COVARIAÇÃO E VARIAÇÃO DE ATRIBUTOS DA FOLHA E DO LENHO EM GRADIENTES AMBIENTAIS

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UNIVERSIDADE ESTADUAL DO NORTE FLUMINENSE DARCY RIBEIRO – UENF

CAMPOS DOS GOYTACAZES - RJ
AGOSTO – 2024

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Tese apresentada ao Centro de Biociências e Biotecnologia da Universidade Estadual do Norte Fluminense Darcy Ribeiro, como parte das exigências para a obtenção do título de Doutor em Ecologia e Recursos Naturais

Orientadora: Profª Drª Angela Pierre Vitória
Coorientadora: Profª Drª Maura Da Cunha

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“The real purpose of scientific method is to make sure Nature hasn’t misled you into thinking you know something you don’t actually know.”

Robert M. Pirsig

SUMÁRIO

LISTA DE ABREVIATURAS

CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico
DNPEA – Departamento Nacional de Pesquisa e Experimentação Agropecuária
EMBRAPA – Empresa Brasileira de Pesquisa Agropecuária
FAO – Food and Agriculture Organization of the United Nations
FAPERJ – Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro
IBGE – Instituto Brasileiro de Geografia e Estatística
ICMBIO – Instituto Chico Mendes de Conservação da Biodiversidade
INEA – Instituto Estadual do Meio Ambiente
INPE – Instituto Nacional de Pesquisas Espaciais
UNEP – United Nations Environment Programme’s
IPCC – Intergovernmental Panel on Climate Change
PRISMA – Preferred Reporting Items for Systematic reviews and Meta-Analyses
SISBIO – Sistema de Autorização e Informação em Biodiversidade
SUDENE – Superintendência do Desenvolvimento do Nordeste

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RESUMO

Gradientes espaciais e temporais podem submeter as espécies a distintas condições abióticas, exigindo delas ajustes em seus atributos funcionais. As estratégias de aquisição e uso dos recursos, resultantes desses ajustes são fundamentais para o *fitness* das espécies. Isto promove a variabilidade na expressão dos atributos, podendo os mesmos se apresentarem de forma mais ou menos covariada, acoplada ou desacoplada a depender da severidade ambiental. Além disso, as relações atributo-atributo mudam ao longo dos gradientes, com distintas contribuições das variações intra- e interespecíficas. Nesse contexto, a presente tese (1) revisou o conhecimento atual através de uma busca bibliográfica (2010-2022) em três bases científicas (*Web of Science, Scopus, Google Scholar*), sobre a variabilidade de atributos funcionais da folha e do lenho ao longo de gradientes abióticos em ecossistemas Neotropicais e sobre o acoplamento e desacoplamento de atributos funcionais em determinados contextos ambientais comparando-os com outras regiões geográficas; (2) determinou como a covariação e variação de sete atributos da folha e do lenho de 74 espécies estão associadas e verificou a existência de *trade-off* entre ambas em um gradiente latitudinal em três áreas da floresta Atlântica (Floresta Ombrófila Densa (FOD), Floresta Semidecidual (FES), Restinga (RES); (3) verificou se a covariação e variação de atributos foliares e do lenho mudou ao longo de um gradiente ambiental espacial local em três espécies coocorrentes em três áreas de sub-bosque de uma FOD. Dentre os principais resultados destaca-se: (1) a maioria dos estudos na região Neotropical esteve relacionada aos gradientes de disponibilidade hídrica e altitude, aos atributos da folha em relação aos atributos do lenho e aos atributos morfológicos em relação aos atributos bioquímicos e anatômicos. Ecossistemas mais restritivos apresentaram uma tendência para atributos mais conservativos e acoplados, enquanto ecossistemas não restritivos apresentaram atributos mais aquisitivos e desacoplados; (2) houve suporte para o *trade-off* entre variação e covariação, como também para uma relação positiva entre ambas entre os ecossistemas FOD, FES e RES. A variação do lenho foi maior na FOD enquanto a covariação do lenho foi maior na FES e RES evidenciando distintos mecanismos das espécies para lidar com restrições hídricas. A variabilidade intraespecífica foi maior que a interespecífica, especialmente na RES onde as condições ambientais restringem mais a expressão de atributos; (3) diferenças sutis entre os atributos foliares entre as espécies e áreas foram encontradas, assim como baixa variação e covariação e ausência de relação entre esses componentes. Adicionalmente, maior contribuição da variabilidade inter- e intraespecíficas na variabilidade dos atributos foi encontrada, indicando haver a ausência de um gradiente abiótico pronunciado entre as áreas de sub-bosque da FOD. Este estudo avança na compreensão da variabilidade de atributos funcionais em ecossistemas neotropicais, revelando como as alterações das condições ambientais moldam as relações entre atributos, especialmente ao destacar novos *insights* nos padrões de variação e covariação de atributos.

Palavras-chave: Ecologia funcional, Estratégias de uso de recursos, *Hotspots* de biodiversidade, Integração de atributos

ABSTRACT

Spatial and temporal gradients can subject species to distinct abiotic conditions, requiring adjustments in their functional traits. Resource-use strategies resulting from these adjustments are fundamental for species fitness. This promotes variation in the expression of these traits, which can present themselves in more or less covariation, coupled, or decoupled forms depending on environmental harshness. Additionally, multiple trait-trait relationships change along environmental gradients, with distinct contributions from intra- and interspecific variability. In this context, the present thesis (1) reviewed current knowledge through a literature search (2010-2022) across three scientific databases (Web of Science, Scopus, Google Scholar), on the variability of leaf and wood functional traits along abiotic gradients in Neotropical ecosystems and on trait coupling and decoupling relationships in specific environmental contexts compared to other geographical regions; (2) determined how the covariation and variation of seven leaf and wood traits of 74 species are associated and verified the existence of a trade-off between them on a latitudinal gradient in three areas of the Atlantic forest (Dense Ombrophilous Forest (DOF), Seasonal Semideciduous Forest (SSF), *Restinga* (RES)); (3) verified whether the covariation and variation of leaf and wood traits changed along a local spatial environmental gradient in three co-occurring species in three areas of a rainforest. Among the main results, this thesis highlights: (1) most studies in the Neotropical region were related to water availability and altitude gradients, leaf traits in relation to wood traits, and morphological traits in relation to biochemical and anatomical traits. Resource-limited ecosystems showed a tendency for more conservative and coupled traits, while resource-rich ones showed more acquisitive and decoupled traits; (2) there was support for the trade-off between variation and covariation, as well as for a positive relationship between them among the DOF, the SSF, and the RES ecosystems. Wood variation was higher in the DOF, while wood covariation was higher in the SSF and RES, evidencing different species mechanisms to deal with water restrictions. Intraspecific variability was greater than interspecific, especially in the RES, where environmental conditions constrain more trait expression; (3) subtle differences in leaf traits between species and areas were observed, along with low variation and covariation, and an absence of a relationship between these components. Additionally, greater contribution of inter- and intraspecific variability was also found, indicating the absence of a sharp abiotic gradient among the understory areas of the FOD. This study enchances our understanding of functional trait variability in Neotropical ecosystems, elucidating how changes in environmental conditions shape trait relationships, particularly by highlighting novel insights into patterns of trait variation and covariation among traits.

Keywords: Functional ecology, Resource use strategies, Biodiversity hotspots, Trait integration

ESTRUTURA DA TESE

Esta tese é composta de:

1. **Uma introdução geral**, apresentando a fundamentação teórica e visão geral sobre a temática dos capítulos seguintes.

2. **Três capítulos redigidos em formato de artigos científicos**, que descrevem diferentes abordagens sobre a variação e covariação de atributos da folha e do lenho em gradientes abióticos em ecossistemas da região Neotropical, com foco para ecossistemas da floresta Atlântica nos capítulos 2 e 3. Cada capítulo possui seu resumo, introdução, material e métodos, resultados, discussão, conclusão e referências conforme cada revista nas quais foram publicados ou submetidos:

    - **Capítulo 1:** A systematic review of leaf and wood traits in Neotropics: environmental gradients and functionality. Situação: publicado no periódico Trees – Structure and Function. https://doi.org/10.1007/s00468-024-02508-7
    - **Capítulo 2:** Functional trait patterns: investigating variation-covariation relationships and the importance of intraspecific variability along distinct vegetation types. Situação: publicado no periódico Community Ecology. https://doi.org/10.1007/s42974-024-00196-4
    - **Capítulo 3:** Leaf and wood trait variability of co-ocurring tree species along a short environmental gradient in an Atlantic tropical rainforest restoration area.

3. **Discussão Geral**, sintetizando os principais resultados descritos nos três capítulos supracitados.

4. **Considerações finais**, ressaltando as contribuições desta tese para a comunidade científica da área.

1. INTRODUÇÃO GERAL

Atributos funcionais das plantas, mensuráveis ao nível do indivíduo, são aqueles que influenciam na reprodução, sobrevivência e crescimento das espécies (Violle et al., 2007; Díaz et al., 2013; Caruso et al., 2020), embora a definição do que é “funcional” para um atributo ainda permaneça em discussão (Mlambo et al., 2014; Garnier et al., 2016; Volaire et al., 2020; Sobral et al., 2021). As relações de causa e efeito entre os diferentes atributos funcionais permitem inferir sobre o posicionamento e diferenciação das espécies dentro de grupos ecológicos (McGill et al., 2006; Adler et al., 2014; Díaz et al., 2016; Belluau e Shipley, 2018). O estudo dessas relações entre atributos permite a melhor compreensão da interação entre as espécies de plantas e seu ambiente (Westoby et al. 2002, Grime e Pierce, 2012).

Neste contexto, surgem os espectros de economia em ecologia, que se caracterizam como dimensões de variação em que os atributos são correlacionados, seja ao nível de órgão ou planta inteira (Wright et al., 2004; Chave et al., 2009; Freschet et al., 2010; Reich, 2014; Díaz et al., 2016; de la Riva et al., 2016). Esses espectros distinguem estratégias ecológicas ao longo de um *continuum* entre aquisição (rápido retorno e baixo custo energético) e conservação de recursos (lento retorno e alto custo energético), auxiliando a entender a variação nas características das espécies em diferentes escalas ecológicas (Wright et al., 2004; Chave et al., 2009; Reich, 2014). Por exemplo, no espectro de economia da folha e da madeira, árvores com maior área foliar específica (i.e. maior investimento em área em relação à sua massa) e menor densidade da madeira (lenho) são encontradas no extremo aquisitivo desse *continuum* de estratégias, enquanto plantas com características opostas são encontradas no extremo conservativo (Wright et al., 2004; Chave et al., 2009). Essa mesma ideia se aplica ao espectro de economia de toda planta, porém com uma única dimensão entre folha, madeira e raiz (de la Riva et al., 2016; Díaz et al., 2016). Avanços na ecologia baseada em atributos foram alcançados com os espectros de economia para avaliar as diferentes interrelações entre atributos e os ajustes das espécies às demandas ambientais. No entanto, se esses espectros representam padrões gerais em diferentes tipos de ecossistemas, escalas espaço-temporais e níveis de organização biológica ainda permanece em debate, como por exemplo, algumas relações entre atributos vistas em escalas regionais que podem não ser encontradas em escalas locais (Funk et al., 2016; Messier et al., 2017).

Os espectros de economia são exemplos representativos das abordagens multivariadas de atributos, as quais têm sido consideradas mais recentemente debates centrais na ecologia baseada em atributos ao considerar múltiplos aspectos do fenótipo (Baraloto et al., 2010; Méndez-Alonzo et al., 2012; Dwyer e Laughlin, 2017; Sanaphre-Villanueva et al., 2022). Abordagens univariadas, que estudam a variação de único atributo em uma condição ou gradiente ambiental, simplificam a complexidade da variação fenotípica (Brown et al., 2022), muitas vezes sem considerar a extensão da variabilidade dos atributos ou as respostas coordenadas entre eles. As distintas relações entre atributos podem ser observadas pelas respostas fenotípicas de variação e/ou covariação nos diferentes órgãos da planta, sendo a primeira a capacidade das espécies em ajustar seus fenótipos às flutuações ambientais e a segunda, as correlações entre vários atributos (Pigliucci, 2003; Valladares et al., 2007; Matesanz et al., 2010; Nicotra et al., 2010; Armbruster et al., 2014). A direção, força e extensão com que essas interrelações entre os atributos funcionais e órgãos da planta ocorrem, assim como a prevalência de estratégias aquisitivas e conservativas, têm sido associadas ao nível de severidade ambiental em que as espécies estão submetidas (Dwyer e Laughlin, 2017).

Sob a ótica da severidade ambiental, estratégias aquisitivas prevalecem em ecossistemas com menores restrições abióticas, como florestas tropicais úmidas, onde a maior amplitude de nicho favorece a maior variação e plasticidade fenotípica. Nesses ecossistemas, atributos da folha e do lenho tem pressões seletivas diferentes e podem operar de forma independente ou desacoplada (Westoby et al., 2002; Baraloto et al., 2010; Donovan et al., 2011; Braga et al., 2016; Dwyer e Laughlin, 2017; Vleminckx et al., 2021). Em contrapartida, em ecossistemas com maiores restrições abióticas onde o espaço de nicho viável é reduzido, como florestas sazonalmente secas, estratégias conservativas, maior covariação e integração fenotípica entre atributos são necessárias, e atributos da folha e do lenho operam de forma interdependente e acoplada (Westoby et al., 2002; Markesteijn et al., 2011; Méndez-Alonzo et al., 2012; Pigliucci, 2003; Dwyer e Laughlin, 2017; Delhaye et al., 2020). Com base nesse contexto, variação (ou plasticidade), e covariação (ou integração) variam em direções opostas, sugerindo que a covariação restringe a variação, seja em gradientes ambientais ou em condições contrastantes (Gianoli, 2004; Gianoli e Palácio-Lopez, 2009; Matesanz et al., 2010).

Contudo, essas hipóteses são recentes na ecologia e ainda pouco testadas, sem consenso entre os estudos. Tem sido observado acoplamento e desacoplamento entre órgãos das plantas em ecossistemas não restritivos e restritivos, com o acoplamento podendo ser fraco em ambientes restritivos (Silva et al., 2018; Medina-Veja et al., 2021; Sanaphre-Villanueva et al., 2022). Estudos recentes também mostram que a variação e covariação podem ocorrer sinergicamente, indicando que a covariação não representa uma restrição à variação, ou ainda, que a plasticidade não é limitada pela integração fenotípica (Zimmermann et al., 2016; Pireda et al., 2019; Matesanz et al., 2021; Borges et al., 2022; Shi et al., 2023; Oyanoghafo et al., 2023). Esses resultados sugerem uma revisão da hipótese de Gianoli e Palácio-López (2009) de que a covariação é uma limitação à variação, e mais estudos são necessários, especialmente porque diferentes fatores podem interferir nessa relação, como a escala espacial, filogenia, grupos funcionais, o órgão da planta estudado, dentre outros (Godoy et al., 2012; Martínez-Cabrera et al., 2011; Messier et al., 2017; Michelaki et al., 2019).

Adicionalmente aos estudos de variação e covariação, a contribuição da variabilidade intraespecífica tem ganhado crescente atenção na ecologia baseada em atributos. Inicialmente assumia-se que a variabilidade entre indivíduos era baixa e negligenciável nas relações entre atributos dentro dos espectros funcionais (McGill et al., 2006). Contudo, essa fonte de variação é maior do que previamente se assumia e tem se mostrado importante na covariação de atributos ao longo de gradientes ambientais (Kichenin et al., 2013; He et al., 2021; Homeier et al., 2021). Quanto maior a amplitude do gradiente ambiental, maior a contribuição da variabilidade intraespecífica (Albert et al., 2010; Auger e Shipley, 2013). Alguns estudos também indicam que a variabilidade intraespecífica pode enfraquecer a covariação de atributos (He et al., 2021). A incorporação dessa variabilidade nas relações de variação e covariação em gradientes ambientais ainda é incipiente, mas vem sendo reavaliada nos diferentes estudos com atributos funcionais.

Portanto, torna-se relevante o estudo da diversidade ecológica e funcional nas regiões tropicais, como por exemplo no contexto das mudanças climáticas, que poderão ter consequências severas para a biodiversidade, afetando a dinâmica de ecossistemas e os serviços ambientais associados (Malhi et al., 2009; Marengo et al., 2009; 2011; Bellard et al., 2012; Allen et al., 2010; Allen et al., 2017; IPCC, 2023). Com as mudanças climáticas em curso, é essencial compreender como ocorre a seleção dos fenótipos em resposta a severidade ambiental servindo como base para predizer como e quais espécies irão sobreviver a estas mudanças em diferentes regiões geográficas.

Nesse contexto, a região Neotropical pode auxiliar na compreensão dessas questões envolvendo a seleção de fenótipos em diferentes condições ambientais. A região Neotropical é considerada uma das regiões mais biodiversas do mundo e, por muitos anos, tem intrigado cientistas de diferentes áreas sobre quais fatores ajudaram a moldar sua alta biodiversidade e heterogeneidade de ecossistemas (Hughes et al., 2013; Morrone et al., 2014; Antonelli et al., 2018; Raven et al., 2020; Jaramillo, 2023). A complexidade da formação dessa região envolveu fatores geológicos, climáticos e oceanográficos, além de processos biológicos em diferentes escalas espaciais e temporais (e.g., adaptação, especiação, competição) (Antonelli e Sanmartín, 2011; Hoorn et al., 2010; Hughes et al., 2013; Jaramillo, 2023). A ampla extensão geográfica da região Neotropical, do México central e ilhas do Caribe à maior parte da América do Sul, resultou na formação de distintos ecossistemas (Morrone et al., 2014; 2022). As formações florestais estão entre os ecossistemas com maiores extensões nessa região, assim como os ecossistemas abertos pertencentes a diagonal seca da América do Sul, sendo eles a Caatinga, o Cerrado e os Chacos (Morrone et al., 2014; Lima et al., 2018).

A região Neotropical também mantém elevada diversidade funcional, taxonômica e filogenética em vários grupos de organismos, especialmente plantas vasculares, superando em mais do dobro as regiões Afrotropical e sudeste da Ásia, que também são altamente diversas (Antonelli e Sanmartín, 2011; Antonelli et al., 2018; Raven et al., 2020). O estudo da diversidade da região Neotropical é prioritário para entender os padrões e processos associados com sua origem e manutenção (Antonelli et al., 2018). Por exemplo, ainda há pouco conhecimento sobre a diversidade funcional nessa região (Antonelli et al., 2018). Em razão dessa alta diversidade e conhecimento ainda incipiente e incompleto, muitas espécies e ecossistemas estão criticamente ameaçados por distúrbios antropogênicos ou eventos climáticos extremos (Antonelli et al., 2022; IPCC, 2023). Neste contexto, somente na região Neotropical, há oito dos 35 *hotspots* mundiais de biodiversidade, incluindo áreas vulneráveis às mudanças climáticas e prioritárias para conservação e restauração, como os Andes, Cerrado e a floresta Atlântica (Myers et al., 2000;

Mittermeier et al., 2011; Bellard et al., 2014; Strassburg et al., 2020; Trew e Maclean, 2021).

Devido à sua extensão geográfica e histórico de formação, a região Neotropical apresenta alta variabilidade ambiental, constituindo diferentes gradientes abióticos e ampla variação funcional e florística (Antonelli e Sanmartín, 2011; Baraloto et al., 2012; Hughes et al., 2013; Vleminckx et al., 2021). Essa heterogeneidade também é evidente na floresta Atlântica, que consiste em um mosaico de fitofisionomias, estendendo-se da região tropical a região subtropical e constituindo diversos gradientes climáticos, topográficos e edáficos (Oliveira-Filho e Fontes, 2000; Ribeiro et al., 2011; Vitória et al., 2019). A distribuição latitudinal e diferenciação de fitofisionomias da floresta Altântica são influenciados principalmente por gradientes de disponibilidade hídrica e temperatura no sentido norte-sul e pela sazonalidade da precipitação no sentido leste-oeste (Joly et al., 2014; Rezende et al., 2018). Entretanto, outros fatores como elevação, topografia e características do solo também moldaram a variação florística e funcional da floresta Atlântica (Eisenlohr e Oliveira-Fillho, 2015; Vitória et al., 2019; Cupertino-Eisenlohr et al., 2021). Por esta razão, a floresta Altântica possui altos níveis de endemismo e riqueza de angiospermas, mas também é uma das florestas tropicais mais ameaçadas no mundo devido à alta perda de cobertura florestal (Mittermeier et al., 2011; Forzza et al., 2012; Joly et al., 2014; Broggio et al., 2024).

Os gradientes ambientais da região Neotropical, e em particular da floresta Atlântica, criaram condições específicas que moldaram a seleção e distribuição das espécies de plantas (Dick e Pennington, 2019; Cupertino-Eisenlohr et al., 2021). A seleção de espécies ocorre continuamente através de vários processos complementares como a estocasticidade de eventos (limitação da dispersão, deriva) e processos determinísticos (interações bióticas e condições abióticas), desde escalas locais a escalas regionais (Vellend e Agrawal, 2010; Kraft et al., 2015; Gilbert e Levine, 2017). Essas pressões seletivas explicam como as plantas lidam com a disponibilidade, duração e intensidade dos recursos e condições abióticas, assim como com interações bióticas (Cornwell e Ackerly, 2009; Kleyer e Minden, 2015; Zanzoterra et al., 2020; Vieira et al., 2021). Espécies que se ajustem a flutuações graduais ou abruptas da disponibilidade hídrica, temperatura, irradiância, disponibilidade de nutrientes, altitude, por exemplo, podem garantir sua manutenção no ambiente e o sucesso reprodutivo pela otimização de seu *fitness* (Garnier et al., 2016; de Bello et al., 2021). Esses aspectos das condições ambientais definem o nicho ecológico das espécies, pois a filtragem e seleção de hábitat agem no *fitness* como um todo (Laughlin e Messier, 2015; Cavender-Bares et al., 2018). A partir dessas flutuações ambientais, o nicho ocupado de uma espécie pode se ampliar ou se estreitar, a partir de determinadas características ou combinações de características que persistem no ambiente (Laughlin, 2014; Laughlin et al., 2020).

Nesse sentido, o estabelecimento de padrões entre as espécies de plantas é importante em regiões e ecossistemas hiperdiversos, como a região Neotropical, para compreender as respostas das espécies às demandas ambientais (Díaz et al., 2016; Pierce et al., 2017; Vitória et al., 2019). Abordagens baseadas em atributos e estratégias ecológicas têm sido uma questão central e crescente em ecologia, especialmente porque essas abordagens simplificam a compreensão do funcionamento e organização das comunidades, independentemente do número de espécies, e melhoram as previsões nas respostas das espécies a diferentes contextos ambientais (Lavorel e Garnier, 2002; McGill et al., 2006; Díaz et al., 2013; 2016; Pérez-Harguindeguy et al., 2013; Reich, 2014; Pierce et al., 2017).

Diante disso, essa tese visou abordar no **Capítulo 1** uma revisão bibliográfica sistemática dos últimos 12 anos (2010-2022) sobre a seleção e variação de atributos em plantas nos principais gradientes abióticos (disponibilidade de água, irradiância, temperatura, fertilidade do solo e elevação), e a variação e covariação (acoplamento e desacoplamento entre folha e lenho) em ecossistemas restritivos e não restritivos; no **Capítulo 2** a variação e covariação de atributos da folha e do lenho em um gradiente latitudinal, buscando compreender a existência de uma relação antagônica ou sinérgica entre esses dois aspectos da variabilidade de atributos, e a contribuição da variabilidade intraespecífica na covariação, ambas no contexto da severidade ambiental e; no **Capítulo 3** a variação e covariação de atributos da folha e do lenho em três espécies coocorrentes em localidades que formam um gradiente ambiental em uma floresta ombrófila da floresta Atlântica, também no contexto da severidade ambiental dentro de um ecossistema mésico e menos restritivo.

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CAPÍTULO 1:

A systematic review of leaf and wood traits in Neotropics: environmental gradients and functionality

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2. CAPÍTULO 1: A sytematic review of leaf and wood traits in Neotropics: environmental gradients and functionality

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Key message Resource-limited environments showed a tendency towards conservative and coupled leaf and wood traits, while displaying an acquisitive and decoupled pattern in resource-rich ones. Water and elevation were the most studied gradients.

Abstract

In the Neotropics, spatial and temporal environmental gradients subject plants to distinct abiotic conditions, requiring functional adjustments. This promotes changes in trait expression, resulting in individual trait variation or covariation. We have systematically reviewed the literature focusing on leaf and wood traits in the Neotropics along major abiotic gradients (water, irradiance, temperature, soil fertility, and elevation). We also assessed their spatial and temporal variation and covariation trends. Thus, we compiled 141 published papers from 2010 to 2022. Most of the studies of leaf and wood traits were related: 1) to the gradients of water avalability and elevation, 2) to leaf traits at the expense of wood traits, with specific leaf area and wood density the most studied traits, respectively, 3) more to the morphological leaf traits than to biochemical, ecophysiological, or anatomical ones. In general, more conservative traits were observed in environments with lower resource availability. Although there is still no consensus, coupling was predominantly linked to water balance during periods of water restriction or in dry ecosystems, and papers have focused on single ecosystems rather than making comparisons across multiple ecosystems.This systematic review highlights the tendency for systems with fewer resources to show a bis towards greater coordination between leaf and wood traits compared to systems with more resources. This review also adresses how traits are expressed based on the integration of more than one environmental driver and the qualitative variations of these resources. Finally, we emphasizethe importance of analyzing different aspects of trait expression when assessing species' responses to environmental gradients, especially in megadiverse regions such as the Neotropics.

Keywords: Abiotic filters, Functional diversity, Phenotypic variation, Trait-based ecology, Trait integration

Introduction

The Neotropics is one of the most diverse biogeographical regions of the world, home to 37% of all plant species with seeds and one of the largest tropical forest areas (Antonelli and Sanmartín 2011; Ulloa et al. 2017; Taubert et al. 2018; FAO and UNEP 2020). This region, located between the latitudes 20° N and 57° S and longitudes 112° W and 35° E, encompasses a large part of Mexico, the countries of Central America, the Caribbean islands, and almost all of South America, comprising ecosystems such as humid and dry tropical forests, subtropical forests, high altitude fields, savannas, and deserts, among others (Hughes et al. 2013; Morrone 2014; Raven et al. 2020; Morrone et al. 2022). Eight of these ecosystems are on the world's 35 biodiversity hotspots list, including regions such as the Andes, *Cerrado*, and the Atlantic Forest (Mittermeier et al. 2011), the last two of which have been listed as world biodiversity hotspots that are particularly vulnerable to climate change (Bellard et al. 2014; Trew and Maclean 2021).

There is evidence that the patterns of diversity and distribution among Neotropic plant species are grounded in complex interactions involving abiotic processes, such as mountains elevations, hydrological and climatic changes, as well as biotic ones, such as dispersion capacity, niche conservation, and edaphic adaptation, indicating diverse environmental gradients (Hoorn et al. 2010; Antonelli and Sanmartín 2011; Hughes et al. 2013; Antonelli et al. 2018; Antonelli 2022). Additional evidence exists, suggesting that the organization of the biodiversity of the Neotropics is more closely related to ecological than geographic processes (Hughes et al. 2013). Such processes include dispersion limitation, a key component in the evolutionary processes of plant species (Hughes et al. 2013). Thus understanding regarding the origin and maintenance of Neotropics biodiversity remains insufficient (Antonelli and Sanmartín 2011; Antonelli et al. 2018; Meseguer et al. 2022).

Given the high biodiversity encountered in the Neotropical region, functional trait-based approaches are essential for establishing patterns between species, simplifying the complexity of communities' organization and functioning, and enhancing understanding of species' responses to environmental demands (McGill et al. 2006; Violle et al. 2007; Díaz et al. 2016; Pierce et al. 2017; Caruso et al. 2020). Functional traits in plants confer measurable phenotypic aspects at the individual level, influencing fitness through their effects on reproduction, growth, and survival of the species (Violle et al. 2007; Díaz et al. 2013; Mlambo et al. 2014; Garnier et al. 2016; Caruso et al. 2020; Volaire et al. 2020; Sobral et al. 2021). Species´ trait-based responses can be accessed through either univariate approaches, focusing on single trait distribution along abiotic gradients, such as the variation in wood density in an elevation or water availability gradient (van der Sande et al. 2016), or multivariate approaches that consider the multidimensional distribution of traits and their multiple relationships (Laughlin 2014; Garnier et al. 2016; Flores-Moreno et al. 2019; Brown et al. 2022). The relationships between traits form axes or dimensions of variation, or even “economic spectra”, that can be explored at both organ and whole-plant levels (Wright et al. 2004; Chave et al. 2009; Freschet et al. 2010; Díaz et al. 2016). These dimensions of variation represent an evolutionary-ecological compromise, allowing the differentiation of species along a continuum between acquisition (fast return and low energy cost) versus resource conservation (slow return and high energy cost), which can enchance the understanding of functional space variation at different spatial and temporal scales (Reich 2014; Caruso et al. 2020; Ribeiro et al. 2022).

In this context, the way the environment acts on the individual expression of traits and the trade-offs between traits determine whether trait variation or covariation will be locally favored (Wood and Brodie 2015; Matesanz et al. 2021). While trait variation is related to a phenotype or trait´s susceptibility to change, trait covariation involves the variation among functionally-related traits (Nicotra et al. 2010; Armbruster et al. 2014). Some researchers have proposed that as environmental harshness increases, the traits of different plant organs tend to function coupled, creating covariation and a reduced niche space (Dwyer and Laughlin 2017; Delhaye et al. 2020; Homeier et al. 2021). In contrast, less severe environmental conditions tend to foster higher trait variation (decoupling among organs) (Dwyer and Laughlin 2017; Delhaye et al. 2020; Homeier et al. 2021). However, multidimensional relations among these traits in response to abiotic gradients and their ecological and adaptive implications for the community functioning has yet to be fully understood, especially in the Neotropics and when the different local, regional, or global spatial scales are considered (Dwyer and Laughlin 2017; Messier et al. 2017; Matesanz et al. 2021; Sanaphre-Villanueva et al. 2022).

Therefore, the aim of this study was to conduct a systematic review focused on the principal abiotic environmental gradients and determine which leaf and wood traits have been most studied in the Neotropics, as well as their principal trends concerning spatial variation and covariation.

Methods

Systematic literature search

We conducted a comprehensive systematic literature review following the PRISMA-adapted protocol (Preferred Reporting Items for Systematic Reviews and Meta-Analyses, Moher et al. 2009; O' Dea et al. 2021). A bibliographic search covering a 12-year period (2010- September 2022) was performed on the online scientific platforms Web of Science, Scopus, and Google Scholar employing a combination of the specific fixed keywords: “plant traits”, “functional variability”, “functional variation”, “environmental gradients”, “abiotic gradients”, combined with the keywords: “Neotropical forests”, “tropical forests”, “coordination”, “covariation”, “integration”, “plasticity”, “phenotypic variation”, “coupling”, “decoupling”, “disentangling”, “intraspecific variation”, “within-species variation”, "interspecific variation”, “between-species variation”, “leaf trait variation”, “wood trait variation”, “South America”, “Central America”, “tropical dry forests”, “tropical rainforests”, “subtropical forests”, “seasonal heath vegetation”, and “*restinga*” (Table S1). The bibliographic search and all information extraction was performed by a single person to avoid any potential bias. We selected only peer-reviewed published scientific papers written in English that met our review aims, scope, and inclusion criteria.

The inclusion criteria established for the selection of papers were as follows: 1) presentation of data pertaining to adult woody shrub-tree species; 2) presentation of leaf or wood traits (at least one trait); 3) relation to native species under natural conditions; and 4) the ability to distinguish descriptive statistics, correlations, regressions, and other analyses, making it possible to identify trait variation in relation to environmental variables in the gradients. We excluded global papers for which it was not possible to extract specific information about the Neotropical region, as well as theoretical papers that did not undergo any statistical analyses or review of plant traits and abiotic gradients. We also included some conceptual or relevant papers published before 2010 or unrelated to the Neotropics region to strengthen the theoretical background of the main topics. Those conceptual or relevant papers were not counted in the paper selection. We found a total of 765 potential papers from the three databases and 141 studies met our inclusion criteria (Fig. 1 and Table S2).

Data extraction

From each selected paper, we collected the following information:

1) Authors, year of publication, country, number of species, number of traits;

2) Plant organ: (i) only leaf; (ii) only wood; and (iii) both leaf and wood;

3) Trait category: (i) ecophysiological (e.g., water potential, chlorophyll fluorescence); (ii) anatomical (e.g., xylem vessel diameter, palisade parenchyma thickness); (iii) morphological (e.g., specific leaf area, wood density) and (iv) biochemical (e.g. leaf carbon isotopic composition, leaf Mg concentration);

4) Abiotic gradient: (i) water availability (air, soil); (ii) irradiance; (iii) temperature; (iv) soil fertility; (v) elevation, and (vi) temporal.

This systematic review was organized as follows: 1) a brief description of paper metrics' results, 2) a description and discussion of the current state of knowledge regarding the variation of leaf and wood traits along the principal abiotic spatial gradients: water availability, irradiance, temperature, soil fertility, and elevation; 3) a summary of the temporal variation of abiotic resources in trait expression; 4) the state of the art regarding leaf and wood coupling and decoupling as a function of resource availability, and 5) a concluding section.

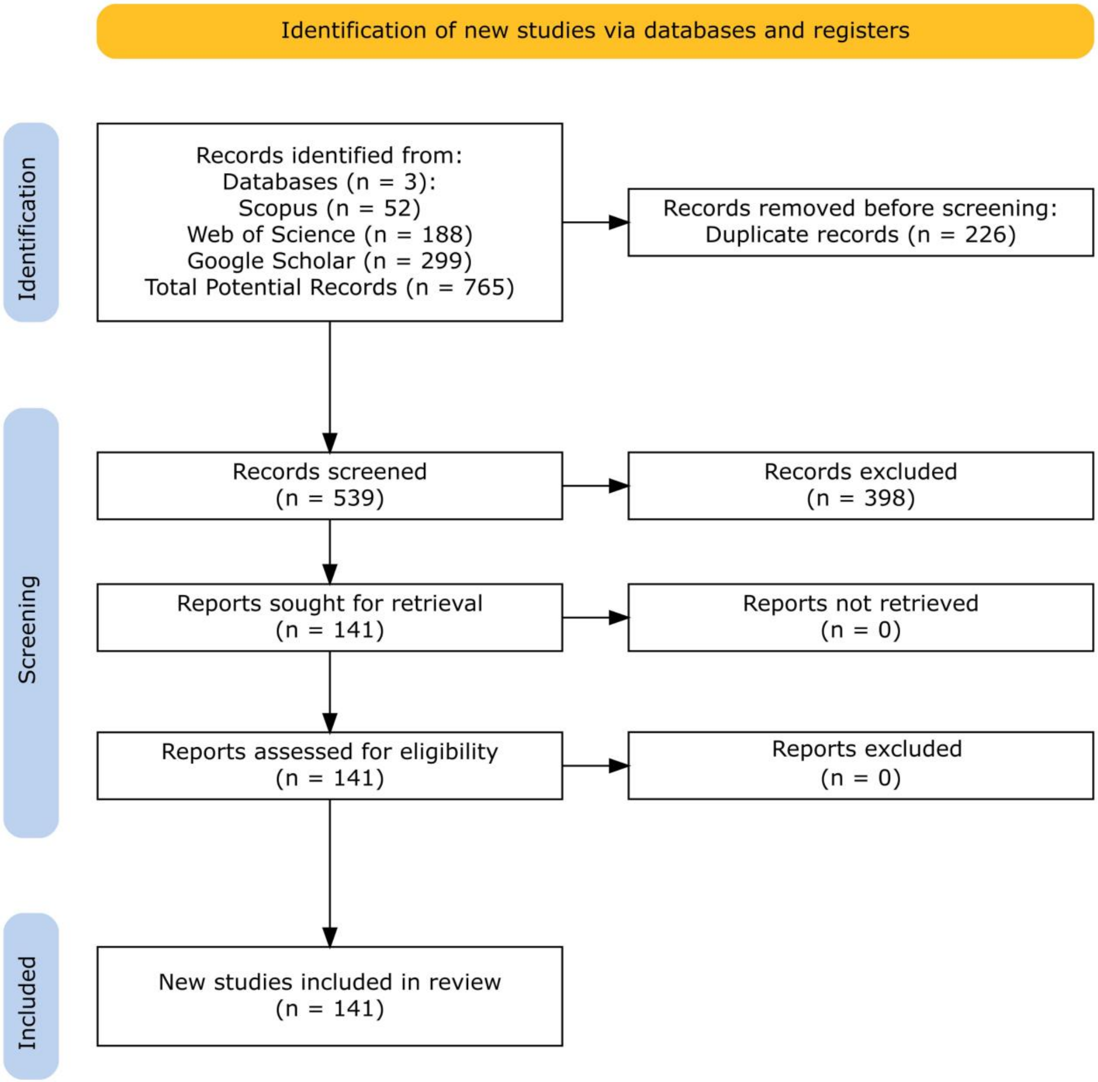

Fig. 1 PRISMA-adapted flowchart for systematic reviews (Moher et al. 2009; O'Dea et al. 2021; Haddaway et al. 2022)

Results and Discussion

A significant exponential increase was observed in the number of papers that relate leaf and wood traits to abiotic gradients, and that report the coupling and decoupling of traits during the analyzed study period (Fig. 2). Among the selected papers, more than 20,000 plant species and over 100 traits were studied in Neotropical countries (Table S2). Brazil had the highest number of papers that examined the abiotic environmental drivers and plant traits, followed by Mexico and Peru (Fig. 3).

Most of the selected papers focused on leaf traits only (n=65) or leaf traits combined with some wood traits (n=62), with a smaller number focusing merely on wood traits (n=16) (Fig. 4a). The most commonly used traits were specific leaf area and leaf Nitrogen for leaves, and wood density, vessel density and vessel diameter for wood (Fig. 4b). The most commonly studied category of traits was morphological, followed by biochemical and ecophysiological ones, with very close values, and anatomical traits (Fig. 4c). Water availability was the most studied environmental driver to leaf and wood traits in the Neotropics, followed by elevation, soil fertility, temperature, irradiance, and temporal variation (Fig. 4d).

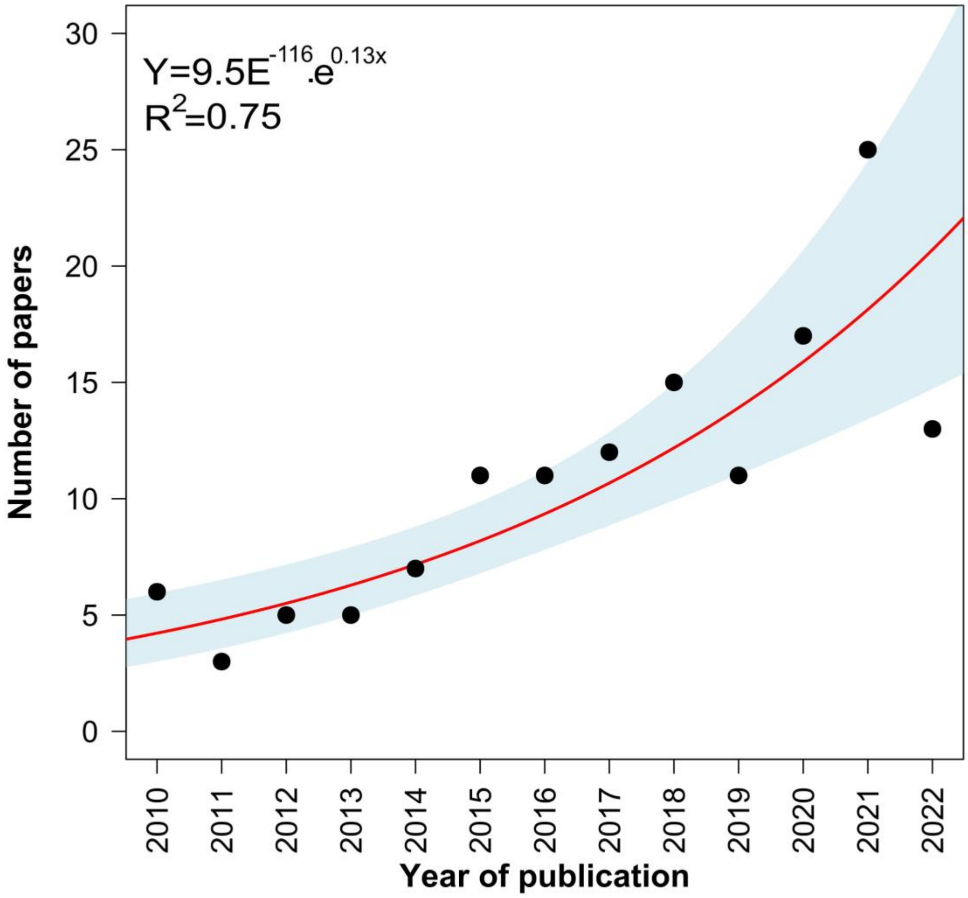

Fig. 2 Correlation between time (2010 to 2022) and number of papers on leaf and wood traits in abiotic gradients

Fig. 3 Map with the Neotropical region in gray following the delimitation proposed by Morrone et al. (2022), and the number of papers (in parentheses) encountered in a systematic review on leaf and wood traits by country in abiotic gradients. The sum of the number of papers passes the total number of review papers due to the fact that some studied more than one Neotropical country

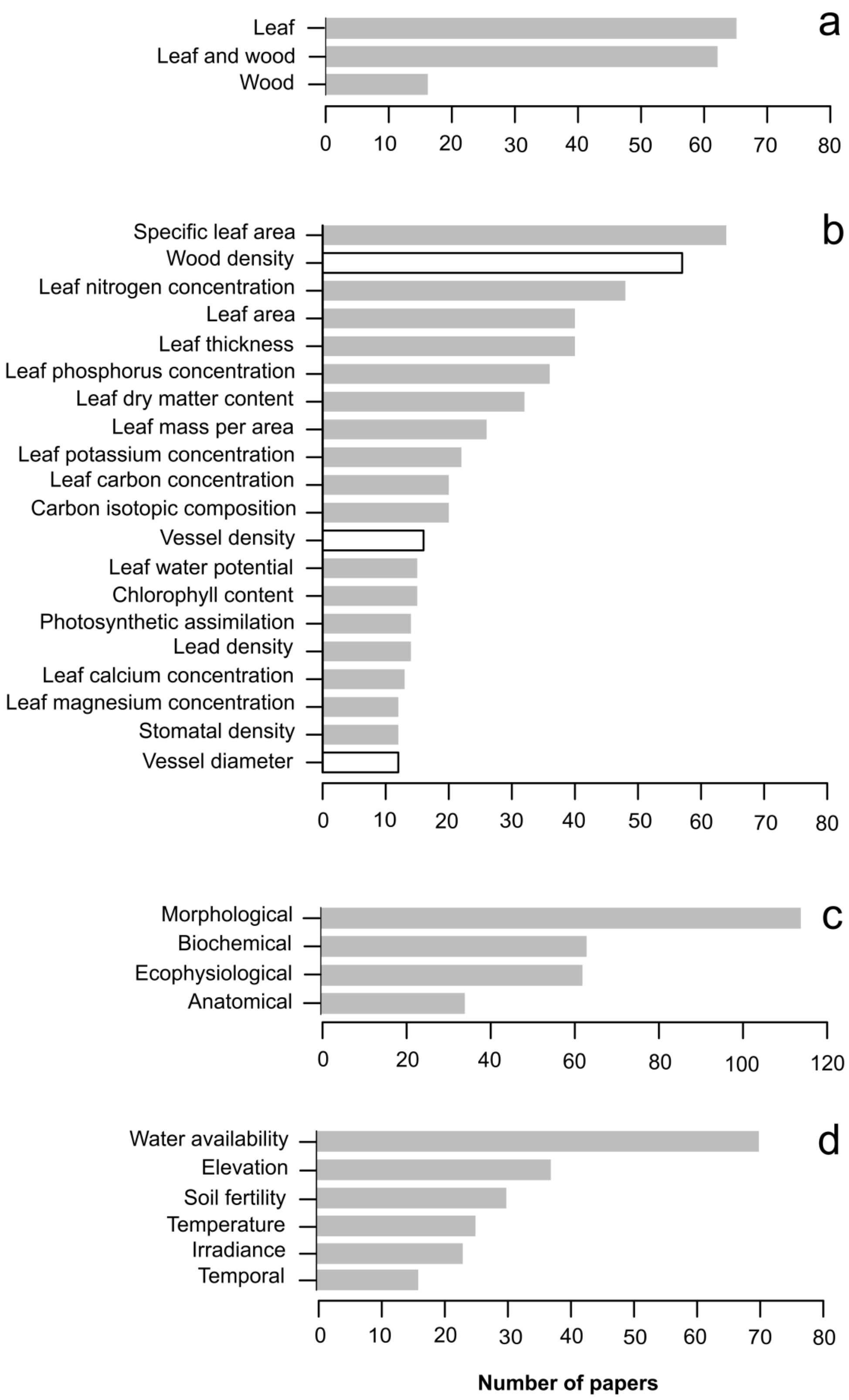

Fig. 4 Metrics of the number of Neotropical papers involving leaf and wood traits. a – organ studied; b – most frequent leaf and wood traits in the papers; c – trait category; d – most studied abiotic gradients

Environmental gradients, leaf and wood traits in Neotropical ecosystems

Environmental gradients generally constitute gradual changes of abiotic resources that are directly related to the environmental preference and sensitivity of a species and therefore its ecological niche (Garnier et al. 2016; de Bello et al. 2021). The changes can occur in only one or several abiotic resources (e.g., water availability + irradiance + temperature), altering the optimal ecophysiological limit of a species and its functional variation, as observed by the distribution of its trait values (Götzenberger et al. 2011; Garnier et al. 2016; de Bello et al. 2021). These changes also determine whether an ecological niche is wider or more reduced. Knowledge about changes in trait variability in environmental gradients allows the establishment of patterns and the ability to make predictions about the community functioning in different environmental contexts, such as those arising from forest management, fragmentation, and climate change (Campbell et al. 2016; Vitória et al. 2016; Heilmeier 2019; Tiwari et al. 2020; Teixeira et al. 2020).

Environmental gradients often involve multiple associated abiotic drivers. However, the identification of individual influences of each resource on trait variability and the composition of functional strategies plays an important role in establishing the main abiotic drivers of communities at different geographic scales (Muscarella et al. 2016, Lourenço Jr. et al. 2022). The variation of leaf and wood traits related to water availability, irradiance, temperature, soil fertility, and elevation gradients are presented below.

Water availability gradient

Water availability is one of the principal limiting resources for shrub-tree species (Padilla and Pugnaire 2007; Rowland et al. 2015). In the Neotropics, the most extensively studied leaf and wood traits in response to the water availability gradient (precipitation, vapor pressure deficit, and air and soil humidity) are morphological (leaf area, specific leaf area, leaf thickness) and anatomical (related to water transport in wood, mechanical support, and wood density) (Table S3).

In the case of wood density, there is no consensus regarding the increase or decrease in the values of this trait as a function of a decrease in water availability (Table S3). This may be related to the lack of agreement between the main anatomical bases that influence wood density, since different anatomical configuration of the xylem (vessel-fiber-parenchyma relationships), for example, are possible for a given wood density in conditions of high water availability (Zieminska et al. 2013, 2015). However, the majority of the studies that presented higher wood density values were carried out comparing two or more arid and seasonal environments (Table S3). An explanation for higher values of wood density in humid locations is related to access to soil water and nutrients, competition for irradiance among tree and shrub species, and increased longevity and resistance to the invasion and deterioration of wood due to pathogens (Lohbeck et al. 2015; van der Sande et al. 2016; Lourenço Jr. et al. 2021).

The majority of leaf trait studies report increased leaf area, specific leaf area, leaf N and P, and reduced water use efficiency, $\delta^{13}C$, and leaf thickness under conditions of increased water availability (Fig. 5 and Table S3). In more humid locations, where plants do not need to store or limit water use, high leaf and specific leaf areas can provide plant advantages, such as enhanced interception of irradiance, water and nutrient absorption from soil, and photosynthetic assimilation (Araújo et al. 2021a). In the same way, higher leaf N and P values are essential for photosynthetic processes. While acting as a structural component of chlorophyll and photosynthetic enzymes, N is related to the most photosynthetic capacity, and P ensures adequate energy transfer during photosynthetic reactions. In addition, the greater availability of moisture, N and P in soil allows plants to accumulate more N and P in their leaves, ensuring the maintenance of photosynthetic processes (Fortunel et al. 2014; van der Sande et al. 2016; Cássia-Silva et al. 2017; Maracahipes et al. 2018; Nascimento et al. 2020). The reduced water use efficiency and $\delta^{13}C$ of plants in locations with little water restriction indicate the low limitation of stomatal conductance, which decreases CO_2 input resistance, increasing the discrimination of ^{13}C (Farquhar and Richards 1984; Vitória et al. 2016, 2018). For its part, low leaf thickness in humid environments facilitates gas exchange, while the investment in high leaf surface area allows the increased interception of irradiance, an important part of photosynthesis (Melo Junior and Boeger 2015; Maya-García et al. 2020). In locations with greater water restriction, species exhibited different levels of xeromorphism, with traits that prevent excessive water loss, such as greater leaf thickness; traits that favor water conservation and nutrient retention, such as high leaf succulence; and traits that favor greater water use efficiency, such as greater stomatal control (Cássia-Silva et al. 2017; Maracahipes et al. 2018; Pireda et al. 2019; Ariano et al. 2022).

In general, these results suggest that Neotropics species exhibit water strategies promoting resistance, tolerance, and drought avoidance that ensure water transport efficiency and safety through habitat differentiation and specialization (Aguilar-Romero et al. 2017; Araújo et al. 2021a; Arenas-Navarro et al. 2021; Lourenço Jr. et al. 2022). Thus, the water strategies observed for mitigating the effects of water restriction, were crucial in preventing and repairing embolisms, as well as in structural strengthening related to hydraulic architecture, among other strategies (Araújo et al. 2021a; Arenas-Navarro et al. 2021; Macieira et al. 2021; Lourenço Jr. et al. 2022).

Another associated environmental driver that can lead to differences of water availability in plants is chronic exposure to wind, which can cause a drying effect and influence plant traits ranging from individual organs to the whole-plant (Gardiner et al. 2016; Zhang et al. 2021). Depending on the intensity of wind exposure, water restriction can cause changes in the leaf boundary layer, consequently affecting photosynthesis and transpiration traits (Anten et al. 2010; Onoda and Anten 2011). In addition to the drying effect, exposure to wind can also induce mechanical effects (touching, rubbing, flexing, breakage), triggering plant responses such as decreased stem, branch, and petiole height and diameter, increased stem, branch, and root wood density, decreased leaf number and area, increased leaf and petiole thickness, favoring leaf shedding, tearing or curling, and promote the formation of flexure and reaction wood to avoid breakage (Anten et al. 2010; Gardiner et al. 2016; Zhang et al. 2021). However, while the effects of chronic wind exposure (unlike exposure to extreme events such as tornadoes and hurricanes) on plant ecophysiological responses are scarce in Neotropical region, they occur more frequently in temperate zones (Gardiner et al. 2016; Momberg et al. 2021; Zhang et al. 2021). Future studies designed to elucidate the effects of wind exposure effects on functional trait variation and its interaction with other environmental gradients are needed.

Against a backdrop of climate change for tropical forests in South America, an increase in the frequency, intensity, and unpredictability of abiotic conditions is forecasted for the coming decades, including an increase in the number and intensity of droughts and the occurrence of intense and irregular precipitation (IPCC 2023). These changes may negatively affect species’ fitness, causing species mortality, for example, due to hydraulic failure in environments affected by more severe droughts (Rowland et al. 2015; Adams et al. 2017; McDowell et al. 2018). Therefore, those species possessing both wood and leaf traits that guarantee hydraulic resistance will have a competitive advantage over those that do not have enough mechanisms for dealing with water restriction (Allen et al. 2017; Menezes-Silva et al. 2019; Chaturvedi et al. 2020). Species that do not yet possess the sets of traits capable of ensuring their survival should be able to acclimate or adapt to new conditions through trait variation or coupling (Matesanz et al. 2010; Ahrens et al. 2019; Stotz et al. 2021). This is essential for adjustments needed for survival to be effectively carried out. Plastic responses to environmental variation are observed at many levels (cells, organs, whole-plant, ecosystems) (Vitória et al. 2019; Tiwari et al. 2020; Schneider 2022). From the perspective of leaf and wood traits, trait variation (phenotypic plasticity) has been extensively documented (Vitória et al. 2019; Stotz et al. 2021; Schneider 2022). While in most reports this trait variation enabled individuals to adapt to new conditions, in some cases, the cost associated with these changes led to increased mortality (Vieira et al. 2021). The coupling of traits as a survival strategy will be discussed in section 3.

Irradiance gradient

Irradiance is another limiting resource that affects the growth and survival of plants (Rabelo et al. 2013; Teixeira et al. 2015, 2018; Vitória et al. 2016, 2019). Its availability and dynamics in the Neotropics vary in quality, intensity, and duration (Rabelo et al. 2013; Silveira et al. 2015; Vitória et al. 2019). It is associated with spatial and temporal variations, most notably in both deciduous and semideciduous ecosystems located farther from the equator (Rabelo et al. 2013; Rossatto et al. 2013; Rosado and Mattos 2010, 2016) and in forest ecosystems due to vegetation stratification and canopy structuring (Silveira et al. 2015). In more open Neotropical ecosystems such as *Cerrado*, *Caatinga*, *restingas*, and *Llanos*, light conditions can vary less than in forest formations. In open environments, traits are more related to photoprotection, acclimation, or adaptation to high irradiance and avoidance of water loss, such as greater thickening of the leaf blade and cuticle, and stomatal density (Table S4). In contrast, in forest ecosystems, leaf traits exhibit more phenotypic plasticity as a means for optimizing the use of the light resource based on the individual position in the vertical profile of the forest (Domingues et al. 2005; Silveira et al. 2015), the natural forest dynamics (clearings, openings, forest edge), or due to anthropogenic causes (forest management, selective logging, restoration) (Rabelo et al. 2013; Campbell et al. 2016; Vitória et al. 2016, 2019; Costa et al. 2020a).

Cloud cover is an environmental driver that can influence irradiance properties (quality, intensity, duration) reaching canopy and understorey tree leaves in tropical forests (Wagner et al. 2016; Berry and Goldsmith 2019). Increased cloud cover can reduce the availability of total and direct irradiance while increasing diffuse irradiance (Graham et al. 2003; Wagner et al. 2016). Additionally, higher cloud cover is associated with increased precipitation and higher elevation, exhibiting a seasonal distribution in tropical forests and exposing plants to periods of cloudy conditions (Wagner et al. 2016; Berry and Goldsmith 2019; Muller-Landau et al. 2020). This distribution of clouds can impact plant traits, especially those related to primary responses to irradiance, such as leaf traits (Graham et al. 2003; Martin et al. 2020). For example, photosynthesis may be limited during the rainy season due to increased cloud cover and higher precipitation (Graham et al. 2003; Berry and Goldsmith 2019). Despite this, while studies considering the influence of cloud cover on plant responses in different environmental contexts in the neotropical region remain scarce, they seem to constitute an emerging field of inquiry, especially in the context of climate change (Kanniah et al. 2012)

Among the most studied traits in response to the irradiance gradient in the Neotropics are morphological leaf traits, such as specific leaf area and leaf thickness, anatomical traits, such as palisade and spongy parenchyma thickness, and stomatal density in addition to ecophysiological traits, such as concentration of photosynthetic pigments, stomatal conductance, transpiration rate, and photosynthetic assimilation (Table S4). Few wood traits related to irradiance variation were studied in the Neotropics (Table S4). However, studies on wood traits involving the irradiance gradient were associated with other resources, such as water availability and temperature (Campbell et al. 2016; Costa et al. 2020a; Borges et al. 2018; Hofhansl et al. 2021; Garcia et al. 2022).

In general, low irradiance can limit the photosynthetic apparatus and C uptake, although it reduce costs associated with photoinhibition (Bedetti et al. 2011; Silveira and Oliveira 2013; Vieira et al. 2015; Silva et al. 2019; Vieira et al. 2021). The principal morpho-anatomical adjustments described for leaf traits in response to low irradiance in the Neotropics are increased leaf area and specific leaf area, lower leaf thickness and stomatal density (Fig. 5 and Table S4) (Vitória et al. 2016; Borges et al. 2018; Maracahipes et al. 2018; Pireda et al. 2019; Zonta et al. 2021). At the opposite extreme, ecosystems with high irradiance have been associated with individuals with higher values of leaf thickness and stomatal density and lower values of specific leaf area (Fig. 5 and Table S4). Together these traits are related to the maximization of light absorption and C fixation, promoting high photosynthetic performance (Rabelo et al. 2013; Melo Junior and Boeger 2015; Maracahipes et al. 2018; Pireda et al. 2019). Increased leaf thickness promotes the penetration and diffusion of direct light optimizing photosynthetic processes (Rabelo et al. 2013; Silveira et al. 2015; Melo Junior and Boeger 2015; Pireda et al. 2019), while high stomatal density more efficiently controls stomatal conductance and, consequently, excessive water loss (Melo Junior and Boeger 2015). On the other hand, high irradiance can damage the functioning of the photosynthetic apparatus through photoinhibition or photodamage, especially when associated with additional environmental drivers, such as soil water deficit and high vapor pressure deficit (VPD), which are commonly observed (Vitória et al. 2016; Silva et al. 2019).

Despite some contradictory results, the majority of studies have found that photoprotection and photoacclimation of individuals increases as the irradiance gradient increases. These changes aim to preserve the photosystem II (PSII) through the reflection of sunlight to prevent leaf overheating, the morpho-anatomical plasticity of leaf traits, such as greater parenchyma thicknening, and investment in more conservative traits, such as lower specific leaf area (Rabelo et al. 2013; Silveira et al. 2015; Silva et al. 2019; Zonta et al. 2021). In addition, strategies associated with drought avoidance and tolerance were reported, due to the fact that high irradiance conditions frequently occur simultaneously with high temperatures and water restriction. High photosynthetic performance under such conditions requires efficient use in water absorption and conservation (Lebrija-Tejos et al. 2010; Rabelo et al. 2013). In general, leaf and wood traits results regarding irradiance variation suggest a strong competitive capacity, manifested by differences among successional stages, leaf ontogenetic stages (young and mature), or by canopy stratification (Rabelo et al. 2013; Silveira et al. 2015; Vitória et al. 2016). The interspecific variation of leaf traits under the same environmental condition also suggests that in addition to the environment influence, responses to irradiance can also be species-specific (Rabelo et al. 2013; Melo Junior and Boeger 2015; Vitória et al. 2016; Vieira et al. 2021).

Temperature gradient

In the Neotropics, the majority of trait studies focused on the effect of the thermic gradient presented morphological and ecophysiological leaf traits related to high temperature tolerance (Table S5). However, fewer studies assessing the temperature gradient were encountered in comparison with those related to water and irradiance gradients. Thus, while temperature was not the central focus for some of the studies included in this section, its effect could be indirectly estimated based on the variation of other resources, most notably irradiance and elevation (Table S5) (Pireda et al. 2019; Homeier et al. 2021; Báez et al. 2022).

The temporal and spatial temperature gradients observed in the Neotropics modulate the expression of traits, especially leaf traits. Daily temperature variations are most pronounced near the poles and diminish the closer one gets to the equator, the latitude at which the lowest variation between diurnal and nocturnal temperatures is observed (see section 2). Seasonal temperature variation in the Neotropics also affects the performance of plants (Nievola et al. 2017), albeit in a less pronounced way than in temperate climate ecosystems.

Some leaf traits, especially ecophysiological ones, are more sensitive to temperature changes than morphological and anatomical traits due to the fact that photosynthesis and, more specifically PSII, is the principal component affected (Moles et al. 2014; Wright et al. 2017; Pérez and Feeley 2020; Araújo et al. 2021b). Resistance to high and low temperatures can vary among species, individuals, or among organs and tissues of a single individual (Larcher 2006; Perez and Feeley 2020). Heating or cooling in a given environment can create conditions that exceed the thermal limits of plants, which is determined by maximum and minimum temperatures tolerated by biological processes (Nievola et al. 2017; Tiwari et al. 2020). Depending on their intensity, duration, and synergistic effects with other environmental resources like water availability and irradiance (Nievola et al. 2017; Lambers and Oliveira 2019), high and low temperatures can negatively affect processes such as growth and photosynthesis and alter the cellular structure of plants (Nievola et al. 2017; Geange et al. 2020).

As a general rule in the Neotropics, temperature increases promote an increase in leaf dry matter content and a decrease of leaf mass per area (Table S5). The leaf mass per area (the opposite of specific leaf area) refers to the investment in C gain per leaf area unit and, depending on the resource availability, is an important trait for species distribution in some environments (Poorter et al. 2009; Reich 2014). Lower values of leaf mass per area are related to species with more acquisitive resource use strategies (Díaz et al. 2016, Fig. 5). Thus, lower leaf mass per area may be associated with an increased leaf turnover, increased deciduousness in areas with more irradiance, and more elevated temperatures (Lara-De La Cruz et al. 2020; Slot et al. 2021). Although unrelated to the studies that encountered lower leaf mass per area at high temperatures (see, however, Enquist et al. 2017), higher leaf N concentration could help explain the possible higher leaf turnover and associated deciduousness due to the fact that deciduous species generally possess higher leaf N and photosynthetic capacity (Table S5) (Enquist et al. 2017; Ribeiro et al. 2022). The higher leaf dry matter content is related to resistance to drought and high and low temperatures. In this sense, higher leaf dry matter content at higher temperatures is mainly associated with more stable nutrient and water retention and greater leaf structural reinforcement (Table S5) (Lebrija-Tejos et al. 2010; Hofhansl et al. 2021; Silva et al. 2021).

While some findings indicate thermotolerance among the species, the mechanisms underlying this strategy have yet to be fully characterized (Tiwari et al. 2020; Araújo et al. 2021b). Other studies have suggested that species thermotolerance to heat and cold is due to enhanced water conservation in leaves, high plasticity in heat dissipation capacity ensuring PSII integrity, and maintenance of the stability of photosynthetic processes as temperature changes along the gradient (Enquist et al. 2017; Salazar et al. 2018; Silva and Rossatto 2022). However, even thermotolerant species may be operating close to or at their thermal limit, and increases in air temperature, as forecast for the coming years, may put species that are incapable of adjusting to these temperature changes at risk (Tiwari et al. 2020; Araújo et al. 2021b; Silva and Rossatto 2022; IPCC 2023). In this sense, individuals inhabiting higher elevations (mountains) tend to experience low temperatures (Ramesh et al. 2023) and may be less affected by global temperature increases than lowland individuals. However, it is important to note that water restriction tends to be more pronounced at higher elevations, and small temperature increases in theses areas could have a synergistic effect with water restriction, exposing conditions that may lead to hydraulic failure. Generally, temperature gradients are associated with irradiance and elevation gradients. At higher elevations, where temperatures are usually lower, plants are exposed to cold-induced constraints (Homeier et al. 2021; Báez et al. 2022). In this context, some traits related to photosynthetic and transpiration processes or water transport may be sensitive to variations in temperature and elevation. For instance, at lower temperatures in higher elevations, plants exhibited higher leaf thickness, lower leaf area, lower leaf N concentration, and lower xylem vessel diameter (Homeier et al. 2021; Báez et al. 2022).

Further studies assessing the combined influence of environmental drivers such as temperature and elevation on leaf and wood traits are needed. Therefore, an increase of between 2 °C and 5 °C in air temperature, for example, may lead to irreversible damage to PSII functioning and even in the presence of plasticity regarding strategies for leaf cooling, such strategies may prove insufficient for ensuring a thermal safety margin (Tiwari et al. 2020; Araújo et al. 2021b). Plant thermotolerance to heat and cold depends on the thermal niche where exposition takes place for given periods of time until a limit is established whereby no metabolic interruptions occur, thereby allowing the plant to withstand increases and decreases in temperature in the harsh environment (Nievola et al. 2017).

Soil fertility gradient

Soil fertility gradients and their effects on traits are directly related to soil texture and the mobilization of macro and micronutrients in plant metabolism (Vitória et al. 2019; Delpiano et al. 2020). Changes in the availability of other abiotic resources, especially water availability and temperature, also affect soil properties, causing fertility to vary simultaneously with other resource gradient (Umaña et al. 2020; Lins et al. 2021). Nutrient concentrations, granulometry, cation exchange capacity, soil pH, and other factors can affect the ecological strategies related to the exploitation and utilization of resources by plants and be reflected in leaf and wood trait variation (Carvalho and Batalha 2013; Becknell and Powers 2014; Delpiano et al. 2020; Lins et al. 2021).

In the Neotropics, it is generally observed that more fertile soils provide higher nutrient concentrations in leaves, promoting more acquisitive trait strategies, such as higher specific leaf area, Ca, P, K, and N concentrations, among others (Fig. 5 and Table S6). In contrast, more conservative trait sets are encountered in less fertile soils (Fig. 5 and Table S6) (Asner et al. 2014a, b; Apaza-Quevedo et al. 2015; Delpiano et al. 2020; Nascimento et al. 2020; Pinto et al. 2021). In such soils, for example, species tend to invest more in leaf chemical and structural defenses, including phenols, tannins, cellulose, lignin, higher ratios of C:N (reduced N), and specific leaf mass (Table S6). This stands in contrast to more fertile soils, having a tendency to present increased concentrations of micro and macronutrients, which increases nutritional quality, the assimilation of plant CO_2, plant growth, and metabolic processes at the expense of greater vulnerability to herbivory (Table S6) (Asner et al. 2014a, b; Asner et al. 2017; Nascimento et al. 2020). In more fertile soils, although most studies suggest an increase in N and P concentrations, there may be a co-limitation of both elements (Delpiano et al. 2020), suggesting that soil nutrients may not always be coupled with leaf nutrients (Álvarez-Yépiz et al. 2017; Delpiano et al. 2020; Nascimento et al. 2020; Damasco et al. 2021).

In a study carried out in Panama involving 106 species along a soil fertility gradient and analyzing leaf and wood N, P, Mg, Ca, and K concentrations, a positive association was observed between leaf and wood nutrients. These results suggest coupling of nutrients between plant organs and between organs and soil nutrients (Heineman et al. 2016). With the exception of N, these results also showed that this coupling and distribution of nutrients between organs does not increase or decrease proportionally, since when leaf nutrient concentrations are no longer limiting photosynthesis, nutrient allocation from the wood increases (Heineman et al. 2016). In this sense, when nutrients are widely available in the environment and photosynthesis is no longer limited by leaf nutrients, plants prioritize the storage of nutrients in the wood structure as a means for ensuring the maintenance and growth of their woody structures (Heineman et al. 2016).

Greater water availability, as occurs in higher precipitation sites, can also influence the availability of other environmental drivers, such as nutrient availability. Under rainy conditions, nutrients may be leached from the system, accelerating soil nutrient loss and significantly impacting plant reponses such as productivity (Santiago et al. 2005; Raulino et al. 2020). The loss of certain soil nutrients directly affects resource availability for plants, and may potentially impact their functional traits. In tropical forests with high precipitation, for example, decreases in P, Ca, K, and Mg nutrient concentrations in canopy trees have been observed (Santiago et al. 2005). In another study, low soil nutrient concentrations, especially P, were found in two Brazilian forests (dry and humid forest), with the authors suggesting that nutrient leaching caused by frequent precipitation could be one of the reasons for the lower nutrient efficiency (Raulino et al. 2020).

Just as there is a nutritional gradient in the soil, there may also be an associated water availability gradient, since the soil structure influences the retention and transport of nutrients with water (Nascimento et al. 2020; Umaña et al. 2020; Lins et al. 2021). Under stressful conditions, nutrient availability can be used as a potential indicator of the species niche (Niklas and Christianson 2011; Lins et al. 2021). For example, under conditions of water restriction, plants tend to increase K uptake, resulting in better control over stomatal openings and osmotic modifications that ensure greater leaf water potential (Lambers and Oliveira 2019; Lins et al. 2021). Interactions with other abiotic resources, such as irradiance or species-specific responses (Melo Junior and Boeger 2015), can significantly interfere in performance, as evidenced in the results of studies investigating fertility gradients and trait variation (Table S6) (Patiño et al. 2012; Heineman et al. 2016; Delpiano et al. 2020; Lins et al. 2021). As an example, the species in a light-edaphic gradient in *restinga* environments in southern Brazil did not exhibit the same leaf area patterns, which may suggest a plastic response of the species more closely related to light than to soil fertility (Melo Junior and Boeger 2015).

Elevation gradient

Elevation has indirect effects on the selection of species related to conditions of water availability, irradiance, temperature, and soil nutrients occurring based on specific features of geographical relief (Körner 2007; Midolo et al. 2019; Hollunder et al. 2022). In the Neotropics, geological formations gave rise to locations with pronounced elevation leading to wide microclimatic variation (Hoorn et al. 2010; Hughes et al. 2013; Antonelli 2022). Species may experience more resource-restrictive scenarios at higher elevations, while at lower ones conditions are considered milder, with more fertile soils and greater water availability, among other conditions (Rosado et al. 2016; Vitória et al. 2019; Hollunder et al. 2022). Most Neotropical studies point to a strong influence of relief on the functional composition of species and on their optimal microclimate. In this sense, the patterns of variation, although diverse, suggest a functional change of more acquisitive species adapted to more humid conditions at lower elevations compared with more conservative species at higher elevations, which are adapted to tolerate cold conditions and water restriction (Fig. 5). The findings also indicate dependence on local environmental heterogeneity as a driver of species responses to elevation, as well as dominant environmental filtering at higher elevations (Hulshof et al. 2013; Apaza-Quevedo et al. 2015; Álvarez-Yépiz et al. 2017; Rosado et al. 2016; Neyret et al. 2016; Vitória et al. 2019; Schmitt et al. 2020; Homeier et al. 2021; Báez et al. 2022; Ferrero et al. 2022; Giraldo-Kalil et al. 2022).

In the Neotropics, trait expression in relation to elevation gradients is quite diverse (Table S7). In some cases the highest or lowest significant values were found only at one elevation extreme (Table S7) (Bosio et al. 2010; Pereira et al. 2022). In others, higher or lower leaf and wood trait values were encountered at intermediate elevations of the gradient (Table S7) (Bosio et al. 2010; Jiménez-Noriega et al. 2017; Martin et al. 2020). Some leaf traits, such as $\delta^{13}C$, venation and trichome density, showed higher values at higher or lower elevations, but did not present a consistent pattern of increase or decrease as a function of the elevation gradient (Table S7) (Lins et al. 2016; Pereira et al. 2022).

In general, the majority of traits studied in the Neotropical elevation gradient mostly involved leaf traits such as leaf mass per area, leaf N concentration, leaf area, and specific leaf area, with a few papers investigating wood traits, most notably vessel element diameter (Table S7). Higher values of leaf mass per area and leaf thickness, and lower values of specific leaf area, leaf area, leaf N, and vessel element diameter were reported at higher elevations (Fig. 5 and Table S7). The highest leaf mass per area and the lowest values for leaf area and specific leaf area are related to maximizing the retention of available nutrients and minimizing water loss, as well as protection from solar radiation (Apaza-Quevedo et al. 2015; Rosado et al. 2016; Neyret et al. 2016; Ochoa-Beltrán et al. 2021; Báez et al. 2022; Ferrero et al. 2022). The lowest values of N and the highest values of leaf mass per area may represent a trade-off related to nutrient conservation and stress tolerance at high elevation at the expense of photosynthetic maximization (Asner et al. 2014a, b; Asner et al. 2017; Martin et al. 2020). The reduced diameter of vessel elements is directly related to protection against embolism induced by freezing and conditions of water restriction at higher elevations (Bosio et al. 2010; Jiménez-Noriega et al. 2017; Báez et al. 2022).

It is important to note that the elevation gradient occurs because other associated gradients, such as temperature and soil fertility gradients are involved. As elevation and temperature change, the availability of certain nutrients, such as N and P, may change and not follow the same pattern. For example, at higher elevations where lower temperatures and soil fertility are expected, it is postulated that there is a limitation of N, while at lower elevations where the opposite temperatures and soil fertility patterns are expected, P may be limiting (Vitousek and Sanford 1986; Fisher et al. 2013). However, based on our results for the neotropical region, this pattern may not hold in some cases (Table S7; Asner et al. 2014ab; Asner et al. 2017; Martin et al. 2020; Peng et al. 2020; Homeier et al. 2021; Báez et al. 2022; Giraldo-Kalil et al. 2022). These findings add greater complexity when evaluating environmental gradients and their interactions in trait selection, as not all nutrients follow the same pattern of higher fertility concerning these environmental drivers.

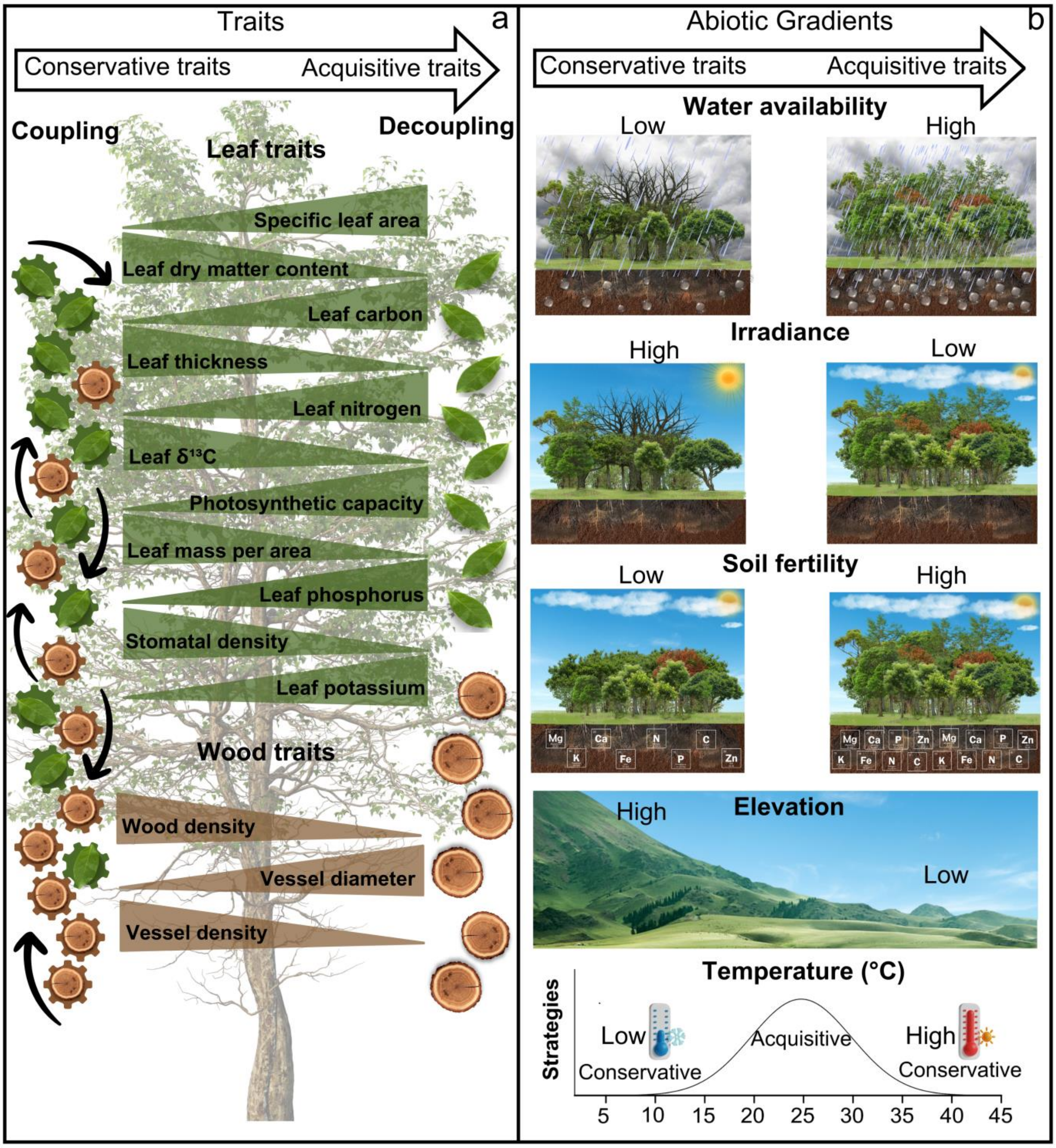

Fig. 5 Relationship of the resource use strategy (conservative or acquisitive) with the expression of leaf and wood traits in Neotropical abiotic gradients. a – trait variation, coupling and decoupling of leaf and wood traits according to the resource use strategy; b – resource use strategy and trait variation in the main abiotic gradients studied

Temporal resource variation

Temporal variation in resource availability, whether daily or seasonal, is linked to both intra- and interannual changes in water availability, irradiance, and temperature (Tonkin et al. 2017; White and Hastings 2020). In the Neotropics, dry season length can vary between 5 and 9 months, with median accumulated precipitation between 50 and 600 mm, with the exception of the Amazon region (600 to 1500 mm), while the wet season length varies between 3 to 6 months, with median accumulated precipitation between 400 and more than 2000 mm (Bombardi et al. 2019). Regarding temperature and irradiance, seasonality tends to increase the farther one moves from the equatorial line (Hajek and Knapp 2021). The transition between the dry and wet seasons can occur gradually and has important effects on plant traits and metabolic processes (Rosado and Mattos 2007; Hasselquist et al. 2010; Kumar et al. 2021; Ribeiro et al. 2022). In general, daily temperatures and irradiance levels increase at dawn and decrease at dusk, reaching the greatest amplitude at midday (De Frenne et al. 2021; Oravec and Greenham 2022). However, latitude, seasonality, and vegetation cover can influence how these two abiotic drivers reach the Earth's surface and influence plant responses (De Frenne et al. 2021; Oravec and Greenham 2022).

While few studies investigating leaf and wood trait responses to seasonal variation in the Neotropics were found during the period analyzed (2010-2022), certain trends were observed, especially for leaf traits (Table S8). In the dry season, the species showed lower water potential and stomatal conductance along with greater water use efficiency; the opposite was true for the wet season (Table S8) (Gotsch et al. 2010; Rosado and Mattos 2010, 2016; Lage-Pinto et al. 2012; Rossatto et al. 2013; Fontes et al. 2018; Garcia et al. 2021). The consistent observation of these variations by many authors and in different locations reinforces the idea of how physiological traits exhibit plasticity in response to environmental variations, such as seasonal resource availability. This physiological capacity for environmental adjustment to optimize water absorption and restrict water loss is shared among several species (Bongers et al. 2017; Vitória et al. 2019). However, many species do not employ this physiological strategy and appear to be less plastic or use other mechanisms, such as morphological adjustments (Vieira et al. 2021). The plasticity or trait variation related to water status control has proven to be a crucial mechanism for the survival of individuals in natural environments (Bongers et al. 2017), particularly when subjected to seasonal resource variation. When under conditions of water restriction (in the soil or air), plants are less able to maintain an adequate water balance, as reflected in lower values of leaf water potential (Rosado and Mattos 2010, 2016; Rossatto et al. 2013). However, lower stomatal conductance may allow more effective water potential maintenance (Silva et al. 2010). This is because the lower stomatal conductance increases resistance of CO_2 uptake to prevent excessive water loss through transpiration, since the atmospheric evaporative demand is higher during the dry period (Lage-Pinto et al. 2012; Rossatto et al. 2013; Garcia et al. 2021). During the dry season some species may thus increase water use efficiency and become more enriched in ^{13}C due to lower resistance to CO_2 uptake (Lage-Pinto et al. 2012; Rossatto et al. 2013).

During periods of drought, with increased leaf fall in deciduous and semi-deciduous ecosystems, photoacclimative adjustments such as photoprotection through heat dissipation and reflection (Gotsch et al. 2010; Rossatto et al. 2013; Costa et al. 2020b), changes in photosynthetic pigment composition (Silva et al. 2010; Lage-Pinto et al. 2012), reductions in photosynthetic activity (Silva et al 2010; Lage-Pinto et al. 2012; Rossatto et al. 2013), and morphophysiological changes pertaining to drought tolerance designed to avoid cavitation and photoinhibition are generally reported (Gotsch et al. 2010; Silva et al. 2010; Rosado and Mattos 2010, 2016; Lage-Pinto et al. 2012; Rossatto et al. 2013; Costa et al. 2020b).

For some species, traits that did not exhibit seasonal variation patterns, such as F_v/F_m and Ψ_{leaf}, were compensated by other traits or environmental conditions, such as the accumulation of photosynthetic pigments and milder conditions during dry periods, including the number of overcast days and water availability in the soil (Silva et al. 2010; Rosado and Mattos 2010, 2016). The results also show great interspecific variation, as some species are considered more photosynthetically efficient, faster to recover from stress, more susceptible to stress, or less stressed than others (Rosado and Mattos 2010, 2016; Fontes et al. 2018).

Coupling and decoupling of leaf and wood traits

From a multivariate perspective, sets of traits from one or more organs and their interactions can be highly related and interdependent or vary independently from each other (Flores-Moreno et al. 2019). These interactions are directly related to resource variation and environmental conditions (Baraloto et al. 2010; Méndez-Alonzo et al. 2012; Flores-Moreno et al. 2019). In Neotropical ecosystems with high resource availability and low seasonal variation (e.g., rainforests), species exhibit traits or organs that vary more independently or in a decoupled manner (Table 1 and S9) (Baraloto et al. 2010; Fortunel et al. 2012; Silva et al. 2015; Braga et al. 2016; Vleminckx et al. 2021; Garcia et al. 2022). This decoupling between leaf and wood under less restrictive environmental conditions has been reported in other regions of the world (Table 1 and S9) (Jager et al. 2015; Valverde-Barrantes et al. 2015; Wang et al. 2017). Such decoupling occurs because less restrictive conditions allow alternative trait sets and ecological strategies, while emphasizing different selective environmental pressures on plant organs, such as soil heterogeneity and precipitation (Baraloto et al. 2010; Fortunel et al. 2012; Silva et al. 2015; Braga et al. 2016; Vleminckx et al. 2021; Garcia et al. 2022).

In contrast, in more severe and abiotically restricted Neotropical ecosystems (e.g., dry forests, savannas, *Caatinga*), species tend to exhibit leaf and wood traits that covary in a coupled manner, even though in some cases this coupling may be weak (Table 1 and S9) (Méndez-Alonzo et al. 2012; Muscarella et al. 2016; Zeballos et al. 2017; Silva et al. 2018; Fagundes et al. 2022). In other biogeographic regions, coupling between organs under more restrictive conditions at different stages, and in different species life forms has also been documented (Table 1 and S9) (Freschet et al. 2010; Laughlin et al. 2010; Pérez-Ramos et al. 2012; Vinya et al. 2012; Fu et al. 2012; Pivovaroff et al. 2014; De la Riva et al. 2016).

Coupling between leaves and wood has mainly been related to water properties and linked to water balance in periods of water restriction, as evidenced by the relationships between phenological and hydraulic traits and with the trade-offs between water efficiency, safety, and acquisitive and conservative strategies (Fig. 5) (Méndez-Alonzo et al. 2012; Muscarella et al. 2016; Zeballos et al. 2017; Fagundes et al. 2022). However, another study carried out in a *restinga* environment in the Brazilian Atlantic forest, showed that coupling between leaf and wood is weak and may be associated with less severe characteristics of the studied *restinga* compared to other environments in which the coupling was found (Silva et al. 2018).

Coupling was observed among leaf, wood, and root traits in seedlings in a study conducted in two tropical forests in Mexico, one of which was dry and the other humid (Sanaphre-Villanueva et al. 2022). Although coupling was found, the trait sets were different in the organs studied for the two forests (Sanaphre-Villanueva et al. 2022). In addition, coupling between leaves and wood was also reported, without distinction between trait sets of two forest ecosystems in Costa Rica and Panama, one seasonal and the other humid, in a study performed with *Costus* species (Ávila-Lovera et al. 2022). In another study carried out in Panama, decoupling was found when relating leaf and wood morphological and hydraulic traits of trees and lianas in a humid evergreen forest and a seasonal dry forest (Medina-Vega et al. 2021). Leaf morphological traits related to the leaf economics spectrum in the two forests operate independently of traits of the wood economics spectrum and wood and leaf hydraulic traits, with the most pronounced decoupling in the seasonally dry forest (Medina-Vega et al. 2021).

Most of the aforementioned studies for both less and more restrictive locations show a pattern in the Neotropics that is consistent with those of other regions of the world (Table 1). In spite of this, the findings of the studies of Sanaphre-Villanueva et al. (2022), Medina-Vega et al. (2021), and Ávila-Lovera et al. (2022) contribute new insights into the environmental components involved in the selection of species traits in different life stages and growth forms. In addition, these results support the theory of environmental severity and the hypothesis that the selection of the same trait differs under different conditions (Dwyer and Laughlin 2017; Flores-Moreno et al. 2019). Recent studies also offer new perspectives regarding coupling among and within plant organs, especially by uncovering changes in the importance of relationships between traits depending on the limiting resource and new dimensions of trait variation, such as those related to root trait variation (Table S9) (Zeballos et al. 2017; Flores-Moreno et al. 2019; Ávila-Lovera et al. 2022; Sanaphre-Villanueva et al. 2022).

In this context, although not included in this review, studies involving root traits play a crucial role in investigations into the coupling of plant organs, because in some cases root traits are coupled to wood traits but decoupled from the leaf ones (Freschet et al. 2010; Fortunel et al. 2012; de la Riva et al. 2016; Li and Bao 2015;

Valverde-Barrantes et al. 2015; Wang et al. 2017; Freschet et al. 2021). This provides evidence that the pattern of coupling and decoupling of organs still does not represent a universal framework, even if only for leaf and wood traits. Therefore, some trait coupling patterns still need to be identified, especially regarding the combinations of traits that plants must prioritize depending on the environmental conditions to which they are exposed (Flores-Moreno et al. 2019).

Studies comparing coupling and decoupling of organs between less and more restrictive ecosystems were investigated to a lesser extent when compared to those that evaluate only one locality (Table 1 and S9). Since studies highlight environmental conditions as strong drivers of viable combinations between traits, comparisons between the coupling and decoupling of plant organs along abiotic gradients can offer alternative means for understanding the changes involved in the trait combinations that result in coupling and decoupling.

Table 1 Trait coupling and decoupling in Neotropical ecosystems and other biogeographical regions

	Number of papers	
	Coupling	Decoupling
Neotropical		
Tropical Dry Forests	5	0
Tropical Rainforests	0	6
Tropical Dry and Rainforests*	2	1
Subtropical Dry Forest	1	0
Some Other Biogeographical Ecossystems		
Seasonally Dry	1	0
Upland Dry and Riparian Birch Forests*	1	0
Semi-arid	1	0
Mediterranean Rangeland	1	0
Seasonally Dry Tropical Forest	1	0
Tropical Dry Forest	1	0
Chaparral - Mediterranean type	1	0
Mediterranean Forests and Shrublands*	1	0
Warm Temperate Rainforest	0	1
Deciduous Hardwood Forest	0	1
Subtropical Evergreen, Temperate Deciduous and Cold-Temperate Coniferous Forest*	0	1

Concluding remarks and future directions

There is a wide range of plant trait responses to changing environmental conditions in the Neotropics. There was an increasing number of papers found for abiotic gradients over the sampled period (2010-2022), showing evidence of the growing importance of this topic within the academic community. Most papers found on abiotic gradients were related to gradients of water availability (soil or air), and elevation, and addressed more leaf traits than wood traits. Specific leaf area and wood density were the most analyzed traits within the abiotic gradients, respectively (Fig. 4b and Tables S1-S8). Additionally, morphological traits were the most studied traits, followed by biochemical and ecophysiological ones, while anatomical traits were studied to a lesser extent. Although studies on ecophysiological traits were frequently encountered, they mostly involved leaf traits. Anatomical traits studies most often involved leaf thickening (palisade and spongy parenchymas, cuticles, and epidermis) and characteristics of vessel elements in the wood (vessel diameter and density; Tables S1-S8). The selection of certain traits (morphological, ecophysiological, biochemical, anatomical) in different environmental contexts described in this review is mostly characterized as soft traits. This is due to their easy measurement and low cost, and some of theses traits are still considered proxies of some ecological strategies (such as specific leaf area and wood density) (Wright et al. 2004; Chave et al. 2009). However, hard traits and other traits not considered in standardized protocols (e.g., chlorophyll parameters) have gaining strength and now standing out in assessments of how trait selection occurs based on specific environmental drivers (Modolo et al. 2021). Although not explicitly functional traits, the use of these traits in environmental gradients also provides an opportunity for reassessing which traits should be selected or added as functional, beyond those that have been previously established (Modolo et al. 2021).

In the Neotropics, the coupling and decoupling of leaf and wood traits have been studied more extensively within a single ecosystem than in comparisons involving multiple ecosystems, with water restriction identified as the predominant environmental driver of trait coupling. Therefore, assessing coupling and decoupling across multiple environments, contrasting environments, or abiotic gradients within a single study remains a knowledge gap to be filled. This would aid the standardization of characteristics to be studied and their sampling, making data more robust.

Although in each ecosystem one resource may be more limiting than another and abiotic gradients have been presented separately, plant responses under natural conditions take place as a result of all the environmental components simultaneously (Garnier et al. 2016; de Bello et al. 2021). Nevertheless, this investigation uncovered few studies assessing the direct effects of temperature and irradiance under natural conditions, most notably those related to temperature, where the papers tended to compare extreme temperature conditions (Tables S5).

Species displayed different mechanisms for dealing with the environmental conditions to which they were exposed in a wide range of morpho-anatomical and ecophysiological trait combinations. In general, this review found that: (1) niche differentiation was one of the main determinants of interspecific responses to the abiotic gradients studied, although a significant contribution from intraspecific variation was possible; (2) studies involving the temporal variation of resources and related plant responses remain scarce when compared to studies addressing spatial variations, a scarcity that is even more pronounced for wood traits in relation to leaf traits; (3) although most studies indicate that traits tend to be more coupled in more restrictive environments, the current literature on the coupling and decoupling of leaf and wood traits suggests that a definitive and universal framework has not yet been established for the multivariate relationships between these sets of traits (Table 1 and S9) (Medina-Vega et al. 2021; Ávila-Lovera et al. 2022; Sanaphre-Villanueva et al. 2022). These results reinforce the importance of local environmental filters for selecting traits, as seen by the species-specific results, mainly those concerning water availability, irradiance, and soil fertility gradients.

Multidimensional relationships among traits have received increasing attention in trait-based ecology in recent years, especially as they involve issues such as integration and plasticity of traits such as 1) trade-offs, 2) phenotypic integration as a key mechanism under restrictive conditions, and 3) the relationships between inter and intraspecific variation in determining correlations within the functional dimensions of traits (Diáz et al. 2016; Laughlin et al. 2017; Flores-Moreno et al. 2019; Freschet et al. 2021; Matesanz et al. 2021). These questions, however, remain controversial, especially when related to abiotic gradients. The definition and better understanding of the functionality and complexity of trait combinations in different environmental contexts represent critical milestones for the enhancement of understanding of trait selection under current climatic conditions while providing a foundation for future climate change scenarios (Laughlin et al. 2017; Helmeier 2019; IPCC 2023; Pereira et al. 2022). This will be particularly important for the Neotropics, for which extreme events are predicted (Mora et al. 2013). As a result of these environmental changes, the filters will become increasingly selective, causing changes to species´ response capacity, promoting trait sets within narrower or wider dimensional spaces depending on the environment and subjecting the species to new environmental conditions (Sterck et al. 2006; Lohbeck et al. 2015; Meir et al. 2018). Therefore, those species that possess traits that optimize their potential for survival and the capacity to tolerate new environmental conditions will have selective advantages over other species, altering the floristics and functioning of ecosystems.

Finally, future studies focusing on the interactions between functional traits and environmenral drivers should not only describe these interactions but also emphasize sharing them by strengthening collaborations among researchers from different countries and among research groups within the same country in the Neotropical region. Furthermore, the sharing of local data on traits, both the commonly used and overlooked ones, will offer researchers a more comprehensive perspective on the drivers of trait variation and covarition at local and regional scales (by comparing neotropical ecosystems) and contribute to studies on a global framework. This is one of the avenues to address gaps in trait-based ecology (and even in other areas) given the lag and underrepresentation of research and information on Neotropical ecosystems compared to other geographic regions (temperate regions) and when biomes within the Neotropical region are compared (Antonelli et al. 2018; Culumber et al. 2019; Vasconcelos 2023). Collaborations are necessary and should be prioritized due to the enormous diversity of ecosystems in the Neotropics, while improvements and information sharing through databases can promote the filling of these gaps and advance future research.

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Declarations

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Supplementary Material

Table S1 Keyword combinations in the bibliographic search databases used in this review

Fixed Keywords	Combinations
“*plant traits*”, “*functional variability*”, “*functional variation*”, “*environmental gradients*”, “*abiotic gradients*”	(1) fixed keywords AND “*neotropical forests*” OR “*tropical forests*” (2) fixed keywords AND “*phenotypic variation*” OR “*coordination*” OR “*covariation*” OR “*integration*”; (3) fixed keywords AND “*phenotypic variation*” OR “*plasticity*” (4) fixed keywords AND “*phenotypic variation*” OR “*coupling*” OR “*decoupling*” OR “*disentangling*” (5) fixed keywords AND “*intraspecific variation*” OR “*within-species variation*” (6) fixed keywords AND "*interspecific variation*” OR “*between-species variation*” (7) fixed keywords AND “*leaf trait variation*” OR “*wood trait variation*” (8) fixed keywords AND “*South America*” OR “*Central America*” (9) fixed keywords AND “*tropical dry forests*” OR “*tropical rainforests*” OR “*subtropical forests*” OR “*seasonal heath vegetation*” OR “*restinga*”

Table S2 List of studies used in the systematic review in the period of 2010-2022, detailed by year, country, number of species and traits. (-) indicates missing information. Neotropics* denotes studies conducted in more than two countries within the Neotropical region

Authors	Year	Country	N° of *spp*	N° of traits	Journal	DOI
Aguilar-Romero et al.	2017	Mexico	9	8	Tree Physiology	10.1093/treephys/tpx033
Álvarez-Yépiz et al.	2017	Mexico	4	7	Oecologia	10.1007/s00442-016-3790-3
Apaza-Quevedo et al.	2015	Bolivia	119	6	Biotropica	10.1111/btp.12232
Araújo et al.[a]	2021	Brazil	4	12	Flora	10.1016/j.flora.2021.151829
Araújo et al.[b]	2021	Brazil	4	6	Environmental Research Letters	10.1088/1748-9326/abe3b9
Arenas-Navarro et al.	2021	Mexico	21	11	AoB Plants	10.1093/aobpla/plab066
Arenas-Navarro et al.	2020	Mexico	21	9	Forests	10.3390/f11080894
Ariano et al.	2022	Brazil	7	8	Flora	10.1016/j.flora.2021.151972
Asner et al.[a]	2014	Peru	1449	21	New Phytologist	10.1111/nph.12895
Asner et al.	2017	Peru	1449	8	New Phytologist	10.1111/nph.14068
Asner et al.[b]	2014	Peru	2420	12	PNAS	10.1073/pnas.1401181111
Assunção et al.	2020	Brazil	75	8	Acta Botanica Brasilica	10.1590/0102-33062020abb0205
Ávila-Lovera et al.	2022	Costa Rica-Panama	17	19	AoB Plants	10.1093/aobpla/plab073
Báez et al.	2022	Ecuador	158	10	PLoS ONE	10.1371/journal. pone.0263508
Baraloto et al.	2010	French Guiana	668	16	Ecology Letters	10.1111/j.1461-0248.2010.01517.x
Baruch	2011	Venezuela	1	12	Acta Oecologica	10.1016/j.actao.2011.05.014
Becknell and Powers	2017	Costa Rica	87	5	Canadian Journal of Forest Research	10.1139/cjfr-2013-0331
Bedetti et al.	2011	Brazil	1	10	Australian Journal of Botany	10.1071/BT10275
Blonder et al.	2017	Peru	100	5	Ecology	10.1002/ecy.1747
Blonder et al.	2018	Peru	136	19	Journal of Ecology	10.1111/1365-2745.12945
Blundo et al.	2015	Argentina	54	10	Acta Oecologica	10.1016/j.actao.2015.09.008
Borges et al.	2018	Brazil	1	7	Australian Journal of Botany	10.1071/BT18114
Bosio et al.	2010	Brazil	1	12	IAWA Journal	10.1163/22941932-90000015
Braga et al.	2016	Brazil	9	7	Biotropica	10.1111/btp.12324
Campbell et al.	2016	Brazil	1	15	Acta Botanica Brasilica	10.1590/0102-33062015abb0267
Camps et al.	2021	Neotropics[1]	1	6	Annals of Botany	10.1093/aob/mcab034
Carvalho and Batalha	2013	Brazil	55	3	Biology Letters	10.1098/rsbl..2013.0412

Cássia-Silva et al.	2017	Brazil	40	9	Plant Ecology	10.1007/s11258-017-0765-3
Chain-Guadarrama et al.	2018	Costa Rica	257	6	Ecography	10.1111/ecog.02637
Cosme et al.	2017	Brazil	28	17	New Phytologist	10.1111/nph.14508
Costa et al.[a]	2020	Brazil	4	28	Forest Ecology and Management	10.1016/j.foreco.2020.118305
Costa et al.[b]	2020	Brazil	1	16	Revista Brasileira de Geografia	-
Damasco et al.	2021	Neotropics[2]	9	8	Scientific Reports	10.1038/s41598-021-88417-y
Dantas and Pausas	2020	Neotropics[3]	1.706	5	Global Ecology and Biogeography	10.1111/geb.13111
Delpiano et al.	2020	Chile	16	11	Plant Soil	10.1007/s11104-020-04515-2
Dória et al.	2016	Brazil	2	19	Flora	10.1016/j.flora.2016.09.002
Enquist et al.	2017	Peru	180	7	Global Ecology and Biogeography	10.1111/geb.12645
Fagundes et al.	2022	Brazil	20	16	Frontiers in Forests and Global Change	10.3389/ffgc.2022.930099
Ferrero et al.	2022	Argentina	2	7	Biological Invasions	10.1007/s10530-021-02722-1
Fontes et al.	2018	Brazil	5	6	Philosophical Transactions of Royal Society B	10.1098/rstb.2018.0209
Fortunel et al.	2019	Ecuador	467	2	Biotropica	10.1111/btp.12643
Fortunel et al.	2018	Ecuador	1047	4	Ecology	10.1002/ecy.2441
Fortunel et al.[a]	2014	French Guiana-Peru	800	15	Journal of Ecology	10.1111/1365-2745.12160
Fortunel et al.[b]	2014	French Guiana	113	15	New Phytologist	10.1111/nph.12632
Fortunel et al.	2012	French Guiana/Peru	758	14	Functional Ecology	10.1111/j.1365-2435.2012.02020.x
Garcia et al.	2021	Brazil	9	11	Oecologia	10.1007/s00442-021-04924-9
Garcia et al.	2022	Brazil	2	5	Journal of Experimental Botany	10.1093/jxb/erab432
Giraldo-Kalil et al.	2022	Mexico	4	5	American Journal of Botany	10.1002/ajb2.16056
Gotsch et al.	2010	Costa Rica	12	10	Plant Ecology	10.1007/s11258-010-9779-9
Grossiord et al.	2019	Neotropics[4]	34	3	Oecologia	10.1007/s00442-019-04513-x
Gvozdevaite et al.	2018	Brazil	89 (65)	5	Tree Physiology	10.1093/treephys/tpy117
Heineman et al.	2016	Panama	106	8	New Phytologist	10.1111/nph.13904
Hofhansl et al.	2021	Costa Rica	34	8	Ecology and Evolution	10.1002/ece3.7256
Homeier et al.	2021	Ecuador	52	12	Scientific Reports	10.1038/s41598-021-89190-8
Hulshof et al.	2013	Costa Rica	275	1	Journal of Vegetation Science	10.1111/jvs.12041
Jancoski et al.	2021	Brazil	21	6	Biotropica	10.1111/btp.13064
Jiménez-Noriega et al.	2017	Mexico	5	9	Journal of Mountain Science	10.1007/s11629-017-4442-8
Kandlikar et al.	2018	Costa Rica	97	7	Journal of Tropical Ecology	10.1017/S0266467418000172
Lage-Pinto et al.	2012	Brazil	2	17	Brazilian Journal of Plant Physiology	10.1590/S1677-04202012000200003

Lara-De La Cruz et al.	2020	Mexico	1	5	Botanical Sciences	10.17129/botsci.2449
Lebrija-Tejos et al.	2010	Mexico	31	23	Ecology	10.1890/08-1449.1
Lins et al.	2016	Brazil	107	1	Trees	10.1007/s00468-016-1368-7
Lins et al.	2021	Brazil	18	11	Rodriguesia	10.1590/2175-7860202172136
Llyod et al.	2015	Brazil-Bolivia	291	15	Biogeosciences	:10.5194/bg-12-6529-2015
Lohbeck et al.	2015	Mexico	132	11	PLoS ONE	10.1371/journal.pone.0123741
Lourenço Jr et al.	2022	Brazil	36	10	New Phytologist	10.1111/nph.17944
Lourenço Jr et al.	2021	Brazil	38	7	Ecosphere	10.1002/ecs2.3629
Macieira et al.	2021	Brazil	1	20	Ecological Indicators	10.1016/j.ecolind.2021.107798
Maracahipes et al.	2018	Brazil	284	12	Perspectives in Plant Ecology, Evolution and Systematics	10.1016/j.ppees.2018.07.006
Maréchaux et al.	2015	French Guiana	71	1	Functional Ecology	10.1111/1365-2345.12452
Martin et al.	2020	Peru	134	19	Frontiers in Plant Science	10.3389/fpls.2019.01810
Maya-García et al.	2020	Mexico-Honduras	1	7	Botanical Sciences	10.17129/botsci.2395
Medina-Vega et al	2021	Panama	16	17	Journal of Ecology	10.1111/1365-2745.13644
Melo-Junior and Boeger	2015	Brazil	3	12	Acta Biológica Colombiana	10.15446/abc.v21n1.47621
Méndez-Alonzo et al.	2012	Mexico	15	15	Ecology	10.1890/11-1213.1
Méndez-Toribio et al.	2017	Mexico	´63	12	Environmental Research Letters	10.1088/1748-9326/aa717b
Miranda et al.	2011	Brazil	5	2	Environmental and Experimental Botany	10.1016/j.envexpbot.2010.08.011
Moraes et al.	2017	Brazil	1	17	Brazilian Journal of Botany	10.1007/s40415-016-0348-x
Muscarella et al.	2019	Puerto Rico	308	2	Journal of Ecology	10.1111/1365-2745.13261
Muscarella et al.	2016	Puerto Rico	250	3	Perspectives in Plant Ecology, Evolution and Systematics	10.1016/j.ppees.2016.09.007
Nardoto et al.	2014	Neotropics[5]	> 400	1	Plant Ecology and Diversity	10.1080/17550874.2013.80752
Nascimento et al.	2020	Brazil	18	12	Plant Ecology and Diversity	10.1080/17550874.2020.1744760
Neves et al.	2017	Brazil	~95	3	Brazilian Journal of Botany	10.1007/s40415-017-0368-1
Neves et al.	2022	Brazil	48	4	Flora	10.1016/j.flora.2022.152090
Neyret et al.	2016	Peru-Brazil	256	1	Ecology and Evolution	10.1002/ece3.2281
Ochoa-Beltrán et al.	2021	Colombia	1099	6	Land	10.3390/land10101057
Oliveira et al.	2018	Brazil	28	1	New Phytologist	10.1111/nph.1546
Oliveira et al.	2020	Brazil	48	13	Science of the Total Environment	10.1016/j.scitotenv.2020.141177
Oliveira et al.	2021	Brazil	1	10	Brazilian Journal of Botany	10.1007/s40415-021-00734-8
Oliveras et al.	2020	Peru-Brasil	367	10	Frontiers in Forests and Global Change	10.3389/ffgc.2020.00018

Patiño et al.	2012	Peru	661	14	Biogeosciences	10.5194/bg-9-775-2012
Peng et al.	2020	Peru	210	6	New Phytologist	10.1111/nph.16447
Pereira et al.	2022	Brazil	1	13	Physiologia Plantarum	10.1111/ppl.13719
Pinho et al.	2019	Brazil	46	7	Basic and Applied Ecology	10.1016/j.baae.2019.08.002
Pinho et al.	2021	Neotropics[6]	3.417	8	Global Ecology and Biogeography	10.1111/geb.13309
Pinto et al.	2021	Brazil	3	9	Plant Ecology	10.1007/s11258-021-01177-7
Pireda et al.	2019	Brazil	3	30	Environmental and Experimental Botany	10.1016/j.envexpbot.2019.05.012
Poorter et al.	2021	Neotropics[7]	Undefined	7	PNAS	10.1073/pnas.2003405118
Poorter et al.	2019	Neotropics[8]	Undefined	1	Nature	10.1038/s41559-019-0882-6
Rabelo et al.	2013	Brazil	3	17	Trees	10.1007/s00468-012-0796-2
Roa-Fuentes et al.	2015	Mexico	4	6	Oecologia	10.1007/s00442-015-3354-y
Rodríguez-Ramírez et al.	2021	Mexico	2	5	Plant Ecology	10.1007/s11258-021-01138-0
Rosado and Mattos	2010	Brazil	10	15	Journal of Vegetation Science	10.1111/j.1654-1103.2009.01119.x
Rosado and Mattos	2016	Brazil	6	6	Annals of the Brazilian Academy of Sciences	10.1590/0001-3765201620150013
Rosado et al.	2015	Brazil	4	12	Trees	10.1007/s00468-015-1165-8
Rosenfield et al.	2019	Brazil	~447	3	Journal of Vegetation Science	10.1111/jvs.12787
Rossatto et al.	2013	Brazil	20	14	Trees	10.1007/s00468-013-0864-2
Salazar et al.	2018	Peru	1	11	Journal of Arid Environments	10.1016/j.jaridenv.2018.01.010
Sanaphre-Villanueva et al	2022	Mexico	95	10	PeerJ	10.7717/peerj.13458
Sánchez-Acevedo et al.	2022	Mexico	1	11	Botanical Sciences	10.17129/botsci.3001
Santiago et al.	2018	French Guiana	14	13	New Phytologist	10.1111/nph.15058
Santos et al.	2021	Brazil	1	5	Rodriguesia	10.1590/2175-7860202172077
Schmitt et al.	2020	French Guiana	5	5	Oikos	10.1111/oik.07488
Scholz et al.	2014	Costa Rica	3	16	IAWA Journal	10.1163/22941932-00000070
Silva and Rossatto	2022	Brazil	30	4	Theoretical Experimental Plant Physiology	10.1007/s40626-022-00244-2
Silva et al.	2019	Brazil	1	12	Flora	10.1016/j.flora.2019.03.003
Silva et al.	2010	Brazil	1	21	Brazilian Journal of Plant Physiology	10.1590/S1677-04202010000400004
Silva et al.	2018	Brazil	33	21	Ecology and Evolution	10.1002/ece3.3547
Silva et al.	2015	Brazil	64	7	Trees	10.1007/s00468-015-1232-1
Silva et al.[a]	2021	Brazil	2.122	7	Journal of Vegetation Science	10.1111/jvs.13049
Silva et al.	2021	Brazil	1.456	7	Plant Ecology	10.1007/ s11258-021-01169-7
Silveira and Oliveira	2013	Brazil	1	6	Brazilian Journal of Biology	10.1590/S1519-69842013000200007

Silveira et al.	2015	Brazil	57	13	Brazilian Journal of Botany	10.1007/s40415-014-0111-0
Slot et al.	2021	Panama	147	6	Plant, Cell & Environment	10.1111/pce.14060
Sonsin et al.	2012	Brazil	11	11	Botanical Journal of the Linnean Society	10.1111/j.1095-8339.2012.01282.x
Souza et al.	2015	Brazil	36	6	Annals of the Brazilian Academy of Sciences	10.1590/0001-376520150381
Souza et al.	2018	Brazil	1	10	PLoS ONE	10.1371/journal.pone.0208512
Terra et al.	2018	Brazil	Undefined	2	Journal of Plant Ecology	10.1093/jpe/rty017
Tiwari et al.	2020	Brazil	7	4	Plant, Cell & Environment	10.1111/pce.13770
Trindade et al.	2020	Brazil	11	7	Journal of Vegetation Science	10.1111/jvs.12896
Umaña and Sweson	2019	Puerto Rico	6	7	Ecology	10.1002/ecy.2745
Umaña et al.	2020	Panama	550	4	Journal of Ecology	10.1111/1365-2745.13442
van der Sande et al.	2016	Neotropics[9]	429	15	Ecological Monographs	10.1890/15-1815.1
Vitória et al.	2016	Brazil	3	17	Forest Ecology and Management	10.1016/j.foreco.2016.07.048
Vitória et al.	2019	Brazil	Undefined	21	Trees	10.1007/s00468-019-01864-z
Vitória et al.	2018	Brazil	38	5	Journal of Tropical Ecology	10.1017/S0266467418000093
Vleminckx et al.	2021	French Guiana	1467	19	Oikos	10.1111/oik.08284
Wagner et al.	2014	French Guiana	53	13	International Journal of Ecology	10.1155/2014/389409
Zeballos et al.	2017	Argentina	37	6	Austral Ecology	10.1111/aec.12455
Zonta et al.	2021	Brazil	1	3	Flora	10.1016/j.flora.2021.151806
Zorger et al.	2019	Brazil	61	5	Biotropica	10.1111/btp.12721

[1] Argentina, Bolivia, Paraguay
[2] Brazil, Colombia, French Guiana, Peru
[3] Not Specified
[4] Brazil, Costa Rica, French Guiana, Panama, Puerto Rico
[5] Bolivia, Brazil, Colombia, Ecuador, Peru, Venezuela
[6] Bolivia, Brazil, Colombia, Costa Rica, Cuba, Ecuador, French Guiana, Guatemala, Guiana, Jamaica, Nicaragua, Panama, Peru, Puerto Rico, Venezuela
[7] Bolivia, Brazil, Costa Rica, French Guiana, Mexico, Panama, Puerto Rico
[8] Bolivia, Brazil, Colombia, Costa Rica, French Guiana, Mexico, Panama, Peru, Puerto Rico, Venezuela
[9] Bolivia, Brazil, Costa Rica, French Guiana

Table S3 Leaf and wood trait variation along a water availability gradient

			Trait variation along a water gradient (from lower to higher availability)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA	Baruch 2011; Bedetti et al. 2011; Fortunel et al. 2014a; Apaza-Quevedo et al. 2015; Roa-Fuentes et al. 2015; van der Sande et al. 2016; Cássia-Silva et al. 2017; Cosme et al. 2017; Borges et al. 2018; Maracahipes et al. 2018; Souza et al. 2018; Zorger et al. 2019; Assunção et al. 2020; Dantas and Pausas 2020; Maya-García et al. 2020; Araújo et al. 2021a; Camps et al. 2021; Lourenço Jr. et al. 2021; Báez et al. 2022; Ferrero et al. 2022	Gotsch et al. 2010; Lohbeck et al. 2015; van der Sande et al. 2016; Chain-Guadarrama et al. 2018; Damasco et al. 2021; Sánchez-Acevedo et al. 2022; Homeier et al. 2021	Oliveira et al. 2020; Trindade et al. 2020; Poorter et al.2021
	Leaf Mass per Area	LMA	Umaña et al. 2020; Oliveira et al. 2021; Garcia et al. 2022	Muscarella et al. 2016; Nascimento et al. 2020; Schmitt et al. 2020	Moraes et al. 2017; Salazar et al. 2018; Grossiord et al. 2019; Muscarella et al. 2019
	Leaf Area	LA	Bedetti et al. 2011; Fortunel et al. 2014a; Apaza-Quevedo et al. 2015; van der Sande et al. 2016; Borges et al. 2018; Chain-Guadarrama et al. 2018; Rosenfield et al. 2019; Zorger et al. 2019; Pireda et al. 2019; Assunção et al. 2020; Nascimento et al. 2020; Schmitt et al. 2020; Pinho et al. 2021; Ferrero et al. 2022	Umaña et al. 2020	Lara-De La Cruz et al. 2020; Hofhansl et al. 2021; Homeier et al. 2021
	Leaf Dry Matter Content	LDMC	Lohbeck et al. 2015; van der Sande et al. 2016; Chain-Guadarrama et al. 2018; Pinho et al. 2019; Homeier et al. 2021	Aguilar-Romero et al. 2017; Rosenfield et al. 2019; Pinho et al. 2021	Roa-Fuentes et al. 2015; Salazar et al. 2018; Zorger et al. 2019; Trindade et al. 2020

Leaf Density	DEN	Wagner et al. 2014; Moraes et al. 2017	Santos et al. 2021	Fortunel et al. 2014a
Leaf Succulence	SUC		Moraes et al. 2017; Pireda et al. 2019; Assunção et al. 2020; Santos et al. 2021	
Leaf Toughness	Ltough	Homeier et al. 2021	Fortunel et al. 2014a; Wagner et al. 2014; Schmitt et al. 2020	
Leaf Width	LW			Camps et al. 2011
Leaf Length	LL			Camps et al. 2011
Leaf Length:Leaf Width Ratio	LL:LW		Maya-García et al. 2020	
Leaf Size	LS	Poorter et al. 2021; Sánchez-Acevedo et al. 2022		
Force to Punch	FP	van der Sande et al. 2016		
Petiole Width	PW		Sánchez-Acevedo et al. 2022	
Petiole Length	PL		Lohbeck et al. 2015	Maya-García et al. 2020; Araújo et al. 2021a; Assunção et al. 2021; Camps et al. 2021
Specific Length of the Petiole	SLP	Souza et al. 2018		
Number of Secondary Veins	NSV	Sánchez-Acevedo et al. 2022		
Venation Density	LVDen		Pireda et al. 2019	
Water Use Efficiency	WUE_i, WUE		Craven et al. 2013; Aguilar-Romero et al. 2017	Baruch et al. 2011; Moraes et al. 2017; Salazar et al. 2018; Oliveira et al. 2021
Carbon Isotopic Composition	$\delta^{13}C$		Baruch et al. 2011; Lloyd et al. 2015; Vitória et al. 2018; Pireda et al. 2019; Damasco et al. 2021	Fortunel et al. 2014a; Wagner et al. 2014
Leaf Water Potential	Ψ_{pd}, Ψ_{md}	Gotsch et al. 2010; Moraes et al. 2017	Moraes et al. 2017; Santos et al. 2021; Neves et al. 2022	Aguilar-Romero et al. 2017; Miranda et al. 2011; Neves et al. 2017
Leaf Turgor Loss Point	π_{tlp}	Maréchaux et al. 2015		

Leaf Water Mass Content	LWC		Araújo et al. 2021a	Salazar er al. 2018
Leaf Phosphorus Concentration	P_{mass}, P_{area}	Fortunel et al. 2014a; van der Sande et al. 2016; Chain-Guadarrama et al. 2018; Maracahipes et al. 2018; Nascimento et al. 2020	Lloyd et al. 2015; Roa-Fuentes et al. 2015; van der Sande et al. 2016; Chain-Guadarrama et al. 2018; Assunção et al. 2020	Wagner et al. 2014; Lloyd et al. 2015; Assunção et al. 2020; Hofhansl et al. 2021; Homeier et al. 2021
Leaf Nitrogen Concentration	N_{mass}, N_{area}	Fortunel et al. 2014a; Wagner et al. 2014; Apaza-Quevedo et al. 2015; van der Sande et al. 2016; Cássia-Silva et al. 2017; Chain-Guadarrama et al. 2018; Maracahipes et al. 2018; Vitória et al. 2018; Nascimento et al. 2020; Hofhansl et al. 2021	Lloyd et al. 2015; Roa-Fuentes et al. 2015; van der Sande et al. 2016; Chain-Guadarrama et al. 2018; Assunção et al. 2020; Damasco et al. 2021; Homeier et al. 2021	Salazar et al. 2018; Poorter et al. 2021
Leaf Potassium Concentration	K_{mass}, K_{area}	Fortunel et al. 2014a; Maracahipes et al. 2018	Lloyd et al. 2015	Souza et al. 2019
Leaf Calcium Concentration	Ca_{mass}, Ca_{area}	Maracahipes et al. 2018	Nascimento et al. 2020; Homeier et al. 2021	Lloyd et al. 2015
Leaf Magnesium Concentration	Mg_{mass}, Mg_{area}	Maracahipes et al. 2018		Lloyd et al. 2015; Homeier et al. 2021
Leaf Carbon Concentration	C	Gotsch et al. 2010	Fortunel et al. 2014a; Cássia-Silva et al. 2017; Maracahipes et al. 2018; Vitória et al. 2018	Apaza-Quevedo et al. 2015; Lloyd et al. 2015; Salazar et al. 2018
Leaf Aluminum Concentration	Al			Homeier et al. 2021
Leaf Carbon:Nitrogen Ratio	C:N		Fortunel et al. 2014a; Wagner et al. 2014; Apaza-Quevedo et al. 2015; Vitória et al. 2018; Nascimento et al. 2020	Baruch et al. 2011
Leaf Nitrogen:Phosphorus Ratio	N:P		Homeier et al. 2021	
Nitrogen Isotopic Composition	$\delta^{15}N$	Vitória et al. 2018; Pireda et al. 2019	Nardoto et al. 2014; Roa-Fuentes et al. 2015	
Trichome Density	TD	Sánchez-Acevedo et al. 2022	Bedetti et al. 2011; Araújo et	

			al. 2021a; Ariano et al. 2022	
Stomatal Density	SD	Ariano et al. 2022	Pireda et al. 2019	Apaza-Quevedo et al. 2015; Salazar et al. 2018; Araújo et al. 2021a; Sánchez-Acevedo et al. 2022
Stomatal Aperture Length	STL	Sánchez-Acevedo et al. 2022		Araújo et al. 2021a
Stomatal Width	SW	Pireda et al. 2019		
Stomatal Length	SL	Pireda et al. 2019		
Abaxial and Adaxial Stomatal Area	SA	Pireda et al. 2019		Salazar et al. 2018
Stomatal Size	SS			Araújo et al. 2021a
Spongy Parenchyma Thickness	SPT		Bedetti et al. 2011; Pireda et al. 2019; Araújo et al. 2021a	
Palisade Parenchyma Thickness	PPT	Ariano et al.2022	Bedetti et al. 2011; Pireda et al. 2019; Araújo et al. 2021a	
Palisade:Spongy Ratio	P:S		Bedetti et al. 2011; Pireda et al. 2019; Araújo et al. 2021a	
Adaxial and Abaxial Cuticle Thickness	ACT	Ariano et al. 2022	Bedetti et al. 2011; Pireda et al. 2019; Araújo et al. 2021a	Gotsch et al. 2010
Adaxial and Abaxial Epidermis Thickness	AET		Bedetti et al. 2011; Pireda et al. 2019; Araújo et al. 2021a	
Midrib Thickness	MTh	Ariano et al. 2022		
Vascular Bundle Thickness	VBTh	Ariano et al. 2022		
Leaf Thickness	LTH	Gotsch et al. 2010; Bedetti et al. 2011; Homeier et al. 2021	Fortunel et al. 2014a; Roa-Fuentes et al. 2015; Cássia-Silva et al. 2017; Moraes et al. 2017; Borges et al. 2018; Maracahipes et al. 2018; Pinho et al. 2019; Pireda et al. 2019; Maya-García et al. 2020; Oliveira et al. 2021; Sánchez-Acevedo et al. 2022	Zorger et al. 2019; Trindade et al. 2020; Hofhansl et al. 2021

	Chlorophyll Content	CC	Wagner et al. 2014; van der Sande et al. 2016; Moraes et al. 2017	Schmitt et al. 2020	Fortunel et al. 2014a
	Chlorophyll a Content	Chl a	Moraes et al. 2017	Pireda et al. 2019	
	Chlorophyll b Content	Chl b	Moraes et al. 2017	Pireda et al. 2019	
	Carotenoid Content	Caro	Moraes et al. 2017	Pireda et al. 2019	
	Chlorophyll:Carotenoid Ratio	Chlo/Car	Pireda et al. 2019		
	Chlorophyll a/b Ratio	Chlo a/b		Pireda et al. 2019	
	Photosynthetic Rate/CO_2 Assmilation	A, A_{max}, A_{mass}, A_{area}	Pireda et al. 2019	Lloyd et al. 2015; Moraes et al. 2017	Baruch et al. 2011; Salazar et al. 2018; Oliveira et al. 2021
	Transpiration Rate	E	Pireda et al. 2019	Moraes et al. 2017	
	Stomatal Conductance	g_s	Pireda et al. 2019	Moraes et al. 2017	Salazar et al. 2018
	C_i/C_a Ratio, C_a, C_i	C_a, C_i, C_i/C_a		Macieira et al. 2021	
	Maximum Quantum Yield of Photosystem II	F_v/F_m	Souza et al. 2018; Pireda et al. 2019		
	Proline	Pro		Pireda et al. 2019	
	Carbohydrates	Carb		Pireda et al. 2019	
	Flavonoids	Fla		Pireda et al. 2019	
	Phenols	Phe		Pireda et al. 2019; Nascimento et al. 2020	
Wood	Wood density	WD, WSG	Lohbeck et al. 2015; van der Sande et al. 2016; Aguilar-Romero et al. 2017; Cássia-Silva et al. 2017; Moraes et al. 2017; Neves et al. 2017; Chain-Guadarrama et al. 2018; Pinho et al. 2019; Dantas and Pausas 2020; Trindade et al. 2020; Garcia et al. 2022; Neves et al. 2022	Fortunel et al. 2014ab; Scholz et al. 2014; Wagner et al. 2014; Blundo et al. 2015; Muscarella et al. 2016; van der Sande et al. 2016; Cosme et al. 2017; Borges et al. 2018; Poorter et al. 2019; Terra et al. 2018; Muscarella et al. 2019; Zorger et al. 2019; Arenas-Navarro et al. 2021; Lourenço Jr. et al. 2021; Poorter et al. 2021; Santos et al. 2021; Silva et al. 2021a; Pinho et al. 2021; Ferrero et al. 2022; Garcia et	Craven et al. 2013; Maracahipes et al. 2018; Grossiord et al. 2019; Assunção et al. 2021; Oliveira et al. 2021; Neves et al. 2022

			al. 2022	
Wood Saturated Water Content	SWC	Aguilar-Romero et al. 2017; Santos et al. 2021; Ferrero et al. 2022		Oliveira et al. 2021; Neves et al. 2022
Maximum Sap Flux Velocity; Sap Flow	V_{max}		Grossiord et al. 2019	
Vessel Frequency/ Density	VF	Arenas-Navarro et al. 2021	Sonsin et al. 2012; Dória et al. 2016; Campbell et al. 2016; Báez et al. 2022; Lourenço Jr. et al. 2022	Bosio et al. 2010; Fortunel et al. 2014b; Cosme et al. 2017; Macieira et al. 2021
Hydraulic and Mean Vessel Diameter	VDh; VDen	Bosio et al. 2010; Sonsin et al. 2012; Dória et al. 2016		Fortunel et al. 2014b; Arenas-Navarro et al. 2021
Vessel Lumen Area	VA	Campbell et al. 2016; Lourenço Jr. et al. 2022	Macieira et al. 2021	
Vessel Length	VL	Bosio et al. 2010	Campbell et al. 2016	Dória et al. 2016
Vessel Wall Thickness	VWT		Lourenço Jr. et al. 2022	
Vessel Grouping Index	VGI	Dória et al. 2016	Lourenço Jr. et al. 2022	Fortunel et al. 2014b; Scholz et al. 2014
Vessel Solitary Fraction	VSF	Lourenço Jr. et al. 2022		
Hydraulic Conductivity	Kh	Arenas-Navarro et al. 2021; Lourenço Jr. et al. 2022		Fortunel et al. 2014b; Cosme et al. 2017
Fibre Diameter	FD		Bosio et al. 2010; Campbell et al. 2016	Dória et al. 2016; Arenas-Navarro et al. 2021
Fibre Length	FL	Bosio et al. 2010	Campbell et al. 2016	
Fibre Wall Thickness	FWT	Dória et al. 2016	Bosio et al. 2010; Fortunel et al. 2014b	Arenas-Navarro et al. 2021
Ray Frequency	RF	Bosio et al. 2010		
Ray Width	RW	Campbell et al. 2016; Dória et al. 2016		
Ray Height	RH	Dória et al. 2016		Bosio et al. 2010
Vessel-Ray Pit Diameter	RVD	Dória et al. 2016		
Intervessel Pit Diameter	IPD	Dória et al. 2016	Campbell et al. 2016	
Conductive	CA	Arenas-Navarro et al. 2021;		Fortunel et al. 2014b

Area/Fraction		Lourenço Jr. et al. 2022		
Parenchyma Area/Fraction	PA	Fortunel et al. 2014b; Lourenço Jr. et al. 2022		
Fibre Area/Fraction	FA		Fortunel et al. 2014b; Lourenço Jr. et al. 2022	
Xylose	Xyl		Macieira et al. 2021	
Soluble Sugars	SS		Macieira et al. 2021	
Galactose, Arabinose, Glucose, Rhamnose, Fucose	Gal, Ara, Glc, Rha, Fuc			Macieira et al. 2021
Starch	Starch	Macieira et al. 2021		
Mannose	Man	Macieira et al. 2021		
Leaf area:Sapwood Area Ratio	LA:SA	Ferrero et al. 2022		Cosme et al. 2017
Water Potential at which 50% Loss of Hydraulic Conductivity	P_{50}	Garcia et al. 2021	Garcia et al. 2022	
Water Potential at which 88% Loss of Hydraulic Conductivity	P_{88}			Garcia et al. 2022
Bark Thickness	BTh		Maracahipes et al. 2018	Fortunel et al. 2014a; Wagner et al. 2014
Huber Value	Hv		Craven et al. 2013; Aguilar-Romero et al. 2017	Scholz et al. 2014

Table S4 Leaf and wood trait variation along an irradiance gradient

			Trait variation along an irradiance gradient (from lower to higher irradiance)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA	Gotsch et al. 2010	Bedetti et al. 2011; Apaza-Quevedo et al. 2015; Melo-Junior and Boeger 2015; Silveira et al. 2015; Vitória et al. 2016; Maracahipes et al. 2018; Silva et al. 2019	Wagner et al. 2014; Maracahipes et al. 2018; Hofhansl et al. 2021; Poorter et al. 2021
	Leaf Mass per Area	LMA	Rabelo et al. 2013; Martin et al. 2020; Garcia et al. 2022		Moraes et al. 2017
	Leaf Area	LA	Souza et al. 2018; Silva et al. 2019	Lebrija-Tejos et al. 2010; Bedetti et al. 2011; Apaza-Quevedo et al. 2015; Melo-Júnior and Boeger 2015; Silveira et al. 2015; Zonta et al. 2021; Borges et al. 2018; Pireda et al. 2019	Rabelo et al. 2013; Hofhansl et al. 2021
	Leaf Dry Matter Content	LDMC	Lebrija-Tejos et al. 2010; Zonta et al. 2021		Rabelo et al. 2013; Silva et al. 2019
	Leaf Density	DEN	Lebrija-Tejos et al. 2010	Rabelo et al. 2013; Moraes et al. 2017	Rabelo et al. 2013; Melo-Júnior and Boeger 2015
	Leaf Succulence	SUC	Moraes et al. 2017; Pireda et al. 2019		Rabelo et al. 2013
	Leaf Toughness	Ltough	Wagner et al. 2014		
	Leaf Length, Leaf Width	LL, LW		Silveira et al. 2015	
	Venation Density	VDen	Pireda et al. 2019		
	Water Use Efficiency	WUE			Silva et al. 2010; Lage-Pinto et al. 2012; Moraes et al. 2017
	Carbon Isotopic Composition	$\delta^{13}C$	Vitória et al. 2016; Pireda et al. 2019; Martin et al. 2020		Wagner et al. 2014
	Leaf Water Potential	Ψ_{pd}, Ψ_{md}	Moraes et al. 2017	Gotsch et al. 2010; Moraes et al. 2017	
	Leaf Water Content	LWC		Melo-Júnior and Boeger	

			2015	
Leaf Phosphorus Concentration	P_{mass}, P_{area}		Maracahipes et al. 2018	Wagner et al. 2014; Hofhansl et al. 2021
Leaf Nitrogen Concentration	N_{mass}, N_{area}		Wagner et al. 2014; Apaza-Quevedo et al. 2015; Maracahipes et al. 2018	Poorter et al. 2021
Leaf Potassium Concentration	K_{mass}, K_{area}		Maracahipes et al. 2018	Wagner et al. 2014
Leaf Calcium Concentration	Ca_{mass}, $Ca_{área}$		Maracahipes et al. 2018	
Leaf Magnesium Concentration	Mg_{mass}, Mg_{area}		Maracahipes et al. 2018	
Leaf Carbon Concentration	C		Gotsch et al. 2010	Apaza-Quevedo et al. 2015
Leaf Carbon:Nitrogen Ratio	C:N	Apaza-Quevedo et al. 2015		
Nitrogen Isotopic Composition	$\delta^{15}N$		Pireda et al. 2019	
Trichome Density, Abaxial Trichome Density	TD	Bedetti et al. 2011	Costa et al. 2020b	
Stomatal Density	SD	Bedetti et al. 2011; Rabelo et al. 2013; Melo-Junior and Boeger 2015; Silveira et al. 2015; Pireda et al. 2019; Costa et al. 2020b		Rabelo et al. 2013; Apaza-Quevedo et al. 2015; Melo-Júnior and Boeger 2015
Stomatal Width	SW		Pireda et al. 2019	
Stomatal Length	SL		Pireda et al. 2019	
Stomatal Area	SA		Pireda et al. 2019; Costa et al. 2020b	
Palisade Parenchyma Thickness	PPT	Silva et al. 2010; Bedetti et al. 2011; Melo-Júnior and Boeger 2015; Silveira et al. 2015; Pireda et al.		Rabelo et al. 2013; Melo-Júnior and Boeger 2015; Costa et al. 2020b

		2019		
Spongy Parenchyma Thickness	SPT	Silva et al. 2010; Bedetti et al. 2011; Silveira et al. 2015; Pireda et al. 2019; Costa et al. 2020b	Melo-Júnior and Boeger 2015	Rabelo et al. 2013; Melo-Júnior and Boeger 2015
Palisade:Spongy Ratio	P:S	Melo-Júnior and Boeger 2015; Silveira et al. 2015; Pireda et al. 2019		Melo-Júnior and Boeger 2015
Adaxial Cuticle Thickness	AdCT	Bedetti et al. 2011; Silveira et al. 2015; Pireda et al. 2019		Rabelo et al. 2013
Abaxial Cuticle Thickness	AbCT	Silveira et al. 2015; Pireda et al. 2019		Silva et al. 2010; Rabelo et al. 2013
Adaxial Epidermis Thickness	AdET	Bedetti et al. 2011; Pireda et al. 2019; Costa et al. 2020b	Silva et al. 2010; Silveira et al. 2015	
Abaxial Epidermis Thickness	AbET	Pireda et al. 2019	Silveira et al. 2015	Costa et al. 2020b
Leaf Thickness	LTH	Silva et al. 2010; Rabelo et al. 2013; Melo-Junior and Boeger 2015; Silveira et al. 2015; Moraes et al. 2017; Borges et al. 2018; Pireda et al. 2019; Silva et al. 2019	Gotsch et al. 2010; Bedetti et al. 2011	Rabelo et al. 2013; Hofhansl et al. 2021
Mesophyll Thickness	MT	Silva et al. 2010; Costa et al. 2020b		
Midrib Thickness	MidT	Costa et al. 2020b		
Vascular Bundle Area of the Midrib	BAMid	Costa et al. 2020b		
Phloem Area of the Midrib	PAMid	Costa et al. 2020b		
Xylem Area of the Midrib	XAMid		Costa et al. 2020b	

Fibre Area of the Midrib	FAMid			Costa et al. 2020b
Nonphotochemical Quenching of Fluorescence	NPQ			Silva et al. 2010; Lage-Pinto et al. 2012; Rabelo et al. 2013; Vitória et al. 2016
Total Chlorophyll	Chlo		Lage-Pinto et al. 2012; Moraes et al. 2017	Silva et al. 2010
Chloprohyll a Content	Chlo a	Pireda et al. 2019	Lage-Pinto et al. 2012; Vitória et al. 2016; Moraes et al. 2017	Silva et al. 2010; Rabelo et al. 2013
Chlorophyll b Content	Chlo b	Pireda et al. 2019	Lage-Pinto et al. 2012; Vitória et al. 2016; Moraes et al. 2017	Silva et al. 2010; Rabelo et al. 2013
Carotenoid Content	Car	Pireda et al. 2019	Lage-Pinto et al. 2012; Moraes et al. 2017; Martin et al. 2020	Silva et al. 2010; Rabelo et al. 2013
Chlorophyll:Carotenoid Ratio	Clo/Car		Lage-Pinto et al. 2012; Vitória et al. 2016; Pireda et al. 2019	Silva et al. 2010
Chlorophyll a/b Ratio	Chlo a/b	Pireda et al. 2019		Silva et al. 2010; Lage-Pinto et al. 2012; Vitória et al. 2016
Photosynthetic Rate/CO_2 Assmilation	A, A_{max}, A_{mass}, A_{area}	Silva et al. 2010; Lage-Pinto et al. 2012; Vitória et al. 2016; Moraes et al. 2017	Pireda et al. 2019	
Transpiration Rate	E	Lage-Pinto et al. 2012; Vitória et al. 2016; Moraes et al. 2017	Pireda et al. 2019	Silva et al. 2010
Stomatal Conductance	g_s	Silva et al. 2010; Lage-Pinto et al. 2012; Vitória et al. 2016; Moraes et al. 2017	Pireda et al. 2019	
Internal CO_2 Concentration	C_i			Lage-Pinto et al. 2012; Vitória et al. 2016
Maximum Quantum Yield of Photosystem II	F_v/F_m		Lage-Pinto et al. 2012; Rabelo et al. 2013; Vitória et al. 2016; Pireda et al. 2019	Silva et al. 2010; Rabelo et al. 2013

	Maximum Primary Yield of Photochemistry of Photosystem II	F_v/F_0		Lage-Pinto et al. 2012; Rabelo et al. 2013	Silva et al. 2010; Rabelo et al. 2013
	Photochemical Quenching of Fluorescence	qP			Silva et al. 2010; Lage-Pinto et al. 2012; Rabelo et al. 2013; Vitória et al. 2016
	Quantum Efficiency of Photosystem II	Φ_{PSII}			Vitória et al. 2016
	Carbohydrates	Carb	Pireda et al. 2019		
	Phenols	Ph	Pireda et al. 2019		
	Proline	Pro	Pireda et al. 2019		
	Flavonoid	Fla	Pireda et al. 2019		
Wood	Wood Density	WD, WSG	Wagner et al. 2014; Borges et al. 2018; Garcia et al. 2022	Moraes et al. 2017; Hofhansl et al. 2021	Maracahipes et al. 2018
	Vessel Frequency/Density	VF	Campbell et al. 2016		
	Vessel Diameter	VDen			Campbell et al. 2016
	Vessel Length	VL	Campbell et al. 2016		
	Vessel Wall Thickness	VWT			Campbell et al. 2016
	Fibre Diameter	FD	Campbell et al. 2016		
	Fibre Length	FL	Campbell et al. 2016		
	Fibre Wall Thickness	FWT	Campbell et al. 2016		
	Fibre Lumen	FLu	Campbell et al. 2016		
	Ray Frequency	RF			Campbell et al. 2016
	Ray Length	RL			Campbell et al. 2016
	Intervessel Pit Diameter	IPD	Campbell et al. 2016		
	Vessel-Ray Pit Diameter	RVD			Campbell et al. 2016
	Fibre Area/Fraction	FA		Costa et al. 2020a	
	Parenchyma Area/Fraction	PA	Costa et al. 2020a		
	Bark Thickness	BTh			Wagner et al. 2014
	Number of Secondary Shoot	NSS		Silveira and Oliveira 2013	

Table S5 Leaf and wood trait variation along a temperature gradient

			Trait variation along a temperature gradient (from lower to higher temperature)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA	Homeier et al. 2021; Silva et al. 2021a; Báez et al. 2022	Araújo et al. 2021a; Silva and Rossatto 2022	Wagner et al. 2014; Pinho et al. 2021
	Leaf Mass per Area	LMA		Enquist et al. 2017; Lara-De La Cruz et al. 2020; Martin et al. 2020; Oliveras et al. 2020; Slot et al. 2021	Salazar et al. 2018
	Leaf Area	LA	Báez et al. 2022	Lebrija-Tejos et al. 2010; Pireda et al., 2019	Lara-De La Cruz et al. 2020
	Leaf Dry Matter Content	LDMC	Lebrija-Tejos et al. 2010; Hofhansl et al. 2021; Silva et al. 2021a	Homeier et al. 2021	Salazar et al. 2018; Oliveras et al., 2020
	Leaf Density	DEN	Lebrija-Tejos et al. 2010		
	Leaf Succulence	SUC	Pireda et al. 2019		
	Petiole Length	PL		Lebrija-Tejos et al. 2010	
	Venation Density	VDen	Blonder et al. 2017		
	Leaf Toughness	Ltough		Homeier et al. 2021; Báez et al. 2022	
	Water Use Efficiency	WUE	Salazar et al. 2018		
	Carbon Isotopic Composition	$\delta^{13}C$	Pireda et al. 2019	Martin et al. 2020	Wagner et al. 2014
	Leaf Water Content	LWC		Salazar et al. 2018	
	Leaf Phosphorus Concentration	P_{mass}, P_{area}	Báez et al. 2022	Oliveras et al. 2020	Wagner et al. 2014; Enquist et al. 2017; Martin et al. 2020
	Leaf Nitrogen Concentration	N_{mass}, N_{area}	Enquist et al. 2017; Martin et al. 2020; Homeier et al. 2021; Báez et al. 2022; Silva et al. 2021a	Wagner et al. 2014	Salazar et al. 2018; Oliveras et al. 2020
	Leaf Potassium Concentration	K_{mass}, K_{area}			Wagner et al. 2014; Oliveras et al. 2020

Leaf Calcium Concentration	Ca_{mass}, Ca_{area}	Homeier et al. 2021		Martin et al. 2020
Leaf Magnesium Concentration	Mg_{mass}, Mg_{area}			Martin et al. 2020
Leaf Carbon Concentration	C			Apaza-Quevedo et al. 2015; Enquist et al. 2017; Salazar et al. 2018; Martin et al. 2020
Leaf Iron Concentration	Fe			Martin et al. 2020
Leaf Zinc Concentration	Zn			Martin et al. 2020
Leaf Manganese Concentration	Mn		Martin et al. 2020	
Leaf Nitrogen:Phosphorus Content	N:P	Homeier et al. 2021		
Leaf Phosphorus:Nitrogen Content	P:N		Enquist et al. 2017	
Nitrogen Use Efficiency	PNUE		Enquist et al. 2017	
Nitrogen Isotopic Composition	$\delta^{15}N$		Pireda et al. 2019	
Trichome Density	TD	Araújo et al. 2021a		
Stomatal Density	SD	Pireda et al. 2019		Salazar et al. 2018 Apaza-Quevedo et al. 2015
Stomatal Width	SW		Pireda et al. 2019	
Stomatal Length	SL		Pireda et al. 2019	
Stomatal Area	AS		Salazar et al. 2018; Pireda et al. 2019	Salazar et al. 2018
Palisade Parenchyma Thickness	PPT	Pireda et al. 2019		
Spongy Parenchyma Thickness	SPT	Pireda et al. 2019		
Cuticle Thickness	CT	Araújo et al. 2021a		
Adaxial and Abaxial Epidermis Thickness		Pireda et al. 2019; Araújo et al. 2021a		

	Leaf Thickness	LTH	Pireda et al. 2019; Silva and Rossatto 2022	Blonder et al. 2017; Oliveras et al. 2020; Homeier et al. 2021; Slot et al. 2021	
	Chlorophyll a Content	Chlo a	Pireda et al. 2019		
	Chlorophyll b Content	Chlo b	Pireda et al. 2019		
	Carotenoid Content	Car	Pireda et al. 2019		Martin et al. 2020
	Chlorophyll:Carotenoid Ratio	Chlo/Car		Pireda et al. 2019	
	Chlorophyll a/b Ratio	Chlo a/b	Pireda et al. 2019		Martin et al. 2020
	Photosynthetic Rate/CO_2 Assmilation	A, A_{max}, A_{mass}, A_{area}, A_{sat}		Pireda et al. 2019	Enquist et al. 2017; Salazar et al. 2018; Oliveras et al. 2020
	Transpiration Rate	E		Pireda et al. 2019	
	Stomatal Conductance	g_s		Pireda et al. 2019	Salazar et al. 2018
	Maximum Quantum Yield of Photosystem II	F_v/F_m		Pireda et al. 2019	Silva and Rossatto 2022
	Temperature associated with the onset of the temperature-induced decline in Fv/Fm	T_5			Tiwari et al. 2020
	Temperature at which Fv/Fm decreased below 95% of the maximum level	T_{95}			Tiwari et al. 2020
	Temperature at which F_v/F_m was reduced to 50%	T_{50}	Silva and Rossatto 2022; Slot et al. 2021	Araújo et al. 2021b	
	Maximum leaf temperature	T_{Lmax}	Araújo et al. 2021b		
	Critical Temperature beyond which F_v/F_m declines	T_{crit}	Slot et al. 2021		
	Thermal Safety Margin	T_{SM}		Araújo et al. 2021b	
	Carbohydrates	Carb	Pireda et al. 2019		
	Proline	Pro	Pireda et al. 2019		
	Flavonoid	Fla	Pireda et al. 2019		

	Phenol	Ph	Pireda et al. 2019	Martin et al. 2020	
	Lignin	Lignin	Martin et al. 2020		
	Cellulose	Cellulose	Martin et al. 2020		
	Non-Structural Carbohydrates	NSC		Martin et al. 2020	
	Tannins	Tannins		Martin et al. 2020	
Wood	Wood Density	WD, WSG	Scholz et al. 2014; Blundo et al. 2015; Terra et al. 2018; Hofhansl et al. 2021; Silva et al. 2021a	Pinho et al. 2021	
	Vessel Frequency/Density	VF	Campbell et al. 2016	Báez et al. 2022	
	Vessel Diameter	VD	Báez et al. 2022		Campbell et al. 2016
	Vessel Area	VA		Campbell et al. 2016	
	Vessel Length	VL	Campbell et al. 2016		
	Vessel Wall Thickness	VWT			Campbell et al. 2016
	Hydraulic Conductivity	Kh			Scholz et al. 2014
	Fibre Diameter	FD	Campbell et al. 2016		
	Fibre Length	FL	Campbell et al. 2016		
	Fibre Wall Thickness	FWT	Campbell et al. 2016		
	Fibre Lumen	FLu	Campbell et al. 2016; Arenas-Navarro et al. 2021		
	Ray Frequency	RF			Scholz et al. 2014
	Ray Length	RL			Campbell et al. 2016
	Ray Width	RW		Campbell et al. 2016	
	Intervessel Pit Diameter	IPD	Campbell et al. 2016		
	Vessel-Ray Pit Diameter	VPD			Campbell et al. 2016
	Fibre Pit Diameter	FPD			Campbell et al. 2016
	Bark Thickness	Bth			Wagner et al. 2014

Table S6 Leaf and wood trait variation along a soil fertility gradient

			Trait variation along a soil fertility gradient (from lower to higher fertility)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA	Bedetti et al. 2011; Carvalho and Batalha 2013; Apaza-Quevedo et al. 2015; Melo-Júnior and Boeger 2015; Souza et al. 2015; Cássia-Silva et al. 2017; Delpiano et al. 2020	Damasco et al. 2021; Giraldo-Kalil et al. 2022	Becknell and Powers 2014; Maracahipes et al. 2018; Hofhansl et al. 2021; Lins et al. 2021
	Leaf Mass per Area	LMA		Asner et al. 2014ab; Vitória et al. 2019; Nascimento et al. 2020	
	Leaf Area	LA	Bedetti et al. 2011; Apaza-Quevedo et al. 2015; Melo-Júnior and Boeger 2015; Nascimento et al. 2020	Pireda et al. 2019	Patiño et al. 2012; Delpiano et al. 2020; Hofhansl et al. 2021; Lins et al. 2021
	Leaf Dry Matter Content	LDMC	Lins et al. 2021		
	Leaf Density	DEN	Pinto et al. 2021	Vitória et al. 2019	Melo-Junior and Boeger 2015
	Leaf Succulence	SUC	Pireda et al. 2019	Vitória et al. 2019	
	Leaf Toughness	Ltough		Carvalho and Batalha 2013	
	Venation density	VDen	Pireda et al. 2019		
	Water Use Efficiency	WUE	Patiño et al. 2012		
	Carbon Isotopic Composition	$\delta^{13}C$	Pireda et al. 2019	Asner et al. 2014ab; Becknell and Powers 2014	
	Leaf Water Potential	Ψ_{leaf}	Lins et al. 2021		
	Leaf Water Content	LWC	Asner et al. 2014ab; Melo-Júnior and Boeger 2015; Nascimento et al. 2020		
	Leaf Phosphorus Concentration	P_{mass}, P_{area}	Patiño et al. 2012; Asner et al. 2014ab; Becknell and Powers 2014; Souza et al. 2015; Heineman et al. 2016; Delpiano et al. 2020; Pinto et al. 2021; Giraldo-Kalil et al. 2022		Hofhansl et al. 2021; Lins et al. 2021
	Leaf Nitrogen Concentration	N_{mass}, N_{area}	Patiño et al. 2012; Carvalho and Batalha 2013; Asner et al.	Álvarez-Yépiz et al. 2017; Damasco et al. 2021	Asner et al. 2014b; Heineman et al. 2016; Cássia-Silva et al.

		2014ab; Becknell and Powers 2014; Apaza-Quevedo et al. 2015; Delpiano et al. 2020; Nascimento et al. 2020; Pinto et al. 2021; Giraldo-Kalil et al. 2022		2017; Lins et al. 2021
Leaf Potassium Concentration	K_{mass}, K_{area}	Patiño et al. 2012; Asner et al. 2014ab; Souza et al. 2015; Heineman et al. 2016; Lins et al. 2021; Delpiano et al. 2020	Pinto et al. 2021	Cássia-Silva et al. 2017
Leaf Calcium Concentration	Ca_{mass}, $Ca_{área}$	Patiño et al. 2012; Asner et al. 2014ab; Heineman et al. 2016; Pinto et al. 2021	Nascimento et al. 2020	
Leaf Magnesium Concentration	Mg_{mass}, Mg_{area}	Patiño et al. 2012; Asner et al. 2014ab; Souza et al. 2015; Pinto et al. 2021		Heineman et al. 2016; Nascimento et al. 2020
Leaf Carbon Concentration	C		Patiño et al. 2012; Asner et al. 2014ab; Becknell and Powers 2014; Cássia-Silva et al. 2017; Maracahipes et al. 2018	Apaza-Quevedo et al. 2015; Nascimento et al. 2020
Leaf Aluminum Concentration	Al		Pinto et al. 2021	
Leaf Iron Concentration	Fe	Asner et al. 2014ab		
Leaf Zinc Concentration	Zn	Asner et al. 2014ab		
Leaf Manganese Concentration	Mn			Asner et al. 2014a
Leaf Boron Concentration	B	Asner et al. 2014ab		
Leaf Sodium Concentration	Na			Lins et al. 2021
Leaf Carbon:Nitrogen Ratio	C:N		Apaza-Quevedo et al 2015; Nascimento et al. 2020	
Leaf Nitrogen:Phosphorus Ratio	N:P	Nascimento et al. 2020		

Leaf Carbon:Phosphorus Ratio	C:P	Nascimento et al. 2020		
Nitrogen Isotopic Composition	$\delta^{15}N$		Pireda et al. 2019	
Abaxial Trichome Density	AbTD		Bedetti et al. 2011	
Stomatal Density	SD	Pireda et al. 2019	Melo-Júnior and Boeger 2015; Damasco et al. 2021	Melo-Junior and Boeger 2015
Stomatal Width	SW		Pireda et al. 2019	
Stomatal Length	SL		Pireda et al. 2019	
Stomatal Area	AS		Pireda et al. 2019	
Palisade Parenchyma Thickness	PPT	Pireda et al. 2019	Bedetti et al. 2011; Melo-Júnior and Boeger 2015	Melo-Junior and Boeger 2015
Spongy Parenchyma Thickness	SPT	Melo-Júnior and Boeger 2015; Pireda et al. 2019	Bedetti et al. 2011	Melo-Junior and Boeger 2015
Palisade:Spongy Ratio	P:S	Pireda et al. 2019	Melo-Júnior and Boeger 2015	Melo-Junior and Boeger 2015
Cuticle Thickness	CT		Bedetti et al. 2011	
Adaxial and Abaxial Epidermis Thickness	AdET, AbET	Pireda et al. 2019	Bedetti et al. 2011	
Leaf Thickness	LTH	Bedetti et al. 2011; Pireda et al. 2019	Melo-Júnior and Boeger 2015; Cássia-Silva et al. 2017; Maracahipes et al. 2018; Vitória et al. 2019; Pinto et al. 2021	Hofhansl et al. 2021
Chlorophyll Content Index	ChlI		Damasco et al. 2021	
Total Chlorophyll Content	Chl	Asner et al. 2014ab		
Chlorophyll a Content	Chlo a	Pireda et al. 2019		
Chlorophyll b Content	Chlo b	Pireda et al. 2019		
Carotenoid Content	Car	Asner et al. 2014ab; Pireda et al. 2019		
Chlorophyll:Carotenoid Ratio	Clo:Car		Pireda et al. 2019	
Chlorophyll a/b Ratio	Chlo a/b	Pireda et al. 2019		

	Photosynthetic Rate/CO_2 Assmilation	A, A_{max}, A_{mass}, A_{area}, A_{sat}		Álvarez-Yépiz et al. 2017; Pireda et al. 2019	
	Transpiration Rate	E		Pireda et al. 2019	
	Stomatal Conductance	g_s		Pireda et al. 2019	
	Maximum Quantum Yield of Photosystem II	F_v/F_m		Pireda et al. 2019	
	Carbohydrates	Carb	Pireda et al. 2019		
	Proline	Pro	Pireda et al. 2019		
	Flavonoid	Fla	Pireda et al. 2019		
	Phenol	Ph	Pireda et al. 2019	Asner et al. 2014ab; Nascimento et al. 2020	
	Lignin	Lignin		Asner et al. 2014ab; Becknell and Powers 2014	
	Cellulose	Cellulose		Asner et al. 2014ab; Becknell and Powers 2014	Asner et al. 2014b
	Soluble Carbon	SC	Asner et al. 2014ab		
	Tannins	Tannins		Asner et al. 2014ab; Becknell and Powers 2014	
	Hemicellulose	HC		Asner et al. 2014ab; Becknell and Powers 2014	
Wood	Wood Density	WG, WSG	Cássia-Silva et al. 2017; Terra et al. 2018	Fortunel et al. 2014b	Becknell and Powers 2014; Maracahipes et al. 2018
	Vessel Frequency/Density	VF		Patiño et al. 2012	Fortunel et al. 2014b
	Vessel Diameter	VD	Damasco et al. 2021		Fortunel et al. 2014b
	Vessel Area	VA			Fortunel et al. 2014b
	Vessel Length	VL	Damasco et al. 2021		Fortunel et al. 2014b
	Vessel Grouping Index	VGI			Fortunel et al. 2014b
	Hydraulic Conductivity	Kh			Fortunel et al. 2014b
	Vessel Lumen Fraction	VLF			Fortunel et al. 2014b
	Vessel Fraction	VF			Fortunel et al. 2014b
	Parenchyma Area/Fraction	PA	Fortunel et al. 2014b		
	Leaf area:Sapwood Area	LA:SA			Patiño et al. 2012

	Ratio				
	Water Potential at which 50% Loss of Hydraulic Conductivity	P50	Oliveira et al. 2019		
	Bark Thickness	Bth		Maracahipes et al. 2018	Cássia-Silva et al. 2017
	Wood Phosphorus Content	P	Heineman et al. 2016		
	Wood Nitrogen Content	N			Heineman et al. 2016
	Wood Potassium Content	K	Heineman et al. 2016		
	Wood Calcium Content	Ca	Heineman et al. 2016		
	Wood Magnesium Content	Mg			Heineman et al. 2016

Table S7 Leaf and wood trait variation along an elevation gradient

			Trait variation along an elevation gradient (from lower to higher elevation)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA	Giraldo-Kalil et al. 2022	Hulshof et al. 2013; Apaza-Quevedo et al. 2015; Rosado et al. 2015; Fortunel et al. 2018; Kandlikar et al. 2018; Vitória et al. 2019; Homeier et al. 2021; Ochoa-Beltrán et al. 2021; Báez et al. 2022; Ferrero et al. 2022; Pereira et al. 2022	Fortunel et al. 2019; Hofhansl et al. 2021
	Leaf Mass per Area	LMA	Neyret et al. 2016; Asner et al. 2014ab; Asner et al. 2017; Martin et al. 2020; Oliveras et al. 2020; Peng et al. 2020; Schmitt et al. 2020; Slot et al. 2021		
	Leaf Area	LA		Apaza-Quevedo et al. 2015; Schmitt et al. 2020; Ochoa-Beltrán et al. 2021; Báez et al. 2022; Ferrero et al. 2022	Fortunel et al. 2019; Umaña and Swenson 2019; Hofhansl et al. 2021; Homeier et al. 2021
	Leaf Dry Matter Content	LDMC	Homeier er al. 2021; Schmitt et al. 2020	Méndez-Toribio et al. 2017	Kandlikar et al. 2018; Oliveras et al. 2020; Ochoa-Beltrán et al. 2021; Slot et al. 2021; Ferrero et al. 2022
	Leaf Density	DEN	Rosado et al. 2015		Slot et al. 2021
	Leaf Toughness	Ltough	Homeier et al. 2021; Ochoa-Beltrán et al, 2021; Báez et al. 2022		
	Leaf Width	LW	Rodríguez-Ramírez et al. 2021		
	Leaf Length	LL		Rodríguez-Ramírez et al. 2021	
	Leaf Length:Width Ratio	LL:LW			Slot et al. 2021
	Petiole Length	PL	Méndez-Toribio et al. 2017		
	Venation Density	VDen	Pereira et al. 2022	Blonder et al. 2017; Blonder et al.	

			2018; Rodríguez-Ramírez et al. 2021	
Leaf Vein Distance	LVD	Blonder et al. 2017		
Leaf Water Content	LWC	Asner et al. 2014ab; Asner et al. 2017	Rosado et al. 2015; Ferrero et al. 2022	
Carbon Isotopic Composition	$\delta^{13}C$	Asner et al. 2014b; Umaña and Swenson 2019; Martin et al. 2020; Pereira et al. 2022		Lins et al. 2016
Leaf Phosphorus Concentration	P_{mass}, P_{area}	Asner et al. 2014ab; Peng et al. 2020	Báez et al. 2022; Giraldo-Kalil et al. 2022	Asner et al. 2014a; Asner et al. 2017; Martin et al. 2020; Hofhansl et al. 2021; Homeier et al. 2021
Leaf Nitrogen Concentration	N_{mass}, N_{area}	Álvarez-Yépiz et al. 2017; Peng et al., 2020	Asner et al. 2014ab; Apaza-Quevedo et al. 2015; Asner et al. 2017; Martin et al. 2020; Homeier et al. 2021; Báez et al. 2022; Giraldo-Kalil et al. 2022	Kandlikar et al. 2018; Umaña and Swenson 2019; Oliveras et al. 2020
Leaf Potassium Concentration	K	Martin et al. 2020		Asner et al. 2104a; Oliveras et al. 2020; Homeier et al. 2021
Leaf Calcium Concentration	Ca		Asner et al. 2014ab; Homeier et al. 2021	Martin et al. 2020; Oliveras et al. 2020
Leaf Magnesium Concentration	Mg			Asner et al. 2014a; Martin et al. 2020; Oliveras et al. 2020; Homeier et al. 2021
Leaf Carbon Concentration	C	Asner et al. 2014ab		Asner et al. 2014b; Apaza-Quevedo et al. 2015; Umaña and Swenson 2019; Martin et al. 2020
Leaf Aluminum Concentration	Al			Homeier et al. 2021
Leaf Iron Concentration	Fe			Asner et al. 2014a; Martin et al. 2020; Oliveras et al. 2020
Leaf Zinc	Zn			Asner et al. 2014a; Martin

Concentration				et al. 2020; Oliveras et al. 2020
Leaf Manganese Concentration	Mn	Asner et al. 2014a; Martin et al. 2020		
Leaf Boron Concentration	B	Martin et al. 2020		Asner et al. 2014a
Leaf Carbon:Nitrogen Ratio	C:N	Apaza-Quevedo et al. 2015		
Leaf Nitrogen:Phosphorus Ratio	N:P	Peng et al. 2020	Homeier et al. 2021	
Nitrogen Isotopic Composition	$\delta^{15}N$			Umaña and Swenson 2019
Trichome Density	TD	Pereira et al. 2022		
Stomatal Density	SD			Apaza-Quevedo et al. 2015; Pereira et al. 2022
Leaf Thickness	LTH	Blonder et al. 2017; Umaña and Swenson 2019; Oliveras et al. 2020; Schmitt et al. 2020; Homeier et al. 2021; Ochoa-Beltrán et al. 2021; Slot et al. 2021	Rosado et al. 2015; Vitória et al. 2019	Hofhansl et al. 2021
Mesophyll Thickness	MT			Jiménez-Noriega et al. 2017
Abaxial Epidermis Thickness	AbET			Jiménez-Noriega et al. 2017
Chlorophyll Content	Chlo	Schmitt et al. 2020	Asner et al. 2014ab	Asner et al. 2017
Carotenoid Content	Car		Asner et al. 2014ab	Martin et al. 2020
Chlorophyll a/b Content	Chlo a/b			Martin et al. 2020
Photosynthetic Rate/CO_2 Assmilation	A	Álvarez-Yépiz et al. 2017		Oliveras et al. 2020
Temperature at	T_{50}		Slot et al. 2021	

	which F_v/F_m was reduced to 50%				
	Critical Temperature beyond which F_v/F_m declines	T_{crit}		Slot et al. 2021	
	Phenol	Ph	Martin et al. 2020		Asner et al. 2014ab; Asner et al. 2017
	Lignin	Lignin		Asner et al. 2014ab; Asner et al. 2017; Martin et al. 2020	
	Cellulose	Cellulose		Asner et al. 2014ab; Martin et al. 2020	
	Tannins	Tannins	Martin et al. 2020		Asner et al. 2014ab; Asner et al. 2017
	Hemicellulose	HC			Asner et al. 2014a
	Non-Structural Carbohydrates	NSC	Asner et al. 2017; Martin et al. 2020		
Wood	Wood Density	WD, WSG	Báez et al. 2022	Scholz et al. 2014; Méndez-Toribio et al. 2017	Rosado et al. 2015; Kandlikar et al. 2018; Ochoa-Beltrán et al. 2021; Ferrero et al. 2022
	Wood Water Content	WWC		Ferrero et al. 2022	
	Vessel Frequency/Density	VF	Báez et al. 2022		Bosio et al. 2010; Jiménez-Noriega et al. 2017
	Vessel Diameter	VD		Bosio et al. 2010; Jiménez-Noriega et al. 2017; Báez et al. 2022	Jiménez-Noriega et al. 2017
	Vessel Length	VL		Bosio et al. 2010	
	Vessel Grouping Index	VGI	Bosio et al. 2010		Scholz et al. 2014
	Hydraulic Conductivity	Kh			Scholz et al. 2014
	Fibre Diameter	FD	Bosio et al. 2010		
	Fibre Length	FL	Bosio et al. 2010		
	Fibre Wall Thickness	FWT	Bosio et al. 2010		
	Ray Frequency	RF	Bosio et al. 2010		
	Ray Height	RL			Bosio et al. 2010
	Leaf area:Sapwood	LA:SA		Vitória et al. 2019; Ferrero et al. 2022	

	Area Ratio			
	Huber value	Hv		Scholz et al. 2014
	Bark Thickness	Bth	Méndez-Toribio et al. 2017	
	Bark Water Content	BWC	Méndez-Toribio et al. 2017	

Table S8 Leaf and wood trait variation in a temporal resource variation

			Trait variation in dry season (opposite values found in wet season)		
Organ	**Traits**	**Symbol**	**Increase**	**Decrease**	**No pattern/variation**
Leaf	Specific Leaf Area	SLA		Gotsch et al. 2010; Rossatto et al. 2013	Bedetti et al. 2011
	Leaf Area	LA			Bedetti et al. 2011
	Leaf Density	DEN		Rosado et al. 2015	
	Leaf Toughness	Ltough		Gotsch et al. 2010	Gotsch et al. 2010
	Water Use Efficiency	WUE	Lage-Pinto et al. 2012; Rossatto et al. 2013		Silva et al. 2010; Lage-Pinto et al. 2012
	Carbon Isotopic Composition	$\delta^{13}C$	Rossatto et al. 2013		
	Leaf Water Potential	Ψ_{leaf}, Ψ_{pd}, Ψ_{md}	Jancoski et al. 2022	Gotsch et al. 2010; Rosado and Mattos 2010; 2016; Rossatto et al. 2013; Fontes et al. 2018	Rosado and Mattos 2010; 2016;
	Leaf Water Content	LWC		Gotsch et al. 2010	Gotsch et al. 2010
	Leaf Phosphorus Concentration	P		Rossatto et al. 2013	
	Leaf Nitrogen Concentration	N		Gotsch et al. 2010; Rossatto et al. 2013	Gotsch et al. 2010
	Leaf Potassium Concentration	K		Rossatto et al. 2013	
	Leaf Calcium Concentration	Ca			Rossatto et al. 2013
	Leaf Magnesium	Mg		Rossatto et al. 2013	
	Leaf Carbon Concentration	C		Gotsch et al. 2010	
	Leaf Nitrogen:Phosphorus Ratio	N:P	Rossatto et al. 2013		
	Trichome Density (Adaxial and Abaxial)	TD			Bedetti et al. 2011; Costa et al. 2020b
	Stomatal Density	SD	Bedetti et al. 2011; Costa et al. 2020b		
	Stomatal Frequency	SF	Costa et al. 2020b		
	Stomatal Area	AS	Costa et al. 2020b		
	Spongy Parenchyma Thickness	SPT	Bedetti et al. 2011; Costa et al. 2020b	Bedetti et al. 2011	
	Palisade Parenchyma Thickness	PPT		Bedetti et al. 2011; Costa et al. 2020b	Costa et al. 2020b

	Epidermis Thickness (Abaxial and/or Adaxial)	ET	Costa et al. 2020b	Bedetti et al. 2011	Costa et al. 2020b
	Cuticle Thickness (Adaxial and/or Abaxial)	CT			Gotsch et al. 2010; Bedetti et al. 2011
	Midrib Thickness	MidT	Costa et al. 2020b		
	Mesophyll Thickness	MT			Costa et al. 2020b
	Vascular Bundle Area of the Midrib	VBAMid	Costa et al. 2020b		
	Xylem Area of the Midrib	XAMid	Costa et al. 2020b		
	Phloem Area of the Midrib	PAMid	Costa et al. 2020b		
	Fibre Area of the Midrib	FAMid	Costa et al. 2020b		
	Leaf Blade Thickness	LBT	Costa et al. 2020b	Bedetti et al. 2011	
	Leaf Thickness	LT	Rosado et al. 2015		Gotsch et al. 2010
	Total Chlorophyll Content	Chlo	Silva et al. 2010; Lage-Pinto et al. 2012		
	Chlorophyll a Content	Chlo a	Silva et al. 2010; Lage-Pinto et al. 2012		
	Chlorophyll b Content	Chlo b	Silva et al. 2010; Lage-Pinto et al. 2012		
	Carotenoid Content	Car	Silva et al. 2010; Lage-Pinto et al. 2012		
	Chlorophyll:Carotenoid Ratio	Chlo/Car		Lage-Pinto et al. 2012	Silva et al. 2010
	Chlorophyll a:Chlorophyll b Ratio	Chlo a/b			Silva et al. 2010; Lage-Pinto et al. 2012
	Photosynthetic Rate/CO_2 Assimilation	A_{mass}, A_{area}, A		Rossatto et al. 2013; Garcia et al. 2021	Silva et al. 2010
	Transpiration Rate	E		Silva et al. 2010; Lage-Pinto et al. 2012; Garcia et al. 2021	
	Stomatal Conductance	g_s		Lage-Pinto et al. 2012; Rossatto et al. 2013; Garcia et al. 2021	Silva et al. 2010; Lage-Pinto et al. 2012
	Maximum Quantum Yield of Photosystem II	F_v/F_m, F_v/F_{mpd}, F_v/F_{mmd}		Lage-Pinto et al. 2012; Rosado and Mattos 2016	Silva et al. 2010
	Maximum Primary Yield of	F_v/F_0	Silva et al. 2010	Lage-Pinto et al. 2012	

	Photochemistry of Photosystem II				
	Photochemical Quenching of Fluorescence	qP	Lage-Pinto et al. 2012	Lage-Pinto et al. 2012	Silva et al. 2010; Lage-Pinto et al. 2012
	Nonphotochemical Quenching of Fluorescence	NPQ	Lage-Pinto et al. 2012	Silva et al. 2010	
	Temperature at which F_v/F_m was reduced to 50%	T_{50}	Tiwari et al. 2020		
Wood	Leaf area:Sapwood Area Ratio	LA:SA	Rosado et al. 2015		
Wood	Hydraulic Safety Margin	HSM_{88}, HSM_{50}		Fontes et al. 2018	

Table S9 Plant organ coupling and decoupling studies in the Neotropic and other biogeographical regions

Authors	Year of Publication	Biogeographical Region	Geographic Zone	Country	Plant Systems	Plant Organ Relationship	Number of species	Plant Organ
Méndez-Alonzo et al.	2012	Neotropical	Tropical	Mexico	Tropical Dry Forest	Coupling	15	Leaves and stems
Muscarella et al.	2016	Neotropical	Tropical	Puerto Rico	Subtropical Dry Forest	Coupling	250	Leaves and stems
Zeballos et al.	2017	Neotropical	Tropical	Argentina	Seasonally Dry Tropical Forest	Coupling	37	Leaves and stems
Silva et al.	2018	Neotropical	Tropical	Brazil	Atlantic Forest - Restinga	Weekly Coupling	33	Leaves and stems
Fagundes et al.	2022	Neotropical	Tropical	Brazil	Seasonally Dry Tropical Forest	Coupling	20	Leaves, stems, and roots
Baraloto et al.	2010	Neotropical	Tropical	French Guiana	Amazon - Tropical Rainforest	Decoupling	758	Leaves and stems
Fortunel et al.	2012	Neotropical	Tropical	French Guiana and Peru	Amazon - Tropical Rainforest	Decoupling	668	Leaves, stems, and roots
Silva et al.	2015	Neotropical	Tropical	Brazil	Atlantic Forest - Ombrophilous	Decoupling	64	Leaves, stems, and seeds
Braga et al.	2016	Neotropical	Tropical	Brazil	Atlantic Forest - Ombrophilous	Decoupling	9	Leaves and stems
Vleminckx et al.	2021	Neotropical	Tropical	French Guiana	Tropical Moist Forest	Decoupling	1467	Leaves, stems, and roots
Garcia et al.	2022	Neotropical	Tropical	Brazil	Amazon - Tropical Rainforest	Decoupling	2	Leaves and stems
Medina-Vega et al.	2021	Neotropical	Tropical	Panama	Seasonally Dry and Wet Evergreen Tropical Forets	Both Decoupling	16	Leaves and stems
Ávila-Lovera et al.[a]	2022	Neotropical	Tropical	Panama and Costa	Seasonal and Wet Forests	Both Coupling	17	Leaves, stems, and roots

				Rica				
Sanaphre-Villanueva et al.[b]	2022	Neotropical	Tropical	Mexico	Tropical Dry and Humid Forest	Both Coupling	95	Leaves, stems, and roots
Ishida et al.	2008	Palearctic	Tropical	Japan	Seasonally Dry Region	Coupling	32	Leaves and stems
Freschet et al.	2010	Palearctic	Temperate	Sweden	Upland Dry and Riparian Birch Forests	Coupling	40	Leaves, stems, and roots
Laughlin et al.	2010	Nearctic	Temperate	United States	Semi-arid Region	Coupling	133	Leaves, seeds, and roots
Pérez-Ramos et al.	2012	Palearctic	Temperate	France	Mediterranean Rangeland	Coupling	16	Leaves and roots
Vinya et al.	2012	Afrotropical	Tropical	Zambia	Seasonally Dry Tropical Forest	Coupling	9	Leaves and stems
Fu et al.	2012	Palearctic/Indo-Malay	Tropical	China	Tropical Dry Forest	Coupling	12	Leaves and stems
Pivovaroff et al.	2014	Nearctic	Temperate	United States	Chaparral - Mediterranean type	Coupling	17	Leaves and stems
De la Riva et al.	2016	Palearctic	Temperate	Spain	Mediterranean Forests and Shrublands	Coupling	38	Leaves, stems, and roots
Jager et al.	2015	Australasian	Temperate	New Zealand	Warm Temperate Rainforest	Decoupling	30	Leaves and stems
Valverde-Barrantes et al.	2015	Nearctic	Temperate	United States	Deciduous Hardwood Forest	Decoupling	34	Leaves and roots
Wang et al.	2017	Palearctic/Indo-Malay	Temperate	China	Subtropical Evergreen, Temperate Deciduous and Cold-Temperate Coniferous Forest	Decoupling	154	Leaves and roots

[a] The only study with seedling life stage included in this review

[b] The only study with an herbaceous genus included in this review

CAPÍTULO 2:

Functional trait patterns: investigating variation-covariation relationships and the importance of intraspecific variability along distinct vegetation types

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3. CAPÍTULO 2: Functional trait patterns: investigating variation-covariation relationships and the importance of intraspecific variability along distinct vegetation types

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Abstract

Plants adjust to abiotic conditions by changing their anatomical, morphological, and physiological traits. Traits can vary independently or in an integrated manner, known as trait variation and covariation, respectively. It has been hypothesized that a trade-off would emerge along a gradient of abiotic constraints in which trait variation would be favored under resource-rich conditions while covariation under resource-limited ones. Although many studies have provided empirical support for this trade-off, a consensus has not yet emerged, due to a lack of support in some cases. This study investigated variation and covariation in three leaf and four wood traits of 74 woody species from a rainforest, a semideciduous forest, and a *Restinga* heath vegetation in the Atlantic Forest, which are subjected to different water-related constraints. We asked: Is there a variation-covariation trade-off within and across vegetation types? How does incorporating intraspecific variability change the magnitude and pattern of trait covariation? We found a variation-covariation trade-off and a positive relationship both within and across vegetation types. Wood variation was higher and covariation was lower in the rainforest, likely due to the greater water availability. Conversely, wood trait covariation was higher and variation was lower in the *Restinga* and seasonal semideciduous forest. Differences between vegetation types are likely related to the species' strategies to prevent hydraulic failure, particularly for *Restinga* species that adjust their wood density and xylem vessel density in a coordinated manner. Accounting for intraspecific trait variability increased covariation across all vegetation types, particularly in the *Restinga*. This highlights the loss of functional information when analyses are based solely on species' mean trait values. Our results also contribute to this discussion by providing evidence that the trade-off or a positive relationship between trait variation and covariation may be context-dependent.

Keywords: Atlantic forest, environmental gradient, phenotypic variation, resource use strategies, trait covariation, integrated traits

Introduction

Changes in resource availability, such as water, light, and nutrients, can significantly affect plant metabolism. These environmental changes may be triggered by shifts in resource management practices, habitat fragmentation, and climate change (Rowland et al. 2015; Campbell et al. 2016; Teixeira et al. 2020; Tiwari et al. 2020). Consequently, plant metabolic and morphological adjustments occur in response to variations in the expression of specific traits under distinct abiotic conditions (Vitória et al. 2019).

Traits refer to a set of measurable characteristics at the individual level of a species, whether morphoanatomical, physiological, molecular, biochemical, or phenological properties (Violle et al. 2007; Caruso et al. 2020). Understanding variation in plant traits is crucial for elucidating community assembly processes, especially in hyperdiverse ecosystems where taxonomic approaches may have limited explanatory power (Wright et al. 2004; Chave et al. 2009; Díaz et al. 2016, Vitória et al. 2019; Ribeiro et al. 2022). Deterministic (i.e., abiotic and biotic interactions) and stochastic (i.e., dispersal limitation and drift in species abundance) processes can act as filters, by selecting particular species and traits within a given environment (Cadotte and Tucker 2017; Gilbert and Levine 2017; Subedi et al. 2019). Trait-based filtering processes can thus determine the functional composition of local assemblages and the identity of dominant species, whose abundance may vary along environmental gradients of abiotic stress and productivity (Fauset et al. 2012; Shipley et al. 2016; Cavender-Bares 2018; Aguirre-Gutiérrez et al. 2019).

The intensity of these filters also determines how trait expression will be locally favored, either through trait independence and variation or through trait integration and covariation (Pigliucci 2003; Nicotra et al. 2010; Laughlin and Messier 2015). Trait variation reflects the flexibility of species in expressing phenotypes that are compatible with prevailing environmental conditions, thereby facilitating their persistence in a given habitat (Valladares et al. 2000). One example is the range of leaf area within a species that can be observed along an irradiance gradient (Vitória et al. 2016). Trait covariation refers to the functional interconnection between traits and is closely related to the phenotypic integration concept (Pigliucci 2003; Armbruster et al. 2014). An example of trait covariation occurs between xylem vessel diameter and xylem hydraulic conductivity, both high in resource-rich environments

(Chave et al. 2009). Although trait variation and covariation may result from environmental changes and correlational selection, they also can result from genetic differences and the developmental architecture of an organism (Matesanz et al. 2010; Armbruster et al. 2014).

It has been proposed that trait covariation increases while trait variation decreases along a gradient of environmental harshness (Schlichting 1989; Pigliucci 2003; Valladares et al. 2005; Dwyer and Laughlin 2017; Delhaye et al. 2020). In resource-rich communities, traits vary more widely as the niche space becomes more available, allowing species to express many trait combinations (Fig. 1a; Violle and Jiang 2009; Dwyer and Laughlin 2017; He et al. 2021). This means that many relationships between traits X and Y could be feasible to optimize species fitness, such as the decoupling between wood and leaf traits in tropical rainforests (Baraloto et al. 2010). On the other hand, resource-limited communities, particularly those related to water availability, select a small number of species with greater trait covariation because a few trait combinations are possible since niche space becomes constrained (Fig. 1b; Dwyer and Laughlin 2017; He et al. 2021). For example, higher values of trait X come with the expression of higher values of trait Y (or *vice-versa*), as seen in species with large seeds that need to adopt taller stature in semi-arid environments (Dwyer and Laughlin 2017). High trait variation in resource-limited environments could also translate to disadvantageous acclimative or adaptive costs (Valladares et al. 2007; Vieira et al. 2021).

Trait variation and covariation can also be influenced to some extent by biophysical constraints (Dywer and Laughlin 2017) since not all traits can vary widely, as they are constrained by other sets of correlated traits besides environmental conditions (Wang and Zhou 2021; Shi et al. 2023). In some cases, both in resource-limited and resource-rich environments, a high trait value must cause a decrease in another trait value, leading to a trade-off between them (Moles 1994; Garland 2014). A trade-off is a negative relationship (linear or not) between two traits, such as the greater seed mass and smaller number of seeds in species in dry woodlands (Moles 1994; Henery and Westoby 2001; Garland 2014).

It also has been suggested that trait covariation may constrain trait variation, although not universally accepted, also leading to a trade-off between them (Fig. 1b; Schlichting 1989; Gianoli 2004; Gianoli and Palacio-López 2009; Matesanz et al. 2010; Godoy et al. 2012). Gianoli and Palacio-López (2009) showed that in resource-limited conditions (e.g. drought and shading), *Convolvulus chilensis* and *Lippia alba* species exhibited traits with lower variation with an increased number of correlations with other traits. However, positive and direct relationships between trait variation and covariation have recently been reported, suggesting that trait covariation may not always act as a constraint on trait variation, even in resource-limited conditions (Fig. 1a; Godoy et al. 2012; Zimmermann et al. 2016; Pireda et al. 2019; Matesanz et al. 2021; Borges et al. 2022; Oyanoghafo et al. 2023; Shi et al. 2023). Matesanz et al. (2021) showed that in *Lepidium subulatum*, traits with higher and similar variation (e.g. flower number) had more correlations with other traits (i.e., linked to more traits) both in resource-limited and resource-rich conditions. These studies emphasize trait variation and covariation as complementary mechanisms of plant functioning and alternative mechanisms to cope with environmental harshness. Therefore, we have summarized the ideas mentioned above into an integrated framework for two scenarios in natural systems (Fig. 1) based on the gradient of environmental harshness framework proposed by Dwyer and Laughlin (2017) and the relationships between trait variation and covariation as demonstrated by Gianoli and Palacio-López (2009) and Matesanz et al. (2021).

The majority of studies evaluating trait variation and covariation relationships have been conducted in controlled greenhouses and natural environments, with a limited number of species (Gianoli 2004; Gianoli and Palacio-López 2009; Zimmermann et al. 2016; Matesanz et al. 2021; Shi et al. 2023). Additionally, most studies have evaluated trait variation and covariation separately (Murren 2002; Pigliucci 2003; van Kleunen and Fisher 2005; Valladares et al. 2007; Poot and Lambers 2008; Vitória et al. 2016; Larson et al. 2019), but this topic is becoming central in trait-based ecology by integrating these two mechanisms. Previous studies have shown that the variation-covariation relationships can depend on the plant organ and trait under consideration (Valladares et al. 2007; Godoy et al. 2012), spatial scale (Messier et al. 2017), phylogeny (Martínez-Cabrera et al. 2011), functional groups (Martínez-Cabrera et al. 2011; Apgaua et al. 2016; Michelaki et al. 2019), and growth form (Martínez-Cabrera et al. 2011; Apgaua et al. 2016), challenging the discussion about the adaptive value of trait variation and covariation (Armbruster et al. 2014; Matesanz et al. 2021).

Both intra- and interspecific trait variability may also influence the strength of trait covariation, and their relative contributions vary depending on the function of environmental conditions (Albert et al. 2010; Tautenhahn et al. 2020). Intraspecific trait variability encompasses the range of trait values exhibited by a group of individuals within a single species. In contrast, interspecific trait variability pertains to the array of trait values exhibited by different species (de Bello et al. 2021). Species with high intraspecific trait variability generally cope better with less constrained environments (Valladares et al. 2000; Valladares and Niinemets 2008; Nicotra et al. 2010). Without resource constraints, different trait sets can be expressed without hindering individuals' performance; the opposite could also be described (He et al. 2021; Silva et al. 2021). For example, high trait covariation is observed in species growing in less fertile soils. However, overall trait covariation may weaken when intraspecific trait variability is considered (He et al. 2021). There has been increasing attention paid to comparisons of trait variation and covariation while accounting for both inter- and intraspecific trait variability and how they change across vegetation types under contrasting environmental conditions, although a consensus has not emerged yet (Kichenin et al. 2013; Laughlin et al. 2017; Messier et al. 2017; Dong et al. 2020; He et al. 2021; Homeier et al. 2021).

Here we evaluated changes in trait variation and covariation for three leaf and four wood traits of 74 woody species within and across three vegetation types with contrasting environmental conditions in the Atlantic Forest: *Restinga* heath vegetation, seasonal semideciduous forest, and rainforest. These three vegetation types form an environmental gradient in terms of climate and soil conditions, ranging from northeastern to southern Brazil, which is expected to create distinct environmental conditions for plants from the *Restinga* to the semideciduous to the rainforest (from the most to the least constrained environment), with the *Restinga* being the harshest soil type.

Therefore, we addressed the following questions: 1) Is there a trade-off between trait variation and covariation within and across the vegetation types? and 2) how does incorporating intraspecific trait variability alter the magnitude and pattern of trait covariation? If the presented conceptual framework is correct, we expect a decrease in trait variation and an increase in trait covariation from the rainforest to the semideciduous forest to the *Restinga* (from high to low resource availability, Fig. 1b). In addition, intraspecific trait variability would lead to weaker trait covariation in all vegetation types (lower number and strength of trait correlations) when compared to interspecific trait variability, especially in the rainforest.

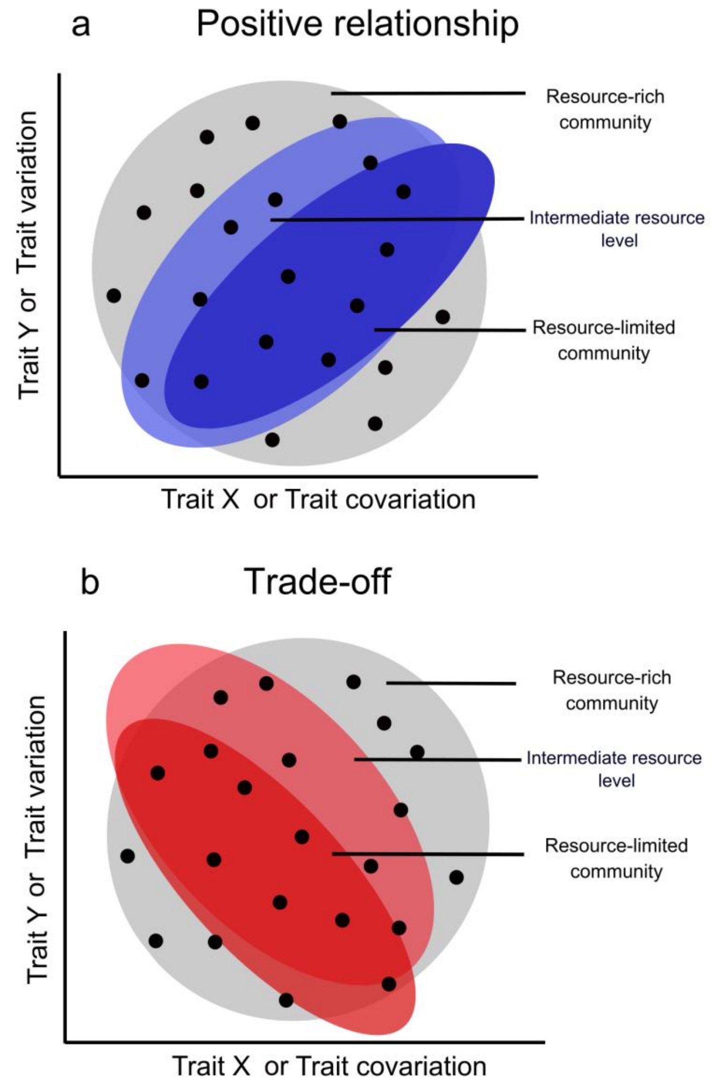

Fig. 1 Conceptual framework based on two possible scenarios for trait-trait or variation and covariation relationships along an environmental gradient. (a) From resource-rich to resource-limited communities, the number of species with viable trait combinations (black dots) and niche space tends to decrease, while trait covariation and trait variation tend to increase, leading to a positive and direct relationship. (b) From resource-rich to resource-limited communities, trait covariation increases, but trait variation decreases, leading to a possible trade-off. As the dimensional space reduces, a few viable combinations are found in both scenarios

Material and Methods

Study areas

This study was conducted in three vegetation types of the Brazilian Atlantic forest: *Restinga* heath vegetation, seasonal semideciduous forest, and rainforest. The *Restinga* is located in a 1900-ha coastal area in the Barreira do Inferno Launch Center, state of Rio Grande do Norte, Brazil (5°54’S, 35°10’W). The climate is tropical with a dry summer (As Köppen climate type; Alvares et al. 2013), a mean annual temperature of 25 ºC, and a mean annual precipitation of 1400 mm (Hijmans et al. 2005). The semideciduous forest is located in a 3260-ha area in the Guaxindiba State Ecological Station, state of Rio de Janeiro, Brazil (21°24’S, 41°04’W). The climate is tropical with a dry winter (Aw, Köppen climate type; Alvares et al. 2013), a mean annual temperature of 23 ºC, and a mean annual precipitation of 1000 mm (Hijmans et al. 2005). The rainforest is located in an 85.6-ha area mostly within the Itajaí-Açu watershed, state of Santa Catarina, Brazil (26°24’S, 50°21’W). The climate is non-seasonal, humid subtropical, with a hot summer toward the east coast (Cfa Köppen climate type; Alvares et al. 2013), a mean annual temperature of 16 ºC, and a mean annual precipitation of 1600 mm (Hijmans et al. 2005 – Table 1). Species and trait data were obtained from field surveys (*Restinga* and semideciduous forest) as well as from the literature (rainforest, Vibrans et al. 2010, Rodrigues et al. 2018, and the Inventário Florístico Florestal de Santa Catarina - www.iff.sc.gov.br).

Table 1 Climatic and edaphic conditions at three vegetation types of the Atlantic forest

		Vegetation types		
Abiotic factors	**Units**	**rainforest**	**semideciduous forest**	***Restinga***
Coordinates		26°24'S, 50°21'W	21°24'S, 41°04'W	5°54'S, 35°10'W
Climate type		Cfa (Non-seasonal humid Subtropical)[a]	Aw (Tropical rainy with dry winter)[a]	As (Tropical with dry summer)[a]
Mean annual temperature	°C	16.6[b]	23.4[b]	25.7[b]
Temperature seasonality	%	331.30[b]	201.88[b]	102.89[b]
Mean annual precipitation	mm	1600[b]	1034[b]	1411[b]
Precipitation seasonality	%	20.64[b]	50.18[b]	71.34[b]
Soil type	-	Yellow-red Podzolic, Cambisol, Gleysol[c]	Cohesive Yellow Latosol[d]	White sand Neosols with patches of Yellow and Red Latosols[e]
Sand content	%	25.71[f]	70.85[g]	96.02[*]
Clay content	%	-	23.90[g]	2.07[*]
Silt content	%	-	5.28[g]	1.92[*]
Soil humidity	%	-	7.90[h]	4.07[i]
pH	Unitless	4.64[f]	5.47[f]	5.66[f]

[a] Abbreviations are based on the Koppen climate classification by Alvares et al. (2013)

[b] Climate variables obtained from the WorldClim Project (Hijmans et al. 2005)

[c] EMBRAPA (2004)

[d] EMBRAPA (2006)

[e] SUDENE/DNPEA (1971)

[f] Soil conditions extracted from the Soil Grid Database (Hengl et al. 2017)

[g] Abreu (2013)

[h] Pireda et al. (2019)

[i] Silva et al. (2016)

[*] Private data

(-) Data not available

Data collection and functional traits

A total of 74 woody species were studied (67 trees and seven shrubs), with 32 species from *Restinga*, ten species from the semideciduous forest, and 32 species from the rainforest (Supplementary Material Table S1). We selected only the most common species in each study area. Despite the number of species used being lower than the species richness found in these vegetation types, particularly in the rainforest, a diversity of genera and families was considered to represent functional diversity, as much as possible. Across vegetation types, leaf and wood traits were collected from the same individuals. Only adult individuals in the reproductive stage were sampled. In the *Restinga*, where the vegetation is shorter due to winds and high intensity of irradiance, the diameter at soil level (DSL) was used, while in other areas the diameter at breast height (DBH) was used.

From the total individuals sampled, we collected data from 5 to 10 individuals for leaf traits, and from 3 to 5 individuals for wood traits per species for each vegetation type. In the *Restinga*, up to ten individuals with DSL ≥ 3 cm were sampled, all in different plots among 80 plots of 25 m^2. In the semideciduous forest, from one to two individuals with DBH ≥ 5 cm were sampled across five plots of 400 m^2. In the rainforest, up to ten individuals with DBH ≥ 10 cm were sampled, all in different plots among 64 plots of 4.000 m^2 (Vibrans et al. 2010).

The functional traits studied were: leaf area (LA - cm^2), specific leaf area (SLA - $cm^2\ g^{-1}$), leaf dry matter content (LDMC - mg g^{-1}), wood density (WD - g cm^{-3}), xylem vessel diameter (VDiam - µm), xylem vessel density (VDens - n° mm^{-2}), and vulnerability index (VI - vessel diameter/density; unitless). All traits were collected and measured according to standardized protocols (Peréz-Harguindeguy et al. 2013). As our trait data came from independently conducted studies, there were differences in methodologies used to collect and measure some traits, including (1) wood density, where samples were obtained from the main stem in the semideciduous forest, from lateral branches in the rainforest, and from the main stem or lateral branches in the *Restinga*; (2) xylem vessels, which were measured by the method of permanent and semi-permanent slides and analyzed using a light microscope with a coupled camera in the semideciduous forest, and by polished wood sections analyzed using a stereo microscope with a coupled camera in the rainforest and *Restinga* (Rodrigues et al. 2018; Campbell et al. 2016; Silva et al. 2018; Pireda et al. 2019; Freitas 2020); and (3) specific leaf area, which was measured from leaf discs or entire leaves in the semideciduous forest (Pireda et al. 2019; Freitas 2020), and from entire leaves in the rainforest and *Restinga* (Rodrigues et al. 2018; Silva et al. 2018). While these methodological differences would not allow the comparison of trait values between vegetation types, it is worth noting that we did not compare trait values, but rather the variation and covariation indices (ranging from 0 to 1) calculated for each set of individuals of each species and vegetation types separately. Therefore, the variables used in the main analyses were the indices, which were related through Pearson correlations, as explained below, eliminating the effects of methodological differences on the results.

Data analysis

Trait data were organized for each vegetation type and plant organ. Missing data represented a very small portion of the overall data (3%, 1.29%, and 1.95% of the total leaf and wood traits for *Restinga*, semideciduous forest, and rainforest, respectively), which were estimated by the multiple imputation for chained equations function of the 'mice' package (van Buuren and Groothuis-Oudshoorn 2011). The missing data imputed for *Restinga* were: 42 values (19 for LA, 19 for SLA, and 4 for WD); semideciduous forest: 4 values for WD; and rainforest: 21 values (2 for LA, 2 for SLA, 1 for LDMC, 4 for VI, 4 for VDiam, 4 for VDens and 5 for WD).

Data were Box-Cox transformed to achieve normality using the 'MASS' and 'rcompanion' packages (Venables and Ripley 2002; Mangiafico 2021) and then used to compute Pearson correlations among traits for each species and for each plant organ separately. Correlation matrices for leaf traits and wood traits for each species in each vegetation type were constructed to represent trait covariation. Subsequently, we computed the mean of the sum of the absolute values of the pairwise correlation coefficients regardless of statistical significance for each matrix, resulting in two covariation values (leaf and wood covariation) for each species in each vegetation type (Armbruster et al. 2014). Non-significant correlations for this computation were considered representative of trait independence, i.e., the decoupling between traits, leading to low trait covariation (values closer to 0). For trait variation, another index was calculated using the difference between the maximum and minimum values divided by the maximum value of each trait in each organ per species in each vegetation type (Valladares et al. 2000). Then, for each species, we obtained three values of leaf trait variation (referring to three leaf traits used) and four values of wood trait variation (referring to four wood traits). Afterward, we averaged the three values of leaf trait variation for each species and averaged the four values of wood trait variation for each species, resulting in two values of trait variation per species in each vegetation type (leaf and wood trait variation). In the end, we obtained four variables related to the indices of variation and covariation: leaf variation and covariation and wood variation and covariation, with the highest amount of trait variation and covariation closest to 1.

To answer our first question (Is there a trade-off between trait variation and covariation within and across the vegetation types?), we performed Pearson correlations between trait variation and covariation indices. The comparisons included: wood variation × wood covariation, leaf variation × wood covariation, leaf covariation × wood covariation, leaf variation × wood variation, leaf covariation × wood variation, and leaf variation × leaf covariation. They were analyzed for all vegetation types together and separately. In addition, comparisons of variation and covariation between vegetation types were performed using an analysis of variance (ANOVA) followed by Tukey test (for all tests $\alpha = 0.05$).

To answer our second question (how does incorporating intraspecific trait variability alter the magnitude and pattern of trait covariation?) we performed network analyses using the *qgraph* function of the 'qgraph' package (Epskamp et al. 2012) for each vegetation type separately based on trait correlations for two different scenarios. One only took into account average differences between species (interspecific trait variability), while the other took into account both the differences between species as well as between individuals (inter + intraspecific trait variability). This framework was based on correlations because there is no assumption of cause-and-effect relationships among traits (Messier et al. 2017; Li et al. 2021a; Homeier et al. 2021). The complexity of intra- and interspecific networks was evaluated by the strength and number of significant correlations. All analyses were performed in the R Software version 4.3.1 (R Core Team 2023).

Results

The wood variation and covariation indices changed across vegetation types (Fig. 2). A higher wood covariation was found in the *Restinga* ($P = 0.0004$) and semideciduous forest ($P = 0.039$) when compared to the rainforest (Fig. 2a), while higher wood variation was found in the rainforest ($P \leq 0.001$ for *Restinga* and $P \leq 0.001$ for semideciduous forest, Fig. 2b). No difference was found for leaf variation and covariation between vegetation types (Fig. 2c-d). All wood and leaf trait values differed significantly between vegetation types (Supplementary Material Figure S1).

Wood density was higher and specific leaf area was lower in the semideciduous forest and *Restinga* compared to the rainforest (Supplementary Material Figure S1c; f)

A negative correlation between wood variation and wood covariation was found (r: -0.45, $p < 0.001$, Fig. 3a), and a positive correlation between wood variation and leaf covariation (r: 0.29, $p = 0.01$, Fig. 3e) for the three vegetation types together (Fig. 3 and Table 2). Within vegetation types, two significant correlations were found: a negative correlation between leaf variation and wood covariation for the rainforest (r: -0.37, $p = 0.04$, Fig. 3b and Table 2), and a positive correlation between wood variation and leaf covariation for the semideciduous forest (r: 0.64, $p = 0.04$; Fig. 3e and Table 2). No relationship between other combinations of leaf and wood trait variation and covariation indices was found (Fig. 3c-d; f)

In all three vegetation types, incorporating intraspecific trait variability (Fig. 4, right column) increased the detection of significant trait correlations within and among plant organs, as well as the number and strength of trait covariation. Intraspecific trait variability contributed more than interspecific trait variability (Fig. 4, left column) in the *Restinga* and the semideciduous forest (four new correlations for each vegetation type, Fig. 4c-f) and much less for the rainforest (one new correlation) (Fig. 4a-b). More correlations were found among wood than leaf traits, and the covariation strength was slightly lower in intraspecific trait variability than that of the interspecific one. The direction of most correlations did not vary across networks, except for leaf area and specific leaf area in comparing intraspecific trait variability networks for the semideciduous forest and *Restinga* (Fig. 4d-f).

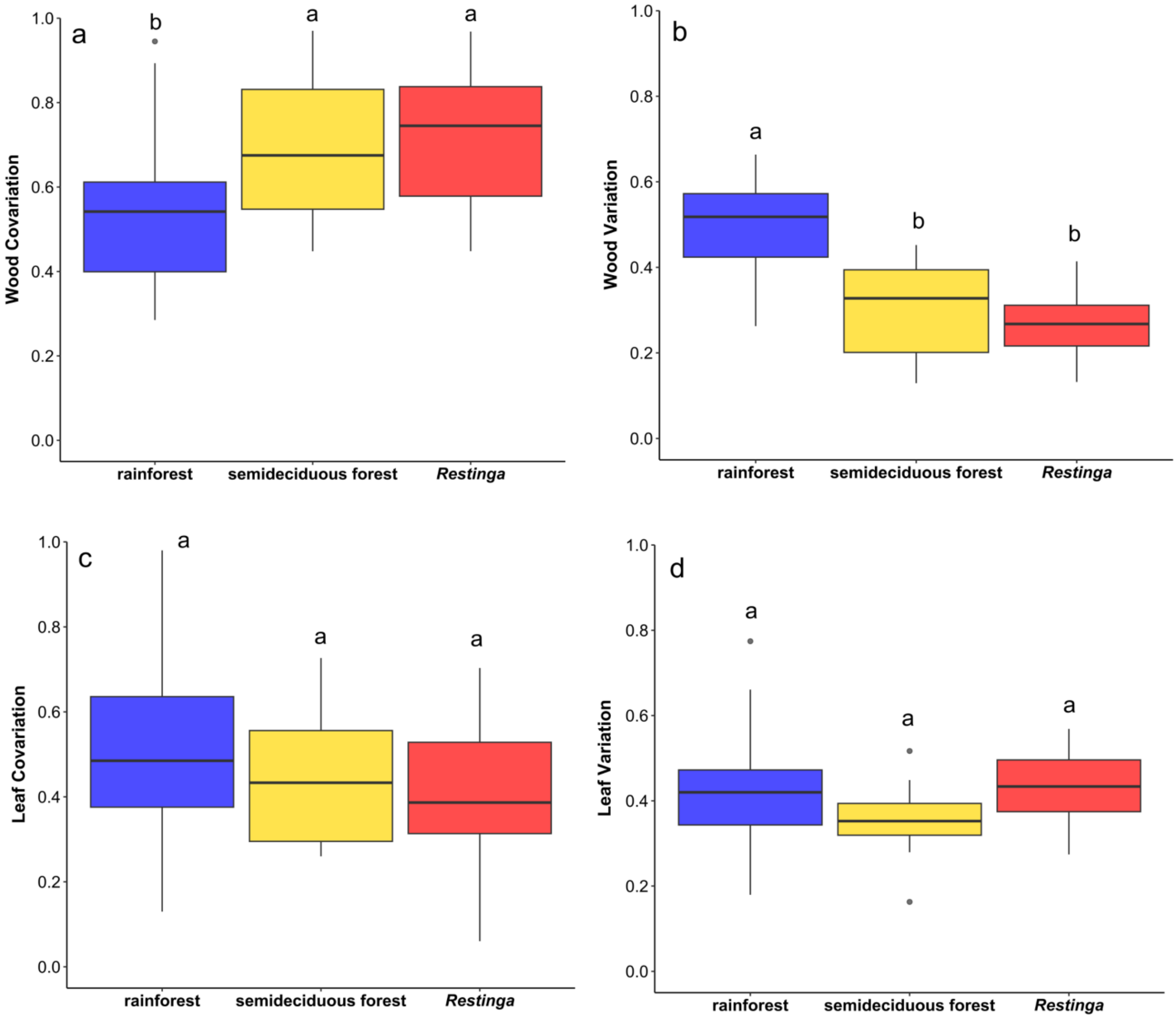

Fig. 2 Boxplots of the four leaf and wood indices. Wood covariation (a), wood variation (b), leaf covariation (c), leaf variation (d). Significant differences between vegetation types are indicated by different letters ($p \leq 0.05$)

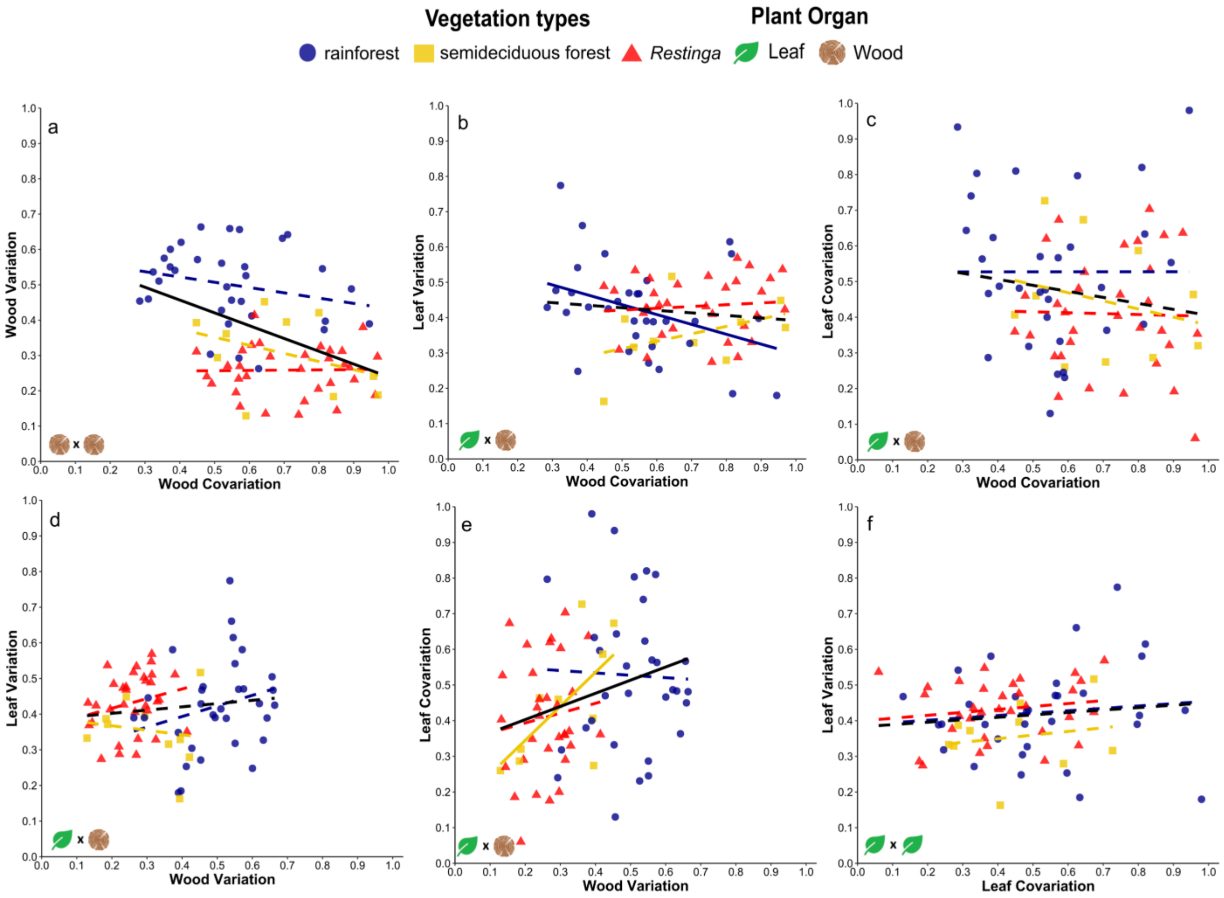

Fig. 3 Relationships between the indices of variation and covariation for leaf and wood traits across and within the three studied vegetation types of the Atlantic forest. Wood variation × wood covariation (a), leaf variation × wood covariation (b), leaf covariation × wood covariation (c), leaf variation × wood variation (d), leaf covariation × wood variation (e), leaf variation × leaf covariation (f). Dashed lines represent non-significant relationships

Table 2 Correlation table for each vegetation type showing the relationship strength and significance (values below and above the diagonal, respectively) between pairs of indices based on the variation and covariation of leaf and wood traits. Values in bold represent significant correlations between pairs of indices

Vegetation type		Correlations			
		Leaf Covar	Wood Covar	Leaf Var	Wood Var
all forests	Leaf Covar		0.294	0.312	0.307
	Wood Covar	0.12		**0.013**	**0.000**
	Leaf Var	0.12	0.29		0.170
	Wood Var	-0.12	-0.45	-0.16	
rainforest	Leaf Covar		0.997	0.560	0.852
	Wood Covar	0.00		**0.039**	0.191
	Leaf Var	0.11	-0.37		0.174
	Wood Var	-0.03	-0.24	0.25	
semideciduous forest	Leaf Covar		0.484	0.620	**0.044**
	Wood Covar	-0.25		0.242	0.288
	Leaf Var	0.18	0.41		0.679
	Wood Var	0.64	-0.37	-0.15	
Restinga	Leaf Covar		0.898	0.375	0.516
	Wood Covar	-0.02		0.609	0.926
	Leaf Var	0.16	0.09		0.207
	Wood Var	0.12	0.02	0.23	

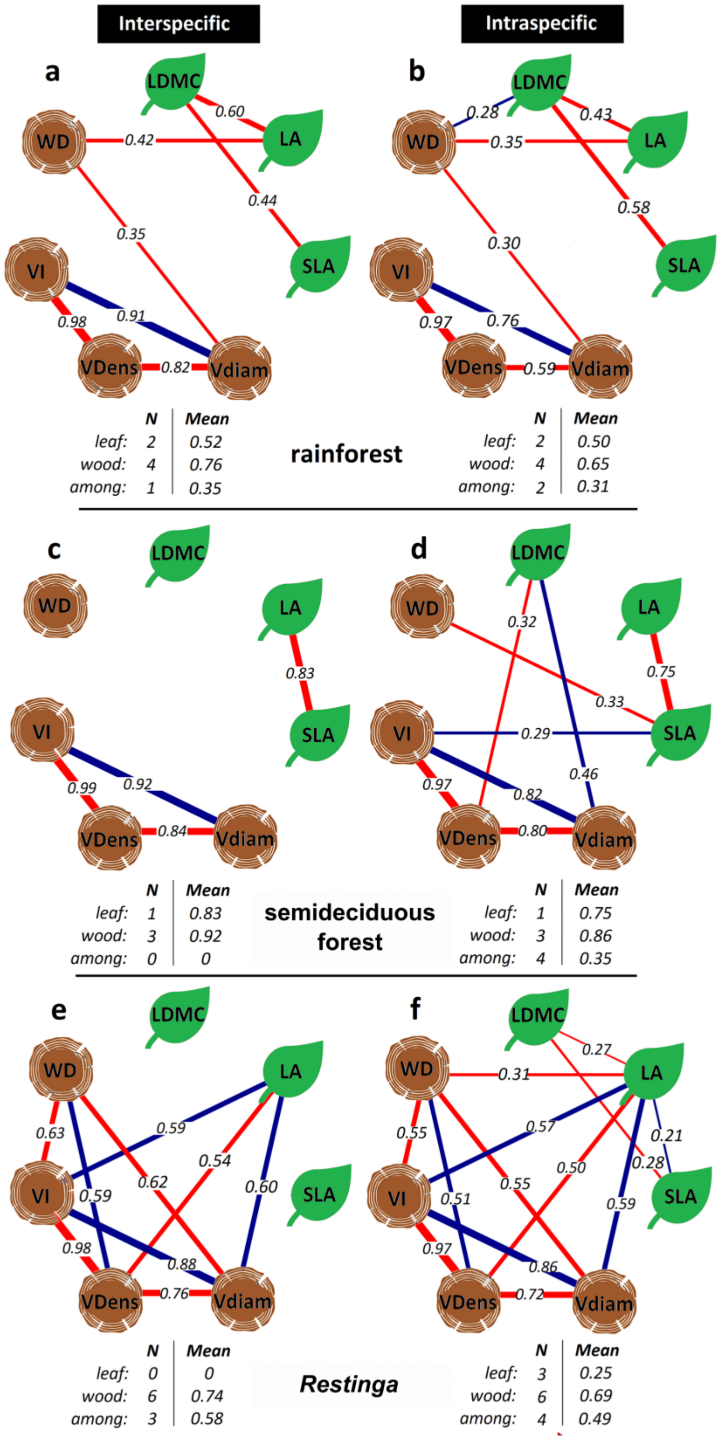

Fig. 4 Leaf and wood trait covariation considering both inter- (a, c, and e) and intraspecific trait variability (b, d, and f) at three vegetation types of the Atlantic Forest. Blue and red lines refer to positive and negative correlations, respectively, and their strength is represented by the line width (correlation coefficients). Acronyms of traits: LDMC, Leaf Dry Matter Content; LA, Leaf Area; SLA, Specific Leaf Area; Vdiam, Vessel Diameter; Vdens, Vessel Density; VI, Vulnerability Index, and WD, Wood Density. N: Number of connections between traits; Mean: mean correlations of the number of connections between traits

Discussion

Our study revealed: 1) the existence of trade-offs between wood variation and wood covariation, and leaf variation and wood covariation as well as a positive association between leaf covariation and wood variation within and across vegetation types; and 2) a higher number of correlations from the rainforest to the *Restinga*, particularly after considering intraspecific trait variability, despite their correlations having slightly lower strength.

According to the conceptual framework underpinning our study (Fig. 1), one would expect a higher covariation between leaf and wood traits in the resource-limited *Restinga*, lower covariation in the resource-rich rainforest, and a trade-off between variation and covariation. Our first hypothesis was partly supported, as we found higher covariation both in the resource-limited *Restinga* and semideciduous forest, and negative and positive associations between variation and covariation for wood and leaves within and across vegetation types. In line with expectations regarding the environment's influence on trait variation and covariation, both resource-limited environments exhibited greater covariation and lower variation compared with the rainforest.

A decrease in trait variation in conjunction with increasing trait covariation has been described in resource-limited conditions, particularly when abiotic constraints are related to irradiance and water (Schlichting 1989; Gianoli 2004; Valladares et al. 2005; Gianoli and Palacio-López 2009; Matesanz et al. 2010; Dwyer and Laughlin 2017). Water availability is a primary limiting resource for trees and shrubs in broad-scale contexts is water availability (Padilla and Pugnaire 2007). Since water can limit plant functioning and trait dimensionality, drier and seasonal environments are associated with a more reduced multifunctional space than non-seasonal, productive ones (Jacobsen et al. 2008; Dwyer and Laughlin 2017; Costa-Saura et al. 2019; He et al. 2021; Silva et al. 2021). Consequently, trait variability is expected to change along with relationships across vegetation types in distinct environmental contexts (de la Riva et al. 2016). In this study, wood traits were more variable in the rainforest than in both seasonal vegetation types (semideciduous forest and *Restinga*). Greater wood variation in the rainforest studied may allow greater resource partitioning for a given species or different species and facilitate their coexistence in this more productive forest (Clark 2010; de la Riva et al. 2018; Michelaki et al. 2019). In mesic environments like the rainforest, intense competition among species has been reported (Rozendaal et al. 2020). The higher variation in functional trait values in this environment may provide organisms with a competitive edge, leading them to occupy many different niches through the adoption of different resource acquisition strategies, mainly if highly overlapping niches occur (Michelaki et al. 2019; Rozendaal et al. 2020). On the other hand, trait variation is often reduced in stressful environments to avoid the costs of maintaining non-adaptive or maladapted phenotypes (Valladares et al. 2007; Vieira et al. 2021). Therefore, high variation may also confer disadvantages in growth and survival if the costs of maintaining it are high (Vieira et al. 2021).

In resource-limited communities (spatially and seasonally) such as *Restingas* and semideciduous forests, species may have competitive advantages over those that do not express their traits in an integrated manner. Thus, individuals with more integrated traits (exhibiting a higher number of stronger trait correlations) are better able to cope with limiting abiotic conditions (Murren 2002; Pigliucci 2003; Delhaye et al. 2020; Silva et al. 2021). For example, the risks of wood embolism formation and hydraulic vulnerability, which will ultimately compromise leaf photosynthetic capacity, may be avoided by increasing the covariation between wood density and xylem vessel diameter/density (Sperry et al. 2008; Chave et al. 2009; Pivovaroff et al. 2014, Simioni et al. 2020). Despite phylogenetic differences among species from the *Restinga* and semideciduous forest, the observed high wood covariation reveals a similar functionality that is probably driven by rainfall seasonality, but could also be to some extent due to biophysical properties such as the relationship between xylem vessel density and diameter (Marks and Lechowicz 2006, Pivovaroff et al. 2016). In the rainforest, there were species with high wood covariation, probably due to structural wood demands since light competition stimulates mature plants to invest in height and a dense canopy, with implications for tree hydraulic architecture (Martínez-Cabrera et al. 2011; Fajardo 2022). Thus, trait variation and covariation may assume distinct roles depending on the environmental demands the species experience.

The present study did not observe, the relationship between wood variation and wood covariation within each vegetation type. However, a trade-off between wood variation and wood covariation was found when all the vegetation types were analyzed together. As overall higher wood covariation reduces maladaptive variation, it may have ecological and evolutionary implications such as a facilitator of plant adaptation (Armbruster et al. 2014). In contrast to leaves, which are short-lived organs that can be replaced during water shortages, the longevity of wood implies long-term exposure to changes in water availability, which reduces variation and could lead to a meaningful trade-off in trait variation and covariation (Poorter et al. 2021; Ribeiro et al. 2022). However, due to the multifaceted functions of wood, greater trait variation may coincide with the presence of weaker trait covariation. The functional variation-covariation pattern observed for the wood was not observed for leaves when considering all vegetation types, probably due to their high plastic capacity and response to other filters that operate at each vegetation type (Violle et al. 2009; Li et al. 2021b). However, two alternative ways were found between leaf and wood within vegetation types, in some cases a vegetation type showing an integrated wood and a variable leaf and *vice-versa*. The leaf-wood variation and covariation relationships found within vegetation types (e.g., rainforest and semideciduous forest) may be an indication that the adaptive value of the same traits could translate into different phenotypes that plants are responding to their local environmental pressures or also being a result of correlational selection (Dwyer and Laughlin et al. 2017; Flores-Moreno et al. 2019; Sanaphre-Villanueva et al. 2022).

Overall, the trade-offs found in our data are consistent with other observational studies, even partially (Gianoli and Palacio-López 2009; Godoy et al. 2012). Additionally, the positive relationships found between trait variation and covariation within and across vegetation types are also in line with the results of previous studies, indicating that both mechanisms can act simultaneously between plant organs. This reinforces recent findings indicating that trait covariation is not always an antagonistic mechanism to variation and that both mechanisms can shift together in a coordinated manner in response to environmental pressures (Zimmermann et al. 2016; Pireda et al. 2019; Matesanz et al. 2021; Borges et al. 2022; Oyanoghafo et al. 2023; Shi et al. 2023). Although higher trait covariation is often expected in resource-limited environments, it is important to note that lower trait covariation could also be found, especially when involving differential plasticity of traits (i.e. two traits differing in their variation, without affecting covariation) (Matesanz et al. 2021). According to Matesanz et al. (2021), differential trait plasticity allows certain flexibility to the covariation structure in different environments. This could also explain the different relationships found between variation and covariation for wood and leaf traits across and within vegetation types. Notably, the mixed results found in those studies and our study can be also attributed to the different indices used to assess trait variation and covariation (Matesanz et al. 2021). Therefore, caution should be taken when evaluating if the expression of trait variation may or may not be constrained by trait covariation because it can depend on what conditions species traits are studied and what metrics are being used.

In addition to the organ and environmental conditions, other factors interfere with the functional patterns of plants, such plant functional groups, growth forms, spatial scale, and phylogenetic relationships (Martínez-Cabrera et al. 2011; Apgaua et al. 2016; Michelaki et al. 2019). In a study, the influence of growth forms and phylogeny on wood trait variation and covariation was analyzed in 200 woody angiosperm plant species (65 shrubs and 135 trees) from dry, mesic, and rainforests (Martínez-Cabrera et al. 2011). It suggested that relationships between vessel traits and wood density differed between growth forms, as while trees showed covariation between vessel traits, wood density, and height, in shrubs wood density and vessel traits were independent. These findings remain consistent even when accounting for phylogenetic relationships (Martínez-Cabrera et al. 2011). Messier et al. (2017), studying 24 saplings of coexisting tree species in a temperate forest found weak and absent correlations at the local scale in the leaf economic spectrum (LES) and wood economic spectrum (WES) while examining the correlation of 20 leaf, branch, stem, and root traits known to be correlated on a global scale. They also found that phylogeny did not play an important role in structuring the correlation of traits related to the LES and WES at a local scale (Messier et al. 2017). This could be a condition found in our local study communities since it has been increasingly found that LES and WES correlated dimensions may not hold locally (Funk and Cornwell 2013; Messier et al. 2017). These studies demonstrate the necessity for a more thorough examination of these factors as drivers of plant trait variation and covariation.

An increasing number of studies comparing inter- and intraspecific trait variability have highlighted its key role in trait expression (Albert et al. 2010; Siefert et al. 2015; He et al. 2021; Homeier et al. 2021). Intraspecific trait variability can weaken overall trait covariation because phenotypic plasticity and ontogeny affect trait expression at small scales (Messier et al. 2017; Anderegg et al. 2018; He et al. 2021). On the other hand, interspecific trait variability results from evolutionary and environmental factors at larger scales, which can strengthen trait relationships

(Messier et al. 2017; Anderegg et al. 2018; He et al. 2021). Weak or non-existent correlations between some pairs of traits, especially within the leaf, suggest the existence of a wide range of trait combinations (He et al. 2021) often observed in tropical forests (Baraloto et al. 2010; Braga et al. 2016; Silva et al. 2021). According to Homeier et al. (2021), the contribution of intraspecific trait variability to trait covariation is substantial but smaller than the interspecific trait variability, and trait covariation is strengthened towards harsher conditions. In our study, the incorporation of intraspecific trait variability is not negligible, as it enhanced the number of trait covariations. Notably, in the *Restinga*, where trait expression is highly influenced by environmental conditions, incorporating intraspecific trait variability yielded the most pronounced effect. In this vegetation type, the chance of detecting significant correlations increased because intraspecific trait variability is reduced, and trait values vary more closely to the overall tendency of the pairwise correlations. As intraspecific trait variability increases toward the rainforest, values vary more independently, thus decreasing this chance. It is worth noting that despite overall differences between individuals, which diminish in seasonal systems, species have a high temporal plasticity regarding dry-to-wet dynamics (Silva et al. 2020). Although intraspecific trait variability enhanced the number of covariations, it is important to note that it slightly reduced the strength of trait covariations across vegetation types, which is in line with a previous study conducted in an evergreen broadleaf forest in eastern China (He et al. 2021).

The variation in water availability marking the vegetation types seems to reflect the internal correlations within each plant organ and interconnectivity among organs, mainly when considering the intraspecific trait variability. As observed elsewhere (Brancalion et al. 2012, He et al. 2021, Dwyer and Laughlin 2017), *Restinga* species need to maintain a more trait connections. This is attributed to the well-drained and oligotrophic sandy soils, which limit trait variation, particularly those associated with water status. Although the semideciduous forest had the least complex trait covariation networks among the three vegetation types, the consideration of intraspecific trait variability revealed new significant correlations that overcame the number of correlations found in the rainforest, which we considered the least environmentally stressful end of the studied environmental gradient. Overall, these results are in line with previous studies that showed evidence that environmental filters may not select trait values independently but rather select viable trait combinations as harshness increases while accounting for intraspecific trait variability (Dwyer and Laughlin et al. 2017; Delhaye et al. 2020; He et al. 2021; Homeier et al. 2021).

The emphasis on trait variation versus covariation has a recent history in community ecology, and further studies are needed to investigate the effects of phylogeny, plant functional groups, growth forms, plant organs, spatial scale, and coarser stress gradients to understand this relationship better. According to Armbruster et al. (2014), having a solid theoretical basis for the proposed predictions is important, making it easier to direct the trait variation and covariation discussions. In addition, the authors suggest that studies comparing indices obtained in different studies should be evaluated with cautiously, as it could represent a bias in the data. In this regard, we believe our results contribute to this discussion by providing evidence that both trade-off and positive relationships between trait variation and covariation may exist in addition to being context-dependent, and by adding some evidence of trait covariation and variation within communities, which is less understood than across communities along environmental gradients (Dywer and Laughlin 2017). Also, distinct vegetation types are marked by significant changes in the number and strength of trait covariation, which seems to be largely caused by environmental conditions and should be further considered in the context of climate change. The intraspecific trait variability was not only important for covariation as well as its absence could have underestimated the differences between species from different tropical vegetation types, highlighting the loss of functional information when relying solely on trait species' means. Therefore, our study also provides further evidence for the connection between intraspecific and interspecific trait variability to trait covariation in forest communities along gradients of resource availability, which is still considered scarce (Kichenin et al. 2013; Schmitt et al. 2020; Homeier et al. 2021).

Extending these discussions about trait variation and covariation to more environmental contexts will help to advance our understanding of how species function under current climatic conditions and potentially serve as a basis for further discussions on the role of climate change in modifying these trait dimensions (Laughlin et al. 2017). Climate change is expected to increase the frequency, intensity, and unpredictability of disturbance events, such as intense precipitation and prolonged droughts, and, consequently, modify species' demographic rates, system composition, structure, and functioning (Marengo et al. 2009; Chou et al. 2014, IPCC 2021). Therefore, it is crucial to understand plant responses to environmental changes, especially in functionally hyperdiverse biomes such as the Atlantic Forest (Silva et al. 2022), one of the three global biodiversity hotspots most vulnerable to climate change (Bellard et al. 2014; Trew and Maclean 2021).

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Statements and Declarations

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Supplementary material

Data that support the findings of this study from the rainforest are freely available in Rodrigues et al. (2018) and the Inventário Florístico Florestal de Santa Catarina (www.iff.sc.gov.br). Supplementary information associated with this article can be found, in the online version.

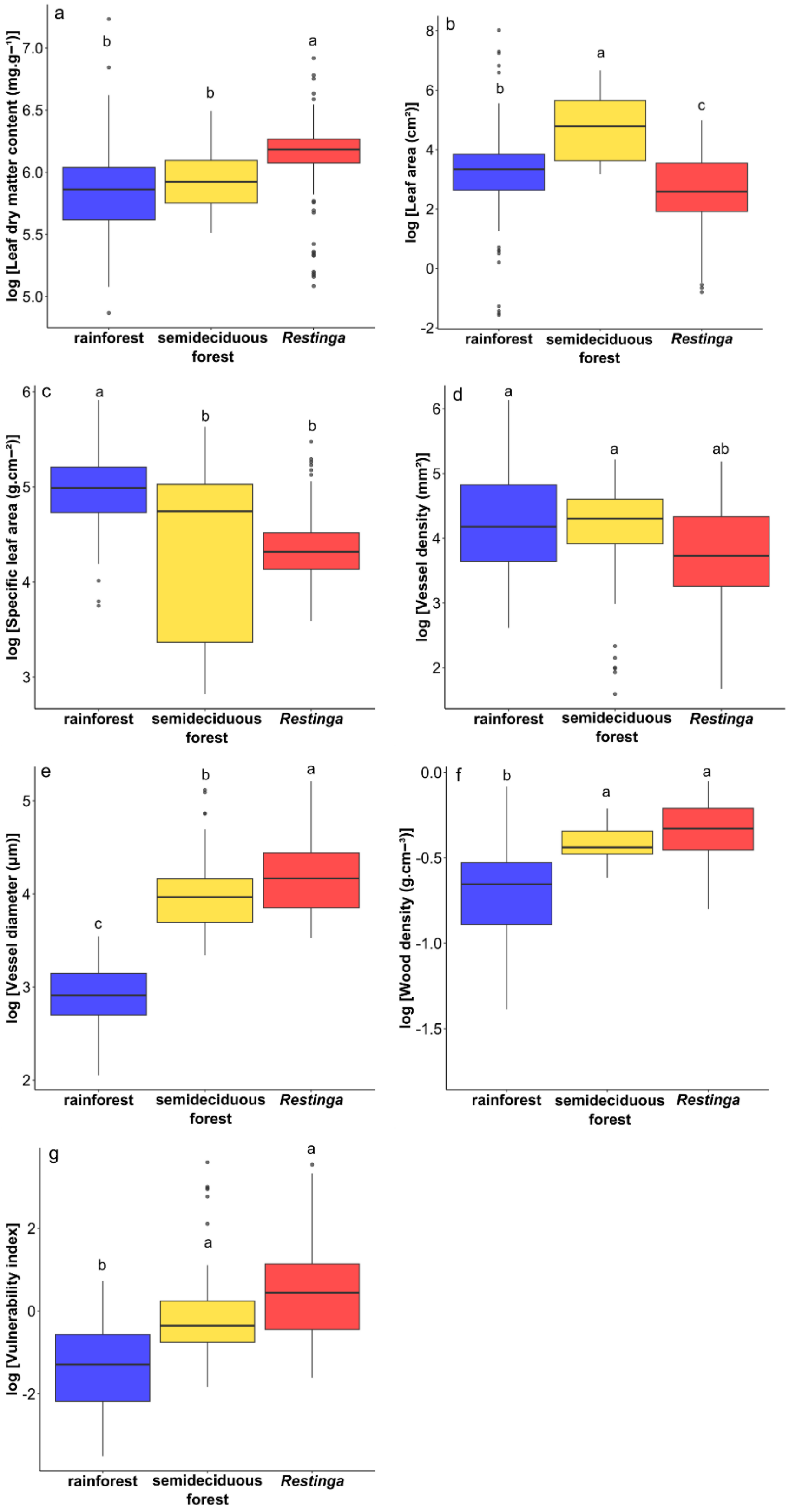
Supplementary Information The online version contains supplementary material available at: https://doi.org/10.1007/s42974--024-00196-4

Supplementary Material

Supplementary Material Table S1 – List of studied species, family, growth form, and vegetation types

Species	Family	Growth form	Vegetation type
Abarema langsdorffii	Fabaceae	tree	rainforest
Amaioua guianensis	Rubiaceae	tree	rainforest
Andira fraxinifolia	Fabaceae	tree	rainforest
Aspidosperma australe	Apocynaceae	tree	rainforest
Aspidosperma parvifolium	Apocynaceae	tree	rainforest
Aspidosperma tomentosum	Apocynaceae	tree	rainforest
Bathysa australis	Rubiaceae	tree	rainforest
Byrsonima ligustrifolia	Malpighiaceae	tree	rainforest
Cabralea canjerana	Meliaceae	tree	rainforest
Campomanesia guaviroba	Myrtaceae	tree	rainforest
Campomanesia reitziana	Myrtaceae	tree	rainforest
Chrysophyllum inornatum	Sapotaceae	tree	rainforest
Copaifera trapezifolia	Fabaceae	tree	rainforest
Coussarea contracta	Rubiaceae	tree	rainforest
Esenbeckia grandiflora	Rutaceae	shrub	rainforest
Eugenia involucrata	Myrtaceae	tree	rainforest
Ficus adhatodifolia	Moraceae	tree	rainforest
Guapira opposita	Nyctaginaceae	tree	rainforest
Hirtella hebeclada	Chrysobalanaceae	tree	rainforest
Inga marginata	Fabaceae	tree	rainforest
Jacaranda puberula	Bignoniaceae	tree	rainforest
Machaerium brasiliense	Fabaceae	tree	rainforest
Muellera campestris	Fabaceae	tree	rainforest
Myrceugenia ovalifolia	Myrtaceae	tree	rainforest
Myrcia brasiliensis	Myrtaceae	tree	rainforest
Myrcia splendens	Myrtaceae	tree	rainforest
Platymiscium floribundum	Fabaceae	tree	rainforest
Posoqueria latifolia	Rubiaceae	tree	rainforest
Psychotria vellosiana	Rubiaceae	tree	rainforest
Sessea regnellii	Solanaceae	tree	rainforest
Solanum sanctae-catharinae	Solanaceae	tree	rainforest
Tapirira guianensis	Anacardiaceae	tree	rainforest
Acanthocladus pulcherrimus	Polygalaceae	tree	semideciduous
Alseis pickelii	Rubiaceae	tree	semideciduous
Brosimum guianense	Moraceae	tree	semideciduous
Inga laurina	Fabaceae	tree	semideciduous
Manilkara subsericea	Sapotaceae	tree	semideciduous
Maytenus obtusifolia	Celastraceae	tree	semideciduous
Metrodorea nigra	Rutaceae	tree	semideciduous
Metternichia princeps	Solanaceae	tree	semideciduous
Paratecoma peroba	Bignoniaceae	tree	semideciduous
Trichilia lepidota	Meliaceae	tree	semideciduous

Anacardium occidentale	Anacardiaceae	tree	*Restinga*
Byrsonima gardneriana	Malpighiaceae	tree	*Restinga*
Byrsonima verbascifolia	Malpighiaceae	tree	*Restinga*
Calliandra parvifolia	Fabaceae	shrub	*Restinga*
Chamaecrista ensiformis	Fabaceae	tree	*Restinga*
Coccoloba laevis	Polygonaceae	shrub	*Restinga*
Coccoloba ramosissima	Polygonaceae	tree	*Restinga*
Coccoloba rosea	Polygonaceae	tree	*Restinga*
Erythroxylum passerinum	Erythroxylaceae	tree	*Restinga*
Eugenia azeda	Myrtaceae	tree	*Restinga*
Eugenia ligustrina	Myrtaceae	tree	*Restinga*
Eugenia luschnathiana	Myrtaceae	tree	*Restinga*
Eugenia punicifolia	Myrtaceae	shrub	*Restinga*
Eugenia umbelliflora	Myrtaceae	tree	*Restinga*
Guapira pernambucensis	Nyctaginaceae	shrub	*Restinga*
Guapira tomentosa	Nyctaginaceae	tree	*Restinga*
Guettarda platypoda	Rubiaceae	shrub	*Restinga*
Hancornia speciosa	Apocynaceae	tree	*Restinga*
Hirtella ciliata	Chrysobalanaceae	tree	*Restinga*
Lecythis pisonis	Lecythidaceae	tree	*Restinga*
Licania parvifolia	Chrysobalanaceae	tree	*Restinga*
Manilkara salzmannii	Sapotaceae	tree	*Restinga*
Maytenus erythroxylon	Celastraceae	tree	*Restinga*
Myrcia ramuliflora	Myrtaceae	tree	*Restinga*
Myrciaria tenella	Myrtaceae	tree	*Restinga*
Ouratea salicifolia	Ochnaceae	tree	*Restinga*
Padrosia restingae	Sapotaceae	tree	*Restinga*
Psidium oligospermum	Myrtaceae	tree	*Restinga*
Schoepfia brasiliensis	Schoepfiaceae	tree	*Restinga*
Strychnos parvifolia	Loganiaceae	shrub	*Restinga*
Tabebuia roseoalba	Bignoniaceae	tree	*Restinga*
Tocoyena sellowiana	Rubiaceae	tree	*Restinga*



Supplementary Material Figure S1 Boxplots of the three leaf (a-c) and four wood (d-g) traits from the three vegetation types of the Atlantic forest. Significant differences between vegetation types are indicated by different letters ($p \leq 0.05$)

CAPÍTULO 3:

Leaf and wood trait variability of co-occurring tree species along a local environmental gradient in an Atlantic tropical rainforest restoration area

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4. CAPÍTULO 3: Leaf and wood trait variability of co-occurring tree species along a local environmental gradient in an Atlantic tropical rainforest restoration area

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Abstract

Changes in forest structure caused by anthropogenic disturbances and forest management, such as those occurring in Atlantic forest ecosystems, can subject species to distinct microclimatic conditions and environmental gradients. To cope with the environmental variability, plants exhibit varying degrees of trait variation and covariation. It has been proposed that lower trait variation and higher trait covariation occur with increasing environmental harshness, although recent studies show contrasting results. In this context, this study investigated trait variability in three forest understory areas of a tropical Atlantic rainforest that form an abiotic gradient. Three co-ocorruing early light-demanding species in three areas were selected and leaf and wood morphological and physiological traits were analyzed to estimate trait variation and covariation. The results showed: 1) subtle differences in leaf traits between individuals, species, and areas; 2) low variation and covariation, and no relationship between these two components and 3) species' responses were more closely related to inter- and intraspecific trait variability than to understory microclimatic conditions. These findings suggest that the subtle differences in traits, along with the observed low variation and covariation, may reflect the absence of a pronounced abiotic gradient among the understory areas due to the homogeneity of the studied Atlantic rainforest. Additionally, the greater influence of inter- and intraspecific variability indicates that species responses are likely more closely associated with the vertical gradient of irradiance than the horizontal gradient across the three understory areas.

Keywords: Intraspecific trait variability, Trait-based ecology, Trait integration

Introduction

Environmental gradients subject plants to different abiotic conditions, selecting species capable of adjusting to changes in these conditions (Garnier et al. 2016; de Bello et al. 2021). As a way of coping with these environmental fluctuations, species exhibit variations in the expression of their morphophysiological, biochemical and phenological traits, presenting a wide functional and phenotypic variation of their characteristics (Violle et al. 2007; Volaire et al. 2020). Trait-based ecology is useful for understanding the responses of species to different environmental contexts, the variability of traits between and within species and populations, grouping them according to their ecological functions and investigating how selection acts on the expression of certain sets of traits (Díaz et al. 2016; Vitória et al. 2019; Ribeiro et al. 2022; Xavier et al. 2023). In some cases, in areas with low irradiance, the selection of species with high leaf area and low leaf thickness may be favored, as a way of increasing the light capture surface, while in locations with higher irradiance, the opposite characteristics may be favored (Díaz et al. 2016; Vitória et al. 2016; Pireda et al. 2019; Freitas et al. 2024a). Similarly, areas with greater water restriction select species with smaller xylem vessel elements and greater wood density, as a mechanism to avoid cavitation and have greater mechanical resistance (Chave et al. 2009; Xavier et al. 2023; Freitas et al. 2024a). In addition, the abrupt or discrete variation in environmental conditions, felt in different ways by plants, restricts the occurrence of species in certain areas or allows some species to be able to occupy and co-occur in contrasting environments (Maracahipes et al. 2018; Pireda et al. 2019; Oliveira et al. 2023).

This environmental filtering acts on the fitness of the species as a whole (Laughlin 2014; Laughlin and Messier 2015). However, approaches that focus exclusively on filtering isolated traits and their average values tend to simplify the complexity of the process, often failing to consider the extent to which trait variability occurs and the coordinated responses between more traits (Boucher et al. 2013; Laughlin 2014; Laughlin and Messier 2015). Trait variation and covariation are the mechanisms involved in the multidimensionality of species responses, reflecting phenotypic plasticity and integration, respectively (Pigliucci 2003; Valladares et al. 2007; Armbruster et al. 2014; Laughlin et al. 2017). Phenotypic variation is the expression of phenotype within species and populations, and can be the result of genetic and environmental factors, as well as the synergy between them (Valladares et al. 2007; Nicotra et al. 2010; Murren et al. 2015). Covariation and integration refer to the level (strength and direction) at which different traits are correlated, and can be the result of selective pressures that favor certain sets of traits that work in a coordinated manner (Murren 2002; Pigliucci 2003; Armbruster et al. 2014). Although both trait variation and covariation presuppose adaptive responses to fitness, they can have a null or non-adaptive value, generating noise in the variation of these traits (van Kleunen and Fisher 2005; Ghalambor et al. 2015; Vieira et al. 2021).

Studies suggest that variation and covariation vary across environmental gradients and are influenced by the level of environmental harshness. In a condition of increased environmental harshness, such as in more seasonal ecosystems, covariation would be favored, with species with greater covariation between traits (i.e. greater strength and number of correlations between them) being more able to pass through more restrictive filters (Gianoli 2004; Dwyer and Laughlin 2017; Delhaye et al. 2020; He et al. 2021). The opposite would be expected for variation in these same conditions of environmental harshness. In more stable and non-restrictive ecosystems, variation tends to increase, given the wider niche range of species due to the greater variation in resources and abiotic conditions (Valladares et al. 2005; Dwyer and Laughlin 2017). In parallel with these expectations and observations, the hypothesis emerged that variation and covariation occur in opposite directions, with variation being constrained by covariation (Gianoli 2001; Valladares et al. 2007; Gianoli and Palacio-López 2009; Matesanz et al. 2010). Despite the proposition of this relationship between variation and covariation, more recent studies have found contradictory and mixed results, showing that both mechanisms may actually act in synergism with species fitness, or may not be related at all (Pireda et al. 2019; Matesanz et al. 2021; Shi et al. 2023a; Freitas et al. 2024b).

Additionally, other studies have found that covariation can be weakened even in more restrictive conditions and ecosystems, due to biophysical constraints between traits, or intraspecific variability (Laughlin et al. 2017; He et al. 2021; Freitas et al. 2024b). Intraspecific variability has been re-evaluated in trait-based ecology studies (Albert et al. 2012; Siefert et al. 2015; Tautenhahn et al. 2020; Westerband et al. 2021). This is because, in studies of plant traits, this portion of variability was often underestimated (Kichenin et al. 2013; Sierfet et al. 2015; Funk et al. 2016).

Therefore, environmental variation tends to influence not only interspecific variability, but also intraspecific variability (Almeida et al. 2013). This has been observed especially in studies on the trait variation and covariation across environmental gradients, such as those evaluating this relationship with environmental harshness (Laughlin et al. 2017; He et al. 2021; Homeier et al. 2021), those evaluating the effect of biotic interactions such as competition (Clark et al. 2010) and those evaluating the interaction between abiotic and biotic factors on intraspecific variability (Helsen et al. 2017). There is evidence for greater intraspecific variability both in ecosystems with high environmental heterogeneity and in more homogeneous and non-restrictive ecosystems (Valladares et al. 2007, Valladares and Niinemets 2008, O'Sullivan et al. 2022).

Tropical forests can be interesting models for studying trait variability at different scales and environmental contexts, as they exhibit high environmental complexity and species diversity, containing around 60% of all vascular plants and one of the largest extensions of land in tropical America (Ulloa et al. 2017; Taubert et al. 2018; Vitória et al. 2019; FAO and UNEP 2020). Despite this high biodiversity and forest cover, a large part of tropical forests have been reduced by anthropogenic activities, such as conversion of areas for pasture and agriculture, exploitation of resources, introduction of exotic species, among others (Vitória et al. 2016; FAO and UNEP 2020; Ngo Bieng 2021; 2022). Currently, most tropical forests are secondary forests resulting from the conversion of primary forests by some kind of human intervention (FAO and UNEP 2020; Ngo Bieng 2021; 2022).

Brazil's Atlantic forest is an example of the result of these anthropogenic disturbances, stretching from the north to the south of the coastal region, and which still faces substantial exploitation throughout its entire extension (Ribeiro et al. 2009; Fundação SOS Mata Atlântica and Instituto de Pesquisas Nacionais Espaciais 2023; Broggio et al. 2024). The Atlantic forest was classified as the second largest tropical forest in South America, but today its extent has been reduced to 26% of its original coverage, also resulting in reduced functionality of this ecosystem (Ribeiro et al. 2009; Joly et al. 2014; Faria et al. 2023; Broggio et al. 2024). Due to deforestation and conversion of primary areas, it is estimated that between 32-40% of the Atlantic forest cover is secondary forest in the early to intermediate stages of regeneration and small fragments of less than 50 ha (Morellato and Haddad 2000; Ribeiro et al. 2009; Joly et al. 2014; Rezende et al. 2018). For this reason, the Atlantic forest is also classified as one of the world's 35 biodiversity hotspots, one of the three regions particularly vulnerable to climate change, urbanization and species invasion, and one of the biomes with a high priority for conservation and restoration (Mittermeier et al. 2011; Bellard et al. 2014; Strassburg et al. 2020; Trew and Maclean 2021). The high environmental heterogeneity found in the Atlantic forest, caused by its wide geographical variation, has enabled the formation of different environmental gradients, including climatic, topographical and edaphic (Oliveira-Filho and Fontes 2000; Ribeiro et al. 2011; Vitória et al. 2019). Identifying the factors that regulate the ecological and physiological processes of plant species is crucial to understanding the functionality of hyperdiverse ecosystems such as the Atlantic forest (Valladares et al. 2014; Vázquez et al. 2015). In addition, knowledge of the functionality of species, through trait variation and covariation, can serve as an important tool for future conservation actions in this ecosystem.

The União Biological Reserve (ReBio União), an integral protection area of the tropical Atlantic forest, has a history of fragmentation and forest management practices, converting the fragments resulting from these disturbances over the years into areas in the secondary regeneration stage, especially after the management and removal of the exotic species *Corymbia citriodora*, through ringing and clear-cutting techniques (Instituto Chico Mendes de Conservação 2008; 2023). Due to this history, these areas have different ages of natural regeneration and, consequently, different abiotic conditions of the forest understory (Vieira et al. 2015; 2021). Some studies have been carried out with the native tree species of this ecosystem in these different fragments of secondary forest, showing different adjustments of their traits to changes in these conditions both spatially and temporally (Teixeira et al. 2015; 2018; 2020; Vieira et al. 2015; 2021; Vitória et al. 2016; 2018). However, studies evaluating variation and covariation in relation to the consequences of forest management on shrub and tree species in this ecosystem are still incipient, as well as this relationship in general ecological studies.

Following the aforementioned discussion, this study of leaf and wood traits of three co-occurring species in three areas of ReBio União, which form a local abiotic gradient, aimed to answer the following questions: 1) Do leaf and wood traits differ between areas and species? 2) How does trait variation and covariation occur and what is the relationship? 3) How much of the total trait variation is explained by interspecific variability, intraspecific variability and understory condition?

Material and Methods

Study sites

This study was conducted in the União Biological Reserve (ReBio União), Rio de Janeiro, Brazil, in the Atlantic Forest domain (Fig. 1, 22° 27' 30" S; 42° 02' 14" W). The vegetation of ReBio União is classified as lowland and submontane dense ombrophilous forest (Instituto Brasileiro de Geografia e Estatística 2012). The region's climate is tropical humid with a dry winter (Aw, Alvares et al. 2013), with average annual temperatures ranging from 18°C to 25°C and average annual rainfall ranging from 1100 to 2400 mm (Instituto Chico Mendes de Conservação 2008; Teixeira et al. 2015; 2018; Vieira et al. 2015; Vitória et al. 2016). The rainy season occurs between October and April, concentrating approximately 80% of the annual rainfall, while the dry season is short, occurring between May and August, with an average monthly rainfall of 50 to 100 mm (Instituto Chico Mendes de Conservação 2008; Braga et al. 2016; Vitória et al. 2018; Teixeira et al. 2020; Vieira et al. 2021). The soils are classified as latosolic dystrophic red-yellow, with sandy clay texture, characterized by their low natural fertility (Miranda et al. 2007; Santos et al. 2018). ReBio União is made up of preserved forest areas, restoration areas with native species and managed areas where clear-cutting, selective cutting and/or ringing of the exotic eucalyptus species *Corymbia citriodora* (Hook.) K.D. & L.A.S. Jonhson have occurred (Instituto Chico Mendes de Conservação 2008; 2023). Forest management in the areas of ReBio União has led to changes in microclimatic conditions, especially in the understory, such as the availability of irradiance, water availability, air and soil temperature, as well as forest cover (Evaristo et al. 2011; Vieira et al. 2015; 2021; Teixeira et al. 2020; Vitória et al. 2016).

For this study, three forest understory areas were selected in 10 x 20 m plots that differ in terms of forest management and preservation (due to the removal of eucalyptus) and microclimatic conditions (Table 1): 1) Exposed Understory: a restoration area with a regenerating understory, with native species planted after eucalyptus cutting, sparse vegetation, with open areas and clearings with a high presence of grasses, with 74% canopy cover and the highest irradiance of the three areas (Table 1); 2) Intermediate Understory: forest area with a well-developed canopy and dense understory of native species with the presence of some clearings and exposed to intermediate irradiance compared to the other two areas, with 90% canopy cover (Table 1); 3) Closed Understory: an area of secondary forest in an advanced successional stage, with a well-developed tree stratum and dense understory, also showing 90% canopy cover and lower irradiance than the other two areas selected (Table 1). Exposed Understory is a restoration area with more recent forest management (occurred in 2013; Vieira et al. 2021).

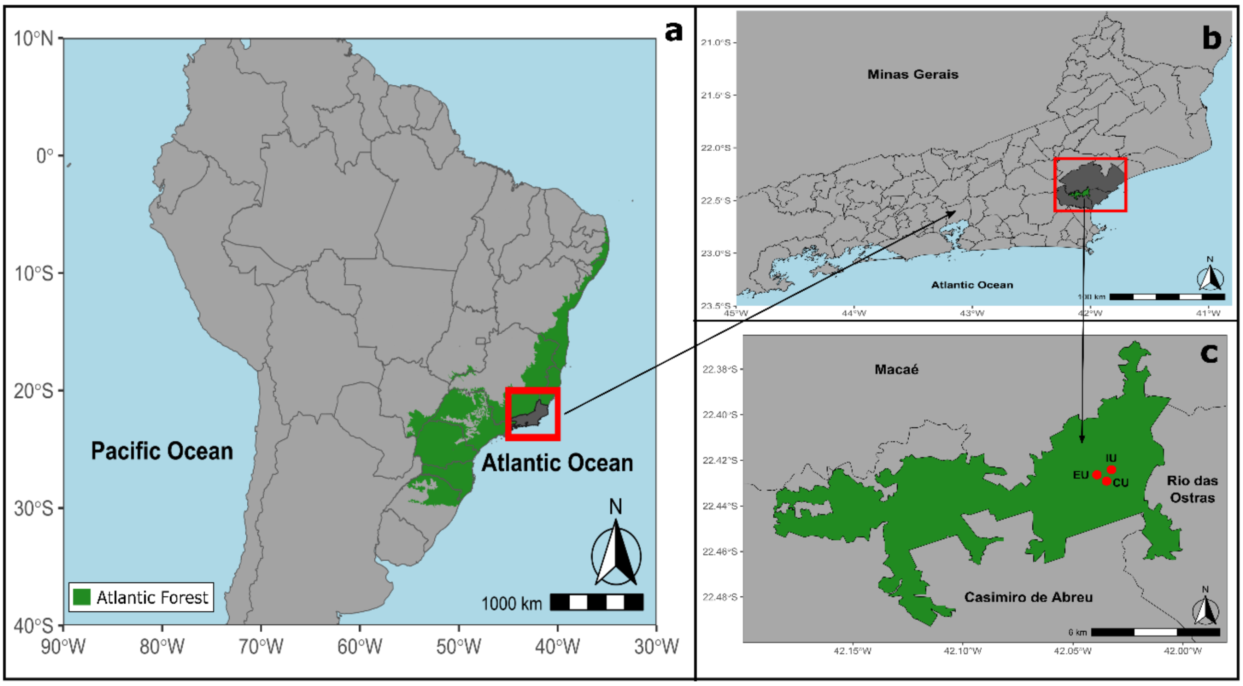


Fig. 1 Location of study areas in ReBio União, Brazil. a – placement of areas within the Atlantic forest domain. b – placement of areas within the state of Rio de Janeiro (RJ), Brazil. c – Boundaries of ReBio União among Casimiro de Abreu, Rio das Ostras e Macaé municipalities, RJ, Brazil. EU: Exposed Understory, CU: Closed Understory, IU: Intermediate Understory

Table 1 Understory microclimatic characteristics between three areas of ReBio União, Brazil. Values represent mean ± standard deviation (n=20). Different letters indicate differences in microclimatic variables between areas ($p < 0.05$)

Microclimatic characteristics*	**Exposed Understory**	**Intermediate Understory**	**Closed Understory**
Irradiance (µmol m^{-2} s^{-1})	824.35 ± 466.70^a	207.43 ± 427.12^b	49.40 ± 69.83^c
Air humidity (%)	57.05 ± 0.87^c	63.33 ± 0.88^b	65.57 ± 1.27^a
Air temperature (°C)	31 ± 0.39^a	30.05 ± 0.32^b	29.80 ± 0.32^b
Wind speed (m/s)	0.88 ± 0.45^a	0.18 ± 0.12^b	0.13 ± 0.14^b
Soil surface temperature (°C)	25.60 ± 1.21^a	23.95 ± 0.99^b	23.41 ± 0.53^b
Vapor pressure deficit (kPa)	1.93 ± 0.07^a	1.56 ± 0.05^b	1.45 ± 0.06^c
Canopy cover (%)	74 ± 25.12^b	89.56 ± 4.55^a	89.92 ± 7.15^a
Understory conditions	Sparse with clearings	Well-developed, with clearings	Dense, well-developed, no clearings

Species selection and data collection

Individuals were tagged in the field and georeferenced using a GPS (GPSMAP 60 CSx, Garmin, USA, Table S1). Three native, evergreen, woody, shrub-tree and co-occurring species were selected in the three areas used in this study: *Xylopia sericea* A. St. -Hill, *Cupania oblongifolia* Mart. and *Miconia cinnamomifolia* (DC. Naud.) (Table 2), *X. sericea* being one of the most abundant species in Rebio União (Evaristo et al. 2011). In each selected area, between 7 and 10 adult individuals with a diameter at breast height ≥ 5 cm of each species were sampled for leaf, wood and height analysis. All the leaves used in the analysis were collected from the third pair, mature, fully expanded, photosynthetically active, free of herbivory and senescence marks. Second and third order branches were collected for wood density analysis. The leaf samples from each individual were collected from the same branch used for the wood samples. The same leaves were used to remove leaf discs and determine photosynthetic pigments, phenolic compounds, chlorophyll content and morphological traits. The maximum plant height (in meters) was estimated from a reference object of known length for each individual in each area based on trigonometric principles (Pérez-Harguindeguy et al. 2013). All the analyses and sampling were carried out during the dry season of 2022, between the months of May and July.

Table 2 Ecological characterization of species selected in the areas of ReBio União, Brazil

Species	Family	Habit	Leaf habit[2]	Leaf division Phyllotaxis[3]	Successional group[2]	Dispersal syndrome[2]	Distribution[3]
Xylopia sericea A.St. -Hill	Annonaceae	Shrub/Tree	Evergreen	Simple, Alternate	Pioneer; Light-demanding early successional	Zoocoric	Amazon, *Cerrado*, Atlantic forest
Cupania oblongifolia Mart.	Sapindaceae	Tree	Evergreen	Compound, Alternate	Light-demanding early successional	Zoocoric	Amazon, *Cerrado*, *Caatinga*, Atlantic forest
Miconia cinnamomifolia (DC.) Naudin	Melastomataceae	Shrub/Tree	Evergreen	Simple, Opposite	Pioneer; Light-demanding early successional	Zoocoric, Autocoric	Atlantic forest

[2]Classification according to Lorenzi (1992; 1998), Carvalho (2003), Ronquim (2021), Vieira et al. (2021)

[3]Classification according to field observations and Flora and Funga do Brasil (2020). https://floradobrasil.jbrj.gov.br/

Measurements of microclimatic parameters

All measurements of microclimatic variables were conducted at 20 points near the study species, between 11:30 and 13:30 h on a sunny day during the dry season, at 1.30 m above ground level. Irradiance was measured using a portable quantum sensor (Li-250A, LICOR Biosciences USA-Canada). Air humidity, air temperature, wind speed, and soil surface temperature (first 5 cm) were measured using a thermo-hygro-anemometer with an external probe (AKSO-AK832). Vapor pressure deficit (VPD) was calculated as: es*ea, where es is the saturated vapor pressure of the air given by the formula 0,61137*EXP((17,502*T°C)/(240,97+T°C)) and ea is the vapor pressure of the air given by the formula (1-(UR%/100)), following Jones (1992). Canopy cover was measured at each cardinal point on a scale from 0 to 100% using a spherical densiometer (Convex Model-A, Forestry Suppliers Inc. USA).

Leaf photosynthetic pigments and phenolic compounds

In each area, five leaves were collected from each individual per species to determine the physiological/biochemical traits ($35 \le n \le 50$ leaves per species). From these five leaves, a 4 mm disk per leaf was taken from each individual to determine the photosynthetic pigments using the Dimethylsulfoxide (DSMO) organic solvent extraction method. The discs were placed in Eppendorf tubes containing 1.5 mL of DMSO, stored in plastic shelves wrapped in aluminum foil and protected from light. After five days, when the pigments had been completely extracted, 250 µl of the solutions were removed using a graduated pipette and placed in microplates (96-well microplate, Cralplast, Brazil). The absorbances of the solutions were determined using an ELISA spectrophotometer (microplate reader, µ-Quant, Bio-Tek Instruments, UK), at wavelengths of 480, 649, and 665 nm using the KC Junior software (Bio-Tek Instruments, UK). All the procedures for quantifying pigment concentrations were carried out in a low-light environment. Using the absorbance values, the concentrations of chlorophyll *a* (1), chlorophyll *b* (2), carotenoids (3), as well as the ratios of chlorophyll *a:b* (4), total chlorophyll *a* + *b* (5) and total chlorophyll:carotenoids ratio (6) were calculated according to Wellburn (1994). The values were obtained in $\mu g.ml^{-1}$ and then converted to $nmol.cm^{-2}$ (6) as described below (Hendry and Price 1993):

(1) [Chlorophyll *a*] ($\mu g.mL^{-1}$) = $12{,}19A_{665} - 3{,}45A_{649}$

(2) [Chlorophyll *b*] ($\mu g.mL^{-1}$) = $21{,}99A_{649} - 5{,}32A_{665}$

(3) [Carotenoid]($\mu g.mL^{-1}$) = ($1000A_{480}$ – 2,14[Chlorophyll *a*] – 70,16[Chlorophyll *b*])/220

(4) [Chlorophyll *a*] / [Chlorophyll *b*]

(5) [Total Chlorophyll] = [Chlorophyll *a*] + [Chlorophyll *b*]

(6) [Total Chlorophyll] / [Carotenoid]

(7) [Pigment] x (Solvent volume) / Leaf disc area

The polyphenolic compounds in the leaves were determined by quantifying the UV absorbance in the leaf epidermis by double excitation of chlorophyll fluorescence (Cerovic et al. 2012; Overbeck et al. 2018) using a DUALEX® Scientific™ portable chlorophyll meter (model FORCE-A, France). DUALEX provides four indices:

anthocyanin (index of phenolics, anthocyanin content), flavonols (index of phenolics, mostly flavonols), chlorophyll content and Nitrogen Balance Index (NBI), which is the ratio between Chlorophyll:Flavonol (Cerovic et al. 2012). These indices can indirectly reflect water and light stress in leaves (Kamphorst et al. 2020).

The total chlorophyll index (SPAD index) was determined using a portable SPAD meter (%, SPAD-502, Soil Plant Analyzer Development, Minolta, Japan). The higher the total chlorophyll content in the leaf, the higher the SPAD index value (Minolta 1989). The SPAD index is generally correlated exponentially with the chlorophyll content in the leaf (Coste et al. 2010).

Leaf morphology

In each area, the same five leaves collected to determine photosynthetic pigments and phenolic compounds were used to analyze morphological traits ($35 \leq n \leq 50$ leaves per species). The leaf area (cm^2) was determined from the whole leaf in simple leaves and in all leaflets of *C. oblongifolia* (compound leaf) (Pérez-Harguindeguy et al. 2013). The leaves were photographed and the images processed using ImageJ software (version 1.53u 15, 2022). The leaves were then weighed on an analytical balance (Shimadzu, model AY220) to obtain their fresh mass (g). After weighing, the leaves were dried in an oven for 72 hours at 60°C to obtain the dry mass (g). The specific leaf area ($cm^2\ g^{-1}$) was determined by the ratio between leaf area and dry mass (Pérez-Harguindeguy et al. 2013). Leaf thickness (mm) was determined using a digital caliper (Worker). In *C. oblongifolia*, thickness measurements were taken on one leaflet per leaf.

Wood density

Branch wood density was measured on one branch per individual per species in each area ($7 \leq n \leq 10$ per species). The samples were hydrated in water for a period of 72 hours at room temperature to fully saturate the sample. After saturation, the samples were weighed, immersed completely in a beaker with water positioned on top of an analytical balance (Shimadzu, model AY220) using the displacement method (Ilic et al. 2000). The displacement mass is considered to be equal to the fresh volume, considering the density of water to be 1 $g.cm^{-3}$ (e.g., 1g = 1 cm^3; Ilic et al. 2000; Williamson and Wiemann 2010). After obtaining the fresh volume, the samples were dried in an oven (Tecnal TE-393/1) at 105 °C for 72 hours (Ilic et al. 2000; Chave et al. 2006; Williamson and Wiemann 2010). At the end, the samples were weighed again on an analytical balance to obtain the dry weight. The wood density ($g.cm^{-3}$) for each individual of each species was determined by the ratio between the dry weight and the fresh volume of the samples (Chave et al. 2006). Lower density woods have a density of less ≤ 0.5 $g.cm^{-3}$, intermediate density woods have a density between 0.5 and 0.7 $g.cm^{-3}$ and denser woods have a density > 0.7 $g.cm^{-3}$ (Chave et al. 2009).

Statistical analyses

All statistical analyses and graphical representations were performed using version 4.4 of the R software (R Core Team 2024). The descriptive statistics mean, standard deviation, median, interquartile range, coefficient of variation, kurtosis and skewness were calculated and reported (Tables S2-S4, *get_summary_stats* and *describeBy* functions, *rstatix* and *psych* packages, Kassambara 2023; Revelle 2024). The distribution of the variables was assessed using graphs of kernel density curves compared with normal distribution curves (Figs. S1-S2, *geom_density* function, *ggplot2* package, Wickham 2016). The data on microclimate variables and traits were also tested for normality of residuals and homogeneity of variances using the Shapiro-Wilk and Levene tests, respectively (*shapiro_test*, *levene_test* functions, *rstatix* package, Kassambara 2023). After testing and observing the metrics and data distribution, most of the variables in both the microclimate and trait data did not meet the assumptions of normality and homogeneity (Tables S2-S4; Figs. S1-S2). The trait data was box-cox transformed in order to proceed with the analysis and meet the assumptions of linearity, normality, homoscedasticity and low residual leverage (*box-cox* function, *MASS* package, Venables and Ripley 2002). For the microclimate data, the mean differences between the three locations were assessed using the non-parametric Kruskal-Wallis test (*kruskal_test* function, *rstatix* package, Kassambara 2023).

To answer the first question (Do leaf and wood traits differ between areas and species?), traits were compared between areas and species using a two-way ANOVA, with species and area as factors (*aov* function, R base). Outliers were removed from this analysis as they were influencing the results of the models, but were presented graphically. A *posteriori* Tukey test, assuming 95% certainty, was carried out to see which variables differed between areas and species (*HSD.test* function, *agricolae* package, de Mendiburu 2023). The collinearity of the variables was tested using the Variance Inflation Factor (VIF), to avoid variables that could overestimate the results of future analyses due to their high correlation values (*corvif* function, Zuur et al. 2010). Variables with VIF ≥ 5 indicate high collinearity and were excluded from analyses involving correlations between traits (Zuur et al. 2010). After excluding these variables, all subsequent analyses were carried out only with the variables with low VIF values.

A principal component analysis was carried out to observe correlations between the variables and whether the set of variables was able to distinguish the functional space between populations and areas (*PCA* function, *FactoMineR* package, Le et al. 2008). In addition, redundant variables were also excluded from the PCA, such as variables used to calculate indices (e.g., Chlorophyll *b* used to calculate Chlorophyll *a:b* ratio). For the PCA, trait and microclimate data were boxcox transformed and scaled as a way of comparing variables of different units of magnitude. The Broken Stick and Kaiser-Guttman criteria (eigenvalue > 1) were used to assess the retention of the principal components. Subsequently, the data was presented separately in a two-dimensional space for the sets of variables (microclimate and traits) (*fviz_pca_biplot* function, *factoextra* package, Kassambara 2020). Ellipses representing the dispersion of the data in relation to the centroids of the variables were incorporated into the PCA as a possible indication of the significance between the groups of variables in the three locations. Subsequently, the scores of the two PCAs were used to check for differences between the main components, using a one-way ANOVA (*aov* function, R base). The overlap between the areas of the ellipses was calculated and presented as a percentage (*maxLikOverlap* function, *SIBER* package, Jackson et al. 2011).

To answer the second question (How does trait variation and covariation occur and what is the relationship?), the variation and covariation indices were determined. For the covariation index, Pearson's correlation matrices were determined for the entire data set, for each area and for each species to observe the pairwise relationships between traits (*rcorr* function, *Hmisc* package, Harrell Jr. 2024). The covariation index was calculated from the correlation matrices as the ratio between the number of total correlations between traits and the number of significant correlations in percentage (eq 1; Gianoli and Palacio-López 2009):

eq 1: (IndC = [(Nº Significant Correlations)/Nº Total Correlations])

The index of variation (IndV) was calculated for all traits and obtained using eq 2 (Valladares et al. 2006):

$$\text{eq 2: } \frac{\text{Maximum Average (Trait x Area) - Minimum Average (Trait x Area)}}{\text{Maximum Average (Trait x Area)}}$$

Subsequently, the indices of covariation and total variation of the species were calculated as the average of the indices for each trait. Indices above 0.5 indicate moderate to high variation and covariation (Valladares et al. 2006, Gianoli and Palacio-López et al. 2009). After determining the indices, linear models were fitted to investigate the relationship between trait variation and covariation for each species and for the entire data set (*lm* function, R base). Although it is postulated that covariation in some cases can restrict variation (i.e., covariation as an independent variable), a Standard Major Axis (SMA) analysis was used as a way of comparing the bivariate relationship between variation and covariation between areas. This analysis compares the slope and elevation of bivariate relationships and does not necessarily require a variable to be classified as dependent or independent (*sma* function, *smatr* package, Warton et al. 2012). We chose to perform the SMA for variation and covariation, since the indices provide information on the traits as a whole and are not evaluated separately for each trait. Variation and covariation were also compared between areas using a one-way ANOVA.

To answer the third question (How much of the total trait variation is explained by interspecific variability, intraspecific variability and understory condition?), a variance partitioning was performed by fitting a linear mixed model using the restricted maximum likelihood method (*lme* function, *lmer* package, Gaussian distribution) and quantifying the different components of variation of the nested traits in descending order (Area, Species and Individual, Liu et al. 2018). The data for this analysis has been logarithmized. The models were then subjected to variance component analysis (*varcomp* function, *ape* package, Paradis and Schliep 2019).

The coefficient of variation of the species in each area was also used to characterize the intraspecific trait variability. The model was built and the variance partitioning analysis was applied for each trait according to Liu et al. (2018).

Results

The PCA carried out with the microclimate data showed that the exposed understory area differed from the intermediate and closed understory areas, the latter also having distinct characteristics (Fig. 2). The analysis of two main components explained 78% of the total variation in the microclimate data (Table S5, Fig. 2). Air temperature, irradiance and humidity were the variables that contributed most to PC1 and differentiating the areas (Table S6). Air temperature and irradiance correlated positively with PC1 (r: 0.80 and 0.89, $p < 0.001$), while air humidity correlated negatively (r: -0.96, $p < 0.001$, Table S7). In PC2, canopy cover contributed significantly and positively to this axis (r: 0.83, $p < 0.001$, Tables S6-S7, Fig. 2). The one-way ANOVA carried out with the scores from this PCA was significant, showing the differentiation between the three areas ($F = 392$, $p < 0.0001$, Fig. S3). The overlap between the ellipses of the intermediate and closed understory areas was approximately 20%. There was no overlap between the exposed understory and the other two areas.

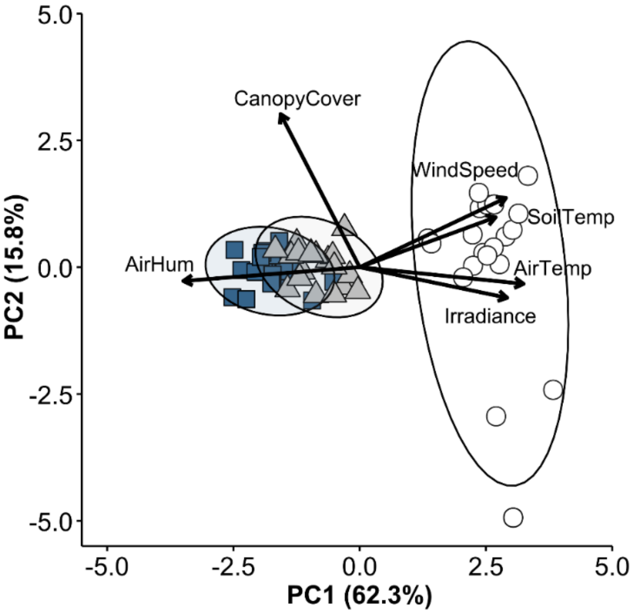


Fig. 2 Principal Component Analysis of microclimatic variables in three areas of ReBio União, Brazil. ○ Exposed Understory, △ Intermediate Understory, ■ Close Understory. AirHum: air humidity, AirTemp: air temperature, SoilTemp: soil surface temperature

These microclimatic differences between areas were reflected in the traits. The two-way ANOVA revealed significant differences between species, areas and the interaction between them in almost all traits evaluated in the abiotic gradient (Tables S8-S9, Fig. 3). Most of the species traits between the exposed and closed understories (extremes of the gradient) showed significant differences (11 of the 15 traits, Tables S8-S9, Fig. 3a-o). For approximately half of the traits, higher values were found in the intermediate and closed understory (7 of the 15 traits, Tables S8-S9, Fig 3f-n, except leaf thickness and chlorophyll *b*). Plant height showed no differences between areas ($p = 0.6$), but did show differences between species, with *M. cinnamomifolia* having greater height compared to *X. sericea* and *C. oblongifolia* ($p < 0.001$, Tables S8-S9, Fig. 3a). Only the content of flavonols and anthocyanins showed higher values in the intermediate area (Fig. 3c-d). Chlorophyll *b* responded increasingly to the abiotic gradient (Exposed - Intermediate - Closed), with higher values for the closed understory compared to the intermediate and exposed ($p < 0.001$, Tables S8-S9, Fig. 3g), with no significant differences between species ($p = 0.6$). In general, no unidirectional pattern of traits was observed among species within each area, with the exception of leaf area and wood density. *C. oblongifolia* had larger leaf areas than *X. sericea* and *M. cinnamomifolia* ($p < 0.05$), due to the intrinsic characteristics of the species (compound leaves in the former and simple leaves in the latter two, Tables S8-S9, Fig. 3n). Higher wood density values were found for *M. cinnamomifolia*, intermediate values for *C. oblongifolia* and lower values for *X. sericea*, at least in the closed and exposed understories (Tables S8-S9, Fig. 3o). Both the environment and the inter- and intraspecific characteristics had an influence on the results found for all traits.

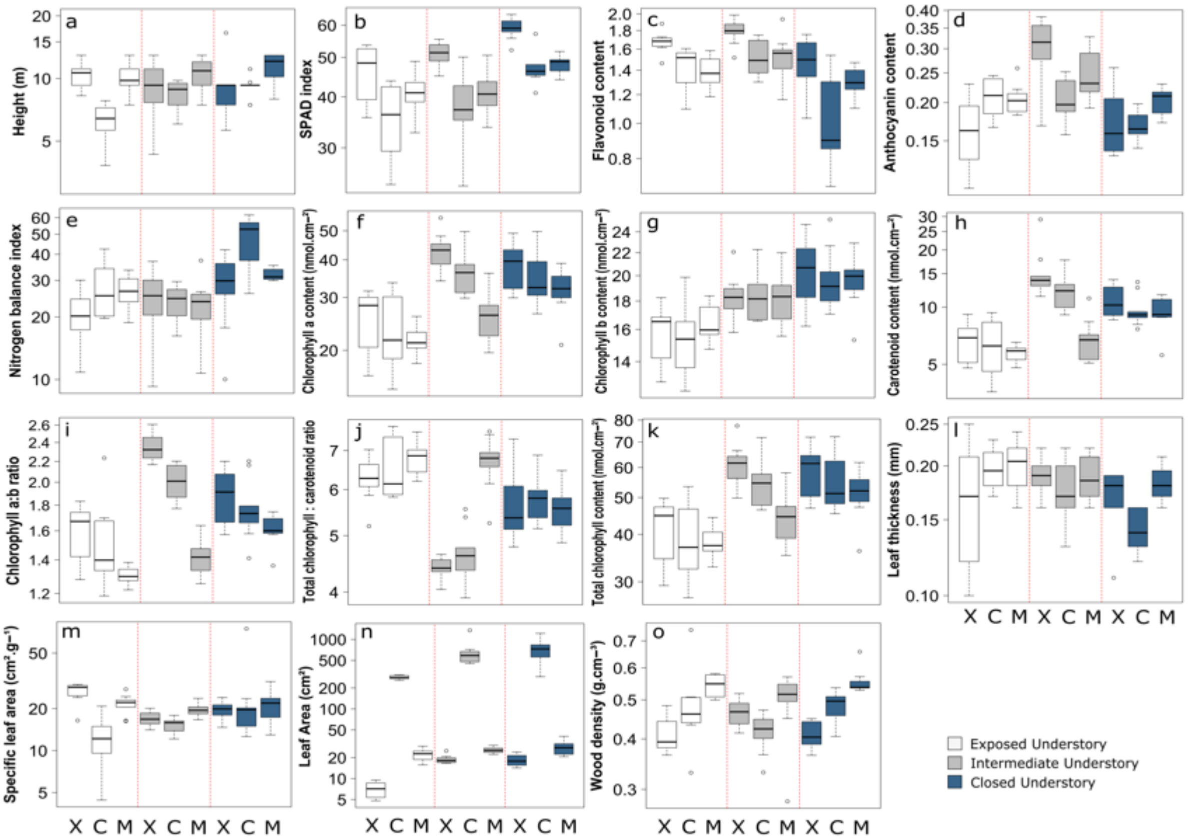


Fig. 3 Leaf and wood trait variation between three co-occurring species of ReBio Uinão, Brazil. X: *Xylopia sericea*, C: *Cupania oblongifolia*, M: *Miconia cinnamomifolia*

When examining the relationships between traits in the PCA, populations from the three areas did not differ regarding the eight selected traits (Fig. 4). The first two principal components explained approximately 46% of the total variation in the data (Table S10, Fig. 4, Fig. S4). The variables that contributed most to PC1 were the SPAD index (r: -0.63, $p < 0.001$), leaf thickness (r: 0.66, $p < 0.001$) and wood density (r: 0.52, $p < 0.001$) and; PC2, flavonol content (r: 0.55, $p < 0.001$), chlorophyll *a:b* ratio (r: 0.66, $p < 0.001$) and specific leaf area (-0.49, $p < 0.001$, Tables S11-S12).

When the analysis of variance of the PC1 and PC2 scores was carried out, statistical differences were found for the first two components ($p < 0.001$, Fig. S5). The overlap of the ellipses ranged from 30% to 45% overlap of the area of exposed understory in relation to intermediate and closed understory; from 23% to 60% overlap of the area of intermediate understory in relation to exposed and closed understory; and from 17% to 60% overlap of the area of closed understory in relation to exposed and intermediate understory. These results corroborate the differences found between traits in the areas, but not for all traits in certain areas and species. Thus, the selected traits are not able to distinguish the areas clearly, with the differences between areas and species being more subtle for the rainforest studied.

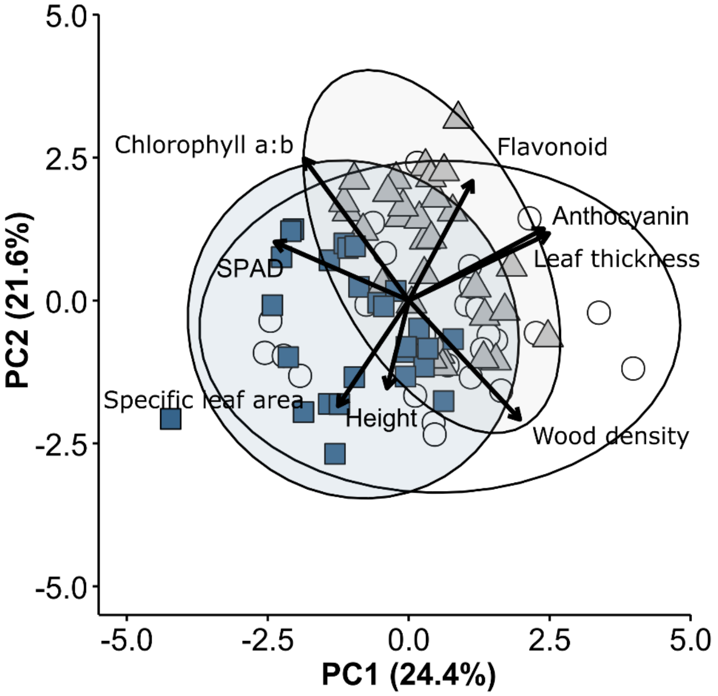
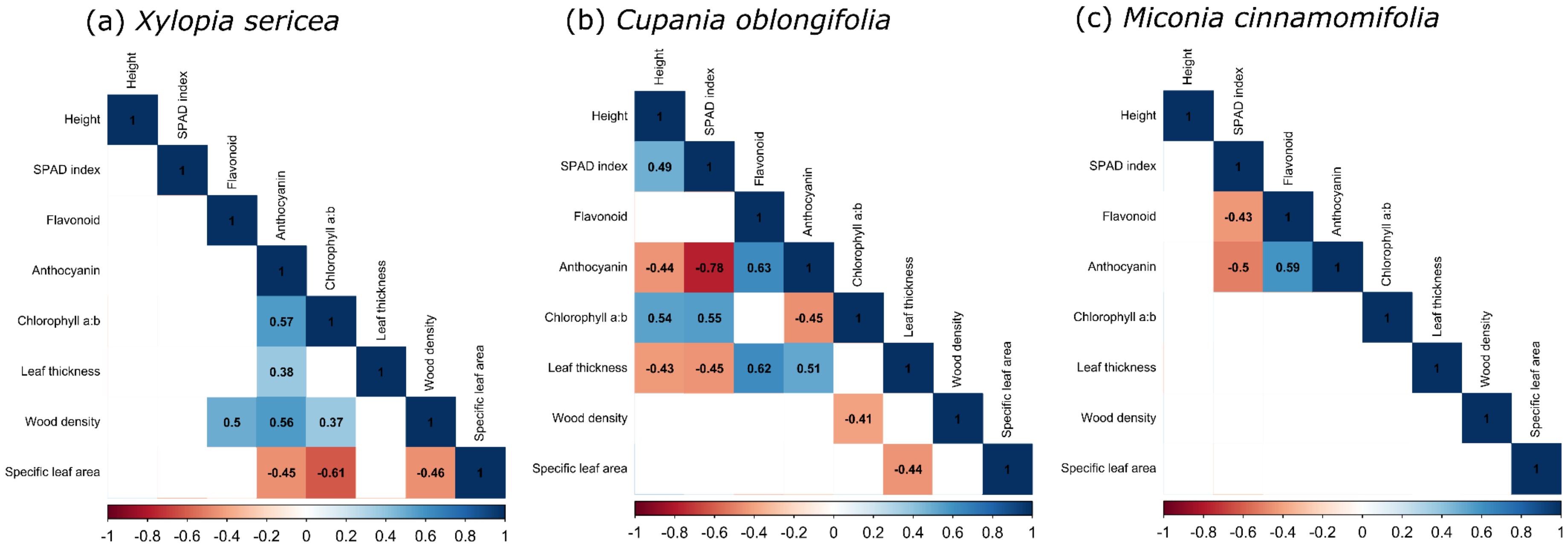


Fig. 4 Principal component analysis of leaf and wood traits in three co-occurring species of ReBio União, Brazil. ○ Exposed Understory, ▲ Intermediate Understory, ■ Close Understory. Each symbol represents an individual measurement.

In general, the species showed low covariation between traits (Fig. 5). *C. oblongifolia* was the species with the highest trait covariation index (IndC: 0.4) with the highest number of significant correlations, followed by *X. sericea* (IndC: 0.3) and *M. cinnamomifolia* (IndC: 0.1, Fig. 5a-c). The covariation of *C. oblongifolia* was significantly higher than the covariation of *M. cinnamomifolia* (F: 8.14, $p < 0.05$). The covariation index was also low depending on the area, with no significant differences observed between them (F: 2.1, p = 0.1, Fig. S6a-S7).

The species evaluated alone or together also showed low variation for all the traits evaluated between the areas (IndV < 0.5, Fig. 6). For *X. sericea*, anthocyanin content was the trait with the highest variation index (Fig. 6b). For *C. oblongifolia*, traits with the highest variation index were leaf thickness and flavonol content and for *M. cinnamomifolia*, anthocyanin content (Fig. 6c-d). The index of variation of species and areas did not differ significantly (F: 2.07, p = 0.15 for species and F: 2.13, p = 0.10 for area, respectively, Fig. S6b).



(a) *Xylopia sericea*

(b) *Cupania oblongifolia*

(c) *Miconia cinnamomifolia*

Fig. 5 Pairwise Pearson correlations matrices of leaf and wood traits as indicators of phenotypic covariation for (a) *X. sericea*, (b) *C. oblongifolia*, (c) *M. cinnamomifolia* in ReBio União, Brazil

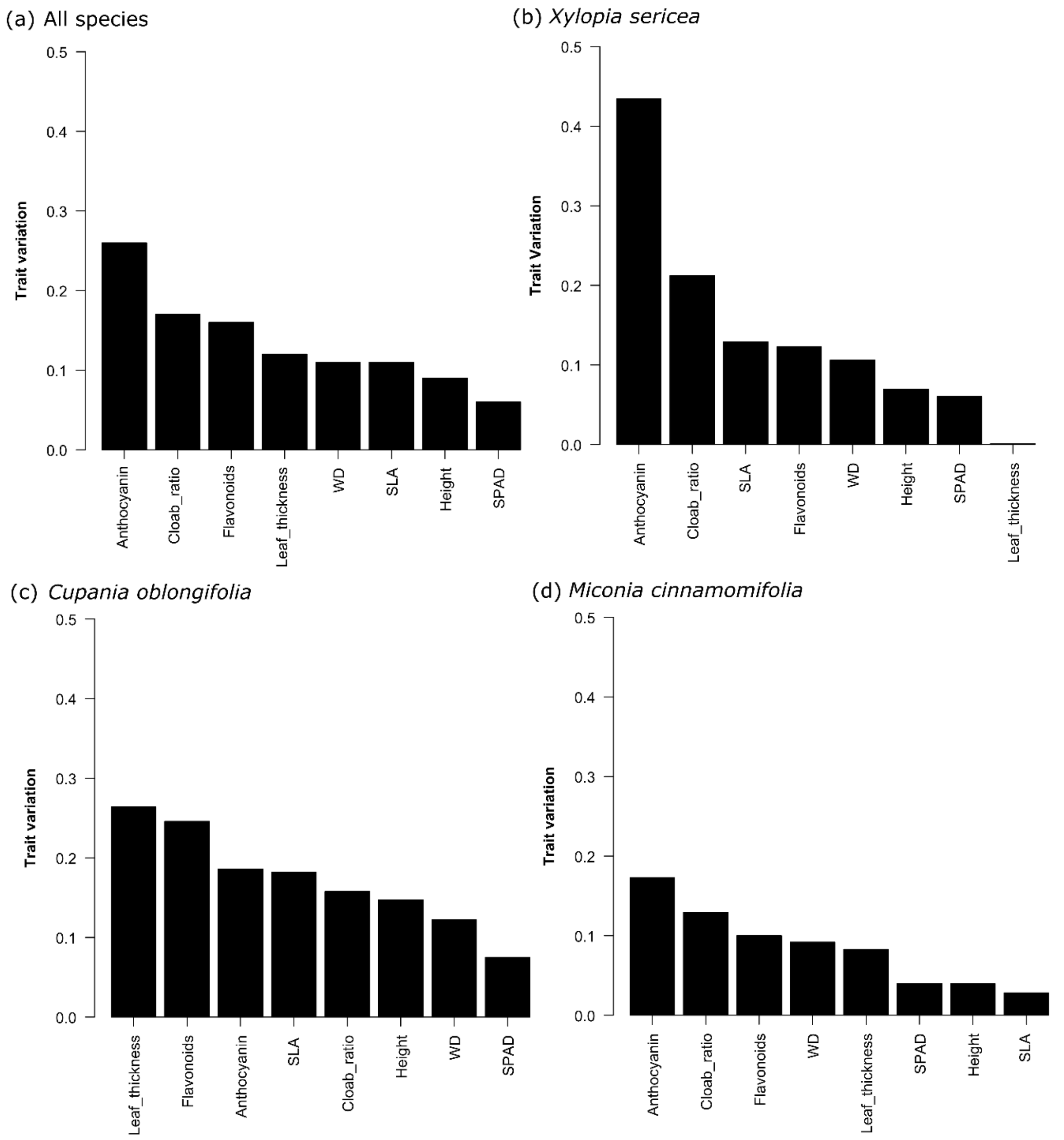
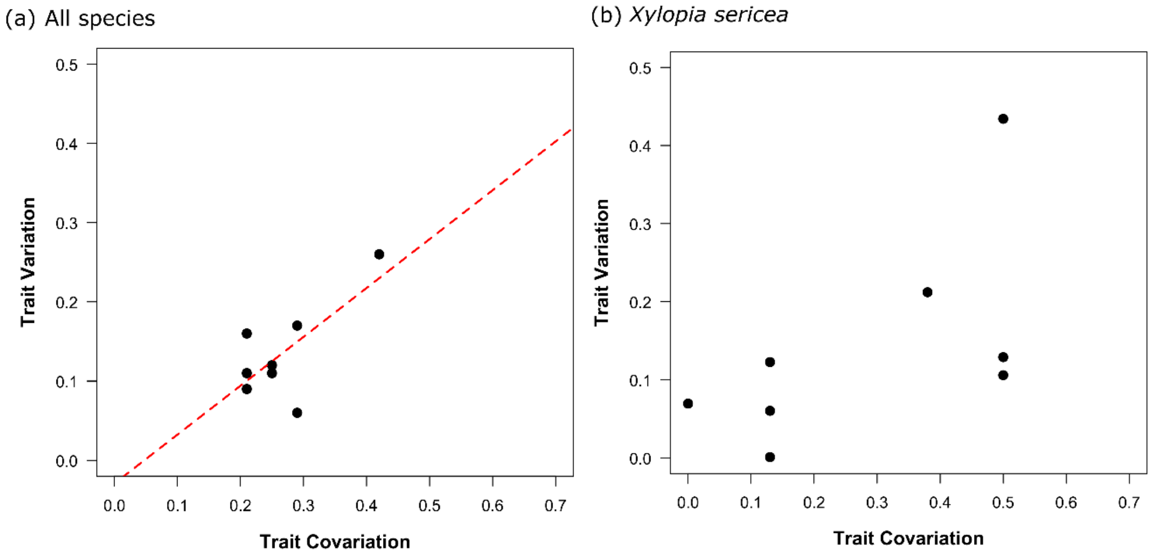
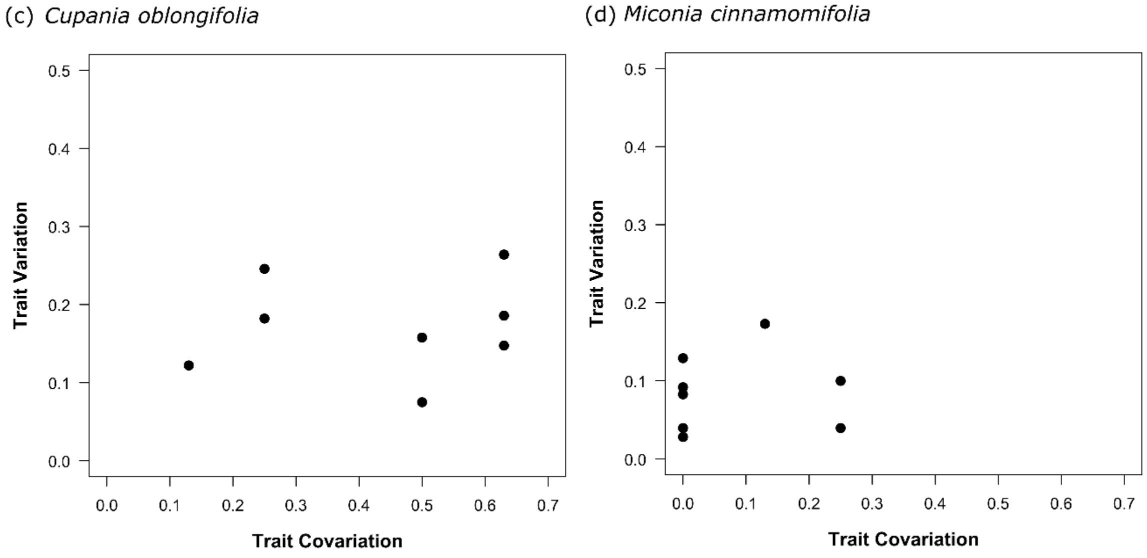


Fig. 6 Trait variation index for each trait across all species and for each species. (a): Trait variation for all species, (b) Trait variation for *X. sericea*, (c) Trait variation for *C. oblongifolia*, (d) Trait variation for *M. cinnamomifolia*. WD: Wood density, SLA: Specific leaf area

Although there are some differences between variation and covariation, no significant relationship was found between these two components of variability when considering all species together (F = 5.93, $R^2 = 0.41$, p = 0.05, Fig. 7a, Table S13) or individually (Fig.7b-d, Table S13). The SMA analysis comparing the bivariate relationship between the indices of variation and covariation reported no differences in the direction and slope of the lines either between species or between areas (Table 3).


(a) All species

(b) *Xylopia sericea*


(c) *Cupania oblongifolia*

(d) *Miconia cinnamomifolia*

Fig. 7 Relationship between trait variation and trait covariation for (a) all species, (b) *X. sericea*, (c) *C. oblongifolia*, (d) *M. cinnamomifolia*. Dashed line indicates a marginally significant relationship

Table 3 Differences in slope and elevation in the bivariate relationships based on SMA analysis between variation and covariation among areas and species in ReBio União. CI: Confidence Intervals. Letters represent SMA pairwise comparisons. The same letters represent no statistical difference in slopes and elevation between areas and species

Understory	**Variation x Covariation**			
	Slope (CI)	Elevation (CI)	r^2	p
Exposed-Intermediate	-0.34 (-0.80 a -0.14)[a]	0.03 (-0.09 a 0.15)[a]	0.05	0.60
Exposed-Closed	0.62 (0.26 a 1.49)[a]	0.07 (-0.02 a 0.18)[a]	0.03	0.66
Closed-Intermediate	0.49 (0.21 a 1.13)[a]	0.02 (-0.09 a 0.12)[a]	0.11	0.41
Species				
X. sericea	0.63 (0.30 a 1.30)[a]	0.01 (-0.11 a 0.13)[a]	0.38	0.10
C. oblongifolia	0.42 (0.17 a 1.02)[a]	0.05 (-0.01 a 0.11)[a]	0.01	0.83
M. cinnamomifolia	0.30 (0.12 a 0.72)[a]	-0.03 (-0.17 a 0.11)[a]	0.01	0.79

When examining the proportion of variance for leaf and wood traits, inter- and intraspecific variability accounted for between 20-40% and 20-60%, respectively, for each trait, especially among morphological traits (Table S14, Fig. 8). The areas explained between 0-25% of the variation in each trait, concentrating on the physiological traits (Table S14, Fig. 8). When observing at intraspecific variability by coefficients of variation, the three species showed low to moderate variability for all traits, except for leaf area and specific leaf area of *C. oblongifolia*, especially in the closed understory, with within-area variability exceeding the total variability for the species (Table S15, Table 4).

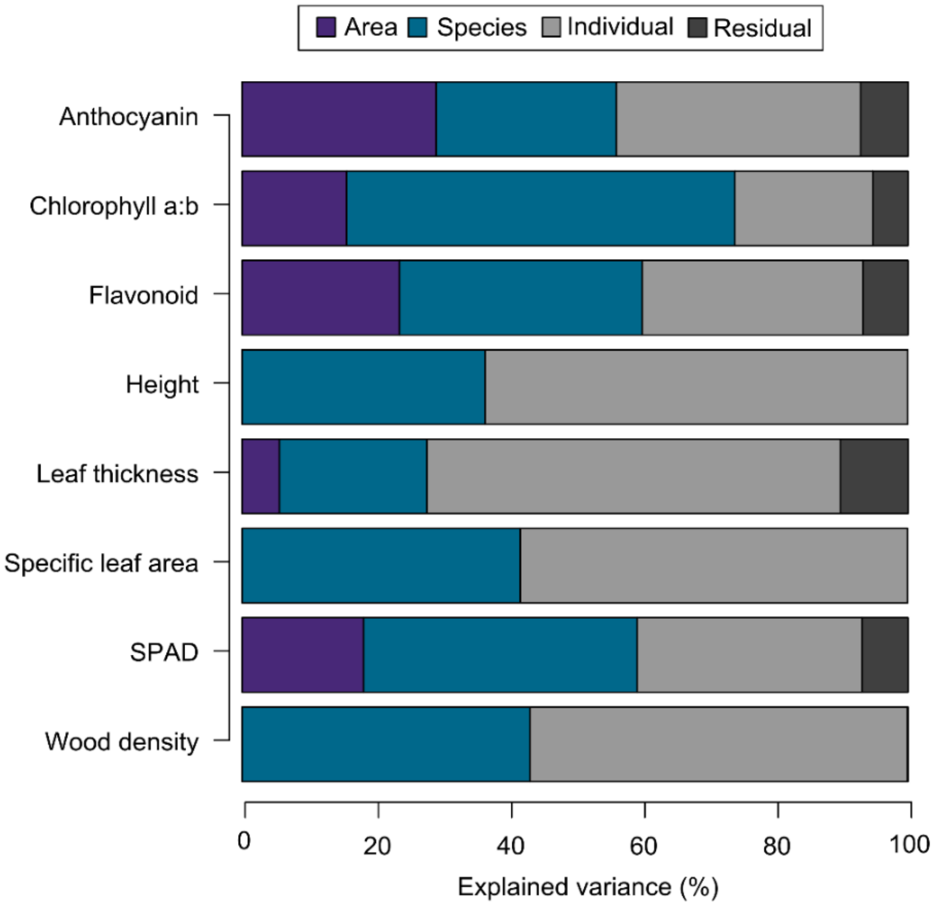


Fig. 8 Source of variation in leaf and wood traits in three areas of ReBio União, Brazil. Variance partitioning in different scales: area, species, individuals and residuals

Table 4 Coefficients of variation of leaf and wood traits of three co-occurring species in ReBio União, Brazil. H: Height, SPAD: Total Chlorophyll SPAD Index, Flav: Flavonoid content, Antho: Anthocyanin content, Chloab: Chlorophyll *a:b* ratio, SLA: Specific leaf area, WD: Wood density. * represent coeficients of variation that exceed total variation within the species

Species	Area	CV H	CV SPAD	CV Flav	CV Antho	CV Chloab	CV LT	CV SLA	CV WD
X. sericea	Exposed	13.63	14.78*	6.99	26.22	11.89	28.07*	15.40	9.54
	Intermediate	29.76*	6.26	7.58	20.45	6.04	9.04	12.10	7.28
	Closed	31.62*	5.78	14.76*	24.57	11.98	14.04	13.49	7.07
	Total	**25.50**	**13.55**	**12.94**	**38.09**	**18.76**	**18.40**	**24.28**	**10.06**
C. oblongifolia	Exposed	20.23	21.25*	12.80	14.76	21.71	10.61	39.89	24.28*
	Intermediate	15.97	19.76	10.94	15.61	8.09	15.91	11.88	10.34
	Closed	11.43	8.82	27.75*	10.71	13.71	10.56	76.21*	8.02
	Total	**20.76**	**19.84**	**23.55**	**17.07**	**17.01**	**18.39**	**68.37**	**16.66**
M. cinnamomifolia	Exposed	18.38*	12.05	9.09	11.17	3.76	12.94*	15.83	5.90
	Intermediate	17.25	12.30	13.04*	18.00*	8.13	11.64	9.73	16.90*
	Closed	16.98	5.71	9.72	10.89	7.84	10.83	28.19*	8.24
	Total	**17.42**	**12.34**	**12.60**	**17.46**	**10.84**	**12.18**	**18.26**	**11.91**

Discussion

The results found for co-occurring species in understory areas in the Atlantic rainforest showed: 1) subtle differences in leaf traits between individuals, species and areas; 2) low variation and covariation and absence of a relationship between these two components, probably associated with the costs of maintaining non-adaptive phenotypes; 3) Inter- and intraspecific variability as main drivers of species' responses to microclimatic conditions.

Leaf traits differ between species and understory areas

Among the understory areas of ReBio União, the exposed understory showed differences in microclimatic conditions compared to the intermediate and closed understories. Irradiance was one of the main abiotic factors influencing the variation between areas. In the intermediate understory, leaf traits were similar to those of both the exposed and closed understories, with no unidirectional variation.

Irradiance acts as a selective filter for species traits in spatial or temporal environmental gradients (Melo-Júnior and Boeger 2015; Vieira et al. 2015; Freitas et al. 2024a). The variation in the content of primary and accessory photosynthetic pigments indicates that the photosynthetic apparatus is influenced by changes in the availability of light (Silva et al. 2010; Freitas et al. 2024a). Flavonols and anthocyanins are phenolic compounds that are most synthesized in response to environmental stresses (Agati et al. 2012; Ferreyra et al. 2012; Landi et al. 2015). In areas subject to high irradiance, such as the exposed understory, photosynthesis can produce more free radicals and the greater synthesis of these pigments serves as antioxidants and filters of excess UV-B radiation, protecting leaf tissues (Gould et al. 2009; Agati et al. 2012; Landi et al. 2015; Shi et al. 2023b). In the intermediate understory, where there is a higher concentration of these pigments, there may be a balance between high photosynthetic capacity and protection against oxidative stress (Albert et al. 2009). In the exposed and intermediate understory, *X. sericea* had a higher content of flavonols and anthocyanins compared to *C. oblongifolia* and *M. cinnamomifolia* (Fig. 3c-d). As *X. sericea* is one of the tallest species in these areas, and consequently forms part of the canopy, photoprotection may be essential for the conditions to which this species is subjected. *C. oblongifolia* and *M. cinnamomifolia* also seem to invest in photoprotection in these areas compared to the closed understory. In addition, flavonols and anthocyanins also act as defenses against herbivory, an essential feature in rainforests (Gould et al. 2009; Ferreyra et al. 2012; Nascimento et al. 2020).

The NBI indirectly measures the allocation of N for vegetative growth, photosynthesis and defense against biotic stresses (Goulas et al. 2004; Cartelat et al. 2005). Lower NBI values in intermediate and exposed understory conditions are possibly a response to the damaging effects of reactive oxygen species, which are frequent in high irradiance conditions (Goulas et al. 2004, Taylor et al. 2004, Fig. 3e). Under these conditions, leaves can increase the biosynthesis of phenolic compounds such as flavonols and anthocyanins, mitigating these effects caused by reactive oxygen species (Overbeck et al. 2018). This behavior is observed in the three species studied in these understory conditions.

The higher NBI values found in the closed understory result from the lower concentration of flavonols in this area (Fig. 3e). The biosynthesis of flavonols may be less critical due to the higher concentration of carotenoids, which are also photoprotective pigments. This high carotenoid concentration could limit the increase in flavonol levels, as there is an interrelationship between the synthesis of these two compounds, especially in environments with lower UV radiation (Harbart et al. 2023). Higher NBI values in the leaves also indicate higher total chlorophyll content, and consequently higher leaf N content (Gaju et al. 2016). Species with higher leaf chlorophyll and N contents tend to have higher photosynthetic assimilation and growth rates, characteristics often found in more mesic and productive areas such as rainforests (Wright et al. 2004; Gray et al. 2019; Freitas et al. 2024a). In milder microclimatic conditions, such as the closed understory, species benefit from higher N content to invest in vegetative growth, such as height, leaf area, and chlorophyll content. *C. oblongifolia* seems to follow this behavior, consistent with a strategy of maximizing photosynthetic assimilation at low irradiance. *M. cinnamomifolia* and *X. sericea*, despite lower NBI values, may also be investing more N in height in this area.

The species differed in height, but this trait did not vary between the areas (Fig. 3a). However, height cannot be analyzed in isolation, as the interaction between area and species was significant (Table S9). The possible allocation of N to vegetative growth, seen indirectly by the NBI, can be explained by the height to diameter ratio (HDR) of the species (Fig. S8a). In the closed understory, the species showed greater HDR compared to those in the intermediate and exposed understory (Fig. S8a-b), indicating a greater investment in vertical growth, which is crucial for a competitive advantage in light acquisition under shaded conditions (Poorter et al. 2005; Ruger et al. 2012; Scalon et al. 2022). These strategies are common in other species under shaded conditions (Alvarenga et al. 2003; Nery et al. 2011; Scalon et al. 2022). In the exposed understory, *M. cinnamomifolia* seems to invest more in diameter, greater wood density and leaf thickness to cope with the restrictive conditions of this area (Fig S8b, Fig. 3l,o). Despite these results, in the closed understory, the HDR between the species was similar, suggesting other investments in traits such as leaf area, leaf thickness and chlorophyll content.

As plants grow taller, they have greater access to light, which initially can promote greater photosynthetic activity, also related to a higher concentration of chlorophylls (Lichtenthaler et al. 2007; Vieira et al. 2015; Gray et al. 2019; Oguchi et al. 2021). However, the need for higher chlorophyll concentration may be reduced when irradiance is in excess, suggesting an acclimatization adjustment to avoid photoinhibition (Lage-Pinto et al. 2012; Vitória et al. 2016). In addition, in areas with high irradiance, there can be rapid decomposition of chlorophylls in the reaction centers, justifying the low concentration of these pigments (Lage-Pinto et al. 2012; Oguchi et al. 2021). In conditions of low irradiance, species tend to have a higher concentration of chlorophylls to maximize light capture and use photoassimilates more efficiently (Niinemets 2010; Oguchi et al. 2021). The higher concentration of chlorophyll *b* in the closed understory may be mainly related to the efficiency in capturing diffuse light (Poorter et al. 2009; Rossatto et al. 2018).

Xylopia sericea and *Cupania oblongifolia* invest more in chlorophyll *a*, chlorophyll *a:b* and total chlorophylls in all three areas, probably due to their greater investment in height and photosynthetic activity to reach higher strata of the forest and use light efficiently, respectively (Fig. 3f,h,i). These species, especially *X. sericea*, also invest in photoprotective pigments such as flavonols, anthocyanins and carotenoids to avoid oxidative stress resulting from increased growth and photosynthesis (Fig. 3c-d,h). On the other hand, *M. cinnamomifolia*, despite investing in height and diameter, seems to prioritize morphological traits to cope with environmental conditions. Similar results for *X. sericea*, *Byrsonima sericea* and *Siparuna guianensis* have been reported for the same rainforest, with regard to chlorophyll concentrations (Silva et al. 2010; Lage-Pinto et al. 2012; 2015; Vieira et al. 2015).

Unexpectedly, the highest carotenoid values were found in the closed and intermediate understory compared to the exposed understory (Fig. 3h), contrary to previous studies at ReBio União (Lage-Pinto et al. 2012; 2015; Teixeira et al. 2015; Vieira et al. 2015). Carotenoids also have an antioxidant action, dissipating excess light energy as heat, neutralizing reactive oxygen species and maintaining the integrity of the photosynthetic apparatus (Sun et al. 2022). Normally, in areas subject to high irradiance, species have high concentrations of carotenoids (Vieira et al. 2015; Pireda et al. 2019). The lower concentration of these pigments in the exposed understory could be related to water stress during the winter and dry season, when the species were collected. The irradiance may not have been enough to cause oxidative damage to the photosynthetic apparatus to increase the concentration of these pigments during this season. However, water stress as a result of this condition may have reduced the concentration of these pigments.

Lage-Pinto et al. (2012) e Silva et al. (2010) showed that the interaction between high irradiance and water stress during the dry season affected the carotenoid concentrations of *B. sericea* and *S. guianensis* in an intermediate understory of the same rainforest, results that contrast with this study. However, the species in this study maintained high concentrations of other photoprotective pigments (anthocyanins and flavonols) which also increase under conditions of water stress (Landi et al. 2015; Li et al. 2021a). In the closed understory, with variable and often limited light, species need to maximize light interception in the lower strata, through sunflecks or by taking advantage of opportunities in canopy openings (Demming-Adams and Adams 2006; Oguchi et al. 2021). In this sense, higher concentrations of carotenoids and chlorophylls are required to optimize photosynthesis without damaging the photosystems, which was observed in all three species in all areas.

In the closed understory, the species showed greater leaf area and lower specific leaf area and thickness compared to the species in the exposed understory. In the exposed understory, species tend to have thicker leaves, with lower leaf area and specific leaf area, to reduce temperature and excessive transpiration, minimizing the risk of overheating and dehydration (Vitória et al. 2016; Pireda et al. 2019; Freitas et al. 2024a). In the closed understory, the larger leaf area increases the surface area for capturing light, and the lower thickness reduces the energy costs of leaf production and maintenance (Niinemets 2010). In the exposed understory, the greater leaf thickening may be a result of the increased thickness of the palisade and spongy parenchyma, epidermis and cuticles (Rabelo et al. 2013; Vieira et al. 2015; Pireda et al. 2019), helping to reflect excess light and reduce water loss (Melo-Junior and Boeger 2015; Maracahipes et al. 2018). Thinner leaves in the closed understory may also have a compact layer of chloroplasts close to the leaf surface, improving light absorption in shaded conditions (Rossatto et al. 2018).

Cupania oblongifolia showed the lowest specific leaf area and thickness, and the highest leaf area, especially in the closed understory (Fig. 3l-n). With several large, thinner and less dense leaflets, *C. oblongifolia* optimizes the area in which diffuse light is captured and maintains an adequate leaf temperature without excessively increasing water loss through transpiration, presenting less energetically costly leaflets (Valladares and Niinemets 2008; Nicotra et al. 2011). These characteristics can help allocate resources to other functions, such as height growth. *M. cinnamomifolia* and *X. sericea*, on the other hand, maintained thicker leaves with greater specific leaf area to cope with the stress in areas of exposed understory and close to the canopy. The greater specific leaf area in the more open areas of this rainforest may indicate a relatively more homogeneous condition in those areas.

Regarding wood density, significant differences were only observed between species, but all had low density, a characteristic associated with mesic and homogeneous environments (Chave et al. 2009; Freitas et al. 2024a). Light-demanding pioneer species generally have lighter woods to optimize growth (Markesteijn et al. 2011). Wood density is more directly influenced by other abiotic factors such as water availability, which is less critical in rainforests (Chave et al. 2009; Freitas et al. 2024a). The variation in wood density between the species in the three areas would be more related to the evolutionary background of the species than to variation in irradiance (Li et al. 2024b).

Therefore, it is suggested that the species evaluated have subtle differences to deal with the variation in irradiance to canopy stratification, common among coexisting species (Falster et al. 2017). In rainforests, competition for light is crucial for the performance and distribution of species (Rozendaal et al. 2020; Matsuo et al. 2021). *C. oblongifolia* invests in the concentration of photosynthetic pigments, efficient use of light and the allocation of resources to leaf area. *X. sericea* invests in height as well as pigments such as flavonols and chlorophylls. *M. cinnamomifolia* also invests in height, but with structures that protect against irradiance and water stresses, such as greater leaf thickness, stem diameter, wood density and phenolic compounds. These characteristics are expected even among species of the same successional stage, which have developed in different environments such as rainforests (Kitajima and Poorter 2008; Vieira et al. 2021). Thus, in general, the species showed more acquisitive traits, typical of light-demanding species (Díaz et al 2016; Cazalvara et al. 2019). This pattern may be a result of the vertical light gradient in tropical forests due to canopy structure (Domingues et al. 2005; Vieira et al. 2015). Despite this, adjustments in traits due to the demand for light are not always strictly related to a successional group (Dos Anjos 2015; Cerqueira et al. 2018; Calzavara et al. 2019).

Although differences in the traits between areas and species were observed, it is important to note that microclimatic conditions show daily and seasonal fluctuations that were not assessed in this study, which may have influenced the results of the leaf traits. Other studies in the same area show variation in morphophysiological traits due to temporal fluctuations (Lage-Pinto et al. 2012; 2015; Teixeira et al. 2015; 2018; 2020; Vieira et al. 2015; 2021; Vitória et al. 2016). Even with a short and mild dry season in ReBio União, it can still be enough to cause changes in the leaf traits of species, especially in the exposed understory (Silva et al. 2010; Lage-Pinto et al. 2012).

Low variation and covariation and no relationship between the two components associated with the costs of maintaining non-adaptive phenotypes

The results showed low covariation between leaf and wood traits for the co-occurring species in ReBio União. Phenotypic covariation refers to the functional coordination between traits (Gianoli 2001; Pigliucci 2003; Armbruster et al. 2014), and the relationships between traits were mostly different between species, with few shared correlations. Only the covariation between *C. oblongifolia* and *M. cinnamomifolia* was statistically different (higher for *C. oblongifolia*), while *X. sericea* showed similar covariation with both. The low covariation and the relationships between traits reflect different responses to the irradiance gradient. The differential investment of *C. oblongifolia* and *M. cinnamomifolia* may be due to subtle differences in light acquisition strategies, with *C. oblongifolia* showing a coordinated response to maximize efficiency in the use of light. This is probably due to the fact that *C. oblongifolia* occupies a lower stratum in the regenerating forest compared to *M. cinnamomifolia*. In ecosystems such as rainforests, light in the understory is variable and reduced in quantity and quality (Matsuo et al. 2021), and *C. oblongifolia* seems to invest in greater covariation of its traits in relation to variation to cope with these conditions.

The greater trait covariation between species may be limited by stronger filters in the area, as overall covariation was low for all species. In mesic and homogeneous ecosystems, covariation between traits tends to be lower, with leaves and wood responding to environmental conditions independently (Baraloto et al. 2010; Braga et al. 2016; Dwyer and Laughlin 2017; Homeier et al. 2021). In contrast, higher covariation is expected in more restrictive and heterogeneous ecosystems (García-Verdugo et al. 2009; Salgado-Negret et al. 2015; Dwyer and Laughlin 2017; Homeier et al. 2021), although some studies have found low covariation in these ecosystems (Tonsor and Scheiner 2007; Boucher et al. 2013). Despite the vertical gradient of irradiance that can affect covariation between species, the rainforest seems to select, in general, phenotypes with low covariation. This is because irradiance and water availability are relatively constant in rainforests, even if they exhibit daily and seasonal fluctuations, allowing for greater trait variation and fewer resource constraints (Oliveira-Filho and Fontes 2000; Valladares et al. 2007; Dwyer and Laughlin et al. 2017).

However, the species and understory also did not show significant differences in trait variation, expressing a low variation. Studies indicate that light-demanding pioneer species generally exhibit high trait variation, especially photosynthetic ones, due to variable irradiance conditions in rainforests (Valladares et al. 2000; Portes et al. 2010). The low variation observed was also reported for this successional group in another study (Rozendaal et al. 2006). These species, which are often more restricted to high irradiance conditions, optimize their mechanisms to reach the canopy or stay in upper strata, being shade avoiders (Valladares and Niinemets 2008; Markesteijn et al. 2011). Although light-demanding species need intermediate to high irradiance to reach larger sizes, they can adjust their morphological and physiological traits to shaded conditions (Poorter and Arets 2003), which could be a particular condition for *C. oblongifolia*.

It is possible that the low trait variation observed in general is due to the cost associated with the ability to adjust to the specific conditions of the understory, which decreases non-adaptive phenotypes frequency (Valladares et al. 2007; Murren et al. 2015; Vieira et al. 2021). For example, species in the closed understory showed greater HDR and total leaf area compared to the other understory conditions, and height varied between the three species, being greater in the species in the higher strata *(X. sericea and M. cinnamomifolia*). In the same rainforest, the low variation observed in *Cytharexylum mirianthum*, another light-demanding species, was attributed to greater investment in growth (Vieira et al. 2021). This relationship between investment in growth and the reduction in costs associated with variation has been observed in other studies (Rosado et al. 2013; dos Anjos et al. 2015; Bongers et al. 2017).

Some studies suggest that if there is a strong selection power of environmental filters, especially in restrictive conditions, covariation between traits will restrict their variation (Gianoli 2004; Matesanz et al. 2010). For example, Gianoli and Palacio-López (2009) showed that, in *Convolvulus chilensis* and *Lippia alba*, the covariation of traits restricted variation under conditions of water restriction and low irradiance. Other studies have shown that phenotypes with greater covariation are selected under restrictive conditions (He et al. 2021; Homeier et al. 2021). However, there is evidence that, in both resource-limited and resource-rich conditions, covariation does not necessarily restrict trait variation and that both can act together in the process of species acclimatization and adaptation (Zimmermann et al. 2016; Pireda et al. 2019; Matesanz et al. 2021; Borges et al. 2022; Shi et al. 2023a; Oyanoghafo et al. 2023). In some cases, the relationship between variation and covariation can be species-specific (Pireda et al. 2019; Borges et al. 2022). Contrary to this evidence, the results indicated a null association between variation and covariation between species and areas, suggesting that these components of the phenotype are independent (Nicotra et al. 2007). More recently, Freitas et al. (2024b) observed a positive association between variation and covariation in a seasonal ecosystem, negative in a rainforest, and absent in both ecosystems between different combinations of leaf and wood traits. According to this study, the relationship between variation and covariation is context-dependent, with both taking on different roles depending on the local demands of each ecosystem (Freitas et al. 2024b). Additionally, covariation can be related to variation if it results from various trade-offs between traits that are sufficient to restrict variation (Jonas and Cioce 2019). Thus, the adaptive value of correlated traits will also depend on the direction of the covariation in order for it to have a significant impact on variation (Laughlin and Messier 2015).

Some authors also point out that the relationship between covariation and variation is influenced by factors other than specific environmental demands, such as the type of trait used, the growth forms, the functional group and the spatial and temporal scale (Apgaua et al. 2016; Martínez-Cabrera et al. 2011; Godoy et al. 2012; Messier et al. 2017; Michelaki et al. 2019). For example, greater covariation in physiological traits may not always lead to less variation in the same trait category (Godoy et al. 2012). However, other studies using morphological and physiological trait have found positive relationships between variation and covariation in non-restrictive and restrictive ecosystems (Pireda et al. 2019; Borges et al. 2022; Shi et al. 2023a). With regard to the spatial scale, it is possible that, at a local scale, relationships commonly described at the community level for regional or global scales may not hold (Messier et al. 2017). This may explain the lack of relationship between variation and covariation observed in this study. On a temporal scale, if species variability can show seasonal and daily variation (Silva et al. 2010; Lage-Pinto et al. 2012; 2015), it is possible to hypothesize that the relationship between variation and covariation may also present a temporal dynamic, an aspect not addressed in this study. Therefore, the differences found between species and the low covariation and variation are more likely attributed to the inter- and intraspecific trait variability in response to the specific conditions of the microhabitat (Jung et al. 2014).

Species' responses were more closely related to intraspecific trait variability than to understory microclimatic conditions

Intraspecific variability refers to trait adjustments within species, resulting from plasticity, genetic variability, or both (Albert et al. 2010). The coefficients of variation observed indicate a certain level of differentiation between microhabitats within ReBio União, since most of the species' traits, at least in one understory condition, exceeded the species' total coefficients of variation (Table 5, S14). These results also suggest considerable intraspecific and intrapopulation phenotypic variation within the areas of ReBio União, indicating that variation in microhabitat and this source of variability generate small differences in species’ responses and probably their fitness. Maintaining a high trait variability can be crucial for the survival of species and populations over time and space (Forsman and Wennersten 2016). However, the low to moderate values of the coefficients of variation suggest that the overall phenotypic variability is relatively stable, but not negligible, and that the differentiation between the understories may be subtle. The expression of intraspecific variation can derive from many components (plasticity, genetics) that are important for differentiating specific traits of a tissue or the whole plant, as well as being context-dependent (Albert et al. 2010; Auger and Shipley 2013; Siefert et al. 2015).

The results of the variance partitioning also reinforce that most of the phenotypic variation is due to the intrinsic characteristics of the species, rather than the specific conditions of the understory (Fig. 8). Intraspecific variability can account for up to 30% of variability in plant communities (Leps et al. 2011; Siefert et al. 2015). The area's low contribution to total variability reinforces that the microclimatic conditions of the understory have a limited impact on phenotypic variation (Fig. 8). Despite this, the particularities of the understory seem to be important in triggering certain phenotypic adjustments related to phenotypic plasticity and acclimatization strategies (Matesanz et al. 2021). In heterogeneous ecosystems, intraspecific variability can be greater, even at very small scales (Opedal et al. 2014).

With regard to traits’ variability, *C. oblongifolia* in the closed understory showed higher coefficients of variation for leaf area and specific leaf area compared to the other two areas, indicating high intraspecific variability related to these traits (Table 4 and S15). This suggests that more variable trait may be more closely linked to environmental variability and the uneven distribution of resources (Albert et al. 2010; Messier et al. 2010). This behavior may be related to the fact that *C. oblongifolia* grows in lower strata, where it needs to invest in light capture surface and biomass allocation in the leaves. Thus, the greater variability reflects local acclimation and the intensity of ecological processes (Jung et al. 2010).

Understory conditions mainly influenced physiological traits, which are more sensitive to environmental variation than morphological ones (Lage-Pinto et al. 2012; 2015; Teixeira et al. 2015; 2018). The greater sensitivity of physiological trait is due to their high plasticity, which is directly related to the regulatory mechanisms that species use to adjust to variation in irradiance (Valladares et al. 2000; Bongers et al. 2017). In ecosystems where local heterogeneity is significant, leaf traits are strongly influenced by fluctuations in environmental conditions, even at the intraspecific level (Boucher et al. 2013; Salgado-Negret et al. 2015), and are fundamental for identifying divergences in inter- and intraspecific populations (Messier et al. 2010).

Intraspecific variability is linked to a species' niche breadth and its ability to occupy different spaces in the ecosystem (Violle and Jiang 2009; Sides et al. 2014). In ReBio União, this variability may also reflect local processes, such as biotic interactions (competition), which may have influenced the low to moderate variation (Almeida et al. 2013). Biotic interactions can vary across environmental gradients and sometimes have a greater impact on variability than abiotic factors (Callaway et al. 2002, Kichenin et al. 2013). High diversity and species richness in more stable and productive communities can intensify competition and lead to an increase in intraspecific variability and this could cause some phenotypic differentiation between species and in their ecological requirements (Boucher et al. 2013). The rainforest of ReBio União is one of the forests with the greatest diversity and richness of native tree species compared to other ecosystems in the region (Rodrigues 2004), and therefore, competition may be an important factor in the differentiation between species.

In ecosystems with fewer environmental restrictions, competition can have a more significant impact (Callaway et al. 2002). The low inter- and intraspecific variability could suggest niche overlap and greater competition (Violle and Jiang 2009; Sides et al. 2014), however, in ReBio União, where these species are abundant, it is more likely that there is greater niche complementarity. Thus, to reduce direct competition, inter- and intraspecific variability can promote light partitioning for these species through vertical stratification (Poorter and Arets 2003; Sides et al. 2014). Therefore, inter- and intraspecific variability contributes to subtle differences in species’ responses, facilitating coexistence through differential investment between traits. Understanding intraspecific variability has proven essential to understanding the diversity of plant communities, both in relation to abiotic and biotic interactions across environmental gradients (Violle et al. 2012; Laughlin et al. 2017) and how these species will respond to predicted climate change.

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Statements and Declarations

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Supplementary Material

Leaf and wood trait variability of co-occurring tree species along a local environmental gradient in an Atlantic tropical rainforest

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Table S1 Geographic location of three co-occurring species in three areas of ReBio União, Brazil

Code	Species	Latitude	Longitude	Area
A1	*Miconia cinnamomifolia*	-22.4289	-42.0358	Closed Understory
A2	*Miconia cinnamomifolia*	-22.4288	-42.0359	Closed Understory
A3	*Miconia cinnamomifolia*	-22.4289	-42.0359	Closed Understory
A4	*Miconia cinnamomifolia*	-22.4288	-42.0358	Closed Understory
A5	*Miconia cinnamomifolia*	-22.4288	-42.0358	Closed Understory
A6	*Miconia cinnamomifolia*	-22.4288	-42.0357	Closed Understory
A7	*Miconia cinnamomifolia*	-22.4292	-42.0359	Closed Understory
A14	*Cupania oblongifolia*	-22.4291	-42.036	Closed Understory
A15	*Cupania oblongifolia*	-22.4294	-42.0361	Closed Understory
A16	*Cupania oblongifolia*	-22.4294	-42.0361	Closed Understory
A17	*Cupania oblongifolia*	-	-	Closed Understory
A18	*Cupania oblongifolia*	-22.429	-42.036	Closed Understory
A19	*Cupania oblongifolia*	-22.429	-42.0361	Closed Understory
A20	*Cupania oblongifolia*	-22.4291	-42.0359	Closed Understory
A21	*Cupania oblongifolia*	-22.4293	-42.0362	Closed Understory
A22	*Cupania oblongifolia*	-22.4294	-42.0361	Closed Understory
A23	*Cupania oblongifolia*	-22.4294	-42.0361	Closed Understory
A24	*Xylopia sericea*	-22.4291	-42.0361	Closed Understory
A25	*Xylopia sericea*	-22.429	-42.0361	Closed Understory
A26	*Xylopia sericea*	-22.4292	-42.036	Closed Understory
A27	*Xylopia sericea*	-22.4292	-42.0359	Closed Understory
A28	*Xylopia sericea*	-22.4292	-42.0359	Closed Understory
A29	*Xylopia sericea*	-	-	Closed Understory
A30	*Xylopia sericea*	-22.4291	-42.0359	Closed Understory
A31	*Xylopia sericea*	-	-	Closed Understory

A32	*Xylopia sericea*	-22.4294	-42.0364	Closed Understory
A33	*Xylopia sericea*	-22.4294	-42.0364	Closed Understory
A44	*Xylopia sericea*	-22.4240	-42.0325	Intermediate Understory
A45	*Cupania oblongifolia*	-22.4241	-42.0324	Intermediate Understory
A46	*Xylopia sericea*	-22.4242	-42.0325	Intermediate Understory
A47	*Cupania oblongifolia*	-22.4242	-42.0325	Intermediate Understory
A48	*Miconia cinnamomifolia*	-22.4242	-42.0326	Intermediate Understory
A49	*Miconia cinnamomifolia*	-22.4243	-42.0325	Intermediate Understory
A52	*Cupania oblongifolia*	-22.4243	-42.0325	Intermediate Understory
A54	*Miconia cinnamomifolia*	-22.4243	-42.0326	Intermediate Understory
A56	*Miconia cinnamomifolia*	-22.4242	-42.0326	Intermediate Understory
A57	*Xylopia sericea*	-22.4242	-42.0327	Intermediate Understory
A58	*Xylopia sericea*	-22.4242	-42.0327	Intermediate Understory
A59	*Xylopia sericea*	-22.4242	-42.0328	Intermediate Understory
A64	*Cupania oblongifolia*	-22.4244	-42.0327	Intermediate Understory
A69	*Cupania oblongifolia*	-22.4246	-42.0329	Intermediate Understory
A71	*Cupania oblongifolia*	-22.4243	-42.0329	Intermediate Understory
A73	*Cupania oblongifolia*	-22.4243	-42.033	Intermediate Understory
A74	*Xylopia sericea*	-22.4244	-42.033	Intermediate Understory
A78	*Miconia cinnamomifolia*	-22.4244	-42.0331	Intermediate Understory
A81	*Xylopia sericea*	-22.4243	-42.0331	Intermediate Understory
A82	*Xylopia sericea*	-22.4243	-42.0331	Intermediate Understory
A84	*Xylopia sericea*	-22.4244	-42.0332	Intermediate Understory
A85	*Miconia cinnamomifolia*	-22.4245	-42.0333	Intermediate Understory
A90	*Cupania oblongifolia*	-22.4243	-42.0329	Intermediate Understory
A92	*Cupania oblongifolia*	-22.4244	-42.0331	Intermediate Understory
A93	*Cupania oblongifolia*	-22.4247	-42.0329	Intermediate Understory
A95	*Miconia cinnamomifolia*	-22.4245	-42.0331	Intermediate Understory

A96	*Miconia cinnamomifolia*	-22.4245	-42.0332	Intermediate Understory
A97	*Miconia cinnamomifolia*	-	-	Intermediate Understory
A98	*Miconia cinnamomifolia*	-	-	Intermediate Understory
A99	*Xylopia sericea*	-	-	Intermediate Understory
A120	*Cupania oblongifolia*	-22.4285	-42.0369	Exposed Understory
A121	*Cupania oblongifolia*	-22.4285	-42.0368	Exposed Understory
A122	*Cupania oblongifolia*	-22.4287	-42.0368	Exposed Understory
A123	*Cupania oblongifolia*	-22.4286	-42.0369	Exposed Understory
A126	*Cupania oblongifolia*	-22.4286	-42.0369	Exposed Understory
A124	*Cupania oblongifolia*	-22.4285	-42.0369	Exposed Understory
A125	*Cupania oblongifolia*	-22.4284	-42.0369	Exposed Understory
A127	*Cupania oblongifolia*	-22.4287	-42.0371	Exposed Understory
A128	*Miconia cinnamomifolia*	-22.4283	-42.037	Exposed Understory
A129	*Miconia cinnamomifolia*	-	-	Exposed Understory
A130	*Miconia cinnamomifolia*	-22.4283	-42.0371	Exposed Understory
A131	*Miconia cinnamomifolia*	-22.4283	-42.0368	Exposed Understory
A132	*Miconia cinnamomifolia*	-22.4284	-42.0368	Exposed Understory
A133	*Miconia cinnamomifolia*	-22.4286	-42.0368	Exposed Understory
A134	*Miconia cinnamomifolia*	-22.4285	-42.0368	Exposed Understory
A135	*Miconia cinnamomifolia*	-22.4285	-42.0371	Exposed Understory
A136	*Miconia cinnamomifolia*	-22.4283	-42.0369	Exposed Understory
A137	*Miconia cinnamomifolia*	-22.4284	-42.0374	Exposed Understory
A138	*Xylopia sericea*	-22.4285	-42.0368	Exposed Understory
A139	*Xylopia sericea*	-22.4285	-42.0368	Exposed Understory
A140	*Xylopia sericea*	-22.4285	-42.0368	Exposed Understory
A141	*Xylopia sericea*	-22.4281	-42.0376	Exposed Understory
A142	*Xylopia sericea*	-22.4281	-42.0376	Exposed Understory
A143	*Xylopia sericea*	-22.4282	-42.0375	Exposed Understory

A144	*Xylopia sericea*	-22.4284	-42.0373	Exposed Understory
A145	*Xylopia sericea*	-22.4282	-42.0374	Exposed Understory
A146	*Xylopia sericea*	-22.4283	-42.0374	Exposed Understory
A147	*Xylopia sericea*	-22.4283	-42.0374	Exposed Understory

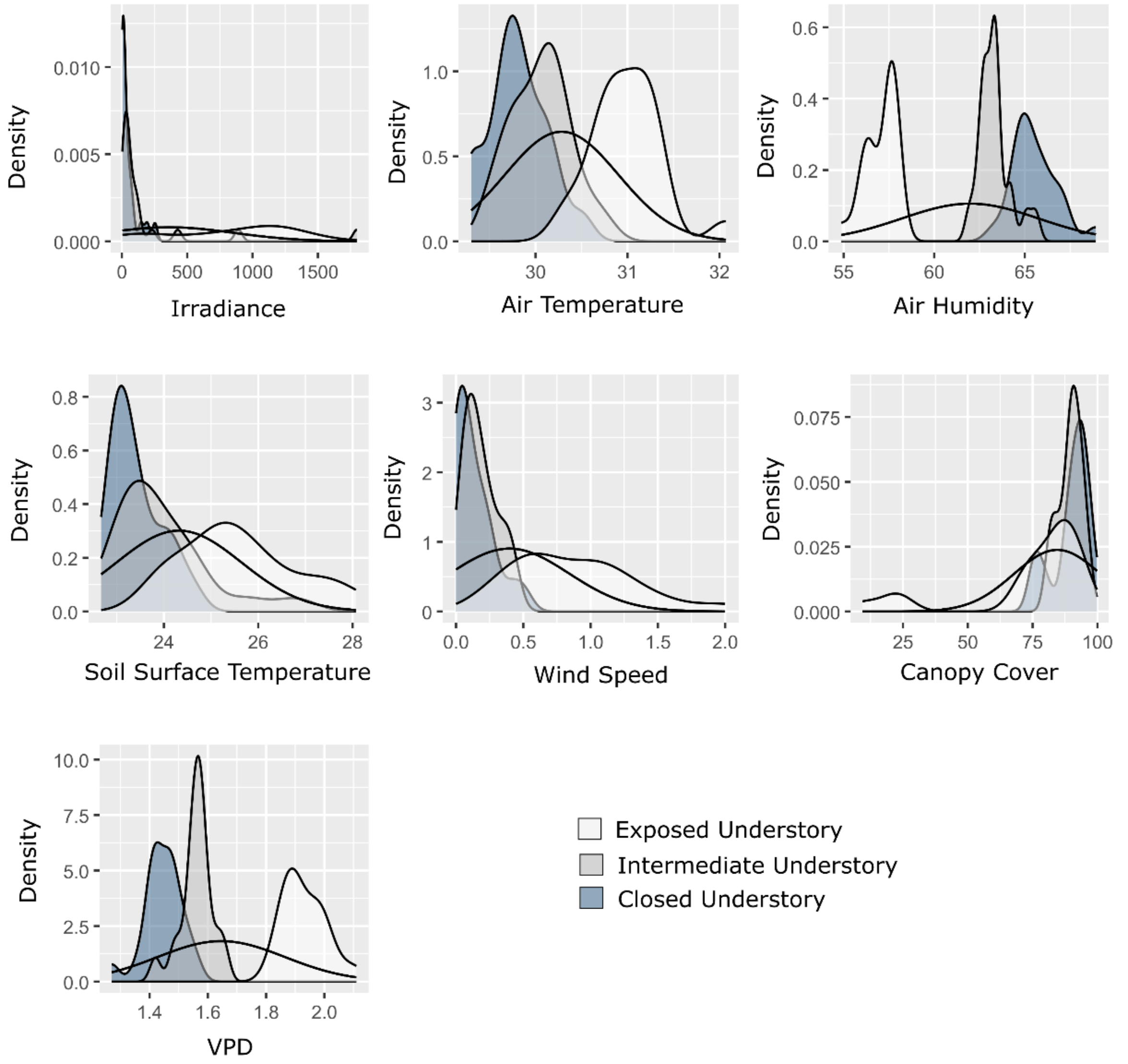

Fig. S1 Kernel density curves for microclimatic variables across three areas in ReBio União, Brazil. The normal distribution is represented by the unfilled black line.

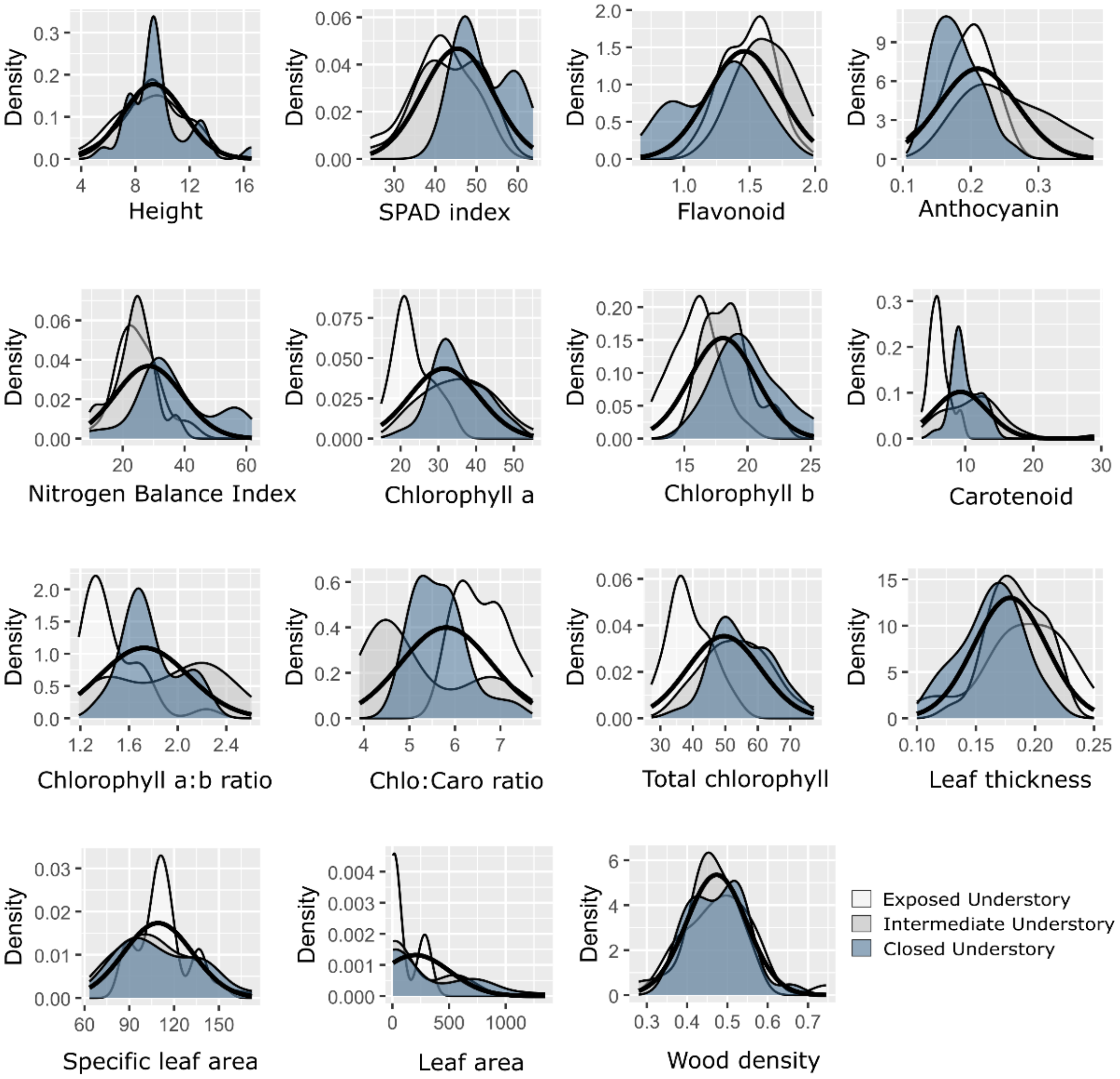

Fig. S2 Kernel density curves for leaf and wood traits in three areas in ReBio União, Brazil. The normal distribution is represented by the unfilled black line.

Table S2 Statistical descriptors of *Xylopia sericea* in three areas of ReBio União, Brazil. N: number of individuals; IQR: interquartile range CV: coefficient of variation

Traits	Exposed Understory					
	N	Min-Max	Median ± IQR	CV	Skewness	Kurtosis
Height (m)	10	8.26 – 12.92	10.65 ± 1.77	13.63	0.13	-1.29
Total chlorophyll (SPAD Index)	10	35.6 – 53.6	48.45 ± 11.65	14.78	-0.38	-1.67
Flavonoid content	8	1.46 – 1.88	1.68 ± 0.07	6.99	-0.08	-0.43
Anthocyanin content	8	0.11 – 0.23	0.16 ± 0.05	26.22	0.25	-1.52
Nitrogen balance index	8	10.84 – 30.03	20.18 ± 6.65	28.19	-0.03	-1.05
Chlorophyll *a* content (nmol.cm^{-2})	10	16.46 – 31.50	28.20 ± 8.81	20.75	-0.43	-1.59
Chlorophyll *b* content (nmol.cm^{-2})	10	12.86 – 18.26	16.53 ± 2.53	11.15	-0.27	-1.54
Carotenoid content (nmol.cm^{-2})	10	4.78 – 9.16	6.90 ± 2.34	22.50	0.14	-1.52
Chlorophyll *a:b* ratio	10	1.28 – 1.83	1.67 ± 0.29	11.89	-0.41	-1.55
Total Chlorophyll:Carotenoid ratio	10	5.19 – 7.03	6.27 ± 0.52	8.34	-0.55	-0.52
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	29.31 – 49.78	44.81 ± 11.76	17.03	-0.41	-1.59
Leaf thickness (mm)	10	0.10 – 0.25	0.17 ± 0.08	28.07	0.05	-1.40
Specific leaf area (cm^{2}.g^{-1})	10	16.43 – 29.81	28.44 ± 3.93	15.40	-1.45	0.97
Leaf area (cm^{2})	10	4.81 – 9.53	7.13 ± 2.90	23.63	-0.02	-1.74
Wood density (g.cm^{-3})	10	0.37 – 0.48	0.39 ± 0.06	9.54	0.59	-1.22
	Intermediate Understory					
Height (m)	10	4.32 – 12.92	9.28 ± 2.99	29.76	-0.19	-1.20
Total chlorophyll (SPAD Index)	10	45.00 – 55.40	51.35 ± 4.60	6.26	-0.37	-1.14
Flavonoid content	10	1.52 – 1.99	1.80 ± 0.10	7.58	-0.50	-0.56
Anthocyanin content	10	0.17 – 0.38	0.32 ± 0.07	20.45	-0.76	-0.24
Nitrogen balance index	10	9.26 – 36.98	25.29 ± 8.88	35.09	-0.40	-1.07
Chlorophyll *a* content (nmol.cm^{-2})	10	34.02 – 55.19	43.08 ± 5.53	13.86	0.41	-0.56
Chlorophyll *b* content (nmol.cm^{-2})	10	15.81 – 22.07	18.29 ± 1.40	9.03	0.64	0.06
Carotenoid content (nmol.cm^{-2})	10	11.39 – 28.95	13.86 ± 1.53	33.26	1.83	2.19
Chlorophyll *a:b* ratio	10	2.17 – 2.61	2.32 ± 0.21	6.04	0.35	-1.38
Total Chlorophyll:Carotenoid ratio	10	4.04 – 4.64	4.40 ± 0.19	3.95	-0.53	-0.63
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	49.83 – 77.27	61.62 ± 7.02	12.28	0.46	-0.35

Leaf thickness (mm)	10	0.16 – 0.22	0.19 ± 0.02	9.04	0.16	-0.75
Specific leaf area ($cm^2.g^{-1}$)	10	14.06 – 20.11	16.80 ± 2.61	12.10	0.11	-1.44
Leaf area (cm^2)	10	16.63 – 24.98	18.11 ± 2.43	13.40	1.26	0.57
Wood density ($g.cm^{-3}$)	10	0.41 – 0.52	0.47 ± 0.05	7.28	0.06	-1.38
Closed Understory						
Height (m)	10	5.64 – 16.56	9.28 ± 1.75	31.62	1.48	1.64
Total chlorophyll (SPAD Index)	10	52.1 – 63.70	58.95 ± 3.48	5.78	-0.54	-0.73
Flavonoid content	10	1.03 – 1.76	1.50 ± 0.29	14.76	-0.49	-0.84
Anthocyanin content	10	0.13 – 0.26	0.16 ± 0.06	24.57	0.75	-1.01
Nitrogen balance index	10	10.02 – 42.05	29.80 ± 9.39	33.98	-0.52	-0.90
Chlorophyll *a* content ($nmol.cm^{-2}$)	10	29.90 – 49.04	39.60 ± 10.42	17.24	0.06	-1.65
Chlorophyll *b* content ($nmol.cm^{-2}$)	10	16.21- 24.74	20.68 ± 3.65	12.70	0.02	-1.29
Carotenoid content ($nmol.cm^{-2}$)	10	8.57 – 13.96	10.25 ± 3.52	18.89	0.23	-1.84
Chlorophyll *a:b* ratio	10	1.57 – 2.20	1.91 ± 0.38	11.98	-0.03	-1.75
Total Chlorophyll:Carotenoid ratio	10	4.78 – 7.33	5.36 ± 0.88	13.48	0.96	-0.12
Total chlorophyll (*a*+*b*) ($nmol.cm^{-2}$)	10	46.86 – 72.12	61.48 ± 12.45	14.40	-0.10	-1.52
Leaf thickness (mm)	10	0.11 – 0.19	0.18 ± 0.03	14.04	-1.45	1.14
Specific leaf area ($cm^2.g^{-1}$)	10	14.67 – 24.01	19.89 ± 2.81	13.49	-0.25	-0.82
Leaf area (cm^2)	10	14.2 – 24.04	17.77 ± 4.87	18.12	0.44	-1.39
Wood density ($g.cm^{-3}$)	10	0.36 – 0.45	0.40 ± 0.05	7.07	-0.02	-1.57

Table S3 Statistical descriptors of *Cupania oblongifolia* in three areas of ReBio União, Brazil N: number of individuals; IQR: interquartile range CV: 202omponentes of variation

Traits	**Exposed Understory**					
	N	**Min-Max**	**Median ± IQR**	**CV**	**Skewness**	**Kurtosis**
Height (m)	8	3.82 – 7.82	6.42 ± 1.48	20.23	-0.59	-0.85
Total chlorophyll (SPAD Index)	8	24.4 – 43.8	36.20 ± 11.05	21.25	-0.31	-1.73
Flavonoid content	8	1.10 – 1.61	1.52 ± 0.24	12.80	-0.65	-1.28
Anthocyanin content	8	0.17 – 0.25	0.21 ± 0.05	14.76	-0.29	-1.70
Nitrogen balance index	8	19.68 – 42.40	25.28 ± 11.53	31.88	0.59	-1.46
Chlorophyll *a* content (nmol.cm^{-2})	8	14.83 – 33.57	21.60 ± 9.25	29.34	0.27	-1.68
Chlorophyll *b* content (nmol.cm^{-2})	8	12.39 – 19.87	15.37 ± 2.52	15.34	0.46	-0.95
Carotenoid content (nmol.cm^{-2})	8	3.58 – 9.36	6.26 ± 2.97	33.96	0.14	-1.65
Chlorophyll *a:b* ratio	8	1.19 – 2.24	1.40 ± 0.31	21.71	1.01	-0.26
Total Chlorophyll:Carotenoid ratio	8	5.82 – 7.70	6.14 ± 1.40	12.37	0.42	-1.88
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	8	27.22 – 53.44	36.97 ± 11.91	23.43	0.25	-1.58
Leaf thickness (mm)	8	0.17 – 0.23	0.20 ± 0.03	10.61	0.21	-1.67
Specific leaf area (cm^{2}.g^{-1})	8	4.41 – 20.81	12.17 ± 4.24	39.89	0.09	-0.94
Leaf area (cm^{2})	8	258.34 – 308.61	283.40 ± 27.49	6.32	-0.06	-1.71
Wood density (g.cm^{-3})	8	0.33 – 0.75	0.46 ± 0.06	24.28	1.00	0.25
	Intermediate Understory					
Height (m)	10	6.04 – 9.78	8.87 ± 1.74	15.97	-0.60	-1.31
Total chlorophyll (SPAD Index)	10	24.2 – 50.1	37.20 ± 6.80	19.76	-0.15	-0.91
Flavonoid content	10	1.30 – 1.75	1.49 ± 0.28	10.94	0.06	-1.71
Anthocyanin content	10	0.16 – 0.25	0.20 ± 0.04	15.61	0.02	-1.54
Nitrogen balance index	10	16.19 – 29.58	24.53 ± 5.85	18.42	-0.39	-1.34
Chlorophyll *a* content (nmol.cm^{-2})	10	29.81 – 49.66	36.27 ± 6.62	17.19	0.63	-0.80
Chlorophyll *b* content (nmol.cm^{-2})	10	16.57 – 22.29	18.16 ± 2.45	10.33	0.63	-0.91
Carotenoid content (nmol.cm^{-2})	10	9.12 – 17.70	12.19 ± 2.79	20.76	0.79	-0.26
Chlorophyll *a:b* ratio	10	1.77 – 2.20	2.01 ± 0.26	8.09	-0.01	-1.67
Total Chlorophyll:Carotenoid ratio	10	3.91 – 5.55	4.62 ± 0.36	11.12	0.35	-1.04
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	46.39 – 71.96	54.56 ± 8.95	14.73	0.66	-0.74

Leaf thickness (mm)	10	0.13 – 0.22	0.17 ± 0.03	15.91	0.09	-1.20
Specific leaf area (cm^2.g^{-1})	10	12.13 – 17.89	15.83 ± 2.44	11.88	-0.23	-1.40
Leaf area (cm^2)	10	449.51 – 1349.82	586.75 ± 173.11	41.62	1.82	2.21
Wood density (g.cm^{-3})	10	0.33 – 0.47	0.42 ± 0.04	10.34	-0.64	-0.82
Closed Understory						
Height (m)	10	7.46 – 11.10	9.28 ± 0.00	11.43	-0.13	-0.41
Total chlorophyll (SPAD Index)	10	40.9 – 57.10	46.25 ± 2.70	8.82	1.11	1.02
Flavonoid content	10	0.67 – 1.54	0.90 ± 0.35	27.75	0.66	-1.22
Anthocyanin content	10	0.14 – 0.20	0.16 ± 0.02	10.71	0.10	-1.43
Nitrogen balance index	10	25.91 – 61.78	52.78 ± 17.48	25.86	-0.56	-1.39
Chlorophyll *a* content (nmol.cm^{-2})	10	26.46 – 49.69	32.35 ± 7.49	20.19	0.84	-0.63
Chlorophyll *b* content (nmol.cm^{-2})	10	17.05 – 25.26	19.13 ± 2.11	13.17	0.96	-0.33
Carotenoid content (nmol.cm^{-2})	10	7.67 – 13.56	9.10 ± 0.59	19.64	1.03	-0.49
Chlorophyll *a:b* ratio	10	1.41 – 2.20	1.73 ± 0.13	13.71	0.56	-0.82
Total Chlorophyll:Carotenoid ratio	10	5.14 – 6.87	5.80 ± 0.56	9.00	0.61	-0.45
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	45.34 – 72.33	51.25 ± 12.00	16.45	0.75	-1.02
Leaf thickness (mm)	10	0.12 – 0.16	0.14 ± 0.03	10.56	-0.14	-1.60
Specific leaf area (cm^2.g^{-1})	10	12.61 – 74.85	19.63 ± 4.22	76.21	2.14	3.17
Leaf area (cm^2)	10	291.14 – 1220.48	727.65 ± 242.13	35.64	0.34	-0.39
Wood density (g.cm^{-3})	10	0.41 – 0.54	0.50 ± 0.04	8.02	-0.72	-0.65

Table S4 Statistical descriptors of *Miconia cinnamomifolia* in three areas of ReBio União, Brazil N: number of individuals; IQR: interquartile range CV: 204omponentes of variation

Traits	Exposed Understory					
	N	**Min-Max**	**Median ± IQR**	**CV**	**Skewness**	**Kurtosis**
Height (m)	10	7.46 – 12.92	9.78 ± 1.75	18.38	0.13	-1.33
Total chlorophyll (SPAD Index)	10	32.70 – 48.9	40.95 ± 3.85	12.05	0.05	-1.01
Flavonoid content	10	1.18 – 1.58	1.37 ± 0.16	9.09	0.19	-1.27
Anthocyanin content	10	0.18 – 0.26	0.20 ± 0.02	11.17	1.05	0.26
Nitrogen balance index	10	18.77 – 33.57	26.57 ± 6.26	17.13	-0.10	-1.34
Chlorophyll *a* content (nmol.cm^{-2})	10	18.07 – 25.91	21.18 ± 2.32	10.23	0.40	-0.73
Chlorophyll *b* content (nmol.cm^{-2})	10	14.74 – 18.39	15.96 ± 1.71	7.09	0.27	-1.46
Carotenoid content (nmol.cm^{-2})	10	4.79 – 6.54	5.88 ± 0.67	10.19	-0.35	-1.35
Chlorophyll *a:b* ratio	10	1.22 – 1.38	1.30 ± 0.06	3.76	0.04	-1.12
Total Chlorophyll:Carotenoid ratio	10	6.20 – 7.54	6.86 ± 0.48	5.88	0.08	-1.08
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	32.80 – 44.31	37.36 ± 3.82	8.76	0.36	-0.94
Leaf thickness (mm)	10	0.16 – 0.24	0.21 ± 0.04	12.94	-0.17	-1.44
Specific leaf area (cm^{2}.g^{-1})	10	16.24 – 27.54	22.16 ± 2.35	15.83	-0.20	-0.92
Leaf area (cm^{2})	10	15.7 – 29.17	22.73 ± 5.19	19.41	-0.07	-1.37
Wood density (g.cm^{-3})	10	0.50 – 0.58	0.55 ± 0.06	5.90	-0.11	-1.79
	Intermediate Understory					
Height (m)	10	7.46 – 12.92	10.89 ± 2.73	17.25	-0.24	-1.47
Total chlorophyll (SPAD Index)	10	33.7 – 50.6	40.65 ± 4.75	12.30	0.40	-0.98
Flavonoid content	10	1.16 – 1.93	1.56 ± 0.15	13.04	0.10	-0.17
Anthocyanin content	10	0.19 – 0.33	0.23 ± 0.07	18.00	0.45	-1.42
Nitrogen balance index	10	10.73 – 37.35	23.68 ± 5.34	31.33	0.27	-0.27
Chlorophyll *a* content (nmol.cm^{-2})	10	19.64 – 36.10	26.17 ± 5.80	18.99	0.50	-0.87
Chlorophyll *b* content (nmol.cm^{-2})	10	5.55 – 21.99	18.34 ± 2.43	10.89	0.36	-1.12
Carotenoid content (nmol.cm^{-2})	10	5.08 – 11.13	6.72 ± 1.59	26.40	1.07	0.27
Chlorophyll *a:b* ratio	10	1.26 – 1.64	1.42 ± 0.14	8.13	0.40	-0.98
Total Chlorophyll:Carotenoid ratio	10	5.25 – 7.55	6.79 ± 0.35	9.75	-0.74	-0.09
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	10	35.19 – 58.10	44.51 ± 8.18	15.65	0.46	-0.95

Leaf thickness (mm)	10	0.16 – 0.22	0.19 ± 0.04	11.64	0.00	-1.77
Specific leaf area (cm^2.g^{-1})	10	16.65 – 23.69	19.44 ± 1.9	9.73	0.51	-0.26
Leaf area (cm^2)	10	22.22 – 29.96	25.41 ± 2.92	9.03	0.37	-0.90
Wood density (g.cm^{-3})	10	0.28 – 0.57	0.52 ± 0.05	16.90	-1.58	1.52
			Closed Understory			
Height (m)	7	7.96 – 12.92	12.10 ± 2.73	16.98	-0.56	-1.42
Total chlorophyll (SPAD Index)	7	44.10 – 51.7	48.80 ± 3.00	5.71	-0.29	-1.57
Flavonoid content	7	1.10 – 1.47	1.29 ± 0.16	9.72	-0.25	-1.49
Anthocyanin content	7	0.17 – 0.23	0.21 ± 0.03	10.89	-0.12	-1.84
Nitrogen balance index	7	29.89 – 35.35	31.13 ± 3.52	7.22	0.42	-1.80
Chlorophyll *a* content (nmol.cm^{-2})	7	20.84 – 38.93	32.09 ± 5.34	18.38	-0.62	-0.88
Chlorophyll *b* content (nmol.cm^{-2})	7	15.31 – 22.90	19.96 ± 1.61	11.98	-0.44	-0.84
Carotenoid content (nmol.cm^{-2})	7	5.59 – 11.61	9.14 ± 2.12	21.71	-0.65	-0.93
Chlorophyll *a:b* ratio	7	1.36 – 1.75	1.60 ± 0.11	7.84	-0.79	-0.66
Total Chlorophyll:Carotenoid ratio	7	4.86 – 6.47	5.57 ± 0.59	9.55	0.34	-1.27
Total chlorophyll (*a*+*b*) (nmol.cm^{-2})	7	36.15 – 61.83	52.05 ± 6.96	15.89	-0.58	-0.86
Leaf thickness (mm)	7	0.16 – 0.21	0.18 ± 0.03	10.93	0.44	-1.68
Specific leaf area (cm^2.g^{-1})	7	12.96 – 31.25	21.89 ± 6.42	28.19	0.26	-1.25
Leaf area (cm^2)	7	20.60 – 40.47	27.72 ± 9.23	25.23	0.47	-1.33
Wood density (g.cm^{-3})	7	0.53 – 0.66	0.54 ± 0.02	8.24	1.36	0.19

Table S5 – Principal components analysis results of microclimatic variables in three areas of ReBio União, Brazil. BS: Broken-Stick Criteria

Principal Components	BS Criteria	Eigenvalues	Variance (%)	Cumulative Variance (%)
PC1	2.45	**3.74**	**62.30**	62.30
PC2	1.45	0.95	**15.80**	78.10
PC3	0.95	0.61	10.25	88.35
PC4	0.62	0.38	6.34	94.69
PC5	0.37	0.25	4.20	98.89
PC6	0.17	0.07	1.16	100

Table S6 Loadings of the first three principal components of microclimatic variables

Variables	PC1	PC2	PC3
Irradiance	**0.42**	-0.17	**0.57**
Air Temperature	**0.46**	-0.09	0.33
Air Humidity	**-0.49**	-0.07	-0.01
Soil Surface Temperature	0.38	0.27	**-0.61**
Wind Speed	0.41	0.39	0.38
Canopy Cover	-0.22	**0.85**	**0.85**

Table S7 Correlation of microclimatic variables with PCA axes. Asterisks indicate: * 0.05; ** 0.01. ***0.001

Traits	PC1	PC2	PC3
Irradiance	**0.80*** **	-0.17	**0.44*** **
Air Temperature	**0.89*** **	-0.09	0.25*
Air Humidity	**-0.96*** **	-0.07	-0.01
Soil Surface Temperature	0.74***	0.27*	**-0.47*** **
Wind Speed	0.80***	0.38**	-0.12
Canopy Cover	-0.43***	**0.83*** **	**0.32* **

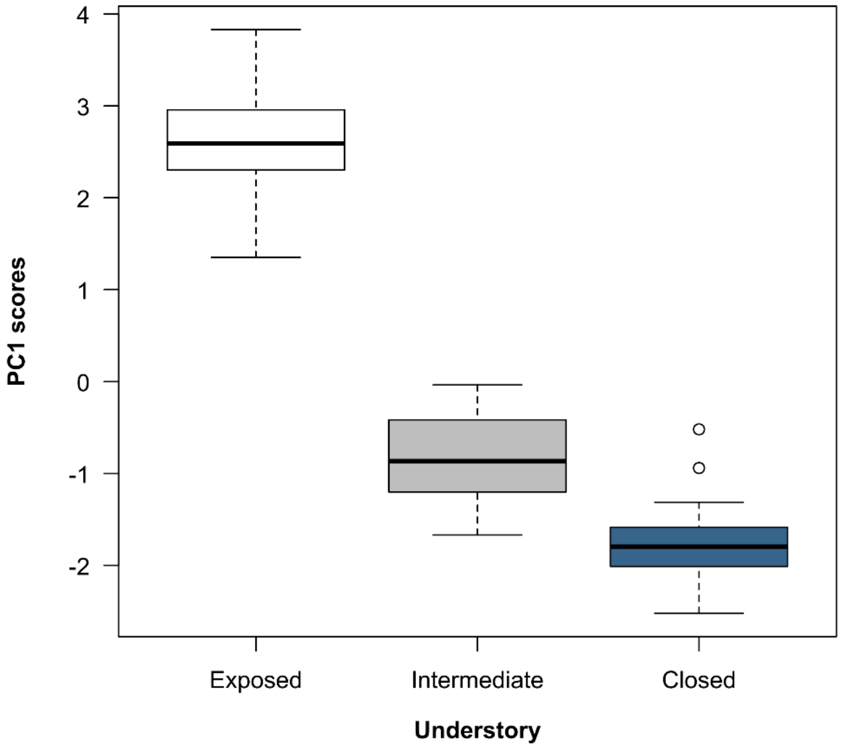

Fig. S3 Scores of the first principal components of microclimatic variables between three areas of ReBio União, Brazil

Table S8 Mean ± standard deviation of leaf and wood traits of three co-occurring species of Rebio União. Different letters represent significant differences between areas and species (p ≤ 0.05, 0.01, 0.001)

Traits	***X. sericea***			***C. oblongifolia***			***M. cinnamomifolia***		
	Exposed Understory	Intermediate Understory	Closed Understory	Exposed Understory	Intermediate Understory	Closed Understory	Exposed Understory	Intermediate Understory	Closed Understory
Height	10.47 ± 1.43^{ab}	8.98 ± 2.67^{a}	9.13 ± 2.89^{bc}	6.28 ± 1.27^{c}	8.45 ± 1.35^{abc}	9.13 ± 1.04^{abc}	10.17 ± 1.87^{ab}	10.69 ± 1.85^{a}	11.31 ± 1.92^{a}
SPAD Index	46.29 ± 6.84^{abc}	51.08 ± 3.20^{ab}	59.03 ± 3.41^{a}	35.53 ± 7.55^{d}	37.99 ± 7.51^{cd}	46.99 ± 4.15^{c}	41.20 ± 4.96^{cd}	41.37 ± 5.09^{cd}	48.00 ± 2.74^{c}
Flavonoid content	1.67 ± 0.12^{ab}	1.80 ± 0.14^{a}	1.47 ± 0.22^{bc}	1.43 ± 0.18^{bc}	1.52 ± 0.17^{abc}	1.02 ± 0.28^{d}	1.39 ± 0.13^{bc}	1.53 ± 0.20^{abc}	1.31 ± 0.13^{c}
Anthocyanin content	0.16 ± 0.04^{c}	0.31 ± 0.06^{a}	0.18 ± 0.04^{c}	0.21 ± 0.03^{c}	0.21 ± 0.03^{bc}	0.17 ± 0.02^{bc}	0.21 ± 0.02^{bc}	0.25 ± 0.05^{b}	0.20 ± 0.02^{bc}
Nitrogen balance index	20.58 ± 5.80^{b}	24.23 ± 8.50^{b}	29.68 ± 10.08^{b}	27.66 ± 8.82^{b}	23.95 ± 4.41^{b}	47.74 ± 12.35^{a}	26.67 ± 4.57^{b}	22.74 ± 7.12^{b}	32.10 ± 2.32^{ab}
Chlorophyll *a* content	25.67 ± 5.33^{cde}	43.04 ± 5.97^{a}	38.41 ± 6.62^{ab}	23.68 ± 6.95^{de}	36.87 ± 6.34^{ab}	34.92 ± 7.05^{bc}	21.62 ± 2.21^{e}	26.16 ± 4.97^{cde}	31.75 ± 5.84^{bcd}
Chlorophyll *b* content	15.76 ± 1.76^{cd}	18.40 ± 1.66^{abc}	20.45 ± 2.60^{a}	15.41 ± 2.37^{d}	18.42 ± 1.90^{ab}	19.62 ± 2.58^{abc}	16.45 ± 1.17^{bcd}	18.25 ± 1.99^{ab}	19.55 ± 2.34^{ab}
Carotenoid content	6.65 ± 1.50^{de}	15.32 ± 5.10^{a}	10.81 ± 2.04^{abc}	6.41 ± 2.18^{e}	12.15 ± 2.52^{ab}	9.68 ± 1.90^{cd}	5.73 ± 0.58^{e}	6.88 ± 1.82^{e}	9.43 ± 2.05^{bc}
Chlorophyll *a:b* ratio	1.60 ± 0.19^{de}	2.35 ± 0.14^{a}	1.89 ± 0.23^{bc}	1.53 ± 0.33^{def}	1.99 ± 0.16^{b}	1.77 ± 0.24^{bcd}	1.30 ± 0.05^{f}	1.42 ± 0.12^{ef}	1.61 ± 0.13^{cde}
Total Chlo:Caro ratio	6.29 ± 0.52^{a}	4.40 ± 0.17^{c}	5.62 ± 0.76^{b}	6.54 ± 0.81^{a}	4.65 ± 0.52^{c}	5.77 ± 0.52^{b}	6.82 ± 0.40^{a}	6.70 ± 0.65^{a}	5.56 ± 0.53^{b}
Total chlorophyll (*a*+*b*)	41.43 ± 7.05^{cde}	61.44 ± 7.55^{a}	58.86 ± 8.47^{ab}	39.09 ± 9.16^{de}	55.29 ± 8.15^{a}	54.54 ± 8.97^{abc}	38.07 ± 3.34^{e}	44.40 ± 6.95^{bcde}	51.30 ± 8.15^{abcd}
Leaf thickness	0.17 ± 0.05^{ab}	0.19 ± 0.02^{a}	0.17 ± 0.02^{a}	0.20 ± 0.02^{a}	0.18 ± 0.03^{a}	0.14 ± 0.02^{b}	0.20 ± 0.03^{a}	0.19 ± 0.02^{a}	0.18 ± 0.02^{a}
Specific leaf area	26.67 ± 4.11^{a}	16.9 ± 2.05^{c}	19.57 ± 2.64^{bc}	12.31 ± 4.91^{d}	15.21 ± 1.81^{cd}	23.89 ± 18.2^{c}	21.68 ± 3.43^{ab}	19.63 ± 1.91^{bc}	21.16 ± 5.97^{bc}
Leaf area	7.16 ± 1.69^{e}	18.88 ± 2.53^{cd}	18.28 ± 3.31^{d}	284.95 ± 18.02^{b}	638.40 ± 265.71^{a}	705.87 ± 251.57^{a}	22.56 ± 4.38^{cd}	25.48 ± 2.30^{c}	28.09 ± 7.09^{c}
Wood density	0.41 ± 0.04^{e}	0.47 ± 0.03^{cd}	0.41 ± 0.03^{e}	0.49 ± 0.12^{bcd}	0.42 ± 0.04^{de}	0.49 ± 0.04^{abc}	0.54 ± 0.03^{a}	0.50 ± 0.08^{ab}	0.56 ± 0.05^{a}

Table S9 Two-way anova table on the influence of individuals, site, and interaction between individuals and site. Df: degrees of freedom. H^2: eta squared (partial) effect size for ANOVA

Trait	Source of Variation	df	F	P	η^2
Height	Individuals	2	15.67	**< 0.001**	0.26
	Site	2	0.5	0.6	0.02
	Individuals:Site	4	5.7	**< 0.001**	0.20
	Residuals	69			
SPAD index	Individuals	2	32.97	**< 0.001**	0.48
	Site	2	8.69	**< 0.001**	0.20
	Individuals:Site	4	1.27	0.29	0.07
	Residuals	71			
Flavonoid content	Individuals	2	22.79	**< 0.001**	0.40
	Site	2	31.11	**< 0.001**	0.47
	Individuals:Site	4	3.31	**0.02**	0.16
	Residuals	69			
Anthocyanin content	Individuals	2	4.37	**0.02**	0.11
	Site	2	38.17	**< 0.001**	0.51
	Individuals:Site	4	11.9	**< 0.001**	0.40
	Residuals	72			
Nitrogen Balance Index	Individuals	2	5.49	**< 0.01**	0.14
	Site	2	17.44	**< 0.001**	0.33
	Individuals:Site	4	3.39	**0.01**	0.16
	Residuals	70			
Chlorophyll *a* content	Individuals	2	16.6	**< 0.001**	0.16
	Site	2	36.37	**< 0.001**	0.50
	Individuals:Site	4	3.38	**0.01**	0.15
	Residuals	74			
Chlorophyll *b* content	Individuals	2	0.39	0.68	0.01
	Site	2	21.59	**< 0.001**	0.37
	Individuals:Site	4	0.72	0.58	0.04
	Residuals	73			
Carotenoid content	Individuals	2	23.51	**< 0.001**	0.41
	Site	2	55.28	**< 0.001**	0.62
	Individuals:Site	4	11.9	**< 0.001**	0.41
	Residuals	69			
Clorophyll *a:b* ratio	Individuals	2	63.2	**< 0.001**	0.64
	Site	2	45.88	**< 0.001**	0.56
	Individuals:Site	4	10.36	**< 0.001**	0.37
	Residuals	72			
Chlorophyll:Carotenoid ratio	Individuals	2	32.27	**< 0.001**	0.48
	Site	2	59.35	**< 0.001**	0.63
	Individuals:Site	4	21.55	**< 0.001**	0.55
	Residuals	70			
Total Chlorophyll	Individuals	2	8.93	**< 0.001**	0.19
	Site	2	31.36	**< 0.001**	0.46

	Individuals:Site	4	2.33	0.06	0.11
	Residuals	74			
Leaf thickness	Individuals	2	5.61	**< 0.01**	0.13
	Site	2	7.38	**< 0.01**	0.16
	Individuals:Site	4	4.69	**< 0.01**	0.20
	Residuals	75			
Specific leaf area	Individuals	2	30.24	**< 0.001**	0.47
	Site	2	9.58	**< 0.001**	0.22
	Individuals:Site	4	12.25	**< 0.001**	0.42
	Residuals	68			
Leaf area	Individuals	2	3069.44	**< 0.001**	0.99
	Site	2	85.02	**< 0.001**	0.70
	Individuals:Site	4	14.46	**< 0.001**	0.44
	Residuals	73			
Wood density	Individuals	2	70.8	**< 0.001**	0.67
	Site	2	0.38	0.69	0.01
	Individuals:Site	4	11.31	**< 0.001**	0.39
	Residuals	70			

Table S10 Principal components analysis results of leaf and wood traits of three co-occurring species in ReBio União, Brazil. BS: Broken Stick Criteria

Principal Components	BS Criteria	Eigenvalues	Variance (%)	Cumulative variance (%)
PC1	2.72	**1.96**	**24.44**	24.44
PC2	1.72	**1.73**	**21.56**	46.00
PC3	1.22	**1.42**	**17.85**	63.85
PC4	0.88	0.86	10.81	74.66
PC5	0.64	0.71	8.90	83.56
PC6	0.44	0.56	7.05	90.61
PC7	0.27	0.44	5.49	96.10
PC8	0.13	0.31	3.92	100.00

Table S11 PCA Loadings of the first four principal components of leaf and wood traits

Traits	PC1	PC2	PC3	PC4
Height	-0.07	-0.31	**0.64**	0.16
SPAD index	**-0.45**	0.21	**0.40**	0.23
Flavonoid	0.21	**0.42**	**0.40**	**-0.45**
Anthocyanin	**0.45**	0.25	0.28	0.29
Chlorophyll a:b	-0.35	**0.50**	0.09	**0.39**
Leaf thickness	**0.47**	0.24	0.16	-0.17
Wood density	**0.37**	**-0.42**	0.15	**0.50**
Specific leaf area	-0.24	**-0.37**	**0.37**	**-0.46**

Table S12 Correlation of leaf and wood traits with PC axes. Asterisks indicate: * 0.05; ** 0.01. ***0.001

Traits	PC1	PC2	PC3	PC4
Height	-0.10	-0.41***	**0.77*** **	0.14
SPAD index	**-0.63*** **	0.27*	**0.47*** **	0.21
Flavonoid	0.30**	**0.55*** **	**0.47*** **	**-0.47*** **
Anthocyanin	**0.63*** **	0.33**	0.33**	0.27*
Chlorophyll a:b	-0.49***	**0.66*** **	0.10	**0.36*** **
Leaf thickness	**0.66*** **	0.31**	0.20	-0.16
Wood density	**0.52*** **	**-0.55*** **	0.18	**0.46*** **
Specific leaf area	-0.33**	**-0.49*** **	**0.45*** **	**-0.43*** **

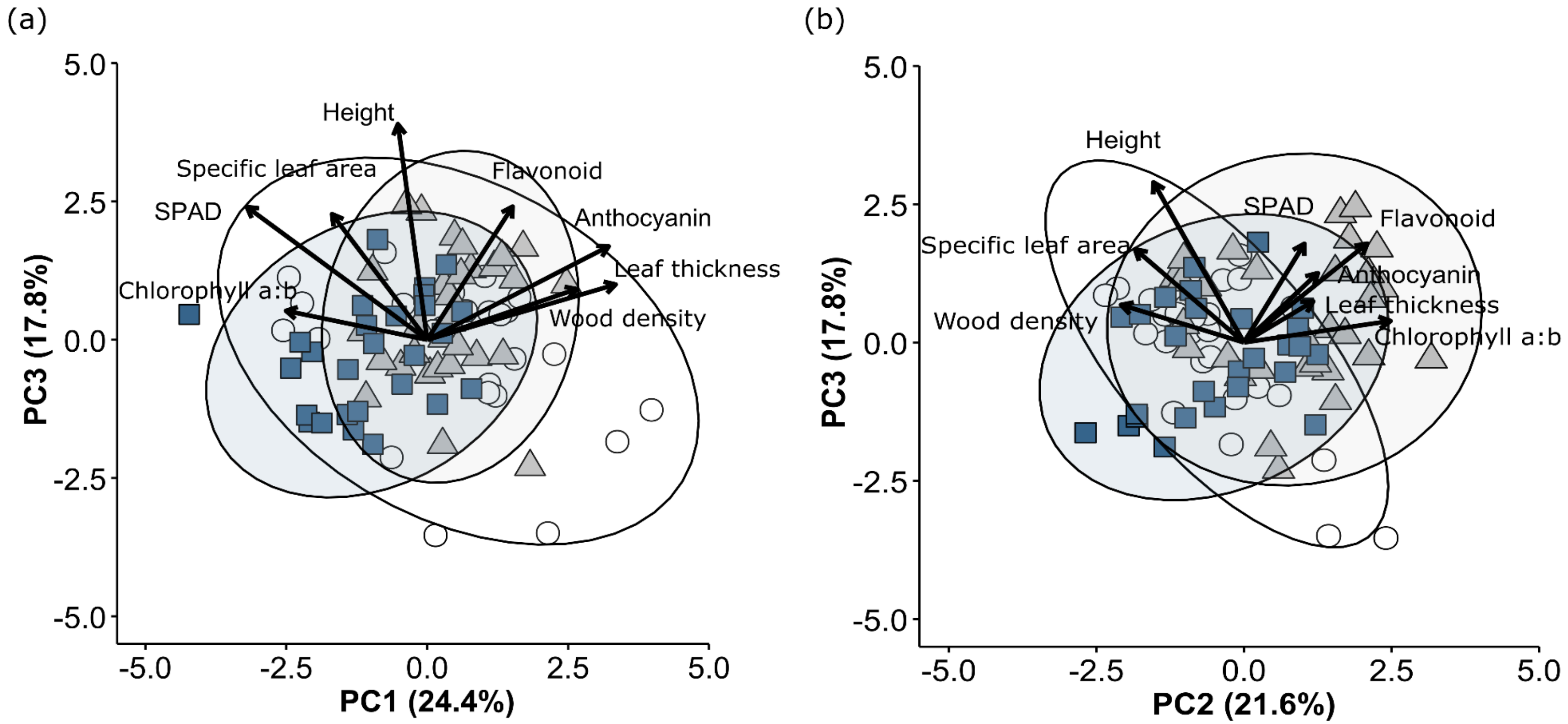

Fig. S4 Principal components analysis of leaf and wood traits in three co-occurring species of ReBio União, Brazil. (a) PC1-PC3. (b) PC2-PC3. ○ Exposed Understory, △ Intermediate Understory, ■ Close Understory

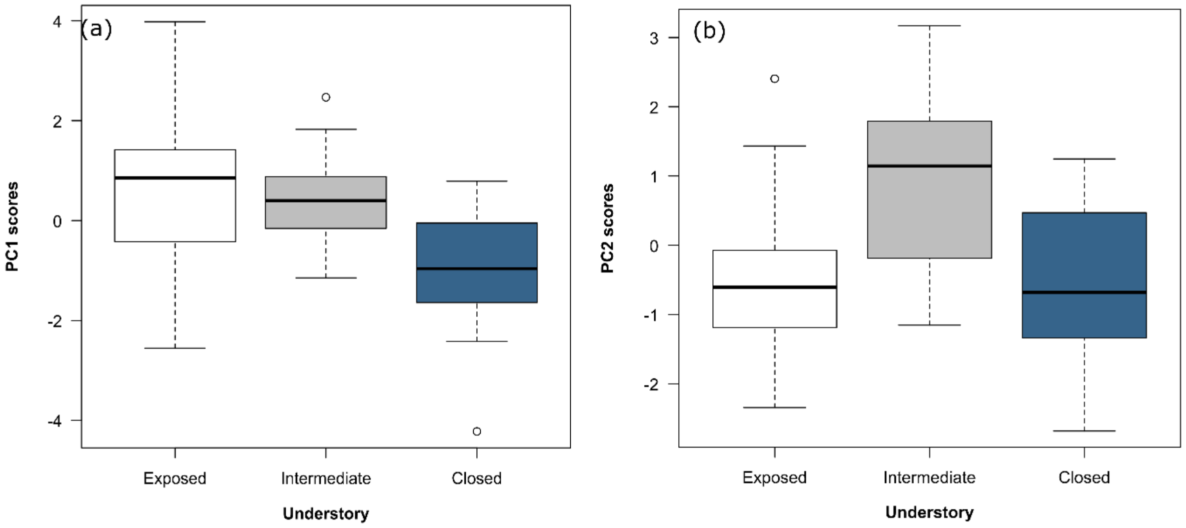

Fig. S5 Scores of the first two principal components of leaf and wood traits between three areas of ReBio União, Brazil

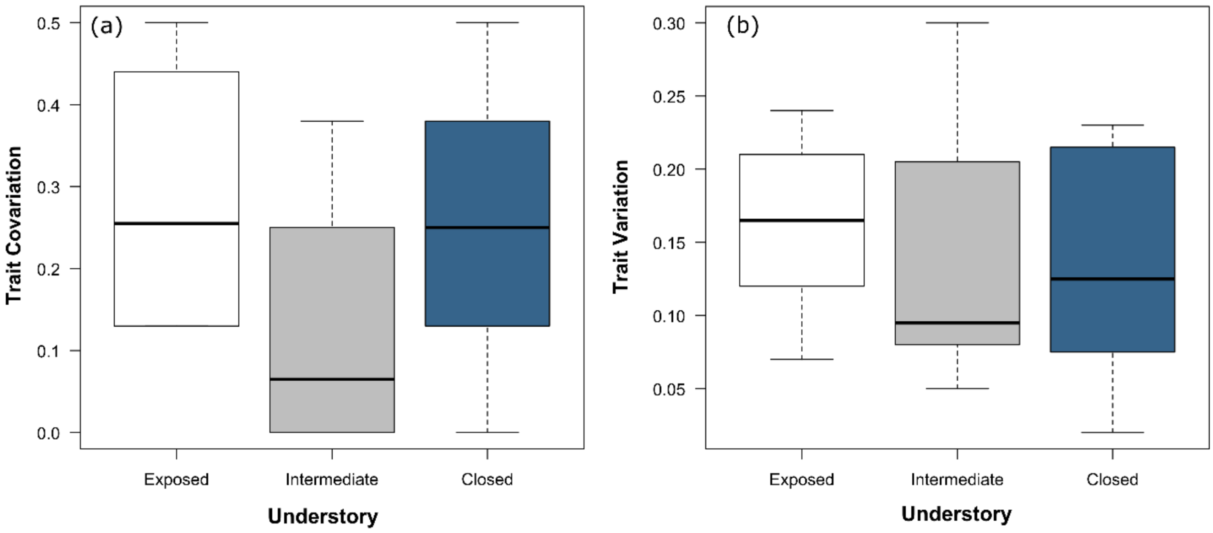

Fig. S6 Trait covariation and variation in three areas of ReBio União, Brazil. (a) Trait covariation (b) Trait variation

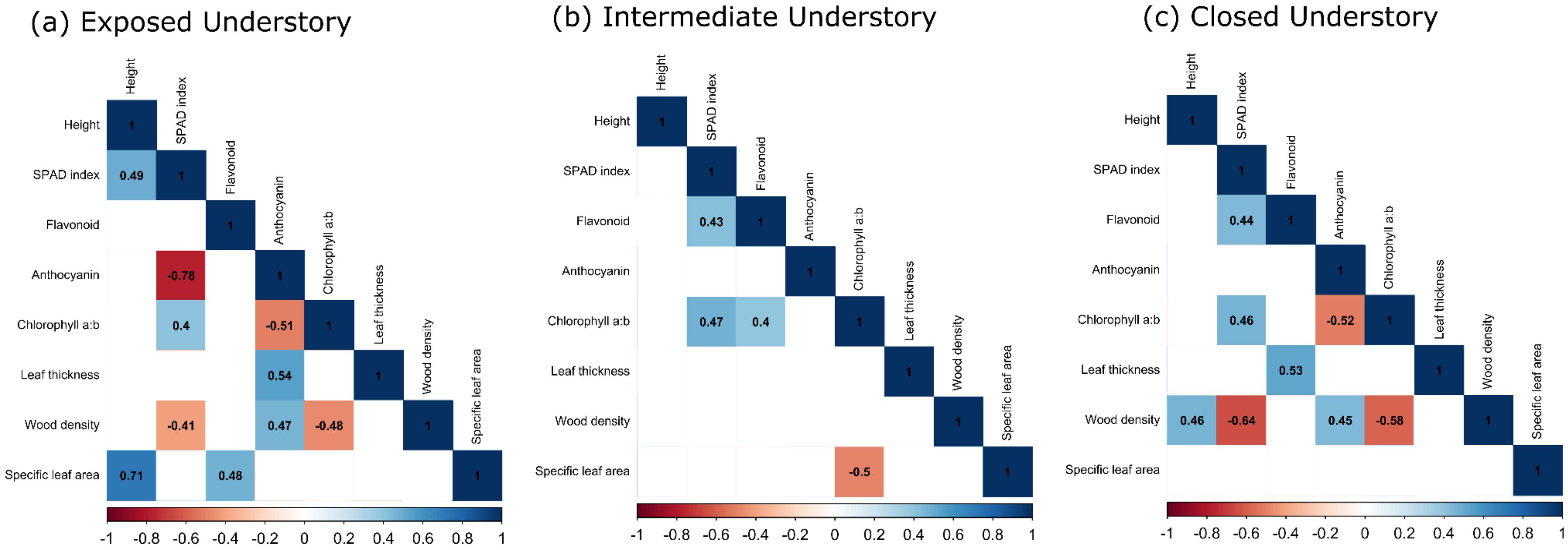

Fig. S7 Pairwise Pearson correlation matrices of leaf and wood traits between areas as indicators of trait covariation (a) Exposed Understory, (b) Intermediate Understory, (c) Closed Understory

Table S13 Results of linear models between trait variation and covariation for all species and for each species. Std: Standard

Species		**Estimate Std**	**Error**	**T value**	**Pr (>| t |)**
All species	(Intercept)	-0.029	0.069	-0.420	0.6890
	Trait covariation	0.616	0.253	2.436	**0.0508**
X. sericea	(Intercept)	0.031	0.072	0.440	0.675
	Trait covariation	0.389	0.209	1.867	0.111
C. oblongifolia	(Intercept)	0.160	0.060	2.665	**< 0.05**
	Trait covariation	0.029	0.125	0.234	0.8230
M. cinnamomifolia	(Intercept)	0.082	0.023	3.519	**< 0.05**
	Trait covariation	0.038	0.176	0.216	0.8360

Table S14 Results of the variance decomposition for leaf and wood traits in ReBio União, Brazil

Traits	**Area**	**Species**	**Individuals**	**Residual (Within)**
Height	0.00	36.49	63.46	0.05
SPAD index	18.26	41.07	33.75	6.91
Flavonoid	23.65	36.40	33.16	6.79
Anthocyanin	29.16	27.03	36.69	7.12
Chlorophyll a:b	15.71	58.30	20.70	5.29
Leaf thickness	5.62	22.12	62.07	10.17
Wood density	0.00	43.24	56.66	0.102
Specific leaf area	0.00	41.77	58.16	0.07

Table S15 Coefficient of variation for leaf traits in three co-occurring species in ReBio União, Brazil

Species	Area	CV NBI	CV CHLA	CV CHLB	CV CAR	CV CHL:CAR	CV TCHL	CV LA
X. sericea	Exposed	28.19	20.75	11.15	22.50	8.34	17.03	23.63
	Intermediate	35.09	13.86	9.03	33.26	3.95	12.28	13.40
	Closed	33.98	17.24	12.70	18.89	13.48	14.40	18.12
	Total	**35.77**	**26.46**	**15.27**	**43.89**	**17.48**	**21.72**	**40.80**
C. oblongifolia	Exposed	31.88	29.34*	15.34	33.96*	12.37	23.43*	6.32
	Intermediate	18.42	17.19	10.33	20.76	11.12	14.73	41.62
	Closed	25.86	20.19	13.17	19.64	9.00	16.45	35.64
	Total	**41.82**	**26.68**	**15.62**	**32.79**	**17.50**	**22.08**	**49.51**
M. cinnamomifolia	Exposed	17.13	10.23	7.09	10.19	5.88	8.76	19.41
	Intermediate	31.33*	18.99	10.89	26.40	9.75	15.65	9.03
	Closed	7.22	18.38	11.98	21.71	9.55	15.89	25.23*
	Total	**23.73**	**22.61**	**12.08**	**29.58**	**11.57**	**18.22**	**19.93**

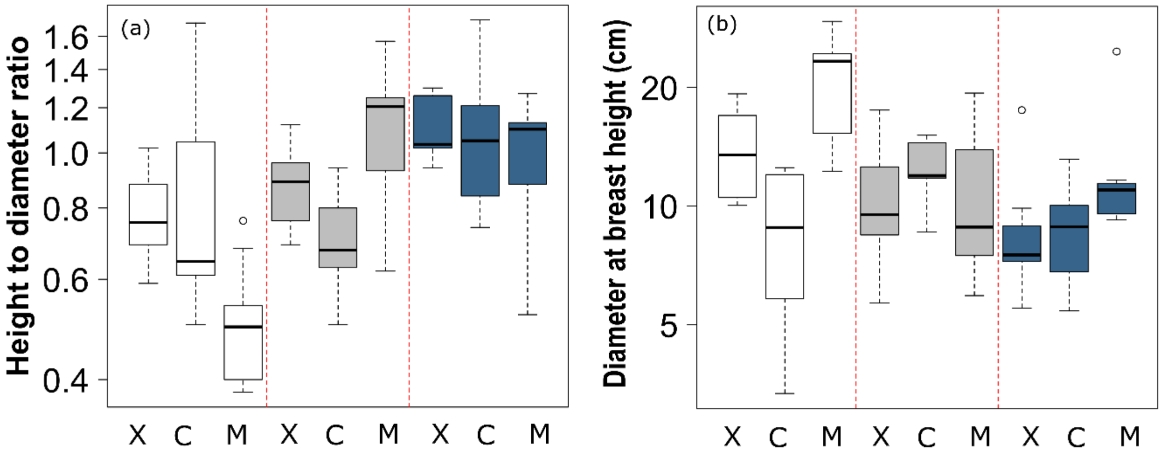

Fig. S8 Height to diameter and diameter at breast height variation between three co-occurring species of ReBio Uinão, Brazil. X: *Xylopia sericea*, C: *Cupania oblongifolia*, M: *Miconia cinnamomifolia*. The species in each area are separated by the dashed red lines.

5. DISCUSSÃO GERAL

Este estudo sobre as respostas dos atributos das plantas em diferentes gradientes abióticos no Neótropico revelou uma ampla gama de respostas morfoanatômicas e fisiológicas inter- e intraespecíficas (**Capítulos 1, 2 e 3**). Observou-se um crescimento temporal sobre os estudos da variação e covariação dos atributos em gradientes ambientais nos últimos 12 anos (**Capítulo 1)**. Esse crescente nos estudos com atributos funcionais na ecologia baseada em atributos deve-se principalmente ao poder de síntese que os atributos podem fornecer para a compreensão de diversos processos biológicos (Shipley et al., 2016). Atributos foliares morfológicos, como a área foliar específica, e do lenho, como a densidade da madeira, foram os mais amplamente investigados. Esses dois atributos são de fácil medição (*soft traits*) em comparação com atributos fisiológicos (*hard traits*) e são considerados *proxies* de estratégias ecológicas e do *fitness* das plantas (Wright et al., 2004, Violle et al., 2007, Chave et al., 2009)

A disponibilidade hídrica foi um dos principais direcionadores ambientais a influenciar na variação dos atributos, como nos padrões de acoplamento e desacoplamento entre folha e lenho e na covariação e variação de atributos do lenho em ecossistemas sazonais e não sazonais (**Capítulos 1 e 2**). A água é um recurso essencial para os sistemas biológicos, como as plantas, e um dos principais recursos a influenciar a distribuição das espécies nos diferentes ecossistemas (Engelbrecht et al., 2007, Padilla e Pugnaire, 2007). Existem inúmeros estudos prevendo que em um futuro breve, a escassez de água em algumas regiões será uma realidade (IPCC, 2023) e espécies que não estejam aptas a lidar com essas mudanças ambientais poderão ser eliminadas dos ecossistemas (McDowell et al., 2018). Além disso, a falha hidráulica é o primeiro processo a acometer as plantas quando esse recurso é restrito (Adams, 2017, McDowell et al., 2018, Menezes-Silva et al., 2019). Observou-se também que os padrões de acoplamento e desacoplamento da folha e do lenho ainda não constituem um padrão geral, tanto para a região Neotropical quanto para outras regiões geográficas, existindo uma lacuna principalmente sobre estudos que comparam esses padrões em mais de um ecossistema, seja em gradientes ambientais ou condições contrastantes (**Capítulo 1**). Muitos mecanismos dentro e entre esses órgãos ainda não estão completamente elucidados, especialmente quais desses mecanismos as plantas “priorizam” em relação as condições ambientais em que estão submetidas (Flores-Moreno et al., 2019).

Seguindo essa mesma busca por padrões, na análise da variação e covariação de atributos da folha e do lenho em um gradiente ambiental latitudinal e em um gradiente ambiental local (principalmente de irradiância), observou-se resultados variados, com relações negativas, positivas e nulas entre esses dois componentes da variação fenotípica nos atributos das espécies (**Capítulos 2 e 3**). Em geral, a variação e covariação dos atributos estiveram relacionadas com as condições ambientais em que as plantas estão submetidas (observado pela ótica da severidade ambiental), mas também, às restrições biofísicas das relações entre atributos, conservadas evolutivamente (Armbruster et al., 2014, Murren et al., 2015, Dwyer e Laughlin 2017). Como resultado disso, a maior covariação do lenho foi encontrada em ecossistemas com maiores restrições espaciais e temporais de recursos (restinga - RN e floresta semidecidual - RJ) e menor variação foi encontrada em um ecossistema produtivo (floresta ombrófila - SC) (**Capítulo 2**), além de baixa covariação da folha e do lenho encontrada em outra floresta ombrófila, na Reserva Biológica União - RJ (**Capítulo 3**).

As associações positivas e negativas entre variação e covariação de atributos foram corroboradas tanto pelo estudo de Gianoli e Palácio-Lopez (2009) quanto pelo estudo de Matesanz et al. (2021) e outros estudos mais recentes (Pireda et al., 2019, Shi et al., 2023, Oyanoghafo et al., 2023). Torna-se evidente em novos estudos a necessidade de uma reavaliação dos mecanismos envolvidos nessa relação entre a variação e covariação de atributos, muitos dos quais também não são completamente compreendidos (Oyanoghafo et al., 2023). Entretanto, os resultados desta tese estão mais direcionados a uma dependência de contexto e ao fato de haver uma nulidade nessas relações, visto pela maioria de relações ausentes entre os atributos da folha e do lenho (**Capítulos 2 e 3**). Ressalta-se que muitas variáveis de confusão podem ter influenciado nessas relações, como o tipo de atributo avaliado, a escala, formas de crescimento e grupos funcionais, os quais são bem estabelecidos de influenciarem a variação inter- e intraespecíficas nas comunidades de plantas (Díaz et al., 2016, Messier et al., 2017, Michelaki et al., 2019).

Por fim, observou-se que a variabilidade intraespecífica teve papel importante no fortalecimento da covariação (em número de correlações) em ecossistemas restritivos e sazonais (**Capítulo 2**) e foi um importante direcionador dos ajustes fenotípicos e estratégias de aclimatação de espécies pioneiras em sub-bosques com diferenças sutis no gradiente ambiental (**Capítulo 3**). Esses resultados reforçam a importância de se considerar a variabilidade intraespecífica nas respostas das espécies (Albert et al., 2010, Siefert et al., 2015) aos diferentes contextos ambientais, bem como nos estudos de ecologia baseada em atributos.

6. CONSIDERAÇÕES FINAIS

O desenvolvimento desta tese contribuiu com novos *insights* e evidências sobre a variação e covariação de atributos da folha e do lenho em diferentes contextos ambientais. Esses componentes da variação fenotípica das plantas vêm ganhando força na ecologia baseada em atributos. Isso porque os valores adaptativos da variação e covariação e suas restrições ecológicas e evolutivas ainda estão sendo explorados e parecem um pouco distantes de serem elucidados. O entendimento desses valores adaptativos da variação e covariação tornam se ainda mais complexos ao reincorporar a variabilidade intraespecífica, que durante um tempo, foi subestimada. Dessa forma, as evidências envolvendo os mecanismos por trás do acoplamento e desacoplamento e/ou da variação e covariação de atributos ainda não são definitivas e carecem de mais respostas, principalmente ao estudar gradientes ambientais.

Portanto, destaca-se a necessidade de estudos que continuem investigando como as plantas reagem aos fatores ambientais abióticos e bióticos, através dos mecanismos de variação e covariação fenotípicas, especialmente ao entender como as plantas respondem como um todo (e não somente avaliando partes isoladas da planta). Esses estudos serão essenciais para aplicação dessas evidências em diferentes escalas e em dois contextos principais: primeiro, para entender como as plantas irão se adaptar às mudanças climáticas previstas e em curso; e segundo, para fornecer a base necessária na implementação e continuidade de políticas e ações de manejo e restauração. Dado que estes organismos já estão experimentando os efeitos das mudanças climáticas e considerando que estamos na década da restauração, este parece um momento oportuno para investigar esses grupos tão diversos nos trópicos e seus mecanismos de respostas.

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