UNIVERSITY OF LEEDS

This is a repository copy of *Toward a coordinated understanding of hydro-biogeochemical root functions in tropical forests for application in vegetation models*.

White Rose Research Online URL for this paper:
https://eprints.whiterose.ac.uk/211418/

Version: Accepted Version

---

**Article:**

Cusack, D.F. orcid.org/0000-0003-4681-7449, Christoffersen, B. orcid.org/0000-0002-4890-9999, Smith-Martin, C.M. orcid.org/0000-0002-6557-1432 et al. (23 more authors) (2024) Toward a coordinated understanding of hydro-biogeochemical root functions in tropical forests for application in vegetation models. New Phytologist, 242 (2). pp. 351-371. ISSN 0028-646X

https://doi.org/10.1111/nph.19561

---

© 2024 The Authors New Phytologist © 2024 New Phytologist Foundation. This is the peer reviewed version of the following article: Cusack, D.F. , Christoffersen, B. , Smith-Martin, C.M. et al. (23 more authors) (2024) Toward a coordinated understanding of hydro-biogeochemical root functions in tropical forests for application in vegetation models. New Phytologist, 242 (2). pp. 351-371. ISSN 0028-646X, which has been published in final form at https://doi.org/10.1111/nph.19561. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Use of Self-Archived Versions. This article may not be enhanced, enriched or otherwise transformed into a derivative work, without express permission from Wiley or by statutory rights under applicable legislation. Copyright notices must not be removed, obscured or modified. The article must be linked to Wiley's version of record on Wiley Online Library and any embedding, framing or otherwise making available the article or pages thereof by third parties from platforms, services and websites other than Wiley Online Library must be prohibited.

**Reuse**

Items deposited in White Rose Research Online are protected by copyright, with all rights reserved unless indicated otherwise. They may be downloaded and/or printed for private study, or other acts as permitted by national copyright laws. The publisher or other rights holders may allow further reproduction and re-use of the full text version. This is indicated by the licence information on the White Rose Research Online record for the item.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing eprints@whiterose.ac.uk including the URL of the record and the reason for the withdrawal request.

White Rose
university consortium
Universities of Leeds, Sheffield & York

eprints@whiterose.ac.uk
https://eprints.whiterose.ac.uk/

Viewpoint:

# Toward a coordinated understanding of hydro-biogeochemical root functions in tropical forests for application in vegetation models

Daniela F. Cusack[1,2*], Bradley Christoffersen[3], Chris M. Smith-Martin[4], Kelly M. Andersen[5], Amanda L. Cordeiro[1,2], Katrin Fleischer[6], S. Joseph Wright[2], Nathaly R. Guerrero-Ramírez[7,8], Laynara F. Lugli[9], Lindsay A. McCulloch[10,11], Mareli Sanchez-Julia[12], Sarah A. Batterman[13,14,2], Caroline Dallstream[15], Claire Fortunel[16], Laura Toro[17], Lucia Fuchslueger[18], Michelle Y. Wong[13,19], Daniela Yaffar[20], Joshua B. Fisher[21], Marie Arnaud[22,23], Lee H. Dietterich[1,24,25,26], Shalom D. Addo-Danso[27], Oscar J. Valverde-Barrantes[28], Monique Weemstra[29], Jing Cheng Ng[5], Richard J. Norby[30]

[1]Department of Ecosystem Science and Sustainability, Warner College of Natural Resources, Colorado State University. Fort Collins, CO 80523-1476, USA

[2]Smithsonian Tropical Research Institute, Apartado 0843–03092, Balboa, Republic of Panama

[3]School of Integrative Biological and Chemical Sciences, The University of Texas Rio Grande Valley, Edinburg, TX 78539, USA

[4]Department of Plant and Microbial Biology, University of Minnesota, St. Paul, Minnesota, 55108, USA

[5]Nanyang Technological University, Singapore, 639798, Singapore

[6]Max-Planck-Institute for Biogeochemistry, Department Biogeochemical Signals, Hans-Knöll-Straße 10, 07745, Jena, Germany

[7]Silviculture and Forest Ecology of Temperate Zones, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen 37077, Germany

[8]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen 37077, Germany

[9]School of Life Sciences, Technical University of Munich, Freising, 85354 Germany

[10]Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St. Cambridge, MA, 02138, USA

[11]National Center for Atmospheric Research, National Oceanographic and Atmospheric Agency, 1850 Table Mesa Dr., Boulder, CO, 80305, USA

[12]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, 70118, USA

[13]Cary Institute of Ecosystem Studies, Millbrook, New York, 12545, USA

[14]School of Geography, University of Leeds, Leeds, LS2 9JT, United Kingdom

[15]Department of Biology, McGill University, 1205 Av. du Docteur-Penfield, Montreal, Quebec, H3A 1B1, Canada

[16]AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, 34398 Montpellier, France

[17]Yale Applied Science Synthesis Program, The Forest School at the Yale School of the Environment, Yale University, New Haven, Connecticut, 06511, USA

[18]Centre for Microbiology and Environmental Systems Science, University of Vienna, 1030 Vienna, Austria

[19]Department of Ecology and Evolutionary Biology, Yale University, 06511, USA

[20]Functional Forest Ecology, Universität Hamburg, 22885 Barsbüttel, Germany

[21]Schmid College of Science and Technology, Chapman University, 1 University Drive, Orange, CA, 92866, USA

[22]Institute of Ecology and Environmental Sciences (IEES), UMR 7618, CNRS-Sorbonne University-INRAE-UPEC-IRD, 75005 Paris, France

[23]School of Geography, Earth and Environmental Sciences & BIFOR , University of Birmingham, Edgbaston, Birmingham, B15 2TT, United Kingdom

[24]Department of Ecosystem Science and Sustainability, Warner College of Natural Resources, Colorado State University, 1231 Libbie Coy Way, A104, Fort Collins, CO, 80523, USA

[25]U.S. Army Engineer Research and Development Center, Environmental Laboratory, Vicksburg, MS, 39180, USA

[26]Department of Biology, Haverford College, Haverford, PA, 19003, USA

[27]Forests and Climate Change Division, CSIR-Forestry Research Institute of Ghana, P.O Box UP 63, KNUST, Kumasi, Ghana

[28]Department of Biological Sciences, International Center for Tropical Biodiversity, Florida International University, Miami, FL 33199, USA

[29]Department of Biological Sciences, International Center for Tropical Biodiversity, Florida International University, Miami, FL 33199, USA

[30]Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

* Author for correspondence (Daniela.Cusack@colostate.edu)

**Social Media**

**On X (previously Twitter): @DanielaCusack and @TropiRoot**

## Summary

Tropical forest root characteristics and resource acquisition strategies are underrepresented in vegetation and global models, hampering prediction of forest-climate feedbacks for these carbon-rich ecosystems. Lowland tropical forests often have globally unique combinations of high taxonomic and functional biodiversity, rainfall seasonality, and strongly weathered infertile soils, giving rise to distinct patterns in root traits and functions compared with higher latitude ecosystems. We provide a roadmap for integrating recent advances in our understanding of tropical forest belowground function into vegetation models, focusing on water and nutrient acquisition. We offer comparisons of recent advances in empirical and model understanding of root characteristics that represent important functional processes in tropical forests. We focus on: 1) fine-root strategies for soil resource exploration, 2) coupling and tradeoffs in fine root water versus nutrient acquisition, and 3) above-belowground linkages in plant resource acquisition and use. We suggest avenues for representing these extremely diverse plant communities in computationally manageable and ecologically meaningful groups in models for above- and belowground hydro-nutrient functions. Tropical forests are undergoing warming, shifting rainfall regimes, and exacerbation of soil nutrient scarcity caused by elevated atmospheric $CO_2$. Accurate model representation of tropical forest functions is crucial for understanding interactions of this biome with climate.

## Key Words

Fine roots, tropical forests, ecosystem vegetation models, plant functional types, root trait clusters, hydraulics, nutrient acquisition, phosphorus uptake

## Introduction

Tropical forests are poorly characterized in vegetation models relative to other ecosystems, and representation of root function lags that of aboveground function (Warren *et al*., 2015; Bonan & Doney, 2018). Tropical forests have the highest rates of net primary production (NPP) on Earth and contain ~30% of terrestrial carbon (C) stocks (Field *et al.*, 1998; Jobbágy & Jackson, 2000; Hengl *et al.*, 2017), with at least 36% of tropical forest NPP allocated belowground (Aragao *et al.*, 2009; Malhi *et al.*, 2011; Huasco *et al.*, 2021). Fine roots are typically considered the absorptive portion of the root structure, which absorb nutrients and water (Guo *et al.*, 2008; McCormack *et al.*, 2015, Table 1). These are typically classified as <2 mm diameter and include branching orders 1 – 3 (e.g., root tips are first order, e.g., https://youtu.be/q_ICrIL62qg, (Freschet *et al.*, 2021a). Understanding and representing tropical forests' water and nutrient cycling is of particular importance in the context of changing tropical forest rainfall regimes and warming (IPCC 2021) and increased relative nutrient scarcity brought on by accelerated photosynthesis of plants grown under elevated atmospheric carbon dioxide ($CO_2$) concentrations (i.e., $CO_2$ fertilization) (Hungate *et al.*, 2003; Fisher *et al.*, 2012; Fleischer *et al.*, 2019).

Tropical forests in particular are distinct from higher latitude ecosystems across several abiotic and biotic dimensions, giving rise to unique patterns of root traits and functions. The unique aspects of tropical forests include combinations of high plant diversity (Eiserhardt *et al.*, 2017), seasonality dominated by rainfall rather than temperature changes, and the predominance of lowland tropical forests on strongly weathered soils poor in phosphorus (P) and base cations, which represent >50% of tropical forests (Holzman, 2008), and commonly leads to P or multi-nutrient limitation to NPP (Vitousek & Sanford, 1986; Cunha *et al.*, 2022). Tropical forests also have large variation in ecosystem characteristics, including exceptions to the above trends such as monodominant stands of particular species or families (e.g., Dipterocarpaceae) (Janzen, 1974; Hart *et al.*, 1989; Peh *et al.*, 2011), high-fertility soils (e.g., Quesada *et al.*, 2011; Cusack *et al.*, 2018), a lack of marked seasonality in rainfall, and/or strong sunlight seasonality because of changes in cloud cover (Yang *et al.*, 2021). Thus, tropical forests have high alpha and beta diversity (Condit *et al.*, 2002), both for organisms and ecosystem characteristics, which create empirical and modeling challenges for characterizing and condensing species into meaningful groups.

Large-scale models have often worked well with only rudimentary root system functionality or none at all (Matamala & Stover 2013), but this functionality can break down when models are confronted with global change factors that alter relationships among soil, plants, and atmosphere (e.g., Zaehle *et al.*, 2014). To address these challenges, vegetation models typically group plants according to common characteristics and functions to simplify the diversity in natural ecosystems (Walker *et al.*, 2014; Medlyn *et al.*, 2015; Fer *et al.*, 2021; Kyker-Snowman *et al.*, 2022), using plant functional type (PFT) groupings. These have generally focused on aboveground traits and temperate ecosystems (Wullschleger *et al.*, 2014; Warren *et al.*, 2015). Several leading vegetation models are now increasing the representation of root functions and inclusion of root characteristics as part of PFTs (Table 2). Model comparisons for tropical forests indicate that including P availability, which has been excluded for representation of temperate ecosystems, can improve representation of outcomes like NPP (Fleischer *et al.*, 2019; Yang *et al.*, 2019; Braghiere *et al.*, 2022; Nakhavali *et al.*, 2022). The time is now ripe to bring together these areas of model development to improve representation of tropical forests: root functional representation, and inclusion of key resource constraints in tropical forests.

An alternative to the PFT approach is "trait-flexible" models, in which traits are re-assigned at every generation to new individuals recruiting into the population, rather than being fixed up-front at the beginning of a simulation as in PFT-based models. Hence, such approaches allow for models to dynamically consider the full trait spaces in a more flexible way (Scheiter *et al.*, 2013; Sakschewski *et al.*, 2015). For example, trait-flexible modeling for the Amazon basin provided greater diversity of belowground trait combinations in response to water scarcity than with PFT approaches (Rius *et al.*, 2023), making this approach attractive for application to these high diversity ecosystems where empirical knowledge about trait combinations is limited. However, most vegetation models representing hydro-biogeochemical functions use the PFT approach. Both the PFT and the trait-flexible modeling approaches would benefit from more accurate representation of critical belowground functions in tropical forests, improving outcomes like NPP and responses to global change.

This Viewpoint provides a roadmap for strengthening our empirical understanding and model representation of the unique root functional characteristics of tropical forests (Fig. 1). We focus on fine roots, including biomass and other traits, with attention to coarse roots (>2 mm diameter) when relevant. We present: **1)** an overview of unique root characteristics in tropical forests in relation to resource acquisition (reviewed in depth in Cusack *et al.,* 2021). **2)** A comparison of our empirical understanding of tropical fine-root function versus root representation in a sampling of leading vegetation models, including the topics: a) soil exploration, b) coordination and tradeoffs in nutrient vs. water acquisition, and c) above-belowground functional linkages for nutrient and water uptake and use. **3)** An assessment of commonly measured tropical root characteristics that are not yet enough understood or are not functionally relevant for model inclusion. Based on this assessment, we call for the development of more balanced above-belowground whole-plant functional types and trait clusters to represent key functions of tropical forests, particularly in relation to P and multi-nutrient acquisition, as well as drought resistance.

## How are fine-root strategies and functions different in tropical forests?

Tropical forests have distinct belowground characteristics relative to other ecosystems, in part because of the unique resource constraints common in tropical forests. First, tropical evergreen forests have the largest stocks of fine-root biomass globally (Jackson *et al.*, 1996). Fine-root production rates are also higher and turnover times are faster in tropical forests versus other forests (Cusack *et al.*, 2021), following trends for tropical forest NPP. For example, tropical forest fine-root productivity in surface soils averaged 596 g $m^{-2}$ $y^{-1}$ versus 428 g $m^{-2}$ $y^{-1}$ in temperate forests and 311 g $m^{-2}$ $y^{-1}$ in boreal forests, and annual root turnover times averaged 1.4 $y^{-1}$ in tropical forests versus 1.2 $y^{-1}$ in temperate forests and 0.8 $y^{-1}$ in boreal forests (Finer *et al.*, 2011). The large and dynamic stocks of root biomass in tropical forests make them important in the global C cycle, since root turnover provides a principal input to the very large soil C stocks in tropical forests (Rasse et al., 2005). The outsized importance of tropical forests in the global C cycle provides further motivation for accurately understanding tropical forest belowground function and representation in vegetation models.

Second, tropical forest roots are more diverse than in other ecosystems across several axes. Similar to the high plant species diversity common in tropical lowland forests, these ecosystems have the highest diversity in fine-root morphological traits (Ma *et al.*, 2018, but see Carmona *et al.*, 2021).

Fewer plant species have been characterized for root traits in tropical forests compared with other biomes (Fig. 2), in part because of the sheer diversity of co-existing species with entangled root systems per unit area. Still, evidence using global databases  suggests that tropical species contribute at least 23% of the unique root trait combinations globally (Guerrero-Ramirez *et al.*, 2021). Related to high species diversity, fine-root traits are less phylogenetically constrained within taxonomic levels compared to other ecosystems globally (Valverde-Barrantes *et al.*, 2021; Weemstra *et al.*, 2023), Asefa et al., 2022). An example in these studies is the "magnoliid" type of root (i.e., thick, fleshy roots) that is largely limited to Magnoleaceae in temperate ecosystems, but is found across multiple families in the tropics (e.g., Moraceae, Malvaceae, and Sapotaceae). Root traits can also be diverse over small spatial scales in tropical forests, with high variation in fine-root traits found within and among individuals of the species, as well as among species (in Box 1), even while the large bioregions of the tropics have some separation in root traits (Addo-Danso *et al.*, 2020). Overall, tropical forests appear to have greater variation and more unique combinations of root traits, both at species and community scales, compared with temperate ecosystems, presenting a special challenge to vegetation modelers.

Third, fine-root strategies are organized around different resources in many tropical forests compared with temperate biomes. Specifically, soil moisture variation and P scarcity appear to drive tropical forest root dynamics and traits (reviewed in Dallstream *et al.,* 2023; Cusack *et al.*, 2021), rather than temperature fluctuations and N scarcity as in many higher latitude ecosystems. Associations with mycorrhizal symbionts in tropical forests are broadly linked to P and water acquisition and include both arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (ECM). Rather than the temperate-ecosystem paradigm of AMF promoting fast decomposition and nutrient cycling versus ECM promoting slow nutrient cycling (Cornelissen *et al.*, 2001; Phillips *et al.*, 2013; Read *et al.*, 2017; Averill *et al.*, 2019; but see Weemstra *et al.*, 2016), in tropical forests, both types of mycorrhizal association have been related to fast and slow nutrient cycling (Chuyong *et al.*, 2000; Keller & Phillips, 2019; Weemstra *et al.*, 2020). Also, in contrast to obligate N fixation by actinorhizal N-fixing trees dominant in temperate and boreal biomes, rhizobial N-fixing trees common in tropical forests can down-regulate N fixation (facultative fixation) (Barron *et al.*, 2011; Menge *et al.*, 2014). Thus, tropical forest root symbionts respond to different types of nutrient limitation with distinct strategies compared with root symbionts in higher latitude ecosystems.

## Integrating multi-functional tropical root representation into vegetation models

We now compare and synthesize current empirical and model understandings of tropical root functions. We organize this section around: 1) root characteristics with strong empirical support for a functional role, and which thus should be prioritized for model integration, versus 2) root traits that are commonly measured but do not yet clearly indicate a root function, or which lack clear relationships to resource availability, and thus are not (yet) suited for model integration. The first part highlights three important functional aspects of roots: a) general soil exploration for resource acquisition, b) coordination and tradeoffs for root nutrient versus water acquisition, and c) above-belowground functional linkages in water and nutrient uptake and use. We consider both the quantity and spatial deployment of roots as well as their activity (Zhang *et al.* 2023). For each of these three areas we describe i.) empirical advances and understanding, ii.) current model representation, and iii.) avenues for model improvement and data needs. We do not advocate that models incorporate all root traits and functions, which would unnecessarily complicate them and increase uncertainty. Rather, we attempt to identify data that is promising for improving functional representation, and model components that are confirmed or at odds with field data following Medlyn *et al*. (2015).

We summarize empirically measured root characteristics (Table 1) alongside an assessment of root function representation in 15 leading vegetation models (Table 2). These models include examples linked to global Earth System Models (ESMs), demographically resolved vegetation models (e.g., representing forest age and structure), and individual-based models. We compare how root characteristics are emphasized in empirical and modeling research (Table 3), showing that some functional root characteristics are understudied relative to their representation in models, while other well-characterized tropical root functions are under-developed in models.

## Root traits strongly linked to tropical forest function – Ripe for models

### Dynamic soil exploration*: empirical advances*

Root characteristics like biomass and depth distribution are clearly linked to soil exploration for resources (Fig. 1), with the largest availability of species-level data from the wet tropics for root biomass, production, turnover, and specific root length (SRL, length/mass) (Fig. 2, Guerrero-Ramírez *et al.*, 2021). Higher SRL increases the volume of soil explored per unit of root biomass (McCormack *et al.*, 2015; demonstrated in https://youtu.be/uHZqG5eKShI). The most prevalent patterns of allocation to root biomass for soil exploration in tropical forests (recently reviewed by Cusack *et al.*, 2021) are: 1) relatively greater root biomass and root production rates in infertile surface soils versus fertile surface soils, likely for rapid uptake of scarce mineral nutrients released from litter decomposition; 2) relatively greater root biomass in surface soils in wetter versus drier conditions, likely because extreme drying in tropical forests causes surface root death; 3) faster fine-root turnover in wetter versus drier conditions and in fertile versus infertile soils, likely indicating a less conservative plant life strategy when resources are abundant; 4) greater fine-root SRL under resource scarcity, both for dry versus wet conditions and infertile versus fertile soils, likely indicating maximization of soil explored per unit biomass; 5) greater root production rates in the subsoil versus surface soils under dry conditions, likely for deep water acquisition. These comparisons were true both across biogeographic gradients and experimental treatments that varied the availability of rock-derived nutrients like P and potassium (K) (e.g., Wurzburger & Wright, 2015; Cusack & Turner, 2021; Reichert *et al.*, 2022), and across seasonal or drought-induced soil moisture variation (e.g., Kummerow *et al.*, 1990; Janos *et al.*, 2008; Metcalfe *et al.*, 2008). These soil exploration patterns of root biomass, production, turnover, and SRL are the best supported by the literature for tropical forests.

### Dynamic soil exploration: *model representation*

Among the 15 models reviewed here (Table 2), root representation was generally implemented as less dynamic in response to moisture or nutrient availability than suggested by the empirical research synthesized above. For example, root turnover was a constant value in the models we assessed. Only two of the models allowed maximum rooting depths to change with tree size (i.e., size-dependent rooting depth), even though 13 of the models had the capacity to resolve tree size

(Table 2). None of the models allowed vertical root depth distributions to respond to changes in soil moisture or nutrient availability.

## Dynamic soil exploration: *avenues for model improvement*

Enabling individual-, cohort-, or PFT-specific rooting distributions and depths, and related resource partitioning is a forefront for model development, which could build on the vertically variable root allocation scheme of Drewniak (2019). Under this type of representation, different plant groups in the community would have different strategies in accordance with some defined resource strategy, which could include coordination between above- and below-ground traits (see section above). Incorporating belowground resource partitioning would allow for a more holistic differentiation between resource-acquisitive vs. -conservative strategies, as well as contrasting strategies for nutrient vs. water acquisition and drought tolerance (see section above). In addition to variable rooting depth by PFTs, increasing model capacity for root systems and functions to respond dynamically to resource changes is an ongoing challenge for vegetation models (Wang *et al.,* 2023). A particular challenge is posed by model structures that are not spatially explicit within grid cells and a given soil layer (Table 2; the gap models reviewed are only spatially explicit aboveground), such that resource partitioning is not possible belowground and resources are shared by all members of the community. Innovative model approaches, which allow for incomplete resource sharing across individuals, cohorts, and/or PFTs while still maintaining mass balance would enable resource-conservative strategies as PFTs to emerge through trait filtering (Scheiter *et al.* 2013). For example, a fraction of the total resource pool could be allocated as PFT-specific (non-shared) and the remainder as shared across the community. Such model developments could be complemented with empirical research, such as species responses to nutrient additions in the field using identification approaches (e.g., DNA barcoding; Jones *et al.,* 2011). This would help assess root exploration patterns and flexibility across species, and could inform the creation of species clustering or PFTs in models.

### Coupled hydro-biogeochemical strategies: *empirical advances*

There are very few empirical data linking root water and nutrient acquisition strategies in tropical forests, but there have been advances to identify clusters of root traits for nutrient acquisition. This recent work could be built on to include clusters of belowground hydraulic traits (as identified above, e.g., rooting depth, root embolism vulnerability). Much of the nutrient acquisition trait work in tropical forests has been for P, developing clusters of traits, or “syndromes,” targeted at P acquisition. Plant P acquisition strategies include different combinations of root phosphatase production, root branching ratios, SRL, mycorrhizal symbioses, root hair length and density, and organic exudates to promote mineralization by decomposers (Ushio *et al.*, 2015; Weemstra *et al.*, 2016; Freschet *et al.*, 2021b, exudate measurement demonstration: https://www.youtube.com/watch?v=n0CQ0lo7pbs). A framework grouped these P acquisition strategies into broader root P “syndromes” for tropical forests, identifying sets of root morphological traits and mycorrhizal types that are often found together, and provide unique strategies for P acquisition from mineral and organic forms (Dallstream *et al.,* 2023). For example, one tropical forest study identified clear tradeoffs in P acquisition strategies among tree species, such as high fine-root phosphatase activity versus increased mycorrhizal hyphal length (Zhu *et al.*, 2023), although morphological tradeoffs were less clearly linked to P acquisition. We have yet to formulate mathematical response surfaces defining which traits are expressed under what nutrient conditions, which would be most useful for models. Such frameworks could be expanded to include strategies for acquisition of other nutrients and water to develop holistic hydro-biogeochemical functional types.

Some work in the tropics has explored plant tradeoffs for the acquisition of different nutrients. It was proposed that N fixation and P acquisition are coordinated in P-scarce tropical forests, because phosphatase enzymes are N-rich proteins (Houlton *et al.*, 2008). Studies in Costa Rica (Nasto *et al.*, 2014; Soper *et al.*, 2019) and Panama (Nasto *et al.*, 2014; Batterman *et al.*, 2018) found mixed support for a relationship between N fixation and root phosphatase activity, indicating that other P acquisition strategies such as mycorrhizal symbiosis and fine-root production should also be assessed for coordination with N acquisition (Lugli *et al.*, 2020; Allen *et al.*, 2020; Braghiere *et al.*, 2022; Reichert *et al.*, 2022). New data presented here from Panama and Singapore demonstrate variation in nutrient uptake rates for different nutrients, with some links to root morphological traits that could be used to further develop resource acquisition syndromes (Box 3, method demonstration (https://youtu.be/4atZ3E0NrX4). Because direct nutrient uptake measures at the root system level are destructive and difficult to scale up (e.g., Cornelissen *et al.*, 2001), more work is needed to explore if they can be related to surrogates, such as lab observations linking P uptake rates to root phosphatase activity (Lee, 1988), and root phosphatase relationships with mycorrhizal colonization, root branching ratio (Yaffar *et al.*, 2021), SRL, and other root morphological traits (Lugli *et al.*, 2020; Cabugao *et al.*, 2021; Han *et al.*, 2022, Box 3), as well as responsiveness of these traits to soil P availability (Ushio *et al.*, 2015; Guilbeault-Mayers *et al.*, 2020; Cabugao *et al.*, 2021; Lugli *et al.*, 2021).

Coupled hydro-biogeochemical strategies: *model representation*

Among the root traits included in the 15 models assessed here (Table 2), water stress or water uptake was represented in 13 models versus only five models that represented nutrient acquisition (N or P), with representation of P dynamics particularly lacking. Similar to the empirical disconnect between nutrient and water acquisition research (discussed above), none of the models explicitly represented coupled hydro-biogeochemical cycling, so we summarize water and nutrient acquisition separately, and generally call for greater coordination of these two areas of model development.

Overall, 13 of the 15 models represented plant hydraulic traits (Table 2). The most common trait representing plant hydraulic function was maximum rooting depth (in 12 of 15 models, Table 2), which was either a constant (four models) or a PFT characteristic and was not responsive to changes in moisture. The next most common hydraulic parameters were "water stress factor" (related to soil moisture, in 10 models), followed by water uptake rate (six models, Table 2). The model with the broadest representation of plant hydraulic traits was FATES-Hydro (with PARTEH module), which additionally represents root hydraulic resistance, embolism vulnerability, fine-root radius, and permeability. Comparing the models with plant hydraulic traits emphasized by empiricists, root phenology, root hair length and density, and mycorrhizal symbiosis were not used to represent plant hydraulics in the models reviewed here (Table 3).

Nutrient uptake processes were represented in fewer models compared with plant hydraulics, with only six of the models representing some aspect of nutrient uptake (Table 2). Root exudation of non-structural carbohydrates was linked to priming and nutrient availability in three of the models, and two models had some representation of symbiotic nutrient uptake, including BNF and mycorrhizal nutrient uptake (Table 2). Representation of N acquisition processes was more developed than P acquisition (Table 2). The most common nutrient parameter functionally related to nutrient uptake in the models was the rate of N uptake, which was responsive to changes in soil nutrient availability (five models), followed by the rate of P uptake (four models, Table 2). Some of the models employed constant nutrient uptake parameters based on diffusion and kinetics, and others accounted for chemical interactions of soil nutrients with minerals and soil microorganisms (Thum *et al.*, 2020; Yu *et al.*, 2020). For example, LM4.1-BNF included many parameters for modeling N uptake (Table 2), including passive nutrient uptake (via transpiration stream), active uptake (via a C cost and Michaelis-Menten dynamics), and symbiotic nutrient acquisition. Meanwhile, P uptake was represented only in four of the models using just one parameter (P uptake rate). Some root characteristics that are empirically related to resource acquisition were included in the models, but without nutrient functionality. For example, vertical root biomass distribution was in 12 of the 15 models (Table 2); however, this parameter was a PFT characteristic and not responsive to changes in resource availability. Of the root characteristics commonly related to plant nutrient acquisition by empiricists (Table 1), SRL, root phenology, root hair length and density, root order distribution, root phosphatase and protease enzyme activities were not represented at all or were not directly linked to nutrient acquisition in the models (Table 3). Based on the empirical advances above, more models could consider implementing coordinated strategies for N and P acquisition, together with plant hydraulics.

## Coupled hydro-biogeochemical strategies: *avenues for model improvement*

Integrating hydraulic and nutrient model components is a forefront for model development. Model development of root dynamics has proceeded on almost entirely independent paths for plant hydraulics versus nutrient acquisition, even within the same model (via separate modules e.g., FATES, LM, LPJ, Table 2), such that coordinated responses to resource changes and C costs for water versus nutrient acquisition are not represented. And, within these parallel model developments, little attention has been given to the unique characteristics of tropical forests (e.g., moisture seasonality, drought, and P scarcity). Model advances have: 1) vertically resolved both water and nutrient transport between layers (e.g., ELM-CNP; Yang et al. 2019), 2) represented the C cost of coarse and fine-root allocation across depths (e.g., Sakschewski et al. 2021), and 3) represented water and nutrient foraging functions of roots across depths (Christoffersen *et al.*, 2016; Xu *et al.*, 2016; Kennedy *et al.*, 2019; Langan *et al.*, 2017; Joshi *et al.*, 2022, Knox et al. 2023). Hydro-biogeochemical model integration would allow better representation of the fast-slow plant lifestyle continuum (Reich 2014) by including trade-offs in nutrient-acquisition (shallow rooted) vs. stable water supply (deep roots). Oliveira et al. (2021) argued that the fast-slow continuum maps onto variation in soil fertility, and the risky-safe hydraulic safety tradeoff occurs across moisture gradients. Hydro-biogeochemical integration would follow in the spirit of allowing ecosystem function and community traits to emerge from competitive ecological interactions (Scheiter *et al.* 2013; Fisher *et al.* 2015). This integration would also enable models to better represent "trait filtering" of plant groups across multiple gradients, such as the sorting of tropical tree species that is observed according to both moisture and P affinities across the Isthmus of Panama (Condit *et al.*, 2013). We argue that the next step in this line of model development to represent tropical forests is to integrate hydraulic and nutrient model components.

### Coupled above-belowground resource strategies: *empirical advances*

While leaves and fine roots are somewhat analogous as aboveground/belowground resource acquisition plant structures, there is variation in the degree to which analogous traits like specific leaf area (SLA) vs. SRL, and leaf vs. root lifespans correlate across biomes (Withington *et al.*, 2006; Jiang *et al.*, 2021).

Very few studies have focused on above-belowground functional linkages in tropical forests, with most attention to plant hydraulics. For example, maximum rooting depth of different species (usually measured for coarse roots), has been linked to deciduousness in tropical forests, particularly in regions with distinct dry seasons and mixed communities of deciduous, semi-deciduous, and evergreen species (Sobrado & Cuenca, 1979; Sampaio, 1995; Smith-Martin *et al.*, 2020). In Amazonian forests designations have been identified for: 1) deep-rooted, evergreen drought avoiders, 2) shallow-rooted, deciduous drought avoiders, and 3) shallow-rooted, evergreen drought tolerators with embolism-resistant vascular systems (Brum *et al.*, 2019; Chitra-Tarak *et al.*, 2021). Interestingly, hydraulic above-belowground linkages appear to be strongest under stressful conditions. In the Amazon, only under dry conditions were there linkages among stem embolism vulnerability and rooting depth (e.g., Oliveira *et al.*, 2019; Laughlin *et al.*, 2021), with these linkages lacking in wet conditions. While these hydraulic groupings are helpful, there can also be large variation in maximum rooting depth among coexisting species of similar lifeform and deciduousness, as demonstrated here for a Costa Rican dry forest (Box 2). To explore this, aboveground hydraulic traits could be linked to belowground traits beyond maximum rooting depth, which is very difficult to measure, including overall root biomass depth distributions, vessel diameter, root embolism vulnerability root embolism vulnerability, and seasonal changes in root production (i.e., phenology) (Germon *et al.*, 2020). Data on the embolism resistance of roots is particularly scarce (e.g., Domec *et al.,* 2006), and could be a focus area for future research to link to aboveground hydraulic vulnerability.

For nutrient above-belowground coordination, a recent global review indicated greater coordination of leaf with root N:P ratios in tropical forests relative to most other biomes, likely related to widespread tropical soil P scarcity and conservation of P in plant tissues (Wang *et al.*, 2022). A broad-scale paper linking remotely-sense canopy traits in Panama with soil data found that canopy greenness (a surrogate for NPP) corresponded to variations in soil fertility and toxicity (Fisher et al., 2020). Also, AMF vs. ECM association has been linked to canopy reflectance properties in tropical forests in Hawai'i (as well as in many temperate sites), likely also indicating plant nutrition linkages (Sousa et al., 2021). While these root-canopy linkages are suggestive, we lack more functional measurements of coordinated root and canopy nutrition in tropical forests.

### Coupled above-belowground resource strategies: *model representation*

Of the 15 vegetation models, several linked aboveground deciduousness with root traits, and most had uneven representation of belowground versus aboveground traits and functions, with an average of ~30 aboveground traits compared to only about eight root traits represented per model

(Table 2). Of the models with explicit linkages, Ecosystem Demography model 2 (ED2) included a trait-driven plant hydraulic module that represents drought deciduousness and plant water stress (Medvigy *et al.*, 2009; Medvigy & Moorcroft, 2012). ED2 also uses three PFTs with different rooting depths: a deeper-rooted evergreen PFT, a shallower-rooted deciduous PFT (Xu *et al.*, 2016; Smith-Martin *et al.*, 2020), and a liana PFT with a different rooting depth from trees (Meunier *et al.*, 2021). The different rooting depths per PFT are linked to data on deciduous and evergreen phenologies for tropical forests (Xu *et al.*, 2016; Smith-Martin *et al.*, 2020). Similarly, LPJmL4.0-VR has adapted a traditional PFT-based model using deciduousness in the Amazon and defined a spectrum of PFTs from shallow to deep-rooted, which are dependent on tree size, including vertically resolved coarse roots (Sakschewski *et al.*, 2021). These groupings follow the empirical data described above. Overall, above-belowground links in plant hydraulics are still in the early stages of development, but these could form the foundation for more integrative plant function in PFTs or trait clusters for tropical forests, with support from the empirical data.

For nutrient acquisition, above-belowground coupling in vegetation models is less developed, and most commonly represented as photosynthate (i.e., C) expenditure for the acquisition of soil nutrients based on plant N demand, including representation of physiological limits to nutrient uptake and efficient optimization of C allocation (reviewed in Davies-Barnard *et al.*, 2022). For example, in the representation of nutrient uptake in the Fixation & Uptake of Nutrients (FUN) model, GPP drives nutrient uptake demand and supplies the C for expenditure (Fisher *et al.*, 2010, Allen *et al.*, 2020). The Davies-Barnard *et al.* (2022) review illustrates that C allocation for nutrient uptake represents a significant advance over older representations, such as biological nitrogen fixation (BNF) as a function of evapotranspiration. Key to the C expenditure approach are the concepts of nutrient limitation and photosynthetic downregulation, which occur when there is not enough C to grow new leaves because of high C costs for soil exploration for scarce nutrients.

Coupled above-belowground resource strategies: *avenues for model improvement*

Integrating more of the hydraulic function of fine and coarse roots into existing above-belowground hydraulic PFTs is an important next step for model development (Fig. 1). In particular, above-belowground linkages for plant hydraulics could be expanded, including the hydraulic function of coarse roots, which are rare in vegetation models and were in only four of the models we assessed (Table 2). Coarse roots in the models were generally represented as support, biomass storage, and root depth distribution, but they were not directly related to water uptake or transport. Moreover, while models sometimes represent the C cost of fine roots, the C cost of coarse roots is only implicitly embedded within an allocation to stem production. Here we advocate that models explicitly represent the C cost of coarse roots that have a direct link to function. This would allow modeled C assimilated aboveground and allocated to coarse roots (investment cost) to be more directly linked to water uptake, following the approach of Sakschewski *et al.* (2021). With the cost of both fine *and* coarse root production explicitly modeled by soil depth, and the returns of such investment represented in terms of water uptake (see plant hydraulic-enabled models, Table 2), models would be in a position to represent the three-way tradeoff presented by Oliveira et al. (2021) among 1) embolism resistance (P50), 2) water table access (deep roots), and 3) water loss control (deciduousness and stomata regulation). An early advance has been made in this direction; the aDGVM2 model has shown how this three-way tradeoff can emerge from variable rooting depth and tradeoffs with P50 and deciduousness

(Langan et al. 2017). Given the empirical support for this three-way tradeoff, and recent advances in the modeling of variable rooting depths and plant hydraulics, we argue that this is a well-justified avenue for data-model integration and development using the small but growing availability of data. Focused collection of data on root hydraulics, such as root embolism resistance, would help to clarify above-belowground coordination of this three-way trade-off.

For above-belowground nutrient coordination in models, there remain outstanding empirical questions—and hypotheses that can be tested in models—of how C allocation and nutrient acquisition interact. For example, what is an accurate tradeoff between C expenditure above versus belowground under nutrient scarcity? To what extent can stoichiometric flexibility of different plant tissues mediate or exacerbate nutrient limitations? How do these individual plant-level processes manifest in larger model grid cells of multiple plants, cohorts, traits, or other plant functional types? Investigations into these types of above-belowground nutrient acquisition questions could then be combined with hydraulic above-belowground linkages to get more coupled hydro-biogeochemical PFTs.

## Tropical root traits not clearly linked to function -- Not ripe for models

It is important to note a set of root traits that are commonly measured and comprise a large portion of our empirical tropical data (Fig. 2), but which thus far have not been demonstrated to link clearly to root function (Table 1). These traits include: root tissue nutrient content and C:N:P stoichiometry, aspects of root morphology (e.g., root tissue density), and mycorrhizal biomass or colonization rates in the absence of functional characterization. Root nutrient content and morphology have been used as proxies for resource acquisition and symbiotic strategies (Addo-

Danso *et al.*, 2018; Bergmann *et al.*, 2020); however, the functional roles of root nutrient content and morphological traits like RDT for resource acquisition are not clear or consistent (Freschet et al, 2021b).

Recently, an expanded global database including root C:N:P and morphology was published as the Global Root Trait (GRooT) database (Guerrero-Ramirez *et al.*, 2021, Fig. 2), which may be useful for further exploration of functional linkages to stoichiometry. To increase the functional utility of this database, these commonly measured traits are being compared and related to smaller data sets for tropical nutrient uptake rates, phosphatase and protease activities. We present an example of this type of exercise using new data, highlighting the difficulty of relating fine-root stoichiometry to functional groupings like N-fixation or mycorrhizal association (Box 4), particularly in the absence of direct measures of N-fixation, such as using $^{15}N_2$ labeling experiments (e.g., https://www.youtube.com/watch?v=7jxM1KZ0f3Q) or direct measures of mycorrhizal-plant C exchange (e.g., https://youtu.be/mNq8eQxDCqM). Given the large availability of root nutrient content data relative to other more functional traits (Fig. 2), it is worth pursuing these comparisons to see if and when we can infer root functionality from stoichiometry, noting that root stoichiometry in models plays an important role for determining nutrient storage and stocks of biomass (Table 2).

Root morphology has been used as an indicator of nutrient acquisition strategies, but there have been very few direct demonstrations of these relationships. Highlighting the difficulty of using morphological root traits to infer function, fine-root traits (diameter, SRL, root tissue density, branching) for 1,467 Amazonian tree species had no significant association with landscape-scale shifts in bulk soil fertility (Vleminckx *et al.*, 2021). This is in contrast to some aboveground tropical forest traits, like canopy greenness and nutrient content, which often covary with soil fertility and soil texture (Fyllas *et al.*, 2012; Fortunel *et al.*, 2014; Fisher *et al.*, 2020). Root diameter, which is functionally most closely related to water conductivity, has been used as a proxy for AMF colonization rate, even though this relationship has not been consistently demonstrated for tropical forests (Kong *et al.*, 2014; Lugli *et al.*, 2020; Yaffar *et al.*, 2021). We present new data from Panama where some root morphological characteristics were strongly correlated to paired measurements of nutrient uptake for two canopy tree species, and nutrient uptake rates were different among nutrients for one different canopy species. However, these relationships were not apparent in similar new data for two species from Singapore, possibly because the Panama data were characterized according to root order (only root tips – 1st order – used, or roots separated for the first three absorptive root orders for morphology, Box 3). Thus, further exploration of if, how, and under what conditions morphological traits are related to nutrient (and water) uptake is warranted, and there appear to be promising relationships if roots are assessed at a scale relevant to absorptive activity.

For mycorrhizae, assessments of colonization, presence, or biomass are the most commonly used methods (Sheldrake *et al.*, 2018; Olsson & Lekberg, 2022), but these measures do not necessarily indicate functional activity since fungal biomass can be present but not active. These measures could be improved if they were related to direct measurements of C or nutrient transfers between tree and fungal symbionts, such as $^{13}CO_2$ pulse labeling of plants and subsequent transfer of $^{13}C$-enriched C to symbionts (Lekberg *et al.*, 2013; Chaudhary *et al.*, 2022, Kaiser *et al.*, 2015; e.g., https://youtu.be/mNq8eQxDCqM), which would allow a better assessment of the functional value of colonization data.

Clarifying the utility of these commonly measured fine-root traits for inferring functions in tropical forests would be useful, given the relatively large quantity of fine-root nutrient, morphological, and colonization data. Absent this, empirical research should shift toward root traits more clearly linked to specific root functions, as described above.

## Achieving data-model integration for a better understanding of tropical root function

We have identified opportunities for improving our understanding of fine-root function in tropical forests, and for integrating key root functions into vegetation models as applied to tropical ecosystems. Our surveys of empirical and modeling approaches to utilizing root data (Table 1-3) demonstrate several broad trends: 1) There are some root characteristics for water acquisition (e.g., root biomass and maximum rooting depth) that are being implemented in models according to our empirical understanding. 2) There have been numerous recent advances in characterization of root traits and functions in tropical forests, but many of these are missing in vegetation models. 3) Models represent some characteristics that are not easily measured and for which there are few data (e.g., nutrient uptake kinetics, water transport by coarse roots). 4) Functional characterization of fine roots is often different in models versus our empirical understanding (Table 3). For example, SRL is used in some models as a PFT characteristic which is unresponsive to resource changes, yet recent data indicate that only ~50% of variation in SRL might be explained by species differences (Box 1), and SRL can be very responsive to resource changes in tropical forests (see discussion above). 5) There are some root characteristics that are well linked to functions in limited empirical studies, such as phosphatase activity, but which have not yet been sufficiently characterized in tropical forests to implement response functions in vegetation models. 6) Some of the most-measured root traits have not been clearly linked to function, and therefore are not immediately useful for representing resource acquisition processes in models (e.g., root nutrient content and diameter). Overall, there is much work left to be done to bring together empirical and modeling research on tropical forest belowground functions, with a need for greater integration going forward.

There are existing frameworks for advancing model-data integration and for comparing models with different modalities (Walker *et al*., 2014; Medlyn *et al*., 2015; Kyker-Snowman *et al*., 2022), but the computational cost of increasing model complexity must be justified by improved model performance. More model ensemble experiments for tropical forest biomes would be useful to test the level of improvement achieved by representing expanded root function (e.g., Koven *et al.*, 2020; Caldararu *et al*., 2023, Fleischer *et al*., 2019). New experiments could also test model-derived hypotheses prior to inclusion of a new process in models. For example, the AmazonFACE experiment (https://amazonface.unicamp.br/) will test hypotheses about P dynamics under elevated $CO_2$ that were developed by using a model inter-comparison (Fleischer *et al*., 2019). Some key questions that arose from these modeling activities are: will $CO_2$ enrichment stimulate root phosphatase activity sufficiently to alleviate P limitation to growth (Yang *et al*., 2019)? And, will including phosphatase production in models improve predictions of tropical forest productivity and responses to elevated $CO_2$?

Close interactions between empiricists and modelers over the course of research projects are essential to meet the challenges we have identified in this research agenda. Model-data integration for tropical forests has improved in the past decade, including efforts such as the U.S. Department of Energy Next Generation Ecological Experiments–Tropics (NGEE-Tropics, https://ngee-tropics.lbl.gov/), the AmazonFACE, the TropiRoot network (https://tropiroottrait.github.io/TropiRootTrait/, described in https://youtu.be/oT2lgeGDnjI), and the Landscape Evolution Observatory at Biosphere 2 (https://www.science.org/doi/full/10.1126/science.abj6789), which bring together field research questions and modeling objectives. Nonetheless, support for these endeavors remains limited. We urge that these collaborations be widespread and supported by funding agencies in order to improve our understanding and prediction of tropical forest function and feedbacks to a changing world.

## Acknowledgements

This Viewpoint resulted in part from a New Phytologist Foundation Workshop grant to DF Cusack, AL Cordeiro, K Andersen, SJ Wright, and RJ Norby on “Coordinating and synthesizing tropical forest root trait studies: Understanding belowground NPP, root responses to global change, and nutrient acquisition dynamics across tropical forests," held in Panama in April, 2023, where the videos referenced in the test were filmed by Ana Endara with the Smithsonian Tropical Research Institute (STRI). Data collection in Panama was supported by DOE Office of Science Early Career Award DE-SC0015898 and NSF Geography & Spatial Studies Grant #BCS-1437591 to D. F. Cusack. Data collection in Puerto Rico was supported by the DOE Office of Science Biological and Environmental Research Program as part of the NGEE-Tropics Program. L. Fuchslueger was supported by the European Union’s Horizon 2020 research and innovation program under the Marie Sklodovska-Curie grant agreement No. 847693 (REWIRE). L. F. Lugli would like to thank the financial support of the Bayerische Staatskanzlei (Bavarian State Chancellery) through the grant associated with the Amazon-FLUX project. L. A. McCulloch would like to thank the financial support of NOAA Climate and Global Change Postdoctoral Fellowship Program, administered by UCAR’s Cooperative Programs for the Advancement of Earth System Science (CPAESS) under award # NA18NWS4620043B to attend the New Phytologist Foundation Workshop. N. G-R would like to thank the financial support of Deutsche Forschungsgemeinschaft (DFG), grant number 316045089/GRK 2300. S. A. Batterman was supported by the United Kingdom Natural Environment Research Council (NE/M019497/1) and the Leverhulme Trust. We also acknowledge support from a National Science Foundation Research Coordination Grant (INCyTE; DEB-1754126) to investigate nutrient cycling in terrestrial ecosystems. We thank Colleen Iversen and Luke McCormack for their critical reviews of early versions of the manuscript, and Rafaël Govaerts for his support extracting data from the World Checklist of Vascular Plants.

## Author contributions

All authors contributed initial ideas, text, and final edits to the manuscript. In-person workshop attendance for discussions and idea development came from: DFC, BC, RN, CSM, KMA, AC, SJW, NG-R, LFL, LM, MS, KF, CD, LT, CF, SB, MW, and LF. Tables were compiled and created by: BC, DFC, SJW and CF. Figure design and finalization came from: DFC, NG-R, LFL, CD, LT, LM, MS, and AC. Data contributions for boxes came from: DFC, ALC, KMA, CSM, and DY. Funding acquisition and coordination were led by: DFC, ALC, RN, SJW and KMA.

## Competing interests

None declared

## Data availability

Data presented in Boxes 1-4 are available in the SI.

## ORCID

Shalom D. Addo-Danso ORCID https://orcid.org/ 0000-0001-5074-1673

Kelly M. Andersen ORCID https://orcid.org/0000-0002-1460-9904

Marie Arnaud ORCID https://orcid.org/0000-0003-4001-6499

Sarah A. Batterman ORCID https://orcid.org/0000-0002-7703-9873

Brad Christoffersen ORCID https://orcid.org/0000-0002-4890-9999

Amanda L Cordeiro ORCID https://orcid.org/0000-0001-7226-0133

Daniela F. Cusack ORCID https://orcid.org/0000-0003-4681-7449

Caroline Dallstream ORCID https://orcid.org/0000-0002-9193-0611

Lee H. Dietterich ORCID https://orcid.org/0000-0003-4465-5845

Joshua B. Fisher ORCID https://orcid.org/0000-0003-4734-9085

Katrin Fleischer ORCID https://orcid.org/0000-0002-9093-9526

Claire Fortunel ORCID https://orcid.org/0000-0002-8367-1605

Lucia Fuchslueger; ORCID https://orcid.org/0000-0002-9615-4439

Nathaly R. Guerrero-Ramírez: ORCID https://orcid.org/0000-0001-7311-9852

Laynara F. Lugli; ORCID https://orcid.org/0000-0001-8404-4841

Lindsay A. McCulloch; ORCID https://orcid.org/0000-0001-6868-2632

Richard J. Norby ORCID https://orcid.org/0000-0002-0238-9828

Mareli Sanchez ORCID https://orcid.org/0009-0001-3193-8259

Chris M. Smith-Martin ORCID https://orcid.org/0000-0002-6557-1432

Laura Toro ORCID https://orcid.org/0000-0002-0550-3294

Oscar J. Valverde Barrantes ORCID https://orcid.org/0000-0002-7327-7647

Monique Weemstra ORCID https://orcid.org/0000-0002-6994-2501

Michelle Y. Wong; ORCID https://orcid.org/0000-0002-7830-8035

S. Joseph Wright ORCID https://orcid.org/0000-0003-4260-5676

Daniela Yaffar ORCID https://orcid.org/0000-0002-8090-7096

# Figures

## Fig. 1

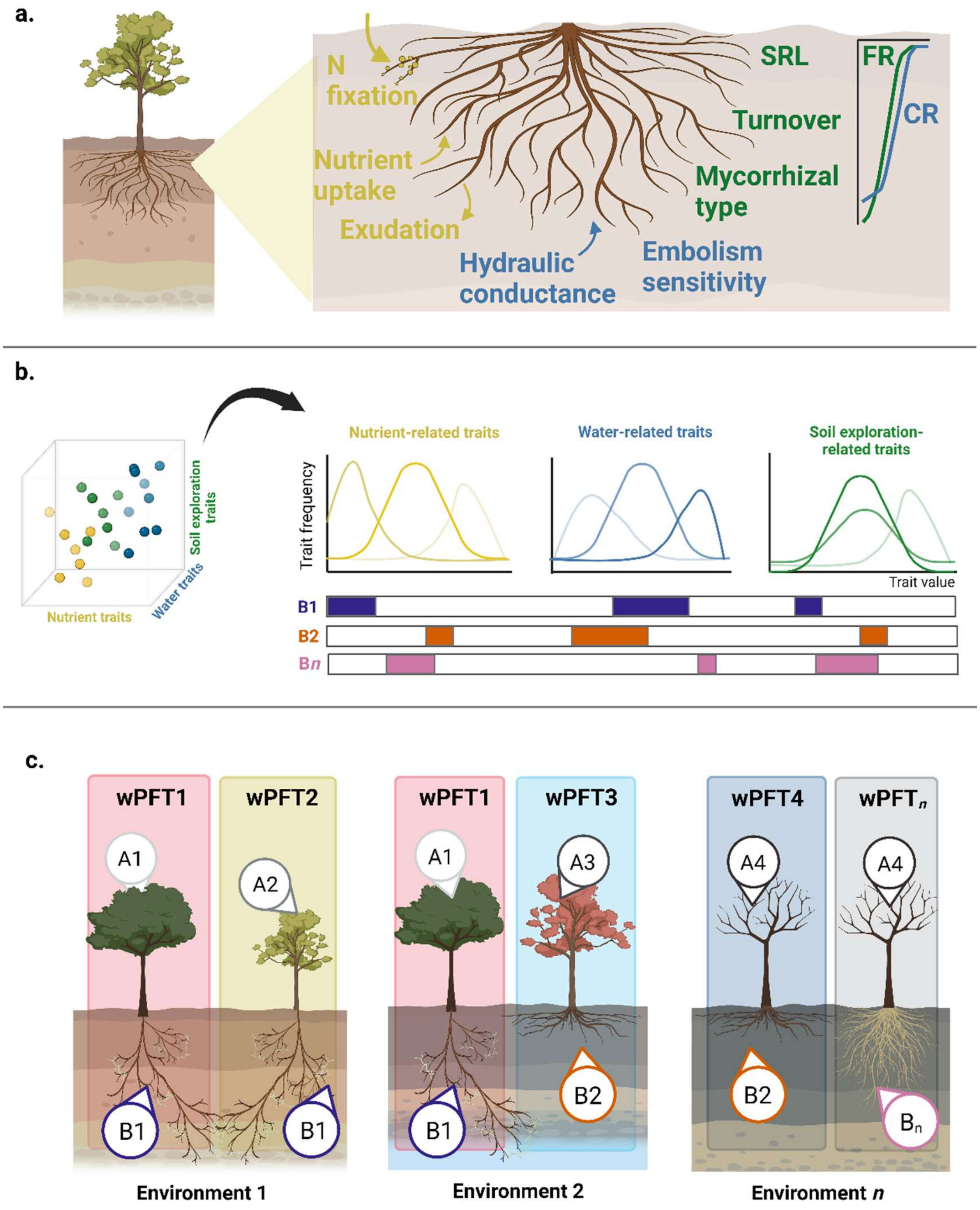


**Figure 1.** A conceptual representation depicts the root traits recommended for further tropical forest research and representation in vegetation models as part of PFTs or trait-clusters. The panels include: **(a.)** a graphical depiction of the root system with a subset of suggested priority root traits for the tropics (see also Table 1), **(b.)** multidimensional trait space and trait distributions that could be used to inform more balanced above-belowground whole-plant functional types (here signaled as ***w***PFTs) for the tropics, and **(c.)** representation of different combinations of belowground trait clusters mixed and matched with aboveground PFTs to test in vegetation models and guide empirical research. Details are as follows: **(a.)** a graphical depiction of root system traits including nutrient uptake traits (in yellow, N-fixation, nutrient uptake rates, carbon exudation), water uptake and drought resistance traits (in blue, hydraulic conductance and embolism sensitivity), and general soil exploration traits (in green, e.g., mycorrhizal type, specific root length (SRL), root turnover). Also shown are hypothetical depth distributions for coarse roots (CR, blue), and fine roots (FR, green, inset). **(b.)** A multidimensional trait space is linked to hypothetical distributions for the root traits depicted in panel (a.), indicating how ranges of the different trait distributions could be selected to form multi-trait belowground functional types (B1, B2, etc.). **(c.)** Belowground and aboveground groupings could be matched to create ***w***PFTs, and then tested in different combinations in vegetation models to assess improvement in predictions of NPP and other emergent properties of ecosystems depicted in vegetation models.

**Figure 2.**

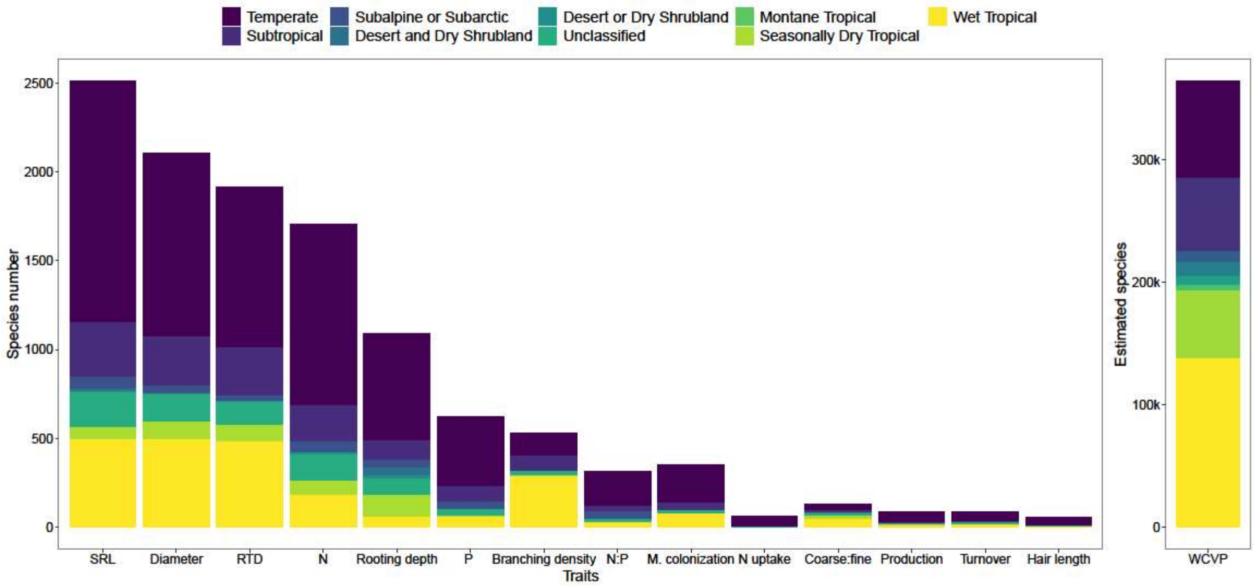


**Fig. 2.** The total number of species for which fine-root traits data are currently available across climatic biomes is shown (left) relative to the total number of known species in each biome (right). Despite much higher species numbers present in wet tropical forests, the highest percentage of available data comes from temperate plant species. Within the tropics, most data are from wet tropical forests (shown in yellow, "wet tropical"). Overall, SRL has been the most commonly measured root trait, while traits particularly important in tropical forests like P uptake are virtually uncharacterized. **Left panel:** the species number in the updated version of the GRooT database (Guerrero-Ramirez *et al.*, 2021) are shown by trait and biome description (colors); traits included are specific root length (SRL, m $g^{-1}$), mean root diameter (Diameter, mm), root tissue density (RTD, g $cm^{-3}$), root nitrogen concentration (N, mg $g^{-1}$), maximum rooting depth (Rooting depth, m), root phosphorus concentration (P, mg $g^{-1}$), root branching density (Branching density, number $cm^{-1}$), root nitrogen to phosphorus ratio (N:P), root mycorrhizal colonization intensity (M. colonization, %), the net uptake rate of nitrogen (N uptake, µmol $g^{-1}$ $day^{-1}$), coarse-to-fine root mass ratio (Coarse:fine), root hair length (Hair length, µm), root production (Production, g $m^{-2}$

year$^{-1}$), root turnover rate (Turnover, year$^{-1}$). Data were filtered to include only fine roots for most of the traits, except coarse-to-fine root mass ratio, maximum rooting depth, and root hair length. **Right panel**: estimate total species number by climate biome from the World Checklist of Vascular Plants (WCVP, Govaerts *et al.*, 2021, POWO 2023). Data sources, climate zone descriptions, and processing details are in SI.

**Table 1.** Root characteristics and trait functions as understood empirically and represented in models

| **Root Trait** | **Units** | **Function in Nature** | **Function in Models** |
|---|---|---|---|
| ***Fine Root Function: Soil Exploration for Water & Nutrient Acquisition*** | | | |
| Fine-root biomass | Mg ha$^{-1}$ | Absorptive tissue | Absorptive tissue |
| Fine-root productivity | Mg ha$^{-1}$ y$^{-1}$ | Absorptive tissue productivity | Absorptive tissue productivity |
| Fine-root turnover (inverse of lifespan) | y$^{-1}$ | Absorptive tissue turnover | Absorptive tissue turnover |
| Specific root length (SRL) | cm g$^{-1}$ | Soil volume explored per cost | Conversion factor (fine root biomass to fine root length), Calculate absorptive area as biomass×SRL×2πr |
| Root growth timing (e.g., phenology/seasonality) | growth or death timing | Align root production & mortality with resource availability | ABSENT |
| Root hair length | µm | Absorptive tissue | ABSENT |
| Root hair density | hairs cm$^{-1}$ | Absorptive tissue | ABSENT |

|  |  |  |  |
|---|---|---|---|
| Depth distribution | Distribution parameter(e.g., β) | Distribute absorptive and transportive tissues | Locate absorptive tissue, characteristic of PFTs in some models |
| Root order distribution (i.e., branching density) | (1+2+3 order) : (4 order) | Absorption per transport | ABSENT (except where vertical distribution of coarse and fine roots are treated separately) |
| Mycorrhizae | Colonization rate, hyphal length, material transfer rate | Exchange C for water, Ps or other nutrients | Exchange C for N and phosphorus |
| ***Fine Root Function: Water Acquisition & Drought Resistance*** |  |  |  |
| Maximum depth | m | Define vertical root domain | Define vertical root domain, characteristic of PFTs in some models |

| | | | |
|---|---|---|---|
| Root hydraulic conductivity | $L_P$; m sec$^{-1}$ MPa$^{-1}$ | Water transport | Water transport |
| P50; pressure at 50% embolism | MPa | Embolism resistance | Embolism resistance |
| Root radius (or diameter) | mm | Possibly related to water c or AMF colonization, function poorly constrained | Soil-root water conductance |
| Root membrane permeability | Mass pressure$^{-1}$ area-$^{1}$ time$^{-1}$ | Water uptake | Water uptake |
| Water uptake rate | mg-$H_2O$ length$^{-1}$ time$^{-1}$ | Water uptake | Water uptake |
| ***Fine-Root Function: Nutrient Acquisition*** | | | |
| Root enzyme activities (e.g., phosphatase, protease) | Degradation rate of | Release organic phosphorus | Release organic phosphorus |

| | | | |
|---|---|---|---|
| | synthetic substrate | | |
| Organic exudate production | C root mass$^{-1}$ (or length$^{-1}$) time$^{-1}$ | Release mineral phosphorus | Release mineral phosphorus, present in few models where it responds to nutrient availability |
| N fixation (nodule biomass and nitrogen fixation rate) | Nodule biomass area$^{-1}$, and fixation rate - mg $N_2$ nodule biomass$^{-1}$ time$^{-1}$ | Acquires N from atmosphere and converts to biologically available forms | Exchange C for N, modeled as C cost, maintenance respiration, or nodule turnover time in response to nutrient availability. Or, modeled as a function of evapotranspiration or NPP. Present in few models, often as a characteristic of PFTs |
| Phosphorus uptake rate | μg P length$^{-1}$ (or root mass$^{-1}$) time$^{-1}$ | Realized phosphorus uptake by root or AMF/ECM symbiont | Realized P uptake, present in few models and varies with nutrient availability |

| | | | |
|---|---|---|---|
| Nitrogen uptake rate | µgN length$^{-1}$ (or root mass$^{-1}$) time$^{-1}$ | Realized nitrogen uptake by root or AMF/ECM symbiont | Realized nitrogen uptake, present in few models and varies with nutrient availability |
| ***Traits without a clear relationship to root resource acquisition*** | | | |
| Tissue N concentration | % | Unclear if correlated with function | |
| Tissue P concentration | % | Unclear if correlated with function | |
| Tissue N-to-P ratio | Ratio | Stoichiometry | ABSENT |
| Tissue C-to-N ratio | Ratio | Stoichiometry | Control N demand, present in most models, part of PFTs |
| Tissue C-to-P ratio | Ratio | Stoichiometry | Control P demand, present in most models, part of PFTs |
| Root tissue density | g cm$^{-1}$ | Defense, possible relation to AMF colonization rate (volume available for colonization) | ABSENT |

| | | | |
|---|---|---|---|
| ***Coarse Root Function: Support & Transport*** | | | |
| Coarse root biomass | Mg ha$^{-1}$ | Support & Water Transport | Track elements in tissues, present in some models as part of PFTs |
| Coarse root productivity | Mg ha$^{-1}$ yr$^{-1}$ | Support | Track elements in tissues |
| Coarse root hydraulic resistance | MPa s$^{-1}$ kg$^{-1}$ $H_2O$ | Water transport | Water transport, present in some models |

Table 1. Root characteristics and traits indicated in this Viewpoint as most relevant to tropical forest function are given, grouped by main function, with common units, and specific function as understood empirically (Function in Nature). Functions in vegetation models are then given, followed by categorical description of how these are included in models (details in Table 2).

**Table 2.** Inclusion of root traits in combination with aboveground traits and parameters in a suite of vegetation models.

Table 2. (Table available as Excel file). Root traits as represented in a sample of 15 vegetation models varying in scope (capability of coupling to Earth system models) and sub-grid resolution (trait assignment and spatial resolution). In general, these models predict plant productivity and other emergent properties of ecosystems depending on changing conditions over time. “Spatially explicit” refers to aboveground processes only (e.g., ray tracing and light competition). Root traits (columns) are grouped by main functions (colors). As an indicator of model complexity in above vs. belowground plant processes, a tally of unique aboveground vs belowground root traits for each model is given. Cells in the table denote where a given root trait varies by PFT or individual (p), size (s), is a global constant (c), is dynamic with moisture (m), is dynamic with nutrients (n), or if it is implicitly considered through other means (i). Blank cells denote traits not represented for a given model. Parentheses with numbers indicate multiple sub-traits or parameters associated with a particular trait. Representative citations for each model are given. Hydraulic-enabled models explicitly represent water transport within plants and include models #4, #5, #6, #7, and #12. Nutrient-enabled models explicitly model N and/or P uptake through direct or symbiotic means and include #1, #5, #7, #9, and #10. Root traits associated with C or biomass storage are not considered here. For a complete description of methods used to construct this table, including definitions of terms and acronyms, and the file or table within each citation that was the specific source for trait information, see the SI.

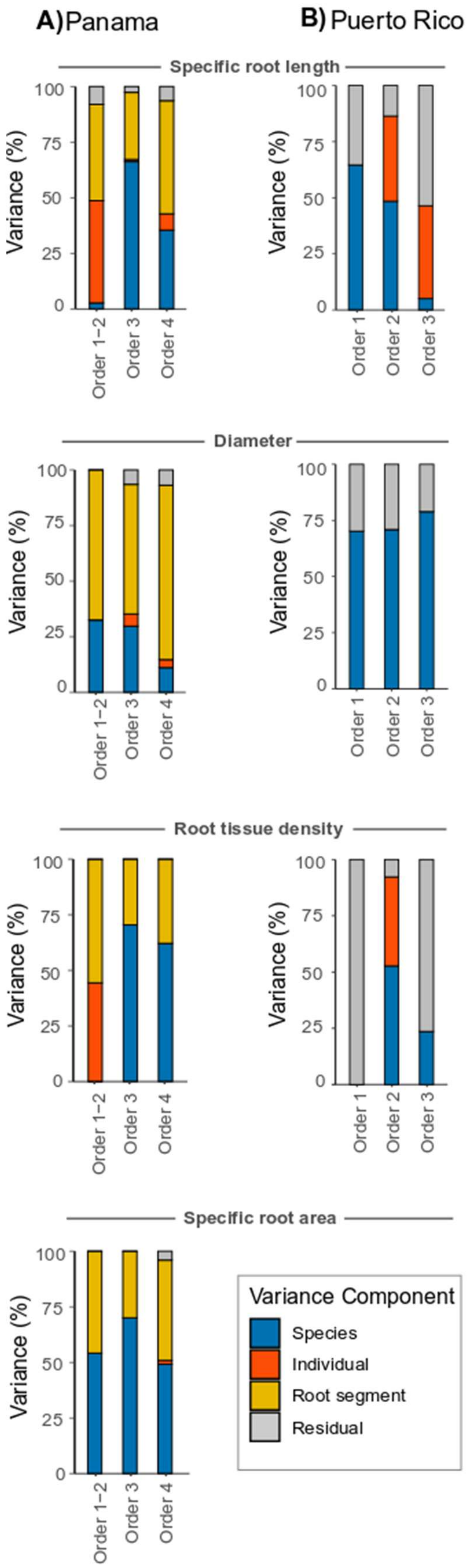
Table 3. A tabulation is presented of the root characteristics present in Table 1 (“1. Empirical research focus”), present in Table 2 (“2. Model focus”), and 3. Common to both models and empirical research, with Caveats when the trait is understood or used differently in empirical work compared with model applications. Note that information is organized in columns such that columns 1, 2 and 3 do not correspond horizontally.

| **1. Empirical research focus (lacking model representation)** | **2. Model focus (lacking empirical focus or understanding)** | **3. Common to models and empirical research** | **Caveats for commonalities between models and empirical research** |
|---|---|---|---|
| Root phenology (seasonality of production/mortality) | Root:Leaf biomass ratio | Root biomass | Models emphasize coarse root biomass as a stock, empirical research emphasizes fine root biomass for resource acquisition |
| Root hair abundance and length | Water stress factor | Max rooting depth and root depth distributions | Models emphasize for water uptake, empirical research combines with root depth distributions for nutrient uptake |
| Root order distributions | Fraction of tree hydraulic resistance in roots | Root tissue CN(P) | Stoichiometry is not clearly functionally important in empirical studies. In models this is commonly used for nutrient accounting and to drive nutrient demand, so in neither case is this a functional trait |
| Root enzyme production (e.g. phosphatase) | Root membrane permeability | Root production and turnover rates | Root turnover rates poorly characterized in tropical empirical data |
| Root tissue density | C cost of N fixation and C cost of mycorrhizal nutrient acquisition | Fine-root SRL (specific root length) | Used as a PFT trait in some models or as a global constant, in empirical work this is responsive more to resource availability and is not clearly distinct among species |

| | | | |
|---|---|---|---|
| | N fix nodule turnover rates | | |
| | | Water and nutrient uptake rates | Poorly characterized for the tropics |
| | Maintenance respiration C cost of nodules | Root diameter | Related to uptake and transport in both models and empirical research |
| | Nutrient uptake rates of AMF vs ECM associations | Root conductance rates and embolism vulnerability (P50) | Very poorly characterized in roots overall, especially in the tropics |
| | | Root organic exudate production | Poorly characterized in tropical empirical data, linked to nutrient uptake |
| | | N fixation rates and nodule biomass | Good empirical understanding of fixation and its function relative to other root traits and represented in most models with improvement needed |
| | | Mycorrhizal type | Type (AMF vs. ECM) related to N uptake rates in models, not supported by tropical data, likely more related to P uptake in tropics but this not in models |

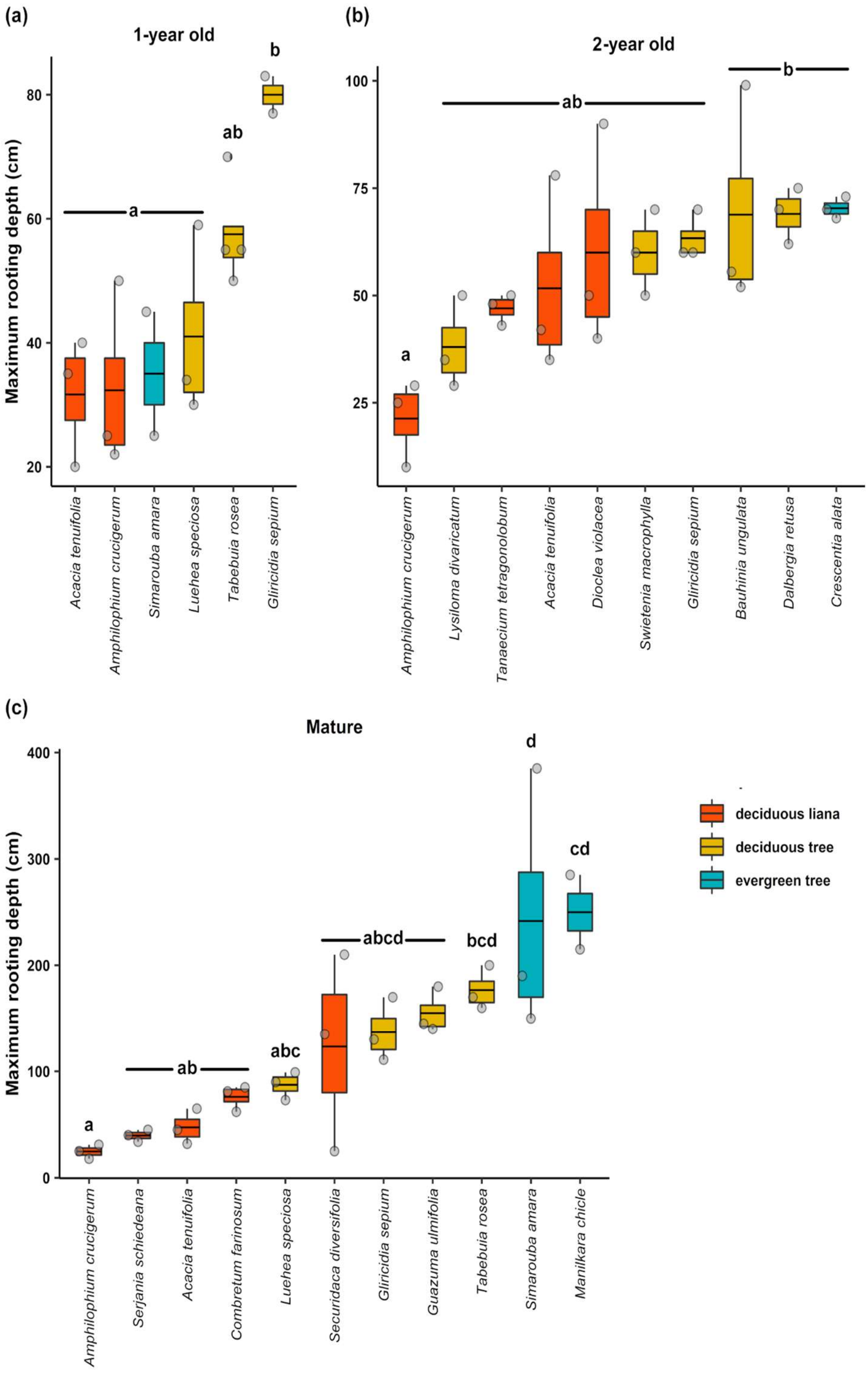
**Box 1. High fine-root trait variation within and among individuals suggests morphological trait flexibility within species in tropical forests**

New data from two tropical forests indicate large intra-specific and individual-scale variation in morphological traits for absorptive roots (orders 1 – 4), comparing the proportion of variation explained by species, individual trees, individual root segments (multiple per individual), and residual (unexplained) variance. The Panama data include 10 replicate individuals for each of two species, and Puerto Rico data include two to three replicate individuals for each of six species to assess inter- and intra-specific variation, with details given in Notes S1. Overall, root segment within individual contributed a large portion of the variance when there was replication at the individual scale (Panama data), When individuals were not well replicated but more species were measured, individual and species contributed similarly to variance for fine-root morphology (Puerto Rico data). Data are provided as Datasets S2 and S3. These data support recent publications indicating that root traits are less phylogenetically conserved in tropical forests (see main text) and suggest that tropical forest community-scale root characteristics are likely dynamic in response to resource shifts. More work must be done to directly link these commonly-measured fine-root morphological traits to functional root activities like nutrient and water uptake and transfer.


A) Panama
B) Puerto Rico
Specific root length
Diameter
Root tissue density
Specific root area
Variance (%)
0
25
50
75
100
Order 1−2
Order 3
Order 4
Order 1
Order 2
Order 3
Variance Component
Species
Individual
Root segment
Residual

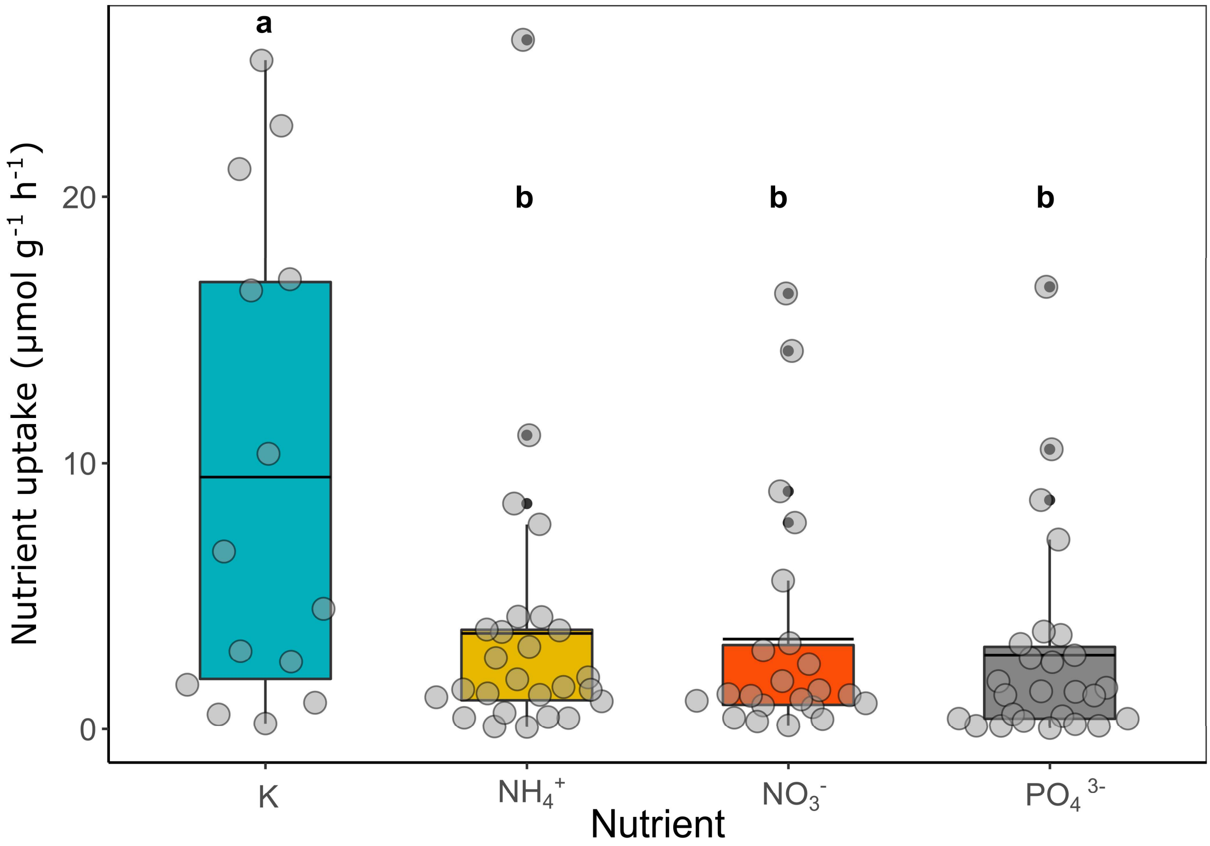
**Box 2: Tropical forest maximum rooting depth linked to life form and deciduousness, but much variation remains**

Deep roots are particularly important for water uptake and redistribution to support transpiration demands during dry periods (Markesteijn & Poorter, 2009), and aboveground phenology has been linked to rooting depths in dry tropical forests (Smith-Martin *et al.*, 2020). Here, a new analysis of data from a dry tropical forest in Costa Rica show relationships between aboveground life form and rooting depth for juvenile and mature trees. This analysis shows that mature evergreen trees had c. 2*x* the maximum rooting depth of co-occurring mature deciduous lianas and trees, indicating above-belowground trait coordination.Letters show means separations using Tukey HSD tests, boxes show means and quartiles. Details are in Notes S1 and data are provided as Dataset S4. These patterns were not present in juvenile trees (top panels), suggesting that belowground niche partitioning develops over time. At the same time, there was substantial variation in maximum rooting depth among mature species that were classified as the same functional type using aboveground deciduousness, suggesting that a more refined understanding of belowground hydraulic strategies within these groups could help separate species into more functionally explicit groupings. Such a holistic below-aboveground representation of water acquisition strategies could contribute to improved tropical forest PFTs or trait clusters, which could then be combined with nutrient acquisition types to improve tropical plant representation in vegetation models.


(a)
1-year old
Maximum rooting depth (cm)
20
40
60
80
a
ab
b
Acacia tenuifolia
Amphilophium crucigerum
Simarouba amara
Luehea speciosa
Tabebuia rosea
Gliricidia sepium
(b)
2-year old
25
50
75
100
a
ab
b
Amphilophium crucigerum
Lysiloma divaricatum
Tanaecium tetragonolobum
Acacia tenuifolia
Dioclea violacea
Swietenia macrophylla
Gliricidia sepium
Bauhinia ungulata
Dalbergia retusa
Crescentia alata
(c)
Mature
Maximum rooting depth (cm)
0
100
200
300
400
a
ab
abc
abcd
bcd
d
cd
Amphilophium crucigerum
Serjania schiedeana
Acacia tenuifolia
Combretum farinosum
Luehea speciosa
Securidaca diversifolia
Gliricidia sepium
Guazuma ulmifolia
Tabebuia rosea
Simarouba amara
Manilkara chicle
deciduous liana
deciduous tree
evergreen tree

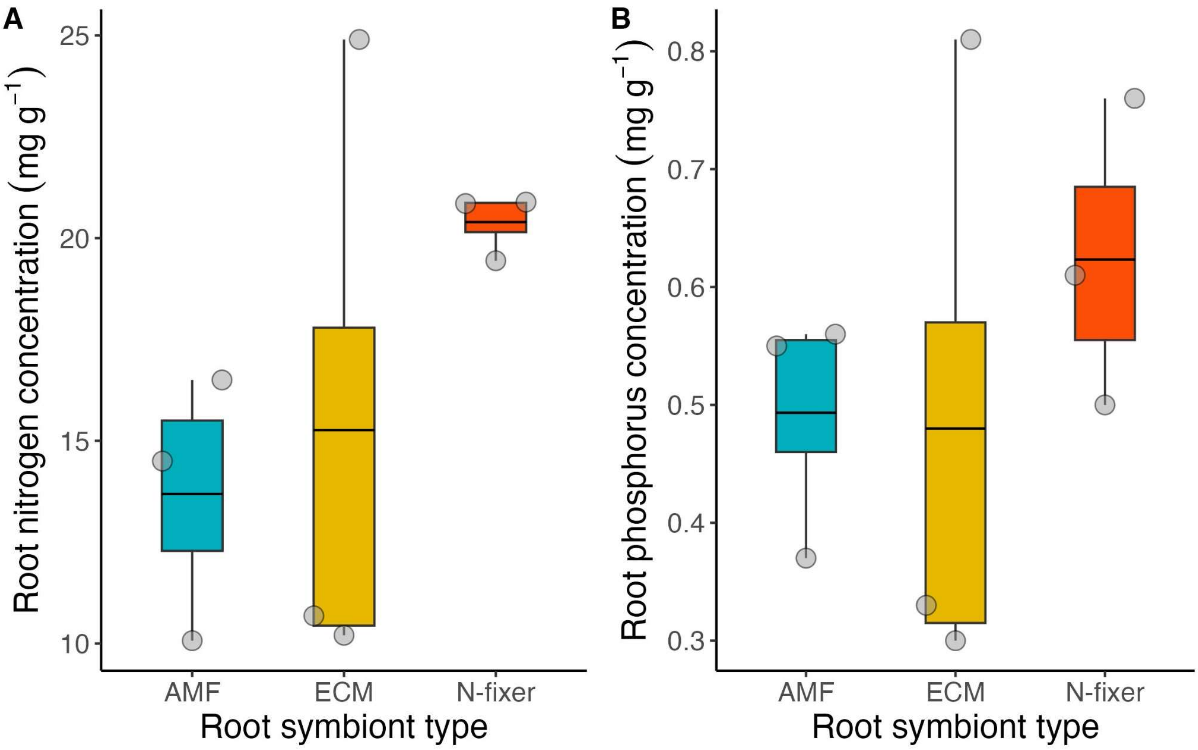
**Box 3: Fine-root nutrient uptake rates and relationships to morphology for tropical trees**

Direct measures of nutrient uptake rates by tropical trees are rare and rarely linked to broader nutrient limitation to NPP studies or to fine root morphological root traits. Here, we present new data for fine-root nutrient uptake rates in a well-characterized lowland Panamanian forest and show relationship between uptake rates and fine-root morphology, with similar data available for two tree species in Singapore. Details are in Notes S1 and data are provided as Datasets S5 and S6. Across 33 mature individuals of a relatively abundant Panamanian lowland species *Protium picramnioides*, there was significantly greater nutrient uptake rates for potassium (K) versus ammonium ($NH_4^+$), nitrate ($NO_3^-$), and phosphate ($PO_4^{3-}$). Figure means are shown with quantiles ($F_{3,87}$=6.78; *P*=0.022), letters indicate significant differences using Tukey HSD tests. This result supports data from a long-term nutrient fertilization experiment in the same site showing that K addition reduced fine-root biomass, length, RDT, and increased SRL (Wurzburger & Wright, 2015), suggesting K limitation to root processes and fine-root dynamic responsiveness to changes in K availability. Data for two other Panamanian species and two species in Singapore also showed variation in uptake rates among nutrients (Notes S1). The Panamanian species had strong correlations between nutrient uptake rates and root morphology, including positive correlations of $NO_3^-$ and $PO_4^{3-}$ with SRL ($r^2$ = 0.83 and 0.88, respectively), negative correlations of uptake with RTD ($r^2$ = 0.99 and 0.71, respectively), and a negative correlation of $PO_4^{3-}$ with root biomass ($r^2$ = 0.75, see Notes S1). This result supports the idea in Box 1 that tropical forest fine-root morphology is responsive to changes in nutrient availability, and that morphology is related to nutrient uptake. Methodological details and raw data are in Notes S1and shown at https://youtu.be/4atZ3E0NrX4). Dynamic nutrient uptake rate measurements within and among sites could be related to fine-root morphological characterization, which could help inform dynamic root responses to changing resources in vegetation models, but considerably more data are required.



## Box 4: Using fine-root stoichiometry as a surrogate for functional traits

Plant tissue stoichiometry could be a relatively easy way to start constraining nutrient acquisition in functional groupings since fine-root C:N:P content is relatively more available than functional trait measurements. However, there remains a knowledge gap across tropical sites linking root stoichiometry directly to nutrient or water acquisition. Fine-root P and N concentrations could reflect fine-root P and N acquisition rates, either directly or via symbiosis. For example, fine-root P is strongly correlated to leaf P concentration (Holdaway *et al.*, 2011), soil inorganic and total P (Holdaway *et al.*, 2011; Schreeg *et al.*, 2014; Freschet *et al.*, 2021b), and soil extractable P (Yaffar *et al.*, 2021). Here we present new data on fine-root N and P content for Panamanian trees with three root symbiont types (arbuscular mycorrhizal (AM), ectomycorrhizal (EM), and N-fixing (Nfix) to explore functional relationships. While N fixers tended to have higher root N content, there were no significant differences in root stiochiometry across these three functional types. Figure showsmeans and quantiles shown for nine tree species (n = 3 individuals per functional type). Details are in Notes S1 and data for each tree species are provided as Dataset S7.. These data highlight the problems with using root stoichiometry to assess symbiotic activity or nutrient uptake rates without additional measurements. Further investigation to confirm whether root stiochiometry is indicative of tropical plant fine-root functional activity would be useful, since root stoichiometry is one of the most abundant types of tropical root data (Fig. 2).


A
Root nitrogen concentration (mg g$^{-1}$)
25
20
15
10
AMF
ECM
N-fixer
Root symbiont type
B
Root phosphorus concentration (mg g$^{-1}$)
0.8
0.7
0.6
0.5
0.4
0.3
AMF
ECM
N-fixer
Root symbiont type

## References

**Addo-Danso SD, Defrenne CE, McCormack ML, Ostonen I, Addo-Danso A, Foli EG, Borden KA, Isaac ME, Prescott CE. 2020.** Fine-root morphological trait variation in tropical forest ecosystems: an evidence synthesis. *Plant Ecology* **221**: 1-13.

**Addo-Danso SD, Prescott CE, Adu-Bredu S, Duah-Gyamfi A, Moore S, Guy RD, Forrester DI, Owusu-Afriyie K, Marshall PL, Malhi Y. 2018.** Fine-root exploitation strategies differ in tropical old growth and logged-over forests in Ghana. *Biotropica* **50**: 606-615.

**Allen K, Fisher JB, Phillips RP, Powers JS, Brzostek ER. 2020.** Modeling the carbon cost of plant nitrogen and phosphorus uptake across temperate and tropical forests. *Frontiers in Forests and Global Change* **3**.

**Andersen KM, Mayor JR, Turner BL. 2017.** Plasticity in nitrogen uptake among plant species with contrasting nutrient acquisition strategies in a tropical forest. *Ecology* **98**: 1388-1398.

**Andersen KM, Turner BL. 2013.** Preferences or plasticity in nitrogen acquisition by understorey palms in a tropical montane forest. *Journal of Ecology* **101**: 819-825.

**Aragao L, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jimenez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, et al. 2009.** Above- and belowground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences* **6**: 2759-2778.

**Asefa M, Worthy SJ, Cao M, Song XY, Lozano YM, Yang J. 2022.** Above- and belowground plant traits are not consistent in response to drought and competition treatments. *Annals of Botany* **130**: 939-950.

**Averill C, Bhatnagar JM, Dietze MC, Pearse WD, Kivlin SN. 2019.** Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proceedings of the National Academy of Sciences of the United States of America* 116: 23163-23168.

**Barron, AR, Purves, DW, & Hedin, LO. 2011.** Facultative nitrogen fixation by canopy legumes in a lowland tropical forest. *Oecologia,* **165:** 511-520.

**Batterman SA, Hall JS, Turner BL, Hedin LO, Walter JKL, Sheldon P, van Breugel M. 2018.** Phosphatase activity and nitrogen fixation reflect species differences, not nutrient trading or nutrient balance, across tropical rainforest trees. *Ecology Letters* **21**: 1486-1495.

**Belda DM, Anthoni P, Warlind D, Olin S, Schurgers G, Tang J, Smith B, Arneth A. 2022.** LPJ-GUESS/LSMv1.0: a next-generation land surface model with high ecological realism. *Geoscientific Model Development* **15**: 6709-6745.

**Bergmann J, Weigelt A, van Der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez NR, Valverde-Barrantes OJ, Bruelheide H, Freschet GT, Iversen CM, et al. 2020.** The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**.

**Braghiere RK, Fisher JB, Allen K, Brzostek E, Shi M, Yang X, Ricciuto DM, Fisher RA, Zhu Q, Phillips RP. 2022.** Modeling global carbon costs of plant nitrogen and phosphorus acquisition. *Journal of Advances in Modeling Earth Systems* **14**.

**Brum M, Vadeboncoeur MA, Ivanov V, Asbjornsen H, Saleska S, Alves LF, Penha D, Dias JD, Aragao L, Barros F, et al. 2019.** Hydrological niche segregation defines forest structure and drought tolerance strategies in a seasonal Amazon forest. *Journal of Ecology* **107**: 318-333.

**Brzostek ER, Fisher JB, Phillips RP. 2014.** Modeling the carbon cost of plant nitrogen acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. *Journal of Geophysical Research-Biogeosciences* **119**: 1684-1697.

**Cabugao KG, Yaffar D, Stenson N, Childs J, Phillips J, Mayes MA, Yang XJ, Weston DJ, Norby RJ. 2021.** Bringing function to structure: Root-soil interactions shaping phosphatase activity throughout a soil profile in Puerto Rico. *Ecology and Evolution* **11**: 1150-1164.

**Caldararu S, Rolo V, Stocker BD, Gimeno TE, Nair R. 2023.** Ideas and perspectives: Beyond model evaluation – combining experiments and models to advance terrestrial ecosystem science. *Biogeosciences Discuss*. [preprint], https://doi.org/10.5194/bg-2023-47.

**Carmona CP, Bueno CG, Toussaint A, Trager S, Diaz S, Moora M, Munson AD, Partel M, Zobel M, Tamme R. 2021.** Fine-root traits in the global spectrum of plant form and function. *Nature* **597**: 683-+.

**Chaudhary VB, Holland EP, Charman-Anderson S, Guzman A, Bell-Dereske L, Cheeke TE, Corrales A, Duchicela J, Egan C, Gupta MM, et al. 2022.** What are mycorrhizal traits? *Trends in Ecology & Evolution* **37**: 573-581.

**Chave J. 1999.** Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling* **124**: 233-254.

**Chitra-Tarak R, Xu CG, Aguilar S, Anderson-Teixeira KJ, Chambers J, Detto M, Faybishenko B, Fisher RA, Knox RG, Koven CD, et al. 2021.** Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist* **231**: 1798-1813.

**Christoffersen BO, Gloor M, Fauset S, Fyllas NM, Galbraith DR, Baker TR, Kruijt B, Rowland L, Fisher RA, Binks OJ, et al. 2016.** Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-Hydro). *Geoscientific Model Development* **9**: 4227-4255.

**Chuyong CB, Newbery DM, Songwe NC. 2000. Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees. *New Phytologist* 148: 493-510.**

**Clark MP, Fan Y, Lawrence DM, Adam JC, Bolster D, Gochis DJ, Hooper RP, Kumar M, Leung LR, Mackay DS, et al. 2015.** Improving the representation of hydrologic processes in Earth System Models. *Water Resources Research* **51**: 5929-5956.

**Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G, et al. 2002.** Beta-diversity in tropical forest trees. *Science* **295**: 666-669.

**Condit R, Engelbrecht, BMJ, Pino, D, Perez, R, Turner BL 2013.** Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America,* **110**(13), 5064-5068.

**Cornelissen JHC, Aerts R, Cerabolini B, Werger MJA, van der Heijden MGA. 2001.** Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia* **129**: 611-619.

**Costa FRC, Schietti J, Stark SC, Smith MN. 2023.** The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought? Palavras-ChavePalabras clave. *New Phytologist* **237**: 714-733.

**Cunha HFV, Andersen KM, Lugli LF, Santana FD, Aleixo IF, Moraes AM, Garcia S, Di Ponzio R, Mendoza EO, Brum B, et al. 2022.** Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature* **608**: 558-+.

**Cusack DF, Addo-Danso SD, Agee EA, Andersen KM, Arnaud M, Batterman SA, Brearley FQ, Ciochina MI, Cordeiro AL, Dallstream C, et al. 2021.** Tradeoffs and synergies in tropical forest root traits and dynamics for nutrient and water acquisition: Field and modeling advances. *Frontiers in Forests and Global Change* **4**.

**Cusack DF, Markesteijn L, Condit R, Lewis OT, Turner BL. 2018.** Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots. *Biogeochemistry* **137**: 253-266.

**Cusack DF, Turner BL. 2021.** Fine root and soil organic carbon depth distributions are inversely related across fertility and rainfall gradients in lowland tropical forests. *Ecosystems* **24**: 1075-1092.

**Davies-Barnard, T., Zaehle, S. and Friedlingstein, P., 2022.** Assessment of the impacts of biological nitrogen fixation structural uncertainty in CMIP6 earth system models. *Biogeosciences*, **19**(14): 3491-3503

**Dallstream C, Weemstra M, Soper FM. 2023.** A framework for fine-root trait syndromes: syndrome coexistence may support phosphorus partitioning in tropical forests. *Oikos*.

**Daly DC, Fine PVA. 2018.** Generic limits re-visited and an updated sectional classification for Protium (tribe Protieae). Studies in Neotropical Burseraceae XXV. *Brittonia* **70**: 418-426.

**de Paula MD, Forrest M, Langan L, Bendix J, Homeier J, Velescu A, Wilcke W, Hickler T. 2021.** Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot. *New Phytologist* **232**: 551-566.

**Domec, J.-C., Scholz, F.G., Bucci, S.J., Meinzer, F.C., Goldstein, G., Villalobos-Vega, R., 2006.** Diurnal and seasonal variation in root xylem embolism in Neotropical savanna woody species: impact on stomatal control of plant water status. *Plant, Cell & Environment* **29**, 26-35.

**Drewniak BA. 2019.** Simulating dynamic roots in the Energy Exascale Earth System Land Model. *Journal of Advances in Modeling Earth Systems* **11**: 338-359.

**Dybzinski R, Kelvakis A, McCabe J, Panock S, Anuchitlertchon K, Vasarhelyi L, McCormack ML, McNickle GG, Poorter H, Trinder C, Farrior CE, 2019**. How are nitrogen availability, fine-root mass, and nitrogen uptake related empirically? Implications for models and theory. *Global Change Biology* **25**: 885-899.

**Eiserhardt WL, Couvreur TLP, Baker WJ. 2017.** Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytologist* **214**: 1408-1422.

**Espeleta JF, Clark DA. 2007.** Multi-scale variation in fine-root biomass in a tropical rain forest: A seven-year study. *Ecological Monographs* **77**: 377-404.

**Fer I, Gardella AK, Shiklomanov AN, Campbell EE, Cowdery EM, De Kauwe MG, Desai A, Duveneck MJ, Fisher JB, Haynes KD, et al. 2021.** Beyond ecosystem modeling: A roadmap to community cyberinfrastructure for ecological data-model integration. *Global Change Biology* **27**: 13-26.

**Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998.** Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* **281**: 237-240.

**Finer L, Ohashi M, Noguchi K, Hirano Y. 2011.** Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. *Forest Ecology and Management* **262**: 2008-2023.

**Fischer R, Bohn F, de Paula MD, Dislich C, Groeneveld J, Gutierrez AG, Kazmierczak M, Knapp N, Lehmann S, Paulick S, et al. 2016.** Lessons learned from applying a forest gap model to understand ecosystem and carbon dynamics of complex tropical forests. *Ecological Modelling* **326**: 124-133.

**Fisher, J.B., Sitch, S., Malhi, Y., Fisher, R.A., Huntingford, C., Tan, S.-Y., 2010.** Carbon cost of plant nitrogen acquisition: A mechanistic, globally-applicable model of plant nitrogen uptake, retranslocation and fixation. *Global Biogeochemical Cycles* **24**: GB1014.

**Fisher JB, Badgley G, Blyth E. 2012.** Global nutrient limitation in terrestrial vegetation. *Global Biogeochemical Cycles* **26**.

**Fisher JB, Perakalapudi NV, Turner BL, Schimel DS, Cusack DF. 2020.** Competing effects of soil fertility and toxicity on tropical greening. *Scientific Reports* **10**.

**Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, Fuchslueger L, Garcia S, Goll DS, Grandis A, Jiang MK, et al. 2019.** Amazon forest response to $CO_2$ fertilization dependent on plant phosphorus acquisition. *Nature Geoscience* **12**: 736-+.

**Fortunel C, Paine CET, Fine PVA, Kraft NJB, Baraloto C. 2014.** Environmental factors predict community functional composition in Amazonian forests. *Journal of Ecology* **102**: 145-155.

**Freschet GT, Pages L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimesova J, Zadworny M, Poorter H, Postma JA, et al. 2021a. A starting guide to root ecology: strengthening ecological concepts and standardising root classification, sampling, processing and trait measurements. *New Phytologist* 232: 973-1122.**

**Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, De Deyn GB, Johnson D, Klimesova J, et al. 2021b.** Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytologist* **232**: 1123-1158.

**Fyllas NM, Quesada CA, Lloyd J. 2012.** Deriving Plant Functional Types for Amazonian forests for use in vegetation dynamics models. *Perspectives in Plant Ecology Evolution and Systematics* **14**: 97-110.

**Germon A, Laclau JP, Robin A, Jourdan C. 2020.** Tamm Review: Deep fine roots in forest ecosystems: Why dig deeper? *Forest Ecology and Management* **466**.

**Guerrero-Ramirez NR, Mommer L, Freschet GT, Iversen CM, McCormack ML, Kattge J, Poorter H, van der Plas F, Bergmann J, Kuyper TW, et al. 2021.** Global root traits (GRooT) database. *Global Ecology and Biogeography* **30**: 25-37.

**Guilbeault-Mayers X, Turner BL, Laliberte E. 2020.** Greater root phosphatase activity of tropical trees at low phosphorus despite strong variation among species. *Ecology* **101**.

**Guo D, Xia M, Wei X, Chang W, Liu Y, Wang Z. 2008. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species.** ***New Phytologist*** **180: 673-683.**

**Han MG, Chen Y, Li R, Yu M, Fu LC, Li SF, Su JR, Zhu B. 2022.** Root phosphatase activity aligns with the collaboration gradient of the root economics space. *New Phytologist* **234**: 837-849.

**Hart TB, Hart JA, Murphy PG. 1989.** Monodominant and species-rich forests of the humid tropics - causes for their co-occurrence. *American Naturalist* **133**: 613-633.

**Haverd V, Smith B, Nieradzik L, Briggs PR, Woodgate W, Trudinger CM, Canadell JG, Cuntz M. 2018.** A new version of the CABLE land surface model (Subversion revision r4601) incorporating land use and land cover change, woody vegetation demography, and a novel optimisation-based approach to plant coordination of photosynthesis. *Geoscientific Model Development* **11**: 2995-3026.

**Hengl T, de Jesus JM, Heuvelink GBM, Gonzalez MR, Kilibarda M, Blagotic A, Shangguan W, Wright MN, Geng XY, Bauer-Marschallinger B, et al. 2017.** SoilGrids250m: Global gridded soil information based on machine learning. *PLOS ONE* **12**.

**Holbrook NM, Whitbeck JL, Mooney HA 1995.** Drought responses of neotropical dry forest trees. In: Medina E, Mooney HA, Bullock SH eds. *Seasonally Dry Tropical Forests*. Cambridge: Cambridge University Press, 243-276.

**Holdaway RJ, Richardson SJ, Dickie IA, Peltzer DA, Coomes DA. 2011.** Species- and community-level patterns in fine root traits along a 120,000-year soil chronosequence in temperate rain forest. *Journal of Ecology* **99**: 954-963.

**Houlton BZ, Wang YP, Vitousek PM, Field CB. 2008.** A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* **454**: 327-U334.

**Huasco WH, Riutta T, Girardin CAJ, Pacha FH, Vilca BPL, Moore S, Rifai SW, del Aguila-Pasquel J, Murakami AA, Freitag R, et al. 2021.** Fine root dynamics across pantropical rainforest ecosystems. *Global Change Biology* **27**: 3657-3680.

**Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB. 2003.** Nitrogen and climate change. *Science* **302**: 1512-1513.

**Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996.** A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389-411.

**Janos DP, Scott J, Bowman D. 2008.** Temporal and spatial variation of fine roots in a northern Australian Eucalyptus tetrodonta savanna. *Journal of Tropical Ecology* **24**: 177-188.

**Janzen DH. 1974.** Tropical black water rivers animals and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**: 69-103.

**Jiang XY, Jia X, Gao SJ, Jiang Y, Wei NN, Han C, Zha TS, Liu P, Tian Y, Qin SG. 2021.** Plant nutrient contents rather than physical traits are coordinated between leaves and roots in a desert shrubland. *Frontiers in Plant Science* **12**.

**Jobbágy EG, Jackson RB. 2000.** The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423-436.

**Jones FA, Erickson DL, Bernal MA, Bermingham E, Kress WJ, Herre EA, Muller-Landau HC, Turner BL. 2011.** The roots of diversity: Below ground species richness and rooting distributions in a tropical forest revealed by DNA barcodes and inverse modeling. *Plos One* **6**.

**Joshi J, Stocker BD, Hofhansl F, Zhou SX, Dieckmann U, Prentice IC. 2022.** Towards a unified theory of plant photosynthesis and hydraulics. *Nature Plants* **8**: 1304-+.

**Kaiser C, Kilburn MR, Clode PL, Fuchslueger L, Koranda M, Cliff JB, Solaiman ZM, Murphy DV. 2015.** Exploring the transfer of recent plant photosynthates to soil microbes: mycorrhizal pathway vs direct root exudation. *New Phytologist* **205**: 1537-1551.

**Keller AB, Phillips RP. 2019. Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. *New Phytologist* 222: 556-564.**

**Kennedy D, Swenson S, Oleson KW, Lawrence DM, Fisher R, da Costa ACL, Gentine P. 2019.** Implementing plant hydraulics in the Community Land Model, Version 5. *Journal of Advances in Modeling Earth Systems* **11**: 485-513.

**Knox RG, Koven CD, Riley WJ, Walker AP, Wright SJ, Holm JA, Wei X, Fisher RA, Zhu Q, Tang J, et al. 2023.** Nutrient dynamics in a coupled terrestrial biosphere and land model (ELM-FATES). [preprint], https://doi.org/10.22541/essoar.167810418.80767445/v1

**Kong DL, Ma CG, Zhang Q, Li L, Chen XY, Zeng H, Guo DL. 2014.** Leading dimensions in absorptive root trait variation across 96 subtropical forest species. *New Phytologist* **203**: 863-872.

**Kou-Giesbrecht S, Malyshev S, Cano IM, Pacala SW, Shevliakova E, Bytnerowicz TA, Menge DNL. 2021.** A novel representation of biological nitrogen fixation and competitive dynamics between nitrogen-fixing and non-fixing plants in a land model (GFDL LM4.1-BNF). *Biogeosciences* **18**: 4143-4183.

**Koven CD, Knox RG, Fisher RA, Chambers JQ, Christoffersen BO, Davies SJ, Detto M, Dietze MC, Faybishenko B, Holm J, et al. 2020.** Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama. *Biogeosciences* **17**: 3017-3044.

**Kummerow J, Castillanos J, Maas M, Larigauderie A. 1990.** Production of fine roots and the seasonality of their growth in a Mexican deciduous dry forest. *Vegetatio* **90**: 73-80.

**Kyker-Snowman E, Lombardozzi DL, Bonan GB, Cheng SJ, Dukes JS, Frey SD, Jacobs EM, McNellis R, Rady JM, Smith NG, et al. 2022.** Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model. *Global Change Biology* **28**: 665-684.

**Langan L, Higgins SI, Scheiter S. 2017.** Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest-savanna boundary in South America? *Journal of Biogeography* **44**: 2319-2330.

**Laughlin DC, Mommer L, Sabatini FM, Bruelheide H, Kuyper TW, McCormack ML, Bergmann J, Freschet GT, Guerrero-Ramirez NR, Iversen CM, et al. 2021.** Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution* **5**: 1123-+.

**Lee RB. 1988.** Phosphate influx and extracellular phosphatase activity in barley roots and rose cells. *New Phytologist* **109**: 141-148.

**Lekberg Y, Rosendahl S, Michelsen A, Olsson PA. 2013.** Seasonal carbon allocation to arbuscular mycorrhizal fungi assessed by microscopic examination, stable isotope probing and fatty acid analysis. *Plant and Soil* **368**: 547-555.

**Longo M, Knox RG, Medvigy DM, Levine NM, Dietze MC, Kim Y, Swann ALS, Zhang K, Rollinson CR, Bras RL, et al. 2019.** The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the Ecosystem Demography model, version 2.2-Part 1: Model description. *Geoscientific Model Development* **12**: 4309-4346.

**Lugli LF, Andersen KM, Aragao L, Cordeiro AL, Cunha HKV, Fuchslueger L, Meir P, Mercado LM, Oblitas E, Quesada CA, et al. 2020.** Multiple phosphorus acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia. *Plant and Soil* **450**: 49-63.

**Lugli LF, Rosa JS, Andersen KM, Di Ponzio R, Almeida RV, Pires M, Cordeiro AL, Cunha HFV, Martins NP, Assis RL, et al. 2021.** Rapid responses of root traits and productivity to phosphorus and cation additions in a tropical lowland forest in Amazonia. *New Phytologist* **230**: 116-128.

**Ma ZQ, Guo DL, Xu XL, Lu MZ, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO. 2018.** Evolutionary history resolves global organization of root functional traits. *Nature* **555**: 94-+.

**Malhi Y, Doughty C, Galbraith D. 2011.** The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B-Biological Sciences* **366**: 3225-3245.

**Marechaux I, Chave J. 2017.** An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: description and applications. *Ecological Monographs* **87**: 632-664.

**Markesteijn L, Poorter L. 2009.** Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* **97**: 311-325.

**Matamala R, Stover DB. 2013.** Introduction to a virtual special issue: Modeling the hidden half - the root of our problem. *New Phytologist* **200**: 939-942.

**McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo DL, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB, et al. 2015.** Redefining fine roots improves understanding of belowground contributions to terrestrial biosphere processes. *New Phytologist* **207**: 505-518.

**McMurtrie RE, Nasholm T. 2018.** Quantifying the contribution of mass flow to nitrogen acquisition by an individual plant root. *New Phytologist* **218**: 119-130.

**Medlyn BE, Zaehle S, De Kauwe MG, Walker AP, Dietze MC, Hanson PJ, Hickler T, Jain AK, Luo YQ, Parton W, et al. 2015.** Using ecosystem experiments to improve vegetation models. *Nature Climate Change* **5**: 528-534.

**Medvigy D, Moorcroft PR. 2012.** Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern North America. *Philosophical Transactions of the Royal Society B-Biological Sciences* **367**: 222-235.

**Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR. 2009.** Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research: Biogeosciences* **114**.

**Menge DNL, Lichstein JW, Angeles-Perez G. 2014.** Nitrogen fixation strategies can explain the latitudinal shift in nitrogen-fixing tree abundance. *Ecology* **95**: 2236-2245.

**Metcalfe DB, Meir P, Aragao L, da Costa ACL, Braga AP, Goncalves PHL, Silva JD, de Almeida SS, Dawson LA, Malhi Y, et al. 2008.** The effects of water availability on root growth and morphology in an Amazon rainforest. *Plant and Soil* **311**: 189-199.

**Nakhavali MA, Mercado LM, Hartley IP, Sitch S, Cunha FV, di Ponzio R, Lugli LF, Quesada CA, Andersen KM, Chadburn SE, et al. 2022.** Representation of the phosphorus cycle in the Joint UK Land Environment Simulator (vn5.5_JULES-CNP). *Geoscientific Model Development* **15**: 5241-5269.

**Nasto MK, Alvarez-Clare S, Lekberg Y, Sullivan BW, Townsend AR, Cleveland CC. 2014.** Interactions among nitrogen fixation and soil phosphorus acquisition strategies in lowland tropical rain forests. *Ecology Letters* **17**: 1282-1289.

**Ng JC. 2022.** Unearthing in-situ nutrient uptake rates: an assessment of underlying assumptions used for their prediction. Final Year Project (FYP), Nanyang Technological University, Singapore. https://hdl.handle.net/10356/156728

**Oliveira RS, Costa FRC, van Baalen E, de Jonge A, Bittencourt PR, Almanza Y, Barros FD, Cordoba EC, Fagundes MV, Garcia S, et al. 2019.** Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. *New Phytologist* **221**: 1457-1465.

**Oliveira RS, Eller CB, Barros FD, Hirota M, Brum M, Bittencourt P. 2021.** Linking plant hydraulics and the fast-slow continuum to understand resilience to drought in tropical ecosystems. *New Phytologist* **230**: 904-923.

**Olsson PA, Lekberg Y. 2022.** A critical review of the use of lipid signature molecules for the quantification of arbuscular mycorrhiza fungi. *Soil Biology & Biochemistry* **166**.

**Peh KSH, Lewis SL, Lloyd J. 2011.** Mechanisms of monodominance in diverse tropical tree-dominated systems. *Journal of Ecology* **99**: 891-898.

**Phillips RP, Brzostek E, Midgley MG. 2013.** The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytologist* **199**: 41-51.

**POWO. 2023.** Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://www.plantsoftheworldonline.org/

**Quesada CA, Lloyd J, Anderson LO, Fyllas NM, Schwarz M, Czimczik CI. 2011.** Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences* **8**: 1415-1440.

**Rasse DP, Rumpel C, Dignac MF. 2005.** Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* **269:** 341-356.

**Read QD, Henning JA, Sanders NJ. 2017.** Intraspecific variation in traits reduces ability of trait-based models to predict community structure. *Journal of Vegetation Science* **28**: 1070-1081.

**Reich, P.B., 2014.** The world-wide “fast–slow” plant economics spectrum: a traits manifesto. *Journal of Ecology* **102**: 275-301

**Reichert T, Rammig A, Fuchslueger L, Lugli LF, Quesada CA, Fleischer K. 2022.** Plant phosphorus-use and -acquisition strategies in Amazonia. *New Phytologist* **234**: 1126-1143.

**Rius BF, Darela JP, Fleischer K, Hofhansl F, Blanco CC, Rammig A, Domingues TF, Lapola DM. 2023.** Higher functional diversity improves modeling of Amazon forest carbon storage. *Ecological Modelling* **481**.

**Russo SE, Kochsiek A, Olney J, Thompson L, Miller AE, Tan S. 2013.** Nitrogen uptake strategies of edaphically specialized Bornean tree species. *Plant Ecology* **214**: 1405-1416.

**Sakschewski B, von Bloh W, Boit A, Rammig A, Kattge J, Poorter L, Penuelas J, Thonicke K. 2015.** Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology* **21**: 2711-2725.

**Sakschewski B, von Bloh W, Druke M, Sorensson AA, Ruscica R, Langerwisch F, Billing M, Bereswill S, Hirota M, Oliveira RS, et al. 2021.** Variable tree rooting strategies are key for modelling the distribution, productivity and evapotranspiration of tropical evergreen forests. *Biogeosciences* **18**: 4091-4116.

**Sampaio EVSB 1995.** Overview of the Brazilian caatinga. In: Medina E, Mooney HA, Bullock SH eds. *Seasonally Dry Tropical Forests*. Cambridge: Cambridge: Cambridge University Press, 35-63.

**Schaphoff S, von Bloh W, Rammig A, Thonicke K, Biemans H, Forkel M, Gerten D, Heinke J, Jagermeyr J, Knauer J, et al. 2018.** LPJmL4-a dynamic global vegetation model with managed land - Part 1: Model description. *Geoscientific Model Development* **11**: 1343-1375.

**Scheiter S, Langan L, Higgins SI. 2013.** Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist* **198**: 957-969.

**Schreeg LA, Santiago LS, Wright SJ, Turner BL. 2014.** Stem, root, and older leaf N:P ratios are more responsive indicators of soil nutrient availability than new foliage. *Ecology* **95**: 2062-2068.

**Seland Ø, Bentsen M, Olivié D, Toniazzo T, Gjermundsen A, Graff LS, Debernard JB, Gupta AK, He YC, Kirkevåg A, et al. 2020.** Overview of the Norwegian Earth System Model (NorESM2) and key climate response of CMIP6 DECK, historical, and scenario simulations. *Geoscientific Model Development* **13**: 6165-6200.

**Sheldrake M, Rosenstock NP, Mangan S, Revillini D, Sayer EJ, Olsson PA, Verbruggen E, Tanner EVJ, Turnerd BL, Wright SJ. 2018.** Responses of arbuscular mycorrhizal fungi to long-term inorganic and organic nutrient addition in a lowland tropical forest. *Isme Journal* **12**: 2433-2445.

**Shi M, Fisher JB, Brzostek ER, Phillips RP. 2016.** Carbon cost of plant nitrogen acquisition: global carbon cycle impact from an improved plant nitrogen cycle in the Community Land Model. *Global Change Biology* **22**: 1299-1314.

**Smith-Martin CM, Muscarella R, Ankori-Karlinsky R, Delzon S, Farrar SL, Salva-Sauri M, Thompson J, Zimmerman JK, Uriarte M. 2022.** Hurricanes increase tropical forest vulnerability to drought. *New Phytologist* **235**: 1005-1017.

**Smith-Martin CM, Xu XT, Medvigy D, Schnitzer SA, Powers JS. 2020.** Allometric scaling laws linking biomass and rooting depth vary across ontogeny and functional groups in tropical dry forest lianas and trees. *New Phytologist* **226**: 714-726.

**Smith B, Warlind D, Arneth A, Hickler T, Leadley P, Siltberg J, Zaehle S. 2014.** Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences* **11**: 2027-2054.

**Sobrado MA, Cuenca G. 1979.** Aspects of water-use of deciduous and evergreen species in a tropical dry forest of Venezuela. *Acta Cientifica Venezolana* **30**: 302-308.

**Soper FM, Nasto MK, Osborne BB, Cleveland CC. 2019.** Nitrogen fixation and foliar nitrogen do not predict phosphorus acquisition strategies in tropical trees. *Journal of Ecology* **107**: 118-126.

**Sousa D, Fisher JB, Galvan FR, Pavlick RP, Cordelli S, Giambelluca TW, Giardina CP, Gilbert GS, Imran-Narahari F, Litton CM, et al. 2021.** Tree canopies reflect mycorrhizal composition. *Geophysical Research Letters* **48**: 1-9.

**Thonicke K, Billing M, von Bloh W, Sakschewski B, Niinemets U, Penuelas J, Cornelissen JHC, Onoda Y, van Bodegom P, Schaepman ME, et al. 2020.** Simulating functional diversity of European natural forests along climatic gradients. *Journal of Biogeography* **47**: 1069-1085.

**Thornton PE, Lamarque JF, Rosenbloom NA, Mahowald NM. 2007.** Influence of carbon-nitrogen cycle coupling on land model response to $CO_2$ fertilization and climate variability. *Global Biogeochemical Cycles* **21**.

**Thum T, Nabel J, Tsuruta A, Aalto T, Dlugokencky EJ, Liski J, Luijkx IT, Markkanen T, Pongratz J, Yoshida Y, et al. 2020.** Evaluating two soil carbon models within the global land surface model JSBACH using surface and spaceborne observations of atmospheric $CO_2$. *Biogeosciences* **17**: 5721-5743.

**Ushio M, Fujiki Y, Hidaka A, Kitayama K. 2015.** Linkage of root physiology and morphology as an adaptation to soil phosphorus impoverishment in tropical montane forests. *Functional Ecology* **29**: 1235-1245.

**Valverde-Barrantes OJ, Authier L, Schimann H, Baraloto C. 2021.** Root anatomy helps to reconcile observed root trait syndromes in tropical tree species. *American Journal of Botany* **108**: 744-755.

**Vitousek PM, Sanford RL. 1986.** Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**: 137-167.

**Vleminckx J, Fortunel C, Valverde-Barrantes O, Paine CET, Engel J, Petronelli P, Dourdain AK, Guevara J, Beroujon S, Baraloto C. 2021.** Resolving whole-plant economics from leaf, stem and root traits of 1467 Amazonian tree species. *Oikos* **130**: 1193-1208.

**Walker AP, Hanson PJ, De Kauwe MG, Medlyn BE, Zaehle S, Asao S, Dietze M, Hickler T, Huntingford C, Iversen CM, et al. 2014.** Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air $CO_2$ enrichment experiments: Model performance at ambient $CO_2$ concentration. *Journal of Geophysical Research: Biogeosciences* **119**: 937-964.

**Wang B, McCormack ML, Ricciuto DM, Yang XJ, Iversen CM. 2023.** Embracing fine-root system complexity in terrestrial ecosystem modeling. *Global Change Biology* **29**: 2871–2885.

**Wang ZQ, Gong HY, Sardans J, Zhou QP, Deng JM, Niklas KJ, Hu HF, Li YL, Ma ZQ, Mipam TD, et al. 2022.** Divergent nitrogen and phosphorus allocation strategies in terrestrial plant leaves and fine roots: A global meta-analysis. *Journal of Ecology* **110**: 2745-2758.

**Warren JM, Hanson PJ, Iversen CM, Kumar J, Walker AP, Wullschleger SD. 2015.** Root structural and functional dynamics in terrestrial biosphere models - evaluation and recommendations. *New Phytologist* **205**: 59-78.

**Weemstra M, Mommer L, Visser EJW, van Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ. 2016.** Towards a multidimensional root trait framework: a tree root review. *New Phytologist* **211**: 1159-1169.

**Weemstra M, Peay KG, Davies SJ, Mohamad M, Itoh A, Tan S, Russo SE. 2020. Lithological constraints on resource economies shape the mycorrhizal composition of a Bornean rain forest. *New Phytologist* 228: 253-268.**

**Weemstra M, Valverde-Barrantes O, Fortunel C, Oblitas Mendoza E, Prata E, Vásquez Pilco M, Vicentini A, Vleminckx J, Baraloto C. 2023. Weak phylogenetic and habitat effects on root trait variation of 218 Neotropical tree species. *Frontiers in Forests and Global Change* 6: 1187127.**

**Weng ES, Malyshev S, Lichstein JW, Farrior CE, Dybzinski R, Zhang T, Shevliakova E, Pacala SW. 2015.** Scaling from individual trees to forests in an Earth system modeling framework using a mathematically tractable model of height-structured competition. *Biogeosciences* **12**: 2655-2694.

**Withington JM, Reich PB, Oleksyn J, Eissenstat DM. 2006.** Comparisons of structure and life span in roots and leaves among temperate trees. *Ecological Monographs* **76**: 381-397.

**Wullschleger SD, Epstein HE, Box EO, Euskirchen ES, Goswami S, Iversen CM, Kattge J, Norby RJ, van Bodegom PM, Xu XF. 2014.** Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany* **114**: 1-16.

**Wurzburger N, Wright SJ. 2015.** Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology* **96**: 2137-2146.

**Xu C, Christoffersen B, Robbins Z, Knox R, Fisher RA, Chitra-Tarak R, Slot M, Solander K, Kueppers L, Koven C, et al. 2023.** Quantification of hydraulic trait control on plant hydrodynamics and risk of hydraulic failure within a demographic structured vegetation model in a tropical forest (FATES-HYDRO V1.0). *EGUsphere* **2023**: 1-32.

**Xu XT, Medvigy D, Powers JS, Becknell JM, Guan KY. 2016.** Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80-95.

**Yaffar D, Defrenne CE, Cabugao KG, Kivlin SN, Childs J, Carvajal N, Norby RJ. 2021.** Trade-offs in phosphorus acquisition strategies of five common tree species in a tropical forest of Puerto Rico. *Frontiers in Forests and Global Change* **4**.

**Yang XJ, Ricciuto DM, Thornton PE, Shi MY, Xu M, Hoffman F, Norby RJ. 2019.** The effects of phosphorus cycle dynamics on carbon sources and sinks in the Amazon region: A Modeling Study Using ELM v1. *Journal of Geophysical Research-Biogeosciences* **124**: 3686-3698.

**Yang XQ, Wu JP, Chen XZ, Ciais P, Maignan F, Yuan WP, Piao SL, Yang S, Gong FX, Su YX, et al. 2021.** A comprehensive framework for seasonal controls of leaf abscission and productivity in evergreen broadleaved tropical and subtropical forests. *Innovation* **2**.

**Yu L, Ahrens B, Wutzler T, Schrumpf M, Zaehle S. 2020.** Jena Soil Model (JSM v1.0; revision 1934): a microbial soil organic carbon model integrated with nitrogen and phosphorus processes. *Geosci. Model Dev.* **13**: 783-803.

**Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T, Luo YQ, Wang YP, El-Masri B, Thornton P, et al. 2014.** Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate free-air $CO_2$ enrichment studies. *New Phytologist* **202**: 803-822.

**Zhang Y, Cao J, Lu M, Kardol P, Wang J, Fan G, Kong D. 2023. The origin of bi-dimensionality in plant root traits. *Trends in Ecology & Evolution* (in press). https://doi.org/10.1016/j.tree.2023.09.002**

**Zhu LQ, Huang RZ, Wang JP, Huang GM, Guan HZ, Lin LJ, Yang MJ, Li YY, Zou XH. 2023.** Litter, root, and mycorrhiza input affected soil microbial community structure in schima superba pure forest in subtropical China. *Diversity-Basel* **15**.

## Supporting Information

| **Filename** | **Description** |
|---|---|
| SI_NotesS1_NewPhytViewpoint_Cusack_Final.pdf | Notes S1 contains methodological details and results for main text and boxes |
| Dataset S2_Box1data_RootTraits_Panama.csv | Dataset S2 provides raw data for Panama roots used in Box 1 |
| Dataset S3_Box1data_RootTraits_PuertoRico.csv | Dataset S3 provides raw data for Puerto Rico roots used in Box 1 |
| Dataset S4_Box2data_MaximumRootingDepthData_CostaRica.csv | Dataset S4 provides raw data for Costa Rica roots used in Box 2 |
| Dataset S5_Box3data_uptake_Panama.csv | Dataset S5 provides raw data for Panama roots used in Box 3 |
| Dataset S6_Box3data_uptake_Singapore.csv | Dataset S6 provides raw data for Singapore roots referenced in Box 3 and in Notes S1 |
| Dataset S7_Box4data_Panama_stoich.csv | Dataset S7 provides raw data for Panama root stoichiometry used in Box 4 |