Czech University of Life Sciences Prague

Faculty of Forestry and Wood Sciences

DYNAMICS OF FOREST GROWTH IN TROPICAL FORESTS OF GHANA

Author: Forzia Ibrahim, M.Sc.

Supervisor: doc. Ing. Radim Matula, Ph.D.

Prague, 2026

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Forestry and Wood Sciences

Ph.D. THESIS ASSIGNMENT

Forzia Ibrahim

Global Change Forestry

Thesis title

Dynamics of forest growth in tropical forests of Ghana

Objectives of thesis

African tropical forests are crucial for biodiversity conservation and carbon storage, yet they remain understudied, particularly in terms of the ecological processes that govern their structure and functioning. These forests are influenced by complex environmental factors such as climate variability, soil moisture, and nutrient availability, all of which play significant roles in shaping species diversity, competitive interactions, and biomass growth. Understanding how these environmental drivers influence forest dynamics is vital for predicting the long-term stability and resilience of these ecosystems, especially in the face of global climate change. While recent studies indicate that West African forests are among the most productive globally, these ecosystems are increasingly threatened by deforestation, fragmentation, and ongoing climate change. In recent years, drought-induced shifts in forest composition have been observed in Ghana, with changes favouring drought-tolerant species as a response to increasingly variable climate conditions. This shift has the potential to significantly impact forest resilience and carbon storage, highlighting the urgent need to understand how broader climate variability influences tropical forest dynamics. Additionally, comprehensive research on the interactions between environmental drivers, particularly at multiple scales, remains limited. This underscores the critical need for targeted research to inform effective conservation strategies and sustainable forest management practices. Given the significant threats facing these ecosystems, this study aims to address critical knowledge gaps by investigating the following objectives:

1. Assess the influence of vapour pressure deficit and soil moisture on biodiversity patterns and conservation value of forest types in Ghana

2. Quantify the role of tree size, wood density and water availability in mediating competitive interactions among tropical tree species in Ghana

3. Investigate biomass growth responses to climate variability and competition in Ghana’s tropical forests

Methodology

The research will be conducted in nine one-hectare (ha) permanent plots within the Global Ecosystem Monitoring (GEM) network along a rainfall gradient in Ghana. These plots span three forest types: Ankasa Conservation Area (ACA, wet evergreen), Bobiri Forest Reserve (BFR, moist semi-deciduous), and Kogyae Strict Nature Reserve (KSNR, dry semi-deciduous). Established in 2011, annual censuses have been conducted since 2012.

All stems with a diameter at breast height (DBH) ≥ 10 cm (measured at 130 cm above ground) are identified to species, tagged, mapped, measured, and assigned a point of measurement (POM) for future monitoring. For trees with buttresses or deformities, the POM is raised 0.5 m above DBH, or up to 4.5 m for species with tall buttresses. Newly recruited stems (DBH ≥ 10 cm) that grew to meet the DBH threshold during the census period have been recorded, tagged, and measured, while trees absent in subsequent censuses have been classified as dead. Diameter and height are measured using a diameter tape and an electronic hypsometer, respectively.

Climate data will be obtained from the ERA5-Land reanalysis dataset (ECMWF) for the dry, wet, and annual periods, including minimum, mean, maximum, and dewpoint temperatures, potential and actual evapotranspiration, rainfall, and soil moisture. Vapour pressure deficit (VPD) will be calculated using the FAO Penman-Monteith equation. Wood density data will be compiled from a global database. Soil samples will be collected and analysed for carbon, nitrogen, and phosphorus content, as well as base cations such as potassium, magnesium, and calcium.

Forest community classification will be conducted using non-metric multidimensional scaling (NMDS)based on species composition. Community diversity will be quantified using Hill numbers to assess species richness, Shannon, and Simpson diversity indices. Conservation value will be evaluated using a Conservation Value Index (CVI), integrating species rarity and threat status. A Redundancy Analysis (RDA) will be conducted to understand the relationships between species abundance and environmental variables. Linear mixed-effects models will be used to examine relationships between community diversity and climate factors while accounting for hierarchical data structure and potential confounders.

Tree growth will be estimated using basal area and above-ground biomass increments derived from standard allometric equations. Competition will be assessed using a spatially explicit neighbourhood approach, modelling tree growth as a function of the size and proximity of neighbouring trees. Growth responses to competition will be analysed using nonlinear regression models for the 15 most common species. Mixed-effects models will be employed to assess the potential effects of climate and competition on biomass growth. The model selection will be based on Akaike's Information Criterion corrected for small sample sizes (AICc), with the most parsimonious model identified by the lowest AICc value. All analyses will be conducted in R (R Core Team, 2024).

The proposed extent of the thesis
50

Keywords

Tree growth, competition, water availability, conservation status, species diversity, tree size, above-ground biomass, rainfall gradient, Ghana

---

Recommended information sources

Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S.L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T.R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K., Phillips, O.L., Oliveras, I., 2020. Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. Nat. Commun. 11, 1–10. https://doi.org/10.1038/s41467-020-16973-4

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

Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G., Hamer, K.C., Swaine, M.D., 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. Ecol. Lett. 15, 1120–1129. https://doi.org/10.1111/j.1461-0248.2012.01834.x

Fortunel, C., Valencia, R., Wright, S.J., Garwood, N.C., Kraft, N.J.B., 2016. Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. Ecol. Lett. 19, 1062–1070. https://doi.org/10.1111/ele.12642

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207. https://doi.org/10.1038/nature16476

Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. African rainforests: past, present and future. Philos. Trans. R. Soc. B Biol. Sci. 368.

Uriarte, M., Condit, R., Canham, C.D., Hubbell, S.P., 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? J. Ecol. 92, 348–360. https://doi.org/10.1111/j.0022-0477.2004.00867.x

Uriarte, M., Lasky, J.R., Boukili, V.K., Chazdon, R.L., 2016. A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. Funct. Ecol. 30, 157–167. https://doi.org/10.1111/1365-2435.12576

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E. M.S., Qin, Z., Quine, T., Sitch, S., Smith, W.K., Wang, F., Wu, C., Xiao, Z., Yang, S., 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Sci. Adv. 5, 1–12.

Zhang-Zheng, H., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Addo-Danso, S.D., Amissah, L., Valentini, R., Djagbletey, G., Anim-Adjei, K., Quansah, J., Sarpong, B., Owusu-Afriyie, K., Gvozdevaite, A., Tang, M., Ruiz-Jaen, M.C., Ibrahim, F., Girardin, C.A.J., Rifai, S., Dahlsjö, C.A.L., Riutta, T., Deng, X., Sun, Y., Prentice, I.C., Oliveras Menor, I., Malhi, Y., 2024. Contrasting carbon cycle along tropical forest aridity gradients in West Africa and Amazonia. Nat. Commun. 15, 1–9. https://doi.org/10.1038/s41467-024-47202-x

Expected date

2024/25 SS – FFWS – State Doctoral Examinations

Thesis supervisor
doc. Ing. Radim Matula, Ph.D.

Supervising department

Department of Forest Ecology

Electronic approval: 10. 11. 2025

prof. Ing. Miroslav Svoboda, Ph.D.
Head of department

Electronic approval: 23. 11. 2025

prof. RNDr. Tomáš Hlásny, PhD.
Chairperson of Field of Study Board

Electronic approval: 12. 12. 2025

prof. Ing. Róbert Marušák, PhD.
Dean

Prague on 02. 01. 2026

Declaration of independence

I hereby declare that this PhD thesis, titled "*Dynamics of forest growth in tropical forests of Ghana*", is the result of my independent research work carried out under the supervision of my supervisor. All sources of information and assistance have been duly acknowledged, and the research was conducted in accordance with the accepted standards and ethical guidelines of scientific research.

I agree with the publication of this PhD thesis according to Czech Law (Act No. 111/1998 Coll. Sb), irrespective of the outcome of the defense.

January 2nd, 2026, Prague   Forzia Ibrahim

Acknowledgement

This thesis forms part of the Global Ecosystem Monitoring Network (GEM) project, which conducts long-term research on forest dynamics, ecosystem productivity and carbon cycling across environmental gradients in major tropical regions. I am deeply grateful to the GEM network, especially the coordinators in Ghana, for providing the framework, access to previous datasets and resources that made this research possible.

I would like to express my sincere gratitude to my supervisors, Ing. doc. Radim Matula and Dr Arne Buechling, for their invaluable guidance, mentorship, and support throughout this project. I am also thankful to my co-supervisors at the Forestry Research Institute of Ghana for their feedback, encouragement and assistance. Special thanks to the field teams and research assistants whose dedication and hard work were crucial to the successful completion of this thesis. I am grateful to the lecturers, researchers and colleagues at the Department of Forest Ecology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, for their continued support and for warmly welcoming me as part of the research community. I acknowledge the support of the internal grant agency of the Faculty of Forestry and Wood Sciences for providing financial assistance to conduct this research and participate in scientific conferences to present my work.

I am deeply grateful to my family, whose unwavering support and encouragement sustained me throughout this journey.

Abstract

African tropical forests are crucial reservoirs of biodiversity and carbon storage, yet the ecological processes shaping their composition, function and resilience remain poorly understood. Predicting forest responses to global change requires an understanding of how abiotic and biotic conditions regulate community structure, biomass accumulation and species interactions. In particular, the extent to which forest physiognomy and function are regulated by nutrient supply, species functional attributes, and the non-additive effects of vapour pressure deficit (VPD) and soil moisture remains largely unexplored. This study addresses these knowledge gaps using a multi-pronged approach to: (1) quantify how moisture availability, nutrients, and VPD shape community diversity and conservation value; (2) investigate the effects of climatic and biotic factors on whole-tree biomass growth; and (3) assess how the functional traits of species together with soil moisture mediate competitive interactions between trees. The analyses draw on a comprehensive 10-year dataset from a network of permanent sampling plots spanning wet evergreen, moist semi-deciduous, and dry semi-deciduous forests in Ghana, West Africa. Forest inventory data were combined with high-resolution climate reanalysis data and soil chemistry measurements to evaluate environmental controls on forest composition, diversity and growth. Tree diversity was quantified using Hill numbers, while conservation value was derived from species rarity and global extinction risk scores. Mixed-effects models were used to estimate the effects of environmental conditions on species diversity indices and aboveground biomass growth. Nonlinear non-parametric models were fitted to examine how biological and abiotic factors modulate competitive interactions between species and how those interactions scale up to influence stem diameter growth.

A total of 3,471 trees representing 242 species were surveyed during the 10-year census interval, of which 17.4% were classified as threatened or near-threatened according to global extinction risk criteria. Species composition, richness and Shannon diversity varied across forest types and

were primarily structured by moisture availability and VPD. Diversity generally increased with soil moisture but declined with higher VPD. Nutrients, particularly calcium and phosphorus, significantly influenced the composition of the moist forest zone. However, evidence for a potential mitigation of VPD impacts by greater soil moisture availability was also detected, leading to a stabilisation of biodiversity levels in more mesic environments. At-risk species were more common in high-rainfall regions relative to drier environments.

Community-level biomass production was highest in the moist forest and increased with structural diversity. However, growth responses to VPD and soil moisture varied among forest types: in dry forests, growth remained suppressed and showed modest declines to increasing VPD; in moist forests, high soil moisture partly buffered against VPD stress; and in wet forests, growth peaked under intermediate moisture conditions. Species-level analyses revealed a consistently positive effect of tree size, and highly taxon-specific responses to competition and the non-additive effects of environmental factors. Variation in the wood density of species modified competitive outcomes, with dense-wooded species exhibiting stronger innate competitive abilities, particularly under moisture-limited conditions. Larger individuals were less sensitive to moisture-dependent competitive pressure, reflecting divergent life history strategies that differentially shape species fitness under varying environmental conditions.

Collectively, these findings demonstrate that tropical forest structure, biodiversity, and productivity are shaped by complex interactions among environmental conditions, species traits, and competitive dynamics. The findings also suggest that aggregating data and analysing processes at a community-level can obscure or mask important species-level variation, underscoring the importance of integrating both species and community-level perspectives to understand forest responses to environmental gradients. The higher concentration of threatened species in wetter forests, coupled with the dynamic nature of competitive interactions, suggests that more prevalent and intense dry season drought episodes, which are forecast for tropical

Africa, may disproportionately affect the physiognomy, function, and biodiversity of these communities. By linking demographic performance, biodiversity and environmental drivers, this thesis highlights the ecological trade-offs that regulate tropical forest carbon dynamics and the critical role of species diversity, functional attributes, and environmental buffering in sustaining forest productivity under changing climatic conditions.

Keywords: Biodiversity, aboveground biomass growth, competition, moisture supply, tree size, wood density, vapour pressure deficit, West Africa.

Table of contents

List of Figures

List of Tables

List of Equations

List of Abbreviations

AGB – Aboveground biomass

AGBI – Aboveground biomass increment

AIC – Akaike information criterion

BA – Basal area

BAI – Basal area increment

CVI – Conservation value index

DBH – Diameter at breast height

GAMM – Generalised additive mixed-effects model

GLMM – Generalised linear mixed-effects model

GTS – Global threatened score

LMM – Linear mixed-effects model

NCI – Neighbourhood crowding index

POM– Point of measurement

RS – Rarity score

SD – Standard deviation

SMI – Soil moisture index

VPD – Vapour pressure deficit

1. INTRODUCTION

Tropical forests play a key role in ameliorating global climate change and harbouring much of the world's biological diversity (Baraloto et al., 2013; Chazdon et al., 2017). Despite their importance, tropical ecosystems are increasingly threatened by intensive resource extraction and changes in land use (Valentini et al., 2014). Recent studies indicate that deforestation rates in tropical regions are increasing, placing even protected forests at risk of substantial ecological degradation (Acheampong et al., 2019; FAO, 2020). For the African continent, climate models forecast monotonic warming trends and greater variability in precipitation regimes, including potentially more severe dry season water deficits (Almazroui et al., 2020; James et al., 2013). In West Africa, a persistent reduction in annual precipitation since 1970, relative to 20th-century mean levels, has already been associated with alterations in forest composition and function (Aguirre-Gutiérrez et al., 2019; Asefi-Najafabady and Saatchi, 2013; Fauset et al., 2012). These climatic shifts are expected to interact with anthropogenic stressors, potentially amplifying negative impacts through non-additive increases in temperatures and drying rates in fragmented or thinned forest patches (Lewis et al., 2015; Martnez-Vilalta and Lloret, 2016). Accurate predictions of tropical forest trajectories require baseline data on species distributions, vulnerabilities, growth dynamics and environmental relationships, but such data are still scarce in many regions, particularly in Africa (Malhi et al., 2013; Réjou-Méchain et al., 2021).

Spatial variation in biotic and abiotic factors fundamentally structures species coexistence, biodiversity and growth patterns across tropical forests (Aguirre-Gutiérrez et al., 2020; Bauman et al., 2022; Esquivel-Muelbert et al., 2019; Peguero et al., 2023). Among the most critical environmental drivers are soil moisture supply and evaporative demand, which jointly regulate water transport through xylem, gas exchanges through leaf stomata, and dependent photosynthetic performance (Novick et al., 2016; Peters et al., 2023). Soil moisture availability reflects the capacity of soils to store and release water to plants, while vapour pressure deficit

(VPD) quantifies atmospheric demand for water and strongly influences transpiration and carbon uptake (López et al., 2021). Although potential responses of forest communities to atmospheric drought have been investigated in some studies (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012), the relative contributions of soil water, VPD and temperature to community-level diversity and growth in tropical systems remain poorly understood (Liu et al., 2020). The conservation implications of these environmental stressors are particularly important in African forests, which often harbour rare and endangered species that contribute disproportionately to functional diversity and ecosystem resilience (Mouillot et al., 2013). Climate change poses a substantial threat to species with restricted distributional ranges or specialised ecological niches, yet high-resolution biogeographical data remain scarce, limiting our ability to anticipate conservation outcomes (Owusu et al., 2022; Sanjeewani et al., 2024). Soil nutrients also influence forest composition and diversity, although evidence for their effects remains inconsistent (Appiah-Badu et al., 2022; Nadeau and Sullivan, 2015). Studies in tropical forests have reported weak, negative or positive associations between soil nutrients and community diversity (Appiah-Badu et al., 2022; Du et al., 2020; LeBauer and Treseder, 2008). These contrasting outcomes are further compounded by a paucity of soil data and the logistical challenges of conducting detailed soil surveys in remote regions.

Biotic interactions, particularly competition for resources, are central to shaping forest productivity and species coexistence (Fortunel et al., 2018; Hubbell et al., 2001; Tilman, 1982; Uriarte et al., 2016). Emerging evidence in tropical systems increasingly highlights the importance of trait-mediated processes in explaining variation in forest composition and function (Enquist and Enquist, 2011; Fortunel et al., 2016). Functional traits associated with water relations and growth capacity provide particularly important axes of competitive differentiation (Fortunel et al., 2016; Kunstler et al., 2016; Rozendaal et al., 2020; Uriarte et al., 2016). The specific architectural characteristics of tree stems may differentially promote plant survival in particular settings. For example, wide xylem conduits facilitate a high water conducting capacity that may confer competitive advantages in resource-rich environments. In contrast, narrow conduits provide greater stability and cavitation resistance, which may promote survival in water-limited habitats (De Guzman et al., 2021; Poorter et al., 2010; Sperry et al., 2006). In other words, species may adopt contrasting strategies of maximising growth in productive environments versus tolerating stress under limiting conditions such as drought (Grime, 1977; Poorter et al., 2010). These trade-offs link biotic interactions directly to environmental gradients. Experimental research across biomes has demonstrated that soil water availability mediates competitive ability among plant species (Angert et al., 2009; Lebrija-Trejos et al., 2023; Pérez-Ramos et al., 2019). Most studies have focused on juvenile life stages, whereas analyses of resource-driven competitive dynamics among canopy trees across environmental gradients in tropical forests remain limited (but see Rozendaal et al., 2020). Overall, tropical forest composition, diversity and productivity are jointly influenced by climate variability, soil nutrient availability, and biotic interactions, yet the combined effects of these drivers on African forest growth remain poorly understood. Understanding these interactions is crucial for uncovering the mechanisms that underpin species coexistence and for predicting how forests will respond to ongoing environmental change.

1.1 Research objectives and scope

West Africa harbours a diverse array of tropical forest systems spanning a pronounced climatic gradient, from wet evergreen forest communities in the southwest to dry semi-deciduous types in the north. These forests sustain high biodiversity and provide critical ecosystem services but remain underrepresented in ecological research relative to the Amazon and Southeast Asia (Fauset et al., 2012; Malhi et al., 2013). Despite their importance, patterns of diversity, conservation value, productivity and their environmental correlates are still poorly characterised. In West Africa, where atmospheric water demand is rising, and soils are increasingly water-limited, few studies have examined how environmental factors such as VPD and soil moisture jointly influence biodiversity, conservation value and aboveground biomass growth across contrasting forest types (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012). Moreover, although competition is widely recognised as a key process structuring species coexistence, limited attention has been given to how competitive interactions, mediated by functional traits and resource availability, shape community assembly in tropical forests (Canham et al., 2006; Kraft et al., 2015). Finally, while soil nutrients are known to influence species composition and productivity, their relative contribution alongside climatic variables remains uncertain, particularly across ecological gradients in this region. To address these knowledge gaps, this thesis integrates analyses of abiotic and biotic drivers across a climatic gradient, combining field surveys, a functional trait dataset and statistical modelling. The study focuses on three overarching interrelated objectives:

1. Disentangling the drivers of floristic composition, diversity and conservation value. This objective was addressed by:
    a. Developing empirically based conservation value indices that account for the relative abundance of at-risk species.
    b. Examining the independent and interactive effects of VPD and soil moisture on diversity patterns.
    c. Assessing the influence of soil nutrient supply on species composition.

It was hypothesised that lower soil moisture availability in drier climatic zones favours species that have an innate capacity for drought tolerance (Aguirre-Gutiérrez et al., 2019), resulting in communities that may be less diverse but potentially more resilient to warming and drying trends. It was further postulated that along the climatic gradient, periods of drought stress and high evaporative demand would have reduced negative impacts on plant performance where soil moisture availability is greater.

2. Determining biomass growth responses to biotic and abiotic factors. To quantify these relationships, I performed the following analyses:
    a. Assessed patterns of biomass growth across forest types.
    b. Determined the synergistic effect of VPD and soil moisture on biomass growth.
    c. Estimated the effect of tree size, competition, and structural diversity on biomass growth.

Higher VPD was expected to accelerate soil moisture depletion, compounding plant water stress and reducing growth by limiting water transport, leaf turgor pressure, and photosynthesis (Grossiord et al., 2020; Novick et al., 2016). The magnitude of these effects was assumed to vary among species and forest types, reflecting differences in ecological strategies and water use traits (Novick et al., 2024). At the individual level, biomass growth was predicted to increase with tree size due to greater crown area and resource acquisition capacity, but to decline under high neighbourhood competition, which intensifies demand for finite resources. Conversely, higher structural diversity was expected to enhance growth through increased light interception and complementary use of belowground resources (Ding et al., 2021; Sapijanskas et al., 2014).

3. Investigating the factors that mediate competitive interactions among tropical tree taxa. This objective was addressed through analyses that:
    a. Identified how species' functional attributes (i.e., wood density and shade tolerance) influence competitive ability.
    b. Assessed the extent to which soil moisture availability regulates competition dynamics.

c. Determined how variation in the abundance, size and proximity of neighbouring trees influences competitive outcomes.

It was hypothesised that competition intensity would increase with greater tree cover, reflecting higher neighbourhood crowding. Competition was also expected to intensify under moisture limitation, as reduced water availability heightens resource scarcity. However, the outcomes of competitive interactions were anticipated to depend strongly on the trait attributes of the interacting species, which reflect their differing life-history strategies and ecological tolerances. For instance, species with denser wood were expected to follow a more conservative resource-use strategy, conferring greater resistance to water limitation and potentially altering their competitive performance.

2. LITERATURE REVIEW

2.1 Growth dynamics of tropical forests: Influence of abiotic and biotic factors

Tropical forests are among the most important components of the global biosphere, occupying approximately 10% of the Earth's land surface and contributing substantially to global terrestrial net primary productivity (Del Grosso et al., 2008; Pan et al., 2011). They store a disproportionate share of the world's forest carbon stocks and regulate nutrient and water cycles (Bonan, 2008; Immerzeel et al., 2020). Projected changes in climate, including rising temperatures and elevated rates of soil drying, are likely to impair key ecological functions by reducing tree growth and altering species distributions (Aguirre-Gutiérrez et al., 2019; Brodribb et al., 2020). Long-term data from large-scale permanent monitoring plots have been central to advancing our understanding of tropical forest dynamics, providing insights into spatial and temporal variation in demographic processes such as growth, mortality and recruitment (Bauman et al., 2022; Claeys et al., 2019; Feeley et al., 2011; Lewis et al., 2004; Phillips and Lewis, 2014; Shen et al., 2013). These datasets have revealed contrasting patterns of forest growth and biomass trends across the tropics. Several studies report long-term increases in tree growth, stem density and aboveground biomass, particularly in South American forests (Laurance et al., 2004; Lewis et al., 2004; Phillips and Lewis, 2014). These changes have often been linked to carbon dioxide fertilisation, which may stimulate photosynthesis and accelerate demographic processes (Lewis et al., 2004; Phillips and Lewis, 2014). Similar patterns have been observed in Africa, Central America, and parts of Asia (Chave et al., 2008; Claeys et al., 2019; Lewis et al., 2009). For example, Claeys et al. (2019) predicted higher rates of growth and recruitment in Central African forests.

In contrast, other studies highlight multidecadal stability in forest dynamics. Research in Barro Colorado Island, Panama, and other tropical sites found that tree growth varied substantially over time, but without consistent directional trends (Clark et al., 2017; Dong et al., 2012; Feeley et al., 2011; Murphy et al., 2013; Rutishauser et al., 2020). These fluctuations have been attributed to interannual variability in climatic conditions and the complex influence of global climate forcing on local demographic processes. Yet other studies have revealed long-term declines in growth or biomass. In the Amazon basin, Brienen et al. (2015) reported decreasing biomass over recent decades, with rising tree mortality rates outweighing productivity gains. Similar declines have been recorded in La Selva, Costa Rica, where canopy tree growth slowed between 1984 and 2000 (Clark et al., 2003), and in monitoring plots in Panama and Malaysia (Feeley et al., 2007). Despite these advances, Africa remains underrepresented in long-term forest monitoring, with relatively few studies assessing growth dynamics across this continent (Bennett et al., 2021; Claeys et al., 2019; Hubau et al., 2020; Rifai et al., 2018). In West Africa, in particular, the scarcity of such data limits understanding of how climatic variability and ecological processes shape forest dynamics. Addressing this gap is crucial for evaluating the capacity of these forests to respond to environmental change.

2.1.1 Abiotic controls on forest productivity: Roles of soil moisture and VPD

Forest productivity is shaped by environmental factors that regulate tree growth and ecosystem carbon balance (Esquivel-Muelbert et al., 2019). Among these, soil moisture and atmospheric VPD are particularly important because they directly influence plant water balance and physiological function within the soil-plant-atmosphere continuum (Fu et al., 2022; McDowell et al., 2020; Sulman et al., 2016). Soil moisture supports xylem water transport by maintaining favourable water potential gradients (Seneviratne et al., 2010). When soil moisture declines, increased xylem tension reduces hydraulic conductivity, constraining transpiration and photosynthesis (Sperry et al., 2016). VPD, which quantifies atmospheric evaporative demand, regulates leaf water loss and associated physiological functions (López et al., 2021). Under high VPD, many plants reduce stomatal conductance to limit transpiration, but this also restricts carbon dioxide uptake and photosynthesis, slowing tissue growth and metabolic activity (Peters et al., 2023; Yuan et al., 2019). These drivers are becoming increasingly important under changing climate conditions. VPD has risen with warming temperatures, while long-term declines in soil moisture and more frequent drought have been observed across tropical regions, with both trends projected to intensify (Bauman et al., 2022; Grossiord et al., 2020; Yuan et al., 2019). Their co-occurrence imposes compounded physiological constraints that limit plant growth and productivity (Liu et al., 2020; McDowell et al., 2008; Qi et al., 2024). Feedback between soil water and VPD can shape outcomes, as adequate soil water may buffer physiological stress under high VPD, whereas dry soils can exacerbate evaporative demand (Liu et al., 2020).

Numerous studies have examined how VPD, temperature, and soil moisture influence vegetation productivity. While these efforts have improved our understanding of climate controls on carbon uptake, the relative importance of VPD and soil moisture remains debated, with effects varying across regions (Chen et al., 2023; Dubey and Ghosh, 2023; Jiang et al., 2023; Lu et al., 2022). In tropical forests, plant growth is generally constrained by soil moisture availability (Jiang et al., 2023). However, long-term field-based monitoring data for African tropical forests remain scarce relative to the Amazon, limiting understanding of how aboveground biomass responds to climate variation (Malhi, 2012). Available evidence from these limited studies suggests that African forests may exhibit regionally variable sensitivity to climate drivers. For instance, in the humid Congo Basin, increased VPD has been linked to declines in growth rates despite stable rainfall, indicating that atmospheric water stress can limit productivity even in moist forests (Jiang et al., 2023; Li et al., 2023). In contrast, large-scale syntheses of data from African forest inventory plots suggest that biomass gains have increased over recent decades, with limited carbon losses even during climate extremes such as the 2015/2016 El Niño (Bennett et al., 2021; Hubau et al., 2020). While the net carbon sink remained positive, it was temporarily reduced during extreme climatic events, highlighting some resistance to short-term climate variability (Williams et al., 2007). Collectively, these findings reveal heterogeneous and context-dependent responses of African tropical forests to climate variation, underscoring the need for detailed, species and site-level investigations of biomass growth dynamics. Importantly, it remains unclear how soil moisture and atmospheric water demand interact to influence growth, and whether these interactions vary across species and forest types. Understanding these complex, interactive effects is crucial for predicting forest responses to ongoing climate change and for linking environmental stressors to ecosystem productivity and resilience.

2.1.2 Biotic influences on tree growth: Effects of competition

Competition plays a central role in shaping community assembly and species coexistence along environmental gradients (Canham et al., 2006; Kraft et al., 2015). Several studies have demonstrated that neighbourhood crowding can suppress tree growth, indicating strong competition for limiting resources such as light, water, and nutrients (Nemetschek et al., 2024; Rozendaal et al., 2020; Weng et al., 2022; Yang et al., 2021). For instance, analyses of long-term forest inventory data in Amazonia and Africa show that elevated levels of crowding (dense stands) reduce growth rates, indicating the strong role of competition in shaping community dynamics (Rozendaal et al., 2020). However, Paine et al. (2008) found weak intraspecific competition among tree seedlings in tropical rainforests, suggesting that factors other than competition could be more influential during early life stages. Similarly, Gourlet-Fleury et al. (2023) reported that competition and site conditions explained only a small portion of growth variability in undisturbed Central African moist forests. The contrasting findings across tropical African forests emphasise the importance of further investigating how neighbourhood crowding affects tree growth.

Several factors, including fluctuations in resource availability, species-specific functional traits and variation in the size and age of trees, can influence competitive outcomes among tree taxa (Fortunel et al., 2016; Kunstler et al., 2016; Rozendaal et al., 2020; Uriarte et al., 2010). Variations in these factors determine how species interact, coexist, and adapt to environmental changes (Gómez-Aparicio et al., 2011). Organism size regulates many biological processes, including resource uptake, metabolism, and primary production in individual plants, as well as species interactions within communities (West et al., 2009, 1997). However, general patterns concerning the influence of size on competitive interactions and demographic rates (growth, survival and recruitment) in forest trees remain unresolved (Forrester, 2019). Contrasting modes of resource competition among individuals have been described, including (1) symmetric processes that are size-independent; (2) size-symmetric interactions, whereby differences among individuals in resource-uptake capacity and hence competitive strength are linearly proportional to plant size; and (3) asymmetric interactions, where uptake capacity varies nonlinearly as a function of size, with a consequence that larger plants acquire a disproportionate share of the local supply of limiting resources (Schwinning and Weiner, 1998). For instance, the interception and attenuation of light by the crowns of large dominant trees is commonly assumed to be a size-mediated asymmetrical competitive effect that suppresses primary production potential in subordinate trees. A long history of competition research has led to the development of spatially explicit neighbourhood models that estimate the consequences of competition in terms of variation in the performance of individual plants (e.g., tree growth) (Pommerening and Sánchez Meador, 2018). Competition effects are quantified using measures of neighbour tree abundance that may be scaled by the size, proximity, genotype, or trait attributes of those neighbours (Weiner, 1984). Associated models can integrate size functions that account for linear (symmetrical) or nonlinear (asymmetrical) size-dependent variation in competitive intensity (Gómez-Aparicio et al., 2011; Uriarte et al., 2004b). These methods provide a mechanistic link between the attributes of neighbouring trees and the nature and intensity of competition dynamics (Weiner, 1990).

Both conspecific (same species) and heterospecific (different species) neighbours can influence competitive interactions in forest communities (Lebrija-Trejos et al., 2014; Stoll and Newbery, 2005). Conspecific neighbours typically compete strongly due to overlapping resource requirements and a shared susceptibility to species-specific pathogens, which can reduce growth, survival and reproduction (Stoll and Newbery, 2005; Uriarte et al., 2004b). In contrast, competition among heterospecifics may be less intense when species differ in resource use strategies, ensuring niche partitioning and potentially mitigating the risk of competitive exclusion (Browne and Karubian, 2016; Chesson, 2000). Negative density dependence, where demographic performance declines with increasing conspecific density, acts as an important stabilising mechanism that promotes species coexistence in both tropical and temperate forests (Janzen, 1970; LaManna et al., 2017).

2.1.2.1 The role of functional attributes and moisture variation on species competitive outcomes

Understanding the factors that mediate species-specific growth responses to competition is fundamental for elucidating forest dynamics and informing sustainable management. Neutral theory proposes that differences in competitive ability are largely unimportant at broad scales (Hubbell, 2006). Under this model, species are assumed to be ecologically equivalent, with stochastic processes such as random dispersal and local extinction generating predictable community patterns (Azaele et al., 2016; Hubbell, 2006; Leibold and McPeek, 2006). Some empirical evidence supports this view. For example, Uriarte et al. (2004a) found that more than half of the species examined showed similar neighbourhood effects on sapling growth, consistent with the assumption of ecological equivalence. However, growing evidence suggests that competition is often mediated by neighbour identity and functional traits. For instance, Uriarte et al. (2004a) reported that sensitivity to neighbourhood crowding varied substantially among taxa, while Kunstler et al. (2016) showed that specific functional traits strongly influenced competition outcomes. These findings suggest that neutral theory, although useful as a null hypothesis, cannot fully account for the directional shifts in composition and function observed in tropical forests (Enquist and Enquist, 2011).

In contrast, niche-based and trait-mediated theories posit that asymmetrical competition is dynamic and underpins community assembly processes (Leibold and McPeek, 2006; Silvertown, 2004). Functional attributes, such as wood density and shade tolerance, influence species' strategies for resource acquisition and stress tolerance (Fortunel et al., 2016; Goldberg, 1990). Classifying species by these attributes provides insights into how biotic interactions shape the performance of trees under varying environmental conditions (Adler et al., 2013; Kunstler et al., 2016). Species with traits that facilitate rapid resource uptake may constrain the performance of proximate neighbours by depleting a disproportionate share of available resources (Goldberg, 1990; Kunstler et al., 2016). Conversely, species possessing attributes that confer tolerance to resource scarcity, for example, physiological mechanisms that promote water- or light-use efficiency (Kobe et al., 1995), tend to be more resistant to competitive pressures (Fortunel et al., 2016; Goldberg, 1990). Wood density is a particularly important functional trait influencing both hydraulic efficiency and drought resilience (Chave et al., 2009; Santiago et al., 2018). Species with higher wood density typically possess smaller, more efficient water-conducting xylem vessels, which reduce the risk of embolism during drought. In contrast, species with low wood density have wider conduits that facilitate rapid water transport but increase their vulnerability to cavitation (Hacke et al., 2001). This trade-off enables high-density wood species to maintain competitiveness in resource-limited environments (Chen et al., 2019). Shade-tolerant species, adapted to low-light understories, grow more slowly but efficiently exploit limited light, giving them an advantage in shaded environments (Kobe et al., 1995). In contrast, shade-intolerant species dominate in high-light conditions, such as canopy gaps, where rapid growth confers a competitive advantage (Bazzaz, 1979). The balance between these contrasting light-use strategies contributes to forest structural and compositional diversity. Although previous studies have shown that functional traits of neighbouring trees influence species-specific growth in diverse tropical forests, such knowledge is limited for African species. In Africa, most research has focused on community-level patterns, with species-level trait-mediated competitive responses largely unexplored (Gourlet-Fleury et al., 2023; Rozendaal et al., 2020).

2.1.3 The role of structural diversity on community-level growth responses

Structural diversity describes heterogeneity in tree size distribution, vertical canopy layering, crown architecture and basal area variation within a forest stand (Dănescu et al., 2016; Deng et al., 2025; LaRue et al., 2023; Liang et al., 2016; Mensah et al., 2023). It is commonly quantified using diameter inequality metrics, tree size or height diversity indices, measures of crown overlap, and composite indices that integrate multiple dimensions of stand structure (Cheng et al., 2024; Dănescu et al., 2016; Fatunsin and Naka, 2025; LaRue et al., 2023; Pommerening, 2002; J. Wang et al., 2025). Traditionally, biodiversity–ecosystem functioning research has focused primarily on tree species diversity, with numerous studies demonstrating positive relationships between species richness and forest carbon storage (Lu et al., 2023; Pellegrini et al., 2016; Ruiz-Jaen and Potvin, 2011). More recent syntheses indicate that stand structure can be a stronger and more consistent predictor of biomass growth than species or functional diversity (Dănescu et al., 2016; Zhai et al., 2024).

Empirical studies show that forests with high structural complexity often exhibit greater productivity and carbon uptake than less complex stands (Dănescu et al., 2016; LaRue et al., 2023; Poorter et al., 2017; Skiadaresis et al., 2025). These gains are commonly attributed to improved whole-canopy light-use efficiency and complementary use of soil resources (Tilman et al., 1997). Multi-layered canopies allow radiation to be intercepted throughout the canopy profile, while variation in tree size facilitates partitioning of soil water and nutrients among individuals occupying different rooting zones (Ding et al., 2021; Sapijanskas et al., 2014). Conversely, other studies have reported that greater structural heterogeneity can increase asymmetric competition for light and soil resources, whereby dominant canopy trees suppress the growth of smaller individuals, particularly under resource-limited conditions (Ali et al., 2019; Forrester and Bauhus, 2016; Kunz et al., 2019). These contrasting findings indicate that structural diversity does not generally enhance productivity and that its effects are strongly context–dependent (Forrester and Bauhus, 2016).

Regional comparisons suggest that biotic composition and environmental constraints differentially influence the impact of structural diversity on productivity across tropical regions. In Neotropical forests, canopy heterogeneity generally enhances biomass accumulation more strongly than in African forests, where distinct species assemblages, functional trait diversity and climatic factors shape growth responses (Aguirre-Gutiérrez et al., 2025b; Mensah et al., 2023). Cross-continental analyses further suggest that African forests often exhibit lower functional trait richness but higher functional divergence, indicating more specialised niche differentiation that may underlie distinct biomass growth responses (Aguirre-Gutiérrez et al., 2025b).

Despite these advances, key gaps remain in our understanding of how structural diversity regulates biomass growth in African tropical forests. Existing studies that quantify structural diversity–biomass relationships in African systems are relatively few and largely focus on aboveground biomass stocks or carbon storage rather than community-level biomass growth dynamics (Mensah et al., 2023; Noulèkoun et al., 2021). Although some studies draw on multiple sites, very few span contrasting natural forest types along strong climatic gradients, and others were conducted in recovery or managed contexts such as grazing exclosures (Noulèkoun et al., 2021). Consequently, it remains unclear whether the positive structural diversity–productivity relationships reported in other tropical regions also apply broadly across the diverse African forest types. Understanding these relationships is crucial for predicting forest productivity and for informing management strategies that sustain ecosystem functioning.

2.2 Abiotic drivers of biodiversity and community composition

Trees are the scaffold of forest communities, shaping stand structure and biodiversity potential (Podlaski, 2019). The composition, richness and diversity of tree species vary across tropical regions and at local scales (Owusu et al., 2022; Poorter et al., 2017). These patterns are strongly influenced by abiotic factors such as water availability, temperature and soil nutrients, which act as environmental filters that structure species abundance and distribution (Khaine et al., 2017; Peguero et al., 2023). Ongoing climate change is expected to intensify abiotic constraints by altering rainfall patterns, increasing VPD and prolonging droughts. The consequences are a potential redistribution of individual taxa, leading to a reshaping of community assembly patterns and the functions dependent on them (Deb et al., 2018; Fauset et al., 2012; Phillips et al., 2009). Indeed, tropical forests are already exhibiting compositional shifts, with drought-tolerant and deciduous species becoming increasingly dominant under intensified water stress (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012; Feeley et al., 2011). Such shifts may reduce taxonomic and functional diversity, leading to ecosystem homogenization and potential declines in ecosystem services such as carbon storage and water cycling (Aguirre-Gutiérrez et al., 2020; Phillips et al., 2009). Although the independent effects of soil moisture, VPD, and temperature on tropical tree diversity are receiving increasing attention (Aguirre-Gutiérrez et al., 2019; Fauset et al., 2012), their interactive influence remains unclear (Liu et al., 2020).

Elevated temperatures, high VPD, and low soil moisture often co-occur, but forest sensitivity varies depending on the baseline climatic and hydrological regimes. Addressing these multi-dimensional drivers is therefore crucial for predicting biodiversity patterns under climate change.

2.2.1 Effect of soil nutrients on species composition

Soil nutrients play a critical role in shaping species composition in tropical forests (Toledo et al., 2011). The supply of plant-essential nutrients, including soil nitrogen, phosphorus, and base cations (e.g., calcium), has been linked to variation in forest diversity and productivity (Peguero et al., 2023; Peña-Claros et al., 2012). Soil chemistry is partially regulated by climate, with temperature and precipitation influencing microbial activity and nutrient mineralisation rates (Deng et al., 2018). Soil nutrient pools are further influenced by climate via transport processes (LeBauer and Treseder, 2008). For example, soils in wet climates (e.g., coastal forests in Ghana) are subject to elevated levels of leaching, which can lead to a potential deficiency of water-soluble nutrients (Fauset et al., 2012). The extent and impact of variation in soil fertility across different forest types and climate regimes remain a topic of debate. While nitrogen and phosphorus are generally recognised as limiting factors of tree productivity globally, their influence appears to be less pronounced in tropical forests (Du et al., 2020; LeBauer and Treseder, 2008). Appiah-Badu et al. (2022) found only weak associations between soil nutrient content and species composition in wet forests in Ghana. Similarly, Nadeau and Sullivan (2015) discovered a weak negative association between soil fertility and tree species richness in the rainforests of Costa Rica. In contrast, nutrient availability has been positively associated with functional diversity in a large-scale study of tropical systems (Aguirre-Gutiérrez et al., 2022). The continued uncertainties in literature are underpinned by the complex interactions between soil nutrient availability, plant species adaptations and varying climatic contexts that modulate nutrient cycling and uptake. Understanding these dynamics is particularly critical for diverse tropical forests, where nutrient limitations may govern species turnover, niche differentiation, and ecosystem functioning under changing environmental conditions.

2.3 Conservation status of tropical tree species: Patterns, threats and implications

Assessing the conservation status of tree taxa using recognised, standardised indices is crucial for understanding species viability and the vulnerability of ecological communities under changing environments (Harvey-Brown et al., 2022). Conservation status integrates a species' population size, ecological range, and probability of persistence (Harvey-Brown et al., 2022; IUCN, 2024). Globally, around 38% of all tree species assessed are threatened, underscoring the urgency of conservation action (IUCN, 2024; Rivers et al., 2023). This concern is particularly acute in tropical forests, which are renowned as biodiversity hotspots and central to maintaining global ecological stability (Myers et al., 2000). In Africa, approximately 31.7% of vascular plant species are likely threatened with extinction, with an additional 33.2% considered rare and potentially at risk of becoming threatened in the near future (Stévart et al., 2019). Notably, in African regions such as Ethiopia, central Tanzania, and the southern Democratic Republic of Congo, over 40% of species are considered to be at risk, emphasising the need for focused conservation strategies in these areas. Comparatively, large-scale assessments in other tropical regions show similar challenges; for instance, in the Amazon, Steege et al. (2015) estimated that 36-57% of ~15,200 tree species qualify as globally threatened under the International Union for Conservation of Nature (IUCN) criteria. The loss of threatened taxa undermines ecological integrity and impairs key processes such as carbon storage, nutrient cycling and hydrological regulation. Recent evidence suggests that climatic niches associated with humid forest types in Africa are likely to shift under climate change, placing many species and communities at risk (Réjou-Méchain et al., 2021).

Despite these concerns, systematic evaluations of the conservation status of tree species in tropical Africa remain limited. While existing studies have identified many endemic and ecologically important species to be at risk of extinction (Kengne et al., 2022; Stévart et al., 2019), few have assessed how conservation value metrics differ among forest communities or how associated indices are shaped by local environmental conditions such as soil moisture and VPD (Sanjeewani et al., 2024). Moreover, quantitative approaches that assess the effects of environmental variation on composite measures of conservation concern (e.g., the conservation value index, which integrates species rarity and global threat levels) have rarely been applied in African tropical forests (but see Owusu et al., 2022). This knowledge gap constrains the understanding of how environmental gradients shape the spatial distribution of threatened taxa and the conservation importance of forest communities. Addressing these issues, the present study examines how key abiotic factors influence community-level conservation metrics across contrasting forest zones in Ghana, providing new insights into how environmental gradients shape conservation priorities in West African forests.

3. METHODOLOGY

3.1 Introduction to the methodology

The methodological framework of this thesis is based on a long-term forest monitoring network established in 2012 across three contrasting forest types in Ghana, West Africa. This network provides a comprehensive basis for evaluating forest growth and biodiversity dynamics in representative tropical ecosystems. This chapter outlines the standardised protocols and analytical approaches employed to address the thesis objectives. It includes descriptions of study sites, establishment of permanent monitoring plots, forest inventory procedures, measurements of tree and stand structures, sampling designs, and calculations of key ecological variables such as basal area increment, neighbourhood competition index, aboveground biomass growth, and species diversity metrics. Detailed descriptions of methods specific to each research objective are provided in subchapters 3.2, 3.3, and 3.4.

3.1.1 Study sites

The study was conducted in three protected forest reserves in Ghana (Figure 1): Ankasa Conservation Area (ACA), Bobiri Forest Reserve (BFR), and Kogyae Strict Nature Reserve (KSNR). These sites are part of the Global Ecosystem Monitoring Network of permanent sampling plots (https://www.globalecosystemmonitoring.com/) established across tropical forest types to monitor forest structure, composition, demographic dynamics and carbon cycling (Marthews et al., 2012). The protected status of these reserves helped to control for the effects of land use on forest dynamics, which could otherwise distort growth and biodiversity assessments and confound their climate relationships. The sampled locations span a latitudinal and environmental gradient ranging from wet coastal areas in the southwest to the drier interior regions of central Ghana. Based on a gridded reanalysis of climate data (Karger et al., 2017) since 1980, mean annual precipitation ranged from ~2057 mm at coastal sites (ACA) to ~1095 mm for northern interior plots (KSNR). Mean annual temperatures ranged from 25.0 °C in the south to 27.0 °C at northern locations (Table 1). All sites experience two rainy seasons (April-July and September-October), interrupted by a distinct dry season (November-March) that increases in length from the coast towards the interior region. Total monthly precipitation during the dry season falls below 100 mm (Hall and Swaine, 1981). Mean elevations are 90 m in ACA, 270 m in BFR, and 225 m in KSNR. The three reserves represent distinct forest types: wet evergreen (ACA), moist semi-deciduous (BFR), and dry semi-deciduous (KSNR) forests, which are characteristic of the forest zone of West Africa and support diverse assemblages of flora and fauna (Hall and Swaine, 1981).

Table 1: Environmental, floristic and structural characteristics of forest types. Shown are long-term mean climate values (1980-2022) with (±) standard deviations.

Ecological characteristics	Forest type		
	Dry	Moist	Wet
Floristics and structure			
Number of individual trees	464	1735	1272
Number of species	53	103	131
Number of genera	46	79	101
Number of families	24	35	40
Shannon diversity	2.72 ± 0.12^{a}	3.07 ± 0.23^{b}	3.46 ± 0.07^{c}
Simpson diversity	0.91 ± 0.12^{a}	0.92 ± 0.23^{a}	0.94 ± 0.14^{b}
Basal area (m^2 ha^{-1})	18.9 ± 0.64^{a}	29.2 ± 0.56^{b}	27.9 ± 0.25^{b}
Stem density (ha^{-1})	180 ± 3.93^{a}	611 ± 20^{b}	456 ± 5.04^{c}
Environmental variables			
Rainfall (mm $year^{-1}$)	1094.97 ± 179.82^{a}	1180.51 ± 171.42^{b}	2057.21 ± 251.26^{c}
Temperature (°C)	27.0 ± 0.41^{a}	26.0 ± 0.43^{b}	25.10 ± 0.29^{c}
Vapour pressure deficit (kPa)	1.72 ± 0.30^{a}	1.25 ± 0.29^{b}	0.48 ± 0.08^{c}

Ecological characteristics	Forest type		
	Dry	Moist	Wet
Relative humidity (%)	77.99 ± 10.19^{a}	82.5 ± 7.41^{b}	90.73 ± 2.12^{c}
Soil moisture (m^3 m^{-3})	0.26 ± 0.03^{a}	0.35 ± 0.02^{b}	0.33 ± 0.03^{c}
Available phosphorus (mg kg^{-1})	14.64 ± 1.02^{a}	18.29 ± 2.33^{b}	15.49 ± 2.07^{a}
Soil nitrogen (g kg^{-1})	4.22 ± 0.17^{a}	3.84 ± 0.57^{b}	5.74 ± 1.57^{c}
Soil carbon (g kg^{-1})	10.60 ± 1.23^{a}	31.81 ± 1.20^{b}	14.53 ± 1.23^{c}
Organic matter (g kg^{-1})	18.14 ± 2.05^{a}	54.85 ± 2.08^{b}	25.07 ± 2.36^{c}
Exchangeable calcium (cmol kg^{-1})	4.09 ± 0.89^{a}	8.60 ± 1.93^{b}	1.55 ± 0.08^{c}
Exchangeable magnesium (cmol kg^{-1})	1.22 ± 0.04^{a}	3.05 ± 0.44^{b}	0.82 ± 0.02^{c}
Exchangeable potassium (cmol kg^{-1})	0.31 ± 0.09^{a}	1.18 ± 0.18^{b}	0.28 ± 0.04^{a}

Notes: Tree basal area was calculated assuming that stems were circular in cross-section (basal area = π x diameter^2/4). Temperature, relative humidity and soil moisture represent conditions for an annual period. Vapour pressure deficit is for the dry season. Differences between forest types were tested using the non-parametric Kruskal-Wallis and post-hoc Dunn tests with a Bonferroni correction. Different letters denote significant differences between types (p<0.05).

3.1.2 Data collection and sampling protocols

Field survey plots were established using a stratified random sampling design (Marthews et al., 2012). In each forest type, three survey plots (1.0 ha each) were established (n = 9 plots total). Individual plots were subdivided into 25 subplots (20×20 m). Within each plot, all living adult trees with diameters at breast height (DBH) ≥ 10 cm were identified to the species level, tagged, and mapped relative to a reference location (southwest plot corner). Stem diameters were measured to the nearest millimetre (0.1 cm) at 1.3 m above ground level. However, the point of measurement (POM) of the diameter was adjusted for some individual trees to account for swelling or buttressing in the basal portions of the bole. Specifically, POMs were raised by fixed increments of 0.5 m up to a maximum level of 4.5 m for individuals when evidence of buttress formation was observed (Marthews et al., 2012). POM levels were painted and documented to ensure measurement consistency across censuses.

Tree mapping and height measurements were conducted using Field-Map technology (IFER – Institute of Forest Ecosystem Research, Jílové u Prahy, Czech Republic; www.fieldmap.cz). Tree positions were recorded in a local Cartesian coordinate system following the standard Field-Map survey procedure (Hédl et al., 2009). A set of permanently established reference points defined the plot framework, and tree x–y coordinates were calculated from laser-measured distances and azimuths obtained with the Field-Map rangefinder–compass unit. Tree heights were measured using the integrated laser rangefinder and clinometer. For each tree, the operator targeted the stem base and the upper crown point, and Field-Map recorded the corresponding distances and vertical angles. The software then automatically computed the total tree height using its internal trigonometric algorithms, which convert angle–distance measurements into vertical height components.

Annual censuses were conducted from 2012, although the three moist forest plots were not censused in 2014, 2019, and 2021. The specific month of data collection was consistent across years but varied by forest type: surveys were conducted in March, June, and September in wet, moist, and dry forests, respectively. During each census, all tagged stems were remeasured and their status (alive or dead) recorded. Newly recruited stems reaching DBH of ≥10 cm during the census were identified, tagged, measured and mapped, while previously recorded stems that were dead or missing were classified as dead.

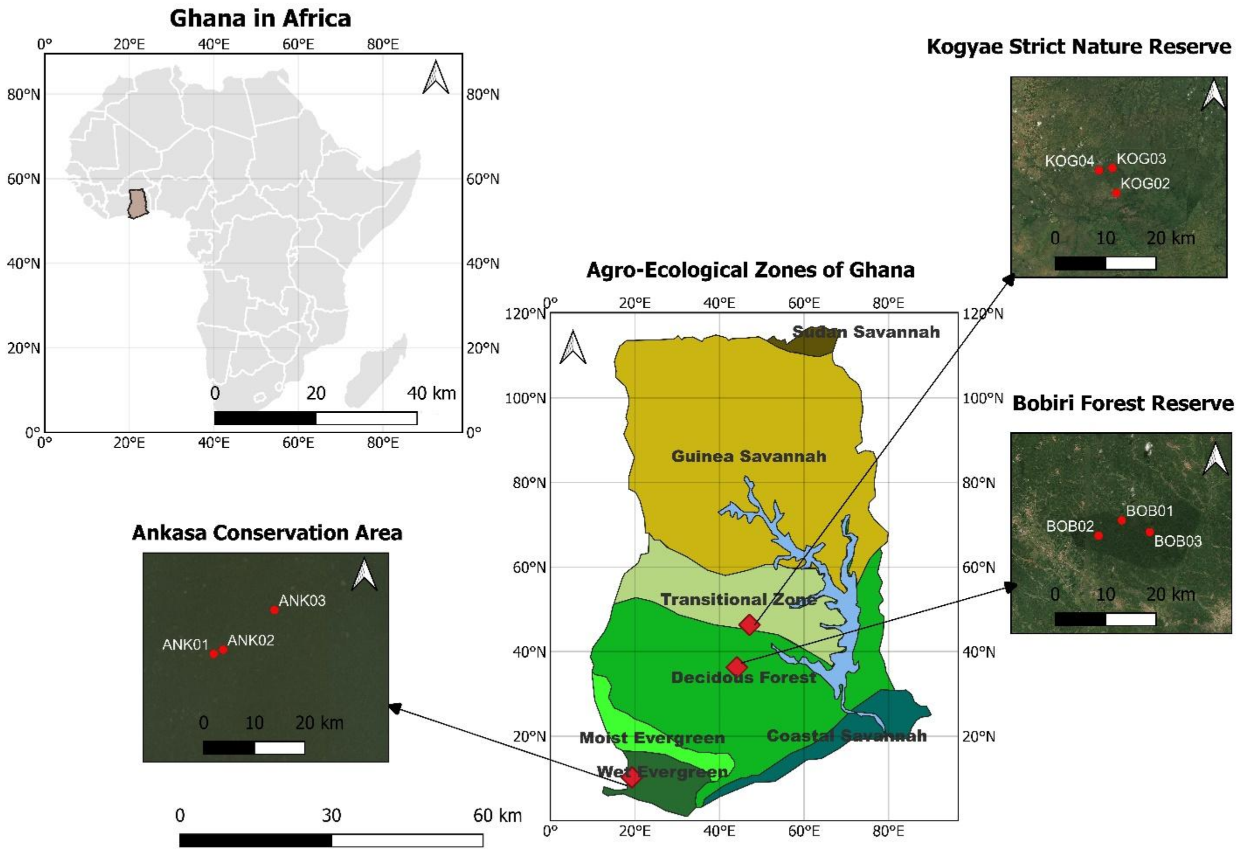

Figure 1: Map of Africa showing the location of study sites in Ghana: Ankasa Conservation Area (wet evergreen forest), Bobiri Forest Reserve (moist semi-deciduous forest), and Kogyae Strict Nature Reserve (dry semi-deciduous forest). The distribution of the individual sampling plots (n = 9) in the smaller panels is overlain on a digital elevation model.

3.1.3 Environmental data

Climate data from a high-resolution climate model (ERA5-Land) developed by the European Centre for Medium-Range Weather Forecasting was used. ERA5-Land provides gridded (spatially continuous), hourly estimates of several climatic variables with global coverage (Muñoz-Sabater et al., 2021). Climate data, including minimum, maximum, dew point, and mean temperatures, precipitation, humidity and soil moisture, were extracted from the ERA5-Land data portal (https://www.ecmwf.int/en/era5-land). The global-scale climate grids were then subset to the geographic extent of the study area. The hourly values for all variables were aggregated to generate daily, monthly, dry season, and annual composites (temperature means and precipitation sums). The dry season across the study sites extends from late November to March. Annual composites were defined to correspond with the different data collection periods of each site, as previously described. Thus, annual climate estimates were generated for the 12 months from March to February for wet forest, June to May for moist, and September to August for dry sites. The 12-month aggregated climate values were then downscaled from 9.0 km to an approximately 900 m (30 arc-second) spatial resolution for each plot using statistical kriging. A USGS digital elevation model and soil hydraulic and thermal parameters, with a spatial resolution of ~900 m, were used as covariates for the kriging-based interpolation (Dai et al., 2013). The entire workflow was performed using R functions from the package *KrigR* (Kusch and Davy, 2022).

After downscaling, soil moisture values were standardised to generate a soil moisture index (SMI; Gao et al., 2016). SMI accounts for low soil water content (wilting point) that is potentially unavailable for root absorption:

$$\mathrm{SMI} = \frac{Qsoil - \min(Qsoil)}{\max(Qsoil) - \min(Qsoil)} \tag{1}$$

where Qsoil is the downscaled, 12-month, volumetric soil moisture fraction ($m^{3}_{H_2O}\ m^{-3}_{soil}$), and min and max represent the corresponding minimum and maximum moisture levels observed for the period of our analyses for each tree location.

VPD was calculated based on the Penman-Monteith approach and equations from Allen et al. (1998):

$$VPD = \ e_{s\,-}\, e_a \tag{2}$$

where e_s and e_a denote saturation and actual vapour pressure deficits, respectively.

$$e_s = \left[\frac{e_{s(T_{max})} + e_{s(T_{min})}}{2}\right] \tag{3}$$

where variables e_s (T_{max}) and e_s (T_{min}) represent saturation pressure at maximum and minimum temperatures.

Saturation vapour pressures (es at T_{max} and T_{min}) were calculated as follows:

$$e_s\,(T_{max}) = 0.6108 \times exp\left(\frac{17.27 \times T_{max}}{T_{max} + 237.3}\right) \quad (4)$$

$$e_s\,(T_{min}) = 0.6108 \times exp\left(\frac{17.27 \times T_{min}}{T_{min} + 237.3}\right) \quad (5)$$

Actual vapour pressure (e_a) was estimated from the dew point temperature (T_{dew}):

$$e_a = 0.6108 \times exp\left(\frac{17.27 \times T_{dew}}{T_{dew} + 237.3}\right) \quad (6)$$

3.1.3.1 Soil data

Soil samples were collected from five randomly selected locations within each forest plot (n = 9) at depths of 0-10 cm, 10-20 cm and 20-30 cm using a soil auger. As mineral concentrations can vary substantially with depth (Jobbágy and Jackson, 2001), subsamples (from different depths) were combined to generate a single representative soil sample for each soil pit. Chemical analyses for carbon and nutrients (nitrogen, phosphorus, potassium, magnesium, calcium) were conducted at the Soil Laboratory of the Faculty of Renewable Natural Resources, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana. To determine total soil nitrogen, the Kjeldahl digestion method was used (Bremner, 1996), while the wet digestion method was employed to quantify soil carbon (Nelson and Sommers, 1982). Soil exchangeable magnesium and calcium were extracted using an atomic absorption spectrophotometer, while potassium was determined using a flame photometer (Chapman, 1965; Rowell, 1994). Available phosphorus was extracted using the Bray II method (Olsen et al., 1982). Soil organic matter was determined using the Walkley–Black method.

3.1.4 Statistical analyses: A general approach

Prior to analyses, collinearity among predictor variables was assessed using Spearman's rank correlation and a single variable was selected from highly correlated ($|r| > 0.70$) pairs (Figures S1.1, S2.1, S2.1.1). Continuous variables were checked for normality using the Shapiro–Wilk test and visualised with histograms. All continuous predictors were standardised (mean-centred and scaled to unit variance) to facilitate model convergence and improve comparability. All analyses were performed using R statistical software (version 4.4.1; R Core Team, 2024).

3.2 Drivers of floristic composition, diversity and conservation value

3.2.1 Forest classification and diversity

To classify the nine survey plots into unique forest community types, ordination analyses were performed. Specifically, non-metric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity metric was used to identify distinct groups based on species composition. The ordination was performed using the *metaMDS* function of the *vegan* package (Oksanen et al., 2022). The significance of compositional differences among forest types was assessed using the analysis of similarity (ANOSIM) test with the *anosim* function from the *vegan* package.

The Importance Value Index (IVI) for each tree species across the different forest types was computed to assess their contribution to the provisioning of community-level ecosystem services (McGill et al., 2007). IVI was calculated following the classical formulation of Curtis and McIntosh (1950), as implemented in the *BiodiversityR* package (Kindt and Coe, 2005). It integrates three components (Eq. 7): relative density (RD), relative frequency (RF), and relative dominance (RBA):

$$IVI = RD + RF + RBA \tag{7}$$

where:

$$RD = \left(\frac{Number\ of\ individuals\ of the\ species}{Total\ number\ of\ individuals\ of\ all\ species}\right) \times 100 \qquad (8)$$

$$RF = \left(\frac{Number\ of\ plots\ in\ which\ the\ species\ occurs}{Total\ number\ of\ plots\ sampled}\right) \times 100 \qquad (9)$$

$$RRBA = \left(\frac{Basal\ area\ of\ the\ species}{Total\ basal\ area\ of\ all\ species}\right) \times 100 \qquad (10)$$

Tree diversity for each forest community type was assessed and compared. To compensate for inherent biases associated with biodiversity assessments that arise due to an uneven distribution of species across space and incomplete (finite) sampling effort, Hill numbers were computed (Roswell et al., 2021). Hill numbers dampen biases by accounting for both richness and relative abundance patterns (Chao et al., 2014). Hill numbers are a family of diversity indices that quantify the effective number of species in a community (the number of equally abundant species in a theoretical community needed to generate a given diversity value). The individual indices of the Hill family differ by a single parameter q. The first three Hill numbers, q = 0, 1, and 2, are related to the more traditional diversity metrics: richness, Shannon, and Simpson, respectively. Methods in Chao et al. (2014) were employed to derive these three Hill numbers for each forest type using the *iNEXT* package (Hsieh et al., 2022). Calculations require the construction of rarefaction and extrapolation curves. We computed 95% confidence intervals around these curves for each forest type, facilitating an assessment of whether diversity levels diverged significantly among forest types.

3.2.2 Conservation value

Community-level conservation values were evaluated by quantifying a Conservation Value Index (CVI). CVI integrates data for both species' rarity and threat status (Capmourteres and Anand, 2016; Owusu et al., 2022) (Eq. 11):

$$CVI = RS + GTS \tag{11}$$

where RS is a rarity score, and GTS is a global threatened score. RS was calculated as the sum of the relative frequency of species (Eq. 12):

$$RS = \sum_{i=1}^{s} \frac{1}{f_i} \tag{12}$$

where f_i is the frequency of the i^{th} species and s denotes the total number of species per forest type. GTS combines and weights the relative threatened status (based on IUCN Red List rankings) of each species in a forest (Eq. 13):

$$GTS = (6 \times EN) + (3 \times VU) + (2 \times NT) + (1 \times LC) + (1 \times NE) \tag{13}$$

where EN, VU, NT, LC, and NE represent the number of taxa belonging to the IUCN categories Endangered, Vulnerable, Near Threatened, Least Concern and Not Evaluated, respectively. ANOVA and Tukey's Honest Significant Difference test were used to compare conservation value indices among forest types.

3.2.3 Statistical analysis: Environmental relationships

Regression analyses were used to assess relationships between community diversity and climate factors. The primary response variable was community richness. Separate analyses were conducted to evaluate the effects of climate on Shannon diversity and the Conservation Value Index (see section 3.2.2). Hierarchical models were developed to investigate how mean annual soil moisture, dry season VPD, and mean annual temperature influenced these response variables. Soil moisture and VPD were selected to reflect soil water availability and atmospheric water demand, while temperature was included to capture the effects of ongoing global warming trends. Mean long-term climate values (1980-2022) were used in our analyses. The full model for community richness assumed the following form (Eq. 14):

$$richness_{ij} \sim \beta_0 + \beta_1(SM_{ij}) + \beta_2(VPD_{ij}) + \beta_3(VPD_{ij}\ x\ SM_{ij}) + b_j + \varepsilon_i \qquad (14)$$

where *richness* is a species count for a 400 m^2 subplot (i) located in a 1.0 ha full plot (j), SM_{ij} is total soil moisture content, VPD_{ij} is vapour pressure deficit, b_j is a random plot effect, β parameters are regression coefficients, and ε_i is residual error. Models assumed that the residuals were independent and normally distributed after accounting for the explanatory variables. Interactions between VPD and SM were tested by fitting separate models with and without interaction terms (*VPD x SM*, Eq. 14). Finally, to evaluate the degree of support for an effect of temperature, VPD was substituted for temperature in alternate models. Temperature and VPD were correlated, but collinearity between all other model terms was low according to tests performed using the *multicollinearity* function of the *performance* package (Lüdecke et al., 2021).

All response variables (n = 3) were analysed separately, but the associated models used the same explanatory terms as shown in Eq. 14. Richness models were formulated as generalised linear mixed-effects models (*glmer* function, *lme4* package, Bates et al., 2015) with a Poisson distribution. The other response variables (Shannon diversity and conservation value index) were fitted as linear mixed effects models (*lmer* function, *lme4* package). Both marginal and conditional coefficients of determination (R^2) were calculated using the *r2* function of the *performance* package to quantify the variance explained by fixed effects versus both fixed and random effects, respectively (Nakagawa et al., 2017). The degree of support for alternate models for a given response variable was assessed by comparing Akaike Information Criterion (AIC) scores and marginal R^2 values.

A Redundancy Analysis (RDA) was performed to understand the relationships between species abundance and a set of climate and soil variables. Species abundance was quantified by the number of individuals for each unique species in the subplots. Species abundance data were $\log_{10}(x + 1)$ transformed. RDA was performed using the forward-backwards selection procedure (*ordistep* function, *vegan* package).

3.3 Biomass growth responses to biotic and abiotic factors

3.3.1 Allometric equations and biomass estimation

Aboveground biomass (AGB) estimation required individual tree height data, which were measured only during the 2020 census. To estimate tree heights for other census years, several candidate height–diameter (H–D) allometric models (log1, log2, Weibull, Michaelis) available in the *BIOMASS R* package were fit to the 2020 height and stem diameter data. Model performance was evaluated using AIC and Residual Standard Error (RSE), with the *log1* model providing the best fit. This model was then used to predict tree heights for other census years based on measured stem diameter.

Species-level wood density values were obtained from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). When species-specific values were unavailable, mean values at the genus, family, or plot level were used, following the approach of Jucker et al. (2018). Annual aboveground biomass for each tree j in year t (AGB_{jt}; Mg) was computed using the pantropical allometric equation from Chave et al. (2014):

$$AGB_{jt} = 0.0673 \times \left(\rho_j \times diameter^2{}_{jt} \times H_{jt}\right)^{0.976} \tag{15}$$

where ρ_j is species-level wood density (g cm^{-3}), $diameter_{jt}$ is measured stem diameter (cm), and H_{jt} is estimated total height (m) of tree j in year t. Biomass estimates were obtained using the *computeAGB* function of the *BIOMASS* package (Réjou-Méchain et al., 2017). Palms and lianas were excluded due to the lack of standardised allometric models (Poorter et al., 2017). Plot-level AGB (Mg ha^{-1}) was obtained by summing tree-level AGB values within each 1-ha full plot. Annual aboveground biomass increment (AGBI; Mg yr^{-1}) was calculated as the difference between successive annual estimates of AGB for each tree. For non-census years in moist forests, mean AGBI was derived from the two-year census interval. Tree-level AGBI values were used for species-level analyses. For community-level analyses, AGBI values for each tree were summed within each subplot (400 m^2) and scaled to a per-hectare basis (Mg ha^{-1} yr^{-1}). Plot-level AGBI was obtained by summing annual biomass increment for all trees in a given 1-ha plot.

3.3.2 Competition

Neighbourhood crowding around each focal tree was quantified using Hegyi's distance-dependent Neighbourhood Crowding Index (NCI; Hegyi, 1974). For each focal tree i, NCI was calculated as:

$$NCI_i = \sum_{j=1}^{n} \frac{(diameter_j)^{\alpha}}{(distance_{ij})^{\beta}} \tag{16}$$

where n is the number of neighbouring trees within 15 m of focal tree i, $diameter_j$ (m) is the stem diameter of neighbour tree j, and $distance_{ij}$ (m) is the horizontal distance between neighbour j and focal tree i. The parameters α and β modulate the influence of neighbour size and distance on competitive intensity, respectively. To standardise competition values, each NCI value was normalised by dividing it by the maximum observed NCI:

$$NCI_{norm} = \frac{NCI}{\max{(NCI)}} \tag{17}$$

3.3.3 Structural diversity

Structural (tree size) diversity was quantified using the Shannon diversity index based on tree basal area distributions across DBH size classes, following established approaches (Fatunsin and Naka, 2025; LaRue et al., 2023). This metric accounts for the relative dominance of different size classes and provides a measure of structural diversity at each subplot (Eq. 18). For each tree, basal area (m^2) was calculated as π (DBH/2)^2, with DBH (cm) converted to metres prior to calculation. Trees were grouped into DBH classes with 10 cm class intervals, ranging from 10 cm (the minimum measured DBH) to the maximum DBH in the dataset. A 10 cm class width was selected to capture size variation and maintain stable class proportions. The total basal area per class was summed within each subplot. Shannon's tree size diversity index (H_d) was then computed as:

$$H_d = -\sum_{i=1}^{D} p_i \ln(p_i) \tag{18}$$

where p_i is the proportion of total basal area of the i^{th} DBH class, and D is the number of DBH classes. Calculations were performed using the *vegan* package (Oksanen et al., 2022).

3.3.4 Statistical analysis: Abiotic and biotic relationships

Differences in AGB, AGBI, soil moisture and VPD across the 2012–2021 monitoring period were examined using linear mixed-effect models, with plot identity included as a random effect. Post hoc pairwise comparisons of estimated marginal means were conducted using Bonferroni correction to evaluate significant differences among forest types. Drivers of AGBI at both species and community levels were investigated using Generalised additive mixed-effects model (GAMMs) fitted with the *gamm* function in the *mgcv* package (Wood, 2017). The response variable, AGBI, was square-root transformed to address right skewness and stabilise variance. GAMMs accommodate nonlinear relationships, hierarchical nesting (where tree identity is nested within subplots and plots), and temporal autocorrelation. At the species-level, separate models were fitted for the 15 most common species across the study sites (Eq. 19). The global model structure was:

$$\sqrt{AGBI_{ijkt}} = \beta_0 + f_1(DBH_{ijkt}) + f_2(NCI_{ijkt}) + te(SMI_{ijkt,}VPD_{ijkt}) + re(TreeID_j/Subplot_k) + \varepsilon_{ijkt} + AR(1)_{t|TreeID_j} \quad (19)$$

where $\sqrt{AGBI_{ijkt}}$ is the square root transformed aboveground biomass increment of tree j in subplot k, plot i, at year t; β_0 is the intercept; f_1 and f_2 are penalised splines for tree diameter (DBH) and neighbourhood crowding index (NCI), respectively; *te*() denotes a tensor product smooth capturing the interaction between soil moisture index (SMI) and VPD; *re*(*TreeID*$_j$/*Subplot*$_k$) accounts for random effects of tree identity nested within subplots; ε_{ijkt} is the residual error, and $AR(1)_{t|TreeID_j}$ models the temporal autocorrelation of repeated measurements within individual trees.

At the community scale, the subplot-level total biomass increment was modelled as a function of structural diversity (SDIV) and the interaction between SMI and VPD, with subplot nested within plots as random effects:

$$\sqrt{AGBI_{ikt}} = \beta_0 + f_1(SDIV_{ikt}) + te(SMI_{ikt,}VPD_{ikt}) + re(Plot_i/Subplot_k) + \varepsilon_{ikt} \quad (20)$$

Penalised splines were restricted to three knots to balance model flexibility and interpretability. Candidate models were constructed by fitting alternative combinations of predictor variables and, where relevant, their interactions (Table S2.1). Model selection at both scales was based on AIC, adjusted R^2, and *concurvity* diagnostics. Competing models with $\Delta AIC < 2$ were considered to have equivalent support (Burnham and Anderson, 2002). Model assumptions, including non-significant levels of temporal autocorrelation, were checked using residual diagnostics and autocorrelation function (ACF) plots of normalised residuals.

3.4 Role of tree size, functional attributes and water availability in mediating competitive interactions among tropical tree species

3.4.1 Growth data

Annual measurements of stem diameter for each adult tree (>10 cm) in all field plots for the 10-year census period (2012-2021) were compiled. Records with missing measurements (N = 310), data for trees that died (N = 705 stems), swamp trees (N = 21), and lianas (N = 16) were removed. A time series of annual basal area increment (BAI, cm^2 $year^{-1}$) was derived from repeated stem diameter measurements for each tree, assuming circular cross sections. For non-census years in moist forests, the average annual BAI was computed using field data from the start and end of the two-year census interval. Growth dynamics were analysed separately for the 15 most common tree species, based on sample size (N>150 trees per species; Table 3).

3.4.2 Species guilds and wood density classification

A prior classification of the regeneration guild of forest taxa in Ghana was used as a proxy for shade tolerance (Hawthorne, 1996, 1995). Hawthorne's semi-quantitative classification was based on a floristic inventory as well as qualitative observations of the environmental correlates of species occurrence (Sheil et al., 2006). Three guild categories were described: (1) a gap-specialist (pioneer) class comprised of light-demanding, shade-intolerant taxa; (2) a shade-tolerant (shade-bearer) class associated with resource-limited closed canopy environments; and (3) a non-pioneer light-demanders (NPLD) category, consisting of species with an intermediate capacity for shade-tolerance (Hawthorne and Abu-Juam, 1995).

For each focal species (N=15), all neighbour taxa were grouped into two or three distinct wood density classes (e.g., low, medium, high) using k-means clustering (Hartigan and Wong, 1979). Preliminary regression models were run comparing the performance of the two-class and three-class groupings. The classification that provided the more parsimonious fit based on corresponding AIC scores was used in subsequent analyses.

3.4.3 Statistical analyses: Effect of wood density, shade tolerance and soil moisture on species-specific competitive outcomes

Competitive effects were quantified by evaluating the extent to which neighbouring individuals constrained the radial growth of focal trees. This analysis focused on how biotic attributes of neighbours and local abiotic conditions modulated competitive pressures. As competition is inherently a neighbourhood-scale phenomenon, the magnitude of neighbour effects was investigated at the level of individual trees. Although the spatial extent of these interactions varies with species and tree size (Stoll and Newbery, 2005; Uriarte et al., 2010), a competitive neighbourhood was defined as a fixed 15 m radius around each focal tree. This threshold is consistent with prior studies demonstrating that competitive interactions among trees predominantly occur within 10–20 m and decline sharply beyond this range (Canham et al., 2006, 2004; Coates et al., 2009; Muscarella et al., 2018; Uriarte et al., 2005). Preliminary analysis (Figure S3.1) further confirmed that neighbour influence was negligible beyond 15 m for most focal species. While variability in competitive interactions across spatial scales and species was acknowledged, the 15 m radius captures a biologically meaningful and computationally feasible scale for our analyses.

Based on an implicit assumption that tree taxa are differentiated in terms of their life-history and resource allocation strategies, and therefore respond uniquely to competition from neighbours, separate sets of nonlinear regression models were formulated for each of 15 focal tree species (Table 3). This study builds on a tradition of neighbourhood modelling approaches in which the demographic performance of an individual tree is analysed in terms of the fine-scale spatial distribution of proximate trees and heterogeneity in the physical environment

(Canham et al., 2004). The statistical framework is based on the application of maximum-likelihood principles to estimate model parameters (Edwards, 1992), contrasting the traditional null-hypothesis testing paradigm that prevails in the dendrochronological literature (Canham and Uriarte, 2006). As in prior studies (e.g., Buechling et al., 2017; Canham et al., 2006; Gómez-Aparicio et al., 2011; Korolyova et al., 2022; Uriarte et al., 2010; Valor et al., 2024), each focal tree species was assumed to have an innate maximum growth potential (i.e. in the absence of neighbours) that is reduced by competitive interactions with neighbouring trees:

$$BAI = PG \times s(diameter) \times \nu(NCI) \tag{21}$$

where BAI is annual basal area increment (cm^2 year^{-1}) at the POM of a given target tree, PG is maximum potential growth rate in the absence of size or competition effects. The functions *s* and ν are nonlinear modifiers that scale PG according to stem diameter and neighbourhood crowding, respectively. PG was treated as a plot-level fixed effect. A unique value for PG was estimated for each of the nine survey plots to account for site-specific variation in growth potential. This approach is consistent with prior neighbourhood modelling frameworks (Buechling et al., 2017; Canham et al., 2006), where plot-specific growth potential is estimated to capture ecological heterogeneity among sites not explained by the other fixed effects of the model. Size and competitive effects were scalar variables (values from 0–1) that fractionally reduced potential growth.

3.4.3.1 Size effects

To quantify the effect of tree size on *PG* in Eq. 21, a lognormal function was used:

$$\text{Size} = \exp\left[-0.5 \times \left(\frac{\ln\left(\frac{\text{diameter} + X_p}{X_0}\right)}{X_b}\right)^2\right] \tag{22}$$

where diameter is an annual time series of stem diameter measurements (cm), X_0 and X_b define the mode and breadth of the function, and X_p is a shift parameter that allows for positive intercepts when stem diameter is zero (Canham and Murphy, 2016). The lognormal generates a unimodal, asymmetrical curve that can fit monotonically increasing, decreasing, or unimodal data distributions (Canham et al., 2004). For those species (N = 6, Table 4) where the POM of diameter varied across individual trees due to stem buttressing, the mode and variance of Eq. 22 were allowed to vary as separate Gaussian functions of POM:

$$X_0 = X_h^{\ddagger} \times \exp\left[-0.5 \times \left(\frac{\mathrm{POM} - X_0^{\ddagger}}{X_b^{\ddagger}}\right)^2\right] \tag{23}$$

and

$$X_b = X_h^{*} \times \exp\left[-0.5 \times \left(\frac{\mathrm{POM} - X_0^{*}}{X_b^{*}}\right)^2\right] \tag{24}$$

where *POM* is the point of measurement of diameter for a given sample tree. The parameters $X_h^{\ddagger}$, $X_0^{\ddagger}$ and $X_b^{\ddagger}$, and X_h^{*}, X_0^{*} and X_b^{*} determine the height, mode and breadth of a given equation, respectively.

3.4.3.2 Competition effects

Competition effects were modelled using a nonlinear exponential decay function (ν in Eq. 21):

$$\nu = exp(-C \times BAratio^{\gamma} \times NCI^{\delta}) \tag{25}$$

where *NCI* is a neighbourhood crowding index that estimates the strength of competitive effects on a target tree based on the configuration and density of trees in a neighbourhood (Eq. 27). The parameters *C* and δ determine the shape of the response in a target tree to variation in NCI. The basal area ratio (BAratio) quantifies the relative size of a target tree compared to its neighbours and is used to adjust the crowding effect in the growth model (Eq. 26). It is defined as the ratio of the mean basal area of all neighbouring trees (within 15 m) to the basal area of the target tree:

$$BAratio_{target} = \frac{\frac{1}{n}\sum_{j}^{n} BA_j}{BA_{target}} \tag{26}$$

where $BAratio_{target}$ is the basal area ratio for the target tree, n is the number of neighbouring trees within 15 m of the target tree, BA_j denotes the basal area of neighbouring tree j, and BA_{target} is the basal area of the target tree.

The neighbouring crowding index (NCI) in Eq. 25 accounts for both the stem diameter and proximity of neighbouring trees relative to a target tree:

$$NCI_{target} = \sum_{i=1}^{K} \lambda_i \left(\sum_{j=1}^{n_i} \frac{(diameter_{ij})^{\alpha}}{(distance_{ij})^{\beta}} \right) \tag{27}$$

where NCI_{target} is the neighbourhood crowding index for the target tree, K is the total number of neighbour groups (e.g., wood density, shade tolerance, taxonomic classes), n_i is the number of neighbours in group i located within 15 m of the target tree, $diameter_{ij}$ (meters) is the stem size of neighbour tree j in group i, and $distance_{ij}$ (meters) is the horizontal distance between the target tree and neighbour j in group i. The exponents α and β adjust the shape of the effects of neighbour diameter and distance, respectively.

The competition coefficient (λ_i) in Eq. 27 scales the aggregated effect of neighbour group i on the target tree, reflecting differences in competitive ability associated with specific functional or taxonomic attributes. In prior studies, unique values of λ_i were estimated based on the taxonomic identity of the neighbours (Buechling et al., 2017; Canham et al., 2004). Here, to test whether resource allocation strategies of neighbours influence their competitive ability, rather than their identity *per se*, individual neighbour taxa were assigned to homogeneous attribute classes and unique λ_i was computed for each class. Independent model fits were formulated and evaluated with alternate attribute classes. Specifically, models were compared using: (1) separate λ_i for K categories of wood density (K=2 or K=3, depending on the focal species); (2) unique λ_i for different guild (shade tolerance) classes (K=3); and (3) separate λ_i values for conspecifics, neighbours of the same family as the target tree, and nonfamilial neighbours (K=3 groups). Additionally, simpler alternate models that treated all neighbour species as equivalent in terms of their competition potential (i.e., λ=1) were fitted.

To capture the full effects of competition on target trees located near plot edges, neighbourhood conditions outside of plot boundaries were simulated (since those trees were not measured during field surveys). Adopting methods from Uriarte et al. (2016), hypothetical populations of trees within 20 m buffer regions surrounding all plot edges were generated. The simulated buffer populations had a size distribution and species composition equivalent to the structure and composition of the surveyed trees that were located inside and within 20 m of plot boundaries. The simulated trees were randomly located within the buffers.

3.4.3.3 Water supply effects

To test whether variation in soil moisture influences the strength of crowding effects from neighbours, the competition-shape parameter C in Eq. 25 was modelled as a Gaussian function of soil moisture:

$$C = Q_h \times \exp\left[-0.5 \times \left(\frac{\mathrm{SMI} - Q_0}{Q_b}\right)^2\right] \tag{28}$$

where SMI is a dimensionless soil moisture index describing mean 12-month soil moisture availability (see Eq. 1), and Q_0, Q_b, and Q_h describe the mode, breadth, and height of the function, respectively. This formulation was chosen a priori based on biological expectations and ecological theory: competition is expected to peak at intermediate moisture levels, where water availability supports physiological activity and resource uptake, and to decline under drought or saturated soil conditions, as stress reduces growth and resource demand (Maestre et al., 2009). Such unimodal responses align with stress gradient theory, which predicts shifts in plant-plant interactions along environmental gradients (Maestre et al., 2009). By allowing the

C parameter to vary unimodally with soil moisture, a nonlinear interaction between competition and water availability was explicitly tested.

3.4.3.4 Model specification and selection

Model parameters were estimated using the maximum likelihood method. A global optimisation algorithm (simulated annealing, Goffe et al., 1994) was used to determine parameter values that maximised the log-likelihood of predicting the observed growth rates for a focal species, given a particular model form (Uriarte et al., 2004b). To quantify uncertainty in parameter estimates, we computed support intervals for each parameter (Edwards, 1992). These intervals define the range of parameter values around the maximum likelihood estimates for which the log likelihood decreases by no more than 2 units. A normal probability density function (PDF) was used to calculate the likelihood. The PDF was modified to account for heteroscedasticity in the model residuals by allowing the standard deviation (SD) to vary as a power function of the mean:

$$SD = a + G^b \tag{29}$$

where a and b are estimated parameters and G is a vector of predicted growth rates (BAI).

Akaike's information criterion, penalised for model complexity, was computed to compare the performance of alternative models (Johnson and Omland, 2004). Model fit was assessed based on the proportion of variation explained (R^2) and prediction bias (slope of the regression of observed vs. predicted BAI). Regression models were fitted using the *likelihood* package (version 1.7; Murphy, 2015).

4. RESULTS

4.1 Drivers of floristic composition, diversity and conservation value

4.1.1 Forest composition and diversity

A total of 3,471 individual trees belonging to 242 species, 166 genera and 50 families were censused (Table 1; Figure S1.2). The species compositional patterns across forest types varied strongly and significantly (Figure 2A; $p = 0.001$). The dominant species of each type, according to the IVI (Table S1.3), included *Sterculia tragacantha*, *Pouteria alnifolia*, and *Manilkara obovata* in dry forests, *Funtumia elastica, Celtis mildbraedii* and *Sterculia rhinopetala* in moist communities, and *Protomegabaria macrophylla*, *Cynometra ananta*, and *Carapa procera* in wet types. *Bombax buonopozense* and *Cola gigantea* were the only generalists occurring in all forests. The prevalent dry forest taxa were shade-intolerant, broad-leaved, and deciduous. In the wet forest, the dominant species were evergreen and shade-tolerant. Moist forest species having high IVI scores were intermediate in terms of shade tolerance. Community-level diversity levels, as quantified by Hill numbers, indicated that wet forests had the highest richness, Shannon diversity, and Simpson's diversity levels relative to moist and dry types (Figure 3; Table 1). Moist and dry forests showed comparable levels of Simpson's diversity.

The RDA results indicate that four soil variables (nitrogen, phosphorus, calcium and moisture content) together with VPD explained 31.9% of the total variation in species composition of the communities (Figure 2B). For wet forests, compositional characteristics were positively associated with nitrogen and negatively with VPD. In contrast, dry forest composition was positively associated with VPD and negatively with nitrogen. The strongest drivers of the variation in the composition of moist forests were soil moisture, phosphorus, and calcium.

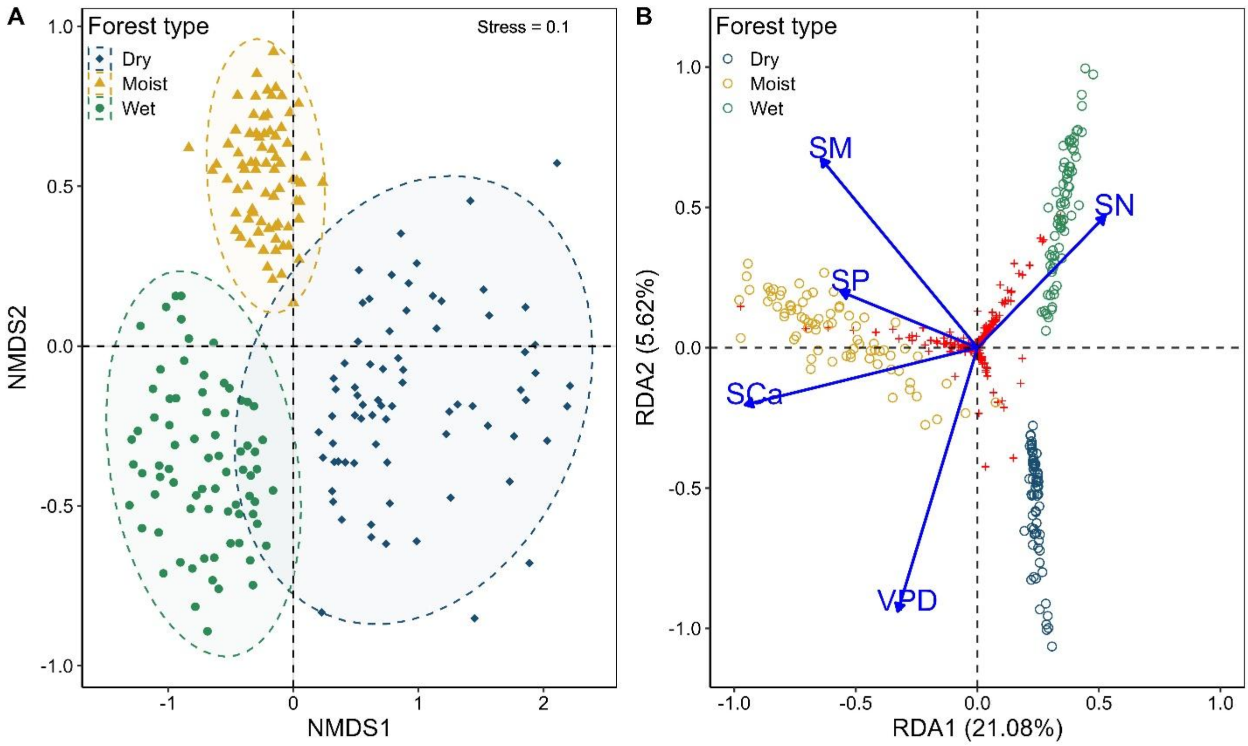

Figure 2: Panel A: NMDS ordination of species abundance data showing clear separation of subplots into wet, moist, and dry forest types, with 95% confidence ellipses. The stress value of 0.1 indicates a good model fit. Panel B: RDA biplot illustrating relationships between species composition (indicated by the "+" sign), subplot (circles), and environmental variables (arrows). The length and direction of the arrows indicate the strength and influence of environmental factors on the composition of the species. Environmental variables include soil moisture (SM), soil nitrogen (SN), vapour pressure deficit (VPD), soil phosphorus (SP), and exchangeable calcium (SCa).

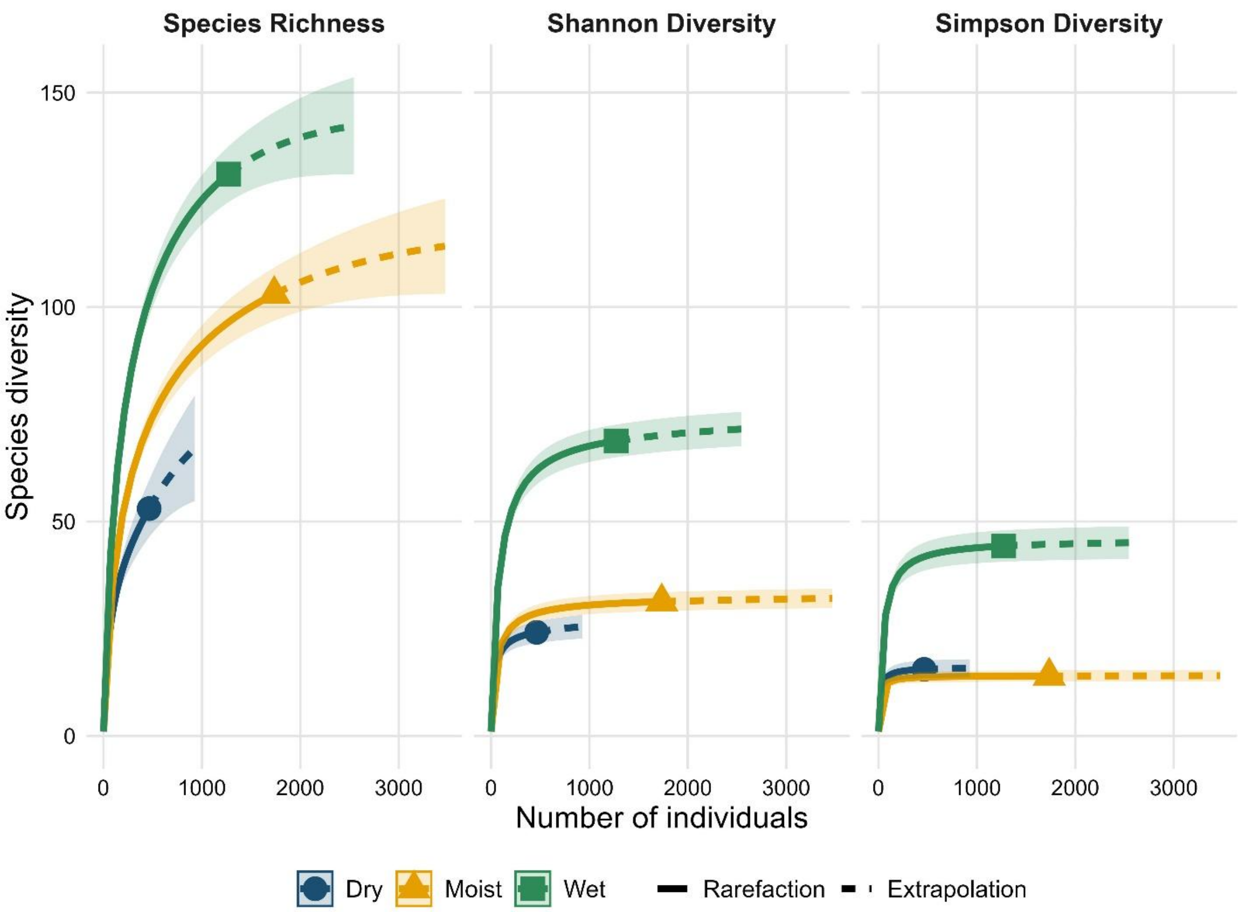

Figure 3: Individual-based rarefaction (solid lines) and extrapolation (dashed lines) curves by forest type for three Hill numbers: q=0 (richness), q=2 (Shannon diversity) and q=3 (Simpson diversity). The shaded areas represent 95% confidence intervals. Non-overlapping intervals indicate significant differences in diversity levels across types.

4.1.2 Diversity-climate relations

Species richness (Figure 4) and Shannon diversity measures (Figure S1.4) responded similarly to variations in environmental factors. Soil moisture was the strongest driver of community diversity, based on a comparison of univariate models fitted alternately with VPD, temperature, and soil moisture (Table 2). Soil moisture availability monotonically increased richness and diversity, while temperature and VPD negatively affected these parameters. The overall best-supported models, by AIC and R^2, included interaction terms (Table 2), suggesting that soil conditions modified the effects of temperature and VPD. Specifically, high soil moisture levels dampened the negative effects of VPD and temperature increases. However, the interaction terms were not significant (*p*>0.05).

Table 2: Summary of the regression results for separate models that estimated the effects of climate on variation in the measures of community diversity (Shannon and Richness) and the Conservation Value Index. Model covariates are dry season vapour pressure deficit (VPD), mean annual soil moisture (SM), mean annual temperature (MAT), and their interactions.

Model covariates	**AIC**	**ΔAIC**	***cR²***	***mR²***	**Rank**
Species Richness					
VPD	1105	22.17	0.74	0.435	6
MAT	1101.14	18.32	0.74	0.544	5
SM	1082.82	0	0.74	0.727	4
VPD + SM	1083.58	0.75	0.74	0.730	3
MAT + SM	1083.29	0.47	0.74	0.731	2
MAT + SM + MAT *x* SM	1084	1.18	0.742	0.736	1
VPD + SM + VPD *x* SM	1083.69	0.87	0.742	0.736	1
Shannon Diversity					
VPD	189.06	21.8	0.708	0.447	6
MAT	185.99	18.73	0.7	0.551	5
SM	170.96	3.7	0.692	0.66	4
VPD + SM	170.66	3.39	0.691	0.68	3
MAT + SM	170.21	2.94	0.691	0.683	2
MAT + SM + MAT *x* SM	167.67	0.41	0.692	0.680	1
VPD + SM + VPD *x* SM	167.26	0	0.693	0.677	1
Conservation Value Index					
VPD	1500.92	29.12	0.658	0.383	6
MAT	1499.44	27.64	0.638	0.470	5

Model covariates	**AIC**	**ΔAIC**	***cR²***	***mR²***	**Rank**
SM	1486.29	14.49	0.633	0.570	4
MAT + SM	1483.00	11.20	0.636	0.587	3
VPD + SM	1482.87	11.07	0.638	0.581	2
MAT + SM + MAT *x* SM	1473.03	1.23	0.639	0.588	1
VPD + SM + VPD *x* SM	1471.80	0	0.642	0.585	1

Notes: Shown are Akaike's Information Criterion (AIC), the difference between the AIC of a given model and the best model (ΔAIC), marginal R^2 (mR^2) representing the variance explained by fixed effects, and conditional R^2 (cR^2), accounting for both fixed and random effects. Rank denotes the model's importance based on AIC scores within each model series. Models with nearly equivalent AIC scores (i.e., ΔAIC ≤ 2) based on marginal R^2 values were secondarily ranked.

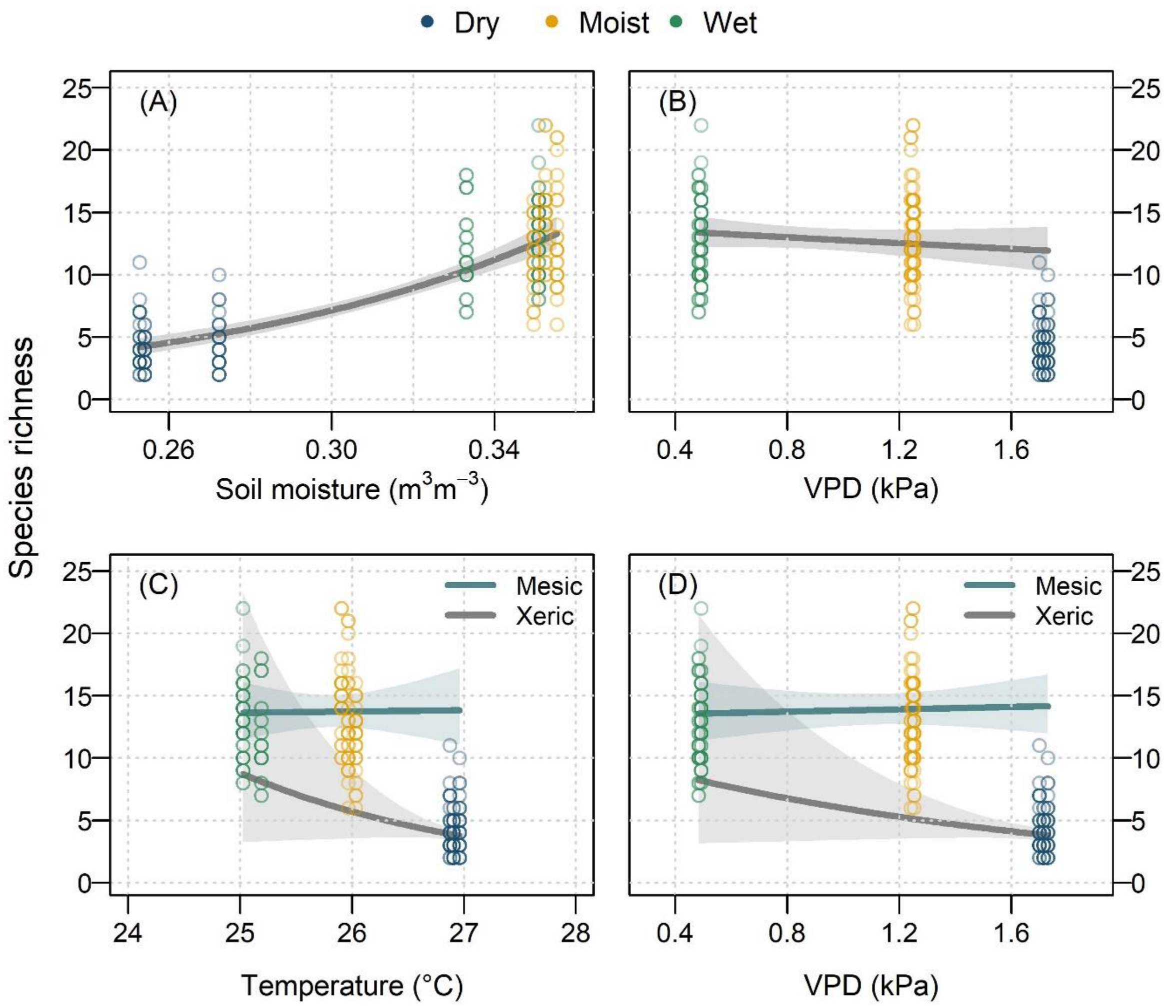

Figure 4: Estimated relationships from GLMMs between species richness and variation in mean annual soil moisture, dry season vapour pressure deficit (VPD) and mean annual temperature. Panel A shows the effect of soil moisture while controlling for VPD (fixed at the observed median level). Panel B shows the estimated association between richness and VPD for constant (median level) soil moisture. In panel C, temperature effects are shown for two levels of soil moisture: mesic conditions (blue curve) are the maximum observed moisture levels and xeric conditions (grey) are the minimum values in the dataset. Panel D shows the effects of VPD in mesic vs. xeric environments. Separate models were fitted with VPD and temperature variables, as VPD was highly correlated with temperature. Only the effects of soil moisture (A) and VPD (B) were statistically significant (p<0.05). Points are the model fitting

data for three forest types (dry, moist, and wet). Models were fitted with subplot data ($n = 225$). The shaded regions delineate 95% confidence intervals.

4.1.3 Conservation rankings and climatic associations

Out of the 242 species identified, 42 were classified as threatened or near threatened. The wet forest supported the highest number of threatened species (VU = 10, EN = 6) compared to the moist (VU=11, EN=1) and dry types (VU=4, EN=2; Figure 5A). The wet forest also had the highest Conservation Value Index (CVI = 156 ± 6.55) and a significantly higher rarity score compared to the moist and dry types (Figure 5B). The global threatened score was lowest in dry forests and did not differ significantly between moist and wet forests (Figure 5B).

Modelled relationships between the community-level Conservation Value Index (CVI) and climate demonstrate evidence of interactions. Specifically, in xeric soils, warming temperatures or increasing VPD were associated with higher CVI scores (Figure S1.5). The conditions of the mesic soil reversed these trends. However, the coefficients of the interaction terms were not statistically significant.

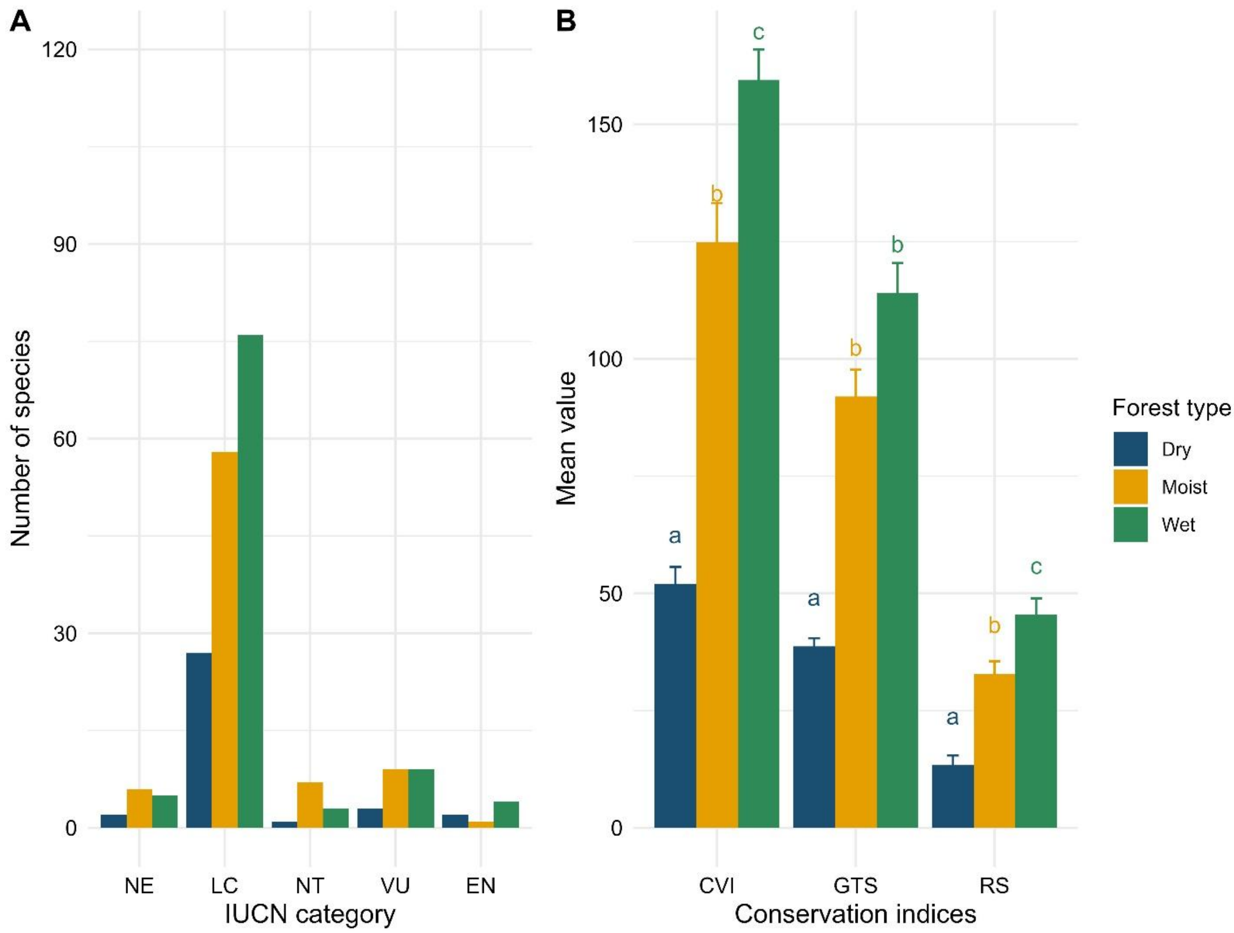

Figure 5: Distribution and conservation status of species for three forest types. (A) number of species based on their conservation status; (B) Conservation value index (CVI), Global Threatened score (GTS) and Rarity score (RS). EN, LC, NE, NT, and VU designate IUCN risk categories Endangered, Least Concern, Not Evaluated, Near Threatened, and Vulnerable, respectively.

4.2 Biomass growth responses to biotic and abiotic factors

4.2.1 Variation in aboveground biomass increment and environmental conditions

AGBI and environmental conditions differed markedly among the classified forest types (Figure 6). Dry season soil moisture was lowest in dry forests and did not differ between moist and wet forests (Figure 6A). Conversely, VPD was highest in dry forests and declined significantly along the gradient towards the wet coastal forests ($p < 0.001$, Figure 6B). Standing

AGB was similar in dry and moist forests but significantly higher in wet forests ($p < 0.001$, Figure 6C). AGBI was generally highest in moist forests, with lower increment rates observed in both wet and dry forests (Figure 6D).

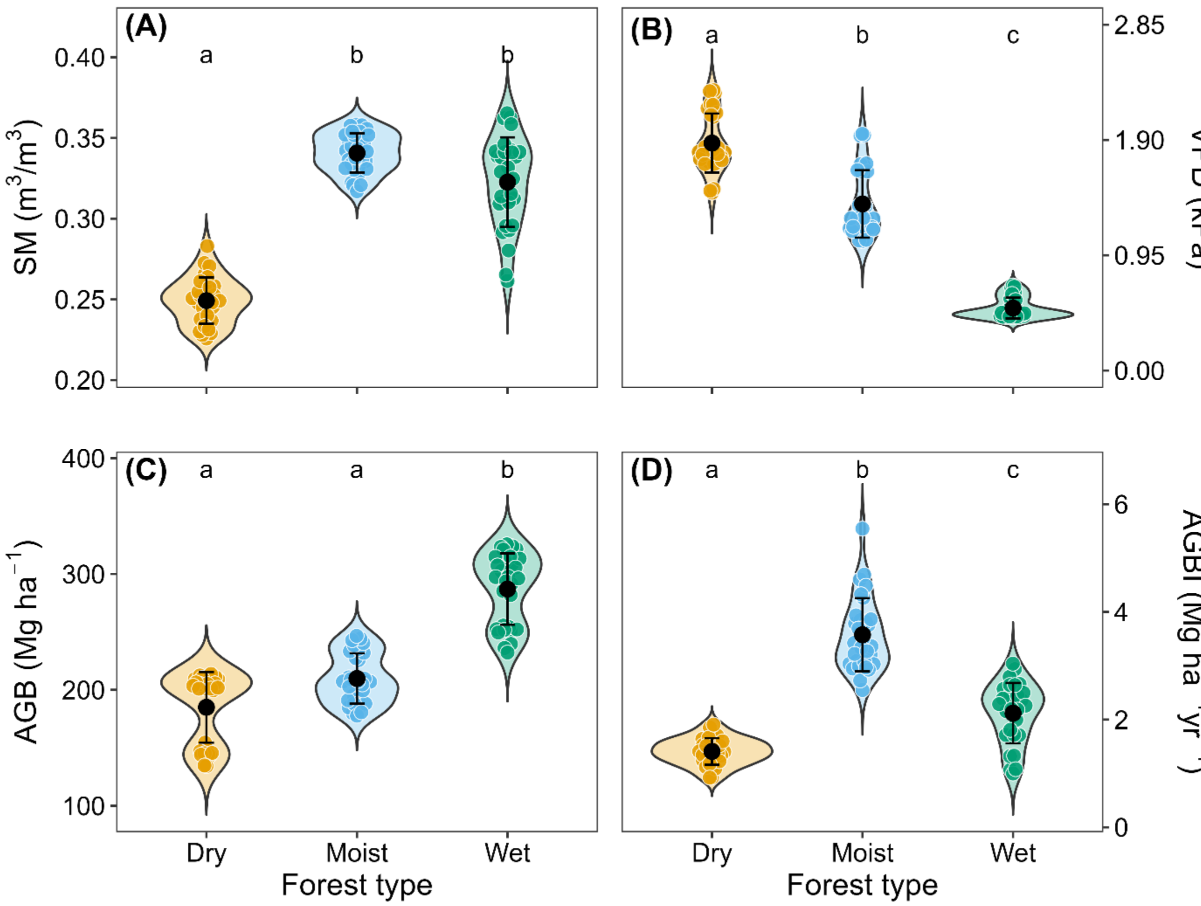

Figure 6: Variation in forest biomass and environmental variables across three forest types. Violin plots show the distribution of individual plot-year values (2012–2021) for (A) dry season soil moisture (SM), (B) dry season vapour pressure deficit (VPD), (C) aboveground biomass (AGB; standing stock recalculated annually), and (D) annual aboveground biomass increment (AGBI; annualised rate of biomass change). Coloured points indicate individual plot-year values, capturing interannual variability. Black points with error bars show model-estimated means ± 95% confidence intervals for each forest type. Different letters denote significant

differences among forest types based on linear mixed-effects models with post-hoc pairwise comparisons (*emmeans*) and the Bonferroni correction ($p < 0.05$).

4.2.2 Community-level responses of biomass growth to biotic and abiotic variables

Community-level AGBI was influenced by both structural diversity and the combined effects of soil moisture and VPD (Table S2.1). The best-fitting GAMM (AIC = 418.6; adjusted R^2 = 54.3) showed that structural diversity increased AGBI across forest types (Figure 7; Table S2.1). The joint effects of soil moisture and VPD varied markedly among forests (Figure 8). In the dry forest, although the interaction between soil moisture and VPD was significant ($F = 6.67$, $p < 0.001$), predicted growth remained uniformly low, exhibiting only minimal variation across the gradient (Figure 8A). In the moist forest, the interaction was more pronounced ($F = 24.97$, $p < 0.001$): growth was highest under high soil moisture and low VPD, and the reduction in growth under high VPD was partially mitigated by elevated soil moisture (Figure 8B). In the wet forest, the strongest interaction ($F = 48.98$, $p < 0.001$) was observed, with peak growth occurring at intermediate soil moisture and VPD levels, but declining at higher soil moisture, even when VPD remained low (Figure 8C).

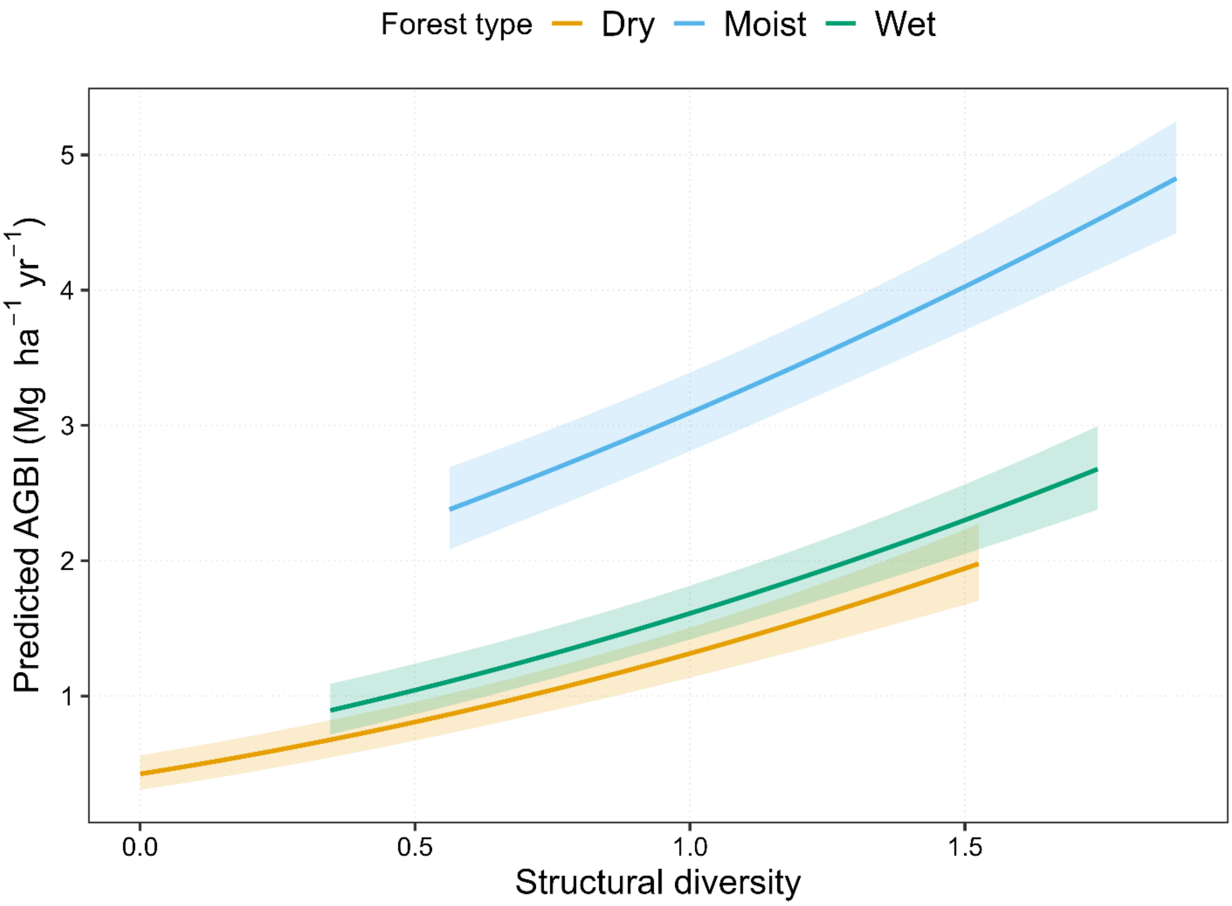

Figure 7: Partial effects of structural diversity on community-level aboveground biomass increment (AGBI; Mg ha^{-1} yr^{-1}) across dry, moist and wet forests. Predictions were derived from Generalised additive mixed-effect models (GAMMs), with soil moisture index and vapour pressure deficit held at their median values. Predicted AGBI values were back-transformed from the modelled sqrt (AGBI) scale. Shaded regions represent 95% confidence intervals.

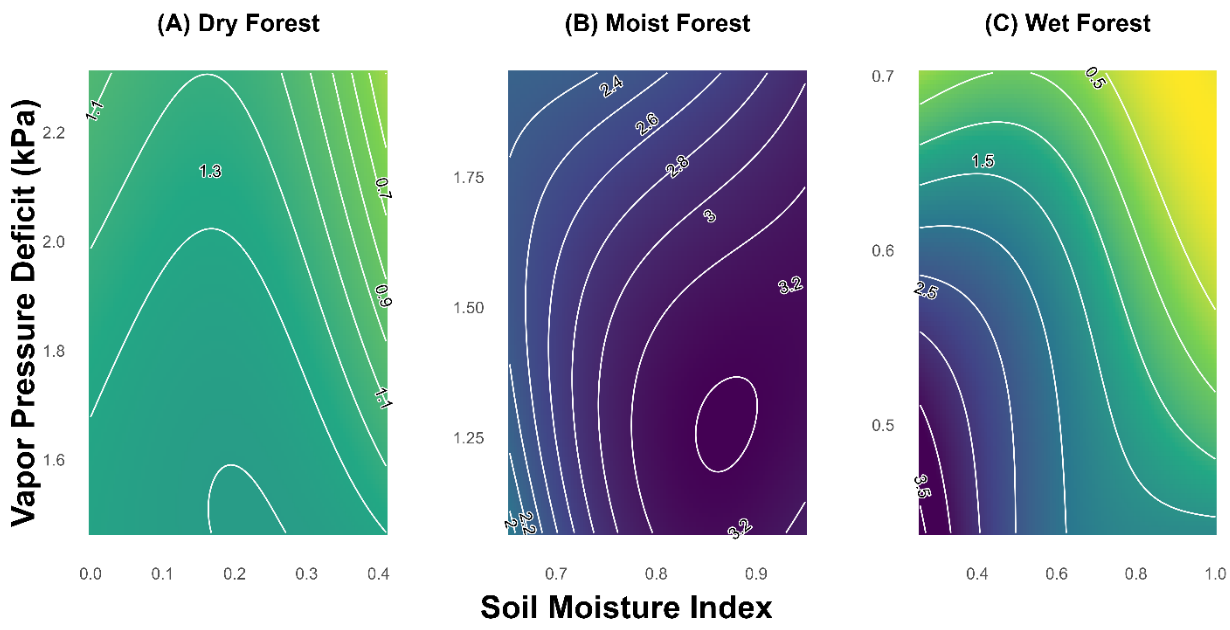

Figure 8: Model-estimated aboveground biomass increment (AGBI; Mg ha^{-1} yr^{-1}) at the community level as a function of the interaction between soil moisture and vapour pressure deficit across dry, moist, and wet forests. Soil moisture is expressed as a dimensionless index of below-ground water availability (Eq. 1). Interaction surfaces are predictions from the best-fitting generalised additive mixed-effects model (GAMM; $n = 2203$), with other covariates held at their median values. Predicted AGBI values were back-transformed from the modelled sqrt (AGBI) scale and plotted using a common colour scale gradient across panels, with lighter to darker colours indicating increasing AGBI. Contour lines represent predicted growth levels. Note that axes show the observed predictor ranges for each forest type; surfaces therefore reflect within-forest responses rather than directly comparable thresholds across forests.

4.2.3 Species-level responses to biotic and abiotic factors

Across the 15 tree species studied, aboveground biomass growth was best explained by models that incorporated tree size (DBH), neighbourhood competition, and the joint effects of soil moisture and VPD (Table S2.2). While DBH consistently emerged as a significant predictor in all models, the importance of environmental and competitive effects varied among species. The variance explained by the best-fitting model for each species ranged from 0.19 to 0.79 (Table S2.2). Estimated concurvity among model terms was low (< 0.5), indicating limited collinearity among predictors.

4.2.3.1 Tree size and competition effects

Predicted biomass growth increased with DBH across all focal species, with no evidence of declines at larger sizes (Figure 9). However, the shape and steepness of this relationship differed among taxa. Some species (e.g., *Heritiera utilis, Sterculia rhinopetala*, *Triplochiton scleroxylon*, *Protomegabaria macrophylla*, and *Nesogordonia papaverifera*) showed a strong monotonic increase in growth with DBH, while other species (e.g., *Celtis mildbraedii*, *Celtis zenkeri*, *Cynometra ananta* and *Erythrophleum suaveolens*) demonstrated more gradual growth across the DBH range.

Responses to neighbourhood competition also varied (Figure S3.1). Some species exhibited a potential for higher rates of biomass growth with increasing levels of neighbour crowding (e.g., *Carapa procera*, *Celtis zenkeri*, *Nesogordonia papaverifera*), while growth capacity in several other taxa (e.g., *Celtis mildbraedii*, *Protomegabaria macrophylla*, *Sterculia rhinopetala*, *Triplochiton scleroxylon, Sterculia tragacantha*, *Pouteria alnifolia*) declined with increasing competition. A few species, including *Heritiera utilis* and *Cynometra ananta* exhibited a hump-shaped response, with growth peaking at intermediate competition levels.

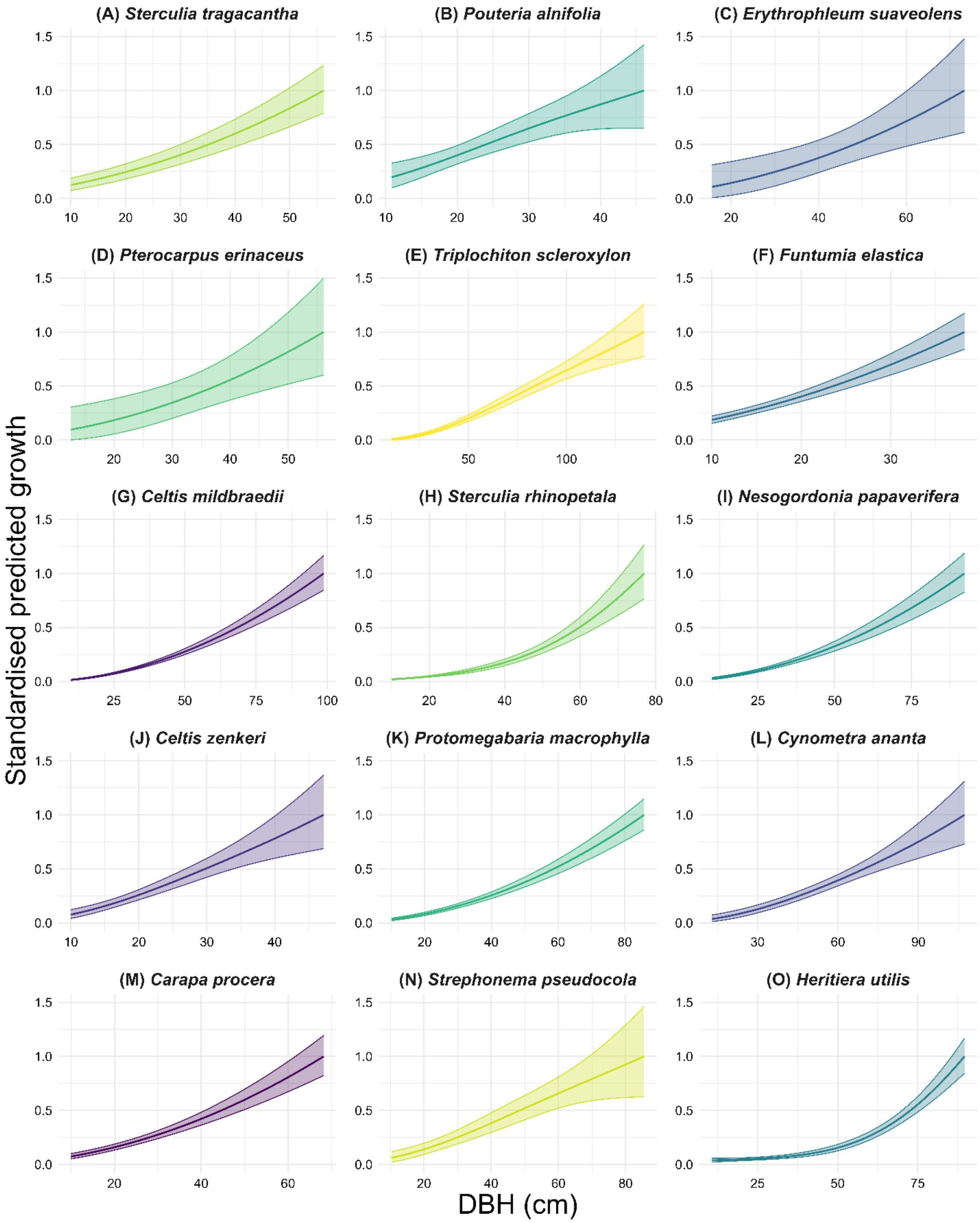

Figure 9: Partial effect of tree diameter at breast height (DBH) on predicted annual aboveground biomass growth at the individual tree scale for 15 tree species. Predictions are based on the best-fitting generalised additive models for each species, incorporating DBH, competition and environmental covariates. Shaded ribbons represent 95% confidence intervals.

All other predictors were held constant at their species-specific median values. Predicted growth estimates were standardised relative to each species' maximum value to allow comparison of response shape across species.

4.2.3.2 Species-specific responses to environmental interactions

The focal species showed distinct growth responses to the combined effects of VPD and soil moisture (Figure 10). Across all taxa, relative biomass growth increased with higher soil moisture and declined with rising VPD, but the magnitude and shape of these relationships varied among species. In the dry forest, species showed a wide range of drought response strategies (Panels A–D). *Erythrophleum suaveolens* was arguably the most tolerant of water limitation (Panel C), exhibiting a relatively high growth potential regardless of soil water levels or VPD. This species was only constrained under the joint effects of very high VPDs and saturated soils. *Pterocarpus erinaceus*, on the other hand, was extremely sensitive to the effects of water stress imposed by soil conditions and the atmosphere (Panel D). The two other dry forest species were mainly inhibited in environments where the effects of low soil water were amplified by high evaporative demand (Panels A, B).

Biomass production of the moist forest taxa was generally constrained when the effects of high VPD were intensified by low water availability, indicating that simultaneous atmospheric and soil water stress heightened growth limitations (Panels E–J). However, greater soil water supplies partially mitigated the negative effects of high VPD in some species (Panels E, F, H, I, J), although this compensatory effect was weak in others (Panel G). In the wet forest, species showed contrasting growth responses to the joint effects of soil moisture and VPD (Panels K–O). *Protomegabaria macrophylla* and *Strephonema pseudocola* exhibited maximum biomass production under low VPD combined with below-average soil moisture, with growth potential decreasing as either VPD or soil moisture increased (Panels K, N). In contrast, *Heritiera utilis* showed strong reductions under dry soils and high VPD, but growth improved consistently with rising soil moisture and remained relatively high even at elevated VPD (Panel O).

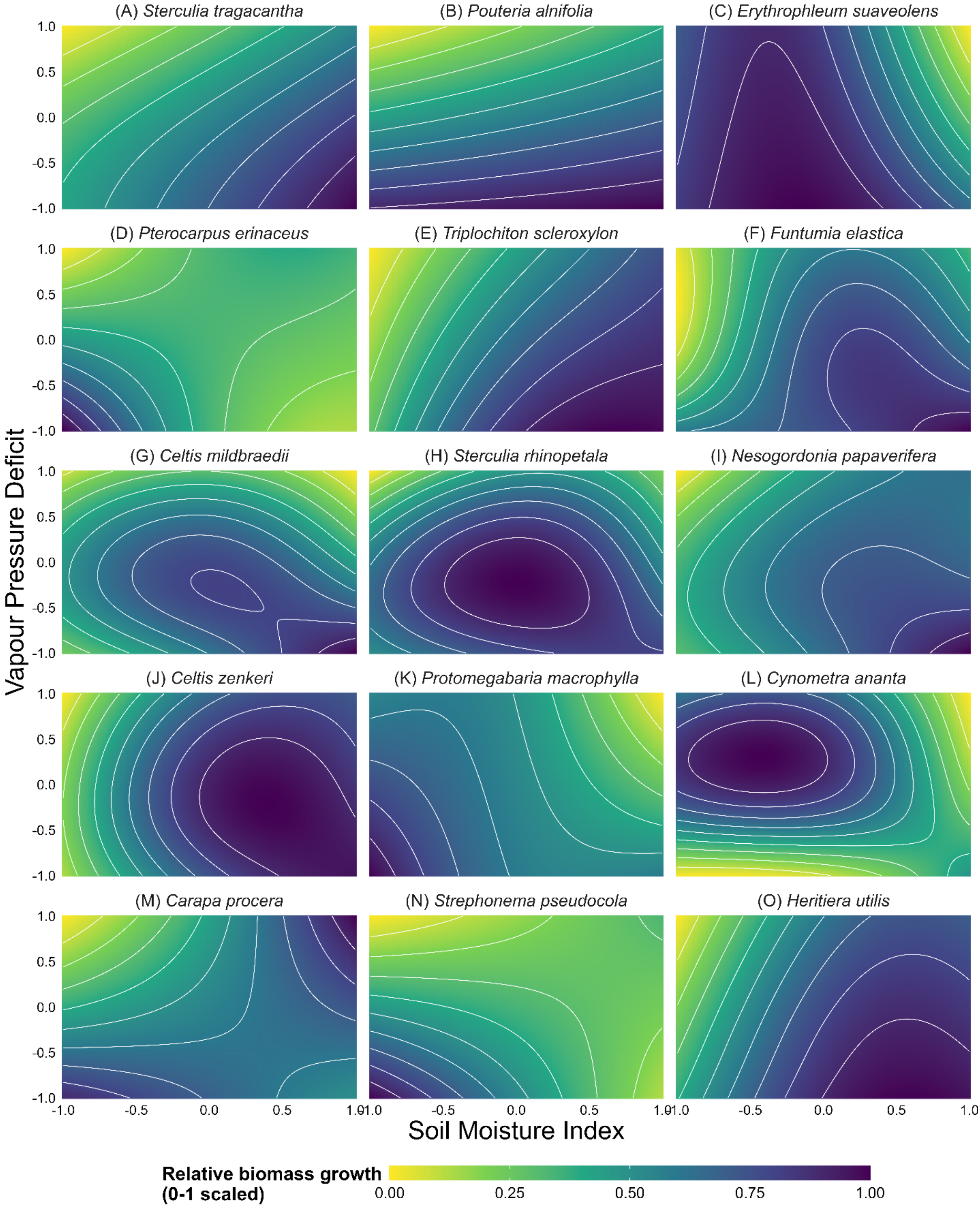

Figure 10: Interactive effects of dry season soil moisture index (SMI) and vapour pressure deficit (VPD) on predicted aboveground biomass growth for all focal species (A–O), estimated

using generalised additive mixed-effect models (GAMMs). Panels are grouped by forest type (dry: A–D; moist: E–J; wet: K–O). Predictions were generated across the standardised (z-score) ranges of SMI and VPD, with other covariates fixed at their median values. The colour gradient represents relative growth, rescaled to range between 0.0 (minimum) and 1.0 (maximum potential growth) within each species. Darker shades indicate higher growth, while lighter shades indicate lower growth. White contour lines show iso-growth curves.

4.3 Role of tree size, functional attributes and water availability in mediating competitive interactions

Seven alternative growth models were tested for the 15 most common tree species in the survey plots. The models explained 16–68% of observed growth variation, depending on species (Table 4; Figure S3.2). All models produced unbiased estimates of growth. Based on information theory, the best-supported models for all focal species accounted for the independent effects of target tree size and neighbour competition.

Table 3: Mean biological and environmental attributes of the 15 focal tree species (5th and 95th percentiles in brackets).

		* Forest type			Biological attribute					
Species (Acronym)	Family	Dry (%)	Moist (%)	Wet (%)	† Guild	‡ Leaf phenology	Wood density ($g\ cm^{-3}$)	Diameter (cm)	Neighbour density (trees ha^{-1})	Rainfall (mm yr^{-1})
Carapa procera (CARAP PROC)	Meliaceae	0	3.8	96.2	ST	E	0.604	14.8 (10.4, 58.3)	439 (212, 736)	2064 (1755, 2484)
Celtis mildbraedii (CELTI MILD)	Ulmaceae	0	100	0	ST	E	0.594	21.3 (11, 58.4)	594 (368, 835)	1238 (932, 1486)
Celtis zenkeri (CELTI ZENK)	Ulmaceae	0	100	0	NPLD	D	0.609	18.8 (11.1, 33.4)	707 (368, 905)	1238 (943, 1500)
Cynometra ananta (CYNOM ANAN)	Leguminosae	0	0	100	ST	E	0.830	51.8 (12.3, 72.2)	460 (297, 665)	2069 (1823, 2511)
Erythrophleum suaveolens (ERYTH SUAV)	Leguminosae	100	0	0	NPLD	D	0.873	41.7 (19.0, 69.1)	156 (71, 255)	1099 (855, 1426)
Funtumia elastica (FUNTU ELAS)	Apocynaceae	0	100	0	NPLD	D	0.424	14.2 (10.4, 25.7)	651 (354, 849)	1196 (943, 1500)
Heritiera utilis (HERIT UTIL)	Malvaceae	0	0	100	NPLD	E	0.480	20.7 (11.2, 71.8)	439 (293, 764)	2008 (1070, 2484)
Nesogordonia papaverifera (NESOG PAPA)	Sterculiaceae	0	100	0	ST	E	0.645	21.6 (11.6, 50.4)	622 (368, 863)	1217 (932, 1486)
Pouteria alnifolia (POUTE ALNI)	Sapotaceae	100	0	0	P	D	0.555	19.6 (11.9, 40.1)	226 (113, 354)	1078 (855, 1426)
Protomegabaria macrophylla (PROTO MACR)	Euphorbiaceae	0	0	100	ST	E	0.602	17.9 (10.9, 44.7)	439 (297, 693)	2064 (1823, 2484)
Pterocarpus erinaceus (PTERO ERIN)	Leguminosae	100	0	0	P	D	0.740	25.3 (12.6, 50.9)	184 (85, 325)	1140 (871, 1436)
Sterculia rhinopetala (STERC RHIN)	Sterculiaceae	0	100	0	NPLD	D	0.673	15.1 (10.6, 40.3)	665 (424, 877)	1238 (926, 1471)
Sterculia tragacantha (STERC TRAG)	Sterculiaceae	85.8	14.2	0	P	D	0.514	20.5 (11.6, 45.9)	283 (127, 736)	1140 (871, 1436)
Strephonema pseudocola (STREP PSEU)	Combretaceae	0	0	100	ST	E	0.633	27.4 (11, 58.0)	424 (297, 653)	2065 (1823, 2484)
Triplochiton scleroxylon (TRIPL SCLE)	Sterculiaceae	0	100	0	P	D	0.335	38.1 (12.7, 109.7)	608 (354, 874)	1238 (932, 1485)

Notes: * Dry, Moist and Wet show the proportional distribution (%) of trees by species across forest types. † Guild classes reflect shade tolerance: NPLD = non-pioneer light demanders; P = Pioneer species; ST = shade-tolerant (see Hawthorne, 1995). ‡ D and E denote deciduous and evergreen species, respectively. Diameter, neighbour density and rainfall are mean values with 5th and 95th percentiles in brackets.

Table 4: Model selection criteria based on AIC scores (penalised for model complexity). Shown are differences in the AIC of a candidate model (*i*) relative to the minimum AIC in a species-specific set of models ($\Delta_i = AIC_i - AIC_{min}$).

		ΔAIC for alternate models							Best model statistics		
Species	Sample size	Null	Size	Bigger tree	Neutral	Taxonomy	Guild	Density	‡NP	Bias	R^2
†*Protomegabaria macrophylla*	1162	1288.1	166.2	**0**	80.2	72.9	202.4	52.4	16	1.12	33.1
Strephonema pseudocola	478	543.5	40.3	**0**	28.1	21.3	14.4	30.2	12	1.04	27.4
†*Celtis mildbraedii*	2144	3449.4	155.9	106.3	118.6	22	**0**	75.1	22	1.08	54.1
Erythrophleum suaveolens	190	158.4	41.2	3	19.1	0	**0**	11.2	18	1.03	44.3
Sterculia rhinopetala	1444	1771.6	116.6	79.9	1.6	6.2	**0**	4.9	18	1.12	44.3
Sterculia tragacantha	984	444.8	131.3	85.6	14.9	4.7	**0**	19	21	0.99	24.7
Carapa procera	523	431.4	53.8	31.3	28.1	**0**	24.6	1.9	19	1.1	36.0
Celtis zenkeri	805	526.8	127.7	152	92.6	**0**	76.3	54.3	18	1.03	27.4
†*Cynometra ananta*	546	644.7	27	17.5	6.9	10.4	6.9	**0**	21	1.01	36.4
Funtumia elastica	3031	1479.7	434.7	365.8	262.4	158	110.8	**0**	17	0.98	17.5
†*Heritiera utilis*	515	916.5	155.8	55	21.5	26.1	8	**0**	24	1.19	63.8
†*Nesogordonia papaverifera*	876	928.4	111.5	54.4	53.7	30.3	38.4	**0**	21	1.02	43.5
Pouteria alnifolia	546	245.2	56	32.7	29.6	11.3	15.3	**0**	18	0.99	16.3
Pterocarpus erinaceus	236	320.1	43.2	4.4	4.1	10.7	10.9	**0**	16	0.97	40.6
†*Triplochiton scleroxylon*	585	1331	272	222.2	109	110.2	127.5	**0**	22	1.08	68.1

Notes: [†]Models account for differences in the height of diameter measurements (POM, see methods). Sample size refers to the model fitting datasets (trees × years). ΔAIC for the best model is zero (bolded). Covariates in alternate models: Null = fit with a single mean value, Size = neighbour diameter only, Bigger tree = competition index based on a simple count of larger neighbour trees, Neutral = equivalent competitors, Taxonomy = competitors classified by identity (3 classes: conspecifics, within family and others), Guild = competitors classified by shade tolerance (3 classes), Density = competitors classified by wood density (2 or 3 classes depending on focal species). [‡] NP is the number of model parameters. Bias is derived from the slope of observed vs predicted growth.

4.3.1 Effects of wood density and shade tolerance

The findings from this study generally reject the hypothesis of equivalent neighbour effects on competition dynamics. By model selection (Table 4), competition outcomes for most focal species (13 of 15) were influenced by biological attributes related to the life-history or resource allocation strategies of their neighbours, such as wood density, shade tolerance, or their taxonomic identity. Only two focal taxa (*Protomegabaria macrophylla* and *Strephonema pseudocola*) were insensitive to any of the modelled attributes of their neighbours, and only responded, in terms of a growth reduction, to the density of larger neighbour trees in their vicinity (within 15 m). The wood density of neighbouring trees modulated competitive interactions for almost half of the focal taxa (7 of 15), controlling for other factors (Table 4). In most cases, neighbour trees with comparatively dense wood were stronger competitors than neighbours with softer or lower wood density (Figure 11A and B). There were two exceptions, as *Nesogordonia papaverifera* and *Pouteria alnifolia* were relatively more sensitive to neighbours with low-density wood. Competition in four of the focal species was influenced by the shade tolerance ability of neighbours. Shade-tolerant neighbours were consistently stronger competitors relative to light-demanding species (pioneers, Figure 11C and D). Competition outcomes for the remaining two focal species were influenced by the taxonomy, but not the resource allocation strategies of the neighbours. For these focal taxa, conspecific neighbours were stronger competitors relative to trees from other species or families (Figure 11E and F).

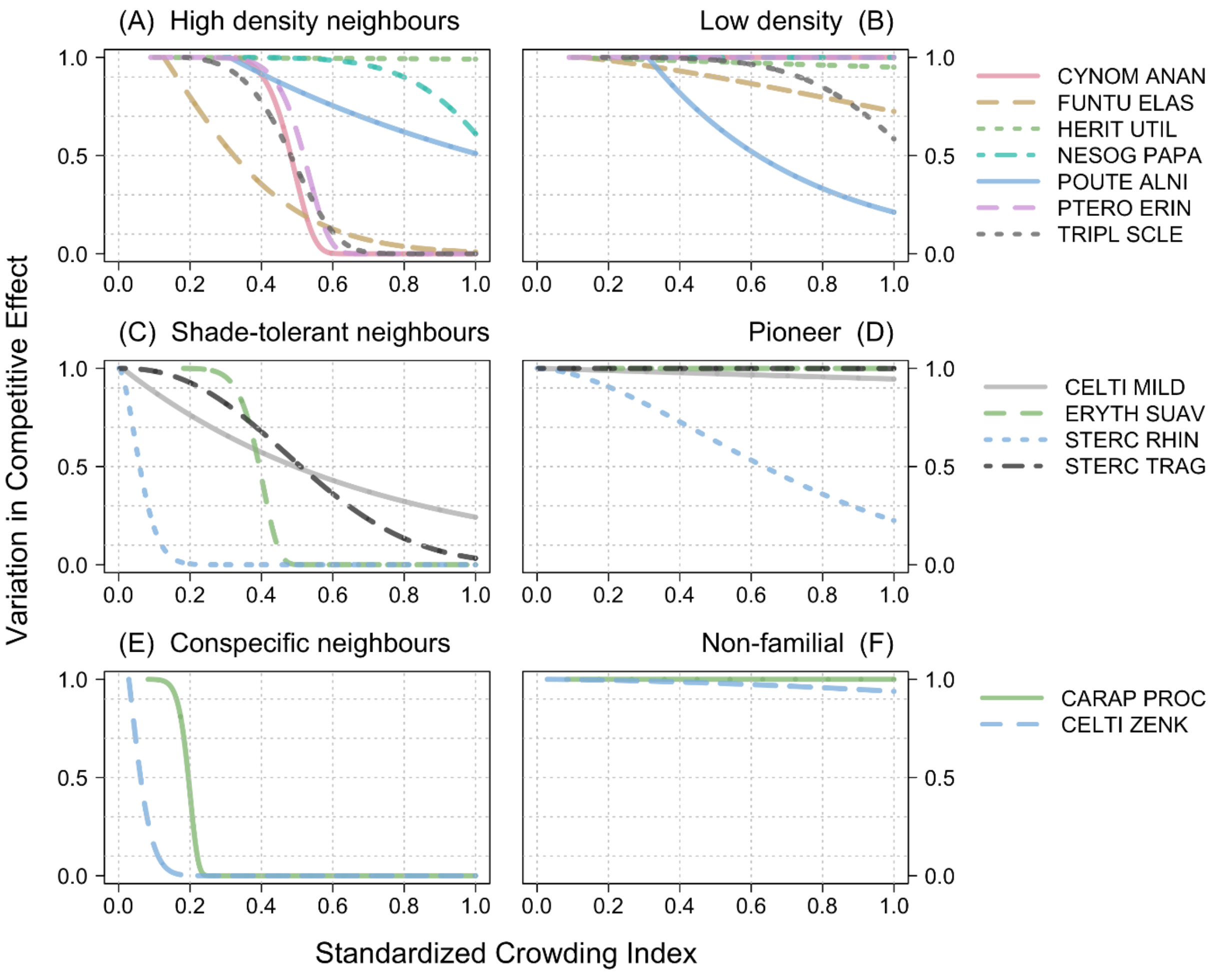

Figure 11: Predicted stem growth in a 30 cm tree for 13 focal species that were sensitive to the biological attributes (i.e. resource allocation strategies) or taxonomy of their neighbours. The best-supported species-specific models (Table 4) were used in these analyses. The response variable is the proportional reduction in maximum potential growth. A standardised crowding index accounts for observed variation in the configuration, density and biological attributes of the neighbouring trees. Growth reductions for each species were predicted under two alternate neighbourhood scenarios: (1) neighbours with dense vs. soft wood (A and B); (2) shade-tolerant vs. light-demanding neighbours (C and D); and (3) conspecific vs. neighbours from other families (E and F). Soil moisture was fixed at the observed mean level for a species.

4.3.2 Moisture, tree size and wood density interactions

Competitive outcomes were regulated by a composite of factors. The strength and shape of these relationships were highly species-specific. For some species (N = 6), moisture limitation independently amplified crowding effects from neighbours, controlling for tree size and trait variation. For example, for a constant density and configuration of neighbours (Crowding index, Eq. 27), potential growth in a 30 cm target tree was progressively reduced along a gradient of decreasing moisture supply and minimised in dense stands and xeric soils (Figure S3.3). Responses in a target tree to neighbourhood crowding effects also depended on tree size. For most focal species (N=9), 10 cm trees were more sensitive to increasing levels of crowding relative to 50 cm individuals, regardless of moisture availability or trait effects (Figure 12A vs. 12D and Figure 12C vs. 12F).

More generally, however, competitive outcomes were determined by the nonadditive effects of target tree size, levels of neighbourhood crowding, the resource allocation strategies of neighbours, and moisture conditions. For example, size-dependent variation in a target tree's response to crowding was modified by soil moisture supply. For most focal species (N=10), 10 cm target trees in xeric environments were substantially more sensitive to elevated crowding levels relative to 50 cm trees in mesic soils (Figure 12B vs. 12F). However, for a few species (e.g., *Sterculia tragacantha* and *Funtumia elastica*), 50 cm trees showed greater sensitivity to neighbourhood crowding than 10 cm trees under xeric conditions (Figure 12A vs Figure 12D). Notably, for these same species, larger trees in wetter conditions were more sensitive to crowding increases relative to smaller trees in xeric sites (Figure 12A vs. Figure 12F). Variations in plant strategies additionally mediated the shape of these relationships. Neighbours having attributes that enhanced their competitive ability (high wood density, shade tolerance, or conspecifics) magnified the negative effects of crowding on small trees in moisture-limited environments (Figure 12A vs. Figure 12F). Again, the shape and magnitude of these responses varied substantially among focal species.

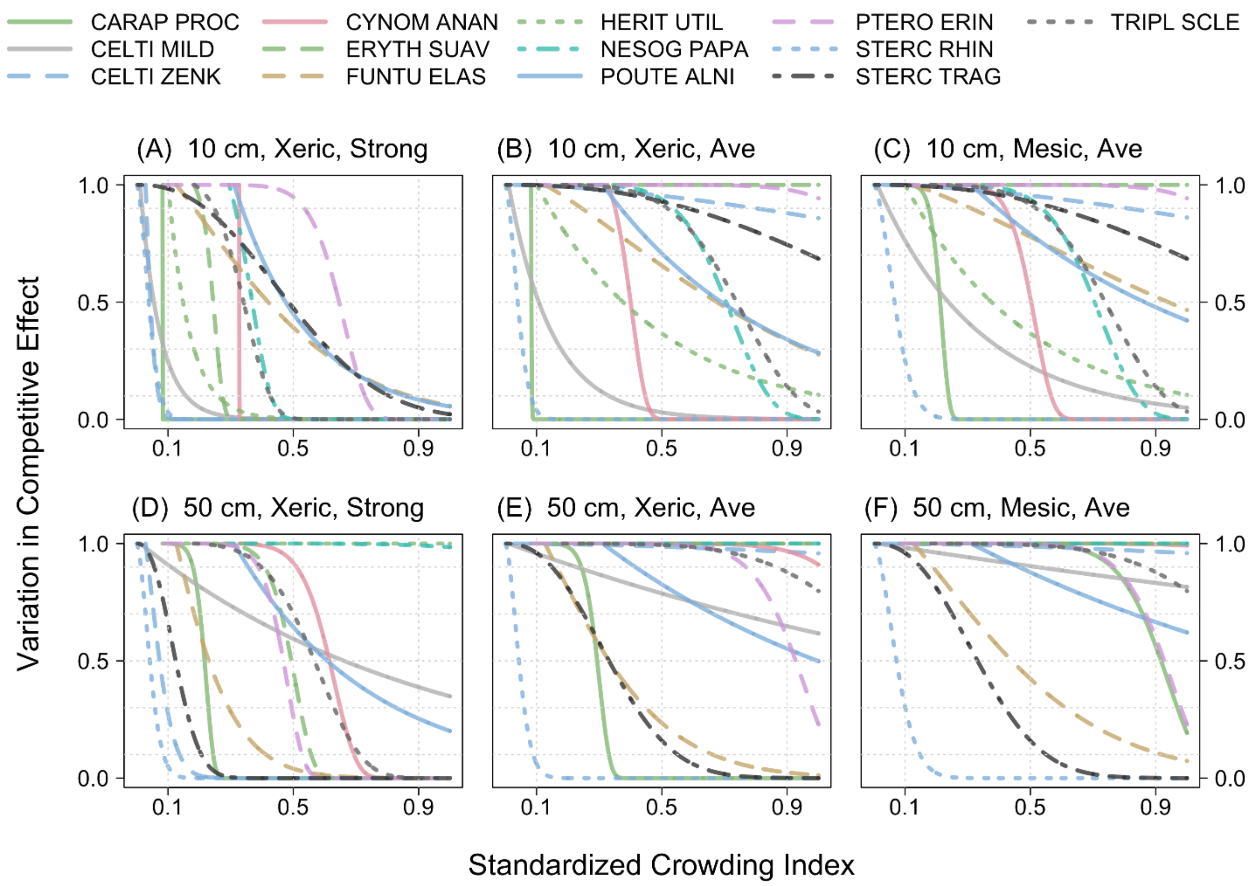

Figure 12: Predicted competitive effects on growth for 13 focal species as a function of tree size, soil moisture conditions and the allocation strategies of the neighbours. The competitive effect (y-axis), calculated from Eqs 25-28, represents the expected proportional reduction in maximum potential growth in a target tree (10 or 50 cm diameter) due to observed variation in the density and configuration of neighbour trees (crowding index) under three alternate soil moisture and neighbour trait scenarios: (1) xeric sites and strong competitors (A and D), (2) xeric sites and average strength competitors (B and E), and (3) mesic sites and average strength competitors (C and F). The crowding index (x-axis) was scaled by the maximum observed value for each species to facilitate comparisons among species. Moisture conditions were set using

percentiles: xeric and mesic were defined by the 5th and 95th percentiles of observed soil moisture. Competitor strength was set by trait level (e.g., average vs. high wood density class).

5. DISCUSSION

5.1 Drivers of floristic composition, diversity and conservation value

5.1.1 Community composition, diversity and environmental associations

The findings from this study revealed significant differences in species assemblages along the wet-to-dry forest gradient, underscoring the distinct ecological characteristics of each forest type (Figure 2A). The observed compositional patterns align with previous classifications of tree assemblages (Hall and Swaine, 1981), further emphasising the uniqueness of these communities. Notably, only two species were common to the three forest types, indicating that most tree taxa are confined to specific niches and may be sensitive to environmental changes. Variation in tree community composition was strongly driven by soil nutrients and climatic factors, consistent with findings from other tropical regions (Esquivel-Muelbert et al., 2018; Peguero et al., 2023). Nitrogen, phosphorus, calcium, soil moisture and VPD were key factors influencing species composition across the gradient, highlighting the importance of soil fertility and climatic conditions in structuring tropical forest communities. In the moist forest, soil moisture, calcium and phosphorus significantly influence species composition. The nutrient-rich and consistent moisture supply in this forest supports species assemblages by promoting growth, survival, and regeneration (Herms and Mattson, 1992). Calcium is essential for root development and nutrient transport, while phosphorus is critical for energy transfer, creating optimal conditions for species with varying nutrient demands (Gang et al., 2023; White, 1998). The combined influence of these nutrients and soil moisture facilitates niche differentiation, allowing various species to coexist by exploiting different resources or adapting to specific microhabitats (Tilman, 1982). Furthermore, higher nitrogen availability in the wet forest positively influenced species composition, underscoring its role in shaping community assembly (LeBauer and Treseder, 2008; Peña-Claros et al., 2012). These findings reinforce the importance of soil fertility in determining plant species distributions in Ghanaian tropical forests and further elucidate the role of edaphic factors in shaping species composition (Swaine, 1996).

Species diversity varied strongly among forest types, with higher levels observed in wet forests and a declining trend toward dry sites (Figure 3). These results suggest that climate is a central driver of species diversity. The marked differences in soil moisture, temperature, and VPD influenced the diversity potential across forest types. Species richness and Shannon diversity increased with soil moisture and declined with elevated VPD (Figure 4A, B & S1.4A, B), consistent with prior research identifying water limitation as a primary constraint on tree species diversity in tropical systems (Abbasi et al., 2022; Aguirre-Gutiérrez et al., 2020; Esquivel-Muelbert et al., 2019). Furthermore, this study provides evidence of feedback mechanisms between VPD and soil water storage. Specifically, in mesic soil environments, community richness and diversity were maintained regardless of temperature conditions or severity of VPD (Figure 4C, D & S1.4C, D). In contrast, in more xeric soils, richness and diversity were comparatively lower and were increasingly reduced by warming trends or a drying atmosphere. These findings support the hypothesis that soil water storage may serve as a resource that ameliorates hydraulic stresses in trees during periods of low humidity and high evaporative demand, thus promoting plant survival (Liu et al., 2020).

The potential moderating effect of below-ground resources on the impacts of atmospheric droughts has implications for the resilience of communities in the face of climate change. Although dry forests are associated with lower biodiversity levels relative to wet forests, they are often characterised by a prevalence of drought-resistant taxa (Aguirre-Gutiérrez et al., 2019). The results of this study similarly suggest that dry community species are tolerant of seasonally high VPD (Figure 2B). Functional traits, such as narrow vessel conduits that are resistant to cavitation or active stomatal regulation to limit evaporative water loss from leaves (Tyree and Sperry, 1989), are most commonly associated with drought tolerance and a consequent stability of communities in dry environments (Fauset et al., 2012). However, fitted models suggest that soil water effects may enhance the resilience of wet and moist forests, where high precipitation inputs contribute to elevated water storage (Table 2). Given the non-significant interaction terms ($p > 0.05$) in the model due to the limited sample size, further large-scale studies are necessary to corroborate these findings and explore the complex dynamics between climate factors and forest community diversity.

5.1.2 Conservation rankings and climate associations

The presence of globally threatened and near-threatened species across forest types accentuates the conservation importance of these ecosystems. This study provides evidence that climate influences the viability of vulnerable taxa. Models indicate that the number of at-risk species, quantified by the Conservation Value Index (CVI), was jointly affected by VPD, soil water, and temperature. Notably, CVI scores increased with rising temperatures or elevated evaporative demand, particularly when soil water storage was low (Figure S1.5 A-B). This suggests that under conditions of reduced moisture availability, warming temperatures contribute to a higher incidence of vulnerable species. In contrast, high soil water mitigated the negative effects of other climate stressors, decreasing the number of vulnerable taxa. The confidence intervals around these modelled relationships were wide, reflecting uncertainty in model outcomes and a need for additional research. Nevertheless, our results suggest that the impacts of above and below-ground factors have the potential to non-additively influence the viability and local extinction risk of species.

The potentially moderating effect of soil water storage on climate stress suggests that high-rainfall environments might be associated with fewer vulnerable species. However, the datasets show that the wet and moist forests contained more at-risk species than dry types (Figure 5A). The precise driver of these patterns is unclear. Low soil nutrient availability may be hypothesised to negatively affect plant function and species fitness (John et al., 2007), which could lead to a higher concentration of endangered species. Although nutrient levels were low in wet forests, presumably due to high leaching rates, nutrient supplies were greater in moist forests than in other types (Table 2). Therefore, the underlying factors driving these patterns require further study.

5.2 Biomass growth responses to biotic and abiotic factors

5.2.1 Community-level responses of aboveground biomass increment to biotic and abiotic variables

Both aboveground standing biomass and biomass production rates exhibited contrasting patterns across forest types. The steep climatic gradient of the study area likely imposes varying levels of physiological constraints on biomass accumulation, consistent with classic water limitation theory in tropical forests (Givnish, 1999). The magnitude of aboveground biomass stocks was similar in moist and dry forests, but substantially higher in the wet forest, suggesting that rainfall and humidity may mediate these patterns (Moore et al., 2018). However, biomass growth was highest in the moist forest, indicating that productivity does not scale linearly with biomass stock or total water supply. This suggests that the intermediate moisture conditions in moist forests optimise growth by balancing resource availability and stress. These conditions support more dynamic biomass accumulation than in wet forests, where dense canopies and high biomass may limit growth through self-shading and density-dependent effects. Productivity is also reduced in dry forests, where water limitation constrains growth. The results obtained in this study align with recent research showing that forest productivity and carbon dynamics can vary substantially along environmental gradients as a consequence of complex interactions between abiotic conditions, resource supply and the biological attributes of the plant communities (Matsuo et al., 2025; Moore et al., 2018; Poorter et al., 2017; Zhang-Zheng et al., 2024).

Community-level responses to soil moisture and VPD further highlight the contrasting growth dynamics across forest types. In the dry forest, predicted growth remained uniformly low across the full range of soil moisture and VPD, showing only modest declines under higher VPD. High VPDs increase evaporative demand, which induces stomatal closure to minimise water loss and to reduce the risk of hydraulic failure (Grossiord et al., 2020; Sulman et al., 2016). This response limits photosynthetic production and the carbohydrates needed to support growth. Plant water stress (low water potentials in plant tissues) due to excessive transpiration fluxes through leaves can also affect growth processes directly by limiting cellular enlargement, which is strongly dependent on adequate turgor pressure (Fatichi et al., 2016; Peters et al., 2023). Literature evidence suggests that cambial growth is more sensitive to water shortages relative to photosynthetic processes (Fatichi et al., 2014; Herms and Mattson, 1992). Together, these mechanisms may explain the strong levels of growth suppression observed in dry forests, consistent with broader evidence from other studies showing that increasing VPD reduces tropical forest productivity and pushes trees closer to hydraulic thresholds beyond which plant performance is compromised (Allen et al., 2017; Novick et al., 2016; Yuan et al., 2019).

In the moist forest, biomass growth was less sensitive to VPD, suggesting that higher baseline soil water availability in this community partially buffers the effects of atmospheric demand (Figure 8B). Sufficient water supply reduces hydraulic resistance within the soil-plant continuum, supporting stomatal conductance and photosynthesis under moderate atmospheric stress (Konings and Gentine, 2017; McDowell et al., 2020). Additionally, higher levels of species richness and functional diversity may contribute to a stabilisation of productivity, as coexisting species likely differ in their sensitivity to drought and strategies of water use (Aguirre-Gutiérrez et al., 2020). These factors likely explain why the moist forest showed the highest biomass growth despite having similar biomass levels relative to the dry forest. Nonetheless, extreme VPD or prolonged drought could constrain biomass accumulation by amplifying the synergistic effects of soil water deficits and atmospheric evaporative demand (Liu et al., 2020; Wang et al., 2025). These findings align with prior studies demonstrating that growth sensitivity to VPD is modulated by soil moisture availability (Sulman et al., 2016; Wen et al., 2023).

The wet forest showed the highest growth under intermediate soil moisture and low-to-moderate VPD, showing that moderate levels of soil drying can enhance productivity by reducing the negative effects of saturated or waterlogged soils in these high rainfall environments. Growth declined sharply under high VPD, even when soil moisture was non-limiting, reflecting the strong constraints of atmospheric drought (Grossiord et al., 2020; Novick et al., 2016). Excessive soil moisture (waterlogging) may induce oxygen limitation in the rhizosphere, limiting root respiration and nutrient uptake (Jackson and Colmer, 2005; Kozlowski and Pallardy, 1997). These patterns indicate that while the wet forests may benefit from moderate amounts of drying, they remain highly vulnerable to both intensifying atmospheric drought and prolonged soil saturation, as expected under scenarios of future climate change (Novick et al., 2016; Phillips et al., 2009).

Structural diversity was also consistently associated with increased biomass growth across all forest types, underscoring the important role of architectural heterogeneity. Structurally complex stands improve light interception across vertical and horizontal strata, reduce competition, and facilitate complementary use of water and nutrients (Dănescu et al., 2016; Sapijanskas et al., 2014). In the moist forest, where structural diversity was highest and environmental stress moderate, these mechanisms allowed trees to exploit available resources, resulting in the strongest positive effects on biomass growth. Empirical evidence across tropical and temperate forest regions corroborates these findings, showing that structural diversity often explains variation in aboveground biomass and growth potential (Mensah et al., 2023; Ouyang et al., 2021; Skiadaresis et al., 2025).

5.2.2 Species-level responses of biomass growth to tree size and competition

The results from this study demonstrate that tree size is a strong predictor of aboveground biomass growth, with the strength and curvature of this relationship varying among species (Figure 9). Across all taxa, growth increased monotonically with DBH, with no evidence of a threshold response at large stem sizes, at least within the range of the model-fitting datasets. For example, some species (e.g., *Heritiera utilis*, *Triplochiton scleroxylon*, *Sterculia rhinopetala*) exhibited steeply accelerating growth trajectories, whereas *Celtis zenkerii* and *Funtumia elastica* displayed more modest, approximately linear increases in growth with size. These differences align with the divergent functional strategies of taxa, highlighting strong links between demographic performance and life-history trade-offs. The strong growth acceleration of pioneer species with soft wood (e.g., *Triplochiton scleroxylon*) likely reflects resource strategies that promote rapid carbon gain in high-light environments. High-density, shade-tolerant species (e.g., *Strephonema pseudocola*) exhibited more gradual growth increases with stem size, aligning with conservative resource-use strategies that prioritise structural support and longevity over rapid biomass accumulation (Poorter et al., 2010). However, other species deviated from these expectations: *Cynometra ananta*, a dense wooded, shade-tolerant species, displayed accelerating growth, while *Pouteria alnifolia*, a pioneer, grew more conservatively. These anomalies emphasise that wood density and functional classification capture part of the variation in size-growth relationships, but additional traits, such as crown architecture, leaf economics, and rooting depth, may further shape growth responses (Herault et al., 2011; Lohbeck et al., 2015; Poorter et al., 2014, 2018). Future studies linking demographic patterns with these traits will help clarify the mechanisms underlying these interspecific differences, as suggested by multi-trait frameworks (Kunstler et al., 2016; Markesteijn et al., 2011; Poorter et al., 2018).

The observed responses of large trees reinforce their role as critical contributors to forest productivity (Lutz et al., 2018; Stephenson et al., 2014). Ontogenetic shifts in resource allocation likely drive this pattern: small understorey trees prioritise height growth to access light, while larger canopy trees benefit from increased light availability, facilitating greater investment in diameter and biomass growth (Newbery and Ridsdale, 2016; Rozendaal and Zuidema, 2011). It is noted that evidence for a unimodal response of growth to size was not detected, although such a pattern has been reported elsewhere (Forrester, 2021; Weiner and Thomas, 2001). A more extensive dataset that captures the dynamics of a larger range of tree sizes may be needed to uncover thresholds or performance peaks in these species.

Responses to neighbourhood competition were highly species-specific (Figure S2.2). Some species maintained growth under increasing levels of crowding, suggesting either a tolerance of competition or the presence of facilitative interactions that are potentially mediated by trait complementarity (Briddon et al., 2025; Brooker et al., 2008). Other species exhibited declining growth with increasing competition, consistent with classical theories of resource limitation (Tilman, 1982). A subset of species (*Heritiera utilis*, *Cynometra ananta*) displayed hump-shaped responses, with growth peaking at intermediate competition before declining. Such patterns suggest a balance between facilitative and inhibitory processes, whereby moderate neighbour densities reduce stress, but higher crowding levels intensify resource limitation (Bertness and Callaway, 1994; Maestre et al., 2009). These findings suggest that aboveground biomass growth is shaped by divergent life-history and resource-use strategies among taxa that differentially mediate size and competitive effects, underscoring the importance of trait diversity for sustaining forest productivity under changing environmental conditions.

5.2.3 Species-specific responses to environmental interactions

Species-level growth responses to the interactive effects of soil moisture and VPD were individualistic, reflecting variation in water sensitivity and ecological strategies. These patterns support our hypothesis that VPD broadly limits growth, but its effects are modulated by soil water availability in species-specific ways. In the dry forest, species-specific responses revealed contrasting drought strategies among dominant taxa, likely contributing to the overall growth suppression observed at the community level. The dry forest species were, in general, tolerant of low soil water availability, in terms of biomass growth (Figure 10A-D), but responded differentially to the combined effects of variation in soil water supply and atmospheric moisture demand. For example, *Erythrophleum suaveolens* was tolerant of both low soil water and high VPD (Figure 10C), while *Sterculia tragacantha* and *Pouteria alnifolia* maintained a positive growth capacity only when high VPDs were slightly buffered by high soil water content (Figure 10A-B). *Pterocarpus erinaceus* was particularly sensitive to above-average soil water supply, irrespective of atmospheric conditions (Figure 10D). These differences in the growth performance of species are consistent with ecological theory that predicts hydraulic trade-offs between drought tolerance and water-use efficiency (Anderegg et al., 2018; Martínez-Vilalta and Garcia-Forner, 2017). Drought-tolerant species may sustain growth under moderate soil moisture deficits through conservative water use and enhanced levels of hydraulic safety, whereas less stress-tolerant species maximise growth under favourable moisture conditions but are more sensitive to resource shortages (Blackman et al., 2019; Chen et al., 2022; de Souza et al., 2020). These contrasting strategies help explain why some species, especially those with conservative life-history strategies, can maintain positive rates of biomass accumulation despite substantial water limitations.

In the moist forest communities, species exhibited comparatively uniform responses to variation in water supply and demand. In general, most species exhibited maximum growth performance under conditions of average, or in many cases, above-average soil moisture content (Figure 10E-J). High VPDs generally reduced growth potential, particularly when soil water availability was below the prevailing average level. Moist forest species differed in the extent to which soil water can buffer the negative effects of high atmospheric demand. The observed patterns align with literature evidence that elevated VPD generally leads to stomatal closure to reduce conductance and water loss to the atmosphere, but this subsequently inhibits photosynthetic carbon gain. The degree to which the behaviour of leaf stomata is regulated is known to vary among species (Grossiord et al., 2020; Novick et al., 2016). These physiological differences among species may buffer whole communities to climatic stress and promote a maintenance of biodiversity and function, whereby drought-resilient taxa sustain productivity under elevated VPD, while more sensitive species maintain performance only when resource supplies are not strongly limiting (Yachi and Loreau, 1999). However, recent trait-based research indicates that prolonged increases in VPD can also alter hydraulic functioning and selectively favour species with attributes that facilitate a tolerance of high levels of evaporative demand (Aguirre-Gutiérrez et al., 2025b; Zhang-Zheng et al., 2025). Over time, such environmental filtering may shift community composition toward drought-tolerant assemblages, with implications for the continuity of forest structure and function across tropical resource gradients (Aguirre-Gutiérrez et al., 2025a, 2019; Fauset et al., 2012).

Wet forest taxa also demonstrated contrasting biomass responses to the combined gradients of soil moisture and VPD, again reflecting diverse hydraulic strategies and a differential tolerance to atmospheric and soil water stress. Several species showed peak biomass accumulation at below-average soil water levels under low VPD, indicating a sensitivity to saturated soil conditions and dependence on well-aerated substrates that support root function and metabolic activity (Figure 10K, M, N). These responses are consistent with research showing that species are adapted or acclimated to microhabitats experiencing periodic drying within otherwise wet landscapes, where short-term declines in soil moisture alleviate chronic hypoxia and improve belowground plant functioning (Jackson and Colmer, 2005; McDowell et al., 2008). The pronounced decline in biomass growth at elevated VPD for some species further indicates a hydraulically conservative strategy, where stomatal closure limits carbon assimilation to maintain xylem safety under increasing atmospheric demand (Choat et al., 2012; Grossiord et al., 2020; McDowell et al., 2008). In contrast, above-average below-ground moisture content buffered the performance of *Heritiera utilis* to the constraints imposed by rising VPDs. This pattern suggests that *H. utilis* is somewhat uniquely adapted to wetter microsites and can sustain hydraulic transport function under high atmospheric evaporative demand when soil water is not limiting.

Together, these species-level patterns across forest types show that variation in VPD and soil moisture interactively regulates the growth capacity of trees, yet taxa differ markedly in their sensitivity to associated stresses. Future studies integrating growth dynamics with functional traits, such as stomatal sensitivity, hydraulic conductivity, rooting depth, and turgor maintenance, will be crucial in elucidating the mechanisms driving divergent life-history strategies. Such a mechanistic understanding will help predict how the expected increases in the frequency and intensity of atmospheric and soil drought may affect the organisation, structure and carbon cycles of tropical communities.

5.3 Role of tree size, functional attributes and water availability in mediating competitive interactions

5.3.1 Effects of wood density and shade tolerance

This study highlights the importance of functional strategy divergence among species and the role of ecological context in shaping neighbourhood processes. Consistent with previous studies in tropical forests (Fortunel et al., 2016; Rozendaal et al., 2020), species with a higher wood density exert stronger competitive effects relative to taxa with comparatively soft wood (Figure 11A). The competitive advantage associated with high wood densities may be attributed to a conservative resource-use strategy (Chave et al., 2009; Kunstler et al., 2016; Lasky et al., 2014). Species with dense wood typically have a reduced innate growth potential, allocating a greater proportion of their resources to structural support and defence functions (Chave et al., 2009; Poorter et al., 2008; Rüger et al., 2012). This allocation strategy enhances their ability to withstand mechanical damage, herbivory and other biotic pressures, while also improving tolerance to resource limitation (Kitajima and Poorter, 2010; Poorter et al., 2014).

In particular, for most focal species, high wood density confers strong competitive advantages under conditions of low water availability (Figure 12A & B and 12D & E). In general, despite variation among taxa, tree species with dense wood have a stress-resistant hydraulic architecture characterised by comparatively narrow xylem vessels (Sperry et al., 2006). Smaller vessels, in terms of both cross-sectional area and length, have a lower transport capacity but are considered to be more resistant to drought-associated low water potentials that can cause wall collapse and dysfunction (Chave et al., 2009; Markesteijn et al., 2011; Markesteijn and Poorter, 2009; Santiago et al., 2018). In contrast, species characterised by a wood structure that is relatively less dense may have wider and longer vessel conduits, which facilitate a greater transport capacity, but are concurrently more vulnerable to embolism and loss of function under water stress (Hacke et al., 2001). Thus, in xeric conditions, this trade-off can favour species with dense wood and a stable xylem architecture, as hydraulic safety facilitates a continuity of water supply to support essential physiological functions, including resource allocation to growth processes (Chen et al., 2019; De Guzman et al., 2021).

However, some studies have shown that wood density, as a species trait, is not always a reliable predictor of competitive ability (Fajardo, 2016), also consistent with our results (Figure 11E & F). Wood density variation within species, driven by divergent adaptations to specific ecological niches (Swenson and Enquist, 2007), may obfuscate the relevance of this trait as a predictor of competitive ability. While wood density is often correlated with hydraulic traits linked to drought resistance, it does not capture the full range of strategies species use to survive in competitive environments. For instance, species with similar wood density may exhibit different drought responses due to variations in vessel size, pit membrane properties, and water storage capacity (Delzon et al., 2010; Wheeler et al., 2005). Some species compensate for low embolism resistance through high water storage capacity, buffering against temporary water deficits (Meinzer et al., 2008; Pineda-García et al., 2013). Additionally, the relatively weak evidence for a universal relationship between xylem efficiency and safety identified in a prior meta-analysis suggests that wood density alone may not consistently determine species' competitive advantage in all environmental contexts (Gleason et al., 2016).

For a minority of species, a capacity for shade tolerance was more important than wood density as a predictor of competitive outcomes. Our results demonstrate that shade-tolerant neighbours exert a stronger competitive effect on focal species relative to pioneer species (Figure 11C & D), corroborating previous studies (Kunstler et al., 2016; Uriarte et al., 2004b). Shade-tolerant species typically invest in traits such as high specific leaf area, which improves light capture efficiency and reduces respiration costs, thereby enhancing photosynthetic performance and net carbon gain under low-light conditions (Chave et al., 2009; Poorter et al., 2008). Additionally, these species allocate more resources towards structural support, promoting long-term persistence and eventual canopy dominance. Consequently, they create a deeper shade and competitively suppress pioneer species, which depend strongly on high light availability for growth (Hu et al., 2020; Rahman et al., 2021). While wood density and shade tolerance were generally stronger predictors of neighbour effects, two focal species deviated from this pattern. *Protomegabaria macrophylla* and *Strephonema pseudocola*, both shade-tolerant evergreens found in wet forests, were insensitive to these traits and responded only to the size of their neighbours. In environments with persistently low light and relatively stable conditions, trait-mediated interactions may be less ecologically relevant (Kraft et al., 2015). For these species, growth appears to be more constrained by physical suppression, such as crowding from large neighbours, than by variation in neighbour function (Uriarte et al., 2004b). This suggests that under conditions of light limitation and low trait contrast, competitive effects may be governed by the spatial structure of stands and the proximity of large neighbours, rather than by functional divergence.

The stronger effects of conspecific neighbours on focal species identified in this study can be explained by their shared occupancy of ecological niches (Guo et al., 2021). This observation aligns with the resource partitioning hypothesis, which predicts more intense competition among conspecific individuals due to matching resource dependency (Lebrija-Trejos et al., 2014; Liu et al., 2021, 2016; Tilman, 1982). As conspecifics share similar growth requirements and phenotypic traits, they are more prone to experience direct competition for limited critical resources, leading to more intense intraspecific competition compared to heterospecifics (Goldberg and Barton, 1992). Only two species were more sensitive to the taxonomic identity of neighbours relative to neighbour trait variation. This study suggests that trait-mediated competitive dynamics are likely prevalent in plant communities in general, but that additional axes of functional variation, not explored (e.g., leaf, hydraulic, or root traits), may influence the competitive responses of *Carapa procera* or *Celtis zenkeri* (Figure 11E, 11F) (Laughlin, 2014).

5.3.2 Moisture, tree size and wood density interactions

This study advances an understanding of how competitive outcomes among tree species are shaped by complex interactions between the individual effects of moisture availability, tree size, and wood density. Larger trees of a given species were less sensitive to competition than their smaller counterparts and demonstrated comparatively lower sensitivity to water stress (Figure

12). These findings underscore the greater capacity of larger trees to maintain growth and survival under water-limited conditions, a trend observed across divergent forested ecosystems (Chen et al., 2019; Germain et al., 2018; Gómez-Aparicio et al., 2011).

Consistent with resource-limitation theory, competitive pressures intensify under moisture scarcity, constraining tree physiological processes essential for growth and survival, such as photosynthesis and nutrient transport (Chen et al., 2019; Dale and Frank, 2022; Tilman, 1988). Under low-moisture conditions, larger trees gain competitive advantages through structural and physiological adaptations. They typically have extensive root systems that access deeper soil layers, tapping into stable water reserves beyond the reach of smaller trees (Canadell et al., 1996; Li et al., 2019; Schwinning, 2010). Additionally, the broad canopies of larger trees intercept a disproportionate share of rainwater, which via stemflow is concentrated in soil reservoirs proximate to their root systems (Crockford and Richardson, 2000; Schume et al., 2004). This resource redistribution may reduce moisture availability for smaller trees, potentially elevating associated physiological and competitive stress (Magalhães et al., 2021). A size-based competitive advantage may also be underlain by a higher photosynthetic capacity associated with a more extensive leaf area, which allows for greater carbon assimilation and storage, supporting growth and survival under competitive and moisture-limited conditions (Hérault et al., 2011; Stephenson et al., 2014). However, it is important to recognise that under severe and prolonged drought conditions, larger trees may experience increased susceptibility to hydraulic constraints, such as higher embolism risks and flow limitations associated with greater tree height. For instance, Stovall et al. (2019) demonstrated that taller trees exhibit elevated mortality risks during intense drought episodes, suggesting that extreme and persistent drought conditions could potentially reverse or significantly alter the patterns observed in this study. These findings are also consistent with aspects of biodiversity research where species-specific responses to temporal variation in the environment, such as fluctuating soil moisture storage, may lead to shifting competitive outcomes (Lebrija-Trejos et al., 2023). More specifically, variability in resource supply may favour distinct taxa at different times, depending on the functional strategies of the coexisting species (Chesson, 1994; Kelly and Bowler, 2002).

Analyses employed focused on the growth potential of trees at a local neighbourhood scale (i.e. within 15 m). This approach was partly pragmatic, facilitating an investigation of the fine-scale biological and abiotic factors shaping competitive interactions between individual trees. It was observed that annual growth capacity declined exponentially for most species at this scale. However, it was also acknowledged that interactions between individuals and environmental effects may encompass larger areas (Uriarte et al., 2010). A recent study has revealed a significant spatial structure in the composition of tropical forests at distances approaching ~100 m (Kalyuzhny et al., 2023). The authors attributed the non-random overdispersion of adult trees of a given species to the strong effects of conspecific negative density dependence (CNDD), such as host-specific pathogen infection or herbivory, that limited the survival of progeny near parent trees. The effects of CNDD acting on juveniles at local scales (<20 m) appear to have propagated over extensive spatial and temporal gradients, influencing the distribution of adult trees and the composition of extant forests (Kalyuzhny et al., 2023). These seemingly contrasting research outcomes are complementary and underscore the importance of different analytical approaches for understanding the complexity of demographic and species assembly processes in tropical forests.

6. CONCLUSIONS

This thesis presents a comprehensive, multi-scale synthesis of how biotic and abiotic drivers shape tropical forest communities along a pronounced climatic gradient in West Africa. By combining analyses of biodiversity potential, community-level productivity, species-specific growth capacity, and inter-tree competitive dynamics, this study demonstrates that tropical forest functioning is governed by an integrated composite of factors, including atmospheric water demand, soil moisture content, nutrient availability, forest structural complexity, and the functional strategies of the component taxa. Water limitation emerges as a primary ecological filter across the gradient, regulating community diversity and conservation value from wet to dry forests, with soil nutrients and forest structure further refining local assemblages. Biodiversity and standing biomass increase concomitantly toward wetter sites, yet maximum biomass growth rates peak in the intermediate moist forest zone, revealing a decoupling between biodiversity potential, carbon storage and carbon flux. At the species-level, growth responses to soil moisture and vapour pressure deficit are strongly individualistic, reflecting diverse physiological and life history strategies among taxa co-occurring within the same environment. The large degree of interspecific variation uncovered by the modelling results supports the relevance of fine-scale analyses of individual-tree behaviour, which may be overlooked in studies conducted at a coarse community scale.

Results show that competitive interactions importantly mediate productivity and biodiversity outcomes through trait- and size-dependent effects. Water limitation can also amplify the intensity of competitive interactions. Smaller trees are shown to be disproportionately sensitive to the combined effects of competition and water shortages. Consequently, regeneration and early growth stages are the most climate-sensitive phases of a tree's life cycle. Climate change impacts are therefore expected to manifest initially through altered recruitment success and shifting competitive hierarchies, leading to a gradual reassembly of the community flora. Forests may thus appear structurally stable in the short term while undergoing substantial demographic reorganisation beneath the canopy. These demographic sensitivities constitute the primary mechanisms through which climate forcing influences forest-scale dynamics.

Forest trajectories under warming and altered rainfall regimes will depend not only on changes in precipitation, but critically on rising evaporative demand from the atmosphere and shifting soil moisture–nutrient relationships. Increasingly severe vapour pressure deficits are likely to suppress productivity even where rainfall remains high, particularly in wet forests where species are adapted to low atmospheric water demand. In drier and transitional forests, declining soil moisture will heighten physiological stress within individuals and intensify competitive interactions between trees, potentially leading to the exclusion of some taxa in favour of species with conservative hydraulic and functional strategies. These processes are expected to drive coordinated shifts in physiological performance, competitive hierarchies, and community assembly, rather than causing simple, uniform declines in growth or diversity. The consequent restructuring of communities will have long-term effects on regional carbon dynamics and the critical climate regulation function of these forests. The strong positive influence of structural diversity on biomass growth further implies that selective logging, which causes a simplification of structure and/or a loss of large trees, will directly reduce carbon uptake potential, even where overall forest cover is maintained.

From a conservation perspective, the results of this study reveal a convergence between ecological value and climatic vulnerability. Wet forests support the highest biodiversity and the greatest proportion of globally threatened and rare species, yet remain sensitive to increasingly severe atmospheric drought. Moist forests function as transitional systems whose productivity and composition depend on the joint balance of water and nutrient availability. Dry forests harbour assemblages adapted to moisture limitation but are nevertheless vulnerable to an escalation of climatic stressors. These contrasts underscore the need for climate-resilient conservation approaches tailored to the distinct ecological roles and vulnerabilities of each forest type. Effective strategies must transcend a static prioritisation of current diversity hotspots and instead address dynamic climate-driven shifts in physiological stress, competitive outcomes, and demographic performance. Protecting wet forests is crucial for safeguarding biodiversity; managing moist forests is vital for sustaining regional carbon uptake under a changing climate; and maintaining dry forests preserves drought-adapted species that may underpin future ecosystem stability. Across all forest types, conserving structural complexity and functional trait diversity will be central to sustaining ecosystem services under future environmental change.

Importantly, by linking compositional, functional, and demographic processes within a unified hydrological and biotic framework, this thesis advances understanding beyond empirical climate-vegetation correlations. It identifies the specific demographic and competitive pathways through which climate forcing reshapes forest structure and function, providing a mechanistic foundation that may inform model forecasts of tropical forest trajectories under alternate future climate scenarios. These insights are also crucial for informing conservation planning and sustainable management aimed at maintaining biodiversity, ecosystem productivity and carbon storage in increasingly variable tropical environments. Future research that integrates long-term demographic monitoring, physiological trait measurements, and fine-scale climatic data will be fundamental for refining these projections and guiding effective, climate-resilient conservation strategies.

7. REFERENCES

Abbasi, U.A., Mattsson, E., Nissanka, S.P., Ali, A., 2022. Biological, structural and functional responses of tropical forests to environmental factors. Biol. Conserv. 276, 109792. https://doi.org/10.1016/j.biocon.2022.109792

Acheampong, E.O., Macgregor, C.J., Sloan, S., Sayer, J., 2019. Deforestation is driven by agricultural expansion in Ghana's forest reserves. Sci. African 5. https://doi.org/10.1016/j.sciaf.2019.e00146

Adler, P.B., Fajardo, A., Kleinhesselink, A.R., Kraft, N.J.B., 2013. Trait-based tests of coexistence mechanisms. Ecol. Lett. 16, 1294–1306. https://doi.org/10.1111/ele.12157

Aguirre-Gutiérrez, J., Díaz, S., Rifai, S.W., Corral-Rivas, J.J., Nava-Miranda, M.G., Gonzálezm, R., Hurtadom, A.B., Revilla, N.S., Vilanova, E., Almeida, E., de Oliveira, E.A., Alvarez-Davila, E., Alves, L.F., de Andrade, A.C.S., da Costa, A.C.L., Vieira, S.A., Aragão, L., Arets, E., Aymard, G.A.C., Baccaro, F., Bakker, Y.V., Baker, T.R., Bánki, O., Baraloto, C., de Camargo, P.B., Berenguer, E., Blanc, L., Bonal, D., Bongers, F., Bordin, K.M., Brienen, R., Brown, F., Prestes, N.C.C.S., Castilho, C. V., Ribeiro, S.C., de Souza, Fernanda Coelho, Comiskey, J.A., Valverde, F.C., Müller, S.C., da Costa Silva, R., do Vale, J.D., de Andrade Kamimura, V., de Oliveira Perdiz, R., del Aguila Pasquel, J., Derroire, G., Fiore, A. Di, Disney, M., Farfan-Rios, W., Fauset, S., Feldpausch, T.R., Ramos, R.F., Llampazo, G.F., Martins, V.F., Fortunel, C., Cabrera, K.G., Barroso, J.G., Hérault, B., Herrera, R., Honorio Coronado, E.N., Huamantupa-Chuquimaco, I., Pipoly, J.J., Zanini, K.J., Jiménez, E., Joly, C.A., Kalamandeen, M., Klipel, J., Levesley, A., Lopez Oviedo, W., Magnusson, W.E., dos Santos, R.M., Marimon, B.S., Marimon-Junior, B.H., de Almeida Reis, S.M., Cruz, O.A.M., Mendoza, A.M., Morandi, P., Muscarella, R., Nascimento, H., Neill, D.A., Menor, I.O., Palacios, W.A., Palacios-Ramos, S., Camacho, N.C.P., Pardo, G., Pennington, R.T., de Oliveira Pereira, L., Pickavance, G., Picolotto, R.C., Pitman, N.C.A., Prieto, A., Quesada, C., Ramírez-Angulo, H., Réjou-Méchain, M., Correa, Z.R., Huaymacari, J.M.R., Rodriguez, C.R., Rivas-Torres, G., Roopsind, A., Rudas, A., Negret, B.S., van der Sande, M.T., Santana, F.D., Santos, F.A.M., Bergamin, R.S., Silman, M.R., Silva, C., Espejo, J.S., Silveira, M., Souza, Fernanda Cristina, Sullivan, M.J.P., Swamy, V., Talbot, J., Terborgh, J.J., van der Meer, P.J., van der Heijden, G., van Ulft, B., Martinez, R.V., Vedovato, L., Vleminckx, J., Vos, V.A., Wortel, V., Zuidema, P.A., Zwerts, J.A., Laurance, S.G.W., Laurance, W.F., Chave, J., Dalling, J.W., Barlow, J., Poorter, L., Enquist, B.J., ter Steege, H., Phillips, O.L., Galbraith, D., Malhi, Y., 2025a. Tropical forests in the Americas are changing too slowly to track climate change. Science (80-.). 387. https://doi.org/10.1126/science.adl5414

Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S.L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T.R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K., Phillips, O.L., Oliveras, I., 2020. Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. Nat. Commun. 11, 1–10. https://doi.org/10.1038/s41467-020-16973-4

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

Aguirre-Gutiérrez, J., Rifai, S.W., Deng, X., ter Steege, H., Thomson, E., Corral-Rivas, J.J., Guimaraes, A.F., Muller, S., Klipel, J., Fauset, S., Resende, A.F., Wallin, G., Joly, C.A., Abernethy, K., Adu-Bredu, S., Alexandre Silva, C., de Oliveira, E.A., Almeida, D.R.A., Alvarez-Davila, E., Asner, G.P., Baker, T.R., Benchimol, M., Bentley, L.P., Berenguer, E., Blanc, L., Bonal, D., Bordin, K., Borges de Lima, R., Both, S., Cabezas Duarte, J., Cardoso, D., de Lima, H.C., Cavalheiro, L., Cernusak, L.A., dos Santos Prestes, N.C.C., da Silva Zanzini, A.C., da Silva, R.J., dos Santos Alves da Silva, R., de Andrade Iguatemy, M., De Sousa Oliveira, T.C., Dechant, B., Derroire, G., Dexter, K.G., Rodrigues, D.J., Espírito-Santo, M., Silva, L.F., Domingues, T.F., Ferreira, J., Simon, M.F., Girardin, C.A.J., Hérault, B., Jeffery, K.J., Kalpuzha Ashtamoorthy, S., Kavidapadinjattathil Sivadasan, A., Klitgaard, B., Laurance, W.F., Dan, M.L., Magnusson, W.E., Campos-Filho, E.M., Manoel dos Santos, R., Manzatto, A.G., Silveira, M., Marimon-Junior, B.H., Martin, R.E., Vieira, D.L.M., Metzker, T., Milliken, W., Moonlight, P., Moraes de Seixas, M.M., Morandi, P.S., Muscarella, R., Nava-Miranda, M.G., Nyirambangutse, B., Silva, J.O., Oliveras Menor, I., Francisco Pena Rodrigues, P.J., Pereira de Oliveira, C., Pereira Zanzini, L., Peres, C.A., Punjayil, V., Quesada, C.A., Réjou-Méchain, M., Riutta, T., Rivas-Torres, G., Rosa, C., Salinas, N., Bergamin, R.S., Marimon, B.S., Shenkin, A., Silva Rodrigues, P.M., Figueiredo, A.E.S., Garcia, Q.S., Spósito, T., Storck-Tonon, D., Sullivan, M.J.P., Svátek, M., Vieira Santiago, W.T., Arn Teh, Y., Theruvil Parambil Sivan, P., Nascimento, M.T., Veenendaal, E., Zo-Bi, I.C., Dago, M.R., Traoré, S., Patacca, M., Badouard, V., de Padua Chaves e Carvalho, S., White, L.J.T., Zhang-Zheng, H., Zibera, E., Zwerts, J.A., Burslem, D.F.R.P., Silman, M., Chave, J., Enquist, B.J., Barlow, J., Phillips, O.L., Coomes, D.A., Malhi, Y., 2025b. Canopy functional trait variation across Earth's tropical forests. Nature 641, 129–136. https://doi.org/10.1038/s41586-025-08663-2

Aguirre-Gutiérrez, J., Berenguer, E., Oliveras Menor, I., Bauman, D., Corral-Rivas, J.J., Nava-Miranda, M.G., Both, S., Ndong, J.E., Ondo, F.E., Bengone, N.N., Mihinhou, V., Dalling, J.W., Heineman, K., Figueiredo, A., González-M, R., Norden, N., Hurtado-M, A.B., González, D., Salgado-Negret, B., Reis, S.M., Moraes de Seixas, M.M., Farfan-Rios, W., Shenkin, A., Riutta, T., Girardin, C.A.J., Moore, S., Abernethy, K., Asner, G.P., Bentley, L.P., Burslem, D.F.R.P., Cernusak, L.A., Enquist, B.J., Ewers, R.M., Ferreira, J., Jeffery, K.J., Joly, C.A., Marimon-Junior, B.H., Martin, R.E., Morandi, P.S., Phillips, O.L., Bennett, A.C., Lewis, S.L., Quesada, C.A., Marimon, B.S., Kissling, W.D., Silman, M., Teh, Y.A., White, L.J.T., Salinas, N., Coomes, D.A., Barlow, J., Adu-Bredu, S., Malhi, Y., 2022. Functional susceptibility of tropical forests to climate change. Nat. Ecol. Evol. 6, 878–889. https://doi.org/10.1038/s41559-022-01747-6

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019. Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests. For. Ecol. Manage. 432, 823–831. https://doi.org/10.1016/j.foreco.2018.10.024

Allen, K., Dupuy, J.M., Gei, M.G., Hulshof, C., Medvigy, D., Pizano, C., Salgado-Negret, B., Smith, C.M., Trierweiler, A., Van Bloem, S.J., Waring, B.G., Xu, X., Powers, J.S., 2017. Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? Environ. Res. Lett. 12. https://doi.org/10.1088/1748-9326/aa5968

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration: Guidelines for computing crop water requirement. FAO Irrig. Drain. Pap. 56. FAO, Rome 300.

Almazroui, M., Saeed, F., Saeed, S., Nazrul Islam, M., Ismail, M., Klutse, N.A.B., Siddiqui, M.H., 2020. Projected Change in Temperature and Precipitation Over Africa from CMIP6. Earth Syst. Environ. 4, 455–475. https://doi.org/10.1007/s41748-020-00161-x

Anderegg, W.R.L., Konings, A.G., Trugman, A.T., Yu, K., Bowling, D.R., Gabbitas, R., Karp, D.S., Pacala, S., Sperry, J.S., Sulman, B.N., Zenes, N., 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. Nature 561, 538–541. https://doi.org/10.1038/s41586-018-0539-7

Angert, A.L., Huxman, T.E., Chesson, P., Venable, D.L., 2009. Functional tradeoffs determine species coexistence via the storage effect. Proc. Natl. Acad. Sci. U. S. A. 106, 11641–11645. https://doi.org/10.1073/pnas.0904512106

Appiah-Badu, K., Anning, A.K., Eshun, B., Mensah, G., 2022. Land use effects on tree species diversity and soil properties of the Awudua Forest, Ghana. Glob. Ecol. Conserv. 34, e02051. https://doi.org/10.1016/j.gecco.2022.e02051

Asefi-Najafabady, S., Saatchi, S., 2013. Response of African humid tropical forests to recent rainfall anomalies. Philos. Trans. R. Soc. B Biol. Sci. 368. https://doi.org/10.1098/rstb.2012.0306

Azaele, S., Suweis, S., Grilli, J., Volkov, I., Banavar, J.R., Maritan, A., 2016. Statistical mechanics of ecological systems: Neutral theory and beyond. Rev. Mod. Phys. 88, 1–31. https://doi.org/10.1103/RevModPhys.88.035003

Baraloto, C., Molto, Q., Rabaud, S., Hérault, B., Valencia, R., Blanc, L., Fine, P.V.A., Thompson, J., 2013. Rapid simultaneous estimation of aboveground biomass and tree diversity across neotropical forests: A comparison of field inventory methods. Biotropica 45, 288–298. https://doi.org/10.1111/btp.12006

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bauman, D., Fortunel, C., Cernusak, L.A., Bentley, L.P., Mcmahon, S.M., Rifai, S.W., Aguirre-, J., Oliveras, I., Bradford, M., Laurance, S.G.W., Delhaye, G., Hutchinson, M.F., Dempsey, R., Mcnellis, B.E., Santos-, P.E., Ninantay-, A.H.R., 2022. Tropical tree growth sensitivity to climate is driven by species intrinsic growth rate and leaf traits 1414–1432. https://doi.org/10.1111/gcb.15982

Bazzaz, F.. A.., 1979. The Physiological Ecology of Plant Succession. Annu. Rev. 10, 351–371.

Bennett, A.C., Dargie, G.C., Cuni-Sanchez, A., Mukendi, J.T., Hubau, W., Mukinzi, J.M., Phillips, O.L., Malhi, Y., Sullivan, M.J.P., Cooper, D.L.M., Adu-Bredu, S., Affum-Baffoe, K., Amani, C.A., Banin, L.F., Beeckman, H., Begne, S.K., Bocko, Y.E., Boeckx, P., Bogaert, J., Brncic, T., Chezeaux, E., Clark, C.J., Daniels, A.K., de Haulleville, T., Kamdem, M.N.D., Doucet, J.L., Ondo, F.E., Ewango, C.E.N., Feldpausch, T.R., Foli, E.G., Gonmadje, C., Hall, J.S., Hardy, O.J., Harris, D.J., Ifo, S.A., Jeffery, K.J., Kearsley, E., Leal, M., Levesley, A., Makana, J.R., Lukasu, F.M., Medjibe, V.P., Mihindu, V., Moore, S., Begone, N.N., Pickavance, G.C., Poulsen, J.R., Reitsma, J., Sonké, B., Sunderland, T.C.H., Taedoumg, H., Talbot, J., Tuagben, D.S., Umunay, P.M., Verbeeck, H., Vleminckx, J., White, L.J.T., Woell, H., Woods, J.T., Zemagho, L., Lewis, S.L., 2021. Resistance of African tropical forests to an extreme climate anomaly. Proc. Natl. Acad. Sci. U. S. A. 118, 1–12. https://doi.org/10.1073/pnas.2003169118

Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. Trends Ecol.

Evol. 9, 191–193. https://doi.org/https://doi.org/10.1016/0169-5347(94)90088-4

Blackman, C.J., Creek, D., Maier, C., Aspinwall, C.J., Drake, J.E., Pfautsch, S., O'Grady, A., Delzon, S., Medlyn, B.E., Tissue, D.T., Choat, B., 2019. Drought response strategies and hydraulic traits contribute to mechanistic understanding of plant dry-down to hydraulic failure. Tree Physiol. 39, 910–924. https://doi.org/https://doi.org/10.1093/treephys/tpz016

Bonan, G.B., 2008. Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. Science (80). 320, 1444–1449. https://doi.org/10.1126/science.1155121

Bremner, J.M., 1996. Nitrogen-total. Methods Soil Anal. Part 3 Chem. Methods 1085–1121. https://doi.org/10.2136/sssabookser5.3.c37

Briddon, C.L., Menéndez García, A., Ghedini, G., 2025. Eco-evolutionary dynamics between multiple competitors reduce phytoplankton coexistence but have limited impacts on community productivity. Proc. R. Soc. B Biol. Sci. 292. https://doi.org/10.1098/rspb.2025.1146

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., 2015. Long term decline of the Amazon carbon sink. Nature 519, 344–348.

Brodribb, T.J., Powers, J., Cochard, H., Choat, B., 2020. Hanging by a thread? Forests and drought. Science (80). 368, 261–266. https://doi.org/10.1126/science.aat7631

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., Tielbörger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2008. Facilitation in plant communities: The past, the present, and the future. J. Ecol. 96, 18–34. https://doi.org/10.1111/j.1365-2745.2007.01295.x

Browne, L., Karubian, J., 2016. Frequency-dependent selection for rare genotypes promotes genetic diversity of a tropical palm. Ecol. Lett. 19, 1439–1447. https://doi.org/10.1111/ele.12692

Buechling, A., Martin, P.H., Canham, C.D., 2017. Climate and competition effects on tree growth in Rocky Mountain forests. J. Ecol. 105, 1636–1647. https://doi.org/10.1111/1365-2745.12782

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second. ed. Springer-Verlag, New York, USA.

Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108, 583–595. https://doi.org/10.1007/BF00329030

Canham, C.D., LePage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. Can. J. For. Res. 34, 778–787. https://doi.org/10.1139/x03-232

Canham, C.D., Murphy, L., 2016. The demography of tree species response to climate: Sapling and canopy tree survival. Ecosphere 7, 1–17. https://doi.org/10.1002/ecs2.1701

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J.,

2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540–554. https://doi.org/10.1890/1051-0761(2006)016[0540:NAOCTC]2.0.CO;2

Canham, C.D., Uriarte, M., 2006. Analysis of neighborhood dynamics of forest ecosystems using likelihood methods and modeling. Ecol. Appl. 16, 62–73. https://doi.org/10.1890/04-0657

Capmourteres, V., Anand, M., 2016. 'Conservation value': A review of the concept and its quantification. Ecosphere 7, 1–19. https://doi.org/10.1002/ecs2.1476

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67. https://doi.org/10.1890/13-0133.1

Chapman, H.D., 1965. Cation-exchange capacity. Methods Soil Anal. Part 2 Chem. Microbiol. Prop. 891–901. https://doi.org/10.2134/agronmonogr9.2.c6

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chave, J., Re´jou-Me´chain, M., Bu´rquez, A., Chidumayo, E., Colgan, M.S., Delitti WBC., et al, 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629

Chave, Jérôme, Olivier, J., Bongers, F., Châtelet, P., Meer, P. Van Der, Norden, N., Riéra, B., Charles-, P., Chave, Jerome, Olivier, J., Bongersf, F., Chateletj, P., Forget, P., Meerf, P. Van Der, Norden, N., Riera, B., Charles-dominique, P., 2008. Above-Ground Biomass and Productivity in a Rain Forest of Eastern South American Above-ground biomass and productivity in a rain forest of eastern South America 24, 355–366. https://doi.org/10.1017/S0266467408005075

Chazdon, R.L., Brancalion, P.H.S., Lamb, D., Laestadius, L., Calmon, M., Kumar, C., 2017. A Policy-Driven Knowledge Agenda for Global Forest and Landscape Restoration. Conserv. Lett. 10, 125–132. https://doi.org/10.1111/conl.12220

Chen, N., Zhang, Y., Yuan, F., Song, C., Xu, M., Wang, Q., Hao, G., Bao, T., Zuo, Y., Liu, J., Zhang, T., Song, Y., Sun, L., Guo, Y., Zhang, H., Ma, G., Du, Y., Xu, X., Wang, X., 2023. Warming-induced vapor pressure deficit suppression of vegetation growth diminished in northern peatlands. Nat. Commun. 14, 1–13. https://doi.org/10.1038/s41467-023-42932-w

Chen, Y., Uriarte, M., Wright, S.J., Yu, S., 2019. Effects of neighborhood trait composition on tree survival differ between drought and postdrought periods. Ecology 100, 1–10. https://doi.org/10.1002/ecy.2766

Chen, Z., Li, S., Wan, X., Liu, S., 2022. Strategies of tree species to adapt to drought from leaf stomatal regulation and stem embolism resistance to root properties. Front. Plant Sci. 13, 1–18. https://doi.org/10.3389/fpls.2022.926535

Cheng, C., Zhang, J., Li, M., Liu, C., Xu, L., He, N., 2024. Vertical structural complexity of plant communities represents the combined effects of resource acquisition and environmental stress on the Tibetan Plateau. Commun. Biol. 7, 1–11.

https://doi.org/10.1038/s42003-024-06076-x

Chesson, P., 2000. General theory of competitive coexistence in spatially-varying environments. Theor. Popul. Biol. 58, 211–237. https://doi.org/10.1006/tpbi.2000.1486

Chesson, P., 1994. Multispecies Competition in Variable Environments. Theor. Popul. Biol.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688

Claeys, F., Gourlet-Fleury, S., Picard, N., Ouédraogo, D.Y., Tadesse, M.G., Hérault, B., Baya, F., Bénédet, F., Cornu, G., Mortier, F., 2019. Climate change would lead to a sharp acceleration of Central African forests dynamics by the end of the century. Environ. Res. Lett. 14. https://doi.org/10.1088/1748-9326/aafb81

Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984 – 2000. Proc. Natl. Acad. Sci. USA 100, 5852–7.

Clark, D.B., Clark, D.A., Oberbauer, S.F., Kellner, J.R., 2017. Multidecadal stability in tropical rain forest structure and dynamics across an old-growth landscape. PLoS One 12, 1–20. https://doi.org/10.1371/journal.pone.0183819

Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130. https://doi.org/10.1111/j.1365-2745.2008.01458.x

Crockford, R.H., Richardson, D.P., 2000. Partitioning of rainfall into throughfall, stemslow∠d interception effect of forest type, ground cover and climate. Hydrol. Process. 14, 2903–2920. https://doi.org/10.1002/1099-1085(200011/12)14:16/17<2903::AID-HYP126>3.0.CO;2-6

Curtis, J., McIntosh, R., 1950. The interrelations of certain analytic and synthetic phytosociological characters. Ecology 31, 434–455.

Dai, Y., Shangguan, W., Duan, Q., Liu, B., Fu, S., Niu, G., 2013. Development of a China dataset of soil hydraulic parameters using pedotransfer functions for land surface modeling. J. Hydrometeorol. 14, 869–887. https://doi.org/10.1175/JHM-D-12-0149.1

Dale, A.G., Frank, S.D., 2022. Water Availability Determines Tree Growth and Physiological Response to Biotic and Abiotic Stress in a Temperate North American Urban Forest. Forests 13, 1–15. https://doi.org/10.3390/f13071012

Dănescu, A., Albrecht, A.T., Bauhus, J., 2016. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. Oecologia 182, 319–333. https://doi.org/10.1007/s00442-016-3623-4

De Guzman, M.E., Acosta-Rangel, A., Winter, K., Meinzer, F.C., Bonal, D., Santiago, L.S., 2021. Hydraulic traits of Neotropical canopy liana and tree species across a broad range of wood density: implications for predicting drought mortality with models. Tree Physiol. 41, 24–34.

de Souza, B.C., Carvalho, E.L.D., Oliveira, R.S., de Araujo, F.S., de Lima, A.L.A., Rodal, M.J.N., 2020. Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest. Oecologia 194, 221–236. https://doi.org/10.1007/s00442-020-04760-3

Deb, J.C., Phinn, S., Butt, N., McAlpine, C.A., 2018. Climate change impacts on tropical forests: Identifying risks for tropical Asia. J. Trop. For. Sci. 30, 182–194. https://doi.org/10.26525/jtfs2018.30.2.182194

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., Hibbard, K., Olson, R., 2008. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology 89, 2117–2126. https://doi.org/doi/pdf/10.1890/07-0850.1

Delzon, S., Douthe, C., Sala, A., Cochard, H., 2010. Mechanism of water-stress induced cavitation in conifers: Bordered pit structure and function support the hypothesis of seal capillary-seeding. Plant, Cell Environ. 33, 2101–2111. https://doi.org/10.1111/j.1365-3040.2010.02208.x

Deng, M., Liu, L., Jiang, L., Liu, W., Wang, X., Li, S., Yang, S., Wang, B., 2018. Ecosystem scale trade-off in nitrogen acquisition pathways. Nat. Ecol. Evol. 2, 1724–1734. https://doi.org/10.1038/s41559-018-0677-1

Deng, R., Liao, J., Rademacher, T., Xu, Z., Du, M., Zheng, J., Fu, L., Zhang, X., 2025. Species-specific influences of competition and tree size on drought sensitivity and resistance for three planted conifers in northern China. For. Ecosyst. 13, 100295. https://doi.org/10.1016/j.fecs.2025.100295

Ding, Y., Nie, Y., Chen, H., Wang, K., Querejeta, J.I., 2021. Water uptake depth is coordinated with leaf water potential, water-use efficiency and drought vulnerability in karst vegetation. New Phytol. 229, 1339–1353. https://doi.org/10.1111/nph.16971

Dong, S.X., Davies, S.J., Ashton, P.S., Bunyavejchewin, S., Nur Supardi, M.N., Kassim, A.R., Tan, S., Moorcroft, P.R., 2012. Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. Proc. R. Soc. B Biol. Sci. 279, 3923–3931. https://doi.org/10.1098/rspb.2012.1124

Du, E., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X., Jackson, R.B., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nat. Geosci. 13, 221–226. https://doi.org/10.1038/s41561-019-0530-4

Dubey, N., Ghosh, S., 2023. The relative role of soil moisture and vapor pressure deficit in affecting the Indian vegetation productivity. Environ. Res. Lett. 18. https://doi.org/10.1088/1748-9326/acd2ef

Edwards, A.W.F., 1992. Likelihoods. London and Baltimor: The Johns Hopkins University Press.

Enquist, B.J., Enquist, C.A.F., 2011. Long-term change within a Neotropical forest: Assessing differential functional and floristic responses to disturbance and drought. Glob. Chang. Biol. 17, 1408–1424. https://doi.org/10.1111/j.1365-2486.2010.02326.x

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J.W., Feldpausch, T.R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B.S., Marimon-Junior, B.H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., Bonal, D., Davila Cardozo, N., Erwin, T., Fauset, S., Hérault, B., Laurance, S., Poorter, L., Qie, L., Stahl, C., Sullivan, M.J.P., ter Steege, H., Vos, V.A., Zuidema, P.A., Almeida, E., Almeida de Oliveira, E., Andrade, A., Vieira, S.A., Aragão, L., Araujo-Murakami, A., Arets, E., Aymard C, G.A., Baraloto, C., Camargo, P.B., Barroso, J.G., Bongers, F., Boot, R., Camargo, J.L., Castro, W., Chama Moscoso, V., Comiskey, J., Cornejo Valverde, F., Lola da Costa, A.C., del Aguila Pasquel, J., Di Fiore, A., Fernanda Duque, L., Elias, F., Engel, J., Flores Llampazo, G., Galbraith, D., Herrera Fernández, R., Honorio Coronado, E., Hubau, W., Jimenez-Rojas, E., Lima, A.J.N., Umetsu, R.K., Laurance, W., Lopez-Gonzalez, G., Lovejoy, T., Aurelio Melo Cruz, O., Morandi, P.S., Neill, D., Núñez Vargas, P., Pallqui Camacho, N.C., Parada Gutierrez, A., Pardo, G., Peacock, J., Peña-Claros, M., Peñuela-Mora, M.C., Petronelli, P., Pickavance, G.C., Pitman, N., Prieto, A., Quesada, C., Ramírez-Angulo, H., Réjou-Méchain, M., Restrepo Correa, Z., Roopsind, A., Rudas, A., Salomão, R., Silva, N., Silva Espejo, J., Singh, J., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres-Lezama, A., Valenzuela Gamarra, L., van de Meer, P.J., van der Heijden, G., van der Hout, P., Vasquez Martinez, R., Vela, C., Vieira, I.C.G., Phillips, O.L., 2018. Compositional response of Amazon forests to climate change. Glob. Chang. Biol. 25, 39–56. https://doi.org/10.1111/gcb.14413

Esquivel-Muelbert, A., Brienen, R.J.W., Baker, T.R., Dexter, K.G., Lewis, S.L., Feldpausch, T.R., Lloyd, J., Monteagudo, A., Arroyo, L., Niro, E.Á., Beatriz, H., Stahl, C., Sullivan, M.J.P., Vos, V.A., Zuidema, P.A., Chama, V., Comiskey, J., Cornejo, F., Antonio, V., Lola, C., José, A., Lima, N., Umetsu, R.K., Gonzalez, G.L., Lovejoy, T., Parada, A., Guido, G., Julie, P., Marielos, P., Claros, P., 2019. Compositional response of Amazon forests to climate change 39–56. https://doi.org/10.1111/gcb.14413

Fajardo, A., 2016. Wood density is a poor predictor of competitive ability among individuals of the same species. For. Ecol. Manage. 372, 217–225. https://doi.org/10.1016/j.foreco.2016.04.022

FAO, 2020. The Forest Landscape Restoration Mechanism. URL https://www.fao.org/in-action/forest-landscape-restoration-mechanism/background/en/ (accessed 4.4.24).

Fatichi, S., Leuzinger, S., Körner, C., 2014. Moving beyond photosynthesis: From carbon source to sink-driven vegetation modeling. New Phytol. 201, 1086–1095. https://doi.org/10.1111/nph.12614

Fatichi, S., Pappas, C., Ivanov, V.Y., 2016. Modeling plant–water interactions: an ecohydrological overview from the cell to the global scale. Wiley Interdiscip. Rev. Water 3, 327–368. https://doi.org/10.1002/wat2.1125

Fatunsin, O.E., Naka, K., 2025. Structural diversity enhances carbon storage in mixed oak-pine forests of the Southeast United States. For. Ecol. Manage. 586, 122719. https://doi.org/10.1016/j.foreco.2025.122719

Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G., Hamer, K.C., Swaine, M.D., 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. Ecol. Lett. 15, 1120–1129. https://doi.org/10.1111/j.1461-0248.2012.01834.x

Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S.P., Foster, R.B., 2011. Directional changes in the species composition of a tropical forest. Ecology 92, 871–882. https://doi.org/10.1890/10-0724.1

Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. Ecol. Lett. 10, 461–469. https://doi.org/10.1111/j.1461-0248.2007.01033.x

Forrester, D.I., 2021. Does individual-tree biomass growth increase continuously with tree size? For. Ecol. Manage. 481, 118717. https://doi.org/10.1016/j.foreco.2020.118717

Forrester, D.I., 2019. Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. For. Ecol. Manage. 447, 139–157. https://doi.org/10.1016/j.foreco.2019.05.053

Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. Curr. For. Reports 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2

Fortunel, C., Lasky, J.R., Uriarte, M., Valencia, R., Wright, S.J., Garwood, N.C., Kraft, N.J.B., 2018. Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. Ecology 99, 2272–2283. https://doi.org/10.1002/ecy.2441

Fortunel, C., Valencia, R., Wright, S.J., Garwood, N.C., Kraft, N.J.B., 2016. Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. Ecol. Lett. 19, 1062–1070. https://doi.org/10.1111/ele.12642

Fu, Z., Ciais, P., Prentice, I.C., Gentine, P., Makowski, D., Bastos, A., Luo, X., Green, J.K., Stoy, P.C., Yang, H., Hajima, T., 2022. Atmospheric dryness reduces photosynthesis along a large range of soil water deficits. Nat. Commun. 13, 1–10. https://doi.org/10.1038/s41467-022-28652-7

Gang, H., Zhonghua, Z., Hongping, W., Lei, L., 2023. Factors influencing the distribution of woody plants in tropical karst hills, south China. PeerJ 11, 1–22. https://doi.org/10.7717/PEERJ.16331

Gao, Y., Markkanen, T., Thum, T., Aurela, M., Lohila, A., Mammarella, I., Kämäraïnen, M., Hagemann, S., Aalto, T., 2016. Assessing various drought indicators in representing summer drought in boreal forests in Finland. Hydrol. Earth Syst. Sci. 20, 175–191. https://doi.org/10.5194/hess-20-175-2016

Germain, R.M., Mayfield, M.M., Gilbert, B., 2018. The ‘filtering’ metaphor revisited: Competition and environment jointly structure invasibility and coexistence. Biol. Lett. 14. https://doi.org/10.1098/rsbl.2018.0460

Givnish, T.J., 1999. On the causes of gradients in tropical tree diversity. J. Ecol. 87, 193–210. https://doi.org/10.1046/j.1365-2745.1999.00333.x

Gleason, S.M., Westoby, M., Jansen, S., Choat, B., Hacke, U.G., Pratt, R.B., Bhaskar, R., Brodribb, T.J., Bucci, S.J., Cao, K.F., Cochard, H., Delzon, S., Domec, J.C., Fan, Z.X., Feild, T.S., Jacobsen, A.L., Johnson, D.M., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mcculloh, K.A., Mencuccini, M., Mitchell, P.J., Morris, H., Nardini, A., Pittermann, J., Plavcová, L., Schreiber, S.G., Sperry, J.S., Wright, I.J., Zanne, A.E., 2016. Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world’s woody plant species. New Phytol. 209, 123–136. https://doi.org/10.1111/nph.13646

Goffe, W.L., Ferrier, G.D., Rogers, J., 1994. Global optimization of statistical functions with simulated annealing. J. Econom. 60, 65–99. https://doi.org/10.1016/0304-4076(94)90038-8

Goldberg, D.E., 1990. Components of Resource Competition in Plant Communities, Perspectives on Plant Competition. Academic Press, Inc. https://doi.org/10.1016/b978-0-12-294452-9.50007-2

Goldberg, D.E., Barton, A.M., 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. Am. Nat. 139, 771–801. https://doi.org/10.1086/285357

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. Glob. Chang. Biol. 17, 2400–2414. https://doi.org/10.1111/j.1365-2486.2011.02421.x

Gourlet-Fleury, S., Rossi, V., Forni, E., Fayolle, A., Ligot, G., Allah-Barem, F., Baya, F., Bénédet, F., Boyemba, F., Cornu, G., Doucet, J.L., Gillet, J.F., Mazengue, M., Mbasi Mbula, M., Van Hoef, Y., Zombo, I., Freycon, V., 2023. Competition and site weakly explain tree growth variability in undisturbed Central African moist forests. J. Ecol. 1–18. https://doi.org/10.1111/1365-2745.14152

Grime, J.P., 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. Am. Nat. 111, 1169–1194.

Grossiord, C., Buckley, T.N., Cernusak, L.A., Novick, K.A., Poulter, B., Siegwolf, R.T.W., Sperry, J.S., McDowell, N.G., 2020. Plant responses to rising vapor pressure deficit. New Phytol. 226, 1550–1566. https://doi.org/10.1111/nph.16485

Guo, Y., Chen, H.Y.H., Wang, B., Xiang, W., Li, D., Li, X., Mallik, A.U., Ding, T., Huang, F., Lu, S., Wen, S., 2021. Conspecific and heterospecific crowding facilitate tree survival in a tropical karst seasonal rainforest. For. Ecol. Manage. 481, 118751. https://doi.org/10.1016/j.foreco.2020.118751

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 457–461. https://doi.org/10.1007/s004420100628

Hall, J.B., Swaine, M.D., 1981. Distribution and ecology of vascular plants in a tropical rain forest: Forest vegetation in Ghana. Dr W. Junk Publishers, The Hague in 1981.

Hartigan, J.A., Wong, M.A., 1979. Algorithm AS 136: a K-means clustering algorithm. J. R. Stat. Soc. Ser. C Appl. Stat. 28, 100–108.

Harvey-Brown, Y., Shaw, K., Davies, K., Rivers, M., 2022. Using the Global Tree Assessment at Multiple Scales of Planning and Action. Diversity 14, 1–6. https://doi.org/10.3390/d14100891

Hawthorne, W.D., 1996. Holes and the sums of parts in Ghanaian forest: Regeneration, scale and sustainable use, Proceedings of the Royal Society of Edinburgh Section B: Biological Sciences. https://doi.org/10.1017/S0269727000006126

Hawthorne, W.D., 1995. Ecological profiles of Ghanaian forest trees. Tropical Forestry Paper no.29. Oxford Forestry Institute, Department of Plant Sciences. Oxford, UK, Oxford, UK.

Hawthorne, W.D., Abu-Juam, M., 1995. Forest Protection in Ghana. IUCN, Glad, Switzerland and Cambridge, UK.

Hédl, R., Svátek, M., Dančák, M., Rodzay, A.W., Salleh, M., Kamariah, A.S., 2009. A new technique for inventory of permanent plots in tropical forests: A case study from lowland dipterocarp forest in Kuala Belalong, Brunei darussalam. Blumea J. Plant Taxon. Plant Geogr. 54, 124–130. https://doi.org/10.3767/000651909X475482

Hegyi, F., 1974. A simulation model for managing jack-pine stands, in: Fries, J. (Ed.), Models for Tree and Stand Simulation. Royal College of Forestry, Stockholm, pp. 74–90.

Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F., Baraloto, C., 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. J. Ecol. 99, 1431–1440. https://doi.org/10.1111/j.1365-2745.2011.01883.x

Herms, D.A., Mattson, W.J., 1992. The dilemma of plants: To grow or defend. Q. Rev. Biol. 67, 283–335. https://doi.org/10.1086/417659

Hsieh, T.C., Ma, K.H., Chao, A., 2022. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 3.0.0. URL http://chao.stat.nthu.edu.tw/wordpress/software-download/.

Hu, J., Herbohn, J., Chazdon, R.L., Baynes, J., Vanclay, J.K., 2020. Long-term growth responses of three Flindersia species to different thinning intensities after selective logging of a tropical rainforest. For. Ecol. Manage. 476, 118442. https://doi.org/10.1016/j.foreco.2020.118442

Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A.K., Ewango, C.E.N., Fauset, S., Mukinzi, J.M., Sheil, D., Sonké, B., Sullivan, M.J.P., Sunderland, T.C.H., Taedoumg, H., Thomas, S.C., White, L.J.T., Abernethy, K.A., Adu-Bredu, S., Amani, C.A., Baker, T.R., Banin, L.F., Baya, F., Begne, S.K., Bennett, A.C., Benedet, F., Bitariho, R., Bocko, Y.E., Boeckx, P., Boundja, P., Brienen, R.J.W., Brncic, T., Chezeaux, E., Chuyong, G.B., Clark, C.J., Collins, M., Comiskey, J.A., Coomes, D.A., Dargie, G.C., de Haulleville, T., Kamdem, M.N.D., Doucet, J.L., Esquivel-Muelbert, A., Feldpausch, T.R., Fofanah, A., Foli, E.G., Gilpin, M., Gloor, E., Gonmadje, C., Gourlet-Fleury, S., Hall, J.S., Hamilton, A.C., Harris, D.J., Hart, T.B., Hockemba, M.B.N., Hladik, A., Ifo, S.A., Jeffery, K.J., Jucker, T., Yakusu, E.K., Kearsley, E., Kenfack, D., Koch, A., Leal, M.E., Levesley, A., Lindsell, J.A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J.C., Makana, J.R., Malhi, Y., Marshall, A.R., Martin, J., Martin, E.H., Mbayu, F.M., Medjibe, V.P., Mihindou, V., Mitchard, E.T.A., Moore, S., Munishi, P.K.T., Bengone, N.N., Ojo, L., Ondo, F.E., Peh, K.S.H., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Qie, L., Reitsma, J., Rovero, F., Swaine, M.D., Talbot, J., Taplin, J., Taylor, D.M., Thomas, D.W., Toirambe, B., Mukendi, J.T., Tuagben, D., Umunay, P.M., van der Heijden, G.M.F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J.T., Zemagho, L., 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature 579, 80–87. https://doi.org/10.1038/s41586-020-2035-0

Hubbell, S.P., 2006. Neutral theory and the evolution of ecological equivalence. Ecology 87, 1387–1398. https://doi.org/10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2

Hubbell, S.P., Ahumada, J.A., Condit, R., Foster, R.B., 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. Ecol. Res. 16, 859–875.

https://doi.org/10.1046/j.1440-1703.2001.00445.x

Immerzeel, W.W., Lutz, A.F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B.J., Elmore, A.C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J.S., Koppes, M., Kraaijenbrink, P.D.A., Kulkarni, A. V., Mayewski, P.A., Nepal, S., Pacheco, P., Painter, T.H., Pellicciotti, F., Rajaram, H., Rupper, S., Sinisalo, A., Shrestha, A.B., Viviroli, D., Wada, Y., Xiao, C., Yao, T., Baillie, J.E.M., 2020. Importance and vulnerability of the world's water towers. Nature 577, 364–369. https://doi.org/10.1038/s41586-019-1822-y

IUCN, 2024. The IUCN Red List of Threatened Species. Version 2024-2. URL https://www.iucnredlist.org/ (accessed 2.20.24).

Jackson, M.B., Colmer, T.D., 2005. Response and adaptation by plants to flooding stress. Ann. Bot. 96, 501–505. https://doi.org/10.1093/aob/mci205

James, R., Washington, R., Rowell, D.P., 2013. Implications of global warming for the climate of African rainforests. Philos. Trans. R. Soc. B Biol. Sci. 368. https://doi.org/10.1098/rstb.2012.0298

Janzen, D.H., 1970. Herbivores and the Number of Tree Species in Tropical Forests. Am. Nat. 104, 501–528. https://doi.org/10.1086/282687

Jiang, X., Albright, R., Creecy, E., Li, K.F., Liang, M.C., Newman, S., Wang, X., Karandana Gamalathge, T.D., Yung, Y.L., 2023. Congo Basin Rainforest Is a Net Carbon Source During the Dry Season. Earth Sp. Sci. 10, 1–12. https://doi.org/10.1029/2022EA002644

Jobbágy, E.G., Jackson, R.B., 2001. The Distribution of Soil Nutrients with Depth. Biogeochemistry 53, 51–77.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., Foster, R.B., 2007. Soil nutrients influence spatial distributions of tropical trees species. Proc. Natl. Acad. Sci. U. S. A. 104, 864–869. https://doi.org/10.1073/pnas.0604666104

Johnson, J.B., Omland, K.S., 2004. Model selection in ecology and evolution. Trends Ecol. Evol. 19, 101–108. https://doi.org/10.1016/j.tree.2003.10.013

Jucker, T., Bongalov, B., Burslem, D.F.R.P., Nilus, R., Dalponte, M., Lewis, S.L., Phillips, O.L., Qie, L., Coomes, D.A., 2018. Topography shapes the structure, composition and function of tropical forest landscapes. Ecol. Lett. 21, 989–1000. https://doi.org/10.1111/ele.12964

Kalyuzhny, M., Lake, J.K., Wright, S.J., Ostling, A.M., Sterculia, A., Celtis, B., Marchand, W., Buechling, A., Rydval, M., Čada, V., Stegehuis, A.I., Fruleux, A., Poláček, M., Hofmeister, J., Pavlin, J., Ralhan, D., Dušátko, M., Janda, P., Mikoláš, M., Vostarek, O., Bače, R., Frankovič, M., Kozák, D., Roibu, C.C., Chaskovskyy, O., Mikac, S., Zlatanov, T., Panayotov, M., Diku, A., Toromani, E., Svoboda, M., 2023. Pervasive within-species spatial repulsion among adult tropical trees. Agric. For. Meteorol. 329, 563–568. https://doi.org/10.1016/j.agrformet.2022.109280

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 1–20. https://doi.org/10.1038/sdata.2017.122

Kelly, C.K., Bowler, M.G., 2002. Coexistence and relative abundance in forest trees. Nature

417, 437–440. https://doi.org/https://doi.org/10.1038/417437a

Kengne, O.C., Feukeng, S.S.K., Ngansop, E.T., Meyan-ya, R.G.D., Zapfack, L., 2022. Floristic composition, growth temperament and conservation status of woody plant species in the Cameroonian tropical rainforests. Ecol. Process. 11. https://doi.org/10.1186/s13717-022-00387-9

Khaine, I., Woo, S.Y., Kang, H., Kwak, M.J., Je, S.M., You, H., Lee, T., Jang, J., Lee, H.K., Lee, E., Yang, L., Kim, H., Lee, J.K., Kim, J., 2017. Species diversity, stand structure, and species distribution across a precipitation gradient in tropical forests in Myanmar. Forests 8, 1–15. https://doi.org/10.3390/f8080282

Kindt, R., Coe, R., 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF).

Kitajima, K., Poorter, L., 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. New Phytol. 186, 708–721. https://doi.org/10.1111/j.1469-8137.2010.03212.x

Kobe, R.K.., Pacala, S.W.., John A . Silander, J., Canham, C.D.., 1995. Juvenile Tree Survivorship as a Component of Shade Tolerance. Ecol. Appl. 5, 517–532. https://doi.org/doi:10.2307/1942040

Konings, A.G., Gentine, P., 2017. Global variations in ecosystem-scale isohydricity. Glob. Chang. Biol. 23, 891–905. https://doi.org/10.1111/gcb.13389

Korolyova, N., Buechling, A., Ďuračiová, R., Zabihi, K., Turčáni, M., Svoboda, M., Bláha, J., Swarts, K., Poláček, M., Hradecký, J., Červenka, J., Němčák, P., Schlyter, F., Jakuš, R., 2022. The Last Trees Standing: Climate modulates tree survival factors during a prolonged bark beetle outbreak in Europe. Agric. For. Meteorol. 322. https://doi.org/10.1016/j.agrformet.2022.109025

Kozlowski, T.T., Pallardy, S.G., 1997. Absorption of Water and Ascent of Sap. Physiol. Woody Plants 237–268. https://doi.org/10.1016/b978-012424162-6/50028-4

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599. https://doi.org/10.1111/1365-2435.12345

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J.H.C., Gourlet-Fleury, S., Hanewinkel, M., Herault, B., Kattge, J., Kurokawa, H., Onoda, Y., Peñuelas, J., Poorter, H., Uriarte, M., Richardson, S., Ruiz-Benito, P., Sun, I.F., Ståhl, G., Swenson, N.G., Thompson, J., Westerlund, B., Wirth, C., Zavala, M.A., Zeng, H., Zimmerman, J.K., Zimmermann, N.E., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529, 204–207. https://doi.org/10.1038/nature16476

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., von Oheimb, G., 2019. Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. Ecol. Lett. 22, 2130–2140. https://doi.org/10.1111/ele.13400

Kusch, E., Davy, R., 2022. KrigR-a tool for downloading and statistically downscaling climate reanalysis data. Environ. Res. Lett. 17. https://doi.org/10.1088/1748-9326/ac48b3

LaManna, J.A., Belote, R.T., Burkle, L.A., Catano, C.P., Myers, J.A., 2017. Negative density dependence mediates biodiversity-productivity relationships across scales. Nat. Ecol. Evol. 1, 1107–1115. https://doi.org/10.1038/s41559-017-0225-4

LaRue, E.A., Knott, J.A., Domke, G.M., Chen, H.Y.H., Guo, Q., Hisano, M., Oswalt, C., Oswalt, S., Kong, N., Potter, K.M., Fei, S., 2023. Structural diversity as a reliable and novel predictor for ecosystem productivity. Front. Ecol. Environ. 21, 33–39. https://doi.org/10.1002/fee.2586

Lasky, J.R., Uriarte, M., Boukili, V.K., Chazdon, R.L., 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. Proc. Natl. Acad. Sci. U. S. A. 111, 5616–5621. https://doi.org/10.1073/pnas.1319342111

Laughlin, D.C., 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. J. Ecol. 102, 186–193. https://doi.org/10.1111/1365-2745.12187

Laurance, W.F., Oliveira, A.A., Laurance, S.G., 2004. Laurance et al._2004_Pervasive alteration of tree communities in undisturbed Amazonian forests(2).pdf. Nature 428, 171–175.

LeBauer, D.., Treseder, K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379. https://doi.org/https://doi.org/10.1890/06-2057.1

Lebrija-Trejos, E., Hernández, A., Wright, S.J., 2023. Effects of moisture and density-dependent interactions on tropical tree diversity. Nature 615, 100–104. https://doi.org/10.1038/s41586-023-05717-1

Lebrija-Trejos, E., Wright, S.J., Hernández, A., Reich, P.B., 2014. Does relatedness matter? Phylogenetic density-dependent survival of seedlings in a tropical forest. Ecology 95, 940–951. https://doi.org/10.1890/13-0623.1

Leibold, M.A., McPeek, M.A., 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87, 1399–1410. https://doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2

Lewis, S.L., Edwards, D.P., Galbraith, D., 2015. Increasing human dominance of tropical forests. Science (80-.). 349, 827–832. https://doi.org/10.1126/SCIENCE.AAA9932

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., Laurance, W.F., 2009. Changing ecology of tropical forests: Evidence and drivers. Annu. Rev. Ecol. Evol. Syst. 40, 529–549. https://doi.org/10.1146/annurev.ecolsys.39.110707.173345

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Brown, S., Chave, J., 2004. Concerted changes in tropical forest structure and dynamics : evidence from 50 South American long-term plots 421–436. https://doi.org/10.1098/rstb.2003.1431

Li, S., Wang, G., Zhu, C., Lu, J., Ullah, W., Fiifi Tawia Hagan, D., Kattel, G., Liu, Y., Zhang, Z., Song, Y., Sun, S., Zheng, Y., Peng, J., 2023. Vegetation growth due to CO2 fertilization is threatened by increasing vapor pressure deficit. J. Hydrol. 619, 129292. https://doi.org/10.1016/j.jhydrol.2023.129292

Li, T., Yang, S., Tan, M., 2019. Simulation and optimization of water supply and demand balance in Shenzhen: A system dynamics approach. J. Clean. Prod. 207, 882–893. https://doi.org/10.1016/j.jclepro.2018.10.052

Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H.Y.H., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L. V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science (80-.). 354. https://doi.org/10.1126/science.aaf8957

Liu, H., Johnson, D.J., Yang, Q., Xu, M., Ma, Z., Fang, X., Shang, Y., Wang, X., 2021. The dynamics of conspecific tree and seedling neighbors on seedling survival in a subtropical forest. For. Ecol. Manage. 483, 118924. https://doi.org/10.1016/j.foreco.2021.118924

Liu, H., Shen, G., Ma, Z., Yang, Q., Xia, J., Fang, X., Wang, X., 2016. Conspecific Leaf Litter-Mediated Effect of Conspecific Adult Neighborhood on Early-Stage Seedling Survival in A Subtropical Forest. Sci. Rep. 6, 1–8. https://doi.org/10.1038/srep37830

Liu, L., Gudmundsson, L., Hauser, M., Qin, D., Li, S., Seneviratne, S.I., 2020. Soil moisture dominates dryness stress on ecosystem production globally. Nat. Commun. 11, 1–9. https://doi.org/10.1038/s41467-020-18631-1

Lohbeck, M., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J.A., Poorter, L., Bongers, F., 2015. Functional trait strategies of trees in dry and wet tropical forests are similar but differ in their consequences for succession. PLoS One 10, 1–15. https://doi.org/10.1371/journal.pone.0123741

López, J., Way, D.A., Sadok, W., 2021. Systemic effects of rising atmospheric vapor pressure deficit on plant physiology and productivity. Glob. Chang. Biol. 27, 1704–1720. https://doi.org/10.1111/gcb.15548

Lu, H., Qin, Z., Lin, S., Chen, X., Chen, B., He, B., Wei, J., Yuan, W., 2022. Large influence of atmospheric vapor pressure deficit on ecosystem production efficiency. Nat. Commun. 13, 10–13. https://doi.org/10.1038/s41467-022-29009-w

Lu, S., Zhang, D., Wang, L., Dong, L., Liu, C., Hou, D., Chen, G., Qiao, X., Wang, Y., Guo, K., 2023. Comparison of plant diversity-carbon storage relationships along altitudinal gradients in temperate forests and shrublands. Front. Plant Sci. 14, 1–13. https://doi.org/10.3389/fpls.2023.1120050

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Softw. 6, 3139. https://doi.org/10.21105/joss.03139

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.W., Chao, K.J., Chao, W.C., Chiang, J.M., Chu, C., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau, B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.F., Hu, Y.H., Hubbell, S.P., Inman-Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson, A.J., Li, Y. De, Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.R., Malhi, Y., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny, V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips, R.P., Reynolds, G., Sack, L., Song, G.Z.M., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R., Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.H., Xu, H., Yamakura, T., Yap, S., Zimmerman, J.K., 2018. Global importance of large-diameter trees. Glob. Ecol. Biogeogr. 27, 849–864. https://doi.org/10.1111/geb.12747

Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. J. Ecol. 97, 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x

Magalhães, J.G. d. S., Amoroso, M.M., Larson, B.C., 2021. What evidence exists on the effects of competition on trees' responses to climate change? A systematic map protocol. Environ. Evid. 10, 1–10. https://doi.org/10.1186/s13750-021-00249-5

Malhi, Y., 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. J. Ecol. 100, 65–75. https://doi.org/10.1111/j.1365-2745.2011.01916.x

Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. African rainforests: Past, present and future. Philos. Trans. R. Soc. B Biol. Sci. 368. https://doi.org/10.1098/rstb.2012.0312

Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. J. Ecol. 97, 311–325. https://doi.org/10.1111/j.1365-2745.2008.01466.x

Markesteijn, L., Poorter, L., Bongers, F., Paz, H., Sack, L., 2011. Hydraulics and life history of tropical dry forest tree species : coordination of species ' drought and shade tolerance 480–495.

Marthews, T., Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Ruiz Jaén, M., Girardin, C., Butt, N., Cain, R., 2012. Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v3.0). http://gem.tropicalforests.ox.ac.uk/.

Martínez-Vilalta, J., Garcia-Forner, N., 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. Plant Cell Environ. 40, 962–976. https://doi.org/10.1111/pce.12846

Martnez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. Glob. Planet. Change 144, 94–108. https://doi.org/10.1016/j.gloplacha.2016.07.009

Matsuo, T., Poorter, L., van der Sande, M.T., Mohammed Abdul, S., Koyiba, D.W., Opoku, J., de Wit, B., Kuzee, T., Amissah, L., 2025. Drivers of biomass stocks and productivity of tropical secondary forests. Ecology 106, 1–18. https://doi.org/10.1002/ecy.4488

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science (80-.). 368. https://doi.org/10.1126/science.aaz9463

McDowell, N.G., Pockman, W., Allen, C., Breshears, D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought : why do some plants survive while others succumb to. New Phytol 178, 719–739.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F., Hurlbert, A.H., Magurran, A.E., Marquet, P.A., Maurer, B.A., Ostling, A., Soykan, C.U., Ugland, K.I., White, E.P., 2007. Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. Ecol. Lett. 10, 995–1015. https://doi.org/10.1111/j.1461-0248.2007.01094.x

Meinzer, F.C., Woodruff, D.R., Domec, J.C., Goldstein, G., Campanello, P.I., Gatti, M.G., Villalobos-Vega, R., 2008. Coordination of leaf and stem water transport properties in tropical forest trees. Oecologia 156, 31–41. https://doi.org/10.1007/s00442-008-0974-5

Mensah, S., Noulèkoun, F., Salako, V.K., Lokossou, C.S.M.J., Akouété, P., Seifert, T., Glèlè Kakaï, R., 2023. Structural and taxonomic diversity predict above-ground biomass better than functional measures of maximum height in mixed-species forests. Appl. Veg. Sci. 26, 1–13. https://doi.org/10.1111/avsc.12732

Moore, S., Adu-Bredu, S., Duah-Gyamfi, A., Addo-Danso, S.D., Ibrahim, F., Mbou, A.T., de Grandcourt, A., Valentini, R., Nicolini, G., Djagbletey, G., Owusu-Afriyie, K., Gvozdevaite, A., Oliveras, I., Ruiz-Jaen, M.C., Malhi, Y., 2018. Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. Glob. Chang. Biol. 24, e496–e510. https://doi.org/10.1111/gcb.13907

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

Muñoz-Sabater, J., Dutra, E., Agustí-Panareda, A., Albergel, C., Arduini, G., Balsamo, G., Boussetta, S., Choulga, M., Harrigan, S., Hersbach, H., Martens, B., Miralles, D.G., Piles, M., Rodríguez-Fernández, N.J., Zsoter, E., Buontempo, C., Thépaut, J.N., 2021. ERA5-Land: A state-of-the-art global reanalysis dataset for land applications. Earth Syst. Sci. Data 13, 4349–4383. https://doi.org/10.5194/essd-13-4349-2021

Murphy, H.T., Bradford, M.G., Dalongeville, A., Ford, A.J., Metcalfe, D.J., Precinct, E., Road, B., Park, D., 2013. No evidence for long-term increases in biomass and stem density in the tropical rain forests of Australia 1589–1597. https://doi.org/10.1111/1365-2745.12163

Murphy, L.E., 2015. Package ‘ likelihood ’. R package version 1.7.

Muscarella, R., Messier, J., Condit, R., Hubbell, S.P., Svenning, J.C., 2018. Effects of biotic interactions on tropical tree performance depend on abiotic conditions. Ecology 99, 2740–2750. https://doi.org/10.1002/ecy.2537

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Complete mitochondrial genome sequence of Gymnopilus junonius. Nature 403, 853–858. https://doi.org/https://doi.org/10.1038/35002501

Nadeau, M.B., Sullivan, T.P., 2015. Relationships between Plant Biodiversity and Soil Fertility in a Mature Tropical Forest, Costa Rica. Int. J. For. Res. 2015, 1–13. https://doi.org/10.1155/2015/732946

Nakagawa, S., Johnson, P.C.D., Schielzeth, H., 2017. The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface 14. https://doi.org/10.1098/rsif.2017.0213

Nelson, D., Sommers, L.E., 1982. MatterMethods of Soil Analysis. Part 2. Chemical and Microbiological Properties. Total Carbon, Org. Carbon, Org. Matter 9, 539–579.

Nemetschek, D., Derroire, G., Marcon, E., Aubry-Kientz, M., Auer, J., Badouard, V., Baraloto, C., Bauman, D., Le Blaye, Q., Boisseaux, M., Bonal, D., Coste, S., Dardevet, E., Heuret, P., Hietz, P., Levionnois, S., Maréchaux, I., McMahon, S.M., Stahl, C., Vleminckx, J., Wanek, W., Ziegler, C., Fortunel, C., 2024. Climate anomalies and neighbourhood crowding interact in shaping tree growth in old-growth and selectively logged tropical forests. J. Ecol. 1–23. https://doi.org/10.1111/1365-2745.14256

Newbery, D.M., Ridsdale, C.E., 2016. Neighbourhood abundance and small-tree survival in a lowland Bornean rainforest. Ecol. Res. 31, 353–366. https://doi.org/10.1007/s11284-016-1345-z

Noulèkoun, F., Birhane, E., Mensah, S., Kassa, H., Berhe, A., Gebremichael, Z.M., Adem, N.M., Seyoum, Y., Mengistu, T., Lemma, B., Hagazi, N., Abrha, H., 2021. Structural diversity consistently mediates species richness effects on aboveground carbon along altitudinal gradients in northern Ethiopian grazing exclosures. Sci. Total Environ. 776, 145838. https://doi.org/10.1016/j.scitotenv.2021.145838

Novick, K.A., Ficklin, D.L., Grossiord, C., Konings, A.G., Martínez-Vilalta, J., Sadok, W., Trugman, A.T., Williams, A.P., Wright, A.J., Abatzoglou, J.T., Dannenberg, M.P., Gentine, P., Guan, K., Johnston, M.R., Lowman, L.E.L., Moore, D.J.P., McDowell, N.G., 2024. The impacts of rising vapour pressure deficit in natural and managed ecosystems. Plant Cell Environ. 47, 3561–3589. https://doi.org/10.1111/pce.14846

Novick, K.A., Ficklin, D.L., Stoy, P.C., Williams, C.A., Bohrer, G., Oishi, A.C., Papuga, S.A., Blanken, P.D., Noormets, A., Sulman, B.N., Scott, R.L., Wang, L., Phillips, R.P., 2016. The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. Nat. Clim. Chang. 6, 1023–1027. https://doi.org/10.1038/nclimate3114

Oksanen, J., Simpson, G.L., Blanchet, F.G., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Durand, S., Beatriz, H., Evangelista, A., Friendly, M., Hannigan, G., Hill, M.O., Lahti, L., Mcglinn, D., Ribeiro, E., Smith, T., Stier, A., Ter, C.J.F., 2022. vegan: Community Ecology Package. R package version 2.6-4. [WWW Document]. URL https://cran.r-project.org/package=vegan

Olsen, S.R., Sommers, L.E., Page, A., 1982. Methods of soil analysis.

Ouyang, S., Xiang, W., Gou, M., Chen, L., Lei, P., Xiao, W., Deng, X., Zeng, L., Li, J., Zhang, T., Peng, C., Forrester, D.I., 2021. Stability in subtropical forests: The role of tree species diversity, stand structure, environmental and socio-economic conditions. Glob. Ecol. Biogeogr. 30, 500–513. https://doi.org/10.1111/geb.13235

Owusu, G., Anning, A.K., Belford, E.J.D., Acquah, E., 2022. Plant species diversity, abundance and conservation status of the Ankasa Resource Reserve, Ghana. Trees, For. People 8, 100264. https://doi.org/10.1016/j.tfp.2022.100264

Paine, C.E.T., Harms, K.E., Schnitzer, S.A., Carson, W.P., 2008. Weak competition among tropical tree seedlings: Implications for species coexistence. Biotropica 40, 432–440. https://doi.org/10.1111/j.1744-7429.2007.00390.x

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world’s forests. Science (80-.). 333, 988–993. https://doi.org/10.1126/science.1201609

Peguero, G., Coello, F., Sardans, J., Asensio, D., Grau, O., Llusià, J., Ogaya, R., Urbina, I., Van Langenhove, L., Verryckt, L.T., Stahl, C., Bréchet, L., Courtois, E.A., Chave, J., Hérault, B., Janssens, I.A., Peñuelas, J., 2023. Nutrient-based species selection is a prevalent driver of community assembly and functional trait space in tropical forests. J. Ecol. 111, 1218–1230. https://doi.org/10.1111/1365-2745.14089

Pellegrini, A.F.A., Socolar, J.B., Elsen, P.R., Giam, X., 2016. Trade-offs between savanna woody plant diversity and carbon storage in the Brazilian Cerrado. Glob. Chang. Biol. 22, 3373–3382. https://doi.org/10.1111/gcb.13259

Peña-Claros, M., Poorter, L., Alarcón, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano, M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L., Toledo, M., 2012. Soil Effects on Forest Structure and Diversity in a Moist and a Dry Tropical Forest. Biotropica 44, 276–283. https://doi.org/10.1111/j.1744-7429.2011.00813.x

Pérez-Ramos, I.M., Matías, L., Gómez-Aparicio, L., Godoy, Ó., 2019. Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-10453-0

Peters, R.L., Kaewmano, A., Fu, P.L., Fan, Z.X., Sterck, F., Steppe, K., Zuidema, P.A., 2023. High vapour pressure deficit enhances turgor limitation of stem growth in an Asian tropical rainforest tree. Plant Cell Environ. 46, 2747–2762. https://doi.org/10.1111/pce.14661

Phillips, O.L., Higuchi, N., Vieira, S., Baker, T.R., Chao, K., Lewis, S.L., 2009. Changes in Amazonian Forest Biomass , Dynamics , and Composition , 1980 – 2002 373–388.

Phillips, O.L., Lewis, S.L., 2014. Recent changes in tropical forest biomass and dynamics. For. Glob. Chang. 77–108. https://doi.org/10.1017/cbo9781107323506.006

Pineda-García, F., Paz, H., Meinzer, F.C., 2013. Drought resistance in early and late secondary successional species from a tropical dry forest: The interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. Plant, Cell Environ. 36, 405–418. https://doi.org/10.1111/j.1365-3040.2012.02582.x

Podlaski, R., 2019. Models of the fine-scale spatial distributions of trees in managed and unmanaged forest patches with Abies alba Mill. and Fagus sylvatica L. For. Ecol. Manage. 439, 1–8. https://doi.org/10.1016/j.foreco.2019.02.031

Pommerening, A., 2002. Approaches to quantifying forest structures. Forestry 75, 305–324. https://doi.org/10.1093/forestry/75.3.305

Pommerening, A., Sánchez Meador, A.J., 2018. Tamm review: Tree interactions between myth and reality. For. Ecol. Manage. 424, 164–176. https://doi.org/10.1016/j.foreco.2018.04.051

Poorter, L., Castilho, C. V., Schietti, J., Oliveira, R.S., Costa, F.R.C., 2018. Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. New Phytol. 219, 109–121. https://doi.org/10.1111/nph.15206

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J.C., Peña-Claros, M., Sterck, F., Villegas, Z., Sass-Klaassen, U., 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol. 185, 481–492. https://doi.org/10.1111/j.1469-8137.2009.03092.x

Poorter, L., Mcneil, A., Hurtado, V.H., Prins, H.H.T., Putz, F.E., 2014. Bark traits and life-history strategies of tropical dry- and moist forest trees. Funct. Ecol. 28, 232–242. https://doi.org/10.1111/1365-2435.12158

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

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manriquez, G., Harms, K.E., Licona, J.C., Martinez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates ? Evidence from five neotropical forests. Ecology 89, 1908–1920.

Qi, G., She, D., Xia, J., Song, J., Jiao, W., Li, J., Liu, Z., 2024. Soil moisture plays an increasingly important role in constraining vegetation productivity in China over the past two decades. Agric. For. Meteorol. 356, 110193. https://doi.org/10.1016/j.agrformet.2024.110193

R Core Team, 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rahman, M., Billah, M., Rahman, O., Datta, D., 2021. Disentangling the role of competition , light interception , and functional traits in tree growth rate variation in South Asian tropical moist forests. For. Ecol. Manage. 483, 118908. https://doi.org/10.1016/j.foreco.2020.118908

Réjou-Méchain, M., Mortier, F., Bastin, J.F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Deblauwe, V., Doucet, J.L., Doumenge, C., Fayolle, A., Garcia, C., Kibambe Lubamba, J.P., Loumeto, J.J., Ngomanda, A., Ploton, P., Sonké, B., Trottier, C., Vimal, R., Yongo, O., Pélissier, R., Gourlet-Fleury, S., 2021. Unveiling African rainforest composition and vulnerability to global change. Nature 593, 90–94.

https://doi.org/10.1038/s41586-021-03483-6

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753

Rifai, S.W., Girardin, C.A.J., Berenguer, E., Del Aguila-Pasquel, J., Dahlsjö, C.A.L., Doughty, C.E., Jeffery, K.J., Moore, S., Oliveras, I., Riutta, T., Rowland, L.M., Murakami, A.A., Addo-Danso, S.D., Brando, P., Burton, C., Ondo, F.E., Duah-Gyamfi, A., Amézquita, F.F., Freitag, R., Pacha, F.H., Huasco, W.H., Ibrahim, F., Mbou, A.T., Mihindou, V.M., Peixoto, K.S., Rocha, W., Rossi, L.C., Seixas, M., Silva-Espejo, J.E., Abernethy, K.A., Adu-Bredu, S., Barlow, J., Da Costa, A.C.L., Marimon, B.S., Marimon-Junior, B.H., Meir, P., Metcalfe, D.B., Phillips, O.L., White, L.J.T., Malhi, Y., 2018. ENSO Drives interannual variation of forest woody growth across the tropics. Philos. Trans. R. Soc. B Biol. Sci. 373. https://doi.org/10.1098/rstb.2017.0410

Rivers, M., Newton, A.C., Oldfield, S., 2023. Scientists' warning to humanity on tree extinctions. Plants People Planet 5, 466–482. https://doi.org/10.1002/ppp3.10314

Roswell, M., Dushoff, J., Winfree, R., 2021. A conceptual guide to measuring species diversity. Oikos 130, 321–338. https://doi.org/10.1111/oik.07202

Rowell, D.L., 1994. Soil Sciecne: Methods and Applications. Longman Group, Harlow.

Rozendaal, D.M.A., Phillips, O.L., Lewis, S.L., Affum-Baffoe, K., Alvarez-Davila, E., Andrade, A., Aragão, L.E.O.C., Araujo-Murakami, A., Baker, T.R., Bánki, O., Brienen, R.J.W., Camargo, J.L.C., Comiskey, J.A., Djuikouo Kamdem, M.N., Fauset, S., Feldpausch, T.R., Killeen, T.J., Laurance, W.F., Laurance, S.G.W., Lovejoy, T., Malhi, Y., Marimon, B.S., Marimon Junior, B.H., Marshall, A.R., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Poorter, L., Reitsma, J., Silveira, M., Sonké, B., Sunderland, T., Taedoumg, H., ter Steege, H., Terborgh, J.W., Umetsu, R.K., van der Heijden, G.M.F., Vilanova, E., Vos, V., White, L.J.T., Willcock, S., Zemagho, L., Vanderwel, M.C., 2020. Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. Ecology 101, 1–11. https://doi.org/10.1002/ecy.3052

Rozendaal, D.M.A., Zuidema, P.A., 2011. Dendroecology in the tropics: A review. Trees - Struct. Funct. 25, 3–16. https://doi.org/10.1007/s00468-010-0480-3

Rüger, N., Wirth, C., Wright, S.J., Condit, R., 2012. Functional traits explain light and size response of growth rates in tropical tree species. Ecology 93, 2626–2636. https://doi.org/10.1890/12-0622.1

Ruiz-Jaen, M.C., Potvin, C., 2011. Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. New Phytol. 189, 978–987. https://doi.org/10.1111/j.1469-8137.2010.03501.x

Rutishauser, E., Wright, S.J., Condit, R., Hubbell, S.P., Davies, S.J., Landau, H.C.M., 2020. Testing for changes in biomass dynamics in large - scale forest datasets 1485–1498. https://doi.org/10.1111/gcb.14833

Sanjeewani, N., Samarasinghe, D., Jayasinghe, H., Ukuwela, K., Wijetunga, A., Wahala, S., De Costa, J., 2024. Variation of floristic diversity, community composition, endemism, and conservation status of tree species in tropical rainforests of Sri Lanka across a wide altitudinal gradient. Sci. Rep. 14, 1–19. https://doi.org/10.1038/s41598-024-52594-3

Santiago, L.S., De Guzman, M.E., Baraloto, C., Vogenberg, J.E., Brodie, M., Hérault, B., Fortunel, C., Bonal, D., 2018. Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. New Phytol. 218, 1015–1024. https://doi.org/10.1111/nph.15058

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. Ecology 95, 2479–2492. https://doi.org/10.1890/13-1366.1

Schume, H., Jost, G., Hager, H., 2004. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. J. Hydrol. 289, 258–274. https://doi.org/10.1016/j.jhydrol.2003.11.036

Schwinning, S., 2010. Ecohydrology Bearing - Invited Commentary. The ecohydrology of roots in rocks. Ecohydrology 3, 238–245. https://doi.org/10.1002/eco

Schwinning, S., Weiner, J., 1998. Mechanisms the degree of size asymmetry determining in competition among plants. Oecologia 113, 447–455.

Seneviratne, S.I., Corti, T., Davin, E.L., Hirschi, M., Jaeger, E.B., Lehner, I., Orlowsky, B., Teuling, A.J., 2010. Investigating soil moisture-climate interactions in a changing climate: A review. Earth-Science Rev. 99, 125–161. https://doi.org/10.1016/j.earscirev.2010.02.004

Sheil, D., Salim, A., Chave, J., Vanclay, J., Hawthorne, W.D., 2006. Illumination-size relationships of 109 coexisting tropical forest tree species. J. Ecol. 94, 494–507. https://doi.org/10.1111/j.1365-2745.2006.01111.x

Shen, Y., Santiago, L.S., Ma, L., Lin, G., Lian, J., Cao, H., Ye, W.-H., 2013. Forest dynamics of a subtropical monsoon forest in Dinghushan , China : recruitment , mortality and the pace of community change Author (s): Yong Shen , Louis S . Santiago , Lei Ma , Guo-Jun Lin , Ju-Yu Lian , Hong-Lin Cao and Wan-Hui Ye Published by : J. Trop. Ecol. 29, 131–145. https://doi.org/10.1017/S02

Silvertown, J., 2004. Plant coexistence and the niche. Trends Ecol. Evol. 19, 605–611. https://doi.org/10.1016/j.tree.2004.09.003

Skiadaresis, G., Leban, J.M., Schnabel, F., Schwarz, J., Guillemot, J., Potvin, C., Bauhus, J., 2025. Interacting and dynamic effects of species and structural diversity promote annual woody biomass production in a tropical tree diversity experiment. For. Ecol. Manage. 593. https://doi.org/10.1016/j.foreco.2025.122844

Sperry, J.S., Hacke, U.G., Pittermann, J., 2006. Size and function in conifer tracheids and angiosperm vessels. Am. J. Bot. 93, 1490–1500. https://doi.org/10.3732/ajb.93.10.1490

Sperry, J.S., Wang, Y., Wolfe, B.T., Mackay, D.S., Anderegg, W.R.L., McDowell, N.G., Pockman, W.T., 2016. Pragmatic hydraulic theory predicts stomatal responses to climatic water deficits. New Phytol. 212, 577–589. https://doi.org/10.1111/nph.14059

Steege, H. Ter, Pitman, N.C.A., Killeen, T.J., Laurance, W.F., Peres, C.A., Guevara, J.E., Salomão, R.P., Castilho, C. V., Amaral, I.L., De Almeida Matos, F.D., De Souza Coelho, L., Magnusson, W.E., Phillips, O.L., De Andrade Lima Filho, D., De Jesus Veiga Carim, M., Irume, M.V., Martins, M.P., Molino, J.F., Sabatier, D., Wittmann, F., López, D.C., Da Silva Guimarães, J.R., Mendoza, A.M., Vargas, P.N., Manzatto, A.G., Reis, N.F.C., Terborgh, J., Casula, K.R., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Montoya, A.J.D., Zartman, C.E., Mostacedo, B., Vasquez, R., Assis, R.L., Medeiros, M.B., Simon, M.F., Andrade, A., Camargo, J.L., Laurance, S.G.W., Nascimento, H.E.M., Marimon, B.S., Marimon, B.H., Costa, F., Targhetta, N., Vieira, I.C.G., Brienen, R., Castellanos, H., Duivenvoorden, J.F., Mogollón, H.F., Piedade, M.T.F., Gerardo, A.A.C., Comiskey, J.A., Damasco, G., Dávila, N., García-Villacorta, R., Diaz, P.R.S., Vincentini, A., Emilio, T., Levis, C., Schietti, J., Souza, P., Alonso, A., Dallmeier, F., Ferreira, L.V., Neill, D., Araujo-Murakami, A., Arroyo, L., Carvalho, F.A., Souza, F.C., Do Amaral, D.D., Gribel, R., Luize, B.G., Pansonato, M.P., Venticinque, E., Fine, P., Toledo, M., Baraloto, C., Cerón, C., Engel, J., Henkel, T.W., Jimenez, E.M., Maas, P., Mora, M.C.P., Petronelli, P., Revilla, J.D.C., Silveira, M., Stropp, J., Thomas-Caesar, R., Baker, T.R., Daly, D., Paredes, M.R., Da Silva, N.F., Fuentes, A., Jørgensen, P.M., Schöngart, J., Silman, M.R., Arboleda, N.C., Cintra, B.B.L., Valverde, F.C., Di Fiore, A., Phillips, J.F., Van Andel, T.R., Von Hildebrand, P., Barbosa, E.M., De Matos Bonates, L.C., De Castro, D., De Sousa Farias, E., Gonzales, T., Guillaumet, J.L., Hoffman, B., Malhi, Y., De Andrade Miranda, I.P., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vela, C.I.A., Vos, V.A., Zent, E.L., Zent, S., Cano, A., Nascimento, M.T., Oliveira, A.A., Ramirez-Angulo, H., Ramos, J.F., Sierra, R., Tirado, M., Medina, M.N.U., Van Der Heijden, G., Torre, E.V., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., De Castro, N., Farfan-Rios, W., Ferreira, C., Mendoza, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Villarroel, D., Zagt, R., Alexiades, M.N., Garcia-Cabrera, K., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W.P., Pansini, S., Pauletto, D., Arevalo, F.R., Sampaio, A.F., Sandoval, E.H.V., Gamarra, L.V., 2015. Estimating the global conservation status of more than 15,000 Amazonian tree species. Sci. Adv. 1, 9–11. https://doi.org/10.1126/sciadv.1500936

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., Van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93. https://doi.org/10.1038/nature12914

Stévart, T., Dauby, G., Lowry, P., Blach-Overgaard, A., Droissart, V., Harris, D.J., Mackinder, A.B., Schatz, G.E., Sonké, B., Sosef, M.S.M., Svenning, J.C., Wieringa, J., Couvreur, T.L.P., 2019. A third of the tropical African flora is potentially threatened with extinction. Sci. Adv. 5. https://doi.org/10.1126/sciadv.aax9444

Stoll, P., Newbery, D.M., 2005. Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. Ecology 86, 3048–3062. https://doi.org/10.1890/04-1540

Stovall, A.E.L., Shugart, H., Yang, X., 2019. Tree height explains mortality risk during an intense drought. Nat. Commun. 10, 1–6. https://doi.org/10.1038/s41467-019-12380-6

Sulman, B.N., Roman, D.T., Yi, K., Wang, L., Phillips, R.P., Novick, K.A., 2016. High atmospheric demand for water can limit forest carbon uptake and transpiration as severely as dry soil. Geophys. Res. Lett. 43, 9686–9695. https://doi.org/10.1002/2016GL069416

Swaine, M.D., 1996. Rainfall and Soil Fertility as Factors Limiting Forest Species

Distributions in Ghana. J. Ecol. 84, 419. https://doi.org/10.2307/2261203

Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. Am. J. Bot. 94, 451–459. https://doi.org/10.3732/ajb.94.3.451

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ, USA.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ, USA.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science (80). 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254–264. https://doi.org/10.1111/j.1365-2745.2010.01741.x

Tyree, M.T., Sperry, J.S., 1989. Vulnerability of Xylem to Cavitation and Embolism. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 19–36. https://doi.org/10.1146/annurev.pp.40.060189.000315

Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., 2004a. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. Ecol. Monogr. 74, 591–614. https://doi.org/10.1890/03-4031

Uriarte, M., Condit, R., Canham, C.D., Hubbell, S.P., 2004b. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? J. Ecol. 92, 348–360. https://doi.org/10.1111/j.0022-0477.2004.00867.x

Uriarte, M., Hubbell, S.P., John, R., Condit, R., Canham, C.D., 2005. Neighbourhood effects on sapling growth and survival in a neotropical forest and the ecological-equivalence hypothesis, in: Burslem, D.F.R.P., Pinard, M.A., Hartley, S.E. (Ed.), Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge University Press, Cambridge, United Kingdom, pp. 89–106. https://doi.org/10.1017/cbo9780511541971.005

Uriarte, M., Lasky, J.R., Boukili, V.K., Chazdon, R.L., 2016. A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. Funct. Ecol. 30, 157–167. https://doi.org/10.1111/1365-2435.12576

Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., John Kress, W., Erickson, D., Forero-Montaña, J., Zimmerman, J.K., Thompson, J., 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: Implications for community assembly. Ecol. Lett. 13, 1503–1514. https://doi.org/10.1111/j.1461-0248.2010.01541.x

Valentini, R., Arneth, A., Bombelli, A., Castaldi, S., Cazzolla Gatti, R., Chevallier, F., Ciais, P., Grieco, E., Hartmann, J., Henry, M., Houghton, R.A., Jung, M., Kutsch, W.L., Malhi, Y., Mayorga, E., Merbold, L., Murray-Tortarolo, G., Papale, D., Peylin, P., Poulter, B., Raymond, P.A., Santini, M., Sitch, S., Vaglio Laurin, G., Van Der Werf, G.R., Williams, C.A., Scholes, R.J., 2014. A full greenhouse gases budget of africa: Synthesis, uncertainties, and vulnerabilities. Biogeosciences 11, 381–407. https://doi.org/10.5194/bg-11-381-2014

Valor, T., Coll, L., Forrester, D.I., Pretzsch, H., Río, M. del, Bielak, K., Brzeziecki, B., Binder, F., Hilmers, T., Sitková, Z., Tognetti, R., Ameztegui, A., 2024. Competitive effect, but not competitive response, varies along a climatic gradient depending on tree species identity. For. Ecosyst. 11. https://doi.org/10.1016/j.fecs.2024.100176

Wang, J., Xu, S., Xie, B., Zhu, C., Wu, X., Ji, K., Du, Q., 2025. Impacts of environment and forest type on the relationship between stand structure diversity and productivity in natural mixed forests. PLoS One 20, 1–18. https://doi.org/10.1371/journal.pone.0329730

Wang, T., Zhang, J., Li, Z., Lin, K., Zhou, W., Wu, G., Pan, M., Chen, X., 2025. Roles of Soil and Atmospheric Dryness on Terrestrial Vegetation Productivity in China - Which Dominates at What Thresholds. Earth's Futur. 13, 1–16. https://doi.org/10.1029/2024EF005469

Weiner, J., 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5, 360–364. https://doi.org/10.1016/0169-5347(90)90095-U

Weiner, J., 1984. Neighbourhood Interference Amongst Pinus Rigida Individuals. J. Ecol. 72, 183–195.

Weiner, J., Thomas, S.C., 2001. The Nature of Tree Growth and the Age-Related Decline in Forest Productivity. Oikos 94, 374–376.

Wen, R., Jiang, P., Qin, M., Jia, Q., Cong, N., Wang, X., Meng, Y., Yang, F., Liu, B., Zhu, M., Zu, J., Chen, N., 2023. Regulation of NDVI and ET negative responses to increased atmospheric vapor pressure deficit by water availability in global drylands. Front. For. Glob. Chang. 6. https://doi.org/10.3389/ffgc.2023.1164347

Weng, X.X., Guo, Y., Tang, Z., 2022. Spatial-temporal dependence of the neighborhood interaction in regulating tree growth in a tropical rainforest. For. Ecol. Manage. 508, 120032. https://doi.org/10.1016/j.foreco.2022.120032

West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric scaling laws in biology. Science (80-.). 276, 122–126. https://doi.org/10.1126/science.276.5309.122

West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. Proc. Natl. Acad. Sci. U. S. A. 106, 7040–7045. https://doi.org/10.1073/pnas.0812294106

Wheeler, J.K., Sperry, J.S., Hacke, U.G., Hoang, N., 2005. Inter-vessel pitting and cavitation in woody Rosaceae and other vessel led plants: A basis for a safety versus efficiency trade-off in xylem transport. Plant, Cell Environ. 28, 800–812. https://doi.org/10.1111/j.1365-3040.2005.01330.x

White, P.J., 1998. Calcium channels in the plasma membrane of root cells. Ann. Bot. 81, 173–183. https://doi.org/10.1006/anbo.1997.0554

Williams, C.A., Hanan, N.P., Neff, J.C., Scholes, R.J., Berry, J.A., Denning, A.S., Baker, D.F., 2007. Africa and the global carbon cycle. Carbon Balance Manag. 2. https://doi.org/10.1186/1750-0680-2-3

Wood, S.N., 2017. Generalized Additive Models: An Introduction with R, Second Edi. ed.

Chapman and Hall/CRC, 2017. https://doi.org/https://doi.org/10.1201/9781315370279

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. 96, 1463–1468. https://doi.org/10.1073/pnas.96.4.1463

Yang, J., Song, X., Zambrano, J., Chen, Y., Cao, M., Deng, X., Zhang, W., Yang, X., Zhang, G., Tang, Y., Swenson, N.G., Cao, M., 2021. Intraspecific variation in tree growth responses to neighbourhood composition and seasonal drought in a tropical forest 26–37. https://doi.org/10.1111/1365-2745.13439

Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong, W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E.M.S., Qin, Z., Quine, T., Sitch, S., Smith, W.K., Wang, F., Wu, C., Xiao, Z., Yang, S., 2019. Increased atmospheric vapor pressure deficit reduces global vegetation growth. Sci. Adv. 5, 1–12. https://doi.org/10.1126/sciadv.aax1396

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

Zhai, L., Will, R.E., Zhang, B., 2024. Structural diversity is better associated with forest productivity than species or functional diversity. Ecology 105, 1–14. https://doi.org/10.1002/ecy.4269

Zhang-Zheng, H., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Addo-Danso, S.D., Amissah, L., Valentini, R., Djagbletey, G., Anim-Adjei, K., Quansah, J., Sarpong, B., Owusu-Afriyie, K., Gvozdevaite, A., Tang, M., Ruiz-Jaen, M.C., Ibrahim, F., Girardin, C.A.J., Rifai, S., Dahlsjö, C.A.L., Riutta, T., Deng, X., Sun, Y., Prentice, I.C., Oliveras Menor, I., Malhi, Y., 2024. Contrasting carbon cycle along tropical forest aridity gradients in West Africa and Amazonia. Nat. Commun. 15, 1–9. https://doi.org/10.1038/s41467-024-47202-x

Zhang-Zheng, H., Malhi, Y., Ziemińska, K., Gvozdevaite, A., Peprah, T., Boakye, M., Adu-Bredu, S., Aguirre-Gutiérrez, J., Moore, S., Sandoval, D., Tang, M., Prentice, I.C., Oliveras Menor, I., 2025. A test of ecophysiological theories on tropical forest functional traits along a VPD gradient. Commun. Biol. 8, 1–13. https://doi.org/10.1038/s42003-025-08420-1

8. SUPPLEMENTARY MATERIAL

Supplement S1

S1.1 Correlation analyses

The effects of soil nutrients, as well as climate, on the composition and diversity of the different forest types were studied using Redundancy Analysis (RDA) and linear mixed-effects models (LMM), respectively. To ensure robust results in the RDA and LMM, multicollinearity between climate and soil variables was tested (Fig. S1.1). One variable from correlated pairs (r > |0.70|) was selected to improve model interpretation.

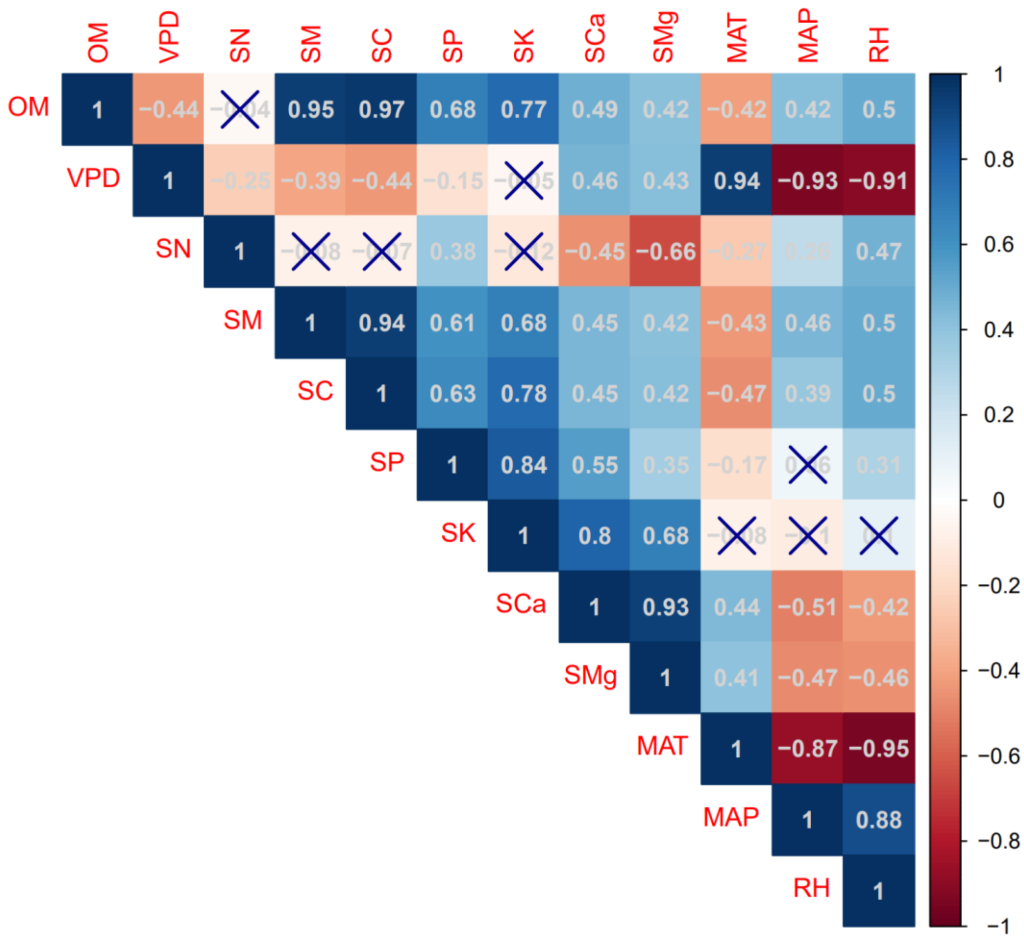

Figure S1.1: Spearman rank correlation matrix between environmental variables (SM = mean annual soil moisture; SC = soil total carbon; OM = soil organic matter; SN = soil total nitrogen; SP = soil available phosphorus; SK = exchangeable soil potassium; SMg = exchangeable soil magnesium; SCa = exchangeable soil calcium; VPD = dry season vapour pressure deficit; MAT

= mean annual temperature; MAP = mean annual precipitation; RH = relative humidity) across study sites. Colour intensity indicates correlation strength, with blue for positive and red for negative correlations. 'X' denotes insignificant correlations (p>0.05).

S1.2 Species abundance by family across forest types

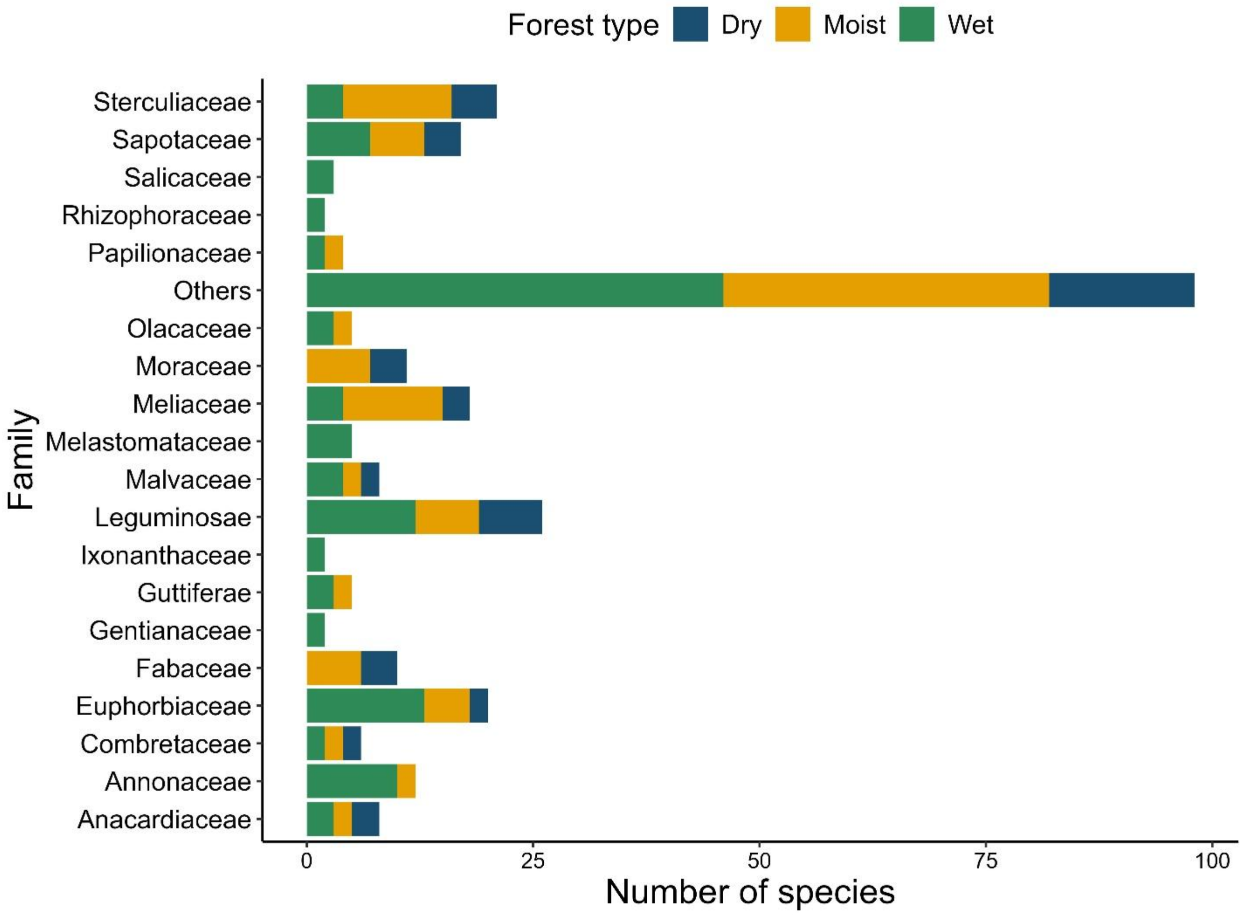

Figure S1.2: Composition of species at the family level across forest types. The category "Others" denotes families with two or fewer species per forest type.

S.1.3 Importance value index of species across forest types.

Table S1.3: List of tree species with the highest Importance Value Index (IVI), their family, relative frequency (RF), relative density (RD) and relative dominance (RBA) scores. Five species with the highest IVI were selected in each forest site.

			Wet forest				Moist forest				Dry forest			
SN	**Species name**	**Family**	**RF**	**RD**	**RBA**	**IVI**	**RF**	**RD**	**RBA**	**IVI**	**RF**	**RD**	**RBA**	**IVI**
1	*Ceiba pentandra*	Bombacaceae	-	-	-	-	1.36	0.97	2.64	4.97	3.70	2.80	12.11	18.62
2	*Celtis mildbraedii*	Ulmaceae	-	-	-	-	1.36	12.05	16.01	29.42	-	-	-	-
3	*Cola gigantea*	Sterculiaceae	0.35	0.16	0.18	0.69	0.91	0.85	0.93	2.69	2.47	6.68	7.87	17.02
4	*Cynometra ananta*	Leguminosae	1.06	4.19	14.13	19.39	-	-	-	-	-	-	-	-
5	*Funtumia elastica*	Apocynaceae	-	-	-	-	1.36	19.50	8.39	29.25	-	-	-	-
6	*Heritiera utilis*	Malvaceae	1.06	3.40	5.71	10.17	-	-	-	-	-	-	-	-
7	*Manilkara obovata*	Sapotaceae	1.06	0.63	0.30	2.00	-	-	-	-	2.47	7.54	7.21	17.22
8	*Nesogordonia papaverifera*	Sterculiaceae	-	-	-	-	1.36	5.06	7.34	13.77	-	-	-	-
9	*Pouteria alnifolia*	Sapotaceae	-	-	-	-	-	-	-	-	3.70	12.50	5.03	21.23
10	*Protomegabaria macrophylla*	Euphorbiaceae	1.06	9.96	8.33	19.36	-	-	-	-	-	-	-	-
11	*Sterculia rhinopetala*	Sterculiaceae	-	-	-	-	1.36	8.53	5.76	15.65	-	-	-	-
12	*Sterculia tragacantha*	Sterculiaceae	-	-	-	-	1.36	0.80	0.71	2.87	3.70	14.66	7.05	25.41
13	*Strephonema pseudocola*	Combretaceae	1.06	3.64	5.63	10.33	-	-	-	-	-	-	-	-
14	*Triplochiton scleroxylon*	Sterculiaceae	-	-	-	-	1.36	3.30	17.05	21.71	-	-	-	-
15	*Uapaca corbisieri*	Euphorbiaceae	1.06	1.82	7.96	10.84	-	-	-	-	-	-	-	-

S1.4 Regression results for Shannon diversity

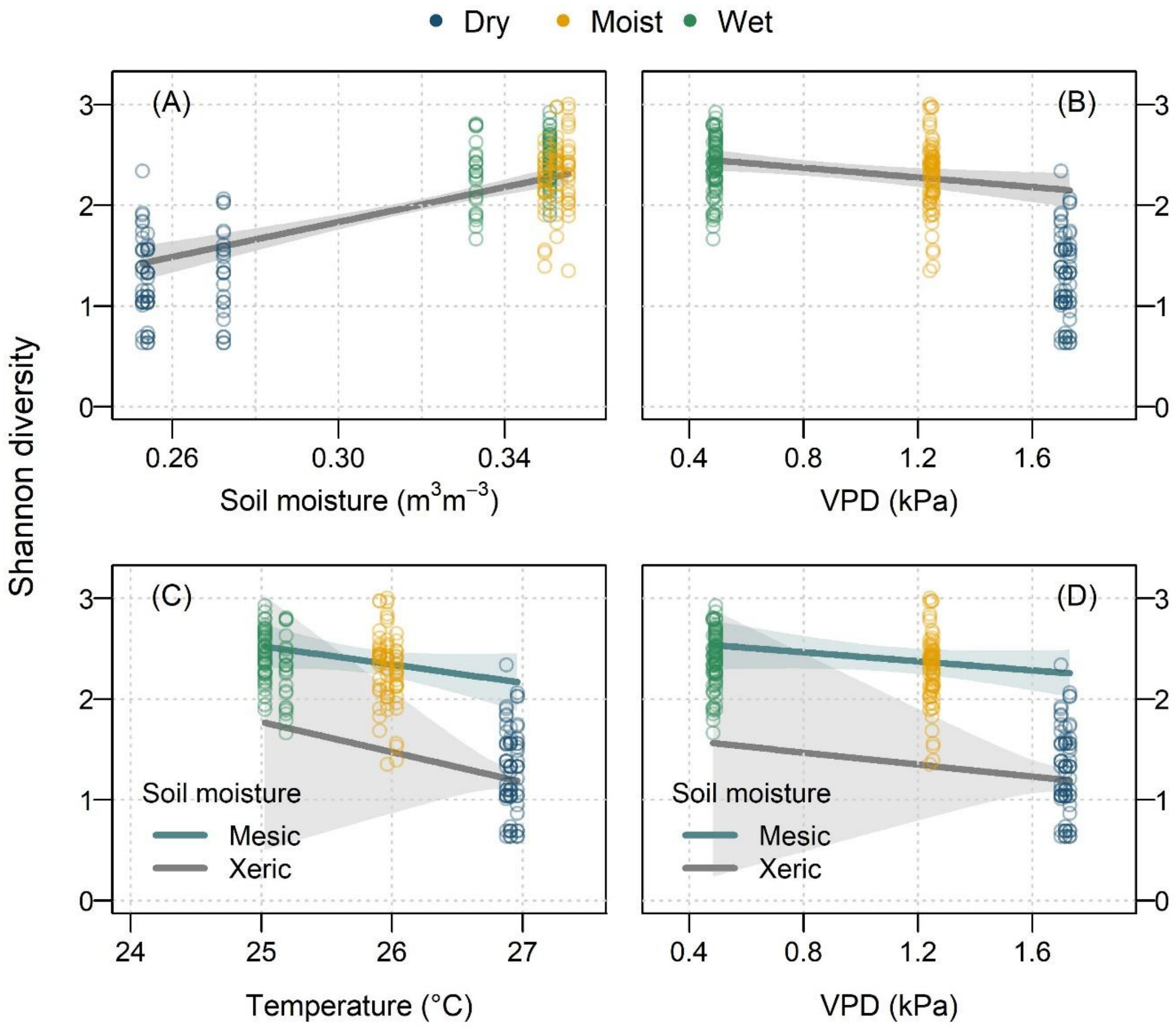

Figure S1.4: Estimated relationships from linear mixed models between Shannon diversity and mean annual soil moisture, dry season vapour pressure deficit (VPD) and mean annual temperature. (A) Effect of soil moisture while controlling for VPD (fixed at the observed median level). (B) Association between Shannon diversity and VPD for constant (median level) soil moisture. (C) Temperature effects for two levels of soil moisture: mesic conditions (blue curve) are the maximum observed moisture content levels; xeric conditions (grey) are the minimum levels. (D) VPD effects are shown in mesic versus xeric environments. Separate models were fitted for VPD and temperature due to their high collinearity. Interactions between temperature and soil moisture (C) and VPD and soil moisture (D) were non-significant

(p>0.05). Points represent subplot data (n = 225) for three forest types, and shaded areas indicate 95% confidence intervals.

S1.5 Regression results of relations between Conservation Value Index (CVI) and climate factors. The CVI accounts for the prevalence of rare species in a community and the number of at-risk species, according to the International Union for Conservation of Nature's (IUCN) Red List Criteria (IUCN, 2024).

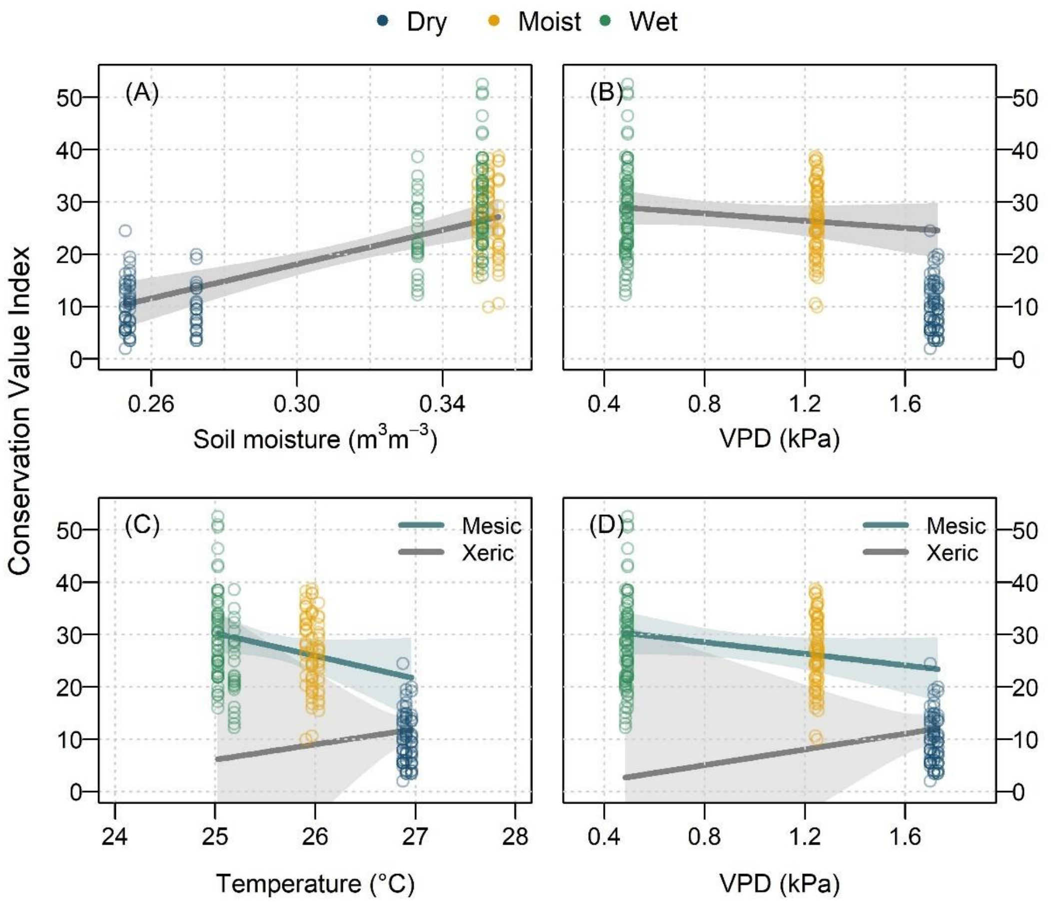

Figure S1.5: Estimated relationships from linear mixed models between Conservation value index (CVI) and variation in mean annual soil moisture, dry season vapour pressure deficit (VPD) and mean annual temperature. Panel A shows the effect of soil moisture while controlling for VPD (fixed at the observed median level). Panel B shows the association between CVI and VPD for constant (median level) soil moisture. In panel C, temperature effects are shown for two levels of soil moisture: mesic conditions (blue curve) are the maximum observed levels of moisture content; xeric conditions (grey) are the minimum levels. In panel D, VPD effects are shown in mesic versus xeric environments. Separate models were fit with VPD and temperature variables, as VPD was highly correlated with temperature. Interactions between temperature and soil moisture (C) and between VPD and soil moisture (D) were both non-significant by traditional p-value thresholds ($p>0.05$). Points are the model fitting data for three forest types (dry, moist and wet). Models were fitted with subplot data (n=225). The shaded regions delineate a 95% confidence interval around fitted lines.

Supplement S2

S2.1 Assessment of correlations among predictors for species and community-level biomass growth

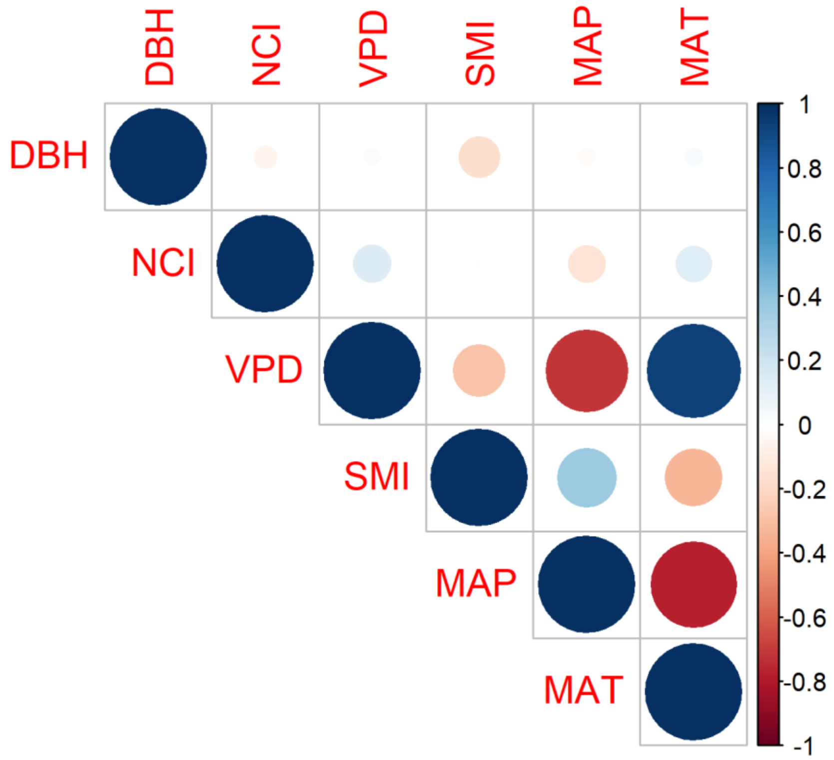

Figure S2.1: Spearman correlation matrix among key predictor variables used in species-specific generalised additive mixed-effect models (GAMMs). Variables include tree diameter at breast height (DBH), neighbourhood crowding index (NCI), and dry season climatic variables, including vapour pressure deficit (VPD), soil moisture index (SMI), mean annual precipitation (MAP), and mean annual temperature (MAT). Colour intensity indicates the strength and direction of correlation (blue = positive, red = negative), while circle size reflects the absolute strength of the correlation (|r|), with larger circles representing stronger relationships.

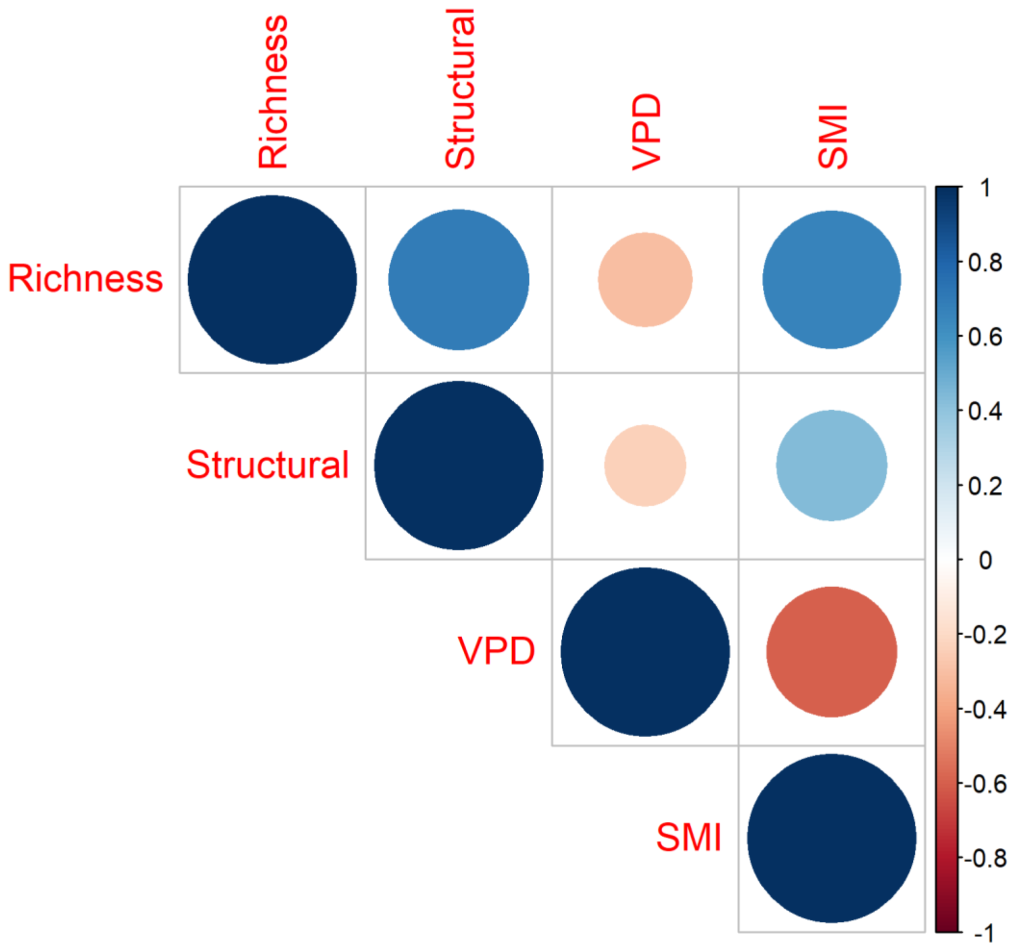

Figure S2.1.1: Spearman correlation matrix showing relationships among key predictor variables included in the community-level generalised additive mixed-effect models (GAMMs). Predictors encompass subplot-level community, structural, and environmental factors: species richness (Richness), structural diversity (Structural), and dry-season vapour pressure deficit (VPD), as well as soil moisture index (SMI). The colour gradient denotes the direction and magnitude of correlations (blue = positive, red = negative), whereas circle size represents the absolute correlation strength (|r|), with larger circles indicating stronger associations.

Table S2.1: Community-level biomass growth responses to biotic and abiotic factors

Model	Explanatory variables	df	AIC	ΔAIC	R^2	Rank
M1	SMI +VPD + forest type	9	742.96	324.32	35.7	3
M2	M1 + Structural	11	645.11	226.46	52.8	2
M3	**Structural + te(SMI × VPD) + forest type**	**22**	**418.64**	**0**	**54.3**	**1**

Notes: Models were fitted using generalised additive mixed effects models (GAMMs). Predictors include soil moisture index (SMI), vapour pressure deficit (VPD), and structural diversity (Structural). df refers to the estimated degrees of freedom for each model, including fixed effect parameters and smooth terms. ΔAIC values are relative to the best-supported model (lowest AIC). Adjusted R^2 represent the proportion of variance explained by the model, accounting for both the number of predictors and smooth terms. *te*(SMI × VPD) denotes a tensor interaction smooth term capturing the joint effect of SMI and VPD.

S.2.2 Effects of neighbourhood crowding index (NCI) on species-specific biomass growth

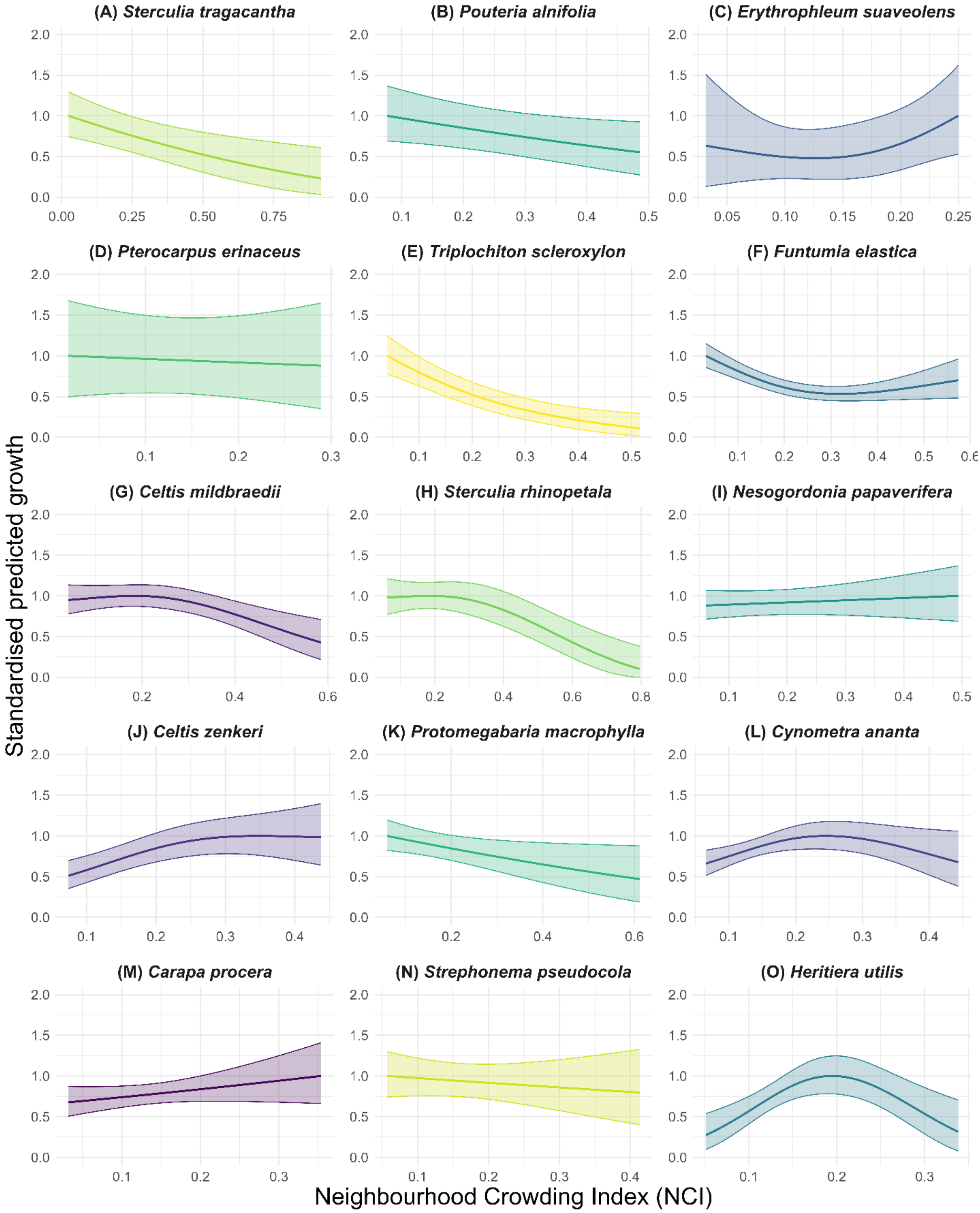

Figure S.2.2: Species-specific effects of neighbourhood crowding index on relative biomass growth. Lines show predicted relative growth from the best species-level GAMMs at the individual tree scale, and shaded areas represent 95% confidence intervals. Predictions were scaled to the maximum growth per species to facilitate comparison across species.

Table S2.2: Summary of best-fitting GAMM models by species

Species names	Model terms	N	AIC	ΔAIC	R^2	Rank
Carapa procera	DBH + NCI	294	1512.22	22.49	0.378	4
	DBH + NCI + SMI	294	1502.56	12.83	0.41	2
	DBH + NCI + SMI + VPD	294	1507.42	17.69	0.411	3
	DBH + NCI + SMI x VPD	294	1489.73	**0**	**0.419**	**1**
Celtis mildbraedii	DBH + NCI	1828	8996.35	82.38	0.631	4
	DBH + NCI + SMI	1828	8925.27	11.30	0.637	3
	DBH + NCI + SMI + VPD	1828	8922.09	8.13	0.638	2
	DBH + NCI + SMI x VPD	1828	8913	**0**	**0.638**	**1**
Celtis zenkeri	DBH + NCI	685	3053.94	61.94	0.348	4
	DBH + NCI + SMI	685	2997.60	5.60	0.383	2
	DBH + NCI + SMI + VPD	685	3001.10	9.10	0.380	3
	DBH + NCI + SMI x VPD	685	2992.79	**0**	**0.380**	1
Cynometra ananta	DBH + NCI	403	2703.66	77.41	0.288	4
	DBH + NCI + SMI	403	2665.32	39.07	0.362	3
	DBH + NCI + SMI + VPD	403	2643.82	17.57	0.396	2
	DBH + NCI + SMI x VPD	403	2626.25	**0**	**0.410**	**1**
Erythrophleum suaveolens	DBH + NCI	150	1012.03	13.78	0.21	4
	DBH + NCI + SMI	150	1010.85	12.60	0.23	3
	DBH + VPD + NCI x SMI	150	1003.14	4.89	0.24	2
	DBH + NCI + SMI x VPD	150	988.25	**0**	**0.27**	**1**

Species names	Model terms	N	AIC	ΔAIC	R^2	Rank
Funtumia elastica	DBH + NCI	2620	9816.88	150.2	0.204	4
	DBH + NCI + SMI	2620	9686.29	19.61	0.22	3
	DBH + NCI + SMI + VPD	2620	9683.47	16.79	0.212	2
	DBH + NCI + SMI x VPD	2620	9666.68	**0**	**0.217**	**1**
Heritiera utilis	DBH + NCI	317	1762.04	30.60	0.659	4
	DBH + NCI + SMI	317	1741.19	9.75	0.686	2
	DBH + NCI + SMI + VPD	317	1744.52	16.79	0.688	3
	DBH + NCI + SMI x VPD	317	1734.23	**0**	**0.686**	**1**
Nesogordonia papaverifera	DBH + NCI	796	4155.70	52.88	0.554	4
	DBH + NCI + SMI	796	4117.94	15.13	0.570	3
	DBH + NCI + SMI + VPD	796	4110.03	7.22	0.571	2
	DBH + NCI + SMI x VPD	796	4102.81	**0**	**0.572**	**1**
Pouteria alnifolia	DBH + NCI	399	2036.46	15.07	0.165	4
	DBH + NCI + SMI	399	2035.97	14.58	0.157	3
	DBH + NCI + SMI + VPD	399	2027.94	6.55	0.194	2
	DBH + NCI + SMI x VPD	399	2021.39	**0**	**0.191**	**1**
Protomegabaria macrophylla	DBH + NCI	506	2732.61	34.64	0.473	4
	DBH + NCI + SMI	506	2708.08	10.11	0.506	2
	DBH + NCI + SMI +VPD	506	2711.99	14.02	0.505	3
	DBH + NCI + SMI x VPD	506	2697.97	**0**	**0.511**	**1**
Pterocarpus erinaceus	DBH + NCI	149	895.72	8.38	0.279	2

Species names	Model terms	N	AIC	ΔAIC	R^2	Rank
	DBH + NCI + SMI	149	898.74	11.39	0.270	4
	DBH + NCI + SMI +VPD	149	898.68	11.34	0.291	3
	DBH + NCI + SMI x VPD	149	887.34	**0**	**0.289**	1
Sterculia rhinopetala	DBH + NCI	1228	5646.19	35.64	0.557	4
	DBH + NCI + SMI	1228	5619.44	8.89	0.561	3
	DBH + NCI + SMI +VPD	1228	5616.62	6.07	0.562	2
	DBH + NCI + SMI x VPD	1228	5610.55	**0**	**0.561**	**1**
Sterculia tragacantha	DBH + NCI	669	3369.06	19.22	0.178	4
	DBH + NCI + SMI	669	3355.10	5.26	0.226	2
	DBH + NCI + SMI +VPD	669	3356.02	6.18	0.228	3
	DBH + NCI + SMI x VPD	669	3349.84	**0**	**0.227**	**1**
Strephonema pseudocola	DBH + NCI	232	1372.63	20.49	0.401	6
	DBH + NCI + SMI	232	1364.90	9.85	0.429	4
	DBH + NCI + SMI +VPD	232	1365.	9.95	0.426	5
	DBH + NCI + SMI x VPD	232	1355.05	**0**	**0.427**	**1**
Triplochiton scleroxylon	DBH + NCI	535	2769.55	25.69	0.790	3
	DBH + NCI + SMI	535	2745.71	1.75	0.795	1
	DBH + NCI + SMI +VPD	535	2750.64	6.78	0.795	2
	DBH + NCI + SMI x VPD	535	2743.86	**0**	**0.794**	**1**

Notes: Each row represents a candidate generalised additive mixed-effects model (GAMM) fitted separately for each focal species. DBH = diameter at breast height; NCI = neighbourhood crowding index; SMI = soil moisture index; VPD = vapour pressure deficit. N = number of observations for each model. Interaction terms (e.g., SMI × VPD) refer to tensor product smooths between predictors. ΔAIC indicates the difference in AIC relative to the best-fitting model for each species (ΔAIC = 0). Models with ΔAIC < 2 were considered to have comparable support. R^2 = adjusted R^2. Rank reflects model ranking based on AIC, with Rank 1 being the best-fitting model per species.

Supplement S3

S3.1 Species-specific distance-dependent competition effects

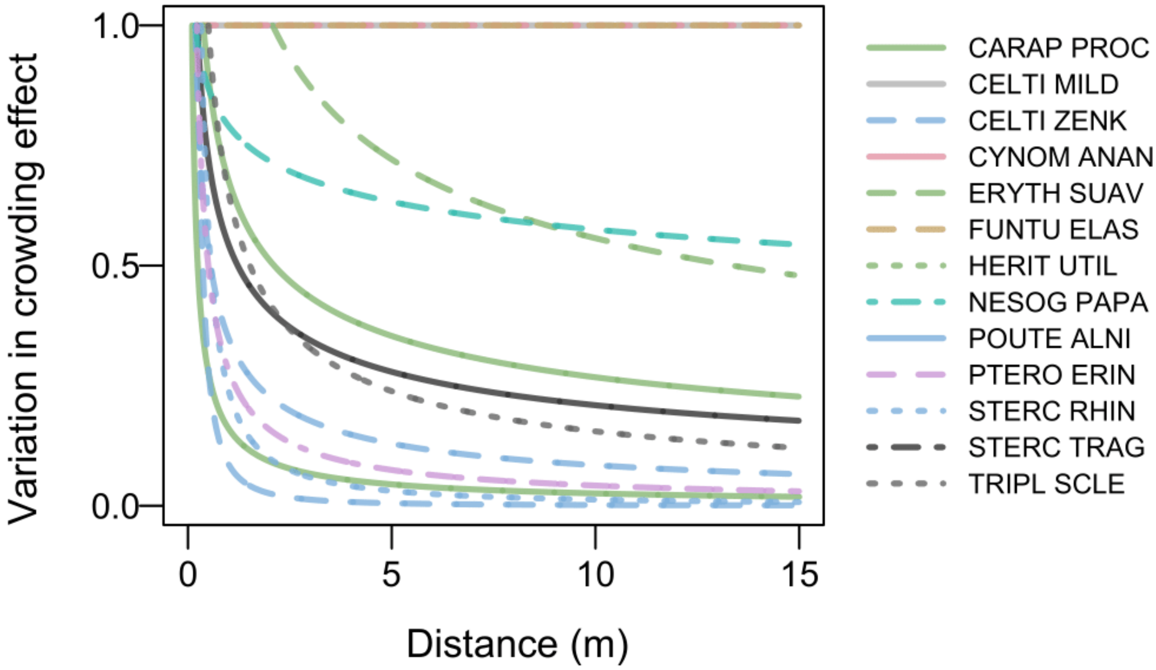

Figure S3.1. Variation in the competition effect of a 30 cm neighbour on an equivalent-sized target tree as a function of distance (for 13 species with non-neutral models). See Table 3 for full species names.

S3.2 Model validation: observed vs. predicted basal area increment for species-specific best model

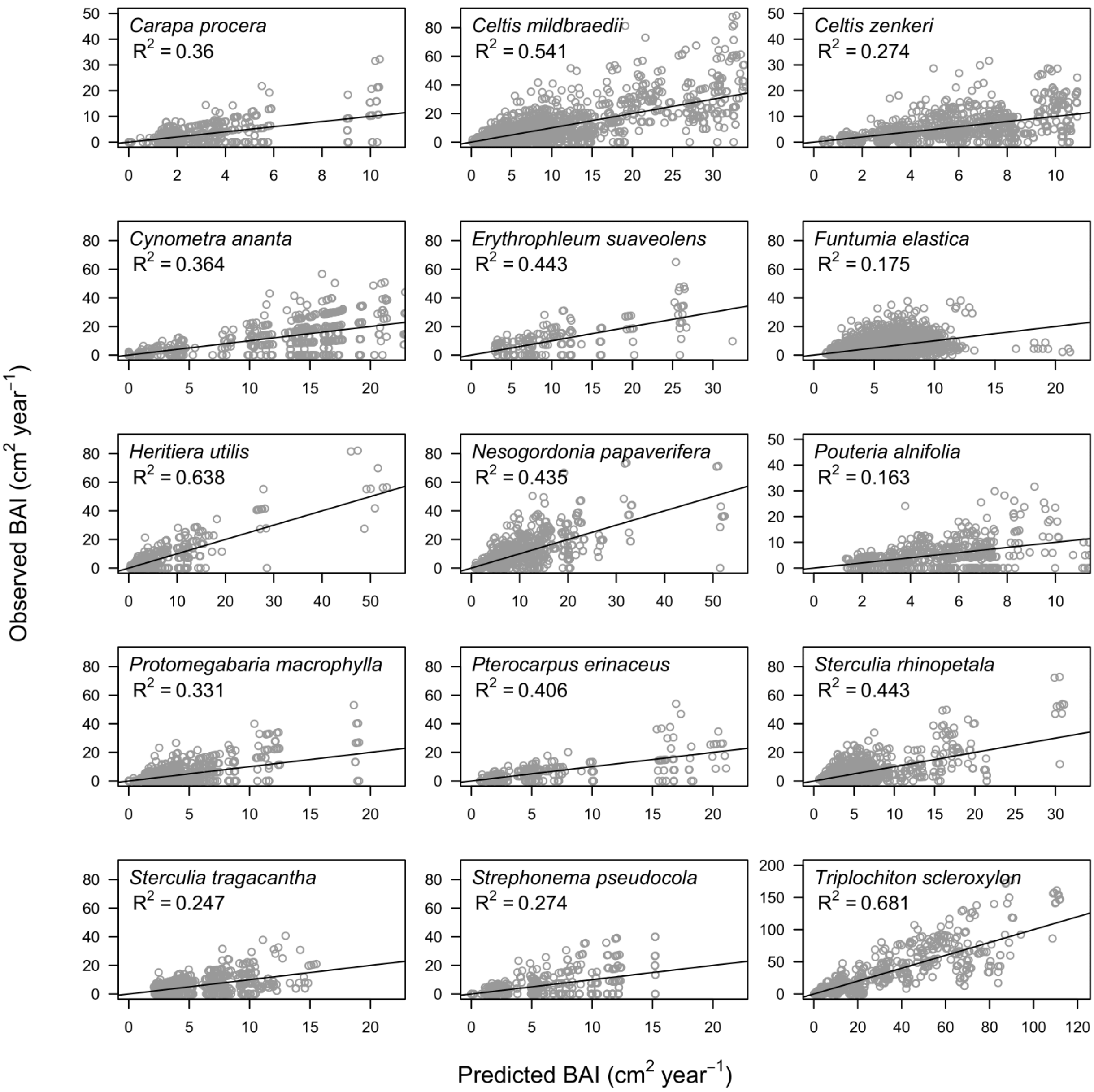

Figure S3.2: Scatterplots showing the relationship between observed and model-predicted annual basal area increment (BAI, cm^2 year^{-1}) for the best model for each species. Each point represents an individual tree measurement. The coefficient of determination (R^2) is reported for each species, indicating the proportion of variance explained by the model.

S3.3 Growth responses to soil moisture and neighbourhood crowding

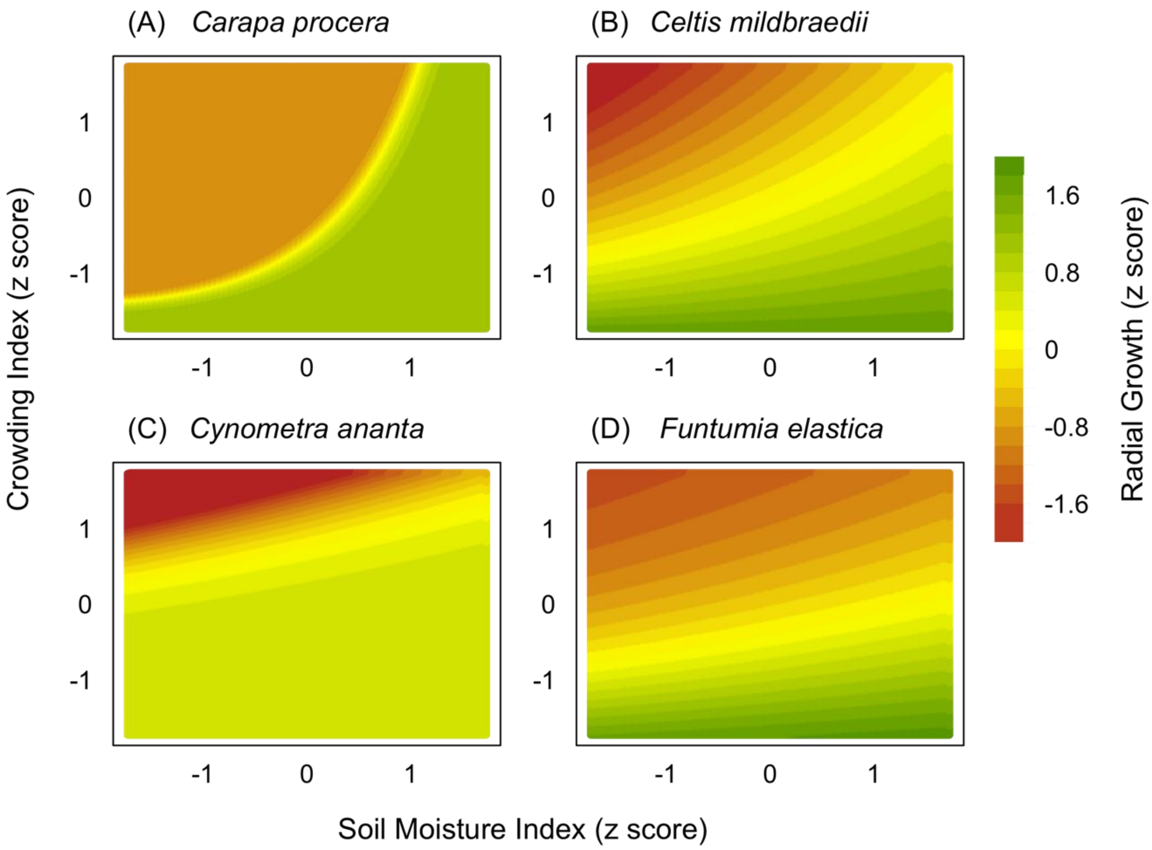

Figure S3.3: Predicted growth responses in a 30 cm tree for a subset (4 of 6) of focal species that were sensitive to the combined effects of variation in soil moisture and variability in the density and configuration of neighbouring trees (competition index). Responses are independent of neighbour trait variation. Neighbour traits are fixed at a mean level. All variables (competition, soil moisture, and radial growth) are shown as z-scores.