UNIVERSIDADE FEDERAL DE VIÇOSA

Drivers of ecosystem functioning in secondary tropical forests: the roles of carbon stocks, endemic species, and anthropogenic disturbance

Nathália Silva
Doctor Scientiae

VIÇOSA - MINAS GERAIS
2025

NATHÁLIA SILVA

Drivers of ecosystem functioning in secondary tropical forests: the roles of carbon stocks, endemic species, and anthropogenic disturbance

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

Adviser: Joao A. Alves Meira Neto

VIÇOSA - MINAS GERAIS
2025

Ficha catalográfica elaborada pela Biblioteca Central da Universidade Federal de Viçosa - Campus Viçosa

T

S586d
2025

Silva, Nathália, 1995-

Drivers of ecosystem functioning in secondary tropical forests: the roles of carbon stocks, endemic species, and anthropogenic disturbance / Nathália Silva. – Viçosa, MG, 2025.

1 tese eletrônica (135 f.): il. (algumas color.).

Texto em português e inglês.

Orientador: João Augusto Alves Meira Neto.

Tese (doutorado) - Universidade Federal de Viçosa, Departamento de Biologia Vegetal, 2025.

Inclui bibliografia.

DOI: https://doi.org/10.47328/ufvbbt.2026.046

Modo de acesso: World Wide Web.

1. Biodiversidade - Conservação - Mata Atlântica. 2. Carbono - Mata Atlântica. 3. Plantas em extinção - Mata Atlântica. 4. Relação humano-planta - Mata Atlântica. I. Meira Neto, João Augusto Alves, 1963-. II. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. III. Título.

CDD 22. ed. 578.7340981

Bibliotecário(a) responsável: Euzébio Luiz Pinto CRB-6/3317

NATHÁLIA SILVA

Drivers of ecosystem functioning in secondary tropical forests: the roles of carbon stocks, endemic species, and anthropogenic disturbance

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

APPROVED: December 5, 2025.

Assent:

Nathália Silva
Author

Joao Augusto Alves Meira Neto
Adviser

Essa tese foi assinada digitalmente pela autora em 11/02/2026 às 14:03:00 e pelo orientador em 11/02/2026 às 14:45:05. As assinaturas têm validade legal, conforme o disposto na Medida Provisória 2.200-2/2001 e na Resolução nº 37/2012 do CONARQ. Para conferir a autenticidade, acesse https://siadoc.ufv.br/validar-documento. No campo 'Código de registro', informe o código **8Q4Z.13NH.7UOP** e clique no botão 'Validar documento'.

ACKNOWLEDGMENTS

Agradeço aos meus pais, Neusa e José, que sempre me apoiaram e instigaram minha curiosidade. Vocês construíram a base da pessoa e da cientista que me tornei. Obrigada por tudo. Às minhas irmãs, Sandra e Ana Lucia; aos meus sobrinhos, Larissa, Thamiris, Anna Gabriella, Chiara, Gabriel, Cecília e Nicolas; à minha querida sobrinha-neta, Olivia; ao meu padrinho, Wilson e a todos os meus tios, tias, primas e primos. Vocês são a melhor família que eu poderia ter.

A todos os meus amigos que fazem parte desta jornada de vida, os do IFES, da graduação, da pós-graduação e os de além-mar. Pelas risadas, choros, sessões de cinema que me mantiveram sã, drinks, fofocas, momentos e memórias: vocês fazem a vida valer a pena.

Agradeço aos amigos e colegas do LEEP, o melhor laboratório da UFV, por toda essa jornada compartilhada na ciência, nos perrengues e em cerca de um milhão de cafezinhos. Vocês tornaram esse caminho mais leve e divertido.

Ao meu orientador, João, por ter me guiado, apoiado e incentivado minha trajetória acadêmica desde a graduação, passando pelo mestrado, pela atuação como pesquisadora colaboradora e no doutorado.

À cidade de Viçosa, esse lugar maravilhoso e acolhedor que me recebeu há 12 anos, quando eu ainda era uma garota cheia de expectativas.

À Universidade Federal de Viçosa e ao Programa de Pós-Graduação em Botânica pela oportunidade de realizar minha formação.

A todos que me acompanharam até aqui, meu muito obrigada!

This work has been sponsored by the following Brazilian research agencies: Coordination for the Improvement of Higher Education Personnel (CAPES; Financing code 001), Minas Gerais State Foundation for Research Aid (FAPEMIG) and National Council of Scientific and Technological Development (CNPq).

“As mentes dos cientistas estão abertas ao explorar mundos novos. Se soubéssemos de antemão o que encontraríamos, seria desnecessário partir.”

Carl Sagan

ABSTRACT

SILVA, Nathália, D.Sc., Universidade Federal de Viçosa, December, 2025. **Drivers of ecosystem functioning in secondary tropical forests: the roles of carbon stocks, endemic species, and anthropogenic disturbance**. Adviser: Joao Augusto Alves Meira Neto.

Understanding the mechanisms that structure biodiversity and determine carbon stocks in tropical forests is central in the face of global change, fragmentation, and intensified anthropogenic disturbances. In this thesis, we investigate the functional, phylogenetic, environmental, and anthropogenic determinants of carbon stocks and the functional diversity of endemic and threatened species in secondary forest fragments of the Atlantic Forest, one of the most endangered biomes on the planet. We used data from 23 fragments, where tree communities were sampled with information on functional traits, phylogenetic structure, and biomass, integrated with environmental variables and disturbance history. In Chapter 1, we evaluate how the mechanisms of niche complementarity and mass ratio regulate aboveground carbon stocks (AGC) and how abiotic factors and anthropogenic disturbances modulate these processes. We hypothesize that (1) the mass ratio mechanism will exert a greater influence on AGC; (2) aboveground carbon stocks will be positively related to environmental factors widely associated with increased productivity and biomass accumulation in tropical forests, such as higher temperature, water availability, and soil fertility; and (3) the influence of ecological mechanisms on carbon stocks will depend on levels of anthropogenic disturbance. In areas with low disturbance, we expect that niche complementarity will play a predominant role, since reduced anthropogenic pressure and greater ecological niche availability can support the coexistence of diverse functional strategies that promote biomass accumulation. Conversely, in highly disturbed areas, the mass ratio mechanism may exert a stronger influence on carbon stocks, as disturbance can select for more resilient or tolerant functional strategies. In Chapter 2, we expand the analysis to explore multiple carbon compartments (AGC, root biomass carbon – RC, and soil organic carbon – SOC), aiming to understand how functional diversity, trait dominance, phylogenetic diversity, and environmental and anthropogenic gradients interact to shape these stocks. We hypothesize that aboveground carbon stocks will be primarily influenced by water availability, soil fertility and functional structure of plants, with communities dominated by species with conservative traits storing more biomass and carbon aboveground. In addition, we expect phylogenetic diversity to have a positive effect on AGC through complementarity and niche partitioning. For root carbon, in addition to sharing similarities with environmental conditions favorable for AGC, since it also represents live biomass, we expect stronger associations with acquisitive functional strategies of plants, since fine roots need to cope with resource fluctuations in the soil. For soil organic carbon, we predict stronger associations with climatic seasonality and edaphic factors, since litter decomposition is constrained during dry periods and organic matter stabilization is favored, and it also appears to be reinforced by resource-conserving strategies that promote stabilization and generate more recalcitrant litter inputs. Finally, in Chapter 3, we explore the role of endemic and threatened species in the functional diversity of secondary tropical forests, evaluating their distribution in functional space and the potential consequences of their loss. We hypothesize that these groups occupy restricted subsets of functional space with more conservative strategies, and that their exclusion would reduce functional richness and dispersion, increasing the regularity of trait distribution. Together, the three chapters provide evidence that maintaining diversity and functional structure is fundamental to sustaining carbon stocks and ecosystem functions in Atlantic Forest remnants, highlighting the importance of conservation strategies that integrate biodiversity, key groups, the influence of anthropogenic degradation, and multiple carbon compartments.

Keywords: ecosystem functioning; biodiversity conservation; trait-based ecology

RESUMO

SILVA, Nathália, D.Sc., Universidade Federal de Viçosa, dezembro de 2025. **Determinantes do funcionamento ecossistêmico em florestas tropicais secundárias: os papéis dos estoques de carbono, das espécies endêmicas e do distúrbio antrópico**. Orientador: Joao Augusto Alves Meira Neto.

A compreensão dos mecanismos que estruturam a biodiversidade e determinam o estoque de carbono em florestas tropicais é central diante das mudanças globais, da fragmentação e da intensificação dos distúrbios antrópicos. Nesta tese, investigamos os determinantes funcionais, filogenéticos, ambientais e antrópicos do estoque de carbono e da diversidade funcional de espécies endêmicas e ameaçadas de extinção em fragmentos florestais secundários da Mata Atlântica, um dos biomas mais ameaçados do planeta. Utilizamos dados de 23 fragmentos, nos quais foram amostradas comunidades arbóreas com informações sobre traços funcionais, estrutura filogenética e biomassa, integradas a variáveis ambientais e históricos de distúrbio. No Capítulo 1, avaliamos como os mecanismos de complementaridade de nicho e razão de massa regulam os estoques de carbono acima do solo (AGC) e de que maneira fatores abióticos e distúrbios antrópicos modulam esses processos. Hipotetizamos que (1) o mecanismo de razão de massa exercerá uma influência maior sobre o AGC; (2) o estoque de carbono acima do solo estará positivamente relacionado a fatores ambientais amplamente associados ao aumento da produtividade e ao acúmulo de biomassa em florestas tropicais, como temperatura mais alta, disponibilidade de água e fertilidade do solo; e (3) a influência dos mecanismos ecológicos sobre o estoque de carbono dependerá dos níveis de distúrbio antrópico. Em áreas com baixos níveis de distúrbio, esperamos que a complementaridade de nicho possa desempenhar um papel predominante, uma vez que a redução da pressão antropogênica e a maior disponibilidade de nichos podem apoiar a coexistência de estratégias funcionais que promovem o acúmulo de biomassa. Em áreas com alto grau de distúrbio, o mecanismo da razão de massa pode exercer uma influência mais pronunciada sobre AGC, uma vez que a perturbação pode selecionar estratégias funcionais mais resilientes ou tolerantes a essas condições desfavoráveis. No Capítulo 2, expandimos a análise para explorar múltiplos compartimentos de carbono (AGC, carbono da biomassa de raízes – RC, e carbono orgânico do solo – SOC), buscando compreender como diversidade funcional, dominância de traços, diversidade filogenética e gradientes ambientais e antrópicos interagem para moldar esses estoques. Nossa hipótese é que AGC seria influenciado principalmente pela disponibilidade de água, fertilidade do solo e espécies com estratégias funcionais conservativas. Além disso, esperamos que a diversidade filogenética tenha um efeito positivo sobre o AGC por meio da complementaridade de nicho. Para o carbono radicular, além de esperarmos similaridades com as condições ambientais favoráveis para AGC, visto que também representa a biomassa viva, esperamos maiores associações com estratégias funcionais aquisitivas, uma vez que as raízes finas precisam lidar com flutuações de recursos no solo. Para o carbono orgânico do solo, prevemos associações mais fortes com a sazonalidade climática e fatores edáficos, visto que a decomposição é restringida durante os períodos secos e a estabilização da matéria orgânica é favorecida. Por fim, no Capítulo 3, exploramos o papel das espécies endêmicas e ameaçadas na diversidade funcional das florestas tropicais secundárias, avaliando sua distribuição no espaço funcional e as consequências potenciais de sua perda. Hipotetizamos que esses grupos ocupam subconjuntos restritos do espaço funcional e com estratégias mais conservativas e que sua exclusão levaria à redução da riqueza e da dispersão funcional, aumentando a regularidade na distribuição dos traços. Em conjunto, os três capítulos oferecem evidências de que a manutenção da diversidade e da estrutura funcional são fundamentais para sustentar estoques de carbono e funções ecossistêmicas nos remanescentes da Mata Atlântica, ressaltando a importância de estratégias de conservação que integrem grupos-chave, a influência da degradação antrópica e múltiplos compartimentos de carbono.

Palavras-chave: funcionamento ecossistêmico; conservação da biodiversidade; ecologia baseada em traços

SUMMARY

INTRODUÇÃO GERAL 10

REFERÊNCIAS..12

CHAPTER 1 - Anthropogenic disturbances shift carbon storage from niche complementarity to mass ratio effects in secondary tropical forests 15

ABSTRACT..16

INTRODUCTION 17

METHODS 20

RESULTS...25

DISCUSSION 30

REFERENCES 35

SUPPLEMENTARY MATERIAL...41

CHAPTER 2 - Drivers of carbon pools in secondary tropical torests: The role of biodiversity and the environment 55

ABSTRACT..55

INTRODUCTION 56

METHODS 59

RESULTS...63

DISCUSSION 67

REFERENCES 72

SUPPLEMENTARY MATERIAL...82

CHAPTER 3 - Functional strategies of endemic and threatened tree species shape the resilience of secondary tropical forests 85

ABSTRACT..85

INTRODUCTION 86

METHODS 88

RESULTS...91

DISCUSSION 100

REFERENCES 104

SUPLEMENTARY MATERIAL 111

CONCLUSÃO GERAL 134

INTRODUÇÃO GERAL

As florestas tropicais desempenham papel central no funcionamento do sistema terrestre, regulando ciclos biogeoquímicos, armazenando grandes quantidades de carbono e sustentando grande parte da diversidade biológica global (Aguirre-Gutiérrez et al., 2022; Bello et al., 2015; Poorter et al., 2021). Entretanto, essas florestas estão sob intensa pressão antrópica, resultando em fragmentação, perda de biodiversidade e alterações na estrutura funcional das comunidades (Da Silva and Tabarelli, 2000; Pyles et al., 2022; Rigueira and Mariano-Neto, 2023). A Mata Atlântica, em particular, é um dos biomas mais ameaçados do mundo, com apenas cerca de 28% de sua cobertura original preservada (Rezende et al., 2018). Marcada por processos de homogeneização funcional e risco de colapso ecológico (Rigueira and Mariano-Neto, 2023), esse bioma é reconhecido como prioridade global de conservação, dada a perda expressiva de habitats ao longo de cinco séculos, em especial nas regiões que concentram os maiores centros populacionais (Marques and Grelle, 2021).

Atualmente, a maior parte da cobertura florestal da Mata Atlântica é composta por fragmentos secundários, em geral pequenos, isolados e desconectados dos grandes remanescentes florestais (Rezende et al., 2018). O curso da sucessão secundária nesses fragmentos é fortemente influenciado por condições bióticas e abióticas locais, o que gera trajetórias distintas de desenvolvimento estrutural e funcional (Chua and Potts, 2018; Craven et al., 2015; Hernández-Vargas et al., 2019; Poorter et al., 2021). Embora essas florestas secundárias possam apresentar redução de alguns serviços ecossistêmicos, como estabilização do solo e provisão hídrica (Marques and Grelle, 2021), estudos recentes demonstram que elas mantêm processos ecossistêmicos fundamentais, além de desempenharem papel relevante para a diversidade funcional e conservação da biodiversidade (Coelho et al., 2024; Matos et al., 2020). Dessa forma, compreender o funcionamento dessas florestas secundárias é essencial para avaliar sua contribuição à resiliência ecológica, ao estoque de carbono e à manutenção de funções ecossistêmicas em paisagens fragmentadas.

Entre os serviços ecossistêmicos mais relevantes prestados por florestas tropicais, destaca-se a regulação climática por meio do sequestro e armazenamento de carbono promovido pela vegetação (Ali and Yan, 2017). Do ponto de vista teórico, dois mecanismos principais explicam as relações entre biodiversidade e funcionamento ecossistêmico: a complementaridade de nicho, que prevê maior acúmulo de biomassa em comunidades com elevada diversidade funcional, e a razão de massa, que enfatiza a dominância de espécies com estratégias funcionais produtivas (Grime, 1998; Tilman et al., 1997). Ambos os mecanismos têm recebido suporte empírico em diferentes contextos e podem atuar de forma sinérgica (Ali et al., 2017; Mensah et al., 2018; Pyles et al., 2022), embora sua importância relativa possa variar conforme condições ambientais e histórico de uso (Borges et al., 2024; Martínez-Ramos et al., 2016). Essa variação abre caminho para novas investigações e reforça a necessidade de estudos que identifiquem quando e por que cada mecanismo prevalece.

O estoque de carbono, por sua vez, envolve não apenas a biomassa aérea, mas também compartimentos subterrâneos, como o carbono em raízes e o carbono orgânico do solo, frequentemente negligenciados em avaliações e estudos (Bu et al., 2019; Gherardi and Sala, 2020; IPCC, 2006; Vieira et al., 2011). Esses compartimentos podem ser influenciados por múltiplos fatores, incluindo condições climáticas, deposição e qualidade da serapilheira, atividade da fauna do solo e interações edáficas (Jobbágy and Jackson, 2000; Luo et al., 2021). Apesar de muitas vezes subestimados, representam frações críticas do ciclo global de carbono (De Miranda et al., 2014; Houghton, 2005). Assim, sua consideração é essencial para uma avaliação abrangente do funcionamento ecossistêmico e do potencial de mitigação das mudanças climáticas pelas florestas tropicais.

Outro aspecto crítico para a conservação funcional das florestas é o papel desempenhado por subconjuntos específicos da flora, como espécies endêmicas e ameaçadas. Para além da riqueza florística geral da Mata Atlântica (Marques and Grelle, 2021), estudos apontam que espécies endêmicas podem representar até mais da metade de sua flora (Brazil Flora Group, 2021; De Lima et al., 2020) e parte igualmente considerável pode estar ameaçada (Da Silva and Tabarelli, 2000; De Lima et al., 2024). Essas espécies podem contribuir de maneira desproporcional para a diversidade funcional e para processos ecossistêmicos essenciais (De Lima et al., 2024; Matos et al., 2020), e sua perda pode gerar lacunas funcionais e reduzir a resiliência das comunidades frente a distúrbios (Carmona et al., 2021). De tal modo, compreender como esses grupos se distribuem no espaço funcional e quais são suas contribuições para o funcionamento dos ecossistemas é fundamental para prever cenários de perda de funções diante das crescentes pressões antrópicas.

Neste contexto, esta tese investigou os determinantes funcionais, filogenéticos, ambientais e antrópicos dos estoques de carbono e da diversidade funcional em 23 fragmentos secundários da Mata Atlântica. Três eixos principais orientaram a investigação: (i) os papéis relativos dos mecanismos de complementaridade de nicho e razão de massa na regulação dos estoques de carbono acima do solo, considerando a modulação exercida pelo distúrbio antrópico; (ii) a influência de fatores bióticos e abióticos sobre diferentes compartimentos de carbono, incluindo biomassa aérea, biomassa radicular e carbono orgânico do solo; e (iii) as contribuições de espécies endêmicas e ameaçadas para a diversidade funcional e os impactos potenciais de sua perda. Em conjunto, esses capítulos buscam aprofundar a compreensão das relações entre biodiversidade e funcionamento ecossistêmico, oferecendo subsídios para estratégias de conservação e manejo de florestas tropicais frente às mudanças globais, especialmente em um bioma marcado pela escassez e fragmentação de áreas remanescentes.

REFERÊNCIAS

Aguirre-Gutiérrez, J., Berenguer, E., Oliveras Menor, I., Bauman, D., Corral-Rivas, J.J., Nava-Miranda, M.G., Both, S., Ndong, J.E., Ondo, F.E., Bengone, N.N., Mihinhou, V., Dalling, J.W., Heineman, K., Figueiredo, A., González-M, R., Norden, N., Hurtado-M, A.B., González, D., Salgado-Negret, B., Reis, S.M., Moraes De Seixas, M.M., Farfan-Rios, W., Shenkin, A., Riutta, T., Girardin, C.A.J., Moore, S., Abernethy, K., Asner, G.P., Bentley, L.P., Burslem, D.F.R.P., Cernusak, L.A., Enquist, B.J., Ewers, R.M., Ferreira, J., Malhi, Y., 2022. Functional susceptibility of tropical forests to climate change. Nat Ecol Evol 6, 878–889. https://doi.org/10.1038/s41559-022-01747-6

Ali, A., Yan, E.-R., 2017. Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review. Tropical Ecology 58, 1–14.

Ali, A., Yan, E.-R., Chang, S.X., Cheng, J.-Y., Liu, X.-Y., 2017. Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Science of The Total Environment 574, 654–662. https://doi.org/10.1016/j.scitotenv.2016.09.022

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, e1501105. https://doi.org/10.1126/sciadv.1501105

Borges, E.R., Réjou-Méchain, M., Gourlet-Fleury, S., Vincent, G., Mortier, F., Bry, X., Cornu, G., Baya, F., Allah-Barem, F., Pélissier, R., 2024. Evolutionary diversity impacts tropical forest biomass and productivity through disturbance-mediated ecological pathways. Journal of Ecology 112, 2344–2358. https://doi.org/10.1111/1365-2745.14399

Brazil Flora Group, 2021. Brazilian Flora 2020 project - Projeto Flora do Brasil 2020. Dataset/Checklist. v393.274 [WWW Document]. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. URL DOI: 10.15468/1mtkaw

Bu, W., Huang, J., Xu, H., Zang, R., Ding, Y., Li, Y., Lin, M., Wang, J., Zhang, C., 2019. Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot. Front. Plant Sci. 9, 1958. https://doi.org/10.3389/fpls.2018.01958

Carmona, C.P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-M., R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M., Toussaint, A., 2021. Erosion of global functional diversity across the tree of life. Sci. Adv. 7, eabf2675. https://doi.org/10.1126/sciadv.abf2675

Chua, S.C., Potts, M.D., 2018. The role of plant functional traits in understanding forest recovery in wet tropical secondary forests. Science of The Total Environment 642, 1252–1262. https://doi.org/10.1016/j.scitotenv.2018.05.397

Coelho, A.J.P., Teixeira, H.M., Verweij, P., Matos, F.A.R., Villa, P.M., Meira-Neto, J.A.A., 2024. Functional richness mediates landscape and management effects on tree biomass and soil fertility during secondary forest succession. Ecological Indicators 162, 112029. https://doi.org/10.1016/j.ecolind.2024.112029

Craven, D., Hall, J.S., Berlyn, G.P., Ashton, M.S., Van Breugel, M., 2015. Changing gears during succession: shifting functional strategies in young tropical secondary forests. Oecologia 179, 293–305. https://doi.org/10.1007/s00442-015-3339-x

Da Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404, 72–74. https://doi.org/10.1038/35003563

De Lima, R.A.F., Dauby, G., De Gasper, A.L., Fernandez, E.P., Vibrans, A.C., Oliveira, A.A.D., Prado, P.I., Souza, V.C., F. De Siqueira, M., Ter Steege, H., 2024. Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383, 219–225. https://doi.org/10.1126/science.abq5099

De Lima, R.A.F., Souza, V.C., De Siqueira, M.F., Ter Steege, H., 2020. Defining endemism levels for biodiversity conservation: Tree species in the Atlantic Forest hotspot. Biological Conservation 252, 108825. https://doi.org/10.1016/j.biocon.2020.108825

De Miranda, S.D.C., Bustamante, M., Palace, M., Hagen, S., Keller, M., Ferreira, L.G., 2014. Regional Variations in Biomass Distribution in Brazilian Savanna Woodland. Biotropica 46, 125–138. https://doi.org/10.1111/btp.12095

Gherardi, L.A., Sala, O.E., 2020. Global patterns and climatic controls of belowground net carbon fixation. Proc. Natl. Acad. Sci. U.S.A. 117, 20038–20043. https://doi.org/10.1073/pnas.2006715117

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecology 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hernández-Vargas, G., Perroni, Y., López-Acosta, J.C., Noa-Carrazana, J.C., Sánchez-Velásquez, L.R., 2019. Do the distribution patterns of plant functional traits change during early secondary succession in tropical montane cloud forests? Acta Oecologica 95, 26–35. https://doi.org/10.1016/j.actao.2019.01.003

Houghton, R.A., 2005. Aboveground Forest Biomass and the Global Carbon Balance. Global Change Biology 11, 945–958. https://doi.org/10.1111/j.1365-2486.2005.00955.x

IPCC, I.P. on C.C., 2006. Good practice guidelines for National Greenhouse gas inventories. Intergovernmental Panel on Climate Change Report, Switzerland.

Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436. https://doi.org/10.1890/1051-0761(2000)010%255B0423:TVDOSO%255D2.0.CO;2

Luo, Z., Viscarra-Rossel, R.A., Qian, T., 2021. Similar importance of edaphic and climatic factors for controlling soil organic carbon stocks of the world. Biogeosciences 18, 2063–2073. https://doi.org/10.5194/bg-18-2063-2021

Marques, M.C.M., Grelle, C.E.V. (Eds.), 2021. The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-55322-7

Martínez-Ramos, M., Ortiz-Rodríguez, I.A., Piñero, D., Dirzo, R., Sarukhán, J., 2016. Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. Proc. Natl. Acad. Sci. U.S.A. 113, 5323–5328. https://doi.org/10.1073/pnas.1602893113

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Global Change Biology 26, 509–522. https://doi.org/10.1111/gcb.14824

Mensah, S., Du Toit, B., Seifert, T., 2018. Diversity–biomass relationship across forest layers: implications for niche complementarity and selection effects. Oecologia 187, 783–795. https://doi.org/10.1007/s00442-018-4144-0

Poorter, L., Rozendaal, D.M.A., Bongers, F., Almeida, de J.S., Álvarez, F.S., Andrade, J.L., Arreola Villa, L.F., Becknell, J.M., Bhaskar, R., Boukili, V., Brancalion, P.H.S., César, R.G., Chave, J., Chazdon, R.L., Dalla Colletta, G., Craven, D., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Díaz García, E., Dupuy, J.M., Durán, S.M., Espírito Santo, M.M., Fernandes, G.W., Finegan, B., Granda Moser, V., Hall, J.S., Hernández-Stefanoni, J.L, 2021. Functional recovery of secondary tropical forests. PNAS 118, e2003405118. https://doi.org/10.1073/pnas.2003405118

Pyles, M.V., Magnago, L.F.S., Maia, V.A., Pinho, B.X., Pitta, G., De Gasper, A.L., Vibrans, A.C., Dos Santos, R.M., Van Den Berg, E., Lima, R.A.F., 2022. Human impacts as the main driver of tropical forest carbon. Sci. Adv. 8, eabl7968. https://doi.org/10.1126/sciadv.abl7968

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rigueira, D.M.G., Mariano-Neto, E., 2023. Structural changes and carbon reduction due to habitat loss in Atlantic Forest. Front. For. Glob. Change 6, 1041448. https://doi.org/10.3389/ffgc.2023.1041448

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Vieira, S.A., Alves, L.F., Duarte-Neto, P.J., Martins, S.C., Veiga, L.G., Scaranello, M.A., Picollo, M.C., Camargo, P.B., Do Carmo, J.B., Neto, E.S., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2011. Stocks of carbon and nitrogen and partitioning between above- and belowground pools in the Brazilian coastal Atlantic Forest elevation range. Ecology and Evolution 1, 421–434. https://doi.org/10.1002/ece3.41

CHAPTER 1 - Anthropogenic disturbances shift carbon storage from niche complementarity to mass ratio effects in secondary tropical forests

Nathália Silva[a], Lhoraynne Pereira Gomes[a,b], Alex Josélio Pires Coelho[a,b], João Augusto Alves Meira-Neto[a].

[a] Laboratory of Ecology and Evolution of Plants – LEEP, Universidade Federal de Viçosa, Viçosa, MG, Brazil
[b] ProBioDiversa Brazil, Association for the Conservation of Biodiversity, Viçosa, MG, Brazil

***Nota**: este capítulo foi publicado na íntegra no periódico **Forest Ecology and Management** (Volume 602, 15 February 2026, 123403); DOI: **10.1016/j.foreco.2025.123403**. A contribuição dos coautores segue conforme descrito no artigo original.*

ABSTRACT

Tropical forests play a significant role in global carbon storage, yet the mechanisms regulating aboveground carbon stocks (AGC) are not entirely elucidated, particularly in human-modified landscapes. This study investigates the influence of functional diversity and dominant traits on AGC across 22 secondary tropical forests in the Atlantic domain, incorporating environmental gradients and disturbance levels. We applied piecewise structural equation models (pSEM) to evaluate the relative contributions of niche complementarity and mass ratio mechanisms, while accounting for abiotic and anthropogenic factors. Our results reveal that functional diversity, particularly functional richness, explained a larger share of AGC variation than dominant traits, emphasizing the importance of niche complementarity in carbon accumulation. Functional dispersion showed negative effects, suggesting that functional clustering stabilizes ecosystem processes, even under environmental variability. Abiotic gradients, including temperature and soil fertility, indirectly influenced AGC through their effects on functional diversity, highlighting the role of environmental filtering in shaping plant strategies. Disturbance levels altered these dynamics, with niche complementarity prevailing in low-disturbance forests and dominant traits becoming more influential in highly disturbed areas. These findings provide new insights into the mechanisms governing carbon stock in secondary forests, demonstrating the combined importance of functional diversity and dominant traits in different contexts. Despite valuable insights, our findings should be interpreted with caution since the small sample size within disturbance groups limits statistical power and generalization. Nonetheless, they highlight the importance of accounting for functional composition, environmental context and degradation in ecological studies and possibly in restoration strategies aimed at enhancing carbon storage in secondary tropical forests.

Keywords: Functional diversity; Ecological strategies; forest ecology; Environmental gradients; Forest resilience; Carbon dynamics.

INTRODUCTION

The factors influencing carbon stock in tropical forests have drawn increasing attention due to their key role in mitigating global change (Ali et al. 2017; Matos et al. 2020; Poorter et al. 2021). Forest carbon dynamics involve tangled processes encompassing species abundance, evolutionary histories, functional strategies, biotic interactions, and relationships with environmental and anthropogenic elements (Bello et al. 2015; Mensah et al. 2021; Ali 2023). Despite the growing number of studies examining biodiversity-carbon relationships in tropical forests, the influence of regional climatic, edaphic, and human-driven factors remains insufficiently explored, especially given that biodiversity declines driven by climate change and land use could lead to substantial losses in stored carbon (Conti and Díaz 2013; Ali et al. 2019; Bu et al. 2019; De La Cruz-Amo et al. 2020; Weiskopf et al. 2024). In light of the imminent worldwide transitions that are projected to alter resource availability and abiotic conditions in the coming years (IPCC 2022), and the current regime shifts in Atlantic Tropical Forests, which are undergoing functional homogenization and collapse (Rigueira and Mariano-Neto 2023), there is an urgent need to deepen our understanding of how plant communities respond to environmental variability and anthropogenic influences.

Prior research indicates that the community-level effects on aboveground carbon stock can be driven by both niche complementarity and the mass ratio among species (Ali and Yan 2017). According to the niche complementarity hypothesis, plant communities with higher functional and species diversity tend to support greater aboveground carbon accumulation through niche partitioning or facilitation (Tilman et al. 1997). However, functional diversity has generally proven to be a weaker predictor of aboveground carbon stock (AGC) (Yuan et al. 2018). Experimental studies have demonstrated positive effects of functional diversity on productivity (Zheng et al. 2021; Larkin et al. 2023). Also, in the Atlantic Forest, similar patterns of positive biodiversity-AGC relationships have been documented (Pyles et al. 2022; Coelho et al. 2024), while in the Amazon, a negative relationship between functional richness and aboveground carbon has been observed (Finegan et al. 2015), suggesting that these dynamics may vary with a regional framework. On the other hand, the mass ratio hypothesis posits that the primary factor regulating aboveground biomass is the functional composition of dominant productive species, which can be assessed through the community-weighted mean of functional traits (CWM) (Grime 1998). This mechanism has received support in multiple studies, both at the global scale (Wang and Ali 2021) in tropical (Finegan et al. 2015; Van Der Sande et al. 2017;

Bu et al. 2019) and subtropical forests (Lin et al. 2016; Bordin et al. 2021). Furthermore, the complex interplay between niche complementarity and mass ratio effects indicates that support can often be found for both hypotheses in a complementary manner (Ali et al. 2017; Pyles et al. 2022; Ali 2023), suggesting that both biodiversity and functional dominance contribute to carbon stock under different ecological contexts. Taking these premises together, they highlight the need for further research to elucidate the conditions under which each mechanism predominates and how they interact to shape the carbon stock in diverse forest ecosystems.

Abiotic factors that influence plant growth and ecological strategies –consequently affecting both biodiversity and carbon stocks – exhibit varied associations, directions, and intensities (Reich et al. 1997; Bu et al. 2019; Van Der Plas 2019). These factors encompass forest age, vegetation types, and a range of environmental conditions, including climate variables, edaphic characteristics, and topographic features (Neves et al. 2017; Gardon et al. 2020; Pyles et al. 2022; Silva et al. 2023). In general, tropical forests aboveground carbon stocks are enhanced in wetter climates with low seasonality, lower altitudes, mild slopes, and nutrient-rich soils (Quesada et al. 2012; Poorter et al. 2017; Coelho De Souza et al. 2019; De La Cruz-Amo et al. 2020). Alternative patterns have also been observed, including higher carbon stocks at high or intermediate altitudes and in low-fertility soils, that may arise due to the diversity of ecological strategies plants adopt to cope with stressful environmental conditions, underscoring the complexity and adaptability of plant communities (Prado-Junior et al. 2016; Aguirre-Gutiérrez et al. 2019; De La Cruz-Amo et al. 2020). This variability in the drivers of carbon stock highlights that both biodiversity and carbon stock patterns should be interpreted within their environmental context (Alves et al. 2010; Van Der Sande et al. 2017; Van Der Plas 2019).

Furthermore, there is evidence that anthropogenic factors tend to modify the relationship between biodiversity and carbon stocks (Van Der Sande et al. 2017; Ferreira et al. 2018). Disturbances such as logging, clear-cutting, invasive species introduction, and forest fragmentation alter the structural and functional diversity of plant communities, often leading to substantial reductions and disruptions in carbon sequestration and storage, especially when biomass is directly removed or severely altered (Mouillot et al. 2013; Magnago et al. 2015; Pyles et al. 2022; Bastos et al. 2024; Weiskopf et al. 2024). The assembly process in such areas often leads to communities filtered by the disturbance, typically exhibiting reduced functional trait diversity (Manhães et al. 2022; Liu et al. 2024). Their remaining functional structure, usually composed of species capable of tolerating or resisting the imposed stressors, may contribute less to carbon stock than more preserved forests (Martínez-Ramos et al. 2016; Lipoma et al. 2024). Moreover, the impacts of disturbance in biodiversity are not uniform and can vary depending on other abiotic factors such as water availability and temperature (Mo et al. 2024). In this context, incorporating historical land-use and disturbance regimes is critical to understand how functional biodiversity, environmental conditions, and aboveground carbon stocks interact amid growing pressures on tropical forests.

Considering the broad effects of mass ratio and niche complementarity (Tilman et al. 1997; Grime 1998; Bu et al. 2019; Ali 2023), as well as broad findings on trait-environment and biodiversity-ecosystem function relationships (Wiesmeier et al. 2019; Bu et al. 2019; De La Cruz-Amo et al. 2020; Ma et al. 2021; Pyles et al. 2022), this study aimed to examine the impact of functional diversity and the dominance of functional traits on aboveground carbon stocks, considering the influence anthropogenic disturbances and abiotic conditions in 22 tropical secondary forests in the Atlantic Forest region, in Brazil. Specifically, we sought to address the following questions: (i) Do niche complementarity and mass ratio mechanisms act jointly to regulate carbon stocks in tropical secondary forests? (ii) How do anthropogenic and abiotic factors influence the balance between these mechanisms in shaping aboveground carbon stocks?

We hypothesized that: (1) The mass ratio mechanism will exert a greater influence on the AGC, suggesting that the presence of dominant traits will have a more significant impact than functional diversity in the studied forests (Conti and Díaz 2013; Finegan et al. 2015; Ali et al. 2017, p. 20; Bu et al. 2019; Wang and Ali 2021; Rodrigues et al. 2023); (2) Aboveground carbon stock will be positively related to environmental factors that are widely associated with increased productivity and biomass accumulation in tropical forests, such as higher temperature, water availability, and soil fertility (Poorter et al. 2017; Ali et al. 2019; Pyles et al. 2022; Ali 2023); (3) The influence of ecological mechanisms on carbon stock will depend on disturbance levels. In areas with low disturbance levels, we expect that niche complementarity might play a predominant role, as the reduced anthropogenic pressure and greater ecological niche availability may support the coexistence of diverse functional strategies that promote biomass accumulation (Martínez-Ramos et al. 2016; Warring et al. 2016; Bentsi-Enchill et al. 2022). In contrast, in areas with a high degree of disturbance, the mass ratio mechanism might exert a more pronounced influence on carbon stocks, given that disturbance could select functional strategies that are more resilient or tolerant to these challenging conditions (Mouillot et al. 2013; Borges et al. 2024).

METHODS

i. Study area and tree inventory

The present study examined 22 secondary forest communities in the Atlantic domain (Fig. 1; Table S1). This global biodiversity hotspot possesses more than 20,000 plant species and high levels of endemism and has suffered significant native vegetation loss, with only about 28% of its original cover remaining (Rezende et al. 2018). The entire region presents matrices with extensive transformations, including conversions to pasture, agriculture, mining, and forestry (Magnago et al. 2015; Matos et al. 2020). The climate varies among the areas according to Koppen's classification, ranging from tropical climates without a dry season (Af, Am, and Aw) to tropical climates with a dry winter (Cwa and Cwc) (Alvares et al. 2013). According to the Brazilian Soil Classification System the region's soils are characterized by dystrophic red and yellow latosols, dystrophic yellow argisols, dystrophic spodosols, and dystrophic cambisols (Santos et al. 2018).

The survey is part of the database of the Laboratory of Plant Ecology and Evolution (LEEP) at the Federal University of Viçosa (UFV), with sampling conducted between 2005 and 2019 (Table S1). In each fragment, an average of fifty 10x10 m plots were sampled, recording height and diameter at breast height for individuals ≥4.8 cm. We excluded a total of 183 non-native and non-specifically identified individuals, as species-level identification was required for trait data collection (de Bello et al. 2021). In this context, a total of 23,364 individuals were sampled and included in the community-level analyses, representing 680 species from 78 botanical families.

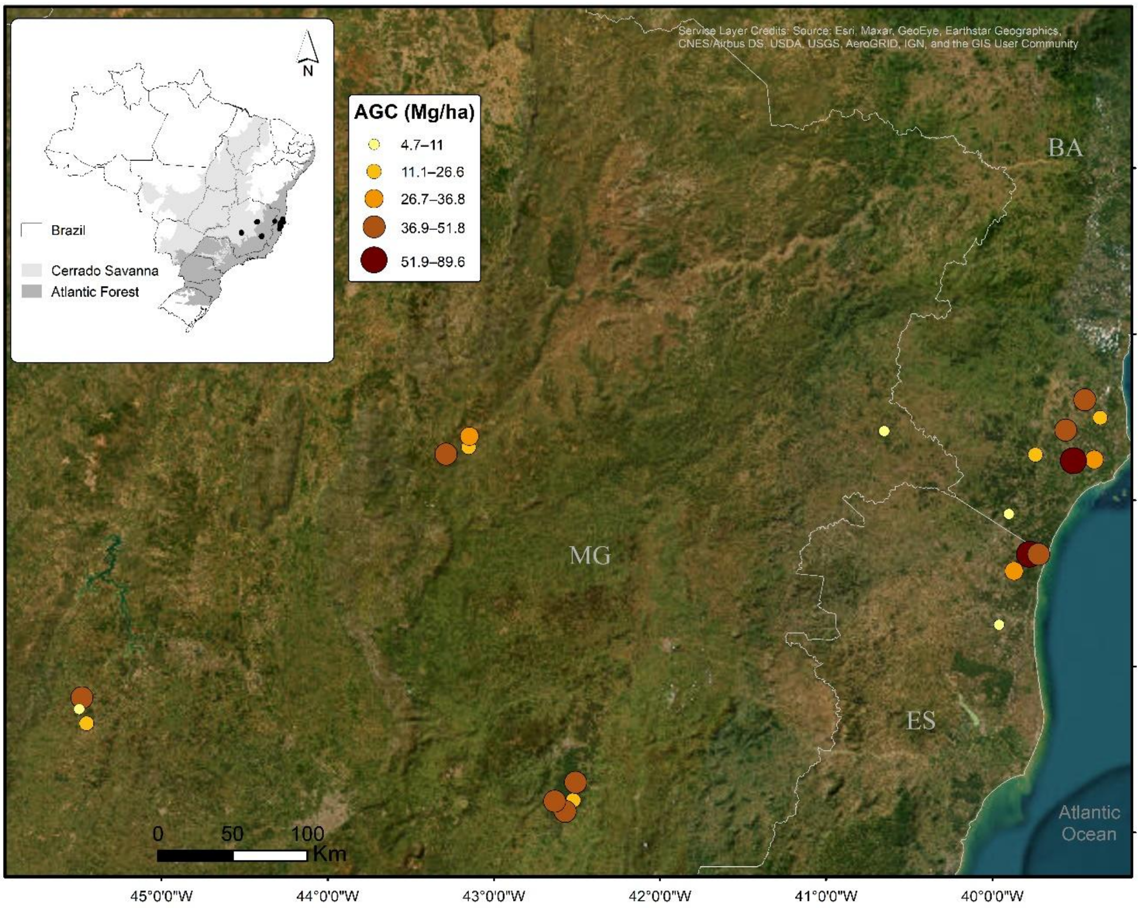

Fig. 1. Atlantic Forest communities sampled. AGC – aboveground carbon stock; BA – Bahia state; ES – Espírito Santo state; MG – Minas Gerais state.

ii. Functional Biodiversity variables

Based on the species lists of each community we collected nine interspecific functional traits linked to key ecosystem processes and functions from the leaf, woody, and reproductive spectra. The traits included leaf area, petiole length, petiole width, fruit length, fruit width, dispersal syndrome (zoochoric or non-zoochoric), leaf habit (evergreen or deciduous), maximum height, and wood density. We obtained the length and width of the leaf blade, petiole, and fruit by measuring exsiccates in virtual herbaria in accordance with the appropriate protocols (Pérez-Harguindeguy et al. 2013; Brazil Flora Group 2021; speciesLink network 2021). The leaf area was calculated using the correction factor of 0.68, which was employed to convert the rectangular product of length and width into leaf area (Li et al. 2020; Schrader et al. 2021). Additional data regarding fruit size, as well as information on dispersal (zoochoric or non-zoochoric) and leaf habit (evergreen or deciduous), were obtained from original articles, books, and specialized websites (Table S2). We extracted the maximum height values from the botanical collection reports using the Reflora virtual herbarium tool (Brazil Flora Group 2021) and wood density values from the Global Wood Density database (Zanne et al. 2009) and books on Brazilian flora (Table S2).

The functional dominance of each community was evaluated using the Community Weighted Mean (CWM) approach. Functional diversity was assessed using multiple-trait indices: Functional Richness (FRic), which quantifies the functional space occupied by the community, and Functional Dispersion (FDis), which captures the distribution of abundances within that space, chosen because it is independent of species richness and consistent regardless of the set of traits used for its calculation (Villéger et al. 2008; Mouchet et al. 2010; Ohlert et al. 2024). Functional diversity and CWM metrics were computed using all traits except wood density, which was excluded to avoid collinearity with AGC, as it is already incorporated into the allometric equation used to estimate aboveground biomass. Categorical traits were transformed into PCoA axes via Gower's distance, and the principal dimensions explaining most variance were used in index calculations (Villéger et al. 2008).

iii. Aboveground carbon stock

The aboveground biomass (AGB – Mg ha^{-1}) of each individual was estimated using the allometric equation proposed by Chave et al. (2014), which is recommended for use in tropical forests, defined as:

$$AGB = 0.0673\ (\rho D^2 H)^{\ 0.976}$$

where D is the stem diameter (Diameter at Breast Height – cm), H is the individual's total height (m), and ρ is the wood density (g cm^{-3}). The aboveground carbon stock (AGC) of each tree and each plot was estimated considering 45.6% of the total AGB (Martin et al. 2018).

iv. Abiotic variables

We gathered a variety of abiotic factors deemed relevant to the region under study: climatic water deficit, altitude, annual temperature, slope, cation exchange capacity (CEC), soil water, soil pH, and anthropogenic disturbance level (Neves et al. 2017; Santos et al. 2018; Pyles et al. 2022; Silva et al. 2023). The climatic water deficit (CWD - mm H_2O) was calculated as the difference between annual actual evapotranspiration (AET) and global potential evapotranspiration (PET), collected using geographical coordinates of each community with a spatial resolution of 1 km using historical averages (Stephenson 1998; Zomer et al. 2022). Data on soil water (mm/cm), CEC (cmolc/kg) and soil pH were obtained from maps made available by EMBRAPA at a spatial resolution of 90m (non-commercial license CC BY NC 3.0 BR), using the geographical coordinates of each community. Using EarthEnv (Amatulli et al. 2018) and Topodata (Valeriano and Rossetti 2012) databases, climatic and topographic data was gathered, including annual temperature (°C), altitude (m) and slope (%) at a spatial resolution of 1km.

We evaluated the level of disturbance of each forest according to a classification system that categorizes the fragments into four levels of disturbance: severe, high, medium, and low, based on the types and intensities of disturbance (clear-cutting, selective logging, burning, etc.) and the time elapsed since the last event before the inventories and/or forest successional stage (initial, early, and late secondary or advanced and old growth) (Pyles et al. 2022). This classification was determined through the historical records available for each area provided by the authors of the original inventories, supported by historical satellite imagery. Although this classification may overlook some within-category variation, it reflects the best available information on disturbance at the fragment level across the Atlantic Forest. It is also consistent with the legal framework and previous large-scale assessments, despite the lack of finer, standardized data in the original surveys (Pyles et al. 2022). The heavy disturbance level, corresponding to early secondary forests clear-cut 10–20 years prior, was not represented in the dataset. The high level represents fragments that underwent clear-cutting between 20 and 50 years before the inventory. The medium level represents fragments that were lightly or sporadically disturbed, with selective logging occurring 50–80 years before the inventory, and the low level represents fragments without disturbance records or those undisturbed for at least 80 years. As the levels formed an ordinal variable, these data were transformed into a continuous variable using ‘ridit scores’.

v. *Data treatment*

CWM metrics and environmental variables were selected to reduce predictors, avoid multicollinearity, and retain those consistently associated with aboveground carbon stock. Environmental variables were selected based on a principal component analysis (PCA). The first and second axes of the PCA explained 45% and 31.3% of the total variance, respectively (Table S4), and were employed as new environmental variables in subsequent analyses. The first axis, named $PC1_{thermal}$, represents a thermal-altitudinal gradient, with positive values associated with higher altitudes and lower annual temperatures, while the second axis, named $PC2_{soil}$, reflects an edaphic gradient, with positive values associated with higher soil pH and greater CEC (Table S4, Fig. S1).

CWM variables were selected using a multiple regression and model selection approach, examining the relationships between CWM variables and AGC. To avoid multicollinearity a global model was used using the Variance Inflation Factor (VIF>5), which led to the exclusion of the CWM variables of petiole length, fruit length, and fruit width; a subsequent synthetic model refined predictor selection, retaining six functional traits relevant to AGC: CWM leaf area, CWM fruit width, CWM maximum height, CWM zoochory, CWM evergreen, and CWM deciduous (Fig. S2).

The biotic variables and the response variable were standardized to ensure comparability across variables with different units and to approximate normal distributions, minimize the impact of outliers, and account for potential non-linear relationships in the regressions and models (Zuur et al. 2009; R Core Team 2022). To address spatial autocorrelation, we applied generalized least squares models for each predictor and AGC. We compared the performance of spatial (with latitudinal and longitudinal coordinates) and non-spatial models using the Akaike Information Criterion (AIC) and R^2_{pseudo} values. The results showed that spatial autocorrelation influenced the variables (Table S5), thus requiring the incorporation of spatial structure into the models. Accordingly, each GLS component in the models was re-fitted with an explicit Gaussian spatial correlation structure “(corGaus(form=~long+lat))” to account for spatial dependence among plots.

vi. Statistical analysis

To evaluate the potential influence of ecological strategies and functional diversity on carbon stocks under diverse environmental conditions, we employed a piecewise structural equation modeling (pSEM) approach. First, we assessed the hypotheses using all the forests together (N=22) to identify overarching patterns for the secondary tropical Forests. Subsequently, we divided the forests into two groups: one labeled "*low disturbance level*" (N=13), which includes the low (N=1) and medium (N=12) categories, since the latter comprises fragments preserved for over 50 years with only light or sporadic disturbances, and another group termed "*high disturbance level*" (N=9), which consists of forests classified under the high disturbance category.

For each data group (all forests, low-disturbance forests, and high-disturbance forests), we built two models: one that considers the possible effects of niche complementarity (FRic and FDis) and one that considers the potential effects of mass ratio (selected CWMs). In both models, three paths were considered: the direct effect of environmental conditions on carbon stock, the direct effect of functional biodiversity indexes (FRic and FDis or CWMs) on the carbon stock, and the indirect effect of abiotic variables through functional biodiversity on the carbon stock. The indirect effect of the abiotic variables was quantified through the interaction of the paths in a route, each abiotic variable for each mediator, and then for the aboveground carbon stock. The effect of each predictor was expressed as a percentage of the total effect sum, quantifying the relative contributions of direct and indirect predictor effects on AGC in the pSEMs.

To balance the number of functional predictors (two diversity metrics and six CWM measures) and avoid overfitting, different combinations of two CWM traits were tested in each mass ratio pSEM resulting in 15 models' total; the final "mass ratio" model was selected based on optimal fit criteria. The best models were selected based on the fit of the pSEMs using Fisher's C statistic ($p>0.05$), AICc, and the p-value ($p>0.05$). Incorporating spatial structure into the pSEM models rendered the inclusion of forest type as a random factor unnecessary, as it did not capture additional variability or improve model fit (data not shown). To assess the potential effects of sample imbalance between disturbance categories ($n=13$ low vs. 9 high), we performed a sensitivity analysis by randomly reducing the low-disturbance group to nine forests across five iterations with different random seeds. Results indicated high model stability, with coefficients and significance levels largely maintained, and consistent directions of effects across iterations (Tables S7 and S8).

Bivariate relationships between AGC, functional biodiversity variables, and environmental variables for highly disturbed forests ($n=9$) were visualized as an exploratory step before performing the pSEM (Figs. S4-S6). We conducted all measures and analyses in R 4.3.1 (R Core Team 2022); details on used packages are in Table S3.

RESULTS

All selected pSEM models demonstrated robust fits to the data, as indicated by Fisher's C p-values greater than 0.05 (Fig. 2; Fig. 3; Fig. 4). Additionally, the tests of directed separation did not reveal any significant residual relationships between the variables ($p > 0.05$ for all tests), suggesting that the models are well specified.

When all forests were analyzed, the niche complementarity model accounted for 69% of the observed variation in aboveground carbon stock. Functional richness and functional dispersion were explained by 53%, respectively (Fig. 2A; bivariate relationships for these models in Fig. S4). $PC2_{Soil}$ ($E=-0.438$, $p=0.01$) and disturbance ($E=-0.658$, $p<0.001$) had a direct negative effect on AGC. This negative effect of $PC2_{Soil}$ means negative effect of soil pH and of CEC (see Table S4, Fig. S1) on carbon stock. Functional dispersion had a negative effect on AGC (E=-0.646, p=0.001), while functional richness showed a strong positive effect (E>0.7) on AGC (E=0.711, p=0.007) and was positively influenced by $PC1_{Thermal}$ (E=-0.699, p=0.001) (Table S6). This suggests an indirect positive effect of $PC1_{Thermal}$ on carbon stock, mediated by functional richness, as indicated by $PC1_{Thermal}$ strong relative indirect contribution of approximately 24% (Fig. 2A). This positive effect of $PC1_{Thermal}$ on carbon stock means positive effect of mean annual temperature and negative effect of altitude (see Table S4, Fig. S1) on carbon stock.

For the same set of forests, the mass ratio model captured 33%, 64%, and 10% of the variation in aboveground carbon stock, CWM leaf area, and CWM of deciduous species, respectively (Fig. 2B). In this model, disturbance was the only variable with a significant negative effect on aboveground carbon stock (E=-0.553, p=0.03) (Table S6). Additionally, the disturbance had a moderate negative effect (E=-0.343, p=0.004), and $PC1_{Thermal}$ had a strong negative effect (E=-1.373, p<0.001) on CWM leaf area (Table S6), as indicated by an indirect relative contribution of approximately 46% for this factor (Fig. 2B). This positive effect of $PC1_{Thermal}$ means positive effect of mean annual temperature and negative effect of altitude (see Table S4, Fig. S1) on CWM leaf area.

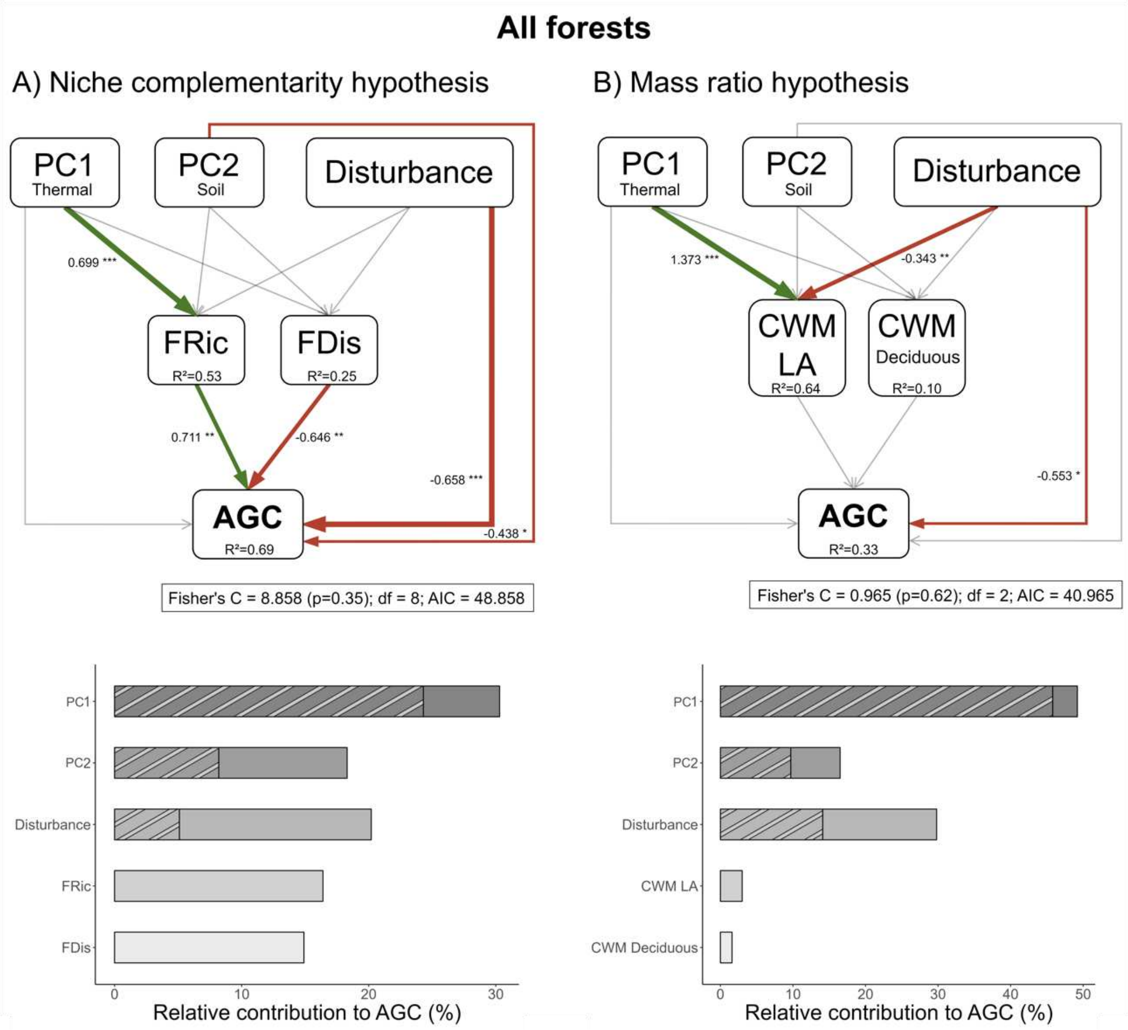

Fig. 2. The best-fit piecewise structural equation models (pSEMs) relating aboveground carbon stock to abiotic variables and FD metrics (niche complementarity model) in (A) and CWM (mass ratio model) in (B), in all forests (N=22). Fisher's C statistics are given for each model. Green arrows indicate significant positive paths ($p<0.05$), red arrows indicate significant negative paths, and gray arrows indicate non-significant paths. The R^2 value is provided for each dependent variable, and standard effect is given for each significant path. For non-significant paths, see Table S6. The bar plots show each predictor's relative contribution, with solid bars representing direct effects and patterned bars indicating indirect effects. AGC = aboveground carbon stock; CWM = community-weighted mean; LA = leaf area; FRic = functional richness; FDis = functional dispersion.

In forests experiencing low disturbance, the niche complementarity model accounted for 59% of the variation in aboveground carbon stock, 62% in functional richness, and 22% in functional dispersion (Fig. 3A; bivariate relationships for these models in Fig. S5). The predictors that explained AGC were $PC2_{Soil}$, which had a strong negative effect (E=-1.654, p=0.002), FDis, also with a strong negative effect (E=-0.788, p=0.007), and FRic, which showed a strong positive effect (E=1.958, p<0.001) and accounted for the largest share of the direct variance explained in AGC, contributing approximately with 31% (Fig. 3A). $PC1_{thermal}$

had a strong positive effect on functional richness (E=-0.779, p=0.003), indirectly influencing carbon stock (Table S6).

In the same low disturbance forests, the mass ratio model explained only 14%, 1%, and 3% of the observed variation in aboveground carbon stock, CWM of maximum height, and CWM of zoochoric species, respectively. However, despite testing across the 15 possible models and achieving satisfactory fits for CWM Hmax and CWM zoochory (Fig. 3B; Table S6), it did not reveal any significantly related variables.

Under high disturbance levels, the niche complementarity model explained 88%, 4%, and 30% of the observed variation in aboveground carbon stock, functional richness, and functional dispersion, respectively (Fig. 4A; bivariate relationships for these models in Fig. S6). In this model, the only significant variable was functional dispersion, which strongly negatively affected AGC (E=-0.891, p=0.02), directly accounting for approximately 30% of the explained AGC variance (Fig. 4A).

The mass ratio model in highly disturbed forests captured 33%, 62%, and 16% for aboveground carbon stock, CWM of maximum height, and CWM of zoochoric species, respectively (Fig. 4B; Table S6). CWM Hmax had a negative effect on AGC (E=-0.481, p<0.001), while $PC1_{Thermal}$ had a strong negative effect on CWM Hmax (E=0.806, p=0.02), suggesting a strong indirect influence of mean annual temperature on AGC, explaining 39% of the AGC variance indirectly (Fig. 4B; Table S6).

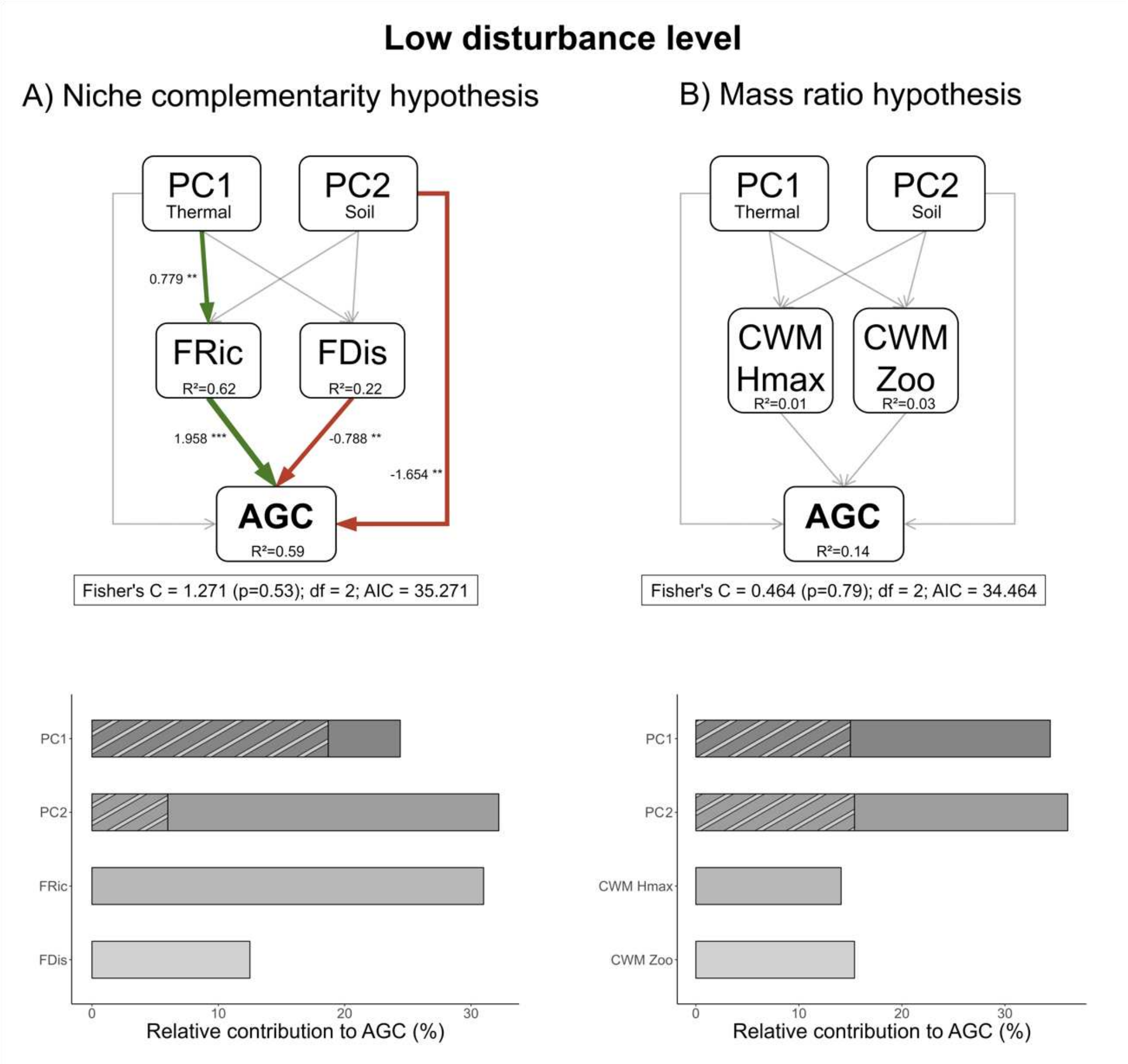

Fig. 3. The best-fit piecewise structural equation models (pSEMs) relating aboveground carbon stock to abiotic variables and FD metrics (niche complementarity model) in (A) and CWM (mass ratio model) in (B), in forests with low disturbance levels (N=13). Fisher's C statistics are given for each model. Green arrows indicate significant positive paths ($p<0.05$), red arrows indicate significant negative paths, and gray arrows indicate non-significant paths. The R^2 value is provided for each dependent variable, and standard effect is given for each significant path. For non-significant paths, see Table S6. The bar plots show each predictor's relative contribution, with solid bars representing direct effects and patterned bars indicating indirect effects. AGC = aboveground carbon stock; CWM = community-weighted mean; Hmax = maximum height; Zoo = zoochory; FRic = functional richness; FDis = functional dispersion.

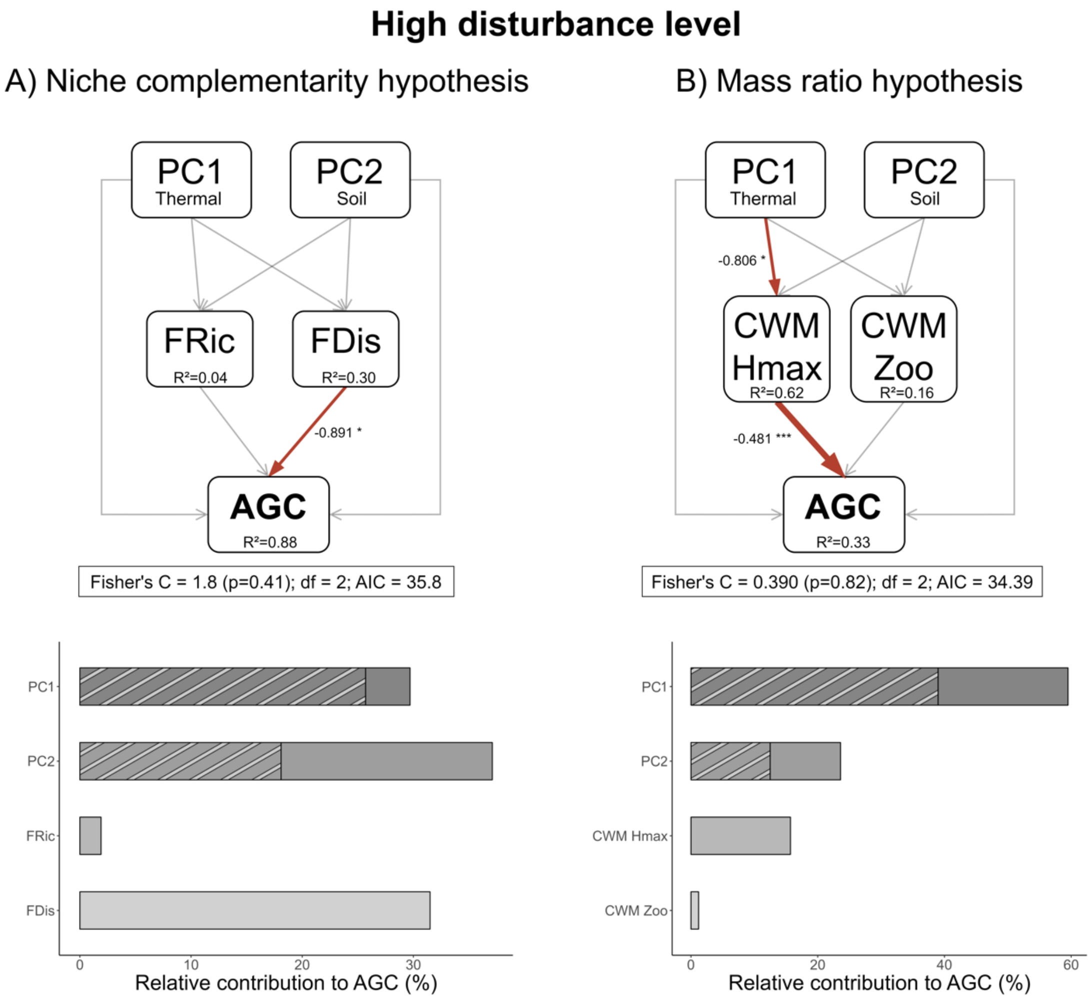

Fig. 4. The best-fit piecewise structural equation models (pSEMs) relating aboveground carbon stock to abiotic variables and FD metrics (niche complementarity model) in (A) and CWM (mass ratio model) in (B), in forests with high disturbance levels (N=9). Fisher's C statistics are given for each model. Green arrows indicate significant positive paths ($p<0.05$), red arrows indicate significant negative paths, and gray arrows indicate non-significant paths. The R^2 value is provided for each dependent variable, and standard effect is given for each significant path. For non-significant paths, see Table S6. The bar plots show each predictor's relative contribution, with solid bars representing direct effects and patterned bars indicating indirect effects. AGC = aboveground carbon stock; CWM = community-weighted mean; Hmax = maximum height; Zoo = zoochory; FRic = functional richness; FDis = functional dispersion.

DISCUSSION

This study revealed that both functional diversity and dominant traits influence aboveground carbon stock in secondary tropical forests, which does not confirm the first hypothesis that anticipated a stronger role for the mass ratio mechanism over niche complementarity. Instead, the niche complementarity model explained a larger proportion of the variation in AGC, highlighting the importance of functional diversity in carbon accumulation, even when all forests were analyzed together. The second hypothesis was partially confirmed since environmental variables influenced AGC, but not entirely as expected: the edaphic gradient (PC2soil) directly negatively affected AGC, suggesting that more fertile soils have reduced biomass accumulation. The third hypothesis was confirmed, indicating that the relative importance of ecological mechanisms depends on disturbance levels. In low-disturbance areas, niche complementarity predominated, whereas in highly disturbed areas, the mass ratio mechanism played a stronger role, suggesting that functional richness is crucial for carbon accumulation in better conserved forests, but dominant species less spread in the functional space are crucial for carbon accumulation in disturbed forests. These findings advance our understanding of how ecological mechanisms and environmental variables interact to regulate carbon stocks in secondary tropical forests, providing support for adaptive conservation and restoration strategies.

i. Niche Complementarity versus Mass Ratio Hypothesis

Our analyses highlight the explanatory power of concurrent ecological mechanisms in tropical forests, particularly niche complementarity, a mechanism that has received less empirical support in tropical forests and terrestrial ecosystems compared to the mass ratio hypothesis (Finegan et al. 2015; Van Der Sande et al. 2017; Bu et al. 2019; Pyles et al. 2022; Coelho et al. 2024). Across all forests, we found that high functional richness combined with low functional dispersion was associated with greater aboveground carbon stocks. Such patterns indicate communities that occupy a broad functional space, reflecting high niche differentiation (Laliberté and Legendre 2010; Coelho et al. 2024), while maintaining efficiency in resource capture and utilization by species close to the centroid of this hypervolume (see Mouillot et al. 2013).

This structure aligns with the mass-ratio hypothesis (Grime 1998), which posits that ecosystem functioning is largely driven by the traits of the most abundant species. In this context, low functional dispersion reflects the convergence of dominant species toward efficient trait syndromes that optimize biomass accumulation and resource use (see Laliberté and Legendre 2010). These dominant functional strategies can enhance productivity by stabilizing ecosystem processes, especially in communities where subordinate species still contribute complementary functions at the margins of the trait space. Thus, the simultaneous presence of broad functional richness and low dispersion suggests that complementarity and mass-ratio effects act together: diverse strategies enable coexistence, while dominance by efficient trait combinations maximizes carbon stock.

ii. Influence of abiotic conditions and disturbance

Abiotic gradients exerted strong indirect effects on aboveground carbon stocks through their influence on functional structure. Higher mean annual temperature increased functional richness and favored larger leaves, which may alleviate the stress of cold winter conditions. This finding aligns with global trends in leaf size, where larger leaves are typically found in warmer tropical climates (Wright et al., 2017). Moreover, since large leaf area is an acquisitive trait, forests with little seasonal variation tend to invest in growth, favoring more acquisitive plant strategies characterized by lower maintenance costs (see Prado-Junior et al. 2016; De Freitas et al. 2024). However, leaf area does not influence aboveground carbon in our findings.

Contrary to expectations, carbon stocks were higher in acidic soils with lower cation exchange capacity. Similar patterns were reported by Coelho et al. (2022) for secondary Atlantic Forests and by Quesada et al. (2012) for Amazonian forests. These findings suggest that low-fertility soils may be dominated by conservative plant strategies (see Prado-Junior et al. 2016; De Freitas et al. 2024) and lead to a greater aboveground carbon stock. These lowland forests (Fig. S3) typically develop on naturally poor soils, shaped by intense pre-weathering and chemical leaching, which consequently keeps most nutrients stored within the biomass (Corrêa et al. 2023). Additionally, there is evidence that older, highly weathered soils tend to harbor greater local diversity and larger species pools, possibly by limiting dominant species and facilitating coexistence (Laliberté et al. 2014).

The decline in aboveground carbon stock with increasing disturbance (Fig. 2) was expected, as the direct removal of biomass results in the immediate loss of carbon from the system. Vegetation loss has been linked to declines in taxonomic and functional biodiversity (Attua et al. 2018; Gautam and Mandal 2018; Bentsi-Enchill et al. 2022), reductions in ecosystem functions (Van Der Sande et al. 2017; Manhães et al. 2022), and decreases in carbon stock (Van Der Sande et al. 2018) in tropical ecosystems. Similar patterns in secondary Amazonian (Ferreira et al. 2018) and Atlantic forests (Pyles et al. 2022) underscore the importance of incorporating historical land-use information to better understand the relationship between biodiversity and ecosystem processes (Lipoma et al. 2024).

iii. Underlying mechanisms of aboveground carbon stock in forests with low disturbance levels

Forests under low disturbance levels provide robust support for the niche complementarity mechanism, a process previously documented in less disturbed mixed temperate forests (Yuan et al. 2018). High functional richness (31%; Fig. 3A) underscores the role of diverse strategies in maintaining ecosystem processes in secondary forests (Mouillot et al. 2013; Warring et al. 2016; Manhães et al. 2022; Coelho et al. 2024). A larger functional space indicates a more balanced functioning among multiple coexisting species (Villéger et al. 2008; Warring et al. 2016; Kunwar et al. 2023), which enhances ecosystem resilience and improves the capacity of communities to adapt to environmental changes (Aguirre-Gutiérrez et al. 2019; Carmona et al. 2021).

The strong negative effect of soil fertility aligns with the patterns observed across all forests and suggests a trend for low-disturbance forests. Fertile soils often coincide with areas of greater historical human pressure, whereas nutrient-poor soils tend to occur in remote or less accessible areas or regions with lower agricultural potential (De Oliveira and Mori 1999; Witcover et al. 2006; Corrêa et al. 2023). These results highlight the key role of minimally disturbed forests on nutrient-poor soils in jointly supporting ecosystem services of carbon stock and functional biodiversity conservation, as limited economic interest helps keep them relatively intact.

iv. Underlying mechanisms of aboveground carbon stock in forests with high disturbance levels

Our results are congruent with findings that the biodiversity-carbon relationship tends to be weaker in disturbed forests (Van Der Sande et al. 2017; Ferreira et al. 2018). A moderate influence of the mass ratio mechanism emerged, mediated by environmental conditions. Specifically, forests at higher altitudes and cooler temperatures showed greater maximum height but lower carbon stocks. While Alves et al. (2010) reported increased AGC with elevation, their findings were primarily linked to intact forests, which generally store more carbon. In contrast, our results show an indirect and restricted association between the thermal-altitudinal gradient and AGC, limited to highly disturbed forests. This divergence may reflect how variations in abiotic filters can dilute the relationships between biodiversity and ecosystem functioning at broader spatial scales (Van Der Plas 2019; Hagan et al. 2021), as evidenced here by the interaction with disturbance levels. Furthermore, the moderate pattern we observed aligns with the notion that the mass ratio mechanism tends to dominate during early stages of secondary succession (Borges et al. 2024); however, the forests in our study are at a more advanced successional stage, which likely attenuates this effect.

Maximum tree height is a common predictor of biomass in tropical and subtropical forests, often showing positive associations with carbon stock (Finegan et al. 2015; Van Der Sande et al. 2017; Yuan et al. 2018; Bordin et al. 2021; Kunwar et al. 2023). However, disturbance can reduce the CWM of maximum height (Jeldu et al. 2023). In contrast to expectations that greater climatic stability promotes acquisitive strategies and growth (Conti and Díaz 2013; Meira-Neto et al. 2019; Bordin et al. 2021), our results indicate that warm, highly disturbed conditions may promote dense understories dominated of numerous small individuals. In our data, disturbance correlated positively with tree abundance (Fig. S7), likely reflecting successional dynamics and structural shifts in the understory. Early- to mid-successional forests often experience recruitment pulses following disturbance events, resulting in higher stem density, especially of shade-tolerant or disturbance-adapted species. These small trees can disproportionately contribute to AGC due to their abundance and conservative traits, such as high wood density and slow turnover, that enhance biomass retention (Poorter et al. 2017; Bu et al. 2019). This pattern diverges from observations in recently disturbed African tropical forests, where biomass gains were primarily driven by the recruitment and growth of large, light-wooded species (Borges et al. 2024). Hence, in some contexts, disturbance may increase AGC through demographic and functional shifts rather than constraining it.

v. *Final Remarks*

While our study provides valuable insights into patterns of carbon stock and biodiversity in secondary tropical forests, it is important to consider the limitation posed by the small number of samples within each disturbance group and in the dataset, which constrains statistical power and generalization. Therefore, our interpretations should be viewed with caution and understood as preliminary trends. Future research should also combine additional abiotic variables, such as nutrient availability and landscape-level factors like fragmentation, to provide a more comprehensive view of the processes regulating carbon stocks, including those of other tropical regions. Furthermore, it is conceivable that other functional traits, particularly "hard" traits and intraspecific variation, which we did not considered due to the lack of field-based trait measurements, are necessary to enhance the precision with which the relationship between biodiversity and carbon stock is captured (Nock et al. 2016). Nevertheless, the robust species-level results presented here have considerable implications for broader regional scales (Diaz et al. 1998; de Bello et al. 2021).

Our findings suggest that the relationship between biodiversity and carbon stocks is not uniform across secondary Atlantic Tropical Forests. The results consistently demonstrated the negative effects of environmental degradation in tropical forests and emphasized the necessity to incorporate and evaluate the impacts of disturbances in ecological analyses. Carbon stocks in forests are below their potential, and there is still room to enhance this ecosystem service in areas where forests have been removed (Mo et al. 2023). In restoration projects with carbon stock as a specific target, our results show that incorporating functional composition information while addressing the climatic and edaphic conditions can yield significant benefits and offer valuable insights into management strategies for the carbon stock capacity of these biodiversity-rich tropical forests.

REFERENCES

Aguirre-Gutiérrez J, Oliveras I, Rifai S, et al (2019) Drier tropical forests are susceptible to functional changes in response to a long-term drought. Ecol Lett 22:855–865. https://doi.org/10.1111/ele.13243

Ali A (2023) Biodiversity–ecosystem functioning research: Brief history, major trends and perspectives. Biological Conservation 285:110210. https://doi.org/10.1016/j.biocon.2023.110210

Ali A, Lin S-L, He J-K, et al (2019) Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. Science of The Total Environment 647:1211–1221. https://doi.org/10.1016/j.scitotenv.2018.08.072

Ali A, Yan E-R (2017) Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review. Tropical Ecology 58:1–14

Ali A, Yan E-R, Chang SX, et al (2017) Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Science of The Total Environment 574:654–662. https://doi.org/10.1016/j.scitotenv.2016.09.022

Alvares CA, Stape JL, Sentelhas PC, et al (2013) Köppen's climate classification map for Brazil. metz 22:711–728. https://doi.org/10.1127/0941-2948/2013/0507

Alves LF, Vieira SA, Scaranello MA, et al (2010) Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). Forest Ecology and Management 260:679–691. https://doi.org/10.1016/j.foreco.2010.05.023

Amatulli G, Domisch S, Tuanmu M-N, et al (2018) A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Sci Data 5:180040. https://doi.org/10.1038/sdata.2018.40

Attua EM, Awanyo L, Antwi EK (2018) Effects of anthropogenic disturbance on tree population structure and diversity of a rain forest biosphere reserve in Ghana, West Africa. Afr J Ecol 56:116–127. https://doi.org/10.1111/aje.12427

Bastos JR, Capellesso ES, Marcilio-Silva V, et al (2024) Mixed effects of climate and species richness on aboveground carbon stock in subtropical Atlantic forests. Science of the Total Environment 945

Bello C, Galetti M, Pizo MA, et al (2015) Defaunation affects carbon storage in tropical forests. Sci Adv 1:e1501105. https://doi.org/10.1126/sciadv.1501105

Bentsi-Enchill F, Damptey FG, Pappoe ANM, et al (2022) Impact of anthropogenic disturbance on tree species diversity, vegetation structure and carbon storage potential in an upland evergreen forest of Ghana, West Africa. Trees, Forests and People 8:100238. https://doi.org/10.1016/j.tfp.2022.100238

Bordin KM, Esquivel-Muelbert A, Bergamin RS, et al (2021) Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests. Forest Ecology and Management 490:119126. https://doi.org/10.1016/j.foreco.2021.119126

Borges ER, Réjou-Méchain M, Gourlet-Fleury S, et al (2024) Evolutionary diversity impacts tropical forest biomass and productivity through disturbance-mediated ecological pathways. Journal of Ecology 112:2344–2358. https://doi.org/10.1111/1365-2745.14399

Brazil Flora Group (2021) Brazilian Flora 2020 project - Projeto Flora do Brasil 2020. Dataset/Checklist. v393.274. In: Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. DOI: 10.15468/1mtkaw

Bu W, Huang J, Xu H, et al (2019) Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot. Front Plant Sci 9:1958. https://doi.org/10.3389/fpls.2018.01958

Carmona CP, Tamme R, Pärtel M, et al (2021) Erosion of global functional diversity across the tree of life. Sci Adv 7:eabf2675. https://doi.org/10.1126/sciadv.abf2675

Chave J, Réjou-Méchain M, Búrquez A, et al (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Change Biol 20:3177–3190. https://doi.org/10.1111/gcb.12629

Coelho AJP, Magnago LFS, Matos FAR, et al (2020) Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. Biodivers Conserv 29:3151–3168. https://doi.org/10.1007/s10531-020-02013-6

Coelho AJP, Ribeiro Matos FA, Villa PM, et al (2022) Multiple drivers influence tree species diversity and above-ground carbon stock in second-growth Atlantic forests: Implications for passive restoration. Journal of Environmental Management 318:115588. https://doi.org/10.1016/j.jenvman.2022.115588

Coelho AJP, Teixeira HM, Verweij P, et al (2024) Functional richness mediates landscape and management effects on tree biomass and soil fertility during secondary forest succession. Ecological Indicators 162:112029. https://doi.org/10.1016/j.ecolind.2024.112029

Coelho De Souza F, Dexter KG, Phillips OL, et al (2019) Evolutionary diversity is associated with wood productivity in Amazonian forests. Nat Ecol Evol 3:1754–1761. https://doi.org/10.1038/s41559-019-1007-y

Conti G, Díaz S (2013) Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. J Ecol 101:18–28. https://doi.org/10.1111/1365-2745.12012

Corrêa MM, de Araújo Filho JC, Schaefer CEGR, Ker JC (2023) Soils of the Coastal Tablelands Under Atlantic Forest (Tabuleiros Costeiros). In: Schaefer CEGR (ed) The Soils of Brazil. Springer International Publishing, Cham, pp 221–238

de Bello F, Carmona CP, Dias A, et al (2021) Handbook of Trait-Based Ecology, 1st edn. Cambridge University Press, Cambridge, UK

De Freitas GV, Da Cunha M, Vitória AP (2024) A systematic review of leaf and wood traits in the Neotropics: environmental gradients and functionality. Trees. https://doi.org/10.1007/s00468-024-02508-7

De La Cruz-Amo L, Bañares-de-Dios G, Cala V, et al (2020) Trade-Offs Among Aboveground, Belowground, and Soil Organic Carbon Stocks Along Altitudinal Gradients in Andean

Tropical Montane Forests. Front Plant Sci 11:106. https://doi.org/10.3389/fpls.2020.00106

De Oliveira AA, Mori SA (1999) A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodiversity and Conservation 8:1219–1244. https://doi.org/10.1023/A:1008908615271

Diaz S, Cabido M, Casanoves F (1998) Plant functional traits and environmental filters at a regional scale. Journal of Vegetation Science 9:113–122. https://doi.org/10.2307/3237229

Ferreira J, Lennox GD, Gardner TA, et al (2018) Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature Clim Change 8:744–749. https://doi.org/10.1038/s41558-018-0225-7

Finegan B, Peña-Claros M, De Oliveira A, et al (2015) Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. Journal of Ecology 103:191–201. https://doi.org/10.1111/1365-2745.12346

Gardon FR, Santos RFD, Rodrigues RR (2020) Brazil's forest restoration, biomass and carbon stocks: A critical review of the knowledge gaps. Forest Ecology and Management 462:117972. https://doi.org/10.1016/j.foreco.2020.117972

Gautam TP, Mandal TN (2018) Effect of disturbance on plant species diversity in moist tropical forest of eastern Nepal. Our Nature 16:1–7. https://doi.org/10.3126/on.v16i1.21558

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecology 86:902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hagan JG, Vanschoenwinkel B, Gamfeldt L (2021) We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. Ecology Letters 24:2537–2548. https://doi.org/10.1111/ele.13874

IPCC (2022) Climate Change 2022: Impacts, Adaptation, and Vulnerability. Cambridge University Press, Cambridge, UK and New York, NY, USA

Jeldu FA, Tolera M, Woldeamanuel T (2023) Functional diversity along disturbance and environmental gradients in Ethiopian moist Afromontane forest. Biosystems Diversity 31:460–469

Kunwar S, Wang L-Q, Kazempour Larsary M, et al (2023) Functional composition of tall-statured trees underpins aboveground biomass in tropical forests. J For Res 34:333–344. https://doi.org/10.1007/s11676-022-01460-x

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Laliberté E, Zemunik G, Turner BL (2014) Environmental filtering explains variation in plant diversity along resource gradients. Science 345:1602–1605. https://doi.org/10.1126/science.1256330

Larkin DJ, Glasenhardt M, Williams EW, et al (2023) Evolutionary history shapes grassland productivity through opposing effects on complementarity and selection. Ecology 104:e4129. https://doi.org/10.1002/ecy.4129

Li Y, Zou D, Shrestha N, et al (2020) Spatiotemporal variation in leaf size and shape in response to climate. Journal of Plant Ecology 13:87–96. https://doi.org/10.1093/jpe/rtz053

Lipoma L, Kambach S, Díaz S, et al (2024) No general support for functional diversity enhancing resilience across terrestrial plant communities. Global Ecol Biogeogr 33:e13895. https://doi.org/10.1111/geb.13895

Liu H, Yin D, He P, et al (2024) Linking plant functional traits to biodiversity under environmental change. Biological Diversity 1:22–28. https://doi.org/10.1002/bod2.12004

Ma H, Mo L, Crowther TW, et al (2021) The global distribution and environmental drivers of aboveground versus belowground plant biomass. Nat Ecol Evol 5:1110–1122. https://doi.org/10.1038/s41559-021-01485-1

Magnago LFS, Magrach A, Laurance WF, et al (2015) Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Glob Change Biol 21:3455–3468. https://doi.org/10.1111/gcb.12937

Manhães AP, Mazzochini GG, Marinho F, et al (2022) Loss of plant cover mediates the negative effect of anthropogenic disturbance on the multifunctionality of a dryland. Applied Vegetation Science 25:e12636. https://doi.org/10.1111/avsc.12636

Martin AR, Doraisami M, Thomas SC (2018) Global patterns in wood carbon concentration across the world's trees and forests. Nature Geosci 11:915–920. https://doi.org/10.1038/s41561-018-0246-x

Martínez-Ramos M, Ortiz-Rodríguez IA, Piñero D, et al (2016) Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. Proc Natl Acad Sci USA 113:5323–5328. https://doi.org/10.1073/pnas.1602893113

Matos FAR, Magnago LFS, Aquila Chan Miranda C, et al (2020) Secondary forest fragments offer important carbon and biodiversity cobenefits. Global Change Biology 26:509–522. https://doi.org/10.1111/gcb.14824

Meira-Neto JAA, Cândido HMN, Miazaki Â, et al (2019) Drivers of the growth–survival trade-off in a tropical forest. Journal of Vegetation Science 30:1184–1194. https://doi.org/10.1111/jvs.12810

Mensah S, Plas F, Noulèkoun F (2021) Do functional identity and divergence promote aboveground carbon differently in tropical semi-arid forests and savannas? Ecosphere 12:. https://doi.org/10.1002/ecs2.3563

Mo L, Crowther TW, Maynard DS, et al (2024) The global distribution and drivers of wood density and their impact on forest carbon stocks. Nat Ecol Evol. https://doi.org/10.1038/s41559-024-02564-9

Mo L, Zohner CM, Reich PB, et al (2023) Integrated global assessment of the natural forest carbon potential. Nature 624:92–101. https://doi.org/10.1038/s41586-023-06723-z

Mouchet MA, Villéger S, Mason NWH, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. Functional Ecology 24:867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot D, Graham NAJ, Villéger S, et al (2013) A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28:167–177. https://doi.org/10.1016/j.tree.2012.10.004

Neves DM, Dexter KG, Pennington RT, et al (2017) Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Diversity Distrib 23:898–909. https://doi.org/10.1111/ddi.12581

Nock CA, Vogt RJ, Beisner BE (2016) Functional Traits. eLS 1–7. https://doi.org/10.1002/9780470015902.a0026282

Ohlert T, Kimmel K, Avolio M, et al (2024) The impact of trait number and correlation on functional diversity metrics in real-world ecosystems. PLoS ONE 19:e0306342. https://doi.org/10.1371/journal.pone.0306342

Pérez-Harguindeguy N, Díaz S, Garnier E, et al (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61:167. https://doi.org/10.1071/BT12225

Poorter L, Rozendaal DMA, Bongers F, et al (2021) Functional recovery of secondary tropical forests. PNAS 118:e2003405118. https://doi.org/10.1073/pnas.2003405118

Poorter L, Van Der Sande MT, Arets EJMM, et al (2017) Biodiversity and climate determine the functioning of Neotropical forests. Global Ecol Biogeogr 26:1423–1434. https://doi.org/10.1111/geb.12668

Prado-Junior JA, Schiavini I, Vale VS, et al (2016) Conservative species drive biomass productivity in tropical dry forests. J Ecol 104:817–827. https://doi.org/10.1111/1365-2745.12543

Pyles MV, Magnago LFS, Maia VA, et al (2022) Human impacts as the main driver of tropical forest carbon. Sci Adv 8:eabl7968. https://doi.org/10.1126/sciadv.abl7968

Quesada CA, Phillips OL, Schwarz M, et al (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9:2203–2246. https://doi.org/10.5194/bg-9-2203-2012

R Core Team (2022) R: A language and environment for statistical computing

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. Proceedings of the National Academy of Sciences 94:13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Rezende CL, Scarano FR, Assad ED, et al (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16:208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rigueira DMG, Mariano-Neto E (2023) Structural changes and carbon reduction due to habitat loss in Atlantic Forest. Front For Glob Change 6:1041448. https://doi.org/10.3389/ffgc.2023.1041448

Rodrigues AC, Villa PM, Silla F, et al (2023) Functional composition enhances aboveground carbon stock during tropical late-secondary forest succession. Plant Biosystems - An International Journal Dealing with all Aspects of Plant Biology 157:1–11. https://doi.org/10.1080/11263504.2022.2073394

Santos HG dos, Jacomine PKT, Anjos LHC dos, et al (2018) Sistema Brasileiro de Classificação de Solos, 5th edn. EMBRAPA, Brasília, DF

Schrader J, Shi P, Royer DL, et al (2021) Leaf size estimation based on leaf length, width and shape. Annals of Botany 128:395–406. https://doi.org/10.1093/aob/mcab078

Silva N, Coelho AJP, Meira-Neto JAA (2023) Functional traits patterns along an altitudinal gradient in a large tropical forest region. Flora 308:152403. https://doi.org/10.1016/j.flora.2023.152403

speciesLink network (2021) Herbário Virtual da Flora e dos Fungos. Dataset/Checklist. http://inct.splink.org.br

Stephenson N (1998) Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J Biogeography 25:855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x

Tilman D, Knops J, Wedin D, et al (1997) The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277:1300–1302. https://doi.org/10.1126/science.277.5330.1300

Valeriano MDM, Rossetti DDF (2012) Topodata: Brazilian full coverage refinement of SRTM data. Applied Geography 32:300–309. https://doi.org/10.1016/j.apgeog.2011.05.004

Van Der Plas F (2019) Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews 94:1220–1245. https://doi.org/10.1111/brv.12499

Van Der Sande MT, Arets EJMM, Peña-Claros M, et al (2018) Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. Functional Ecology 32:461–474. https://doi.org/10.1111/1365-2435.12968

Van Der Sande MT, Poorter L, Kooistra L, et al (2017) Biodiversity in species, traits, and structure determines carbon stocks and uptake in tropical forests. Biotropica 49:593–603. https://doi.org/10.1111/btp.12453

Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301. https://doi.org/10.1890/07-1206.1

Wang L-Q, Ali A (2021) Climate regulates the functional traits – aboveground biomass relationships at a community-level in forests: A global meta-analysis. Science of The Total Environment 761:143238. https://doi.org/10.1016/j.scitotenv.2020.143238

Warring B, Cardoso FCG, Marques MCM, Varassin IG (2016) Functional diversity of reproductive traits increases across succession in the Atlantic forest. Rodriguésia 67:321–333. https://doi.org/10.1590/2175-7860201667204

Weiskopf SR, Isbell F, Arce-Plata MI, et al (2024) Biodiversity loss reduces global terrestrial carbon storage. Nat Commun 15:4354. https://doi.org/10.1038/s41467-024-47872-7

Wiesmeier M, Urbanski L, Hobley E, et al (2019) Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales. Geoderma 333:149–162. https://doi.org/10.1016/j.geoderma.2018.07.026

Witcover J, Vosti SA, Carpentier CL, De Araújo Gomes TC (2006) Impacts of soil quality differences on deforestation, use of cleared land, and farm income. Envir Dev Econ 11:343–370. https://doi.org/10.1017/S1355770X0600283X

Yuan Z, Wang S, Ali A, et al (2018) Aboveground carbon storage is driven by functional trait composition and stand structural attributes rather than biodiversity in temperate mixed forests recovering from disturbances. Annals of Forest Science 75:67. https://doi.org/10.1007/s13595-018-0745-3

Zanne AE, Lopez-Gonzalez G, Coomes DA, et al (2009) Towards a worldwide wood economics spectrum. 2047488 bytes

Zheng L, Chen HYH, Biswas SR, et al (2021) Diversity and identity of economics traits determine the extent of tree mixture effects on ecosystem productivity. Journal of Ecology 109:1898–1908. https://doi.org/10.1111/1365-2745.13614

Zomer RJ, Xu J, Trabucco A (2022) Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. Sci Data 9:409. https://doi.org/10.1038/s41597-022-01493-1

Zuur AF, Ieno EN, Walker N, et al (2009) Mixed effects models and extensions in ecology with R. Springer New York, New York, NY

SUPPLEMENTARY MATERIAL

Table S1. Identification (regional name) and size of the sampled areas of each forest fragment studied in southeastern Brazil.

Identification	Vegetation Type	Sampling year
11D	Rain forest	2011
11F	Rain forest	2011
13C	Rain forest	2011
14E	Semideciduous forest	2011
15A	Rain forest	2011
21B	Rain forest	2011
21C	Rain forest	2011
21D	Rain forest	2011
22B	Rain forest	2011
APP SB	Riverine forest	2006
Capim	Semideciduous forest	2011
Carbonita	Riverine forest	2010
Córrego Fundo	Riverine forest	2010
Fazendinha	Riverine forest	2011
Mombaça	Semideciduous forest	2010
Palhal	Rain forest	2005
PERD	Semideciduous forest	2019
Lagoa capim	Semideciduous forest	2012
Santa Cruz	Semideciduous forest	2012
Sombra da Tarde	Rain forest	2014
Ticó	Riverine forest	2011
Três Rios	Rain forest	2012

Table S2. Main additional sources of functional trait collection.

Source / Title	References
Articles	
Myrcia (Myrtaceae) in the Vale Natural Reserve, Linhares, Espírito Santo, Brazil	Scaravelli et al. 2022
Annonaceae from Natural Reserve Vale, Linhares, Espírito Santo	Lopes & Mello-Silva 2014
Books	
Angiospermas da Reserva Natural Vale, na floresta atlântica do Norte do Espírito Santo	Rolim et al. 2016
Árvores Brasileiras Vol. 1, 2 e 3	Lorenzi 1992; Lorenzi 1998; Lorenzi 2008
Espécies Arbóreas Brasileiras Vol. 1, 2, 3, 4 e 5	Carvalho 2014
Guia de árvores com valor econômico	Campos Filho & Sartorelli 2015
Lista de árvores nativas do sul da Bahia	Sambuichi et al. 2009
Sementes florestais da mata atlântica: um guia para o manejo de espécies da Hileia Baiana	Albuquerque et al. 2022
Specialized websites	
Userful Tropical Plants Database	https://tropical.theferns.info
Encyclopedia of Life	https://eol.org

Table S3. List of the main functions and packages used in the analyses and calculations of indices.

Analysis/indices	Package	References
Community-Weighted Mean (CWM)	FD	Laliberté et al. 2014
Functional Diversity	fundiversity	Grenié & Gruson 2023
generalized least-squares (GLS) models	nlme	Pinheiro et al., 2023
Principal Component analysis (PCA)	FactoMineR	Lê et al., 2008
Principal Coordinate Analysis (PCoA)	vegan and ape	Paradis & Schliep 2019; Oksanen et al. 2022
Piecewise structural equation models (pSEM)	piecewiseSEM	Lefcheck, 2016
Simple linear regressions	stats	R Core Team 2022
Synthetic model selection	MuMIn	Barton 2020
Variance inflation factor (VIF)	car	Fox & Weisberg 2019

Table S4. Contributions of the abiotic variables to the first two principal components (PCA1 and PCA2) of the Principal Component Analysis (PCA). The contributions are expressed as percentages and indicate the relative importance of each variable in forming the PCA axes. The percentages of variance explained by each component are included. For easier interpretation, the PC1 scores and all subsequent calculations were multiplied by -1, so that higher positive scores correspond to higher temperatures. Since all values of PC1 were uniformly adjusted, the underlying data integrity is preserved.

Variables	***PC1***	***PC2***
CWD	16.52	2.48
Altitude	**18.57**	-13.17
Annual Temperature	**- 19.85**	11.06
Slope	12.07	21.81
CEC	14.46	**22.67**
Soil Water	16.37	-0.36
Soil pH	2.16	**28.46**
Percentage of variance	45%	31.30%
Cumulative	45%	76.30%

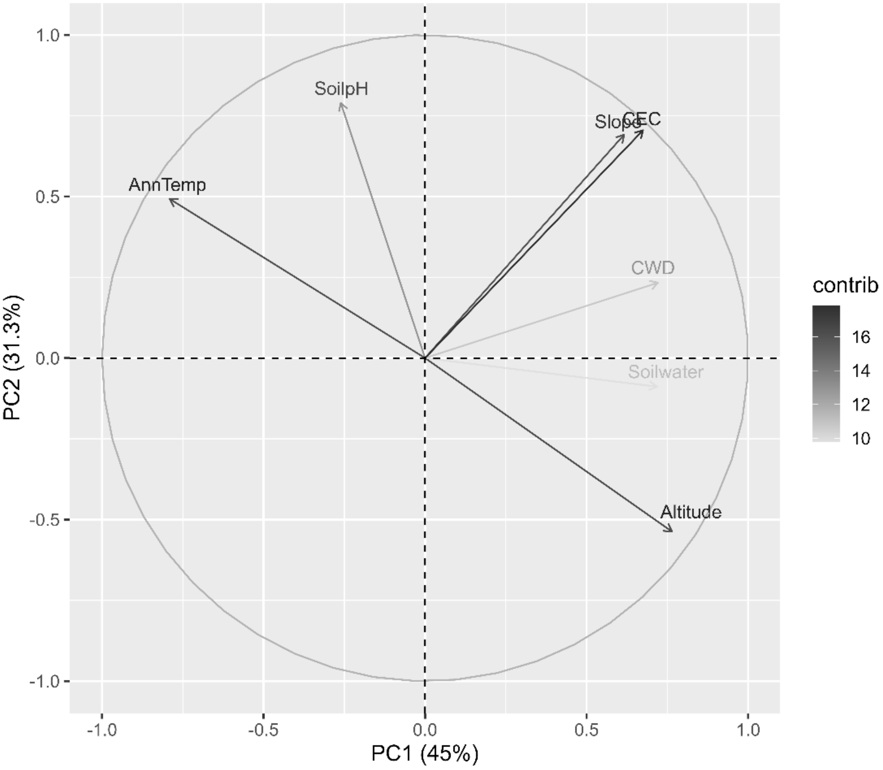

Fig. S1. Principal component analysis (PCA) axes 1 and 2 showing the abiotic variables patterns in all forests (n=22). The percentage of contribution for each variable is indicated in Table S4. Alt = altitude; AnnTemp = annual temperature; CWD = climatic water deficit. For easier interpretation, the PC1 scores in Table S4 and all subsequent calculations were multiplied by -1, so that higher positive scores correspond to higher temperatures. Since all values of PC1 were uniformly adjusted, the underlying data integrity is preserved.

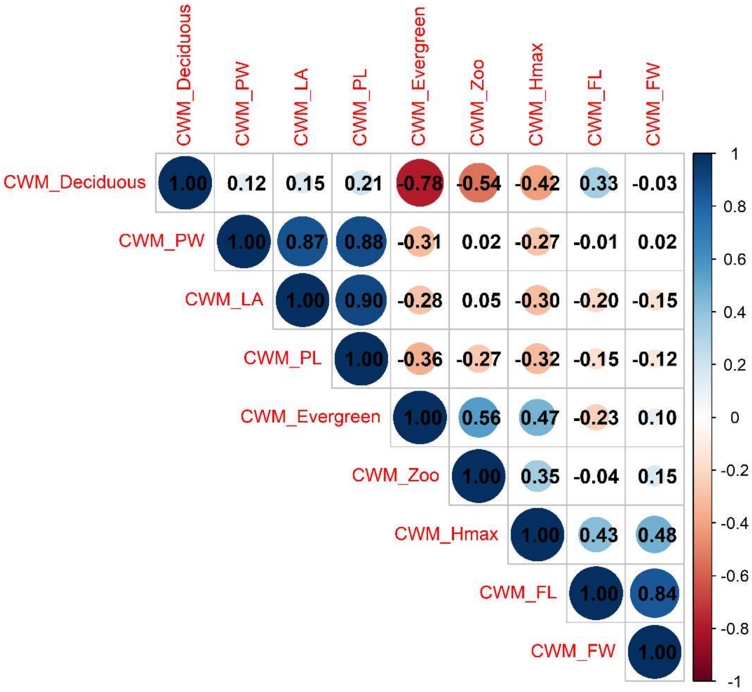

Fig. S2. Correlation map (Pearson correlation) for the set of biotic variables of functional composition (CWM). Blue dots represent positive correlations, red dots represent negative correlations.

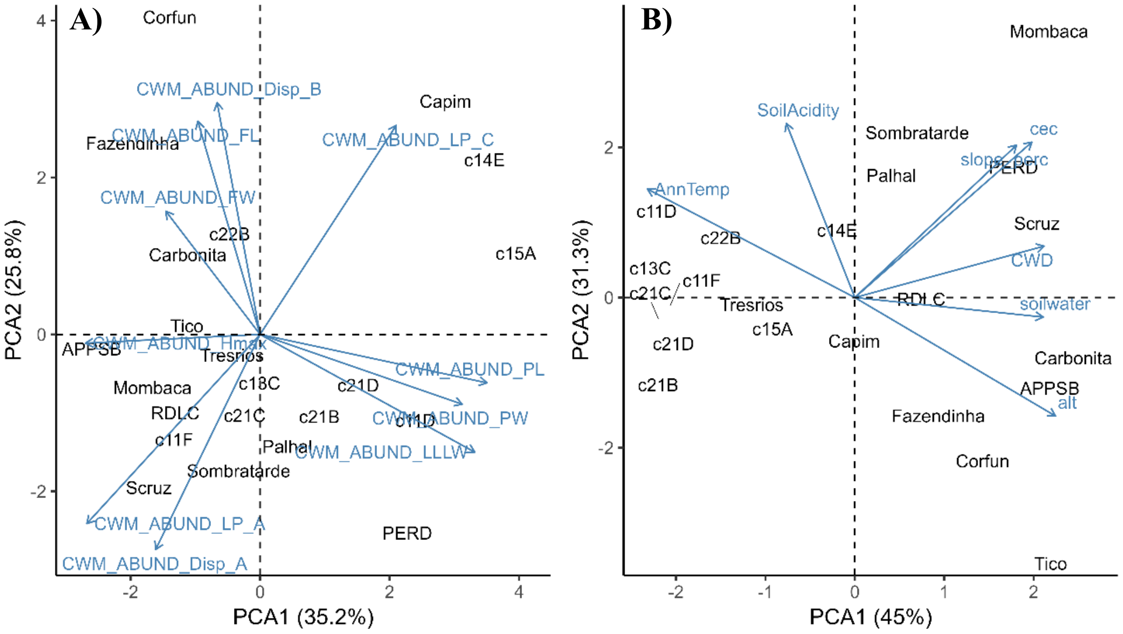

Fig. S3. Principal component analysis (PCA) axes 1 and 2 showing the relations between the plot sites and the CWM functional traits (A) and the abiotic variables (B) for all sites (n=22). The functional traits are zoochoric dispersion (Dips_A), non-zoochoric dispersion (Disp_B), maximum height (Hmax), fruit length (FL), fruit width (FW), leaf area (LLLW), petiole length (PL), petiole width (PW), evergreen (LP_A) and deciduous (LP_C). The abiotic variables are altitude (Alt), annual temperature (AnnTemp), climatic water deficit (CWD) and cation exchange capacity (cec).

Table S5. Summary of the generalized least-squares (GLS) models to test spatial autocorrelation for biotic and abiotic drivers with aboveground carbon stock (AGC).

GLS model	Intercept	SE	t-value	P-value	AIC	R^2_{pseudo}
AGC ~ $PC1_{Climate}$	0.011	0.085	0.131	0.897	56.445	-0.065
AGC ~ $PC1_{Climate}$ + Spatial Cor.	0.109	0.074	1.471	0.157	46.518	0.187
AGC ~ $PC2_{Soil}$	-0.074	0.100	-0.737	0.469	55.592	-0.047
AGC ~ $PC2_{Soil}$ + Spatial Cor.	-0.119	0.062	-1.912	0.070	45.011	0.219
AGC ~ Disturbance level	-0.428	0.219	-1.953	0.065	50.920	0.052
AGC ~ Disturbance + Spatial Cor.	-0.370	0.195	-1.895	0.072	44.274	0.234
AGC ~ FRic	0.483	0.965	0.501	0.622	51.362	0.042
AGC ~ FRic + Spatial Cor.	1.603	0.994	1.613	0.122	45.707	0.204
AGC ~ FDis	-1.057	0.778	-1.359	0.189	50.197	0.066
AGC ~ FDis + Spatial Cor.	0.333	0.299	1.113	0.279	47.137	0.174
AGC ~ CWM LA	-0.319	2.530	-0.126	0.901	49.678	0.077
AGC ~ CWM LA + Spatial Cor.	2.343	1.298	1.805	0.086	45.827	0.201
AGC ~ CWM FW	0.110	1.744	0.063	0.950	50.434	0.061
AGC ~ CWM FW + Spatial Cor.	-0.731	1.251	-0.584	0.565	47.588	0.164
AGC ~ CWM Hmax	1.474	1.256	1.173	0.254	49.697	0.077
AGC ~ CWM Hmax + Spatial Cor.	-1.136	0.729	-1.559	0.135	46.927	0.178
AGC ~ CWM Evergreen	0.517	0.261	1.982	0.061	50.472	0.061
AGC ~ CWM Evergreen + Spatial Cor.	0.362	0.216	1.673	0.109	49.095	0.132
AGC ~ CWM Deciduous	-0.276	0.173	-1.593	0.126	52.542	0.017

AGC ~ CWM Deciduous + Spatial Cor.	0.088	0.083	1.058	0.302	47.276	0.171
AGC ~ CWM Zoochory	1.043	0.419	2.490	0.021	47.619	0.121
AGC ~ CWM Zoochory + Spatial Cor.	0.874	0.382	2.282	0.033	47.301	0.170

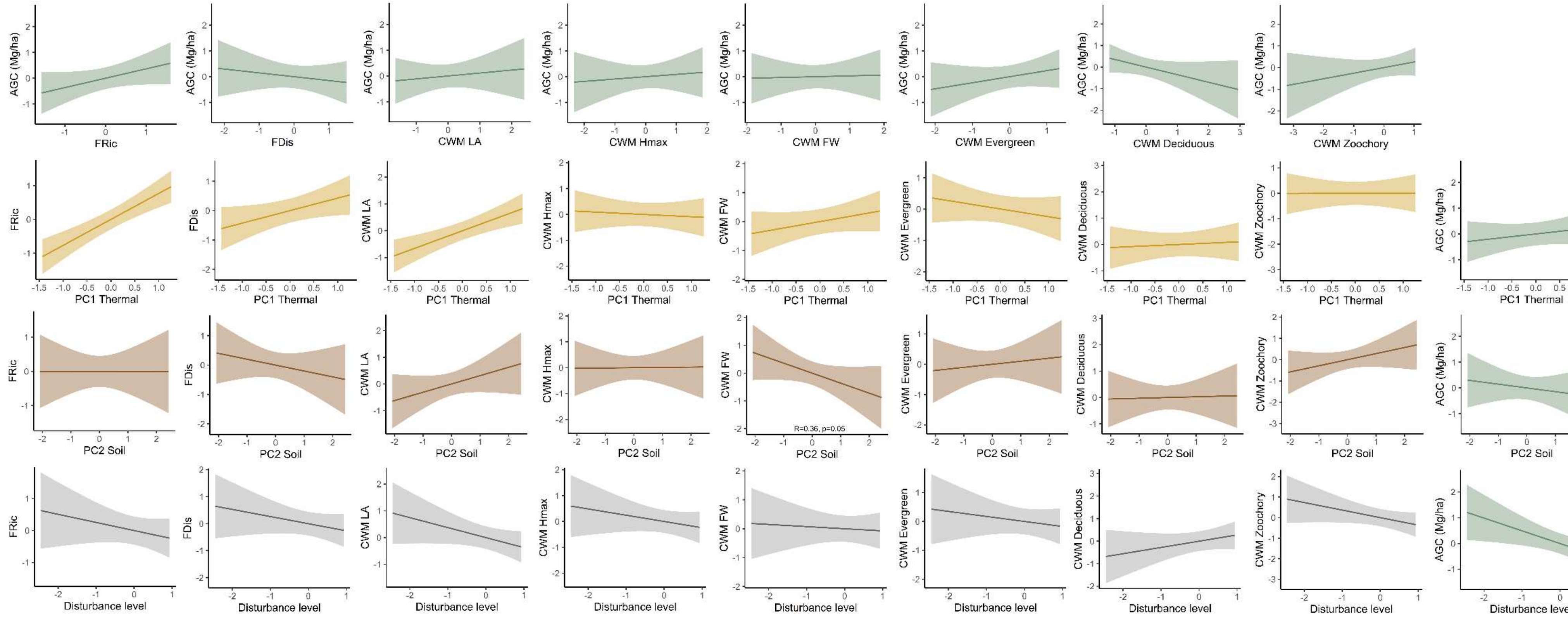

Fig. S4. Bivariate relationships between aboveground carbon stock (AGC), functional variables, and environmental variables for all forests; n=22.

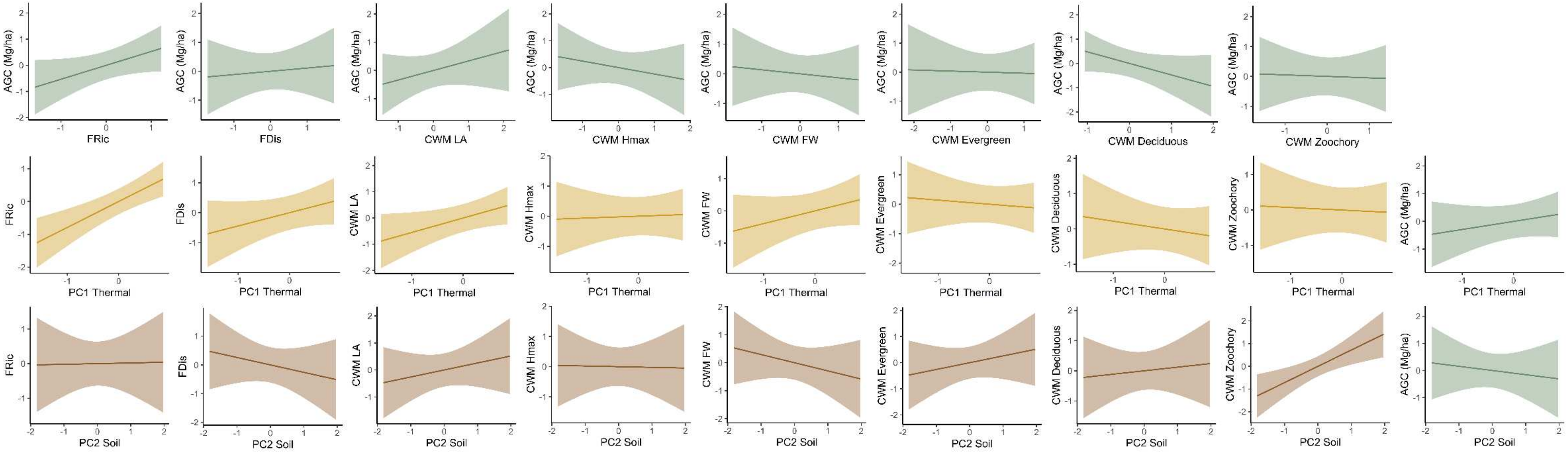

Fig. S5. Bivariate relationships between aboveground carbon stock (AGC), functional variables, and environmental variables for forests with low levels of disturbance; n=13.

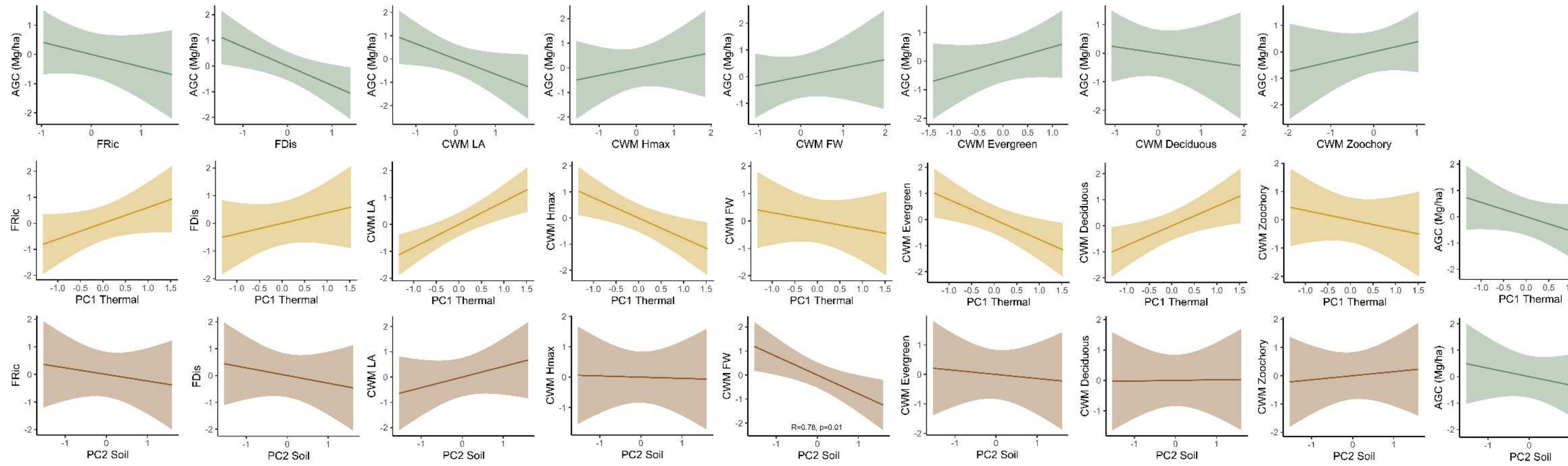

Fig. S6. Bivariate relationships between aboveground carbon stock (AGC), functional variables, and environmental variables for forests with high levels of disturbance; n=9.

Table S6. Standardized effects on AGC based on structural equation models (pSEMs). Abbreviations in Fig. 2 and 3.

Predictors To AGC		**Complementarity Model**		**Mass Ratio Model**	
		Effect	p	Effect	p
		All forests			
PCA1$_{Thermal}$		-0.260	0.256	0.092	0.763
	FRic	0.699	**0.0009**	-	-
	FDis	0.355	0.124	-	-
	CWM LA	-	-	1.373	**0.0000**
	CWM Deciduous	-	-	0.182	0.443
PCA2$_{Soil}$		-0.438	**0.01**	-0.240	0.292
	FRic	0.136	0.406	-	-
	FDis	-0.221	0.305	-	-
	CWM LA	-	-	-0.165	0.286
	CWM Deciduous	-	-	0.176	0.458
Disturbance		-0.658	**0.0006**	-0.553	**0.03**
	FRic	0.037	0.827	-	-
	FDis	-0.184	0.421	-	-
	CWM LA	-	-	-0.343	**0.004**
	CWM Deciduous	-	-	0.154	0.355
FRic		0.711	**0.006**	-	-
FDis		-0.646	**0.002**	-	-
CWM LA		-	-	-0.106	0.725
CWM Deciduous		-	-	-0.055	0.779
		Low disturbance level forests			
PCA1$_{Thermal}$		-0.361	0.588	0.247	0.499
	FRic	0.779	**0.003**	-	-
	FDis	0.405	0.182	-	-
	CWM Hmax	-	-	0.092	0.794
	CWM Zoo	-	-	0.099	0.792
PCA2$_{Soil}$		-1.654	**0.002**	-0.263	0.591
	FRic	0.191	0.361	-	-
	FDis	-0.188	0.520	-	-
	CWM Hmax	-	-	-0.055	0.871
	CWM Zoo	-	-	-0.141	0.495
FRic		1.958	**0.0003**	-	-
FDis		-0.788	**0.007**	-	-
CWM Hmax		-	-	-0.179	0.613
CWM Zoo		-	-	0.196	0.693
		High disturbance level forests			
PCA1$_{Thermal}$		-0.114	0.679	-0.628	0.101
	FRic	-0.251	0.546	-	-
	FDis	0.476	0.226	-	-
	CWM Hmax	-	-	-0.806	**0.02**

	CWM Zoo	-	-	-0.388	0.352
PCA2$_{Soil}$		-0.535	0.065	-0.339	0.305
	FRic	0.113	0.807	-	-
	FDis	-0.399	0.301	-	-
	CWM Hmax	-	-	0.149	0.588
	CWM Zoo	-	-	0.235	0.564
FRic		0.053	0.855	-	-
FDis		-0.891	**0.02**	-	-
CWM Hmax		-	-	-0.481	**0.0003**
CWM Zoo		-	-	0.036	0.400

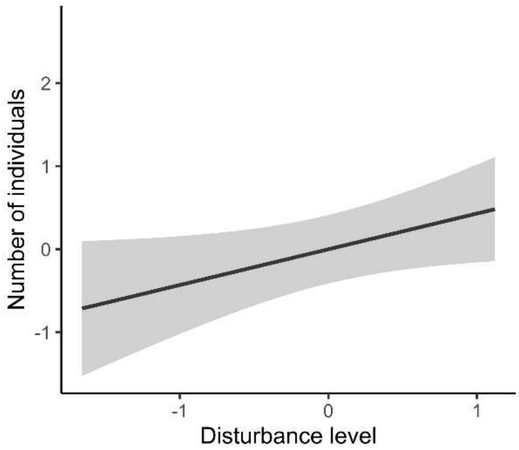

Fig. S7. Linear relationship between the number of individuals and the level of disturbance (R^2=0.43; p=0.04); n=22.

Table S7. Sensitivity analysis of niche complementarity models addressing sample imbalance. Low-disturbance forests originally had n=13 and high-disturbance forests n=9. To evaluate the robustness of the results to unequal sample sizes, we randomly reduced the low-disturbance group to n=9 using five random seeds. Forests excluded in each iteration were: set.seed 1 – c21D, Corfun, PERD, Tico; set.seed 2 – c11F, c13C, c22B, Sombratarde; set.seed 3 – c11D, c21D, Mombaca, Tresrios; set.seed 4 – c11D, c11F, Mombaca, Tresrios; set.seed 5 – c21D, c22B, Corfun, Tico. Code to remove after set.seed: [sample(1:nrow(lowdist), size = 9, replace = FALSE),], lowdist[!(lowdist$Sites %in% lowdist_sampled$Sites),], com[!(com$Sites %in% lowdist_removed$Sites),].

MODEL	**AIC**	**R²(AGC)**	**R²(FRIC)**	**R²(FDIS)**	**SIGNIFICANT VARIABLES**
ALL FORESTS (**ORIGINAL N=22**)	48.85	0.69	0.53	0.25	AGC ~ PC2soil (-0.43) AGC ~ disturbance level (-0.65) AGC ~ FRic (+0.71) AGC ~ FDis (-0.69) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 1, N=18)	48.85	0.76	0.53	0.25	AGC ~ PC2soil (-0.70) AGC ~ disturbance level (-0.89) AGC ~ FDis (-0.65) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 2, N=18)	48.85	0.64	0.53	0.25	AGC ~ PC2soil (-0.38) AGC ~ disturbance level (-0.61) AGC ~ FDis (-0.65) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 3, N=18)	48.85	0.68	0.53	0.25	AGC ~ PC2soil (-0.44) AGC ~ disturbance level (-0.66) AGC ~ FRic (+0.66) AGC ~ FDis (-0.65) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 4, N=18)	48.85	0.67	0.53	0.25	AGC ~ PC2soil (-0.46) AGC ~ disturbance level (-0.65) AGC ~ FDis (-0.61) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 5, N=18)	48.85	0.82	0.53	0.25	AGC ~ PC2soil (-0.65) AGC ~ disturbance level (-0.81) AGC ~ FRic (+0.51) AGC ~ FDis (-0.67) FRic ~ PC1thermal (-0.69)
LOW DISTURBANCE (**ORIGINAL N=13**)	35.27	0.59	0.62	0.22	AGC ~ PC2soil (-1.65) AGC ~ FRic (+1.95) AGC ~ FDis (-0.78) FRic ~ PC1thermal (-0.77)
LOW DISTURBANCE (SET.SEED 1, N=9)	35.27	0.57	0.62	0.22	AGC ~ PC2soil (-2.01) AGC ~ FRic (+2.23) FRic ~ PC1thermal (-0.77)
LOW DISTURBANCE (SET.SEED 2, N=9)	35.27	0.56	0.62	0.22	AGC ~ PC2soil (-2.33) AGC ~ FDis (-0.93) FRic ~ PC1thermal (-0.77)
LOW DISTURBANCE (SET.SEED 3, N=9)	35.27	0.51	0.62	0.22	AGC ~ FRic (+0.84) AGC ~ FDis (-1.38) FRic ~ PC1thermal (-0.77)
LOW DISTURBANCE (SET.SEED 4, N=9)	35.27	0.45	0.62	0.22	AGC ~ PC2soil (-2.12) FRic ~ PC1thermal (-0.77)
LOW DISTURBANCE (SET.SEED 5, N=9)	35.27	0.57	0.62	0.22	AGC ~ PC2soil (-2.91) AGC ~ FRic (+2.47) AGC ~ FDis (-1.23) FRic ~ PC1thermal (-0.77)

Table S8. Sensitivity analysis of mass ratio models addressing sample imbalance. Low-disturbance forests originally had n=13 and high-disturbance forests n=9. To evaluate the robustness of the results to unequal sample sizes, we randomly reduced the low-disturbance group to n=9 using five random seeds. Forests excluded in each iteration were: set.seed 1 – c21D, Corfun, PERD, Tico; set.seed 2 – c11F, c13C, c22B, Sombratarde; set.seed 3 – c11D, c21D, Mombaca, Tresrios; set.seed 4 – c11D, c11F, Mombaca, Tresrios; set.seed 5 – c21D, c22B, Corfun, Tico. Code to remove after set.seed: [sample(1:nrow(lowdist), size = 9, replace = FALSE),], lowdist[!(lowdist$Sites %in% lowdist_sampled$Sites),], com[!(com$Sites %in% lowdist_removed$Sites),].

MODEL	**AIC**	**R^2(AGC)**	**R^2(CWM_LA)**	**R^2(CWM_DECIDUOUS)**	**SIGNIFICANT VARIABLES**
ALL FORESTS (**ORIGINAL N=22**)	41.85	0.36	0.64	0.12	AGC ~ disturbance level (-0.51) CWM_LA ~ PC1thermal (+1.37) CWM LA ~ disturbance level (-0.34)
ALL FORESTS (SET.SEED 1, N=18)	66.62	0.57	0.53	0.25	AGC ~ PC2soil (-0.95) AGC ~ disturbance level (-1.36) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 2, N=18)	66.62	0.22	0.53	0.25	FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 3, N=18)	66.62	0.22	0.53	0.25	AGC ~ disturbance level (-0.59) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 4, N=18)	66.62	0.40	0.53	0.25	AGC ~ disturbance level (-0.61) FRic ~ PC1thermal (-0.69)
ALL FORESTS (SET.SEED 5, N=18)	66.62	0.48	0.53	0.25	AGC ~ disturbance level (-0.78) FRic ~ PC1thermal (-0.69)
			R^2(CWM_Hmax)	**R^2(CWM_Zoochoric)**	
LOW DISTURBANCE (**ORIGINAL N=13**)	34.46	0.14	0.03	0.01	- (model was statistically accepted, but without significant variables)
LOW DISTURBANCE (SET.SEED 1, N=9)	35.27	0.57	0.62	0.22	FRic ~ PC1thermal (-0.77) *statistically rejected
LOW DISTURBANCE (SET.SEED 2, N=9)	35.27	0.62	0.62	0.22	FRic ~ PC1thermal (-0.77) *statistically rejected
LOW DISTURBANCE (SET.SEED 3, N=9)	67.18	0.45	0.62	0.22	AGC ~ CWM zoochoric (+2.02) FRic ~ PC1thermal (-0.77) *statistically rejected
LOW DISTURBANCE (SET.SEED 4, N=9)	67.18	0.49	0.62	0.22	AGC ~ PC2soil (-2.60) FRic ~ PC1thermal (-0.77) *statistically rejected
LOW DISTURBANCE (SET.SEED 5, N=9)	67.18	0.39	0.62	0.22	FRic ~ PC1thermal (-0.77) *statistically rejected

*statistically rejected = Fisher’s C and p-value significant ($p<0.05$).

References (tables S2 and S3)

Albuquerque, N., Moraes, C., & Souza, M. (2022) *Sementes florestais da mata atlântica: um guia para o manejo de espécies da Hileia Baiana*. Programa Arboretum de Conservação e Restauração da Diversidade Florestal: Teixeira de Freitas, BA.

Barton, K. (2020) MuMIn: Multi-Model Inference.

Campos Filho, E.M., & Sartorelli, P.A.R. (2015) Guia de árvores com valor econômico. *São Paulo: Agroicone*.

Carvalho, P.E.R. (2014) *Espécies arbóreas brasileiras*. EMBRAPA.

Fox, J., & Weisberg, S. (2019) *An {R} Companion to Applied Regression*. Sage: Thousand Oaks CA.

Grenié, M., & Gruson, H. (2023) fundiversity: a modular R package to compute functional diversity indices. *Ecography*, 2023(3). https://doi.or/10.1111/ecog.06585

Laliberté, E., Legendre, P., & Shipley, B. (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology.

Lê, S., Josse, J., & Husson, F. (2008) FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software*, 25(1). https://doi.or/10.18637/jss.v025.i01

Lefcheck, J.S. (2016) piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. https://doi.or/10.1111/2041-210X.12512

Lopes, J.D.C., & Mello-Silva, R.D. (2014) Annonaceae da Reserva Natural Vale, Linhares, Espírito Santo. *Rodriguésia*, 65(3), 599–635. https://doi.or/10.1590/2175-7860201465304

Lorenzi, H. (1992) *Árvores brasileiras: Manual de Identificação de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil*. Ed. Plantarum: Nova Odessa.

Lorenzi, H. (2008) *Árvores Brasileiras: Manual de Identificação de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil*. Ed. Plantarum: Nova Odessa.

Lorenzi, H. (1998) *Árvores brasileiras: Manual de Identificação e Cultivo de Plantas Arbóreas Nativas do Brasil*. Ed. Plantarum: Nova Odessa.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022) vegan: Community Ecology Package.

Paradis, E., & Schliep, K. (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. https://doi.or/10.1093/bioinformatics/bty633

Pinheiro, J., Bates, D., & R Core Team. (2023) nlme: Linear and Nonlinear Mixed Effects Models.

R Core Team. (2022) R: A language and environment for statistical computing.

Rolim, S.G., Peixoto, A.L., Pereira, O.J., Araujo, D. de, Nadruz, M., Siqueira, G., & Menezes, L. de. (2016) Angiospermas da Reserva Natural Vale, na floresta atlântica do norte do Espírito Santo. *Floresta Atlântica de Tabuleiro: diversidade e endemismo na Reserva Natural Vale*, 1, 167–230.

Sambuichi, R.H.R., Mielke, M.S., & Pereira, C.E. (2009) Lista de árvores nativas do sul da Bahia. *Nossas árvores: conservação, uso e manejo de árvores nativas no sul da Bahia*. Editus: Ilhéus, BA.

Scaravelli, F.S., Gaem, P.H., Valdemarin, K.S., Lucas, E., & Mazine, F.F. (2022) Myrcia (Myrtaceae) in the Vale Natural Reserve, Linhares, Espírito Santo, Brazil. *Rodriguésia*, 73, e02352020. https://doi.or/10.1590/2175-7860202273024

CHAPTER 2 - Drivers of carbon pools in secondary tropical forests: The role of biodiversity and the environment

ABSTRACT

Secondary tropical forests play a key role in the global carbon cycle, yet assessments often focus on aboveground biomass, overlooking substantial belowground pools such as roots and soil organic carbon. Understanding how biotic and abiotic factors jointly shape different carbon compartments is essential for effective management and climate change mitigation. We evaluated aboveground, root, and soil carbon stocks (AGC, RC, and SOC) across 21 secondary Atlantic Forest fragments in Brazil, integrating functional and phylogenetic diversity metrics with environmental and anthropogenic variables. Exploratory statistical models were used to identify the main drivers of each carbon compartment. Carbon stocks varied markedly among plots: AGC accounted for 12-57% of total carbon, roots for 4-26%, and soil for 22-84%. AGC increased with phylogenetic diversity and evergreen dominance, supporting the roles of niche complementarity and conservative strategies in sustaining long-term biomass accumulation. Root carbon was positively associated with precipitation and evergreen dominance but negatively related to functional evenness, indicating hierarchical rather than complementary effects on belowground allocation. SOC was primarily driven by abiotic factors, with higher soil water content enhancing carbon storage and higher mean annual temperature reducing it, highlighting the vulnerability of soil carbon to climate warming. Functional traits revealed clear trade-offs: nitrogen-fixing and tall acquisitive species contributed less to long-term SOC, whereas conservative traits promoted soil carbon accumulation. Overall, our results show that carbon compartments in secondary tropical forests respond to distinct combinations of environmental, functional, and phylogenetic drivers. The predominance of belowground pools in many sites underscores the limitations of assessments based solely on AGC, particularly in restoration contexts. Integrated, compartment-specific approaches that incorporate functional diversity are therefore crucial for improving carbon management, conservation, and ecosystem service valuation in tropical forests.

Key words: trait-based ecology; carbon allocation; phylogenetic structure.

INTRODUCTION

Secondary tropical forests, with their varied structures, types, biodiversity, and environmental conditions, play crucial roles in ecological processes and ecosystem services, including nutrient cycling, water regulation, biodiversity maintenance, and carbon sequestration (Brandon, 2014; Matos et al., 2020). The latter has become increasingly prominent due to its critical role in regulating atmospheric carbon dioxide levels and mitigating the effects of global change (Bennett et al., 2020; Ferreira et al., 2023; Mitchard, 2018). Consequently, the majority of studies and restoration projects, including those involving carbon credits, focus on the patterns and forms of tree biomass accumulation potential (Coelho et al., 2022; Cuesta et al., 2023; Gardon et al., 2020; Pichancourt et al., 2014; Randazzo et al., 2023). However, other forms of carbon storage, which may be equally or more substantial in terms of volume, particularly belowground, are often overlooked, as are the dynamics between different carbon compartments and their relationships with biodiversity, plant functional strategies, and environmental factors (Ali and Yan, 2017; Bieluczyk et al., 2023; Brancalion et al., 2018; Gherardi and Sala, 2020; Moreira et al., 2020). Understanding these connections is essential for developing effective conservation strategies and mitigate anthropogenic effects in an integrated and comprehensive manner.

There are four main reservoirs for determining carbon stocks in an ecosystem, as defined by the IPCC (2006): live aboveground biomass (AGB) and belowground biomass (BGB), dead organic matter, including fallen wood and litter, and carbon in soil organic matter (SOC). Of these, the carbon stocks in aboveground and root biomass, as well as soil carbon, are the most accessible from phytosociological data and geoscientific information. Above and belowground biomass stocks mainly consist of woody stem material and fine roots (IPCC, 2006; McCormack et al., 2015). Organic carbon stocks in the soil encompass a complex set of decomposed materials, including root remains, fruits, seed banks, litter, microbiota, mesofauna, macrofauna, and the various biotic interactions present in the soil matrix (Denardin et al., 2014; IPCC, 2006; Wiesmeier et al., 2019). These carbon compartments contribute substantially to the overall carbon dynamics in tropical forests and to the multifunctionality of these ecosystems, providing a valid estimate of the carbon that the ecosystem can store in the long term (De La Cruz-Amo et al., 2020; McCormack et al., 2015; Vieira et al., 2011).

Several processes have been identified as primary contributors to carbon accumulation. The main drivers of carbon in stem and root biomass include forest age and type, climate, soil quality and structure, dominant species, functional and phylogenetic structures (De La Cruz-Amo et al., 2020; Satdichanh et al., 2023; Wiesmeier et al., 2019). Soil organic carbon is also shaped by multiple factors, such as organic matter deposition, decomposition rates in the rhizosphere and by microbiota, litter characteristics, and the size and depth of the root system (Gherardi and Sala, 2020; Jobbágy and Jackson, 2000; Lee et al., 2024; Poirier et al., 2018; Sena et al., 2018; Wiesmeier et al., 2019). Moreover, human activities such as deforestation and land use changes represent substantial threats to this ecosystem process, given their capacity to modify the ecosystem's natural carbon storage capacity and impact biodiversity (Costa et al., 2009; Denardin et al., 2014; Rigueira and Mariano-Neto, 2023; Wiesmeier et al., 2019). The diversity and complexity of interactions between biotic and abiotic factors indicate that carbon stocks in tropical forests result from multifactorial processes, whose investigation requires an integrated approach that considers these multiple dimensions.

Plant functional traits provide a mechanistic link between biodiversity, environmental filters, and ecosystem functioning, as they reflect trade-offs in resource acquisition, use, and conservation (Diaz et al., 2004; Violle et al., 2007). In tropical forests, plant strategies are often described along an acquisitive-conservative spectrum, in which acquisitive species are characterized by fast growth, nutrient-rich tissues, and rapid resource turnover, whereas conservative species exhibit traits associated with slow growth, high wood density, tougher tissues, longer tissue lifespan, and greater investment in structural support and maintenance (Poorter et al., 2017; Reich, 2014; Wright et al., 2004). These contrasting strategies are shaped by climatic, edaphic, and disturbance gradients and have direct implications for carbon dynamics, as acquisitive strategies tend to promote rapid biomass accumulation but lower residence time, while conservative strategies are often linked to greater biomass persistence, slower turnover, and enhanced carbon storage, particularly in woody tissues and soil organic matter (Díaz et al., 2009; Finegan et al., 2015; Mensah et al., 2021). Consequently, the dominance and diversity of functional strategies within communities can strongly modulate how carbon is allocated and retained across aboveground, root, and soil compartments.

Despite the importance of the topic, there are few studies that simultaneously address the multiple carbon pools in forest ecosystems (e.g., Bieluczyk et al., 2023; Dantas et al., 2020; De La Cruz-Amo et al., 2020; Doetterl et al., 2015; Lee et al., 2024; Ma et al., 2021; Vieira et al., 2011). Even rarer are those that investigate the multiple drivers that influence carbon stocks in an integrated manner, considering climate, soil, disturbances, functional structure, and phylogeny. The majority of extant research focuses on the effects of these factors on a single compartment, typically aboveground carbon (e.g. Borges et al., 2021; Bu et al., 2019; Cavanaugh et al., 2014; Coelho De Souza et al., 2019; Ferreira et al., 2023; Mensah et al., 2021; Noulèkoun et al., 2024; Pyles et al., 2022; Wang and Ali, 2021; Zang, 2019), neglecting the large stocks in the soil - the third largest global carbon stock, behind only ocean and geological reservoirs (Gherardi and Sala, 2020). Previous studies indicate that, in tropical forests, the soil can store twice or even three times the amount of carbon present in the aboveground biomass, highlighting its critical importance for the global carbon balance (Houghton, 2005; Kendie et al., 2021; Vieira et al., 2011). Therefore, understanding how biotic and abiotic factors shape carbon stock across compartments is crucial for guiding management and conservation strategies, given the central role of tropical forests in the global carbon cycle.

In this context, we aimed to assess the organic carbon stocks in secondary Atlantic Forests in a highly fragmented region under strong human pressure (De Lima et al., 2024; Pyles et al., 2022; Rezende et al., 2018; Rigueira and Mariano-Neto, 2023), across aboveground biomass, roots, and soil, and identify their main drivers. Here, we investigated the effects of functional dominance, functional diversity, and phylogenetic diversity on carbon stocks in each compartment above and belowground, also considering climatic, edaphic, and anthropogenic gradients that may modulate these relationships on a regional scale. We hypothesize that (1) aboveground carbon stocks will be primarily influenced by water availability, soil fertility, and functional structure of plants, with communities dominated by species with conservative traits storing more biomass and carbon aboveground (Diaz et al., 2004; Mensah et al., 2021; Poorter et al., 2017). In addition, we expect functional and phylogenetic diversity to have a positive effect on AGC through complementarity and niche partitioning, as more diverse communities may capture and use resources more efficiently (Ali and Yan, 2017; Satdichanh et al., 2019). (2) for root carbon (RC), in addition to sharing similarities with environmental conditions favorable for AGC, since it also represents live biomass, we expect stronger associations with acquisitive functional strategies of plants, since fine roots need to cope with resource fluctuations in the soil (Kong et al., 2016; Lugli et al., 2020). And (3) for soil organic carbon, we anticipate stronger links with both climatic seasonality, edaphic factors and conservative functional strategies, since litter decomposition is constrained during dry periods and organic matter stabilization is favored, and it also seems to be enhanced by functional strategies related to resource conservation that promote stabilization and generate more recalcitrant litter inputs (Luo et al., 2021; Parsons et al., 2014; Yu et al., 2019).

METHODS

i. *Study area*

This study included 21 fragments of secondary forests within the Atlantic Forest domain, located across the states of Minas Gerais, Espírito Santo, and Bahia (Figure 1). The sampled forests have been undergoing secondary succession for four to six decades after different land-use histories, primarily selective logging and clear-cutting, within complex landscapes that have experienced extensive transformations, including conversion to pasture, agriculture, mining, and silviculture (Coelho et al., 2022; Matos et al., 2020). The areas encompass three main vegetation types: rainforests, semideciduous forests and riverine (gallery) forests (Figure 1), primarily differentiated by water availability, landscape topography, and soil depth, drainage and texture, which drive regional variations in floristic, functional, and phylogenetic community composition (Neves et al., 2017; Vitória et al., 2019). The region encompasses a climatic gradient from tropical without a dry season (Af, Am, Aw) to tropical with a dry winter (Cwa, Cwc), following the Köppen classification, and local soils are mainly dystrophic red and yellow latosols, dystrophic yellow argisols, spodosols, and cambisols (Santos et al., 2018).

The inventories were conducted between 2005 and 2019. In each fragment, 50 plots of 10x10 meters (0.5 ha) were established, where all individuals with a diameter at breast height (DBH) ≥ 4.8 cm were recorded, including measurements of height and circumference. In total, 23,026 individuals from 644 species and 71 families were sampled. Morphospecies (aff.) and individuals identified only to the family level were excluded from subsequent analyses, since functional trait data must be species-specific.

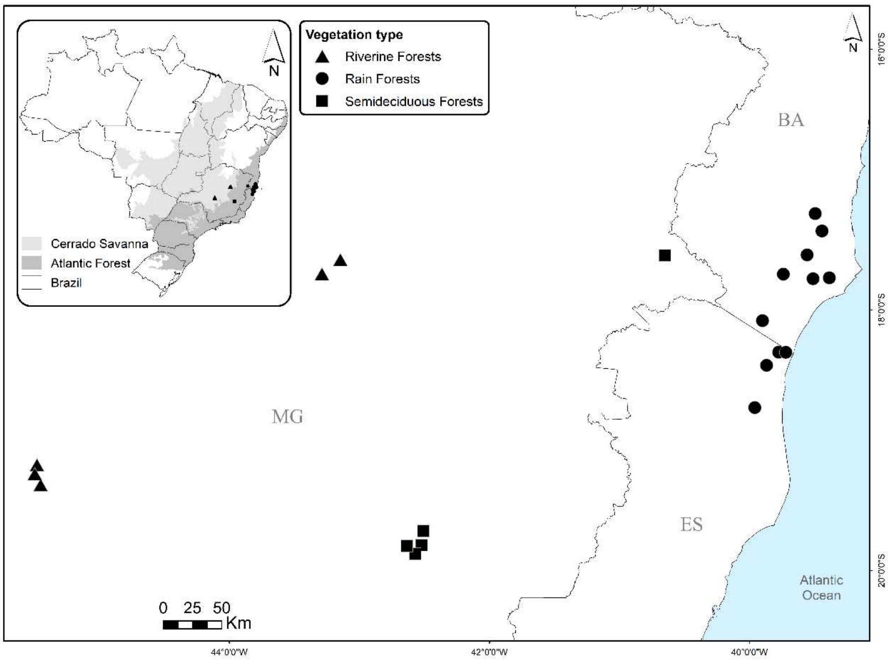

Figure 1. Location of rain, semideciduous, and riverine (gallery) forest communities. BA – Bahia state; ES – Espírito Santo state; MG – Minas Gerais state.

ii. Environmental variables

Climatic variables of average (annual), variation (seasonality), and extremes (maximum) of temperature and precipitation were obtained via WorldClim at a spatial resolution of 1 km (Fick and Hijmans, 2017). Soil variables related to water availability, texture, and soil fertility proxies (CEC – cation exchange capacity, pH, clay, sand and water content in the soil) were acquired from GeoInfo - Embrapa (non-commercial use license CC BY NC 3.0 BR) at a spatial resolution of 90 meters (Santos et al., 2018).

Landscape and anthropogenic variables relevant to the ecology of the Atlantic Forest were considered, including fragment isolation (measured by Euclidean distance, in meters, to the nearest fragment) (Bender et al., 2003) and the level of anthropogenic disturbance. The latter was quantified using a four-level classification (high, medium, low, and severe) based on disturbance type and intensity (e.g., clear-cutting, selective logging, fire), time since the last event, and successional stage, following Pyles et al. (2022). This classification relied on historical records from original inventories, complemented by satellite imagery, and represents the most robust fragment-level information available across the Atlantic Forest, despite limited within-category resolution and the absence of standardized fine-scale data. In the dataset, early secondary forests subjected to severe disturbance were not represented; high disturbance corresponded to clear-cutting 20-50 years before sampling, medium disturbance to sporadic or selective logging 50-80 years prior, and low disturbance to forests undisturbed or without records for at least 80 years. As disturbance levels were ordinal, they were converted into a continuous variable using ridit scores.

iii. Functional and phylogenetic metrics

We obtained information on ten functional traits at the interspecific level by measuring virtual herbaria, databases, books, and scientific articles, following the appropriate protocols (Brazil Flora Group, 2021; de Bello et al., 2021; Kattge et al., 2020; Pérez-Harguindeguy et al., 2013; speciesLink network, 2021; Tedersoo et al., 2018; Zanne et al., 2009): leaf area, fruit length and width, seed length and width, maximum height, wood density, leaf habit (evergreen or deciduous), nitrogen fixation capacity, and dispersal type (biotic or abiotic). When species-specific values were not available, we used an imputation procedure to estimate the values of functional traits, using the average method for the genus, focusing mainly on neotropical regions (Chave et al., 2006; de Bello et al., 2021; Flores and Coomes, 2011).

The functional dominance of communities was estimated using the abundance-weighted mean of functional traits (CWM). Functional diversity was assessed based on multi-trait metrics, allowing us to characterize the volume, distribution, and dispersion of traits in communities. Due to the presence of categorical functional traits, a Principal Coordinate Analysis (PCoA) with Gower's distance was applied, selecting the dimensions that best explained the variation for the calculation of the indices. The metrics used were: Functional Richness (FRic), which expresses the breadth of the functional space occupied by the community; Functional Dispersion (FDis), which quantifies the distribution of species in relation to the centroid of the functional space, weighted by abundances; Functional Divergence (FDiv), which measures the degree to which the most abundant species deviate from the centroid, indicating functional specialization; and Functional Evenness (FEve), which assesses the regularity in the distribution of abundances throughout the functional space (Mouchet et al., 2010; Villéger et al., 2008).

Using the phylogenetic tree generated from all sampled woody angiosperms, we calculated the following phylogenetic metrics: Faith’s phylogenetic Index (PD), Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD), and their standardized effect sizes (*ses*), which minimizes the effect of species richness of each plot based on the ‘phylogeny.pool’ null model. PD is determined by the number of species and their phylogenetic dissimilarity (Faith, 1992). MPD represents the average distance between all pairs of taxa in the sample, while MNTD measures the average distance to the nearest taxon, focusing on the extent of the terminal cluster (Webb, 2000).

iv. Carbon stock pools

We estimated aboveground biomass (AGB Mg ha^{-1}) for each individual using the allometric equation of Chave et al. (2014), widely used for tropical forests, defined as:

$$AGB = 0.0673\ (\rho D^2 H)^{\ 0.976}$$

Where D is the diameter of the stem (DBH – cm), H is the height of the individual (m), and ρ is the wood density (g cm^{-3}).

Belowground biomass (BGB Mg ha^{-1}) was estimated for each individual using the allometric equation of Kachamba et al. (2016), which uses tree diameter (D – DBH) in the following formula:

$$BGB = 0.285\ \times\ D^{1.993}$$

The above-ground carbon stock (AGC) and root carbon stock (RC) of each individual was estimated considering 45.6% of the total biomass (AGB e BGB) (Martin et al., 2018).

Soil organic carbon stock (SOC Mg ha^{-1}) for the 0-30 cm depth layer was obtained from maps provided by GeoInfo - Embrapa (Santos et al., 2018), using the same spatial resolution and licensing conditions as the other edaphic variables. These maps were generated through digital soil mapping based on legacy soil data and freely available geospatial covariates, within the framework of the Brazilian National Soil Survey Program (PronaSolos). SOC values were obtained using the geographic coordinates of each forest fragment and aggregated to a total sampled area of 0.81 ha per plot. We analyzed both the total carbon value across areas, as well as the ratios among compartments (sum of carbon stock/total*100).

v. Statistical analyses

To assess which environmental, edaphic, landscape, phylogenetic and functional variables influence each carbon compartment (AGC, RC, and SOC), we adopted a stepwise exploratory modeling approach, a process of construction and simplification of models to reduce the risk of overfitting and collinearity. Initially, we verified the bivariate relationships between each predictor variable and carbon stocks transformed into logarithms using simple linear regressions. For AGC, we did not include WD as a predictor, since it is already incorporated into the allometric equation used to calculate AGC, and its inclusion would introduce circularity. For regressions showing statistical significance or marginal significance ($p \leq 0.05$), we evaluated spatial autocorrelation in the residuals using Moran's test applied to generalized linear models (GLS). The presence of spatial autocorrelation would indicate dependence among nearby observations, violating the independence of errors assumption and potentially biasing results; however, no significant spatial autocorrelation was detected (Table S1). Subsequently, significant predictors were included in global generalized linear models (GLMs) to identify the main drivers of each carbon compartment (R Core Team, 2022). Given the absence of spatial autocorrelation and the limited number of levels in the grouping factors (21 areas and 3 forest types), we used glms rather than glmms (mixed), as random effects could not be reliably estimated and often resulted in singular or unidentifiable fits. Model robustness was assessed by checking multicollinearity among predictors using the variance inflation factor (VIF), excluding variables with VIF>4 (Figure S1). Model selection and averaging were then conducted using the dredge function of the MuMIn package (Barton, 2024). Candidate models were generated by fitting all possible combinations of predictors from the global model, and models were ranked according to Akaike's Information Criterion (AIC). To reduce multicollinearity, only models with a maximum pairwise correlation among predictors ≤0.6 were retained. From this reduced candidate set, models with ΔAIC<2 were considered equally plausible and included in the final model-averaging procedure. Model-averaged parameter estimates were then obtained using the *model.avg* function. All analyses were conducted in the R statistical environment (R Core Team, 2022).

RESULTS

Aboveground carbon stock (AGC) varied widely among plots, ranging from 4.73 to 89.60 Mg ha^{-1} across all fragments (Table 1; Figure 2A) and between 12 and 57% of the total carbon stock (Figure 2B). On average, AGC accounted for approximately 39% of total carbon. Carbon stock in roots varied between 1.8 and 36.5 Mg ha^{-1} (Table 1; Figure 2A) and between 4 and 26% of the total proportion (Figure 2B), representing on average 20% of the total. Finally, organic carbon stock in the soil varied between 30.7 and 46.2 Mg ha^{-1} (Table 1; Figure 2A) and between 22 and 84% of the total carbon proportion (Figure 2B), with a mean contribution of about 41%.

Table 1. Carbon stocks by compartment in secondary tropical forests (mean ± standard deviation and observed range – Mg/ha^{-1}).

Compartment	**Mean ± sd (%)**	**Min. – Max.**
Aboveground carbon (AGC)	36.06 ± 20.60 (39)	4.73 – 89.60
Root carbon (RC)	18.18 ± 8.14 (20)	1.83 – 36.50
Soil organic carbon (SOC)	38.83 ± 4.49 (41)	30.70 – 46.20
Total carbon stock	93.07 ± 27.50	40.95 – 155.84

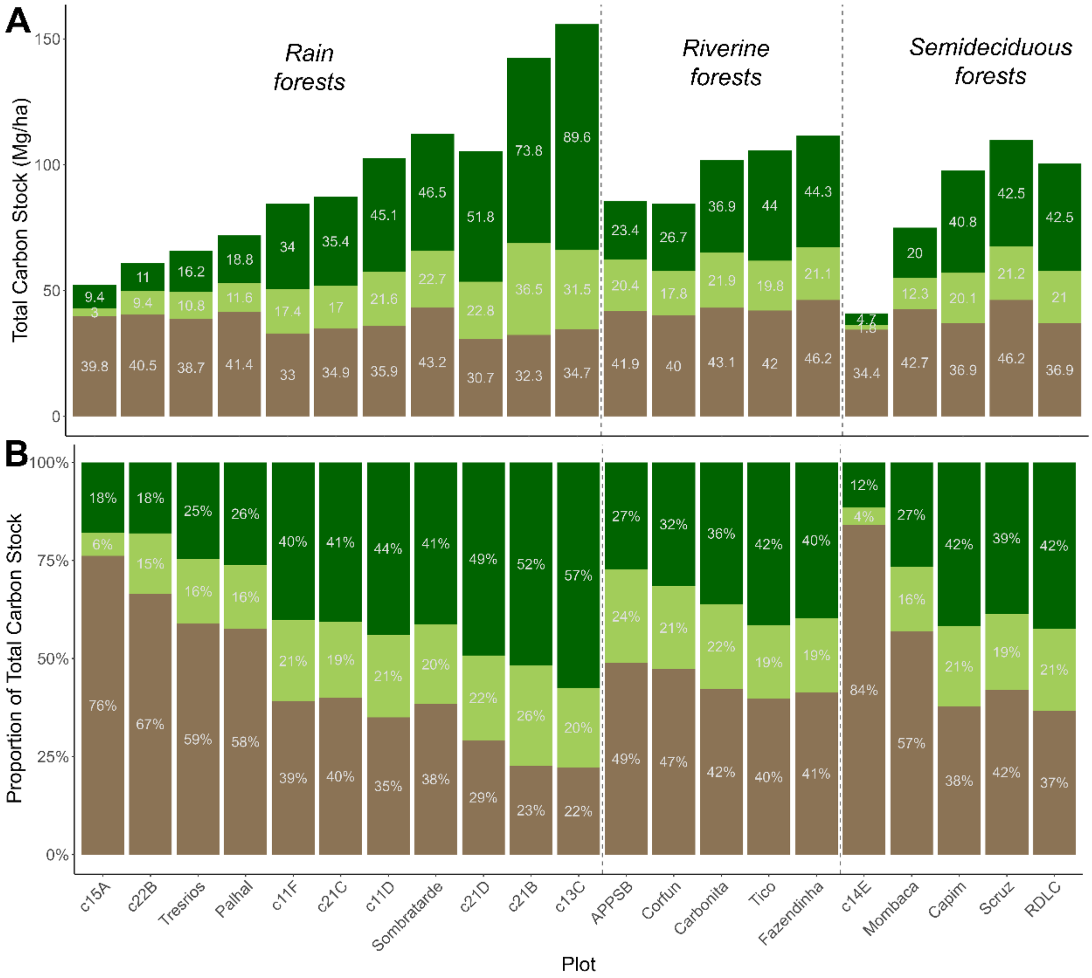

Figure 2. Carbon stock compartments across different plots and forest types: (A) absolute value (Mg/ha^{-1}) and (B) relative proportions (%) for rainforests (n=11) riverine forests (n=5), and semideciduous forests (n=5). Aboveground carbon (AGC) is shown in dark green at the top, root carbon (RC) in light green in the middle, and soil organic carbon (SOC) in brown at the bottom.

Bivariate regressions were first used to identify general trends in the relationships between variables. Aboveground carbon (AGC) and root carbon (RC) responded to a total of 7 and 10 variables, respectively, with a tendency for these relationships to involve more biotic factors (Table 2). In contrast, soil organic carbon (SOC) responded to a total of 12 variables, predominantly abiotic (Table 2). Based on these significant bivariate relationships, three global generalized linear models (GLMs) were subsequently constructed (Supplementary text 1), one for each carbon compartment. AGC showed a positive relationship with observed phylogenetic diversity (p=0.03) and the proportion of evergreen species (p=0.02) and a negative relationship with the proportion of nitrogen fixing species (p=0.004) (Figure 3; Table S2). Annual precipitation (p=0.27) and disturbance level (p=0.59) were selected but did not show significant relationships. The RC model exhibited a positive relationship with annual precipitation (p=0.005) and the proportion of evergreen species (p=0.02), and a negative relationship with soil functional evenness (p=0.01) (Figure 4; Table S2). The variables selected in the model but without significant relationships with RC were sesMPD (p=0.42), and sesMNTD (p=0.35). For the SOC model, a positive relationship was observed with soil water content (p=0.003) and a negative relationship with annual temperature (p=0.01) and CWM of maximum height (p=0.001) (Figure 5; Table S2). a marginal relationship was found for and CEC (p=0.05). Variables included in the models but without statistical significance were clay content (p=0.53) and CWM fruit width (p=0.13).

Table 2. Variables significantly associated with carbon stocks in the aboveground (AGC), root (RC) and soil (SOC) compartments in three forest types (simple regressions). Arrows (↓↑) indicate direction of the effect; significance levels: p=0.05‘.’, p<0.05*, p<0.01**, p<0.001***; coefficient of determination (R^2) in parentheses.

Variables groups	*Independent variable*	*AGC*	*RC*	*SOC*
Climate	Annual temperature	-	-	↓** (0.29)
	Annual precipitation	↑** (0.26)	↑. (0.17)	↓. (0.16)
	Precipitation seasonality	-	-	↑* (0.22)
	Temperature seasonality	-	-	-
	Maximum precipitation	-	-	↑* (0.22)
	Maximum temperature	-	-	-
Soil	Water content	-	-	↑*** (0.57)
	Sand content	-	-	↓*** (0.70)
	Clay content	-	-	↑* (0.20)
	Soil pH	-	-	-
	CEC	-	-	↑** (0.41)
Landscape	Patch isolation	-	-	-
	Disturbance level	↓. (0.16)	-	-
Phylogenetic diversity	sesPD	-	-	-
	PD obs.	↑* (0.24)	-	-
	sesMPD	-	↑* (0.24)	-
	MPD obs.	-	-	-
	sesMNTD	↑* (0.21)	↑. (0.18)	-
	MNTD obs.	-	-	-

Functional diversity	FRic	-	-	-
	FDiv	-	-	-
	FDis	-	↓. (0.18)	-
	FEve	-	↓* (0.23)	-
Functional dominance	CWM leaf area	-	-	↓** (0.40)
	CWM fruit length	-	↓* (0.23)	↓* (0.28)
	CWM fruit width	-	-	↓* (0.28)
	CWM seed length	-	-	-
	CWM seed width	-	-	-
	CWM maximum height	-	-	↓** (0.40)
	CWM wood density	-	-	-
	CWM evergreen	↑. (0.16)	↑** (0.26)	-
	CWM deciduous	-	↓. (0.19)	-
	CWM N fixing	↓** (0.40)	↓** (0.36)	-
	CWM biotic dispersion	↑* (0.23)	↑** (0.32)	-
	CWM abiotic dispersion	-	-	-

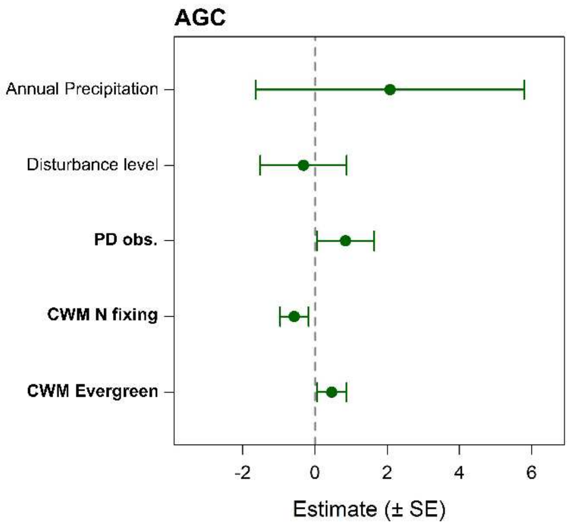

Figure 3. Effects of environmental, phylogenetic and functional variables on aboveground carbon (AGC) stocks. Significant variables in bold.

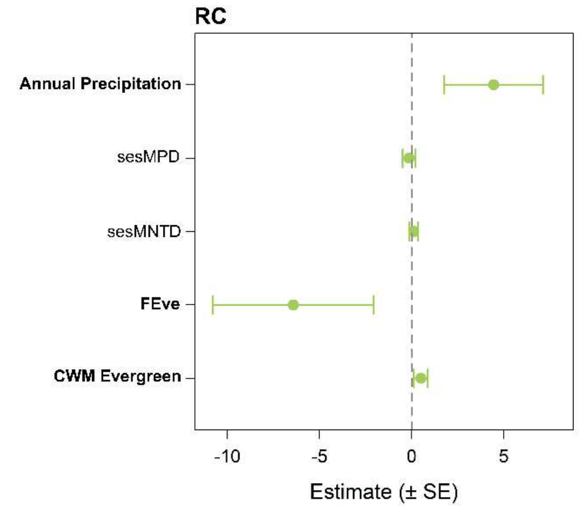

Figure 4. Effects of environmental, phylogenetic and functional variables on root carbon (RC) stocks. Significant variables in bold.

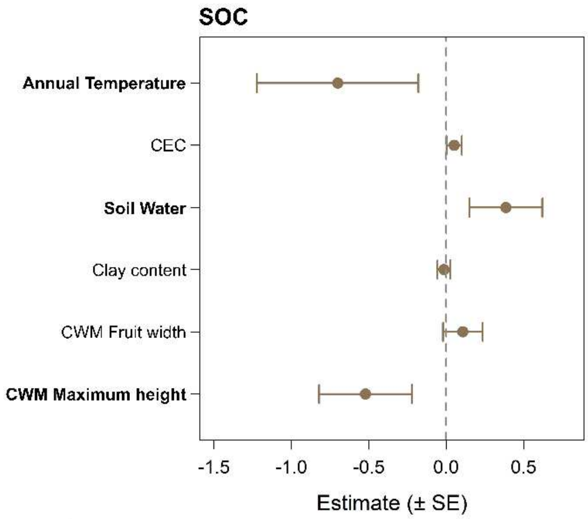

Figure 5. Effects of environmental, phylogenetic and functional variables on soil organic carbon (SOC) stocks. Significant variables in bold.

DISCUSSION

Our results reveal distinct patterns of carbon stock in the Atlantic Forest and provide partial support for the proposed hypotheses, highlighting both the role of biotic diversity and the influence of abiotic conditions in shaping carbon stocks across compartments. Aboveground carbon was positively associated with phylogenetic diversity, confirming the expectation that higher phylogenetic diversity enhances carbon storage through complementarity and niche partitioning (Ali and Yan, 2017; Satdichanh et al., 2019), while functional dominance by conservative strategies also contributed to greater aboveground biomass (Adler et al., 2014;

Diémé et al., 2019). For root carbon, the positive effects of annual precipitation and evergreen dominance indicate that belowground carbon is favored by water availability and conservative strategies, contrary to our initial hypothesis that acquisitive traits would be more strongly associated with root allocation. Soil organic carbon showed the strongest links to abiotic gradients, with positive associations with soil water content and negative associations with temperature, corroborating the hypothesis that climatic and edaphic conditions are primary drivers of SOC dynamics (Davidson and Janssens, 2006; Luo et al., 2021). Together, these results demonstrate that although functional diversity and dominance shape above and belowground carbon differently, environmental filters remain the main determinants of soil carbon. This underscores the importance of adopting compartment-specific and multivariate perspectives to understand carbon allocation in tropical forests, as the mechanisms underlying AGC, RC, and SOC are not only distinct but also interact with climate and soil in complex ways, with direct implications for predicting ecosystem responses to global change.

i. *Patterns in carbon compartments*

The carbon pools values observed in the areas covered by this study were generally within the ranges reported for tropical forests or proportional to total stock estimates (De La Cruz-Amo et al., 2020; Jones et al., 2019; Kendie et al., 2021; Vieira et al., 2011). For exemple, Bieluczyk et al. (2023) reported that in a primary Atlantic Forest, AGC accounted for 50% (54.1 Mg ha^{-1}) and SOC for 44% (47.4 Mg ha^{-1}), with the remainder presented in litter. In restored forests, the same authors identified 37.7% AGC and 53.2% SOC, suggesting that the edaphic compartment tends to recover more quickly than plant biomass. Similarly, Dantas et al. (2020) reported that in a semideciduous secondary forest, 35.23% of the total carbon was stored aboveground, a value very close to the 39% recorded in our plots, although they recorded a higher proportion of SOC (62.22% vs. 42% in our data). In contrast, the belowground carbon fraction was substantially lower in their study (1.54% vs. 20% in our data), likely due to different methodologies: Dantas et al. performed direct measurements of soil and root carbon, whereas we relied on spatial data for SOC and allometric estimates for root carbon. This suggests that spatial models as the one we used here may underestimate the actual soil carbon levels in secondary tropical forests, while allometric equations may be overestimating root carbon stocks (Handavu et al., 2021; Kotowska et al., 2015).

The wide variation in aboveground carbon stocks among the evaluated plots (4.73 a 89.6 Mg ha^{-1}; Table 1) may reflect different successional stages, disturbance histories, and functional compositions of plant communities, factors widely recognized to influence vegetation structure and biomass accumulation (Lasky et al., 2014; Poorter et al., 2021; Pyles et al., 2022). In this study, the larger number of plots sampled in rainforests, which tend to have taller and denser vegetation (Marques et al., 2011; Scarano, 2002), contributed to an higher average total carbon value. Given that aboveground carbon can represent less than half of the total stock in certain areas, estimates based solely on aboveground biomass may substantially underestimate the carbon storage potential of tropical forests (Bieluczyk et al., 2023; Handavu et al., 2021; Houghton, 2005; Kotowska et al., 2015). The high percentages of organic carbon in the soil, reaching up to 84% of the total in some plots (Figure 2B), underscore its role as the main carbon reservoir in the studied ecosystems, even accounting for potential underestimates from spatial data. Moreover, the lower range and variability of soil carbon stocks, compared to aboveground biomass, suggest greater temporal stability in this compartment, which is less affected by recent disturbances and successional dynamics (Bieluczyk et al., 2023; Kendie et al., 2021; Satdichanh et al., 2023).

ii. Carbon drivers in secondary Atlantic forests

The differential influence of biotic and abiotic variables on the distinct carbon compartments above and belowground has already been reported in several biomes, including temperate forests (Lee et al., 2024), savanna formations (Terra et al., 2023) and other tropical forest regions (Doetterl et al., 2015; Saimun et al., 2021). Annual precipitation had a positive influence on RC, reinforcing the central role of water availability and its importance for photosynthetic demand as key drivers of primary productivity and biomass accumulation in tropical forests (Aguirre-Gutiérrez et al., 2019; Ali et al., 2019; Lammerant et al., 2023). SOC showed a positive relationship with soil water content, suggesting that higher moisture availability enhances carbon stabilization. Soils with higher water content are more likely to experience waterlogging and anaerobic conditions, which slows down nutrient cycling, mineralization, and losses due to microbial respiration, and hinders the decomposition of plant tissues, promoting greater accumulation and stabilization of carbon in the soil (De La Cruz-Amo et al., 2020; Pantaleão et al., 2024; Saimun et al., 2021; Wiesmeier et al., 2019). In contrast, we found that increasing mean annual temperature was associated with lower SOC, consistent with the expectation that warmer environments accelerate microbial activity and nutrient cycling, thereby reducing long-term carbon storage (Davidson and Janssens, 2006; De La Cruz-Amo et al., 2020; Parsons et al., 2014). These findings align with global evidence that temperature is a key regulator of soil carbon turnover (Davidson and Janssens, 2006) and highlight the vulnerability of SOC stocks to ongoing climate warming, which is projected to exacerbate losses through enhanced decomposition processes (Luo et al., 2021).

Phylogenetic diversity had a positive effect on AGC, supporting the niche complementarity hypothesis, which predicts that more distantly related species use resources in complementary ways and thereby enhance ecosystem functioning (Cadotte, 2013; Coelho De Souza et al., 2019; Larkin et al., 2023; Satdichanh et al., 2019; Tilman et al., 1997). In contrast, the negative relationship between functional evenness and RC suggests that communities dominated by particular strategies occupying asymmetrical positions in trait space, rather than evenly distributed functional values, can be more effective in driving belowground carbon storage. This pattern likely reflects the disproportionate importance of carbon-hyperdominant species, whose functional traits exert strong influence on ecosystem processes through the mass ratio effect (Borges et al., 2021; Da et al., 2023; Kong et al., 2016; Poirier et al., 2018; Tolmos et al., 2024).

Functional traits revealed contrasting strategies across compartments. A higher proportion of evergreen species was associated with greater AGC and RC, reinforcing the role of conservative traits in sustaining long-term biomass accumulation, and contrary to what was found by Rodrigues et al. (2023) for a semideciduous forest in Minas Gerais State. Conversely, the negative effect of nitrogen-fixing species supports the idea that acquisitive strategies, while favoring rapid resource uptake, may trade off with long-term carbon storage (Bu et al., 2019; Mensah et al., 2021). In addition, the observed association between lower maximum height and higher SOC stocks, a pattern also reported for mixed semi-deciduous forests in the Congo (Doetterl et al., 2015), suggests that acquisitive, tall species may contribute less to SOC, whereas conservative strategies that generate more recalcitrant litter inputs, likely including shorter, dense-wooded understory species, promote soil carbon stabilization (Parsons et al., 2014; Sterck et al., 2011; Yin et al., 2019; Yu et al., 2019). Altogether, these findings highlight the prevalence of conservative strategies, potentially reflecting the dominance of shade-tolerant, slow-growing species, which are known to enhance organic matter conservation processes (Bruelheide et al., 2018; Chave et al., 2006; Kazakou et al., 2009).

The weak or insignificant effects of disturbance, even when included in the models, suggest either a low sensitivity of carbon compartments to the evaluated disturbance gradient or the presence of indirect effects mediated by other factors not captured in our global analyses (Silva et al., 2025, submitted). The strong correlation observed between AGC and RC ($r = 0.93$)

is largely explained by the allometric approach used to estimate RC from tree diameter, which directly reflects aboveground biomass accumulation; this may also explain overlapping patterns detected for the proportion of evergreen species. Moreover, although integrated analyses across the three carbon compartments would be informative, the limited number of replicates (21 fragments) and the large number of predictors considered (35 abiotic and biotic variables) restricted more complex modeling approaches, leading us to adopt a more exploratory perspective focused on identifying key associations. Structural differences among Atlantic Forest types (rainforest, riverine, and semi-deciduous), which may drive variation in floristic, phylogenetic, and functional dimensions, could not be fully addressed due to the low and uneven replication across forest types (11, 5, and 5 fragments, respectively). Future studies should account for these limitations by incorporating broader sampling across forest types and scales, while also valuing local studies with direct measurements of soil and root carbon, which remain crucial for improving the accuracy of compartment-specific estimates.

iii. Final remarks

The contrasting patterns between carbon compartments reinforce the need for a compartmentalized approach to understanding and managing carbon stocks in tropical forests. The distinct explanatory factors for aboveground, root, and soil carbon indicate that the ecological mechanisms underlying each fraction often operate autonomously, requiring differentiated and integrated management, conservation, and restoration strategies. Importantly, this study provides a robust exploratory analysis, with SOC and RC estimates derived indirectly rather than measured directly in the field, and few studies of comparable scope and comparative design exist, so these results should be interpreted with appropriate carefulness.

Despite the predominance of AGC as a standard metric in the carbon market for ecological restoration initiatives, our data reveal that this compartment represents, on average, less than half of the total carbon stored in the ecosystems studied. The sum of the fractions of carbon in roots and soil corresponds to a significant portion of the total (more than 50% in many cases; Figure 2). This suggests that ecosystems with smaller tree sizes may be undervalued in environmental compensation schemes that rely exclusively on aboveground biomass. The inclusion of subterranean pools is still rare in carbon market methodologies, which often operate with simplified approaches focused on rapid quantification of aboveground biomass (Brancalion et al., 2018; Matzek et al., 2015). The organic carbon stock in the soil, due to its greater temporal stability and lower vulnerability to short-term disturbances, emerges as a key component of the resilience of tropical ecosystems (Bieluczyk et al., 2023; Kendie et al., 2021; Mantovani et al., 2024; Satdichanh et al., 2023).

Furthermore, it raises important questions about the suitability of the carbon markets as effective instruments for conservation and ecological restoration: by prioritizing carbon alone, they tend to neglect biodiversity and critical ecosystem functions, and perpetuate a logic of limited valuation and underestimation of the ecological value of certain forest formations (Bordin et al., 2023; Ferreira et al., 2018). Tropical forest ecosystems provide a range of essential ecosystem services that are often overlooked by the one-dimensional metrics of carbon markets (Kittur et al., 2023). The ability of these formations to provide habitat for fauna, regulate the hydrological regime, stabilize the soil, promote nutrient cycling, among other ecosystem services, reinforces their importance beyond carbon storage (Díaz-García et al., 2020; Harrison et al., 2014; Martínez-Ramos et al., 2016). By failing to consider these multiple benefits, traditional compensation mechanisms may fail to recognize the true functional value of forests, especially those in early stages of succession or with low aboveground biomass but high potential for providing other ecosystem services.

REFERENCES

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C., Franco, M., 2014. Functional traits explain variation in plant life history strategies. PNAS 111, 740–745. https://doi.org/10.1073/pnas.1315179111

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T.R., Feldpausch, T.R., Gvozdevaite, A., Hubau, W., Kraft, N.J.B., Lewis, S.L., Moore, S., Niinemets, Ü., Peprah, T., Phillips, O.L., Ziemińska, K., Enquist, B., Malhi, Y., 2019. Drier tropical forests are susceptible to functional changes in response to a long-term drought. Ecol Lett 22, 855–865. https://doi.org/10.1111/ele.13243

Ali, A., Lin, S.-L., He, J.-K., Kong, F.-M., Yu, J.-H., Jiang, H.-S., 2019. Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. Science of The Total Environment 647, 1211–1221. https://doi.org/10.1016/j.scitotenv.2018.08.072

Ali, A., Yan, E.-R., 2017. Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review. Tropical Ecology 58, 1–14.

Barton, K., 2024. MuMIn: Multi-Model Inference.

Bender, D.J., Tischendorf, L., Fahrig, L., 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18, 17–39. https://doi.org/10.1023/A:1022937226820

Bennett, A.C., Penman, T.D., Arndt, S.K., Roxburgh, S.H., Bennett, L.T., 2020. Climate more important than soils for predicting forest biomass at the continental scale. Ecography. https://doi.org/10.1111/ecog.05180

Bieluczyk, W., Asselta, F.O., Navroski, D., Gontijo, J.B., Venturini, A.M., Mendes, L.W., Simon, C.P., Camargo, P.B.D., Tadini, A.M., Martin-Neto, L., Bendassolli, J.A., Rodrigues, R.R., Van Der Putten, W.H., Tsai, S.M., 2023. Linking above and belowground carbon sequestration, soil organic matter properties, and soil health in Brazilian Atlantic Forest restoration. Journal of Environmental Management 344, 118573. https://doi.org/10.1016/j.jenvman.2023.118573

Bordin, K.M., Esquivel-Muelbert, A., Klipel, J., Picolotto, R.C., Bergamin, R.S., Da Silva, A.C., Higuchi, P., Capellesso, E.S., Marques, M.C.M., Souza, A.F., Müller, S.C., 2023. No relationship between biodiversity and forest carbon sink across the subtropical Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 21, 112–120. https://doi.org/10.1016/j.pecon.2023.02.003

Borges, E.R., Dexter, K.G., Pyles, M.V., Bueno, M.L., Santos, R.M.D., Fontes, M.A.L., Carvalho, F.A., 2021. The interaction of land-use history and tree species diversity in driving variation in the aboveground biomass of urban versus non-urban tropical forests. Ecological Indicators 129, 107915. https://doi.org/10.1016/j.ecolind.2021.107915

Brancalion, P.H.S., Bello, C., Chazdon, R.L., Galetti, M., Jordano, P., Lima, R.A.F., Medina, A., Pizo, M.A., Reid, J.L., 2018. Maximizing biodiversity conservation and carbon stocking in restored tropical forests. CONSERVATION LETTERS 11, e12454. https://doi.org/10.1111/conl.12454

Brandon, K., 2014. Ecosystem Services from Tropical Forests: Review of Current Science. SSRN Journal. https://doi.org/10.2139/ssrn.2622749

Brazil Flora Group, 2021. Brazilian Flora 2020 project - Projeto Flora do Brasil 2020. Dataset/Checklist. v393.274 [WWW Document]. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. URL DOI: 10.15468/1mtkaw

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodt, F., Mahecha, M.D., Peet, R.K., Sandel, B., Van Bodegom, P., Altman, J., Alvarez-Dávila, E., Arfin Khan, M.A.S., Attorre, F., Aubin, I., Baraloto, C., Barroso, J.G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J.H.C., Craven, D., Dainese, M., Derroire, G., De Sanctis, M., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T.R., Fenton, N.J., Garnier, E., Guerin, G.R., Gutiérrez, A.G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D.N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A.Y., Kühn, I., Laughlin, D.C., Lens, F., Loos, J., Louault, F., Lyubenova, M.I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J.V., Munzinger, J., Myers-Smith, I.H., Neill, D.A., Niinemets, Ü., Orwin, K.H., Ozinga, W.A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O.L., Pärtel, M., Reich, P.B., Römermann, C., Rodrigues, A.V., Sabatini, F.M., Sardans, J., Schmidt, M., Seidler, G., Silva Espejo, J.E., Silveira, M., Smyth, A., Sporbert, M., Svenning, J.-C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., Jandt, U., 2018. Global trait–environment relationships of plant communities. Nat Ecol Evol 2, 1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Bu, W., Huang, J., Xu, H., Zang, R., Ding, Y., Li, Y., Lin, M., Wang, J., Zhang, C., 2019. Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot. Front. Plant Sci. 9, 1958. https://doi.org/10.3389/fpls.2018.01958

Cadotte, M.W., 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. Proc. Natl. Acad. Sci. U.S.A. 110, 8996–9000. https://doi.org/10.1073/pnas.1301685110

Cavanaugh, K.C., Gosnell, J.S., Davis, S.L., Ahumada, J., Boundja, P., Clark, D.B., Mugerwa, B., Jansen, P.A., O’Brien, T.G., Rovero, F., Sheil, D., Vasquez, R., Andelman, S., 2014. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale: Biodiversity and aboveground carbon storage. Global Ecology and Biogeography 23, 563–573. https://doi.org/10.1111/geb.12143

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H.T., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16, 2356–2367. https://doi.org/10.1890/1051-0761(2006)016%255B2356:RAPVOW%255D2.0.CO;2

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob Change Biol 20, 3177–3190. https://doi.org/10.1111/gcb.12629

Coelho, A.J.P., Villa, P.M., Matos, F.A.R., Heringer, G., Bueno, M.L., de Paula Almado, R., Meira-Neto, J.A.A., 2022. Atlantic Forest recovery after long-term eucalyptus plantations: The role of zoochoric and shade-tolerant tree species on carbon stock. Forest Ecology and Management 503, 119789. https://doi.org/10.1016/j.foreco.2021.119789

Coelho De Souza, F., Dexter, K.G., Phillips, O.L., Pennington, R.T., Neves, D., Sullivan, M.J.P., Alvarez-Davila, E., Alves, Á., Amaral, I., Andrade, A., Aragao, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C., G.A., Bánki, O., Baraloto, C., Barroso, J.G., Boot, R.G.A., Brienen, R.J.W., Brown, F., Camargo, J.L.C., Castro, W., Chave, J., Cogollo, A., Comiskey, J.A., Cornejo-Valverde, F., Da Costa, A.L., De Camargo, P.B., Di Fiore, A., Feldpausch, T.R., Galbraith, D.R., Gloor, E., Goodman, R.C., Gilpin, M., Herrera, R., Higuchi, N., Honorio Coronado, E.N., Jimenez-Rojas, E., Killeen, T.J., Laurance, S., Laurance, W.F., Lopez-Gonzalez, G., Lovejoy, T.E., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Mendoza, C., Monteagudo-Mendoza, A., Neill, D.A., Vargas, P.N., Peñuela Mora, M.C., Pickavance, G.C., Pipoly, J.J., Pitman, N.C.A., Poorter, L., Prieto, A., Ramirez, F., Roopsind, A., Rudas, A., Salomão, R.P., Silva, N., Silveira, M., Singh, J., Stropp, J., Ter Steege, H., Terborgh, J., Thomas-Caesar, R., Umetsu, R.K., Vasquez, R.V., Célia-Vieira, I., Vieira, S.A., Vos, V.A., Zagt, R.J., Baker, T.R., 2019. Evolutionary diversity is associated with wood productivity in Amazonian forests. Nat Ecol Evol 3, 1754–1761. https://doi.org/10.1038/s41559-019-1007-y

Costa, O.V., Cantarutti, R.B., Fontes, L.E.F., Costa, L.M.D., Nacif, P.G.S., Faria, J.C., 2009. Estoque de carbono do solo sob pastagem em área de tabuleiro costeiro no sul da Bahia. Rev. Bras. Ciênc. Solo 33, 1137–1145. https://doi.org/10.1590/S0100-06832009000500007

Cuesta, F., Calderón-Loor, M., Rosero, P., Miron, N., Sharf, A., Proaño-Castro, C., Andrade, F., 2023. Mapping Above-Ground Carbon Stocks at the Landscape Scale to Support a Carbon Compensation Mechanism: The Chocó Andino Case Study. Forests 14, 1903. https://doi.org/10.3390/f14091903

Da, R., Fan, C., Zhang, C., Zhao, X., Von Gadow, K., 2023. Are absorptive root traits good predictors of ecosystem functioning? A test in a natural temperate forest. New Phytologist 239, 75–86. https://doi.org/10.1111/nph.18915

Dantas, D., Terra, M.D.C.N.S., Pinto, L.O.R., Calegario, N., Maciel, S.M., 2020. Above and belowground carbon stock in a tropical forest in Brazil. Acta Sci. Agron. 43, e48276. https://doi.org/10.4025/actasciagron.v43i1.48276

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. https://doi.org/10.1038/nature04514 de Bello, F., Carmona, C.P., Dias, A., Gotzenberger, L., Moretti, M., Berg, M.P., 2021. Handbook of Trait-Based Ecology, 1st ed. Cambridge University Press, Cambridge, UK.

De La Cruz-Amo, L., Bañares-de-Dios, G., Cala, V., Granzow-de La Cerda, Í., Espinosa, C.I., Ledo, A., Salinas, N., Macía, M.J., Cayuela, L., 2020. Trade-Offs Among Aboveground, Belowground, and Soil Organic Carbon Stocks Along Altitudinal Gradients in Andean Tropical Montane Forests. Front. Plant Sci. 11, 106. https://doi.org/10.3389/fpls.2020.00106

De Lima, R.A.F., Dauby, G., De Gasper, A.L., Fernandez, E.P., Vibrans, A.C., Oliveira, A.A.D., Prado, P.I., Souza, V.C., F. De Siqueira, M., Ter Steege, H., 2024. Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383, 219–225. https://doi.org/10.1126/science.abq5099

Denardin, R.B.N., Mattias, J.L., Wildner, L.D.P., Nesi, C.N., Sordi, A., Kolling, D.F., Busnello, F.J., Cerutti, T., 2014. Estoque de carbono no solo sob diferentes formações florestais, Chapecó - SC. Ciênc. Florest. 24, 59–69. https://doi.org/10.5902/1980509813323

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science 15, 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x

Díaz-García, J.M., López-Barrera, F., Pineda, E., Toledo-Aceves, T., Andresen, E., 2020. Comparing the success of active and passive restoration in a tropical cloud forest landscape: A multi-taxa fauna approach. PLoS ONE 15, e0242020. https://doi.org/10.1371/journal.pone.0242020

Diémé, J.S., Armas, C., Rusch, G.M., Pugnaire, F.I., 2019. Functional responses of four Sahelian tree species to resource availability. Flora 254, 181–187. https://doi.org/10.1016/j.flora.2018.10.009

Doetterl, S., Kearsley, E., Bauters, M., Hufkens, K., Lisingo, J., Baert, G., Verbeeck, H., Boeckx, P., 2015. Aboveground vs. Belowground Carbon Stocks in African Tropical Lowland Rainforest: Drivers and Implications. PLoS ONE 10, e0143209. https://doi.org/10.1371/journal.pone.0143209

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Ferreira, I.J.M., Campanharo, W.A., Fonseca, M.G., Escada, M.I.S., Nascimento, M.T., Villela, D.M., Brancalion, P., Magnago, L.F.S., Anderson, L.O., Nagy, L., Aragão, L.E.O.C., 2023. Potential aboveground biomass increase in Brazilian Atlantic Forest fragments with climate change. Global Change Biology 29, 3098–3113. https://doi.org/10.1111/gcb.16670

Ferreira, J., Lennox, G.D., Gardner, T.A., Thomson, J.R., Berenguer, E., Lees, A.C., Mac Nally, R., Aragão, L.E.O.C., Ferraz, S.F.B., Louzada, J., Moura, N.G., Oliveira, V.H.F., Pardini, R., Solar, R.R.C., Vieira, I.C.G., Barlow, J., 2018. Carbon-focused conservation may fail to protect the most biodiverse tropical forests. Nature Clim Change 8, 744–749. https://doi.org/10.1038/s41558-018-0225-7

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Intl Journal of Climatology 37, 4302–4315. https://doi.org/10.1002/joc.5086

Flores, O., Coomes, D.A., 2011. Estimating the wood density of species for carbon stock assessments: *Wood density estimation*. Methods in Ecology and Evolution 2, 214–220. https://doi.org/10.1111/j.2041-210X.2010.00068.x

Gardon, F.R., Santos, R.F.D., Rodrigues, R.R., 2020. Brazil's forest restoration, biomass and carbon stocks: A critical review of the knowledge gaps. Forest Ecology and Management 462, 117972. https://doi.org/10.1016/j.foreco.2020.117972

Gherardi, L.A., Sala, O.E., 2020. Global patterns and climatic controls of belowground net carbon fixation. Proc. Natl. Acad. Sci. U.S.A. 117, 20038–20043. https://doi.org/10.1073/pnas.2006715117

Handavu, F., Syampungani, S., Sileshi, G.W., Chirwa, P.W.C., 2021. Aboveground and belowground tree biomass and carbon stocks in the miombo woodlands of the Copperbelt in Zambia. Carbon Management 12, 307–321. https://doi.org/10.1080/17583004.2021.1926330

Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamănă, N., Geertsema, W., Lommelen, E., Meiresonne, L., Turkelboom, F., 2014. Linkages between biodiversity attributes and ecosystem services: A systematic review. Ecosystem Services 9, 191–203. https://doi.org/10.1016/j.ecoser.2014.05.006

Houghton, R.A., 2005. Aboveground Forest Biomass and the Global Carbon Balance. Global Change Biology 11, 945–958. https://doi.org/10.1111/j.1365-2486.2005.00955.x

IPCC, I.P. on C.C., 2006. Good practice guidelines for National Greenhouse gas inventories. Intergovernmental Panel on Climate Change Report, Switzerland.

Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436. https://doi.org/10.1890/1051-0761(2000)010%255B0423:TVDOSO%255D2.0.CO;2

Jones, I.L., DeWalt, S.J., Lopez, O.R., Bunnefeld, L., Pattison, Z., Dent, D.H., 2019. Above- and belowground carbon stocks are decoupled in secondary tropical forests and are positively related to forest age and soil nutrients respectively. Science of The Total Environment 697, 133987. https://doi.org/10.1016/j.scitotenv.2019.133987

Kachamba, D., Eid, T., Gobakken, T., 2016. Above- and Belowground Biomass Models for Trees in the Miombo Woodlands of Malawi. Forests 7, 38. https://doi.org/10.3390/f7020038

Kattge, J., Bönisch, D., Díaz, S., Lavorel, S., Prentice, I., Leadley, P., Tautenhahn, S., Werner, G., 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Kazakou, E., Violle, C., Roumet, C., Pintor, C., Gimenez, O., Garnier, E., 2009. Litter quality and decomposability of species from a Mediterranean succession depend on leaf traits but not on nitrogen supply. Annals of Botany 104, 1151–1161. https://doi.org/10.1093/aob/mcp202

Kendie, G., Addisu, S., Abiyu, A., 2021. Biomass and soil carbon stocks in different forest types, Northwestern Ethiopia. International Journal of River Basin Management 19, 123–129. https://doi.org/10.1080/15715124.2019.1593183

Kittur, B.H., Raj, A., Upadhyay, A.P., Jhariya, M.K., Banerjee, A., 2023. Eco-Restoration of Degraded Forest Ecosystems for Sustainable Development, in: Raj, A., Jhariya, M.K., Banerjee, A., Nema, S., Bargali, K. (Eds.), Land and Environmental Management through Forestry. Wiley, pp. 273–291. https://doi.org/10.1002/9781119910527.ch11

Kong, D.L., Wang, J.J., Kardol, P., Wu, H.F., Zeng, H., Deng, X.B., Deng, Y., 2016. Economic strategies of plant absorptive roots vary with root diameter. Biogeosciences 13, 415–424. https://doi.org/10.5194/bg-13-415-2016

Kotowska, M.M., Leuschner, C., Triadiati, T., Meriem, S., Hertel, D., 2015. Quantifying above- and belowground biomass carbon loss with forest conversion in tropical lowlands of S umatra (I ndonesia). Global Change Biology 21, 3620–3634. https://doi.org/10.1111/gcb.12979

Lammerant, R., Rita, A., Borghetti, M., Muscarella, R., 2023. Water-limited environments affect the association between functional diversity and forest productivity. Ecology and Evolution 13, e10406. https://doi.org/10.1002/ece3.10406

Larkin, D.J., Glasenhardt, M., Williams, E.W., Karimi, N., Barak, R.S., Leavens, E., Hipp, A.L., 2023. Evolutionary history shapes grassland productivity through opposing effects on complementarity and selection. Ecology 104, e4129. https://doi.org/10.1002/ecy.4129

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W., Chazdon, R.L., 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol Lett 17, 1158–1167. https://doi.org/10.1111/ele.12322

Lee, Y.-J., Lee, H.-I., Lee, C.-B., Lee, K.-H., Kim, R.-H., Ali, A., 2024. Abiotic and stand age-induced changes in tree diversity and size inequality regulate aboveground biomass and soil organic carbon stock in temperate forests of South Korea. CATENA 237, 107827. https://doi.org/10.1016/j.catena.2024.107827

Lugli, L.F., Andersen, K.M., Aragão, L.E.O.C., Cordeiro, A.L., Cunha, H.F.V., Fuchslueger, L., Meir, P., Mercado, L.M., Oblitas, E., Quesada, C.A., Rosa, J.S., Schaap, K.J., Valverde-Barrantes, O., Hartley, I.P., 2020. Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. Plant Soil 450, 49–63. https://doi.org/10.1007/s11104-019-03963-9

Luo, Z., Viscarra-Rossel, R.A., Qian, T., 2021. Similar importance of edaphic and climatic factors for controlling soil organic carbon stocks of the world. Biogeosciences 18, 2063–2073. https://doi.org/10.5194/bg-18-2063-2021

Ma, H., Mo, L., Crowther, T.W., Maynard, D.S., Van Den Hoogen, J., Stocker, B.D., Terrer, C., Zohner, C.M., 2021. The global distribution and environmental drivers of aboveground versus belowground plant biomass. Nat Ecol Evol 5, 1110–1122. https://doi.org/10.1038/s41559-021-01485-1

Mantovani, V.A., Terra, M.C.N.S., Rodrigues, A.F., Silva, C.A., Guo, L., Mello, J.M. de, Mello, C.R. de, 2024. Unprecedentedly high soil carbon stocks and their spatial variability in a seasonally dry Atlantic Forest in Brazil. Catena 235. https://doi.org/10.1016/j.catena.2023.107696

Marques, M.C.M., Swaine, M.D., Liebsch, D., 2011. Diversity distribution and floristic differentiation of the coastal lowland vegetation: implications for the conservation of the Brazilian Atlantic Forest. Biodivers Conserv 20, 153–168. https://doi.org/10.1007/s10531-010-9952-4

Martin, A.R., Doraisami, M., Thomas, S.C., 2018. Global patterns in wood carbon concentration across the world's trees and forests. Nature Geosci 11, 915–920. https://doi.org/10.1038/s41561-018-0246-x

Martínez-Ramos, M., Ortiz-Rodríguez, I.A., Piñero, D., Dirzo, R., Sarukhán, J., 2016. Anthropogenic disturbances jeopardize biodiversity conservation within tropical rainforest reserves. Proc. Natl. Acad. Sci. U.S.A. 113, 5323–5328. https://doi.org/10.1073/pnas.1602893113

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Global Change Biology 26, 509–522. https://doi.org/10.1111/gcb.14824

Matzek, V., Puleston, C., Gunn, J., 2015. Can carbon credits fund riparian forest restoration? Restoration Ecology 23, 7–14. https://doi.org/10.1111/rec.12153

McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmisaari, H., Hobbie, E.A., Iversen, C.M., Jackson, R.B., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., Zadworny, M., 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytologist 207, 505–518. https://doi.org/10.1111/nph.13363

Mensah, S., Plas, F., Noulèkoun, F., 2021. Do functional identity and divergence promote aboveground carbon differently in tropical semi-arid forests and savannas? Ecosphere 12. https://doi.org/10.1002/ecs2.3563

Mitchard, E.T.A., 2018. The tropical forest carbon cycle and climate change. Nature 559, 527–534. https://doi.org/10.1038/s41586-018-0300-2

Moreira, S.L.S., Imbuzeiro, H.M.A., Silvert, C., Dietrich, O.H.S., Pimentel, L.D., Fernandes, R.B.A., 2020. Above- and below-ground carbon accumulation in cultivated macauba palm and potential to generate carbon credits. Journal of Cleaner Production 265, 121628. https://doi.org/10.1016/j.jclepro.2020.121628

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. Functional Ecology 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Neves, D.M., Dexter, K.G., Pennington, R.T., Valente, A.S.M., Bueno, M.L., Eisenlohr, P.V., Fontes, M.A.L., Miranda, P.L.S., Moreira, S.N., Rezende, V.L., Saiter, F.Z., Oliveira-Filho, A.T., 2017. Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Diversity Distrib 23, 898–909. https://doi.org/10.1111/ddi.12581

Noulèkoun, F., Mensah, S., Dimobe, K., Birhane, E., Kifle, E.T., Naab, J., Son, Y., Khamzina, A., 2024. Both the selection and complementarity effects underpin the effect of structural diversity on aboveground biomass in tropical forests. Global Ecol Biogeogr 33, 325–340. https://doi.org/10.1111/geb.13800

Pantaleão, L.C., Moraes, L.F.D.D., Cesário, F.V., Moser, P., Dias, A.T.C., Amorim, T.A., Sansevero, J.B.B., 2024. Linking plant functional traits to soil properties in tropical forest restoration. Forest Ecology and Management 563, 121976. https://doi.org/10.1016/j.foreco.2024.121976

Parsons, S.A., Valdez-Ramirez, V., Congdon, R.A., Williams, S.E., 2014. Contrasting patterns of litterfall seasonality and seasonal changes in litter decomposability in a tropical rainforest region. Biogeosciences 11, 5047–5056. https://doi.org/10.5194/bg-11-5047-2014

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167. https://doi.org/10.1071/BT12225

Pichancourt, J., Firn, J., Chadès, I., Martin, T.G., 2014. Growing biodiverse carbon-rich forests. Global Change Biology 20, 382–393. https://doi.org/10.1111/gcb.12345

Poirier, V., Roumet, C., Munson, A.D., 2018. The root of the matter: Linking root traits and soil organic matter stabilization processes. Soil Biology and Biochemistry 120, 246–259. https://doi.org/10.1016/j.soilbio.2018.02.016

Poorter, L., Rozendaal, D.M.A., Bongers, F., Almeida, de J.S., Álvarez, F.S., Andrade, J.L., Arreola Villa, L.F., Becknell, J.M., Bhaskar, R., Boukili, V., Brancalion, P.H.S., César, R.G., Chave, J., Chazdon, R.L., Dalla Colletta, G., Craven, D., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Díaz García, E., Dupuy, J.M., Durán, S.M., Espírito Santo, M.M., Fernandes, G.W., Finegan, B., Granda Moser, V., Hall, J.S., Hernández-Stefanoni, J.L., Jakovac, C.C., Kennard, D., Lebrija-Trejos, E., Letcher, S.G., Lohbeck, M., Lopez, O.R., Marín-Spiotta, E., Martínez-Ramos, M., Meave, J.A., Mora, F., de Souza Moreno, V., Müller, S.C., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Oliveira, R.S., Paz, H., Sanchez-Azofeifa, A., Sanaphre-Villanueva, L., Toledo, M., Uriarte, M., Utrera, L.P., van Breugel, M., van der Sande, M.T., Veloso, M.D.M., Wright, S.J., Zanini, K.J., Zimmerman, J.K., Westoby, M., 2021. Functional recovery of secondary tropical forests. PNAS 118, e2003405118. https://doi.org/10.1073/pnas.2003405118

Poorter, L., Van Der Sande, M.T., Arets, E.J.M.M., Ascarrunz, N., Enquist, B.J., Finegan, B., Licona, J.C., Martínez-Ramos, M., Mazzei, L., Meave, J.A., Muñoz, R., Nytch, C.J., De Oliveira, A.A., Pérez-García, E.A., Prado-Junior, J., Rodríguez-Velázques, J., Ruschel, A.R., Salgado-Negret, B., Schiavini, I., Swenson, N.G., Tenorio, E.A., Thompson, J., Toledo, M., Uriarte, M., Hout, P.V.D., Zimmerman, J.K., Peña-Claros, M., 2017. Biodiversity and climate determine the functioning of Neotropical forests. Global Ecol Biogeogr 26, 1423–1434. https://doi.org/10.1111/geb.12668

Pyles, M.V., Magnago, L.F.S., Maia, V.A., Pinho, B.X., Pitta, G., De Gasper, A.L., Vibrans, A.C., Dos Santos, R.M., Van Den Berg, E., Lima, R.A.F., 2022. Human impacts as the main driver of tropical forest carbon. Sci. Adv. 8, eabl7968. https://doi.org/10.1126/sciadv.abl7968

R Core Team, 2022. R: A language and environment for statistical computing.

Randazzo, N.A., Gordon, D.R., Hamburg, S.P., 2023. Improved assessment of baseline and additionality for forest carbon crediting. Ecological Applications 33, e2817. https://doi.org/10.1002/eap.2817

Reich, P.B., 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. Journal of Ecology 102, 275–301. https://doi.org/10.1111/1365-2745.12211

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rigueira, D.M.G., Mariano-Neto, E., 2023. Structural changes and carbon reduction due to habitat loss in Atlantic Forest. Front. For. Glob. Change 6, 1041448. https://doi.org/10.3389/ffgc.2023.1041448

Rodrigues, A.C., Silla, F., Meira-Neto, J.A.A., Gomes, L.P., Villa, P.M., Neri, A.V., 2023. Carbon and biodiversity cobenefits of second-growth tropical forest: The role of leaf phenology. Forest Ecology and Management 546, 121377. https://doi.org/10.1016/j.foreco.2023.121377

Saimun, Md.S.R., Karim, Md.R., Sultana, F., Arfin-Khan, M.A.S., 2021. Multiple drivers of tree and soil carbon stock in the tropical forest ecosystems of Bangladesh. Trees, Forests and People 5, 100108. https://doi.org/10.1016/j.tfp.2021.100108

Santos, H.G. dos, Jacomine, P.K.T., Anjos, L.H.C. dos, Lumbreras, J.F., Coelho, M.R., Almeida, J.A. de, Araujo Filho, J.C. de, 2018. Sistema Brasileiro de Classificação de Solos, 5th ed. EMBRAPA, Brasília, DF.

Satdichanh, M., Dossa, G.G.O., Yan, K., Tomlinson, K.W., Barton, K.E., Crow, S.E., Winowiecki, L., Vågen, T., Xu, J., Harrison, R.D., 2023. Drivers of soil organic carbon stock during tropical forest succession. Journal of Ecology 111, 1722–1734. https://doi.org/10.1111/1365-2745.14141

Satdichanh, M., Ma, H., Yan, K., Dossa, G.G.O., Winowiecki, L., Vågen, T., Gassner, A., Xu, J., Harrison, R.D., 2019. Phylogenetic diversity correlated with above-ground biomass production during forest succession: Evidence from tropical forests in Southeast Asia. Journal of Ecology 107, 1419–1432. https://doi.org/10.1111/1365-2745.13112

Scarano, F.R., 2002. Structure, Function and Floristic Relationships of Plant Communities in Stressful Habitats Marginal to the Brazilian Atlantic Rainforest. Annals of Botany 90, 517–524. https://doi.org/10.1093/aob/mcf189

Sena, P.H.A., Lins-e-Silva, A.C.B., Gonçalves-Souza, T., 2018. Integrating trait and evolutionary differences untangles how biodiversity affects ecosystem functioning. Oecologia 188, 1121–1132. https://doi.org/10.1007/s00442-018-4269-1

speciesLink network, 2021. Herbário Virtual da Flora e dos Fungos. Dataset/Checklist. [WWW Document]. URL http://inct.splink.org.br

Sterck, F., Markesteijn, L., Schieving, F., Poorter, L., 2011. Functional traits determine trade-offs and niches in a tropical forest community. PNAS 108, 20627–20632. https://doi.org/10.1073/pnas.1106950108

Tedersoo, L., Laanisto, L., Rahimlou, S., Toussaint, A., Hallikma, T., Pärtel, M., 2018. Global database of plants with root-symbiotic nitrogen fixation: Nod DB. J Vegetation Science 29, 560–568. https://doi.org/10.1111/jvs.12627

Terra, M.C.N.S., Nunes, M.H., Souza, C.R., Ferreira, G.W.D., Prado-Junior, J.A. do, Rezende, V.L., Maciel, R., Mantovani, V., Rodrigues, A., Morais, V.A., Scolforo, J.R.S., Mello, J.M. de, 2023. The inverted forest: Aboveground and notably large belowground carbon stocks and their drivers in Brazilian savannas. Science of the Total Environment. https://doi.org/10.1016/j.scitotenv.2022.161320

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tolmos, M.L., Guerrero-Ramirez, N.R., Ameztegui, A., Barajas Barbosa, M.P., Craven, D., Kreft, H., 2024. Biogeographic context mediates multifaceted diversity-productivity relationships in island and mainland forests. Journal of Ecology 1365-2745.14270. https://doi.org/10.1111/1365-2745.14270

Vieira, S.A., Alves, L.F., Duarte-Neto, P.J., Martins, S.C., Veiga, L.G., Scaranello, M.A., Picollo, M.C., Camargo, P.B., Do Carmo, J.B., Neto, E.S., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2011. Stocks of carbon and nitrogen and partitioning between above- and belowground pools in the Brazilian coastal Atlantic Forest elevation range. Ecology and Evolution 1, 421–434. https://doi.org/10.1002/ece3.41

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vitória, A.P., Alves, L.F., Santiago, L.S., 2019. Atlantic forest and leaf traits: an overview. Trees 33, 1535–1547. https://doi.org/10.1007/s00468-019-01864-z

Wang, L.-Q., Ali, A., 2021. Climate regulates the functional traits – aboveground biomass relationships at a community-level in forests: A global meta-analysis. Science of The Total Environment 761, 143238. https://doi.org/10.1016/j.scitotenv.2020.143238

Webb, C.O., 2000. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. The American Naturalist 156, 145–155. https://doi.org/10.1086/303378

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., Von Lützow, M., Marin-Spiotta, E., Van Wesemael, B., Rabot, E., Ließ, M., Garcia-Franco, N., Wollschläger, U., Vogel, H.-J., Kögel-Knabner, I., 2019. Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales. Geoderma 333, 149–162. https://doi.org/10.1016/j.geoderma.2018.07.026

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403

Yin, Q., Tian, T., Han, X., Xu, J., Chai, Y., Mo, J., Lei, M., Wang, L., Yue, M., 2019. The relationships between biomass allocation and plant functional trait. Ecological Indicators 102, 302–308. https://doi.org/10.1016/j.ecolind.2019.02.047

Yu, M., Wang, Y., Jiang, J., Wang, C., Zhou, G., Yan, J., 2019. Soil Organic Carbon Stabilization in the Three Subtropical Forests: Importance of Clay and Metal Oxides. JGR Biogeosciences 124, 2976–2990. https://doi.org/10.1029/2018JG004995

Zang, R., 2019. Plant Functional Traits Are the Mediators in Regulating Effects of Abiotic Site Conditions on Aboveground Carbon Stock-Evidence From a 30 ha Tropical Forest Plot. Frontiers in Plant Science 9, 10.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. https://doi.org/10.5061/DRYAD.234

SUPPLEMENTARY MATERIAL

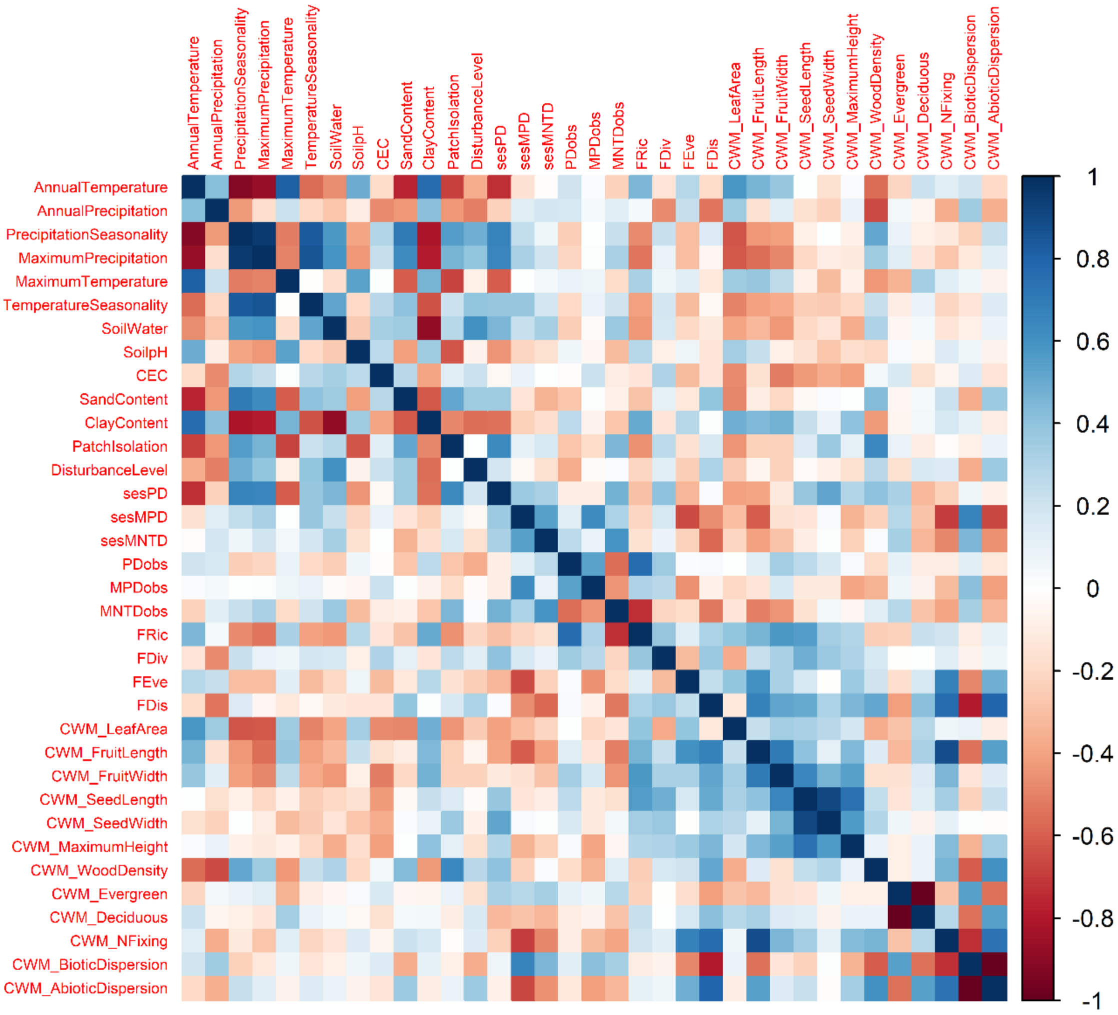

Figure S1. Correlation matrix between environmental, phylogenetic and functional variables in the studied forests.

Table S1. Results of Moran's test applied to the residuals of generalized least squares (GLS) models to assess spatial autocorrelation in riverine, rain, and semideciduous forests. No model showed evidence of significant spatial dependence.

Model		***Observed***	***SD***		***p***
AGC	~ Annual precipitation	0.06923138	0.1537474	-0.05	0.43
	~ Disturbance level	0.009213356	0.1517807		0.69
	~ sesMNTD	-0.007452215	0.1515713		0.77
	~ CWM Evergreen	-0.03272338	0.1509127		0.90
	~ CWM N fixing	-0.1561283	0.1513871		0.48
	~ CWM Biotic dispersion	-0.07147552	0.1540573		0.88
RC	~ Annual precipitation	0.1540372	0.1422692	-0.05	0.15
	~ sesMPD	-0.01984282	0.1494644		0.84
	~ sesMNTD	0.07130312	0.1438632		0.39
	~ FEve	0.01138162	0.1510394		0.68
	~ FDis	0.06677269	0.148853		0.43
	~ CWM fruit length	-0.006683938	0.1497597		0.77
	~ CWM Evergreen	-0.02167487	0.1428549		0.84
	~ CWM Deciduous	-0.05212218	0.1451007		0.98
	~ CWM Biotic dispersion	0.005073696	0.14534		0.70
	~ CWM Abiotic dispersion	0.03427009	0.1473916		0.56
SOC	~ Annual temperature	0.09577849	0.1547939	-0.05	0.34
	~ Annual precipitation	0.2151533	0.1518245		0.08
	~ Precipitation seasonality	0.1573871	0.1546946		0.18
	~ Maximum precipitation	0.1440153	0.1551194		0.21
	~ Soil water	0.08788829	0.1562305		0.37
	~ Sand content	0.1269065	0.1528535		0.24
	~ Clay content	0.1343247	0.1517153		0.22
	~ CEC	0.1005407	0.1516045		0.32
	~ CWM Leaf area	0.0335922	0.1546322		0.58
	~ CWM fruit length	0.1057041	0.1549923		0.31
	~ CWM fruit width	0.08705953	0.1549514		0.37
	~ CWM fruit maximum height	0.4283871	0.1548692		0.06

Supplementary Text 1. Global generalized linear models (GLMs) for AGC (1), RC (2) and SOC (3). All continuous predictor variables and response variables were log-transformed prior to model fitting.

(1) AGC ~ AnnPrec + disturblvl + pdobs + sesmntd + CWM_EVER + CWM_NF + CWM_DBIO

(2) RC ~ AnnPrec + sesmpd + sesmntd + fdis + feve + CWM_NF + CWM_FL + CWM_DECI + CWM_EVER + CWM_DBIO

(3) SOC ~ AnnTemp + AnnPrec + soilwater + cec + TeorArg_cat + CWM_LA + CWM_FW + CWM_HMAX

Table S2. Results of generalized linear models for aboveground carbon (AGC), root carbon (RC), and soil organic carbon (SOC).

Compartment	**Predictor**	**Estimate**	**Std. Error**	**Adj. SE**	**z / t value**	**P-value**
AGC	Intercept	-8.2183	9.1210	9.5407	0.861	0.38903
AGC	CWM_NF	-0.5733	0.1862	0.2000	2.866	0.00416
AGC	CWM_EVER	0.4655	0.1903	0.2055	2.266	0.02347
AGC	pdobs	0.8465	0.3731	0.4028	2.102	0.03559
AGC	disturblvl	0.3204	0.5651	0.6102	0.525	0.59958
AGC	AnnPrec	2.0766	1.7408	1.8931	1.097	0.27267
RC	Intercept	-26.0245	9.3802	–	-2.774	0.01417
RC	AnnPrec	4.4511	1.3637	–	3.264	0.00523
RC	sesmpd	-0.1430	0.1744	–	-0.820	0.42515
RC	sesmntd	0.1134	0.1197	–	0.947	0.35849
RC	feve	-6.4289	2.2176	–	-2.899	0.01101
RC	CWM_EVER	0.5013	0.1936	–	2.589	0.02053
SOC	Intercept	6.57978	1.08997	1.18115	5.571	< 2e-16
SOC	AnnTemp	-0.70067	0.26610	0.28746	2.437	0.01479
SOC	cec	0.05162	0.02527	0.02739	1.884	0.05951
SOC	CWM_FW	0.10745	0.06583	0.07173	1.498	0.13410
SOC	CWM_HMAX	-0.52173	0.15297	0.16491	3.164	0.00156
SOC	soilwater	0.38577	0.12013	0.13061	2.954	0.00314
SOC	TeorArg	-0.01452	0.02117	0.02317	0.627	0.53088

CHAPTER 3 - Functional strategies of endemic and threatened tree species shape the resilience of secondary tropical forests

ABSTRACT

The loss of endemic and threatened species in tropical forests can compromise essential ecosystem functions, yet the magnitude of their effects on functional diversity remains uncertain. In this study, we evaluated the functional role of these groups in 23 secondary fragments of the Atlantic Forest, a global biodiversity hotspot where endemism and threat strongly converge. We compiled data for 714 tree species and 12 functional traits associated with growth, persistence, and regeneration strategies. Species were classified according to endemism and threat status, and their functional differences were assessed through univariate and multivariate comparisons. Functional space was estimated using hypervolumes and functional diversity metrics, followed by progressive species removal simulations under four scenarios: endemic, threatened, endemic-threatened, and random removals, the latter serving as a null model. Our results show that endemic species are significantly overrepresented among threatened taxa (87%), with Fabaceae, Myrtaceae, and Lauraceae standing out as key families. Endemic and threatened species exhibited distinctive traits, such as larger fruits and seeds, lower maximum height, and higher wood density, suggesting conservative resource-use strategies in these groups. Despite substantial functional overlap with widespread species, the removal of these groups led to contraction of functional space, reduced functional richness and divergence, and shifts in trait distribution within the hypervolume. The loss of endemics was particularly critical, driving sharp declines in functional diversity and increasing the relative redundancy of widespread species. These findings demonstrate that, although partial compensation mechanisms exist, the loss of endemic and threatened species creates functional gaps that are difficult to replace, undermining the stability and resilience of tropical communities. Thus, conserving these groups is essential not only because of their biogeographic uniqueness but also due to their disproportionate contribution to functional diversity.

Key words: biodiversity loss; endemism; functional vulnerability.

INTRODUCTION

Tropical biodiversity faces unprecedented pressures from global change, habitat fragmentation, and human exploitation, leading to accelerated loss of native vegetation and threatening not only individual species but also the functional structure and ecosystem processes that sustain forest resilience (Cadotte et al., 2011; De Lima et al., 2024; Mouillot et al., 2013b; Pimm et al., 2014). In this context, forest resilience is understood as the capacity of ecosystems to absorb disturbances, reorganize, and maintain key functions, structure, and processes over time (Falk et al., 2022; Lipoma et al., 2024). From a functional perspective, resilience is closely linked to the diversity, redundancy, and distribution of plant functional traits that enable communities to resist or recover from environmental and anthropogenic stressors (Mouillot et al., 2013b). Endemism, in particular, is often a focal point in conservation efforts due to the higher extinction risk faced by endemic species and the strong links between this vulnerability and environmental, socioeconomic, biological, and climatic factors (Da Silva and Tabarelli, 2000; De Lima et al., 2020b; Pouteau et al., 2022; Scarano, 2009). In tropical regions such as the Atlantic Forest, a global biodiversity hotspot (Myers et al., 2000), up to 65% of plant species are endemic, and a comparable fraction is threatened (Brazil Flora Group, 2021; De Lima et al., 2024), only 28% of its native vegetation remains (Rezende et al., 2018), and ongoing habitat loss is driving forest homogenization and functional collapse (Rigueira and Mariano-Neto, 2023). Within this context, understanding the functional roles of endemic and threatened species in shaping community structure and diversity is essential to anticipate ecosystem function losses and guide robust conservation strategies (Brazil Flora Group, 2021; Hofhansl et al., 2021; Matos et al., 2020).

Endemic species represent taxa restricted to specific geographic areas, often originating from or concentrated within centers of endemism, and constitute distinctive components of regional biodiversity (DaSilva et al., 2015; De Lima et al., 2020b; Werneck et al., 2011). Although not necessarily rare, their occurrence is scale-dependent (Behroozian et al., 2020; DaSilva, 2011; Nery et al., 2023). Threatened species, in turn, are defined by multiple criteria, including population decline, limited geographic range, and small population size (IUCN, 2022). Evidence suggests that certain subsets of species contribute disproportionately to specific ecosystem functions, such as carbon storage by hyperdominant species (Rodrigues et al., 2019), while rare species sustain low functional redundancy and high functional richness, thereby enhancing ecosystem stability and other key functions (Ames et al., 2017; Leitão et al., 2016; Mouillot et al., 2013a; Säterberg et al., 2019; Tang et al., 2023; Zhang et al., 2022).

Endemic and threatened species often belong to these key functional groups, playing critical roles in carbon storage, forest regeneration, and plant-animal interactions (De Lima et al., 2024; Magnago et al., 2015; Matos et al., 2020; Pineda-Zapata et al., 2024). Therefore, assessing their functional strategies and how these differ from widely distributed species can provide valuable insights into their contributions to ecosystem functioning.

Functional ecology provides conceptual and analytical tools to quantify how functional traits (morphological, physiological, dispersal, growth, and persistence attributes) influence community structure and ecosystem processes (Diaz et al., 2016; Mouillot et al., 2013b; Violle et al., 2007). Plant ecological strategies can vary according to environmental conditions, phylogenetic relationships, phenotypic plasticity, and biotic interactions, among other factors (An et al., 2024; Baraloto et al., 2012; De Freitas et al., 2024; Heilmeier, 2019; Silva et al., 2023). Functional space analysis, defined as the multidimensional representation of trait diversity within a community, allows for the assessment of trait variety, distribution, similarity, and divergence among species (Carmona et al., 2024; de Bello et al., 2021; Mouillot et al., 2013b). The use of hypervolumes as a representation of functional space enables a precise quantification of the occupied niche breadth by integrating multiple trait dimensions simultaneously (Galán Díaz et al., 2021). This framework helps identify functional gaps, assess redundancy and specialization, and predict community resilience.

Despite major advances in understanding ecological strategies and community-level functional diversity, the specific roles of endemic and threatened groups remain underexplored (Hofhansl et al., 2021; Leitão et al., 2016; Violle et al., 2007). Some studies have shown that endemic and widespread species can be functionally equivalent (Cutts et al., 2023; Hanz et al., 2022), suggesting that functional redundancy may buffer the impacts of endemic species loss if remaining taxa share similar traits (Chua et al., 2019; Leitão et al., 2016). In contrast, other evidence indicates that endemic species may occupy a narrow subset of functional space, reflecting reduced niche breadth (Nery et al., 2023). Such a pattern could increase ecosystem vulnerability to their loss, as extinction would generate functional gaps unlikely to be compensated by widespread species (Carmona et al., 2021).

Uncertainties therefore persist regarding the magnitude of the impacts arising from the loss of endemic and threatened species and the potential for functional compensation within tropical forests. This study investigates the functional strategies of endemic and threatened tree species in secondary fragments of the Atlantic Forest, assessing how these groups contribute to community functional structure and diversity. We also explore the potential impacts of their loss on functional diversity. We hypothesize that (1) endemic and threatened species predominantly exhibit conservative resource-use strategies, showing higher functional clustering and occupying a narrower subset of functional space (Nery et al., 2023). Consequently, we expect that (2) their loss will lead to reductions in functional richness and diversity, reflecting a lower variety of traits within multidimensional space, along with a more regular trait distribution, indicating reduced balance in functional space occupancy among remaining species.

METHODS

i. Study area

This study considered tree species recorded in 23 secondary forest fragments within the Atlantic Forest domain, encompassing rainforests, semideciduous, and riverine forest types (Figure S1). This global biodiversity hotspot concentrates over 15,000 plant species and exhibits remarkably high levels of endemism (Brazil Flora Group, 2021; Werneck et al., 2011). The surrounding landscape has undergone extensive transformation, including conversion to pasture, agriculture, mining, and forestry (Amaral et al., 2025; Coelho et al., 2022; Matos et al., 2020). Climate across the region varies according to the Köppen classification, ranging from tropical without a dry season (Af, Am, Aw) to tropical with a dry winter (Cwa, Cwc) (Alvares et al., 2013). The main soil types include According to the Brazilian Soil Classification System the region's soils are characterized by dystrophic red and yellow latosols, dystrophic yellow argisols, dystrophic spodosols, and dystrophic cambisols (Santos et al., 2018).

Field surveys were conducted between 2005 and 2019. For each fragment, individual tree height and diameter at breast height (DBH) were recorded for individuals ≥4.8 cm within 10x10 m plots. Non-native individuals or those identified only to the genus or family level were excluded to ensure consistency in species-level functional data and analyses (de Bello et al., 2021).

ii. Functional traits

For each species, we compiled twelve functional traits associated with key ecological processes and ecosystem functions: leaf area (Larea; mm^2), petiole length and width (PL and PW; mm), fruit length and width (FL and FW; mm), seed length and width (SL and SW; mm), maximum species height (Hmax; m), wood density (WD; $g\ cm^{-3}$), dispersal syndrome (Disp; biotic or abiotic), leaf phenology (LP; evergreen or deciduous), and nitrogen fixation (NF;

fixing or non-fixing). Trait information was obtained at the interspecific level from measurements of herbarium specimens, floras, and published literature, following standardized protocols (Brazil Flora Group, 2021; de Bello et al., 2021; Pérez-Harguindeguy et al., 2013; speciesLink network, 2021). Additional data were sourced from trait databases on nitrogen fixation (Tedersoo et al., 2018), wood density (Zanne et al., 2009) and general plant traits (TRY database; Kattge et al., 2020). When species-specific values were unavailable, trait values were imputed using the genus mean restricted to the Neotropical region (Chave et al., 2006; de Bello et al., 2021; Flores and Coomes, 2011).

iii. Endemism and threat status

Taxonomic information was harmonized, and endemism classification was obtained from the Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br – Brazilian Flora Project), one of the most comprehensive databases of the Brazilian flora. Species restricted to the Atlantic Forest domain and to the Brazilian territory were classified as endemic. Threat status followed the IUCN Red List criteria (http://www.iucnredlist.org). Species listed as ‘Least Concern’ and ‘Near Threatened’ were considered non-threatened, whereas ‘Endangered’, ‘Critically Endangered’, and ‘Vulnerable’ species were classified as having some level of threat of extinction. It is worth noting that these assessments were conducted in 2022, and both threat status and endemism classification may be constantly updated as new sampling efforts and taxonomic revisions become available. Families with the highest proportions of endemic species (≥4%) were highlighted, as well as the proportion of endemic species among threatened and non-threatened categories.

iv. Functional diferences among groups

Differences in quantitative functional traits among widespread, endemic, threatened, and endemic–threatened species were assessed using complementary nonparametric approaches tailored to the structure of the comparisons. For contrasts involving widespread species versus each restricted group (endemic, threatened, and endemic-threatened), we applied the Brunner-Munzel test, which is robust to heteroscedasticity and does not assume identical distribution shapes across groups (Neubert and Brunner, 2007). This property is particularly important in our dataset, where group sizes are unbalanced and variance heterogeneity among species categories is expected due to differences in ecological strategies and rarity. Effect sizes for these comparisons were calculated as the difference between group means divided by the global standard deviation to facilitate comparability across traits.

Differences among the restricted groups themselves (endemic, threatened, and endemic-threatened) were evaluated using the Kruskal-Wallis test, which provides a global, rank-based assessment of differences across more than two groups without assuming normality (R Core Team, 2022). When the Kruskal-Wallis test indicated significant effects, post hoc pairwise comparisons were conducted using Dunn's test with appropriate adjustment for multiple comparisons to identify which group pairs differed significantly (Dinno, 2024). This two-step approach allowed us to disentangle broad contrasts between widespread and restricted species from finer-scale differences among restricted categories while respecting the distributional properties of the data. For categorical functional traits (nitrogen fixation, leaf phenology, and dispersal mode), differences among species groups were assessed using Fisher's exact test, as several contingency tables included expected cell frequencies below five, violating the assumptions of chi-square tests.

v. Functional space and species loss simulations

We simulated species loss to evaluate how different extinction scenarios could affect functional structure and diversity (Text S1) (Leitão et al., 2016). The baseline (0%) represented the functional space of all species. Then, progressive removals from 5% to 95%, in 5% intervals, were simulated (Violle et al., 2017), totaling 19 removals (Table S1), under four distinct scenarios: (1) removal of endemic species, (2) removal of threatened species, (3) removal of endemic and threatened species, and (4) random species removal (null model).

Functional diversity metrics FRic (functional richness), FDiv (functional divergence), FEve (functional evenness), and FDis (functional dispersion), were computed using the "fundiversity" package (Grenié and Gruson, 2023) for the original community and all simulated scenarios. Simple linear regressions were fitted between the proportion of species removed and each functional metric. Model assumptions (homoscedasticity, normality, and residual's independence) were verified. In some cases, FRic, FEve, and FDiv returned missing (zero) values due to a low number of species relative to the number of traits in certain scenarios (Table S1).

Functional spaces for the original metacommunity and the 95% removal scenarios were visualized based on FRic and FDiv using the "funspace" package (Carmona et al., 2024). The *funspaceDim* function was used to determine the number of PCA-derived dimensions required, indicating two dimensions. PCA was performed using *princomp* on the functional trait dataset (R Core Team, 2022). The *funspace* function was then used to construct the functional space, while *funspaceNull* tested statistical differences between observed and theoretical uniform distributions. Moreover, the "TPD" package was used to estimate trait probability density functions (TPDs), quantifying shared trait space among groups (Carmona et al., 2019). All analyses and visualizations were performed in R version 4.2.3.

RESULTS

Across the 23 forest fragments, we recorded 24,251 individuals belonging to 714 species and 78 botanical families (Table S2). The dataset included 364 endemic species (51%) and 350 widespread species (49%). Of all species recorded, 503 had IUCN assessments available: 432 were classified as non-threatened and 71 as threatened (Table S2). Endemic species were significantly overrepresented among threatened species (χ^2=43.152; p<0.001; residuals for endemic-threatened = 4.37; non-endemic-threatened = -4.41), with 87.3% of threatened species being endemic (Figure 1). Among the 78 botanical families recorded, 62 contained endemic species and 21 included threatened species. The most representative families among endemics were Fabaceae, Myrtaceae, and Lauraceae, while among threatened species the most frequent were Myrtaceae, Fabaceae, and Meliaceae (Table 1). Endemic threatened species were mostly concentrated within Fabaceae, Myrtaceae, and Lauraceae (Table 1).

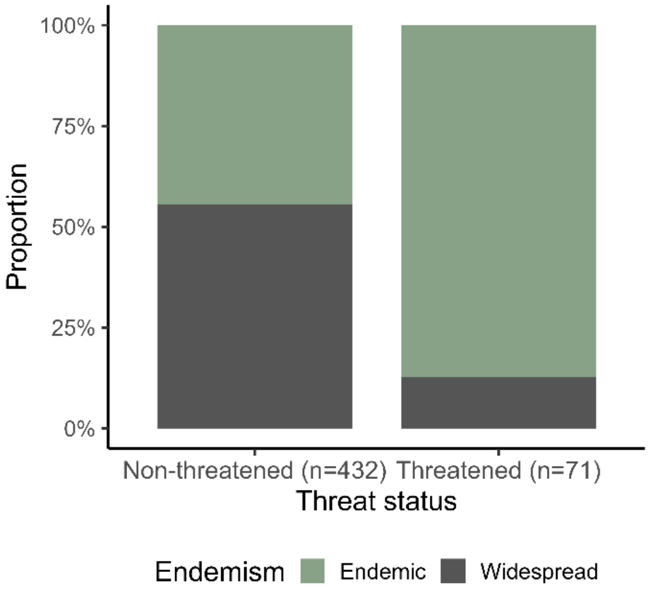

Figure 1. Proportion of endemic and widespread species among non-threatened and threatened groups.

Table 1. Proportion of endemic and threatened species in each botanical family above 4% representation.

Endemic	**%**	**Threatened**	**%**	**Endemic threatened**	**%**
Fabaceae	14.6	Myrtaceae	18.6	Fabaceae	14.8
Myrtaceae	14.3	Fabaceae	14.3	Myrtaceae	10.9
Lauraceae	6.9	Meliaceae	7.1	Lauraceae	6.2
Sapotaceae	4.4	Moraceae	5.7	Sapotaceae	4.8
Annonaceae	4.1	Lauraceae	4.3	Rubiaceae	4.3
		Rubiaceae	4.3		

Mean values of functional traits varied among species groups (Table 2), except for leaf traits (leaf area and petiole size). Endemic species showed larger seed size (SL and SW) and lower maximum height than the widespread mean. Threatened species had significantly larger fruit size (FL and FW) compared to the widespread mean. Endemic threatened species further diverged from the general trend, exhibiting larger fruits (FL and FW), larger seeds (SL and SW), lower maximum height, and higher wood density, all differing significantly from the widespread mean. Among endemic, threatened, and endemic-threatened groups, significant differences (indicated by the letters in Table 2) were found for fruit width and seed size (SL and SW) between endemics and endemic-threatened species, with higher values in the latter. In addition, maximum height differed significantly between endemics and threatened species, being higher among threatened ones

For categorical functional traits, no significant differences were observed among groups regarding nitrogen fixation, with similar proportions of fixers and non-fixers in all categories (Table 3). In contrast, leaf phenology differed significantly: endemic threatened species were predominantly evergreen (77.4%), whereas threatened species were mostly deciduous (77.8%) (Table 3). We also detected differences in dispersal syndrome, with endemic threatened species being predominantly zoochoric (85.5%), while threatened species were mostly abiotically dispersed (55.6%) (Table 3).

Table 2. Comparison of quantitative functional trait values among widespread, endemic, threatened, and endemic–threatened tree species. Values are shown as mean±standard deviation. Comparisons with widespread species were conducted using the Brunner-Munzel test; the corresponding p-values and effect sizes (in parentheses) indicate whether each restricted group differs from widespread species. Comparisons among restricted groups (endemic, threatened, endemic–threatened) were performed using the Kruskal-Wallis test followed by Dunn's post hoc tests. Different lowercase letters indicate statistically significant differences among these restricted groups (Dunn's test, $p<0.05$).

Functional trait	*Widespread species trait mean (sd)*	*Endemic species trait mean (sd)*	*p (Effect size)*	*Threatened species trait mean (sd)*	*p (Effect size)*	*Endemic threatened species trait mean (sd)*	*p (Effect size)*
Leaf area	44731.93 ± 407722.97	39876.24 ± 228021.24 ^{a}	0.73 (0.01)	19069.4 ± 19254.87 ^{a}	0.32 (0.06)	27152.5 ± 133401.22 ^{a}	0.51 (0.05)
PL	31.45 ± 64.62	31.97 ± 70.71 ^{a}	0.54 (-0.01)	48.37 ± 46.4 ^{a}	0.22 (-0.26)	22.81 ± 38.33 ^{a}	0.34 (0.14)
PW	2.63 ± 11.08	2.24 ± 3.36 ^{a}	0.70 (0.05)	1.93 ± 0.73 ^{a}	0.55 (0.06)	2.48 ± 3.75 ^{a}	0.55 (0.01)
FL	45.48 ± 68.01	47.16 ± 58.24 ^{a}	0.22 (-0.03)	78.04 ± 88.21 ^{a}	**0.01** (-0.47)	54.44 ± 64.21 ^{a}	**0.01** (-0.13)
FW	20.45 ± 19.23	22.84 ± 22.72 ^{a}	0.25 (-0.11)	34.42 ± 32.67 ^{ab}	**0.002** (-0.71)	26.44 ± 20.46 ^{b}	**0.002** (-0.31)
SL	11.72 ± 9.25	14.15 ± 13.84 ^{a}	**0.03** (-0.21)	12.32 ± 5.95 ^{ab}	0.35 (-0.07)	17.26 ± 13.7 ^{b}	**<0.001** (-0.54)
SW	7.9 ± 6.17	9.52 ± 8.42 ^{a}	**0.01** (-0.22)	10.77 ± 7.7 ^{ab}	0.23 (-0.46)	11.08 ± 7.33 ^{b}	**<0.001** (-0.49)
Hmax	22.52 ± 9.36	20.34 ± 9.33 ^{a}	**0.003** (0.23)	30.78 ± 13.31 ^{b}	0.14 (-0.87)	19.61 ± 8.06 ^{a}	**0.01** (0.32)
WD	0.66 ± 0.16	0.68 ± 0.16 ^{a}	0.14 (-0.16)	0.62 ± 0.18 ^{a}	0.48 (0.26)	0.69 ± 0.12 ^{a}	**0.05 (-0.23)**

Table 3. Relative frequency (%) of categoric functional trait values among each group (endemic, threatened, endemic threatened species) relative to the overall species. Significant differences are shown in bold (Fisher's exact test).

Functional trait		*Widespread species trait %*	*Endemic species trait %*	*Threatened species trait %*	*Endemic threatened species trait %*	*p*
LP	Evergreen	58.4	60.9	22.2	**77.4**	**0.002**
	Deciduous	41.6	39.1	**77.8**	22.6	
NF	N fixing	15.2	14.6	11.1	14.5	0.99
	Not N fixing	84.8	85.4	88.9	85.5	
Dispersion	Biotic	77.7	73.5	44.4	**85.5**	**0.02**
	Abiotic	22.3	26.5	**55.6**	14.5	

Functional space analyses revealed key patterns. In the original scenario, representing the current composition of tropical forests, the global functional space was 59.11 with high divergence (0.95) (Table 4; Figure 2). Within this space, endemic threatened species occupied 21.07 units (divergence 0.72), endemics 44.86 (0.94), widespread 39.86 (0.89), threatened 22.22 (0.73), and non-threatened 58.17 (0.94), highlighting the larger space of endemics and non-threatened species compared to other groups. These values indicate substantial overlap among groups, with overlap analyses showing high functional similarity between endemics and widespread (91%) and between threatened and non-threatened species (90%), while endemic threatened species shared 85% of their functional space with endemics and 100% with threatened species (Table 5).

When simulating the removal of 95% of endemic and threatened species, the global functional space showed a slight reduction (58.69), with divergence remaining stable (0.94) (Table 4; Figure 3). The endemic-threatened group experienced a sharp contraction, reducing to 4.34 units with a marked drop in divergence (0.36). Endemics showed a modest reduction (43.83), while widespread species slightly expanded their space (40.65). Threatened species overall lost space (14.09), whereas non-threatened species remained stable (58.84). In this scenario, functional overlap between endemics and widespread species decreased (87%), as well as between threatened and non-threatened species (86%), while endemic-threatened species shared 100% of their functional space with both endemics and threatened species (Table 5).

Under the scenario of 95% endemic species loss, the global functional space decreased more markedly (53.24), and functional divergence dropped to 0.85 (Table 4; Figure S2). The endemic group was consequently the most affected, losing nearly half of its space (22.73; divergence 0.58). Endemic-threatened species also contracted (14.97; divergence 0.52), while widespread species substantially expanded their functional volume (51.51; divergence 0.86). Threatened species as a whole maintained values close to the original (22.31), and non-threatened species declined slightly (51.40). This scenario showed a strong reduction in functional overlap between endemics and widespread species (73%) and between threatened and non-threatened species (65%), while endemic-threatened species shared 65% of their functional space with endemics and 73% with threatened species (Table 5).

In the scenario of 95% threatened species removal, the global functional space remained virtually unchanged (59.68) (Table 4; Figure S3). Nonetheless, endemic-threatened species experienced a pronounced contraction (5.99; divergence 0.43), matching the total functional space occupied by all threatened species, indicating that these are entirely contained within the endemic-threatened group. In contrast, endemics (44.57), widespread (40.92), and non-threatened (59.73) species remained stable. In this scenario, functional overlap between endemics and widespread species was high (88%), and complete overlap (100%) occurred between threatened and non-threatened species, endemic-threatened and endemics, and endemic-threatened and threatened species (Table 5).

Finally, under the scenario of random loss of 95% of species, the global functional space was slightly larger than the original (61.69), but divergence dropped sharply (0.63), reflecting the drastic reduction in the number of species (36 compared to the initial 714) occupying the hypervolume (Table 4; Figure S4). Despite this, groups such as endemic-threatened (22.84), non-endemic (60.90), and widespread (60.98) species maintained or expanded their space, though with a parallel reduction in divergence (ranging from 0.35 to 0.65). In this scenario, endemics and widespread species shared 78% of their functional space, and threatened and non-threatened species shared 90%. Endemic-threatened species shared 100% of their functional space with both endemics and threatened species (Table 5).

Table 4. Functional metrics of the original assemblage and under simulated species loss scenarios (95% quantile removal): endemic threatened species loss, endemic species loss, threatened species loss, and random species loss. Metrics include functional space (FRic) and functional divergence (FDiv) calculated for the whole assemblage (Global) and for each subset of species (endemic, widespread, threatened, non-threatened, and threatened endemic).

Functional diversity metrics	*Original*	*Threatened endemic species loss (95%)*	*Endemic species loss 95%*	*Threatened species loss (95%)*	*Random species loss (95%)*
	n=714	n=655	n=368	n=647	n=36
			Global		
Functional space	59.11	58.69	53.24	59.68	61.69
Functional divergence	0.95	0.94	0.85	0.94	0.63
			Threatened endemic		
Functional space	21.07	4.34	14.97	5.99	22.84
Functional divergence	0.72	0.36	0.52	0.43	0.35
			Endemic		
Functional space	44.86	43.83	22.73	44.57	43.93
Functional divergence	0.94	0.94	0.58	0.94	0.48
			Widespread		
Functional space	39.86	40.65	51.51	40.92	60.9
Functional divergence	0.89	0.89	0.86	0.90	0.65
			Threatened		
Functional space	22.22	14.09	22.31	5.99	22.84
Functional divergence	0.73	0.63	0.59	0.43	0.35
			Non-threatened		
Functional space	58.17	58.84	51.40	59.73	60.98
Functional divergence	0.94	0.94	0.86	0.94	0.64

Table 5. Dissimilarity and proportion of shared functional space (p-shared) among the groups of endemic and widespread species, threatened and non-threatened species and endemic threatened species.

Functional space	*Groups*	*Dissimilarity*	*p-shared*
Original	Endemic – widespread	0.314	0.91
	Threatened – non-threatened	0.286	0.90
	Endemic threatened – endemic	0.183	0.85
	Endemic threatened – threatened	0.419	1
Threatened endemic species loss (95%)	Endemic – widespread	0.256	0.87
	Threatened – non-threatened	0.543	0.86
	Endemic threatened – endemic	0.738	1
	Endemic threatened – threatened	0.400	1
Endemic species loss 95%	Endemic – widespread	0.501	0.73
	Threatened – non-threatened	0.425	0.65
	Endemic threatened – endemic	0.380	0.65
	Endemic threatened – threatened	0.489	0.73
Threatened species loss (95%)	Endemic – widespread	0.267	0.88
	Threatened – non-threatened	0.603	1
	Endemic threatened – endemic	0.259	1
	Endemic threatened – threatened	0.608	1
Random species loss (95%)	Endemic – widespread	0.624	0.78
	Threatened – non-threatened	0.287	0.90
	Endemic threatened – endemic	0.200	1
	Endemic threatened – threatened	0.200	1

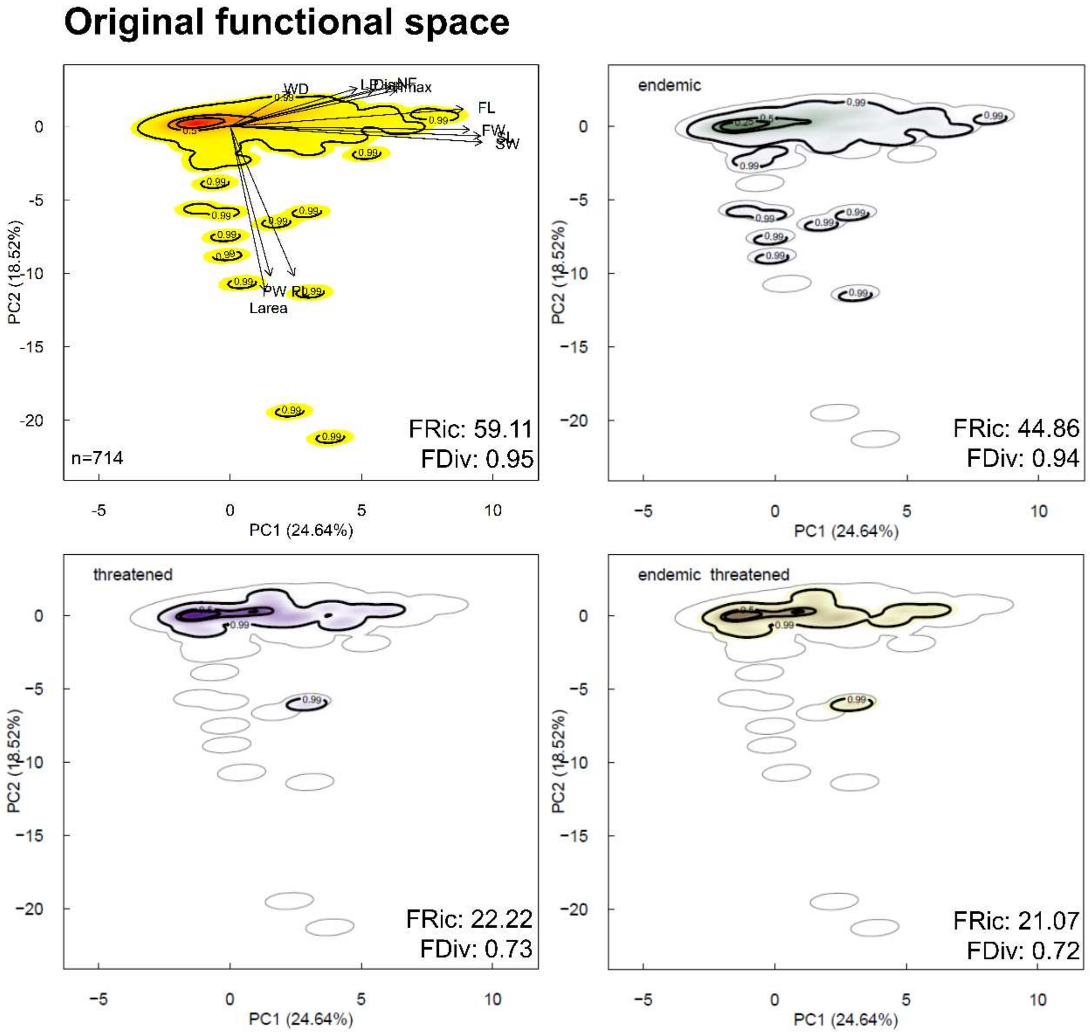

Figure 2. Original functional space of tree species in the Atlantic Forest (n=714). The top left panel shows the global functional space (null space=280.3; SES=-101.8; p=0.98), defined by the first two PCA axes (PC1=24.64% and PC2=18.52% of variance explained). Other panels depict the probabilistic species distribution of endemic, threatened, and endemic threatened species. Functional space size (FRic), functional divergence (FDiv), dissimilarity (D), and proportion of shared space (p-shared) are indicated. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

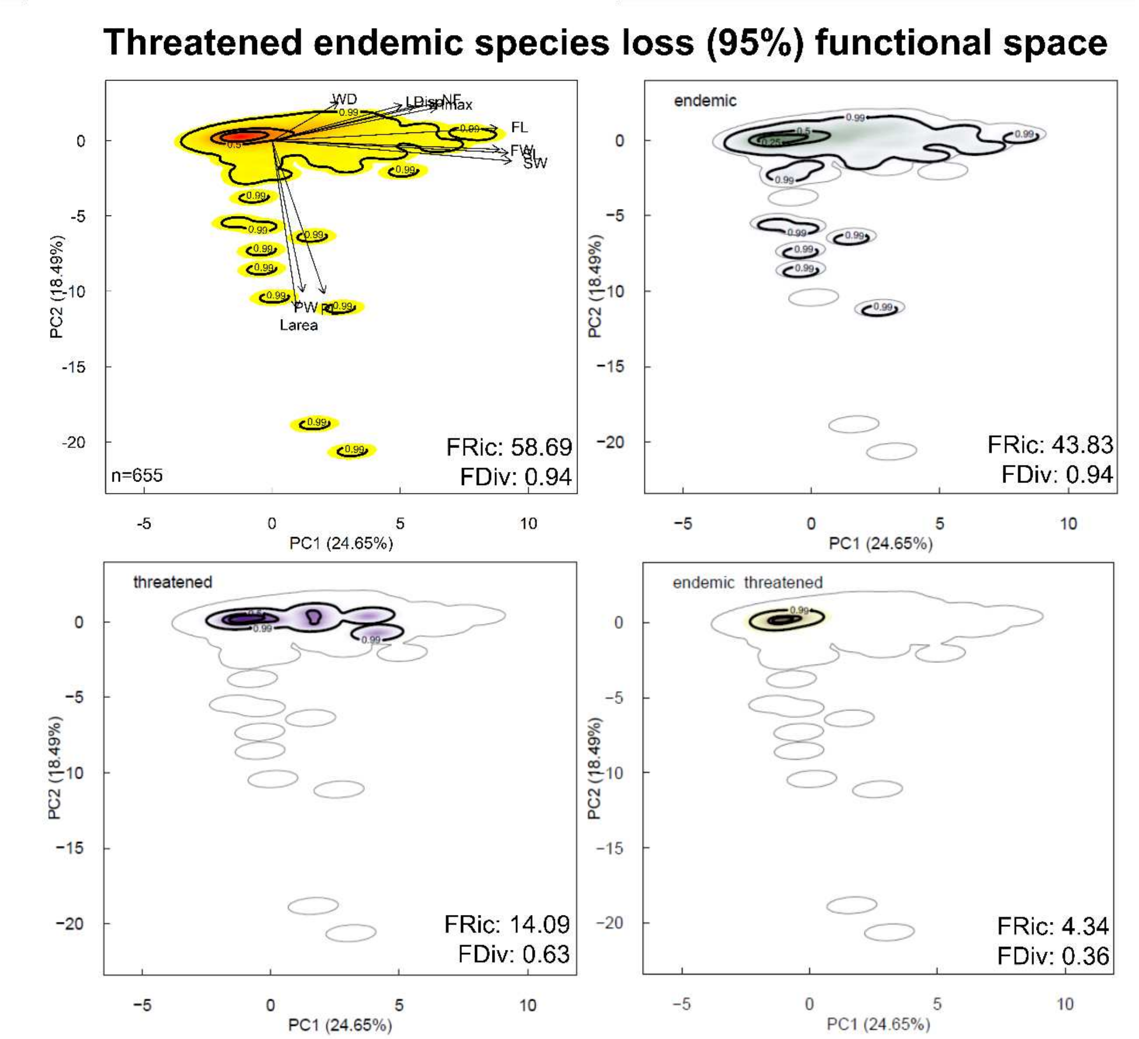

Figure 3. Functional space of tree species in the Atlantic Forest after the removal of 95% of threatened endemic species (n=655). The top left panel shows the global functional space (null space=272.65; SES=-82.94; p=0.98) defined by the first two PCA axes (PC1=24.65% and PC2=18.49% of variance explained). Other panels depict the probabilistic species distribution of endemic, threatened, and endemic threatened species. Functional space size (FRic), functional divergence (FDiv), dissimilarity (D), and proportion of shared space (p-shared) are indicated. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

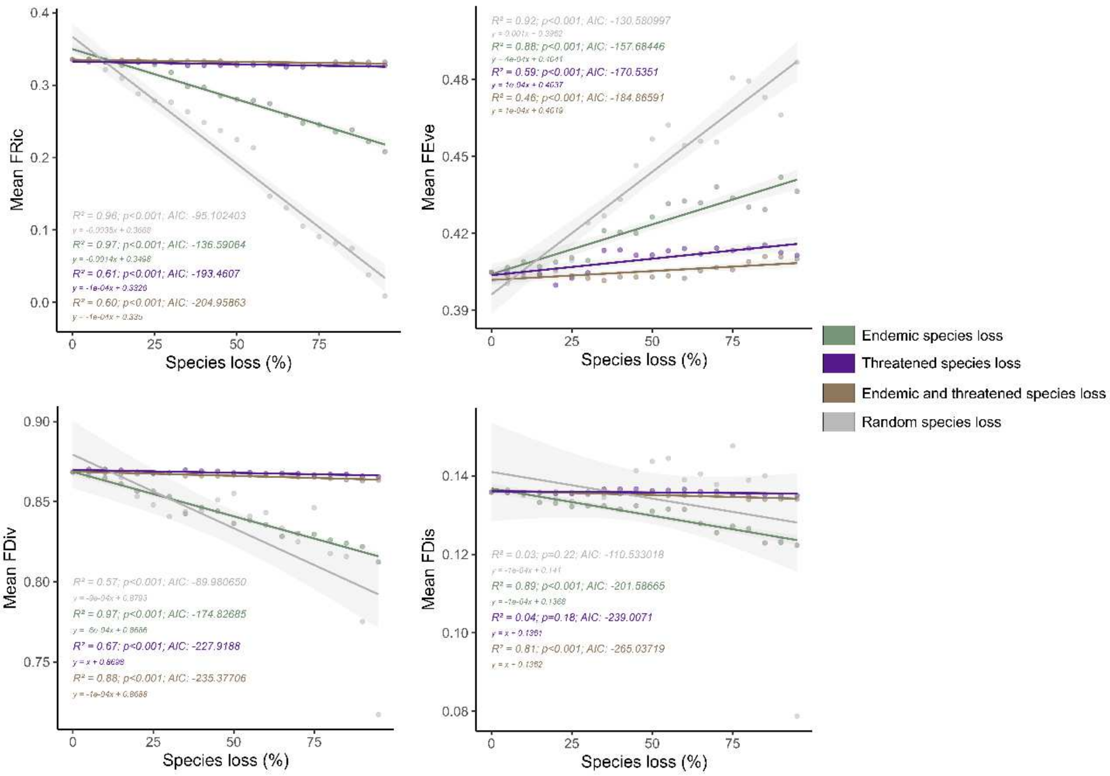

Figure 4. Linear regressions showing the relationship between species loss (%) under different removal scenarios and functional diversity metrics: functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), and functional dispersion (FDis). Each panel represents one metric, with fitted lines indicating the slope of functional change under each scenario.

Linear regressions revealed consistent effects of species loss on functional diversity metrics (Figure 4). Functional richness declined significantly across all scenarios, indicating a progressive reduction in the range of functional strategies available within communities. Functional divergence was negatively associated with species removal, particularly when endemic species were lost. Functional dispersion also decreased, but only under the removal of endemic and endemic-threatened species. Conversely, functional evenness increased consistently across all scenarios, suggesting that species loss leads to the elimination of rare traits and greater redundancy among the remaining ones. The regression equations allowed estimating the rate of functional loss per unit of species removal. For example, in the scenario of endemic-threatened species loss (Fric = -1×10^{-4}x + 0.335), each unit of removal corresponded to an approximate 0.33% reduction in functional richness.

DISCUSSION

This study provides relevant contributions by demonstrating that endemic and threatened species of the Atlantic Forest exhibit distinct functional strategies and ecological structures. We confirmed the hypothesis that these groups predominantly share conservative strategies, particularly along reproductive and structural axes. Although they are relatively well represented in the mean functional strategies (central 25% quantile), we also observed distinct functional clusters, reinforcing the hypothesis that they occupy a restricted subset of the functional space. Furthermore, the simulated loss of these groups led to reduced functional diversity and increased functional evenness, supporting our expectations. These findings reinforce that, under the context of global change, certain strategies tend to be favored while others, especially those associated with restricted-range species and conservative traits, become more vulnerable (Carmona et al., 2021; De Lima et al., 2020). In this sense, our results confirm that endemic and threatened species are particularly susceptible to impacts due to both their limited geographic distributions and conservative strategies. Their loss may reconfigure the successional trajectory of secondary tropical forests, favoring widespread, fast-growing species at the expense of late-successional, shade-tolerant ones with dense woods, biotic dispersal, and slow life cycles, traits whose decline may negatively affect carbon storage and other ecosystem services (Bello et al., 2015; Da Silva and Tabarelli, 2000; De Lima et al., 2020b; Matos et al., 2020; Rigueira and Mariano-Neto, 2023; Rocha-Santos et al., 2017).

i. Trait syndromes and taxonomic patterns underlying vulnerability

Endemic threatened species showed marked differentiation in conservative strategies compared to other groups, including larger fruits and seeds, a higher proportion of zoochoric dispersal, smaller maximum height, higher wood density, and greater proportion of evergreen species. Reproductive traits such as large fruits and seeds are generally associated with dependence on specialized dispersers, such as large vertebrates, which increases their vulnerability in scenarios of dispersers decline (Bello et al., 2017, 2015; Galetti et al., 2013; Tabarelli and Peres, 2002), further compounding the extinction risk of threatened endemics. Similar tendencies toward high wood density and shorter stature were observed by Hofhansl et al. (2021) in lowland tropical forests of Costa Rica, though without statistical significance. Moreover, these conservative structural strategies, including evergreen habit, reflect slow growth in well-protected tissues, typically advantageous under water-limited environments, common in semideciduous Atlantic forests, and are strongly associated with ecosystem-level carbon stock (Conti and Díaz, 2013; De Freitas et al., 2024; Diémé et al., 2019; Neves et al., 2017), as are endemic and threatened species (Magnago et al., 2015; Matos et al., 2020).

Myrtaceae and Fabaceae emerged as prominent families among endemic and threatened species, reinforcing both their functional relevance and associated vulnerability. Both families rank among the most representative of Atlantic Forest flora, encompassing abundant understory species that are shade-tolerant and animal-dispersed (Bello et al., 2017; De Lima et al., 2020a; Rocha-Santos et al., 2017), as well as emergent, carbon-hyperdominant species (Rodrigues et al., 2019), highlighting their broad ecological and structural importance, now further confirmed by the high proportion of vulnerable species. Other families highlighted among endemics and threatened species, such as Rubiaceae, Sapotaceae, Annonaceae, and Lauraceae, also include typically shade-tolerant species with dense wood and known susceptibility to habitat loss (Joly et al., 2014; Rigueira and Mariano-Neto, 2023; Rocha-Santos et al., 2017). This association between endemism, dominance of specific families, and conservative strategies suggests that historical processes of specialization, geographic restriction, and environmental filtering have shaped particularly vulnerable functional profiles (Ames et al., 2017; Hofhansl et al., 2021).

ii. Functional space structure and consequences of species loss

Most of the original functional space was concentrated in species with small fruits and seeds (Figure 2), but distinct clusters were also observed, occupied by species with large fruits and seeds (ex.: *Inga edulis*, widespread; *Lecythis pisonis*, endemic) and by species with large petioles and leaves, mainly palms (Figure S5). The Arecaceae family stood out as a functionally distinct clade, with about 70% of its species being endemic (this study; Table S2), playing disproportionate trophic and structural roles, such as providing resources to frugivores and shaping understory dynamics (Benchimol et al., 2017; De Souza et al., 2020; Elias et al., 2019). The restricted functional space of endemics corroborates Nery et al. (2023), who found higher specialization among endemic species (using the genus *Miconia* [Melastomataceae] as a model) attributed to the strong environmental gradients of the Atlantic Forest. Still, functional overlap between endemic and widespread species, as well as between threatened and non-threatened ones, suggests partial redundancy in the functional space, though threatened endemics tend to occupy narrower niches.

In the removal scenarios, threatened endemic species were strongly replaced by other groups within the functional space. The exclusion of endemics caused the sharpest drop in divergence, evidencing their disproportionate contribution to functional diversity. The relative stability of the functional space occupied by widespread species, and even its expansion after the removal of endemics, may indicate a niche-release effect associated with partial trait overlap (Behroozian et al., 2020; Chua et al., 2019). This process has been documented in the Atlantic Forest, with the gradual replacement of endemic by widespread species (De Lima et al., 2020a). Although such replacement may maintain aggregate ecosystem functioning, it results in greater homogenization and the loss of unique strategies, compromising the functional resilience of secondary forests (Carmona et al., 2021; De Lima et al., 2020a; Zhang et al., 2022). Similar results have been reported for rare species across ecosystems, reinforcing that the loss of specialized groups cannot be fully compensated by generalists (Ames et al., 2017; Leitão et al., 2016; Mouillot et al., 2013a; Zhang et al., 2022). It is noteworthy that many Atlantic Forest endemics are concentrated in rainforests of Espírito Santo and Bahia states (De Lima et al., 2020b), regions that, along with Minas Gerais state, are current deforestation hotspots, accounting for nearly half of mature forest losses in the biome (Amaral et al., 2025), highlighting the urgency of conserving these particularly vulnerable species groups.

The removal of threatened species had more limited effects on the global functional space, as most overlap with threatened endemics and are partially compensated by other categories. Nonetheless, their extinction should not be overlooked: 25.2% of species with some threat level have already been lost in the Atlantic Forest (De Lima et al., 2020a), and we found that threatened species display distinctive traits such as deciduous habit, abiotic dispersal, and large fruits, the latter frequently linked to higher extinction risk (Da Silva & Tabarelli, 2000). These traits may relate to the high proportion of Fabaceae species within the threatened group (Table 1). In the random removal scenario, the global functional space remained wide but with very low divergence, indicating increasing uniformity and reduced functional differentiation. This result also highlights that the interpretation of functional space size requires caution: since the metric is calculated only from the remaining species, even random space of just 36 species produced a space slightly larger (61.69; Table 4) than the original scenario (59.11, with 714 species). This shows that average loss may obscure apparent impacts, as functional space adjusts to the relative distribution of surviving species. In contrast, directed removals reveal structural vulnerabilities, emphasizing the importance of specialized functional groups for ecosystem resilience, even though we simulated the loss of 5% random species within each group and real extinction is a much more deterministic process (Carmona et al., 2021; De Lima et al., 2020a).

The decline in both richness and functional divergence across all removal scenarios reinforces that species loss inevitably reduces the range of functional strategies and distant niche positions (Mouchet et al., 2010; Villéger et al., 2008). Because FRic measures occupied volume, its reduction indicates that even the exclusion of only 5% of species already compromises total functional diversity, especially because species in peripheral positions are lost. The drop in functional dispersion, which measures niche differentiation among species (Laliberté and Legendre, 2010), under the loss of endemic and threatened endemic species (but not under threatened or random scenarios), points to the elimination of unique, non-redundant functions, particularly marked in the threatened endemic group. Meanwhile, the increase in evenness suggests that removal eliminates rare traits, leading to more redundant and less complex ecosystems (Ames et al., 2017; Chua et al., 2019).

iii. Conservation implications

Our study identified that 87% of endemic species are threatened, a slightly higher proportion than that reported by Lima et al. (2024) (82%), reinforcing the high vulnerability of this group to anthropogenic pressures and climate change (Joly et al., 2014; Pouteau et al., 2022). This pattern reflects both evolutionary processes of isolation and local radiation (Giatzouzaki et al., 2022) and exposure to fragmentation and habitat loss (De Lima et al., 2024). However, our sampling focused on secondary fragments and covered a narrow latitudinal extent of the Atlantic Forest (Figure S1), a characteristic of this biome that drives major floristic, functional, and phylogenetic variation (Bordin et al., 2021; Brown et al., 2020; Marcilio-Silva et al., 2017; Rezende et al., 2021; Silva et al., 2021). Consequently, some centers of endemism were not included, which could help further refine the observed patterns (DaSilva et al., 2015). Moreover, the results depend directly on the criteria used to define endemism and threat status. For instance, the species *Euterpe edulis* Mart., a keystone Atlantic Forest species, is considered endemic and threatened in some sources (Gatti et al., 2014; Joly et al., 2014; Leal et al., 2022), but listed as non-endemic and of lower concern in Flora do Brasil and the IUCN, respectively. Future analyses could therefore adopt alternative endemism definitions (De Lima et al., 2020b) and integrate multiple red lists (e.g., CNCFlora, state-level lists) to achieve a broader view of the Atlantic Forest, incorporating regional variations and cross-biome connections.

The fact that threatened endemic species are almost entirely contained within the threatened group highlights the need to integrate endemism and threat criteria into conservation planning. Prioritizing this group is strategic, as their loss entails not only taxonomic erosion but also the elimination of unique functional strategies sustaining a portion of functional diversity. Protecting endemics, particularly from key families like Myrtaceae and Fabaceae, may prevent local collapses of specialized functions not captured by global metrics. However, only a small fraction of these species currently occur within protected areas (Werneck et al., 2011), emphasizing the need to conserve secondary forests that shelters them. Preserving these groups safeguards not only immediate ecological functions but also evolutionary history and genetic diversity (Veron et al., 2017). At the same time, our results show that growing redundancy under species loss may sustain basic functions in the short term but at the expense of long-term functional diversity. This pattern suggests that maintaining functional richness may mask the erosion of more sensitive metrics such as divergence and dispersion, indicating the fragility of functional complexity and the vulnerability of unique ecosystem services. Thus, conserving threatened endemic species should be regarded not merely as biodiversity preservation, but as an essential strategy to ensure the functional resilience of tropical forests under anthropogenic and global change pressures.

REFERENCES

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. metz 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507

Amaral, S., Metzger, J.P., Rosa, M., Adorno, B.V., Gonçalves, G.C., Guedes Pinto, L.F., 2025. Alarming patterns of mature forest loss in the Brazilian Atlantic Forest. Nat Sustain 8, 256–264. https://doi.org/10.1038/s41893-025-01508-w

Ames, G.M., Wall, W.A., Hohmann, M.G., Wright, J.P., 2017. Trait space of rare plants in a fire-dependent ecosystem. Conservation Biology 31, 903–911. https://doi.org/10.1111/cobi.12867

An, N., Lu, N., Chen, W., Chen, Y., Shi, H., Wu, F., Fu, B., 2024. Spatial mapping of key plant functional traits in terrestrial ecosystems across China. Earth Syst. Sci. Data 16, 1771–1810. https://doi.org/10.5194/essd-16-1771-2024

Baraloto, C., Hardy, O.J., Paine, C.E.T., Dexter, K.G., Cruaud, C., Dunning, L.T., Gonzalez, M.-A., Sabatier, D., Savolainen, V., Chave, J., 2012. Using functional traits and phylogenetic trees to examine the assembly of tropical tree communities. Journal of Ecology 12.

Behroozian, M., Ejtehadi, H., Memariani, F., Pierce, S., Mesdaghi, M., 2020. Are endemic species necessarily ecological specialists? Functional variability and niche differentiation of two threatened Dianthus species in the montane steppes of northeastern Iran. Sci Rep 10, 11774. https://doi.org/10.1038/s41598-020-68618-7

Bello, C., Galetti, M., Montan, D., Pizo, M.A., Mariguela, T.C., Culot, L., Bufalo, F., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W.R., Da Silva, F.R., Ovaskainen, O., Jordano, P., 2017. Atlantic frugivory: a plant–frugivore interaction data set for the Atlantic Forest. Ecology 98, 1729–1729. https://doi.org/10.1002/ecy.1818

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, e1501105. https://doi.org/10.1126/sciadv.1501105

Benchimol, M., Talora, D.C., Mariano-Neto, E., Oliveira, T.L.S., Leal, A., Mielke, M.S., Faria, D., 2017. Losing our palms: The influence of landscape-scale deforestation on Arecaceae diversity in the Atlantic forest. Forest Ecology and Management 384, 314–322. https://doi.org/10.1016/j.foreco.2016.11.014

Bordin, K.M., Esquivel-Muelbert, A., Bergamin, R.S., Klipel, J., Picolotto, R.C., Frangipani, M.A., Zanini, K.J., Cianciaruso, M.V., Jarenkow, J.A., Jurinitz, C.F., Molz, M., Higuchi, P., Silva, A.C.D., Müller, S.C., 2021. Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests. Forest Ecology and Management 490, 119126. https://doi.org/10.1016/j.foreco.2021.119126

Brazil Flora Group, 2021. Brazilian Flora 2020 project - Projeto Flora do Brasil 2020. Dataset/Checklist. v393.274 [WWW Document]. Instituto de Pesquisas Jardim Botanico do Rio de Janeiro. URL DOI: 10.15468/1mtkaw

Brown, J.L., Paz, A., Reginato, M., Renata, C.A., Assis, C., Lyra, M., Caddah, M.K., Aguirre-Santoro, J., d'Horta, F., Raposo Do Amaral, F., Goldenberg, R., Lucas Silva-Brandão, K., Freitas, A.V.L., Rodrigues, M.T., Michelangeli, F.A., Miyaki, C.Y., Carnaval, A.C., 2020. Seeing the forest through many trees: Multi-taxon patterns of phylogenetic diversity in the Atlantic Forest hotspot. Diversity and Distributions 26, 1160–1176. https://doi.org/10.1111/ddi.13116

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48, 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Carmona, C.P., De Bello, F., Mason, N.W.H., Lepš, J., 2019. Trait probability density (TPD): measuring functional diversity across scales based on TPD with R. Ecology 100, e02876. https://doi.org/10.1002/ecy.2876

Carmona, C.P., Pavanetto, N., Puglielli, G., 2024. funspace: An R package to build, analyse and plot functional trait spaces. Diversity and Distributions 30, e13820. https://doi.org/10.1111/ddi.13820

Carmona, C.P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-M., R., González-Suárez, M., Salguero-Gómez, R., Vásquez-Valderrama, M., Toussaint, A., 2021. Erosion of global functional diversity across the tree of life. Sci. Adv. 7, eabf2675. https://doi.org/10.1126/sciadv.abf2675

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H.T., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16, 2356–2367. https://doi.org/10.1890/1051-0761(2006)016%255B2356:RAPVOW%255D2.0.CO;2

Chua, K.W.J., Tan, H.H., Yeo, D.C.J., 2019. Loss of endemic fish species drives impacts on functional richness, redundancy and vulnerability in freshwater ecoregions of Sundaland. Biological Conservation 234, 72–81. https://doi.org/10.1016/j.biocon.2019.03.019

Coelho, A.J.P., Villa, P.M., Matos, F.A.R., Heringer, G., Bueno, M.L., de Paula Almado, R., Meira-Neto, J.A.A., 2022. Atlantic Forest recovery after long-term eucalyptus plantations: The role of zoochoric and shade-tolerant tree species on carbon stock. Forest Ecology and Management 503, 119789. https://doi.org/10.1016/j.foreco.2021.119789

Conti, G., Díaz, S., 2013. Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. J Ecol 101, 18–28. https://doi.org/10.1111/1365-2745.12012

Cutts, V., Hanz, D.M., Barajas-Barbosa, M.P., Schrodt, F., Steinbauer, M.J., Beierkuhnlein, C., Denelle, P., Fernández-Palacios, J.M., Gaüzère, P., Grenié, M., Irl, S.D.H., Kraft, N., Kreft, H., Maitner, B., Munoz, F., Thuiller, W., Violle, C., Weigelt, P., Field, R., Algar, A.C., 2023. Links to rare climates do not translate into distinct traits for island endemics. Ecology Letters 26, 504–515. https://doi.org/10.1111/ele.14169

Da Silva, J.M.C., Tabarelli, M., 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404, 72–74. https://doi.org/10.1038/35003563

DaSilva, M.B., 2011. Areas of endemism: do species live anywhere, where they can, or where they historically evolved and speciated? RB 7, 12–17. https://doi.org/10.7594/revbio.07.03

DaSilva, M.B., Pinto-da-Rocha, R., DeSouza, A.M., 2015. A protocol for the delimitation of areas of endemism and the historical regionalization of the B razilian Atlantic Rain Forest using harvestmen distribution data. Cladistics 31, 692–705. https://doi.org/10.1111/cla.12121

de Bello, F., Carmona, C.P., Dias, A., Gotzenberger, L., Moretti, M., Berg, M.P., 2021. Handbook of Trait-Based Ecology, 1st ed. Cambridge University Press, Cambridge, UK.

De Freitas, G.V., Da Cunha, M., Vitória, A.P., 2024. A systematic review of leaf and wood traits in the Neotropics: environmental gradients and functionality. Trees. https://doi.org/10.1007/s00468-024-02508-7

De Lima, R.A.F., Dauby, G., De Gasper, A.L., Fernandez, E.P., Vibrans, A.C., Oliveira, A.A.D., Prado, P.I., Souza, V.C., F. De Siqueira, M., Ter Steege, H., 2024. Comprehensive conservation assessments reveal high extinction risks across Atlantic Forest trees. Science 383, 219–225. https://doi.org/10.1126/science.abq5099

De Lima, R.A.F., Oliveira, A.A., Pitta, G.R., De Gasper, A.L., Vibrans, A.C., Chave, J., Ter Steege, H., Prado, P.I., 2020a. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nat Commun 11, 6347. https://doi.org/10.1038/s41467-020-20217-w

De Lima, R.A.F., Souza, V.C., De Siqueira, M.F., Ter Steege, H., 2020b. Defining endemism levels for biodiversity conservation: Tree species in the Atlantic Forest hotspot. Biological Conservation 252, 108825. https://doi.org/10.1016/j.biocon.2020.108825

De Souza, F.G., De Araújo, F.F., De Paulo Farias, D., Zanotto, A.W., Neri-Numa, I.A., Pastore, G.M., 2020. Brazilian fruits of Arecaceae family: An overview of some representatives with promising food, therapeutic and industrial applications. Food Research International 138, 109690. https://doi.org/10.1016/j.foodres.2020.109690

Diaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/doi:10.1038/nature16489

Diémé, J.S., Armas, C., Rusch, G.M., Pugnaire, F.I., 2019. Functional responses of four Sahelian tree species to resource availability. Flora 254, 181–187. https://doi.org/10.1016/j.flora.2018.10.009

Dinno, A., 2024. dunn.test: Dunn's Test of Multiple Comparisons Using Rank Sums.

Elias, G.A., Colares, R., Antunes, A.R., Padilha, P.T., Lima, J.M.T., Santos, R., 2019. Palm (Arecaceae) Communities in the Brazilian Atlantic Forest: a Phytosociological Study. Floresta Ambient. 26, e20180413. https://doi.org/10.1590/2179-8087.041318

Falk, D.A., Van Mantgem, P.J., Keeley, J.E., Gregg, R.M., Guiterman, C.H., Tepley, A.J., Jn Young, D., Marshall, L.A., 2022. Mechanisms of forest resilience. Forest Ecology and Management 512, 120129. https://doi.org/10.1016/j.foreco.2022.120129

Flores, O., Coomes, D.A., 2011. Estimating the wood density of species for carbon stock assessments: *Wood density estimation*. Methods in Ecology and Evolution 2, 214–220. https://doi.org/10.1111/j.2041-210X.2010.00068.x

Galán Díaz, J., De La Riva, E.G., Funk, J.L., Vilà, M., 2021. Functional segregation of resource-use strategies of native and invasive plants across Mediterranean biome communities. Biol Invasions 23, 253–266. https://doi.org/10.1007/s10530-020-02368-5

Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimarães, Jr., Brancalion, P.H., Ribeiro, M.C., Jordano, P., 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340, 1086–1090. https://doi.org/:%252010.1126/science.1233774

Gatti, M.G., Campanello, P.I., Villagra, M., Montti, L., Goldstein, G., 2014. Hydraulic architecture and photoinhibition influence spatial distribution of the arborescent palm Euterpe edulis in subtropical forests. Tree Physiology 34, 630–639. https://doi.org/10.1093/treephys/tpu039

Giatzouzaki, D., Delhaye, G., Meerts, P.J., 2022. Trait divergence between endemic plants of Aegean islands and their widespread congeners. Plant Ecol 223, 507–523. https://doi.org/10.1007/s11258-022-01224-x

Grenié, M., Gruson, H., 2023. fundiversity: a modular R package to compute functional diversity indices. Ecography 2023. https://doi.org/10.1111/ecog.06585

Hanz, D.M., Beloiu, M., Wipfler, R., Beierkuhnlein, C., Field, R., Jentsch, A., Vetaas, O.R., Irl, S.D.H., 2022. High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island. J Vegetation Science 33, e13120. https://doi.org/10.1111/jvs.13120

Heilmeier, H., 2019. Functional traits explaining plant responses to past and future climate changes. Flora 254, 1–11. https://doi.org/10.1016/j.flora.2019.04.004

Hofhansl, F., Chacón-Madrigal, E., Brännström, Å., Dieckmann, U., Franklin, O., 2021. Mechanisms driving plant functional trait variation in a tropical forest. Ecol. Evol. 11, 3856–3870. https://doi.org/10.1002/ece3.7256

IUCN, 2022. The IUCN Red List of Threatened Species [WWW Document]. URL https://www.iucnredlist.org (accessed 3.14.22).

Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. New Phytologist 204, 459–473. https://doi.org/10.1111/nph.12989

Kattge, J., Bönisch, D., Díaz, S., Lavorel, S., Prentice, I., Leadley, P., Tautenhahn, S., Werner, G., 2020. TRY plant trait database – enhanced coverage and open access. Global Change Biology 26, 119–188. https://doi.org/10.1111/gcb.14904

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1

Leal, A., Benchimol, M., Costa, H.C.M., Faria, D., Cazetta, E., 2022. Impacts of landscape-scale forest loss and a dry event on the demographic structure of the endangered palm Euterpe edulis Mart. in the Atlantic Forest. Front. For. Glob. Change 5, 909901. https://doi.org/10.3389/ffgc.2022.909901

Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proc. R. Soc. B. 283, 20160084. https://doi.org/10.1098/rspb.2016.0084

Lipoma, L., Kambach, S., Díaz, S., Sabatini, F.M., Damasceno, G., Kattge, J., Wirth, C., Abella, S.R., Beierkuhnlein, C., Belote, T.R., Bernhardt-Römermann, M., Craven, D., Dolezal, J., Eisenhauer, N., Isbell, F., Jentsch, A., Kreyling, J., Lanta, V., Le Stradic, S., Lepš, J., Manninen, O., Mariotte, P., Reich, P.B., Ruppert, J.C., Schmidt, W., Tilman, D., Van Ruijven, J., Wagg, C., Wardle, D.A., Wilsey, B., Bruelheide, H., 2024. No general support for functional diversity enhancing resilience across terrestrial plant communities. Global Ecol Biogeogr 33, e13895. https://doi.org/10.1111/geb.13895

Magnago, L.F.S., Magrach, A., Laurance, W.F., Martins, S.V., Meira-Neto, J.A.A., Simonelli, M., Edwards, D.P., 2015. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Glob Change Biol 21, 3455–3468. https://doi.org/10.1111/gcb.12937

Marcilio-Silva, V., Zwiener, V.P., Marques, M.C.M., 2017. Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest. Diversity and Distributions 23, 1110–1119. https://doi.org/10.1111/ddi.12616

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Global Change Biology 26, 509–522. https://doi.org/10.1111/gcb.14824

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules: Functional diversity measures. Functional Ecology 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., Thuiller, W., 2013a. Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. PLoS Biol 11, e1001569. https://doi.org/10.1371/journal.pbio.1001569

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013b. A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution 28, 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501

Nery, E.K., Caddah, M.K., Santos, M.F., Nogueira, A., 2023. The evolution of ecological specialization underlies plant endemism in the Atlantic Forest. Annals of Botany 131, 921–940. https://doi.org/10.1093/aob/mcad029

Neubert, K., Brunner, E., 2007. A studentized permutation test for the non-parametric Behrens–Fisher problem. Computational Statistics & Data Analysis 51, 5192–5204. https://doi.org/10.1016/j.csda.2006.05.024

Neves, D.M., Dexter, K.G., Pennington, R.T., Valente, A.S.M., Bueno, M.L., Eisenlohr, P.V., Fontes, M.A.L., Miranda, P.L.S., Moreira, S.N., Rezende, V.L., Saiter, F.Z., Oliveira-Filho, A.T., 2017. Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. Diversity Distrib 23, 898–909. https://doi.org/10.1111/ddi.12581

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 61, 167. https://doi.org/10.1071/BT12225

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752. https://doi.org/10.1126/science.1246752

Pineda-Zapata, S., González-Ávila, S., Armenteras, D., González-Delgado, T.M., Morán-Ordoñez, A., 2024. Mapping the way: identifying priority potential corridors for protected areas connectivity in Colombia. Perspectives in Ecology and Conservation 22, 156–166. https://doi.org/10.1016/j.pecon.2024.02.003

Pouteau, R., Brunel, C., Dawson, W., Essl, F., Kreft, H., Lenzner, B., Meyer, C., Pergl, J., Pyšek, P., Seebens, H., Weigelt, P., Winter, M., Van Kleunen, M., 2022. Environmental and socioeconomic correlates of extinction risk in endemic species. Diversity and Distributions 28, 53–64. https://doi.org/10.1111/ddi.13438

R Core Team, 2022. R: A language and environment for statistical computing.

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspectives in Ecology and Conservation 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Rezende, V.L., Pontara, V., Bueno, M.L., Berg, E., Silva de Miranda, P.L., Oliveira-Filho, A.T., Dexter, K.G., 2021. Phylogenetic regionalization of tree assemblages reveals novel patterns of evolutionary affinities in the Atlantic Forest. J. Biogeogr. 48, 798–810. https://doi.org/10.1111/jbi.14038

Rigueira, D.M.G., Mariano-Neto, E., 2023. Structural changes and carbon reduction due to habitat loss in Atlantic Forest. Front. For. Glob. Change 6, 1041448. https://doi.org/10.3389/ffgc.2023.1041448

Rocha-Santos, L., Benchimol, M., Mayfield, M.M., Faria, D., Pessoa, M.S., Talora, D.C., Mariano-Neto, E., Cazetta, E., 2017. Functional decay in tree community within tropical fragmented landscapes: Effects of landscape-scale forest cover. PLoS ONE 12, e0175545. https://doi.org/10.1371/journal.pone.0175545

Rodrigues, A.C., Villa, P.M., Neri, A.V., 2019. Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. Ecological Indicators 102, 208–217. https://doi.org/10.1016/j.ecolind.2019.02.033

Santos, H.G. dos, Jacomine, P.K.T., Anjos, L.H.C. dos, Lumbreras, J.F., Coelho, M.R., Almeida, J.A. de, Araujo Filho, J.C. de, 2018. Sistema Brasileiro de Classificação de Solos, 5th ed. EMBRAPA, Brasília, DF.

Säterberg, T., Jonsson, T., Yearsley, J., Berg, S., Ebenman, B., 2019. A potential role for rare species in ecosystem dynamics. Sci Rep 9, 11107. https://doi.org/10.1038/s41598-019-47541-6

Scarano, F.R., 2009. Plant communities at the periphery of the Atlantic rain forest: Rare-species bias and its risks for conservation. Biological Conservation 142, 1201–1208. https://doi.org/10.1016/j.biocon.2009.02.027

Silva, J.L.A., Souza, A.F., Vitória, A.P., 2021. Historical and current environmental selection on functional traits of trees in the Atlantic Forest biodiversity hotspot. J Veg Sci 32. https://doi.org/10.1111/jvs.13049

Silva, N., Coelho, A.J.P., Meira-Neto, J.A.A., 2023. Functional traits patterns along an altitudinal gradient in a large tropical forest region. Flora 308, 152403. https://doi.org/10.1016/j.flora.2023.152403

speciesLink network, 2021. Herbário Virtual da Flora e dos Fungos. Dataset/Checklist. [WWW Document]. URL http://inct.splink.org.br

Tabarelli, M., Peres, C.A., 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. Biological Conservation 106, 165–176. https://doi.org/10.1016/S0006-3207(01)00243-9

Tang, R., Li, S., Lang, X., Huang, X., Su, J., 2023. Rare species contribute greater to ecosystem multifunctionality in a subtropical forest than common species due to their functional diversity. Forest Ecology and Management 538, 120981. https://doi.org/10.1016/j.foreco.2023.120981

Tedersoo, L., Laanisto, L., Rahimlou, S., Toussaint, A., Hallikma, T., Pärtel, M., 2018. Global database of plants with root-symbiotic nitrogen fixation: Nod DB. J Vegetation Science 29, 560–568. https://doi.org/10.1111/jvs.12627

Veron, S., Davies, T.J., Cadotte, M.W., Clergeau, P., Pavoine, S., 2017. Predicting loss of evolutionary history: Where are we?: Predicting loss of evolutionary history. Biol Rev 92, 271–291. https://doi.org/10.1111/brv.12228

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., Livingstone, S.W., Mouillot, D., 2017. Functional Rarity: The Ecology of Outliers. Trends in Ecology & Evolution 32, 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Werneck, M.D.S., Sobral, M.E.G., Rocha, C.T.V., Landau, E.C., Stehmann, J.R., 2011. Distribution and Endemism of Angiosperms in the Atlantic Forest. Nat. Conserv. 9, 188–193. https://doi.org/10.4322/natcon.2011.024

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. https://doi.org/10.5061/DRYAD.234

Zhang, S., Zang, R., Sheil, D., 2022. Rare and common species contribute disproportionately to the functional variation within tropical forests. Journal of Environmental Management 304, 114332. https://doi.org/10.1016/j.jenvman.2021.114332

SUPLEMENTARY MATERIAL

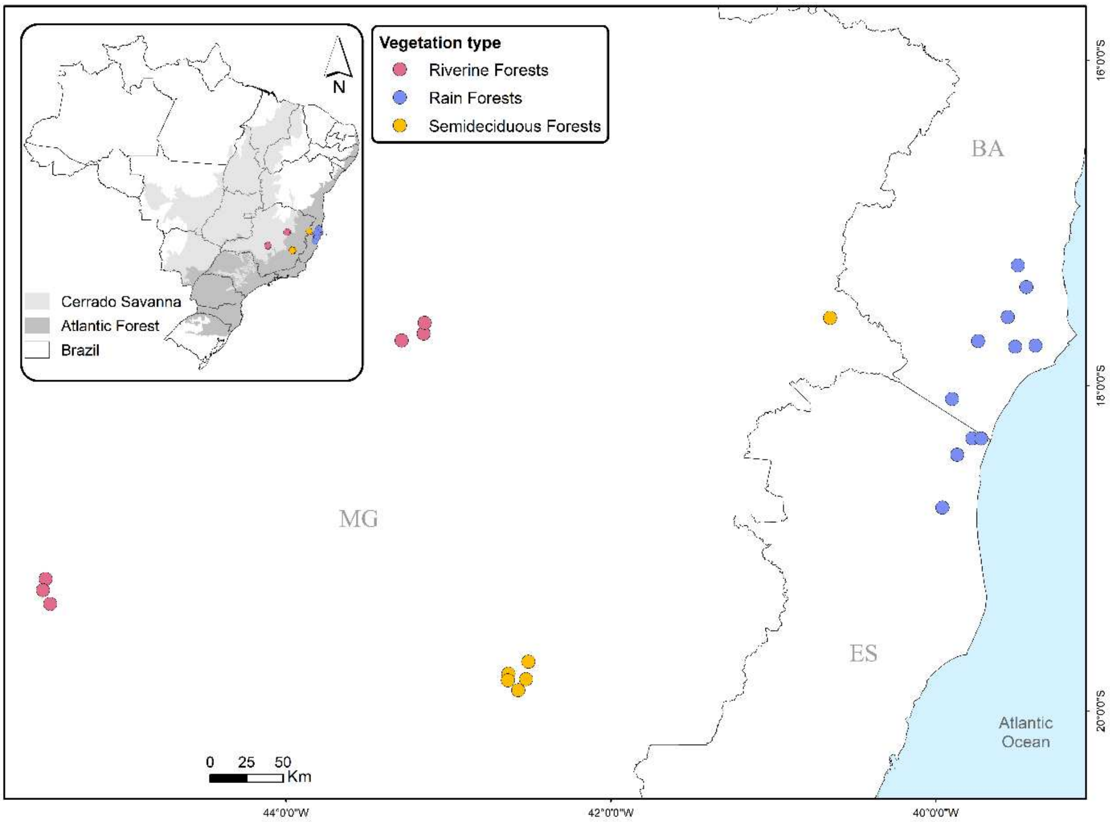

Figure S1. Fig. 1. Atlantic Forest communities sampled; BA – Bahia state; ES – Espírito Santo state; MG – Minas Gerais state.

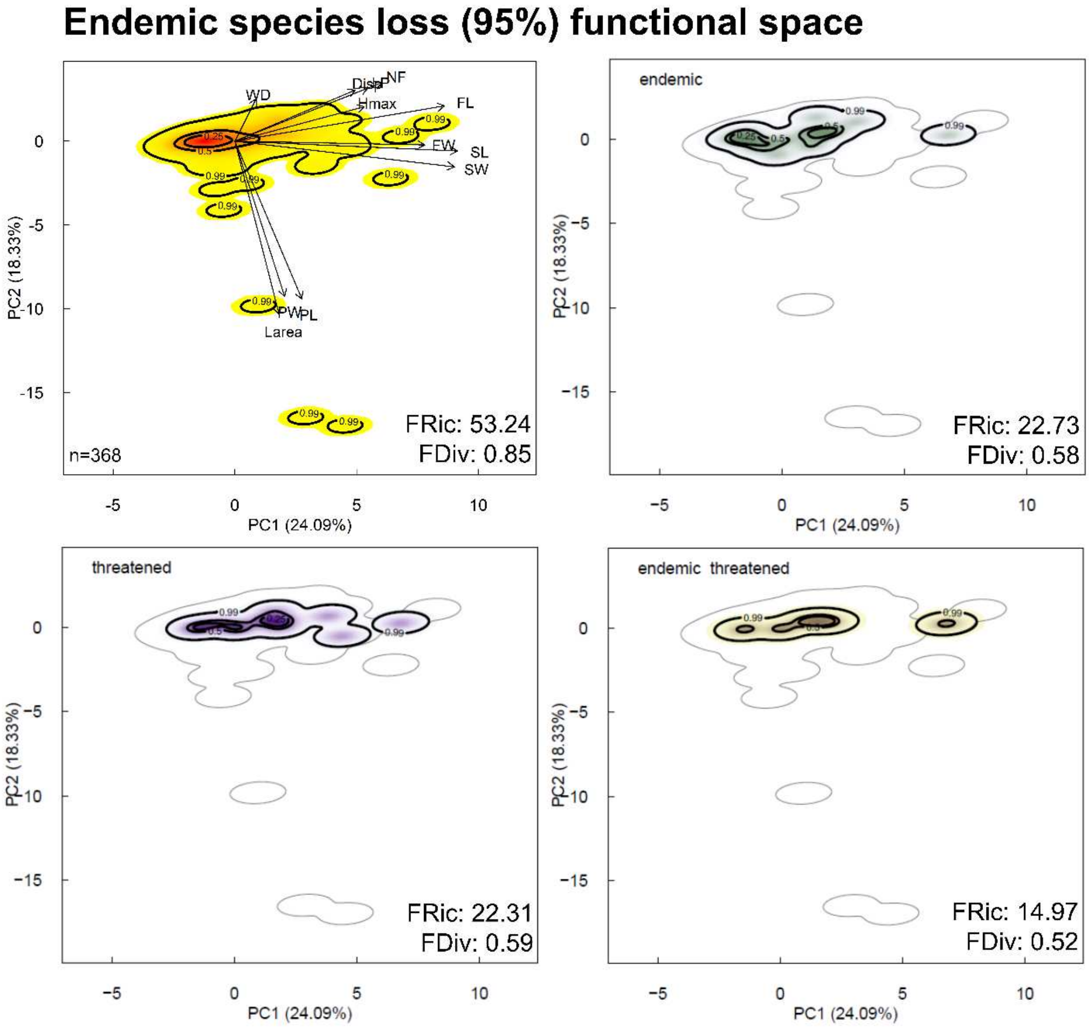

Figure S2. Functional space of tree species in the Atlantic Forest after the removal of 95% of endemic species (n=368). The top left panel shows the global functional space (null space=235.97; SES=-64.13; p=0.98) defined by the first two PCA axes (PC1=24.09% and PC2=18.33% of variance explained). Other panels depict the probabilistic species distribution of endemic, threatened, and endemic threatened species. Functional space size (FRic), functional divergence (FDiv), dissimilarity (D), and proportion of shared space (p-shared) are indicated. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

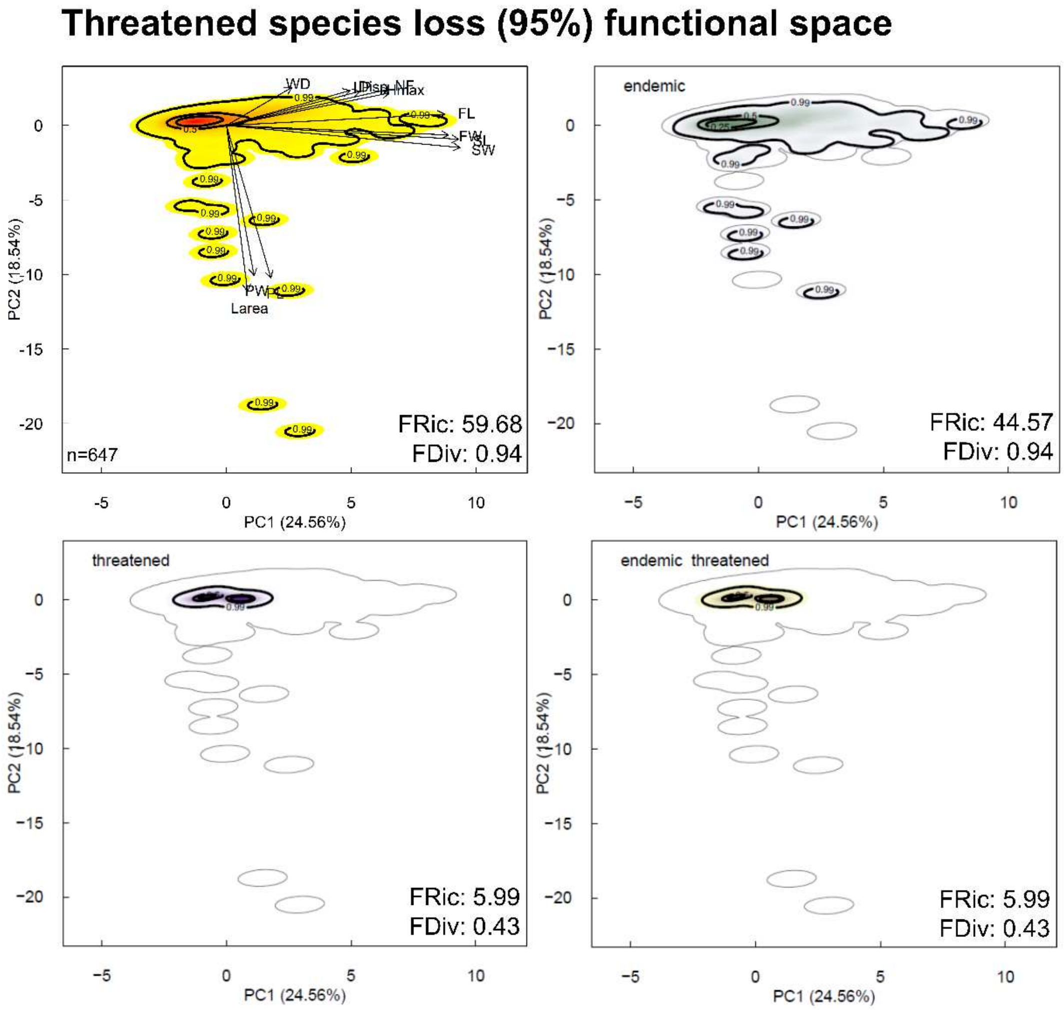

Figure S3. Functional space of tree species in the Atlantic Forest after the removal of 95% of threatened species (n=647). The top left panel shows the global functional space (null space=273.91; SES=-94.31; p=0.98) defined by the first two PCA axes (PC1=24.56% and PC2=18.54% of variance explained). Other panels depict the probabilistic species distribution of endemic, threatened, and endemic threatened species. Functional space size (FRic), functional divergence (FDiv), dissimilarity (D), and proportion of shared space (p-shared) are indicated. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

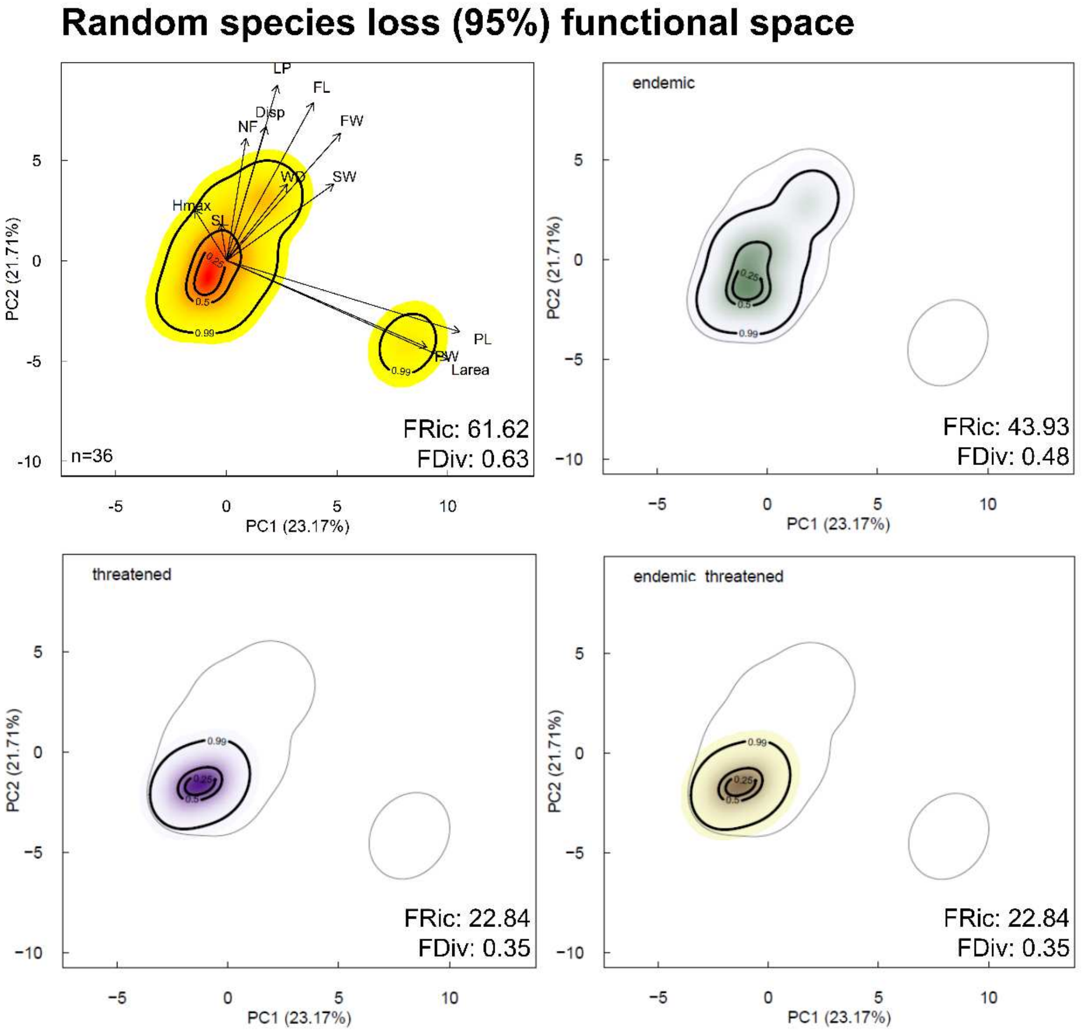

Figure S4. Functional space of tree species in the Atlantic Forest after the removal of 95% of random species (n=36). The top left panel shows the global functional space (null space=120.69; SES=-10.7; p=0.98) defined by the first two PCA axes (PC1=23.17% and PC2=21.71% of variance explained). Other panels depict the probabilistic species distribution of endemic, threatened, and endemic threatened species. Functional space size (FRic), functional divergence (FDiv), dissimilarity (D), and proportion of shared space (p-shared) are indicated. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

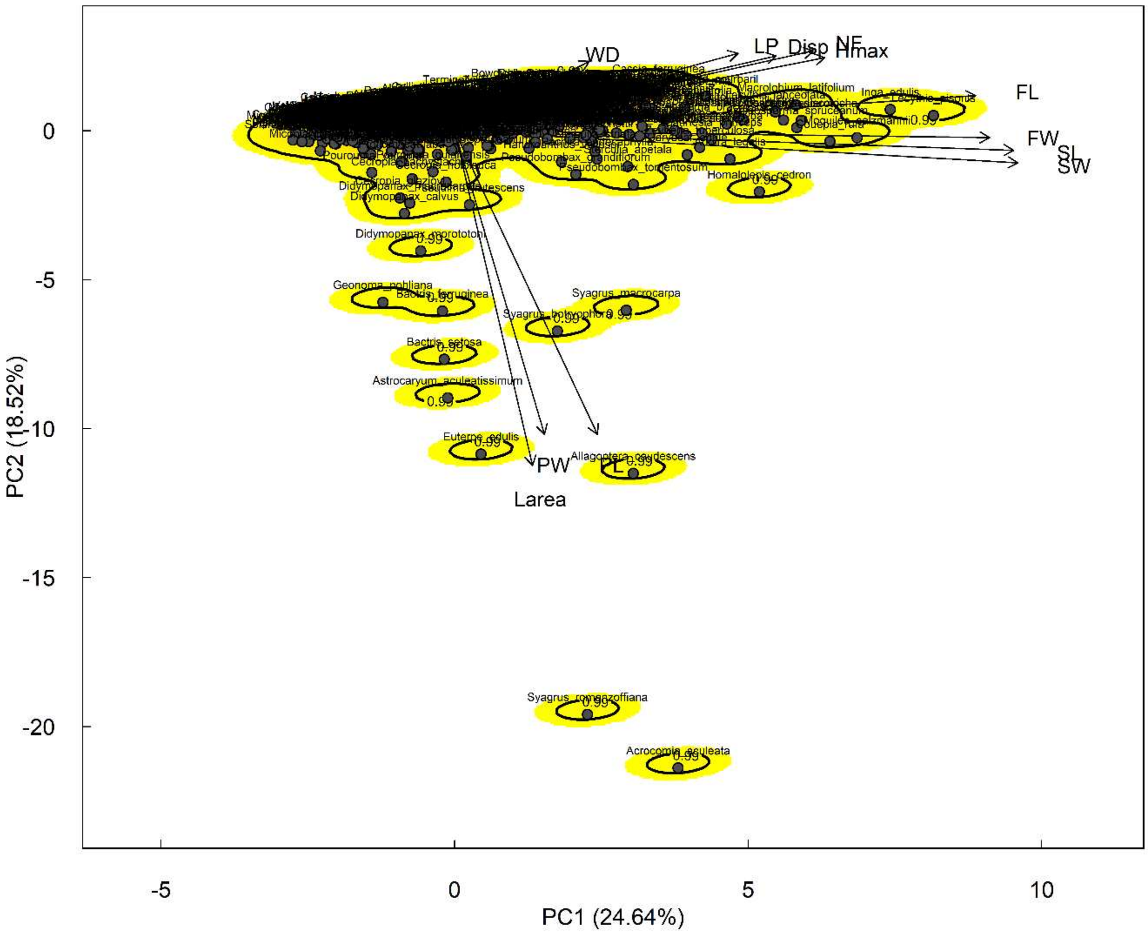

Figure S5. Original global functional space of tree species in the Atlantic Forest. The gray dots represent individual species, with their scientific names. Arrows show trait directions and weights. Color gradients represent species density (darker = higher), and black contours indicate outer limits and 0.25, 0.5, and 0.99 quantiles.

Supplementary Text 1: Code used to simulate species removals in four scenarios (endemic, threatened, endemic threatened, and random) for functional and abundance datasets. Exemple for 5% removal.

```
# Funcion
set.seed(123)
remove_species <- function(species_list, category, ecol_data, category_value) {
  species_to_remove <- sample(
    ecol_data$spp[ecol_data[[category]] == category_value],
    size = round(0.05 * sum(ecol_data[[category]] == category_value))
  )
  return(species_list[!species_list %in% species_to_remove])
}
# Scenario 1
cenario1_species <- remove_species(species_abund, "Endemism", ecol, "endemic")
cenario1_abund <- abund2[abund2$spp %in% cenario1_species, ]
cenario1_traits <- traits2[traits2$spp %in% cenario1_species, ]
# Scenario 2
cenario2_species <- remove_species(species_abund, "IUCN", ecol, "threatened")
cenario2_abund <- abund2[abund2$spp %in% cenario2_species, ]
cenario2_traits <- traits2[traits2$spp %in% cenario2_species, ]
# Scenario 3
endemic_threatened_species <- ecol$spp[ecol$Endemism == "endemic" & ecol$IUCN ==
"threatened"]
species_to_remove <- sample(endemic_threatened_species, size = round(0.05 *
length(endemic_threatened_species)))
cenario3_species <- species_abund[!species_abund %in% species_to_remove]
cenario3_abund <- abund2[abund2$spp %in% cenario3_species, ]
cenario3_traits <- traits2[traits2$spp %in% cenario3_species, ]
# Cenário 4 (random)
species_to_remove <- sample(species_abund, size = round(0.05 * length(species_abund)))
cenario4_species <- species_abund[!species_abund %in% species_to_remove]
cenario4_abund <- abund2[abund2$spp %in% cenario4_species, ]
cenario4_traits <- traits2[traits2$spp %in% cenario4_species, ]
```

Table S1. Number of species removed under different species loss scenarios (5-95%) for each category: endemic, widespread, threatened, threatened endemic, and random removal. The baseline (0%) corresponds to the original species pool.

Scenario	*Endemic*	*Threatened*	*Endemic and threatened*	*Random*
	Number of species removed			
0 (original)	18	4	3	36
5%	18	4	3	36
10%	36	7	6	71
15%	55	11	9	107
20%	73	14	12	143
25%	91	18	16	178
30%	109	21	19	214
35%	127	25	22	250
40%	146	28	25	286
45%	164	32	28	321
50%	182	36	31	357
55%	200	39	34	393
60%	218	43	37	428
65%	237	46	40	464
70%	255	50	43	500
75%	273	53	46	536
80%	291	57	50	571
85%	309	60	53	607
90%	328	64	56	643
95%	346	67	59	678

Table S2. List of species recorded across the 23 forest fragments (metacommunity), including their endemism status (according to Flora do Brasil 2020) and conservation status (DD: Data Deficient; LC: Least Concern; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; NE: Not Evaluated) (evaluation in 2022).

Species	**Endemism**	**Threat status**
Abarema_brachystachya	Endemic	NE
Abarema_villosa	Endemic	LC
Acanthocladus_pulcherrimus	Endemic	NE
Acosmium_lentiscifolium	Endemic	LC
Acrocomia_aculeata	Widespread	NE
Actinostemon_concolor	Widespread	LC
Actinostemon_klotzschii	Widespread	LC
Aegiphila_verticillata	Widespread	NE
Albizia_pedicellaris	Widespread	NE
Albizia_polycephala	Widespread	LC
Alchornea_glandulosa	Widespread	LC
Alchornea_triplinervia	Widespread	LC
Alibertia_edulis	Widespread	LC
Allagoptera_caudescens	Endemic	NE
Allophylus_edulis	Widespread	LC
Allophylus_leucoclados	Endemic	NE
Allophylus_petiolulatus	Widespread	NE
Allophylus_puberulus	Endemic	NE
Allophylus_semidentatus	Widespread	NE
Alseis_floribunda	Widespread	LC
Alseis_involuta	Endemic	NE
Amaioua_guianensis	Widespread	LC
Amaioua_intermedia	Widespread	LC
Ampelocera_glabra	Endemic	LC
Amphirrhox_longifolia	Widespread	LC
Anadenanthera_colubrina	Widespread	LC
Anadenanthera_peregrina	Widespread	LC
Andira_fraxinifolia	Endemic	LC
Andira_legalis	Endemic	LC
Andira_ormosioides	Endemic	LC
Aniba_firmula	Endemic	LC
Annona_acutiflora	Endemic	LC
Annona_cacans	Widespread	LC
Annona_coriacea	Widespread	NE
Annona_crassiflora	Widespread	LC
Annona_dolabripetala	Endemic	LC
Apeiba_tibourbou	Widespread	LC
Apuleia_leiocarpa	Widespread	LC
Arapatiella_psilophylla	Endemic	VU
Aspidosperma_cylindrocarpon	Widespread	LC

Aspidosperma_darienense	Widespread	LC
Aspidosperma_desmanthum	Widespread	LC
Aspidosperma_discolor	Endemic	LC
Aspidosperma_illustre	Endemic	NT
Aspidosperma_olivaceum	Endemic	NE
Aspidosperma_parvifolium	Endemic	NE
Aspidosperma_spruceanum	Endemic	LC
Aspidosperma_subincanum	Widespread	LC
Astrocaryum_aculeatissimum	Endemic	LC
Astronium_concinnum	Endemic	NE
Astronium_fraxinifolium	Widespread	NE
Astronium_graveolens	Widespread	NE
Astronium_urundeuva	Widespread	DD
Athenaea_velutina	Endemic	LC
Austrocritonia_velutina	Endemic	LC
Baccharis_platypoda	Widespread	NE
Bactris_ferruginea	Endemic	NE
Bactris_setosa	Endemic	NE
Banara_brasiliensis	Endemic	VU
Banara_parviflora	Endemic	LC
Bathysa_australis	Widespread	NE
Bauhinia_forficata	Widespread	LC
Beilschmiedia_linharensis	Endemic	NE
Bixa_arborea	Widespread	LC
Blepharocalyx_eggersii	Widespread	LC
Blepharocalyx_salicifolius	Widespread	NE
Bonnetia_stricta	Endemic	LC
Bowdichia_virgilioides	Widespread	LC
Brasiliocroton_mamoninha	Endemic	LC
Brosimum_gaudichaudii	Widespread	NE
Brosimum_glaucum	Endemic	NE
Brosimum_glaziovii	Endemic	EN
Brosimum_guianense	Widespread	LC
Brosimum_lactescens	Widespread	LC
Brunfelsia_brasiliensis	Endemic	NE
Byrsonima_basiloba	Endemic	LC
Byrsonima_crassifolia	Widespread	LC
Byrsonima_crispa	Widespread	LC
Byrsonima_intermedia	Endemic	NE
Byrsonima_pachyphylla	Widespread	LC
Byrsonima_sericea	Widespread	LC
Byrsonima_stipulacea	Widespread	LC
Cabralea_canjerana	Widespread	LC
Callisthene_major	Widespread	LC
Callisthene_minor	Endemic	LC
Calophyllum_brasiliense	Widespread	LC

Campomanesia_aurea	Widespread	NE
Campomanesia_espiritosantensis	Endemic	VU
Campomanesia_guazumifolia	Widespread	LC
Campomanesia_laurifolia	Endemic	EN
Campomanesia_lineatifolia	Widespread	LC
Campomanesia_xanthocarpa	Widespread	NE
Caraipa_densifolia	Widespread	LC
Cariniana_legalis	Endemic	VU
Cariniana_parvifolia	Endemic	NE
Carpotroche_brasiliensis	Endemic	LC
Caryocar_edule	Endemic	NE
Casearia_arborea	Widespread	LC
Casearia_commersoniana	Endemic	LC
Casearia_decandra	Widespread	NE
Casearia_gossypiosperma	Widespread	NE
Casearia_javitensis	Widespread	LC
Casearia_lasiophylla	Endemic	DD
Casearia_mariquitensis	Widespread	LC
Casearia_obliqua	Endemic	LC
Casearia_oblongifolia	Endemic	LC
Casearia_sylvestris	Widespread	LC
Casearia_ulmifolia	Endemic	LC
Cassia_ferruginea	Widespread	LC
Cecropia_glaziovi	Endemic	LC
Cecropia_hololeuca	Endemic	LC
Cecropia_pachystachya	Widespread	NE
Cedrela_fissilis	Widespread	VU
Cedrela_odorata	Widespread	VU
Ceiba_pubiflora	Widespread	NE
Ceiba_speciosa	Widespread	LC
Cenostigma_pluviosum	Widespread	NE
Centrolobium_sclerophyllum	Endemic	NE
Chaetocarpus_echinocarpus	Widespread	LC
Chamaecrista_bahiae	Endemic	LC
Chomelia_pohliana	Endemic	LC
Chromolaena_barbacensis	Endemic	NE
Chrysophyllum_gonocarpum	Widespread	LC
Chrysophyllum_imperiale	Endemic	EN
Chrysophyllum_januariense	Endemic	CR
Chrysophyllum_lucentifolium	Widespread	LC
Chrysophyllum_marginatum	Widespread	LC
Chrysophyllum_splendens	Endemic	VU
Cinnamomum_sellowianum	Endemic	LC
Citharexylum_myrianthum	Widespread	NE
Citronella_paniculata	Widespread	NE
Clarisia_ilicifolia	Widespread	LC

Clarisia_racemosa	Widespread	LC
Cnidoscolus_oligandrus	Endemic	LC
Coccoloba_glaziovii	Endemic	LC
Coccoloba_salicifolia	Endemic	NE
Coccoloba_warmingii	Endemic	LC
Connarus_suberosus	Widespread	NE
Copaifera_langsdorffii	Widespread	LC
Copaifera_lucens	Endemic	LC
Cordia_acutifolia	Endemic	LC
Cordia_bicolor	Widespread	LC
Cordia_ecalyculata	Widespread	NE
Cordia_magnoliifolia	Endemic	LC
Cordia_sellowiana	Endemic	LC
Cordia_sericicalyx	Widespread	LC
Cordiera_concolor	Widespread	NE
Couepia_carautae	Endemic	CR
Couepia_grandiflora	Widespread	NE
Couepia_rufa	Endemic	LC
Couepia_schottii	Endemic	VU
Couratari_asterotricha	Endemic	CR
Coussapoa_microcarpa	Endemic	LC
Coutarea_hexandra	Widespread	LC
Croton_floribundus	Widespread	NE
Cryptocarya_aschersoniana	Widespread	LC
Cupania_emarginata	Endemic	LC
Cupania_hispida	Widespread	LC
Cupania_ludowigii	Endemic	LC
Cupania_oblongifolia	Endemic	LC
Cupania_paniculata	Endemic	LC
Cupania_rugosa	Endemic	LC
Cupania_scrobiculata	Widespread	LC
Cupania_vernalis	Widespread	LC
Cybianthus_brasiliensis	Endemic	NE
Dalbergia_brasiliensis	Endemic	NE
Dalbergia_elegans	Endemic	NE
Dalbergia_foliolosa	Endemic	NT
Dalbergia_nigra	Endemic	VU
Davilla_elliptica	Widespread	NE
Deguelia_densiflora	Widespread	NE
Deguelia_hatschbachii	Endemic	VU
Dendropanax_brasiliensis	Endemic	LC
Dendropanax_cuneatus	Widespread	LC
Dialium_guianense	Widespread	LC
Diatenopteryx_sorbifolia	Widespread	NE
Dictyoloma_vandellianum	Widespread	LC
Didymopanax_calvus	Widespread	NE

Didymopanax_macrocarpus	Endemic	LC
Didymopanax_morototoni	Widespread	LC
Dilodendron_bipinnatum	Widespread	NE
Dimorphandra_jorgei	Endemic	LC
Dimorphandra_mollis	Widespread	LC
Diospyros_brasiliensis	Endemic	NT
Diospyros_inconstans	Widespread	LC
Diospyros_lasiocalyx	Widespread	LC
Diospyros_riedelii	Endemic	EN
Diospyros_sericea	Widespread	NE
Diploon_cuspidatum	Widespread	LC
Diplotropis_ferruginea	Endemic	LC
Diplotropis_incexis	Endemic	LC
Diplotropis_purpurea	Widespread	LC
Duguetia_chrysocarpa	Endemic	LC
Duguetia_furfuracea	Widespread	LC
Duguetia_lanceolata	Endemic	LC
Duroia_valesca	Endemic	VU
Ecclinusa_ramiflora	Widespread	LC
Emmotum_acuminatum	Endemic	NE
Emmotum_nitens	Endemic	LC
Endlicheria_glomerata	Endemic	LC
Endlicheria_paniculata	Widespread	LC
Enterolobium_contortisiliquum	Widespread	LC
Eriotheca_candolleana	Endemic	LC
Eriotheca_gracilipes	Widespread	NE
Eriotheca_macrophylla	Endemic	LC
Eriotheca_pubescens	Widespread	NE
Erythroxylum_campestre	Widespread	NE
Erythroxylum_citrifolium	Widespread	LC
Erythroxylum_daphnites	Widespread	LC
Erythroxylum_pelleterianum	Widespread	LC
Erythroxylum_pulchrum	Endemic	NE
Erythroxylum_suberosum	Widespread	LC
Eschweilera_ovata	Endemic	LC
Eugenia_aurata	Endemic	NE
Eugenia_bahiensis	Endemic	NE
Eugenia_beaurepairiana	Endemic	LC
Eugenia_brasiliensis	Endemic	NE
Eugenia_cymatodes	Endemic	VU
Eugenia_dodonaeifolia	Endemic	LC
Eugenia_dysenterica	Endemic	LC
Eugenia_florida	Widespread	LC
Eugenia_fluminensis	Widespread	DD
Eugenia_gemmiflora	Endemic	NE
Eugenia_hirta	Endemic	LC

Eugenia_inversa	Endemic	EN
Eugenia_itapemirimensis	Endemic	LC
Eugenia_ligustrina	Widespread	NE
Eugenia_macrosperma	Endemic	LC
Eugenia_pisiformis	Endemic	NE
Eugenia_platyphylla	Endemic	LC
Eugenia_platysema	Endemic	NE
Eugenia_plicatocostata	Endemic	NT
Eugenia_prasina	Endemic	VU
Eugenia_ramboi	Widespread	NE
Eugenia_subterminalis	Endemic	NE
Eugenia_sulcata	Endemic	LC
Eugenia_ternatifolia	Endemic	LC
Euterpe_edulis	Widespread	NE
Exellodendron_gracile	Endemic	NE
Exostyles_venusta	Endemic	LC
Faramea_atlantica	Endemic	VU
Faramea_bahiensis	Endemic	NE
Ficus_adhatodifolia	Widespread	NE
Ficus_citrifolia	Widespread	LC
Ficus_gomelleira	Widespread	LC
Ficus_obtusifolia	Widespread	LC
Ficus_pulchella	Widespread	VU
Garcinia_brasiliensis	Endemic	LC
Garcinia_gardneriana	Widespread	LC
Geissospermum_laeve	Widespread	NE
Genipa_americana	Widespread	LC
Geonoma_pohliana	Endemic	NE
Glycydendron_espiritosantense	Endemic	VU
Goniorrhachis_marginata	Endemic	LC
Guapira_graciliflora	Endemic	LC
Guapira_laxiflora	Endemic	NE
Guapira_noxia	Endemic	LC
Guapira_opposita	Widespread	LC
Guapira_venosa	Endemic	LC
Guarea_guidonia	Widespread	LC
Guarea_kunthiana	Widespread	LC
Guarea_macrophylla	Widespread	LC
Guarea_pendula	Endemic	LC
Guatteria_australis	Endemic	LC
Guatteria_campestris	Endemic	LC
Guatteria_ferruginea	Endemic	LC
Guatteria_macropus	Endemic	LC
Guatteria_pogonopus	Endemic	LC
Guatteria_sellowiana	Endemic	LC
Guatteria_villosissima	Endemic	LC

Guazuma_ulmifolia	Widespread	LC
Guettarda_angelica	Endemic	LC
Guettarda_viburnoides	Widespread	NE
Handroanthus_arianeae	Endemic	NE
Handroanthus_chrysotrichus	Widespread	NE
Handroanthus_cristatus	Endemic	NE
Handroanthus_heptaphyllus	Widespread	LC
Handroanthus_impetiginosus	Widespread	NT
Handroanthus_ochraceus	Widespread	NE
Handroanthus_riodocensis	Endemic	NE
Handroanthus_serratifolius	Widespread	EN
Handroanthus_vellosoi	Endemic	LC
Heisteria_ovata	Widespread	LC
Helicostylis_pedunculata	Widespread	NE
Helicostylis_tomentosa	Widespread	LC
Henriettea_stellaris	Widespread	LC
Heteropterys_byrsonimifolia	Endemic	LC
Heteropterys_campestris	Widespread	NE
Hieronyma_oblonga	Widespread	LC
Himatanthus_bracteatus	Endemic	LC
Himatanthus_phagedaenicus	Widespread	LC
Hirtella_bicornis	Widespread	LC
Hirtella_bullata	Widespread	LC
Hirtella_burchellii	Widespread	LC
Hirtella_hebeclada	Endemic	LC
Hirtella_racemosa	Widespread	LC
Homalolepis_cedron	Widespread	LC
Homalolepis_subcymosa	Endemic	NE
Hortia_brasiliana	Widespread	LC
Humiriastrum_dentatum	Endemic	LC
Humiriastrum_mussunungense	Endemic	VU
Hydrogaster_trinervis	Endemic	LC
Hymenaea_courbaril	Widespread	LC
Hymenolobium_janeirense	Endemic	NE
Hymenopus_heteromorphus	Widespread	LC
Ilex_affinis	Widespread	LC
Ilex_cerasifolia	Endemic	LC
Ilex_floribunda	Endemic	LC
Inga_cabelo	Endemic	EN
Inga_capitata	Widespread	LC
Inga_cylindrica	Widespread	LC
Inga_edulis	Widespread	LC
Inga_exfoliata	Endemic	EN
Inga_flagelliformis	Widespread	LC
Inga_hispida	Endemic	VU
Inga_ingoides	Widespread	LC

Inga_laurina	Widespread	LC
Inga_leptantha	Endemic	VU
Inga_schinifolia	Endemic	LC
Inga_subnuda	Endemic	LC
Inga_thibaudiana	Widespread	LC
Inga_unica	Endemic	VU
Inga_vera	Widespread	LC
Ixora_bahiensis	Endemic	EN
Ixora_brevifolia	Widespread	LC
Ixora_gardneriana	Endemic	LC
Jacaranda_caroba	Endemic	LC
Jacaranda_macrantha	Endemic	NE
Jacaranda_puberula	Endemic	LC
Jacaratia_heptaphylla	Widespread	NE
Jacaratia_spinosa	Widespread	LC
Joannesia_princeps	Endemic	VU
Kielmeyera_albopunctata	Endemic	VU
Kielmeyera_elata	Endemic	EN
Kielmeyera_occhioniana	Endemic	NE
Lacistema_aggregatum	Widespread	LC
Lacistema_hasslerianum	Widespread	NE
Lacistema_pubescens	Endemic	LC
Lacmellea_pauciflora	Endemic	EN
Lacunaria_crenata	Widespread	LC
Lafoensia_vandelliana	Widespread	NE
Lamanonia_ternata	Widespread	LC
Lecythis_lanceolata	Endemic	DD
Lecythis_lurida	Endemic	DD
Lecythis_pisonis	Endemic	NE
Leptobalanus_octandrus	Widespread	NE
Leptolobium_dasycarpum	Widespread	LC
Licania_belemii	Endemic	NE
Licania_discolor	Widespread	LC
Licania_hypoleuca	Widespread	LC
Licania_kunthiana	Endemic	LC
Licania_spicata	Endemic	LC
Licaria_bahiana	Endemic	LC
Licaria_guianensis	Widespread	LC
Lithraea_molleoides	Widespread	LC
Lonchocarpus_cultratus	Widespread	NE
Luehea_grandiflora	Widespread	NE
Mabea_fistulifera	Widespread	NE
Mabea_pulcherrima	Widespread	LC
Machaerium_brasiliense	Widespread	LC
Machaerium_fulvovenosum	Endemic	NE
Machaerium_hirtum	Widespread	LC

Machaerium_nyctitans	Widespread	LC
Machaerium_opacum	Endemic	LC
Machaerium_ovalifolium	Endemic	LC
Machaerium_villosum	Widespread	VU
Machaonia_acuminata	Widespread	LC
Maclura_tinctoria	Widespread	LC
Macoubea_guianensis	Widespread	LC
Macrolobium_latifolium	Endemic	LC
Macrothumia_kuhlmannii	Endemic	LC
Malouetia_cestroides	Endemic	NE
Manilkara_bella	Endemic	EN
Manilkara_elata	Endemic	EN
Manilkara_rufula	Endemic	NT
Manilkara_salzmannii	Endemic	LC
Margaritaria_nobilis	Widespread	NE
Matayba_elaeagnoides	Widespread	LC
Matayba_guianensis	Widespread	LC
Melanopsidium_nigrum	Endemic	NE
Melanoxylon_brauna	Endemic	NE
Melicoccus_espiritosantensis	Endemic	NE
Melicoccus_oliviformis	Endemic	NE
Meliosma_sellowii	Endemic	LC
Metrodorea_nigra	Endemic	LC
Miconia_albicans	Widespread	LC
Miconia_calvescens	Widespread	LC
Miconia_cinnamomifolia	Endemic	LC
Miconia_holosericea	Widespread	LC
Miconia_hypoleuca	Widespread	LC
Miconia_ibaguensis	Widespread	NE
Miconia_latecrenata	Endemic	LC
Miconia_ligustroides	Endemic	LC
Miconia_macrothyrsa	Widespread	NE
Miconia_paucidens	Widespread	NE
Miconia_prasina	Widespread	LC
Miconia_rimalis	Endemic	NE
Miconia_rubiginosa	Endemic	LC
Miconia_sellowiana	Endemic	LC
Miconia_splendens	Widespread	LC
Micropholis_crassipedicellata	Endemic	DD
Micropholis_gardneriana	Widespread	LC
Micropholis_venulosa	Widespread	LC
Mimosa_schomburgkii	Widespread	LC
Mollinedia_lamprophylla	Endemic	CR
Mollinedia_schottiana	Endemic	LC
Monilicarpa_brasiliana	Endemic	NE
Monteverdia_evonymoides	Widespread	NE

Monteverdia_floribunda	Widespread	NE
Monteverdia_gonoclada	Endemic	LC
Monteverdia_samydiformis	Endemic	NE
Moquilea_salzmannii	Endemic	LC
Moquiniastrum_pulchrum	Widespread	NE
Mouriri_arborea	Endemic	LC
Mouriri_elliptica	Endemic	LC
Mouriri_glazioviana	Endemic	NE
Myrcia_aethusa	Endemic	VU
Myrcia_amazonica	Widespread	LC
Myrcia_cordiifolia	Endemic	NE
Myrcia_crocea	Endemic	NE
Myrcia_eugenioides	Endemic	VU
Myrcia_eumecephylla	Endemic	VU
Myrcia_excoriata	Endemic	LC
Myrcia_ferruginosa	Endemic	EN
Myrcia_grandifolia	Endemic	NE
Myrcia_guianensis	Widespread	LC
Myrcia_hebepetala	Endemic	NE
Myrcia_hirtiflora	Endemic	LC
Myrcia_loranthifolia	Endemic	NE
Myrcia_multiflora	Widespread	LC
Myrcia_mutabilis	Endemic	LC
Myrcia_neoblanchetiana	Endemic	NE
Myrcia_neoestrellensis	Endemic	CR
Myrcia_neolucida	Widespread	LC
Myrcia_obversa	Endemic	VU
Myrcia_racemosa	Endemic	LC
Myrcia_retorta	Endemic	LC
Myrcia_riodocensis	Endemic	EN
Myrcia_rufipes	Endemic	LC
Myrcia_splendens	Widespread	LC
Myrcia_sucrei	Endemic	VU
Myrcia_tijucensis	Endemic	NE
Myrcia_tomentosa	Widespread	LC
Myrcia_vittoriana	Endemic	NE
Myrciaria_floribunda	Widespread	LC
Myrciaria_strigipes	Endemic	LC
Myrocarpus_frondosus	Widespread	DD
Myrsine_coriacea	Widespread	NE
Myrsine_umbellata	Widespread	LC
Naucleopsis_oblongifolia	Widespread	VU
Nectandra_grandiflora	Endemic	NE
Nectandra_lanceolata	Endemic	LC
Nectandra_megapotamica	Widespread	LC
Nectandra_membranacea	Widespread	LC

Nectandra_oppositifolia	Widespread	LC
Nectandra_rigida	Widespread	NE
Neea_floribunda	Widespread	LC
Neea_theifera	Widespread	NE
Neomitranthes_stictophylla	Endemic	NE
Neoraputia_alba	Endemic	LC
Ocotea_aciphylla	Widespread	LC
Ocotea_acutifolia	Widespread	LC
Ocotea_argentea	Endemic	LC
Ocotea_beulahiae	Endemic	NE
Ocotea_bicolor	Widespread	NE
Ocotea_brachybotrya	Endemic	LC
Ocotea_confertiflora	Endemic	NE
Ocotea_corymbosa	Widespread	LC
Ocotea_diospyrifolia	Widespread	LC
Ocotea_dispersa	Endemic	LC
Ocotea_divaricata	Endemic	LC
Ocotea_fasciculata	Widespread	LC
Ocotea_floribunda	Widespread	NE
Ocotea_glauca	Endemic	LC
Ocotea_indecora	Endemic	LC
Ocotea_lanata	Endemic	LC
Ocotea_lancifolia	Widespread	LC
Ocotea_laxa	Endemic	NE
Ocotea_longifolia	Widespread	LC
Ocotea_nitida	Endemic	LC
Ocotea_odorifera	Endemic	NE
Ocotea_pluridomatiata	Endemic	EN
Ocotea_prolifera	Endemic	LC
Ocotea_silvestris	Endemic	NE
Ocotea_spixiana	Endemic	NE
Ocotea_velutina	Endemic	LC
Ormosia_arborea	Endemic	LC
Ormosia_nitida	Endemic	NT
Ouratea_castaneifolia	Widespread	NE
Ouratea_cuspidata	Endemic	NE
Ouratea_hexasperma	Widespread	NE
Ouratea_parvifolia	Endemic	NE
Oxandra_espintana	Widespread	LC
Pachira_endecaphylla	Endemic	LC
Pachystroma_longifolium	Widespread	LC
Palicourea_rigida	Widespread	NE
Panopsis_rubescens	Widespread	LC
Parapiptadenia_pterosperma	Endemic	LC
Paratecoma_peroba	Endemic	NE
Parinari_brasiliensis	Endemic	NE

Parinari_parvifolia	Widespread	NT
Parkia_pendula	Widespread	LC
Pausandra_trianae	Endemic	LC
Pavonia_calyculosa	Endemic	LC
Peltogyne_angustiflora	Endemic	NT
Peltogyne_confertiflora	Widespread	NE
Peltophorum_dubium	Widespread	LC
Pera_glabrata	Widespread	LC
Pera_heteranthera	Endemic	LC
Phyllostemonodaphne_geminiflora	Widespread	EN
Picramnia_glazioviana	Endemic	LC
Picramnia_parvifolia	Widespread	NE
Picramnia_ramiflora	Endemic	LC
Pilocarpus_riedelianus	Endemic	LC
Pilocarpus_spicatus	Endemic	LC
Piper_arboreum	Widespread	NE
Piptadenia_gonoacantha	Widespread	LC
Piptadenia_paniculata	Endemic	LC
Piptocarpha_macropoda	Endemic	LC
Piptocarpha_rotundifolia	Widespread	NE
Pisonia_ambigua	Widespread	NE
Plathymenia_reticulata	Widespread	NE
Platymiscium_floribundum	Endemic	LC
Platypodium_elegans	Widespread	LC
Pleroma_granulosum	Endemic	NE
Plinia_grandifolia	Endemic	NT
Plinia_involucrata	Widespread	NE
Plinia_renatiana	Endemic	NE
Plinia_rivularis	Widespread	LC
Poecilanthe_falcata	Endemic	LC
Pogonophora_schomburgkiana	Widespread	LC
Pourouma_guianensis	Widespread	LC
Pourouma_mollis	Widespread	LC
Pourouma_velutina	Widespread	LC
Pouteria_bangii	Widespread	LC
Pouteria_bullata	Endemic	VU
Pouteria_butyrocarpa	Endemic	EN
Pouteria_caimito	Widespread	LC
Pouteria_coelomatica	Endemic	EN
Pouteria_cuspidata	Widespread	LC
Pouteria_filipes	Widespread	LC
Pouteria_gardneri	Widespread	LC
Pouteria_glomerata	Widespread	LC
Pouteria_grandiflora	Endemic	NT
Pouteria_guianensis	Widespread	LC
Pouteria_macrophylla	Widespread	LC

Pouteria_oxypetala	Endemic	EN
Pouteria_pachycalyx	Endemic	CR
Pouteria_psammophila	Endemic	NT
Pouteria_torta	Widespread	LC
Pouteria_venosa	Widespread	LC
Pradosia_lactescens	Endemic	NE
Protium_aracouchini	Widespread	LC
Protium_atlanticum	Endemic	NE
Protium_catuaba	Endemic	EN
Protium_glaziovii	Endemic	EN
Protium_heptaphyllum	Widespread	LC
Protium_ovatum	Endemic	LC
Protium_warmingianum	Endemic	LC
Prunus_brasiliensis	Widespread	NE
Prunus_myrtifolia	Widespread	NE
Pseudima_frutescens	Widespread	LC
Pseudobombax_grandiflorum	Endemic	NE
Pseudobombax_tomentosum	Widespread	LC
Pseudopiptadenia_contorta	Endemic	NE
Pseudoxandra_spiritus-sancti	Endemic	EN
Psidium_cattleyanum	Endemic	NE
Psidium_guajava	Widespread	LC
Psidium_guineense	Widespread	LC
Psidium_macahense	Endemic	NE
Psidium_oblongatum	Endemic	LC
Psidium_rufum	Endemic	LC
Psidium_sartorianum	Widespread	NE
Psychotria_carthagenensis	Endemic	NE
Psychotria_pedunculosa	Widespread	NE
Pterocarpus_rohrii	Widespread	NE
Pterygota_brasiliensis	Endemic	LC
Qualea_cryptantha	Endemic	NE
Qualea_grandiflora	Widespread	LC
Qualea_multiflora	Widespread	LC
Qualea_parviflora	Widespread	NE
Quararibea_penduliflora	Endemic	NE
Quiina_glaziovii	Endemic	LC
Ramisia_brasiliensis	Endemic	LC
Randia_armata	Widespread	LC
Rauvolfia_capixabae	Endemic	EN
Ravenia_infelix	Endemic	NT
Rinorea_bahiensis	Endemic	NE
Rudgea_sessilis	Endemic	NE
Rudgea_viburnoides	Widespread	NE
Sacoglottis_mattogrossensis	Widespread	LC
Salacia_elliptica	Widespread	LC

_Sapium_glandulosum_	Widespread	LC
_Schinus_terebinthifolia_	Widespread	NE
_Schizolobium_parahyba_	Widespread	LC
_Schoepfia_brasiliensis_	Widespread	NE
_Senefeldera_verticillata_	Endemic	LC
_Senegalia_polyphylla_	Widespread	LC
_Senna_macranthera_	Widespread	LC
_Simarouba_amara_	Widespread	LC
_Simira_alba_	Endemic	NE
_Simira_grazielae_	Endemic	NE
_Simira_sampaioana_	Widespread	LC
_Siparuna_bifida_	Widespread	NE
_Siparuna_guianensis_	Widespread	LC
_Siparuna_reginae_	Widespread	NE
_Sloanea_garckeana_	Widespread	LC
_Sloanea_granulosa_	Widespread	NE
_Sloanea_guianensis_	Widespread	LC
_Sloanea_hirsuta_	Endemic	NE
_Sloanea_sinemariensis_	Widespread	NE
_Solanum_alatirameum_	Endemic	NE
_Solanum_lycocarpum_	Widespread	LC
_Solanum_sooretamum_	Endemic	NE
_Solanum_swartzianum_	Widespread	LC
_Sorocea_bonplandii_	Widespread	NE
_Sorocea_guilleminiana_	Endemic	VU
_Sparattosperma_leucanthum_	Widespread	LC
_Spondias_macrocarpa_	Endemic	LC
_Spondias_mombin_	Widespread	LC
_Stephanopodium_blanchetianum_	Endemic	LC
_Sterculia_apetala_	Widespread	LC
_Sterculia_excelsa_	Endemic	LC
_Sterculia_striata_	Endemic	LC
_Stryphnodendron_adstringens_	Endemic	NE
_Stryphnodendron_guianense_	Widespread	LC
_Stryphnodendron_pulcherrimum_	Widespread	LC
_Stryphnodendron_rotundifolium_	Widespread	LC
_Styrax_ferrugineus_	Widespread	NE
_Swartzia_acutifolia_	Endemic	LC
_Swartzia_apetala_	Endemic	LC
_Swartzia_linharensis_	Endemic	NE
_Swartzia_myrtifolia_	Widespread	LC
_Swartzia_pinheiroana_	Endemic	LC
_Swartzia_polyphylla_	Widespread	LC
_Swartzia_simplex_	Widespread	LC
_Sweetia_fruticosa_	Widespread	LC
_Syagrus_botryophora_	Endemic	NT

Syagrus_macrocarpa	Endemic	EN
Syagrus_romanzoffiana	Widespread	NE
Symphonia_globulifera	Widespread	LC
Symplocos_estrellensis	Endemic	LC
Symplocos_pubescens	Widespread	LC
Symplocos_pycnobotrya	Endemic	EN
Tabebuia_cassinoides	Endemic	NE
Tabebuia_elliptica	Endemic	LC
Tabebuia_obtusifolia	Endemic	NE
Tabebuia_roseoalba	Widespread	NT
Tabernaemontana_laeta	Endemic	LC
Tabernaemontana_salzmannii	Endemic	LC
Tachigali_aurea	Widespread	NE
Tachigali_paratyensis	Endemic	LC
Tachigali_pilgeriana	Endemic	EN
Tachigali_rugosa	Endemic	NE
Tachigali_subvelutina	Widespread	NE
Tachigali_vulgaris	Endemic	LC
Tapirira_guianensis	Widespread	LC
Tapirira_obtusa	Widespread	LC
Terminalia_argentea	Widespread	LC
Terminalia_fagifolia	Widespread	LC
Terminalia_glabrescens	Widespread	NE
Terminalia_kleinii	Endemic	NT
Ternstroemia_brasiliensis	Endemic	NE
Thyrsodium_spruceanum	Widespread	LC
Toulicia_elliptica	Widespread	NE
Toulicia_patentinervis	Widespread	NE
Toulicia_stans	Endemic	CR
Tovomita_guianensis	Widespread	LC
Trichilia_casaretti	Endemic	VU
Trichilia_catigua	Widespread	NE
Trichilia_glabra	Widespread	LC
Trichilia_lepidota	Widespread	LC
Trichilia_magnifoliola	Endemic	VU
Trichilia_pallens	Endemic	NT
Trichilia_pallida	Widespread	NE
Trichilia_pseudostipularis	Endemic	NT
Trichilia_quadrijuga	Widespread	LC
Trichilia_silvatica	Endemic	VU
Trigoniodendron_spiritusanctense	Endemic	NE
Unonopsis_guatterioides	Widespread	LC
Urbanodendron_verrucosum	Endemic	VU
Vatairea_heteroptera	Endemic	LC
Vataireopsis_araroba	Endemic	NT
Vernonanthura_divaricata	Widespread	LC

Vernonanthura_polyanthes	Widespread	NE
Virola_bicuhyba	Endemic	NE
Virola_gardneri	Endemic	LC
Virola_officinalis	Endemic	LC
Virola_sebifera	Widespread	LC
Virola_surinamensis	Widespread	EN
Vismia_brasiliensis	Endemic	LC
Vismia_guianensis	Widespread	LC
Vismia_martiana	Endemic	NE
Vitex_megapotamica	Widespread	LC
Vitex_mexiae	Endemic	LC
Vitex_polygama	Endemic	LC
Vitex_sellowiana	Endemic	LC
Vitex_triflora	Widespread	LC
Vochysia_angelica	Endemic	NE
Xylopia_aromatica	Widespread	LC
Xylopia_brasiliensis	Endemic	NE
Xylopia_laevigata	Endemic	LC
Xylopia_ochrantha	Endemic	LC
Xylopia_sericea	Widespread	LC
Xylosma_prockia	Widespread	LC
Zanthoxylum_compactum	Widespread	LC
Zanthoxylum_fagara	Widespread	LC
Zanthoxylum_rhoifolium	Widespread	LC
Zanthoxylum_riedelianum	Widespread	LC
Zeyheria_montana	Endemic	NE
Zeyheria_tuberculosa	Widespread	VU
Zollernia_glabra	Widespread	LC
Zollernia_ilicifolia	Widespread	LC
Zollernia_modesta	Endemic	NE

CONCLUSÃO GERAL

Esta tese investigou como atributos bióticos, estratégias funcionais e condições ambientais moldam o funcionamento de ecossistemas em florestas tropicais secundárias, com ênfase no estoque de carbono e no papel ecológico de espécies endêmicas e ameaçadas. Ao longo dos três capítulos, integramos análises empíricas de carbono acima e abaixo do solo, estrutura funcional e filogenética, e a vulnerabilidade de grupos-chave de espécies, oferecendo uma compreensão abrangente das respostas do estoque de carbono a distúrbios, filtros ambientais e erosão da biodiversidade. Em conjunto, os resultados ressaltam a natureza icomplexa dos mecanismos ecológicos que estruturam florestas secundárias e reforçam a necessidade de incorporar perspectivas funcionais ao planejamento da restauração e da conservação.

No primeiro capítulo, os resultados demonstraram que tanto a diversidade funcional quanto os traços dominantes regulam os estoques de carbono acima do solo, mas sua importância relativa depende fortemente do histórico de distúrbio. Enquanto a complementaridade de nicho prevaleceu em florestas menos perturbadas, efeitos de razão de massa ganharam destaque sob maior distúrbio, revelando mecanismos ecológicos dependentes do contexto que moldam o acúmulo de carbono. Fatores ambientais, especialmente gradientes edáficos, também influenciaram os estoques de carbono. Esses achados reforçam a necessidade de considerar antecedentes de distúrbio e a diversidade funcional em avaliações do potencial de carbono de florestas, sobretudo em paisagens sujeitas à degradação acelerada.

O segundo capítulo expandiu essa perspectiva examinando a alocação de carbono em três compartimentos, na biomassa aérea, nas raízes e no solo, mostrando que cada um responde a combinações distintas de variáveis abióticas e traços funcionais. O carbono acima do solo foi determinado conjuntamente pela diversidade filogenética e por estratégias conservativas dominantes, enquanto o carbono radicular foi influenciado principalmente pelo clima. O carbono orgânico do solo apresentou a maior dependência de condições edáficas e climáticas, evidenciando a dinâmica lenta e a elevada sensibilidade ambiental desse reservatório. Importante destacar que o capítulo mostra que o carbono acima do solo representa menos da metade do carbono total do ecossistema das florestas secundárias analisadas, indicando que estratégias de restauração e metodologias de mercados de carbono podem subestimar o carbono florestal caso os componentes subterrâneos não sejam incorporados.

Por fim, o terceiro capítulo demonstrou que espécies endêmicas e ameaçadas ocupam regiões restritas do espaço funcional e tendem a apresentar estratégias conservativas, o que as torna particularmente vulneráveis a mudanças ambientais e à perda de espécies. Extinções simuladas desses grupos resultaram em redução da diversidade e maior uniformidade funcional, indicando a erosão de estratégias únicas e a homogeneização da estrutura funcional das florestas tropicais secundárias. A perda de espécies conservativas e tardias na sucessão, muitas delas endêmicas, pode direcionar trajetórias sucessionais para espécies amplamente distribuídas e aquisitivas, com efeitos em cascata sobre o estoque de carbono de longo prazo e a resiliência dos ecossistemas. Esses resultados destacam a importância estratégica de conservar espécies endêmicas ameaçadas como repositórios de traços funcionais e história evolutiva insubstituíveis.

De modo geral, esta tese mostra que o funcionamento de florestas tropicais secundárias emerge da interação entre diversidade funcional, estratégias dominantes e filtros ambientais, com o histórico de distúrbio exercendo influência decisiva em funções e serviços ecossistêmicos. Combinados, nossos resultados enfatizam que ações eficazes de conservação e restauração devem considerar não apenas os estoques de carbono, mas também as dimensões funcional e filogenética da biodiversidade, incluindo a proteção de espécies endêmicas vulneráveis. Ao integrar mecanismos que operam acima e abaixo do solo e ao longo de múltiplas dimensões da diversidade, este trabalho contribui para uma compreensão mais profunda dos processos que sustentam serviços ecossistêmicos em florestas tropicais secundárias e oferece uma base para o delineamento de estratégias que ampliem o estoque de carbono, preservem a resiliência funcional e salvaguardem a biodiversidade em um cenário de mudanças globais aceleradas.