Viewpoints

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

Summary

Tropical forest root characteristics and resource acquisition strategies are underrepresented in vegetation and global models, hampering the 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 trade-offs in fine-root water vs nutrient acquisition, and (3) aboveground–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 linked aboveground–belowground hydro-nutrient functions. Tropical forests are undergoing warming, shifting rainfall regimes, and exacerbation of soil nutrient scarcity caused by elevated atmospheric CO_2. The accurate model representation of tropical forest functions is crucial for understanding the interactions of this biome with the climate.

Introduction

Tropical forests are poorly characterized in vegetation models relative to other ecosystems, and the 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 *c.* 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. the first-order root tips, 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 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 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 results in 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 of 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

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 and nutrient acquisition			
Fine-root biomass	Mg ha^{-1}	Absorptive tissue	Absorptive tissue
Fine-root productivity	Mg ha^{-1} yr^{-1}	Absorptive tissue productivity	Absorptive tissue productivity
Fine-root turnover (inverse of lifespan)	yr^{-1}	Absorptive tissue turnover	Absorptive tissue turnover
Specific root length (SRL)	cm g^{-1}	Soil volume explored per unit biomass	Conversion factor (fine-root biomass to fine-root length), Calculate absorptive area as biomass $\times$ SRL $\times$ $2\pi r$
Root growth timing (e.g. phenology/ seasonality)	Growth or death timing	Align root production and 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 function)	Distribute absorptive and transportive tissues through soil profile according to resources	Locate absorptive tissue in soil, characteristic of PFTs in some models
Root order distribution (i.e. branching density)	Ratio of (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 plant C for water and/or other nutrients	Exchange C for nitrogen and phosphorus
Fine-root function: water acquisition and drought resistance			
Maximum depth	m	Define vertical root domain	Define vertical root domain, characteristic of PFTs in some models
Root hydraulic conductivity	L_P; ms^{-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 conductance or AMF colonization, function poorly constrained	Soil–root water conductance
Root membrane permeability	Mass per pressure per area per time	Water uptake	Water uptake
Water uptake rate	mg-H_2O per length per time	Water uptake	Water uptake
Fine-root function: nutrient acquisition			
Root enzyme activities (e.g. phosphatase and protease)	Degradation rate of organic compounds	Release mineral nutrients from organic matter	Release mineral phosphorus
Organic exudate production	C root per mass (or per length) per time	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 per area, and fixation rate – mg N_2 fixed per nodule biomass per time	Acquire nitrogen from the atmosphere and convert to biologically available forms	Exchange C for nitrogen, 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, sometimes a characteristic of PFTs
Phosphorus uptake rate	µg P per length of root (or per mass) per time	Phosphorus uptake by root or AMF/ECM symbiont	Realized phosphorus uptake, present in few models and varies with nutrient availability
Nitrogen uptake rate	µg N per length of root (or per mass) per time	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 : P ratio	Ratio	Stoichiometry	ABSENT
Tissue C : N ratio	Ratio	Stoichiometry	Control nitrogen demand, present in most models, part of PFTs
Tissue C : P ratio	Ratio	Stoichiometry	Control phosphorus 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 and transport			
Coarse root biomass	Mg ha^{-1}	Structural support and 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

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 functions 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). AMF, arbuscular mycorrhizal fungi; NPP, net primary production; PFT, plant functional type.

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

No.	Model name	ESM-capable	Trait assignment: PFT, Cohort, IBM	Spatially explicit	No. of above-/below-ground plant traits	Support, storage, distribution				Longevity, stoichiometry, mass-length conversion				Water uptake						Direct nutrient uptake + priming			Symbiotic nutrient uptake							Reference
					Function	Coarse root biomass	Fine root leaf biomass or area ratio	Vertical root distribution parameter(s)	Maximum rooting depth	Fine root CN ratio	Fine root CP ratio	Fine root turnover rate (unit biomass/yr)	Specific root length or area	Water stress factor (relative soil water availability)	Fraction of total tree resistance in root system	Water uptake per unit fine-root C or length	Transporting root P50	Fine root radius (controls soil–root conductance)	Root membrane permeability	Rate of N uptake per root length (active or passive)	Rate of P uptake per root length (active or passive)	Rate of root exudation per unit NSC	N fixation rate per unit nodule biomass	Nodule biomass	Fixation cost: (nodule C spent per unit N acquired)	Nodule maintenance respiration rate	Nodule turnover time	Rate of AM inorganic N uptake per AM biomass	Rate of EM inorganic N uptake per unit N decomp	
1	E3SM-ELM-CNP	✓	PFT		NA/10	p	p	p	c	c	c	p		m						n	n									Thornton *et al*. (2007); Yang *et al*. (2019)
2	LPJmL4.0	✓	PFT		31/6		p,m	p	p	p		p		m																Schaphoff *et al*. (2018)
3	LPJmL4.0-VR	✓	Cohort		31/7	p,s[2]	p,m	p	p,s	p		p		m																Sakschewski *et al*. (2021)
4	ED2.2-[HYD][1]	✓	Cohort		52/6		p	p	p,s			p		m,s		m														Xu *et al*. (2016); Longo *et al*. (2019)
5	FATES-[Hydro] [PARTEH]	✓	Cohort		23/15	p,s	p,n	p	p	p,n	p,n	p	p	m	p	m	p	p	m(2)	n	n	n	i			i				Koven *et al*. (2020); Knox *et al*. (2023); Xu *et al*. (2023)
6	LM3-PPA-TV	✓	Cohort		37/9		p	p	p			p	c			m		c	c			c								Weng *et al*. (2015); Martinez Cano *et al*. (2020)
7	LM4.1-BNF	✓	Cohort		21/31		p	p	c	c		p	c			m		c	c	n(5), m		n(2)	p	n	c	c	c	n(5)	n(6)	Weng *et al*. (2015); Kou-Giesbrecht *et al*. (2021)
8	LPJ-GUESS	✓	Cohort		19/6		p,m,n	p	c	n		p		m																Smith *et al*. (2014); Belda *et al*. (2022)
9	LPJ-GUESS-NTD	✓	Cohort		19/11		p,m,n,s	p	c	n		p		m						n(3)	n(2)									Dantas de Paula *et al*. (2021)
10	CABLE-POP	✓	Cohort		16/9		p	p	p	p	c	p		m						n	n									Haverd *et al*. (2018)
11	LPJml-FIT		IBM		32/6		p,m	p	p	p		p		m																Sakschewski *et al*. (2015); Thonicke *et al*. (2020)
12	aDGVM2		IBM		22/9	p[3]	p	p	p				p		m	m	p	c												Scheiter *et al*. (2013); Langan *et al*. (2017)
13	CAETE		IBM		15/5		p			p		p		m,s		m														Rius *et al*. (2023)
14	FORMIND		IBM	✓	63/0																									Fischer *et al*. (2016)
15	TROLL		IBM	✓	25/0																									Chave (1999); Marechaux & Chave (2017)

Root traits as represented in a sample of 15 vegetation models are presented that vary in scope (e.g. 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 in response to changing conditions over time. 'Spatially explicit' refers to aboveground processes only (e.g. light competition). Root biomass and traits (columns) are grouped by main functions (top row). 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. Models are grouped into three main approaches for assigning plant traits within which trait values are held constant over the lifespan of an individual; we are not aware of any approaches that explicitly allow for trait plasticity over ontogeny: 'PFT' – plant functional type represented by a single average individual with characteristic trait values; 'Cohort' – an average individual within a tree size class, functional type, and in most cases, a particular canopy layer or light environment; 'IBM' – individual based modeling of every tree within a patch. A subset of IBMs use spatially explicit locations of trees, termed gap models. With a few exceptions, we tallied traits and parameters rather than dynamic state or rate quantities, to give an idea of how many unique field root variables would need quantification for executing the model in a tropical forest. Cells in the table denote where a given root trait varies by PFT/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 no. 4, 5, 6, 7, and 12. Nutrient-enabled models explicitly model nitrogen and/or phosphorus uptake through direct or symbiotic means and include models no. 1, 5, 7, 9, and 10. Root traits associated only 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 Supporting Information Notes S1.

[1] This model is not yet coupled to an ESM but is ESM-capable.

[2] Coarse roots are distributed with depth and serve a physical support function.

[3] Coarse roots are implicit with storage and serve a storage/resprouting function.

comparisons for tropical forests indicate that including P availability, which has been excluded for the representation of temperate ecosystems, can improve the 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 the 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 reassigned 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 vs root representation in a sampling of leading vegetation models, including the topics: (a) soil exploration, (b) coordination and trade-offs in nutrient vs water acquisition, and (c) aboveground–belowground functional linkages for nutrient and water uptake and use. (3) An assessment of commonly measured

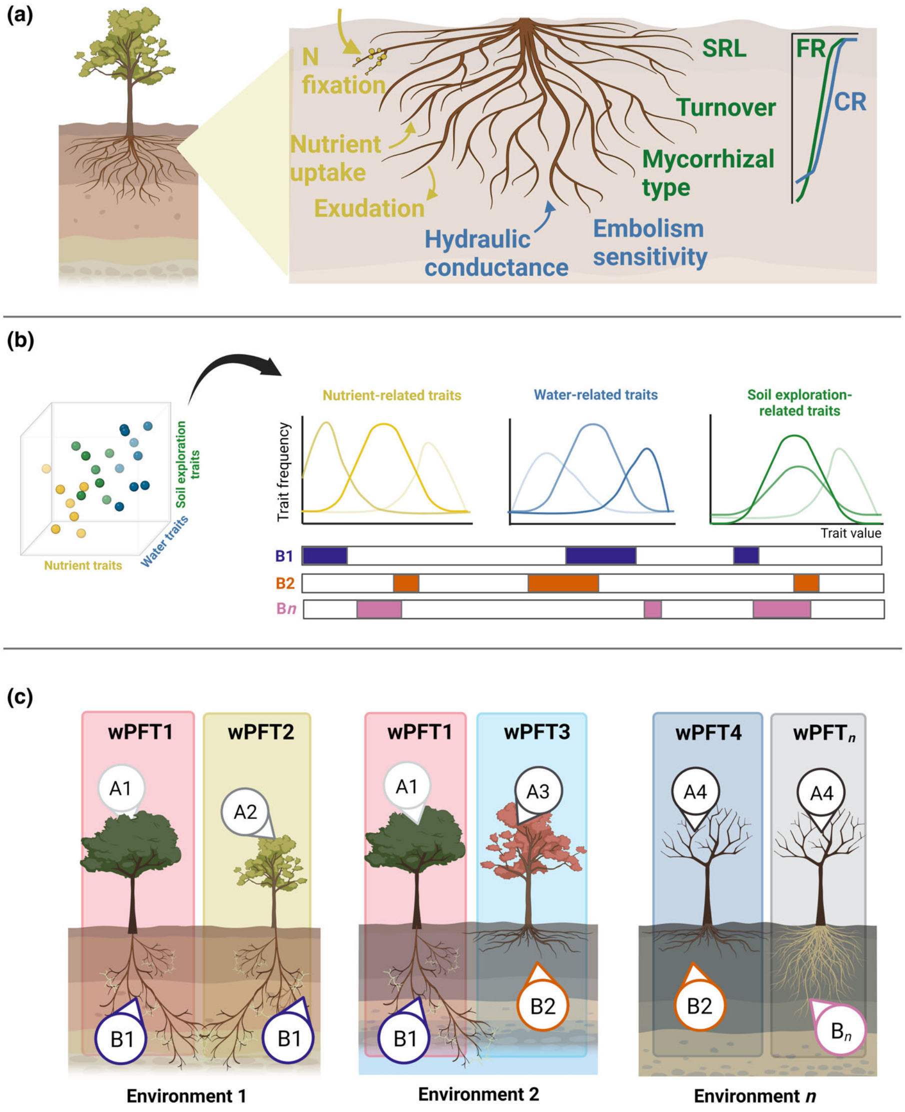


Fig. 1 Conceptual representation depicts the root traits recommended for further tropical forest research and representation in vegetation models as part of whole-plant functional types (PFTs) or trait clusters. The panels include (a) a graphical depiction of the root system with a subset of suggested 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 aboveground–belowground whole PTFs (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, C 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 net primary production (NPP) and other emergent properties of ecosystems depicted in vegetation models.

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 aboveground–belowground PFTs 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 than in 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} yr^{-1} vs 428 g m^{-2} yr^{-1} in temperate forests and 311 g m^{-2} yr^{-1} in boreal forests, and annual root turnover times averaged 1.4 yr^{-1} in tropical forests vs 1.2 yr^{-1} in temperate forests and 0.8 yr^{-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 coexisting 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 with other ecosystems globally (Valverde-Barrantes *et al.*, 2021; Asefa *et al.*, 2022; Weemstra *et al.*, 2023). 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

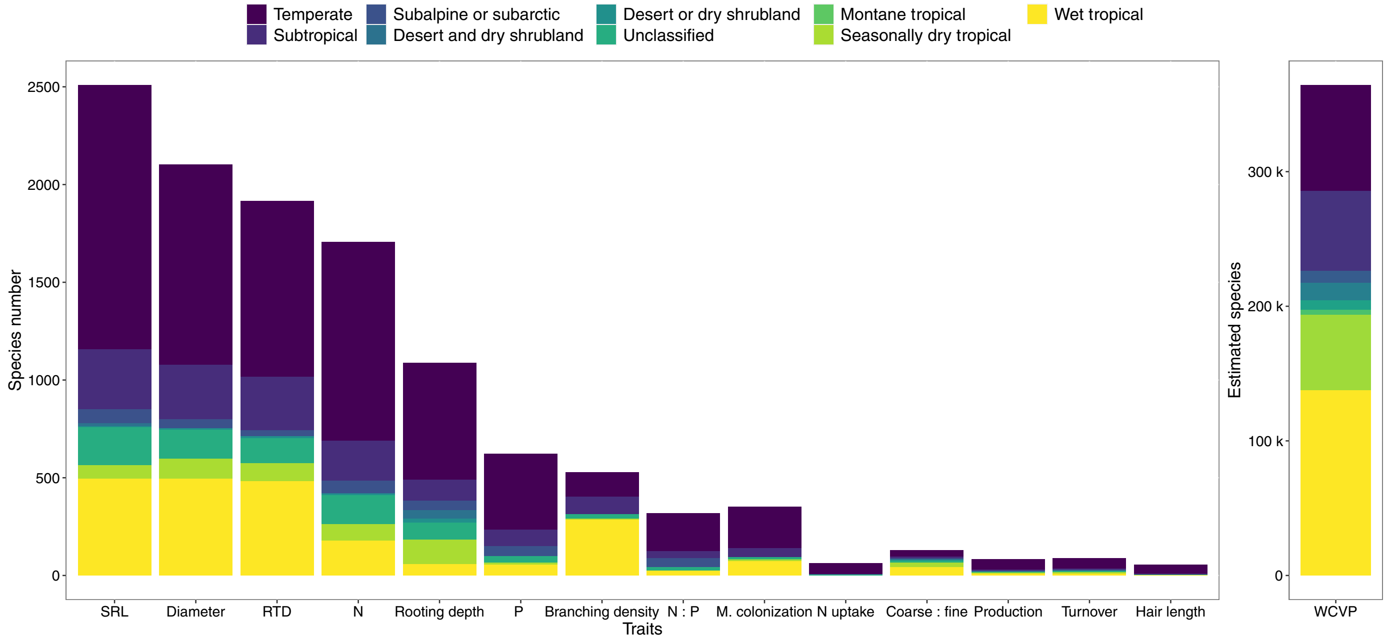


Fig. 2 Total number of species for which fine-root traits data are currently available across climatic biomes is shown (left) relative to the total number of known species in each biome (right). Despite much higher species numbers present in wet tropical forests, the highest percentage of available data comes from temperate plant species. Within the tropics, most data are from wet tropical forests (shown in yellow, 'wet tropical'). Overall, specific root length (SRL) has been the most commonly measured root trait (note that total root biomass not shown), 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 root trait and biome description (colors); traits included are 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} d^{-1}), coarse-to-fine root mass ratio (Coarse : fine), root hair length (Hair length, μm), root production (Production, g m^{-2} yr^{-1}), and root turnover rate (Turnover, yr^{-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 Supporting Information.

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 a species, as well as among species (in Box 1). At the same time, 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 vs 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 downregulate 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, vs (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 trade-offs for root nutrient vs water acquisition, and (c) aboveground–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 (1) empirical advances and understanding, (2) current model representation, and (3) 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 the data that are promising for improving functional representation, and model components that are confirmed or at odds with field data (e.g. Medlyn *et al.*, 2015).

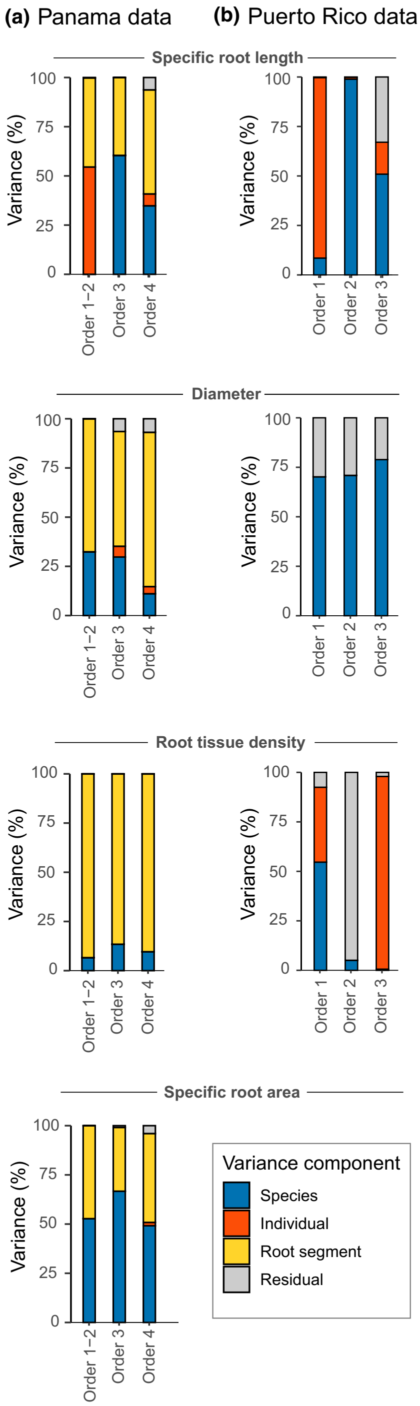
We summarize empirically measured root characteristics (Table 1) alongside an assessment of root function representation in 15 leading vegetation models (Table 2). These models include some linked to global Earth system models (ESMs), demographically resolved vegetation models (e.g. representing forest 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-Ramirez *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 as follows: (1) relatively greater root biomass and root production rates in infertile surface soils vs 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 vs drier conditions, likely because extreme drying in tropical forests causes surface root death; (3) faster fine-root turnover in wetter vs drier conditions and in fertile vs 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 vs wet conditions and infertile vs fertile soils, indicating maximization of soil explored per unit biomass; and (5) greater root production rates in the subsoil vs surface soils under dry vs wet conditions, likely of 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 for root biomass, production, turnover, and SRL are the best supported by the literature for tropical forest root characteristics.

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

Box 1 High fine-root trait variation within and among individuals suggests morphological trait flexibility 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). A comparison of the proportion of variation explained by species, individual trees, individual root segments (replicated 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 segments within individuals 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 S1 and S2. Bars show the percent of variance explained by each component, with statistical methods in Notes S1. 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.

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 the forefront of 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 belowground traits (see section below). Incorporating

Table 3 Tabulation is presented of the root characteristics present in Table 1 ('1. Empirical research focus'), and in Table 2 ('2. Model focus'), and present in both (3. Common), comparing empirical understanding with model use (Caveats).

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 water uptake, empirical research combines with root depth distributions for nutrient uptake also
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 production and turnover rates are understood similarly in empirical and modeling work, but are poorly characterized in tropical empirical data
Root tissue density	C cost of N fixation and C cost of mycorrhizal nutrient acquisition	Fine-root specific root length (SRL)	Used as a PFT trait in some models or as a global constant; in empirical work SRL is responsive to resource availability within and among tropical species and is not clearly distinct among species
	N fix nodule turnover rates	Water and nutrient uptake rates	Understood similarly in empirical and modeling work, but 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	Exudation rates and chemistry are poorly characterized in tropical empirical data, appear linked to nutrient uptake
		N fixation rates and nodule biomass	Relatively good empirical understanding of N fixation and its function relative to other root traits; 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

Root characteristics in Tables 1 and 2 are combined. Column 3 gives characteristics 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. AMF, arbuscular mycorrhizal fungi; ECM, ectomycorrhizal fungi.

belowground resource partitioning would allow for a more holistic differentiation between resource-acquisitive and resource-conservative strategies, as well as contrasting strategies for nutrient and water acquisition and drought tolerance. 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 given soil layers (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 (nonshared) 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 in identifying clusters of root traits for nutrient acquisition. This recent work could be built on to include clusters of belowground hydraulic traits (Table 1, e.g. rooting depth and 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 root P acquisition '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 trade-offs in P acquisition strategies among tree species, such as high fine-root phosphatase activity vs increased mycorrhizal hyphal length (Zhu *et al.*, 2023), although morphological trade-offs were less clearly linked to P acquisition. We have yet to formulate mathematical response surfaces defining which trait combinations 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 trade-offs 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 (Allen *et al.*, 2020; Lugli *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 2), 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 whether nutrient uptake rates can be related to surrogates, such as laboratory 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 2), 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). Acquisition of different nutrients could then be explored in relation to water uptake.

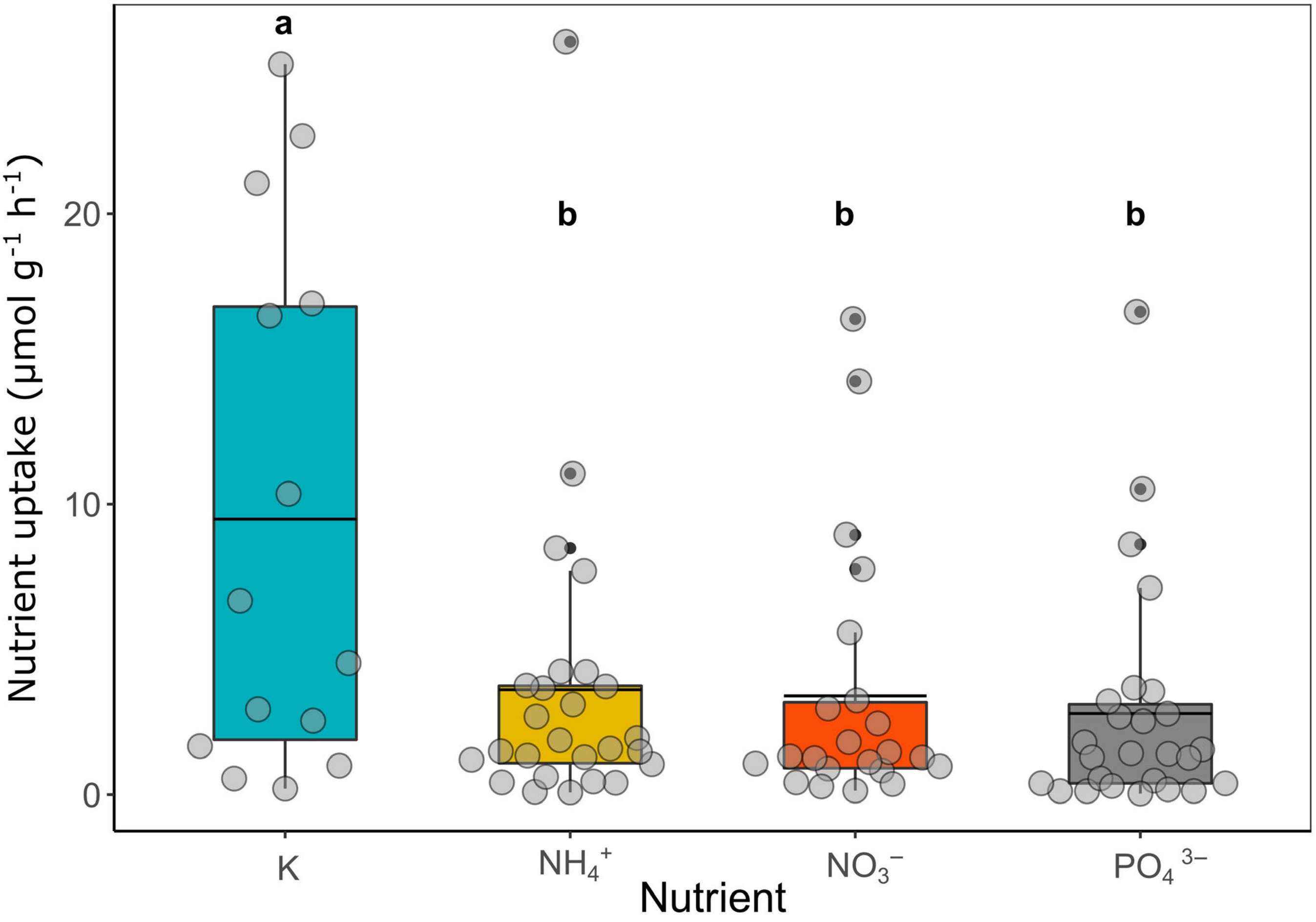
Coupled hydro-biogeochemical strategies: *model representation* Among the root traits included in the 15 models assessed here (Table 2), water stress or water uptake was represented in 13 models vs only five models that represented nutrient acquisition (N or P), with representation of P dynamics particularly 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 to plant hydraulic traits emphasized by empiricists, root phenology, root hair length and density, and mycorrhizal symbiosis were not used in the models to represent plant hydraulics (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 nonstructural carbohydrates was linked to priming and nutrient availability in three of the models, and two models had some representation of symbiotic nutrient uptake, including biological nitrogen fixation (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

Box 2 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 measured in relation to broader nutrient limitation to net primary production (NPP) 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 in Notes S1. Details and additional results are in Notes S1 and data are provided as Datasets S3 and S4. Across 33 mature individuals of a relatively abundant Panamanian lowland species *Protium picramnioides*, there were significantly greater nutrient uptake rates for potassium (K) vs 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, data shown in gray points. 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 S1 and shown at https://youtu.be/4atZ3E0NrX4. Dynamic nutrient uptake rate measurements within and among sites should be measured with fine-root morphological characterization, which could help inform dynamic root responses to changing resources in vegetation models. Considerably more data are required.



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 the forefront of vegetation model development. Model development of root dynamics has proceeded on almost entirely independent paths for plant hydraulics vs nutrient acquisition, even within the same model (via separate modules, e.g. FATES, LM, and LPJ; Table 2), such that coordinated responses to resource changes and C costs for water vs 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 toward coordinating water and nutrient uptake include: (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; Langan *et al*., 2017; Kennedy *et al*., 2019; Joshi *et al*., 2022; Knox *et al*., 2023). Hydro-biogeochemical model integration would allow a 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 trade-off 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 aboveground–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).

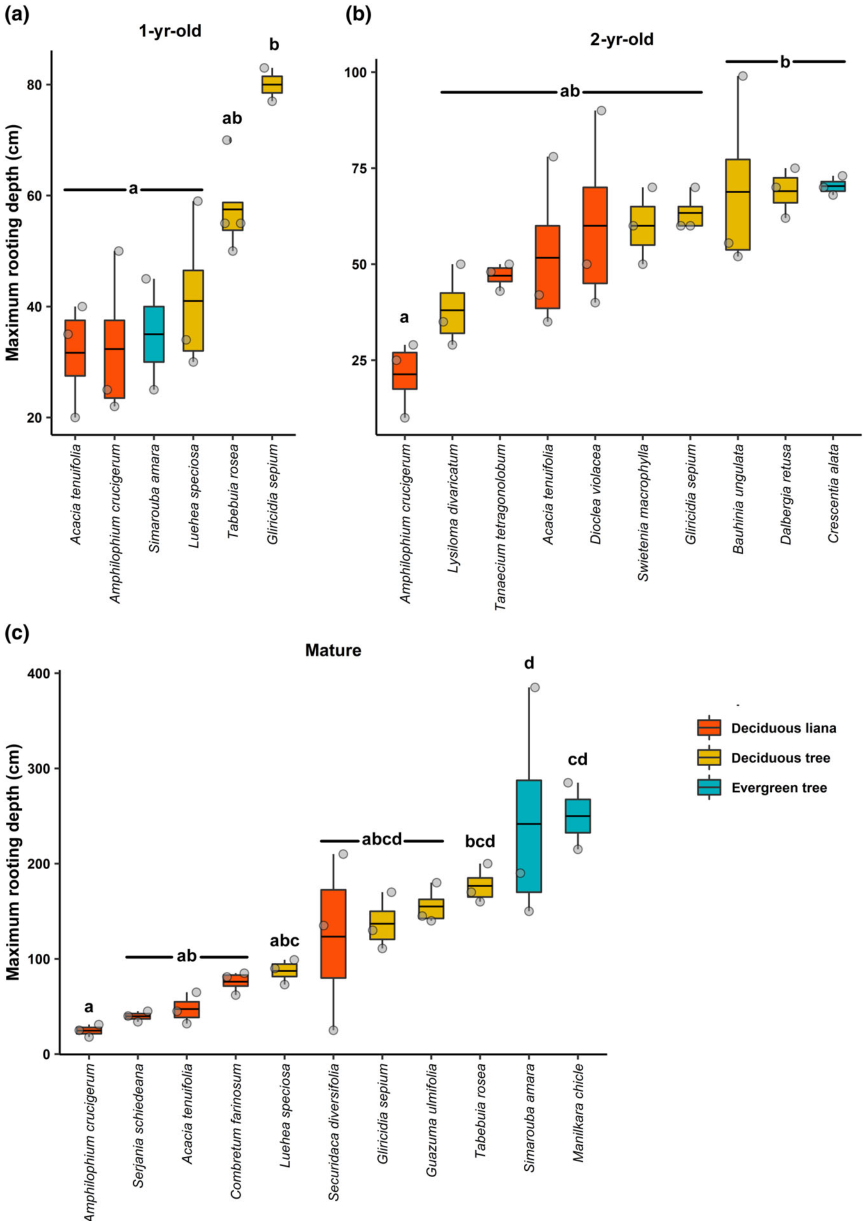
Very few studies have focused on aboveground–belowground functional linkages in tropical forests, with most attention to plant hydraulics. For example, maximum rooting depth of different species (usually measured for coarse roots) has been linked to deciduousness in tropical forests, particularly in 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 aboveground–belowground linkages appear to be strongest under stressful conditions. In the Amazon, only under dry conditions were there linkages between 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 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 3). To explore this, aboveground hydraulic traits could be linked to belowground traits beyond maximum rooting depth, which is very difficult to measure, such as overall root biomass depth distributions, vessel diameter, root embolism vulnerability, and seasonal changes in root production (i.e. phenology; Germon *et al*., 2020). Data on the embolism resistance of roots are 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 aboveground–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 aboveground–belowground 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 strategies in tropical forests.

Coupled aboveground–belowground resource strategies: *model representation* Of the 15 vegetation models, several linked aboveground deciduousness with root traits, and most had an uneven representation of belowground vs aboveground traits and functions, with an average of *c*. 30 aboveground traits compared with 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 used 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 of 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 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, aboveground–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.

Box 3 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 shows 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 aboveground–belowground trait coordination. Letters show means separations using Tukey HSD tests; boxes show means and quartiles; data are shown in gray points. Details are provided in Notes S1, and data are provided as Dataset S5. 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 plant functional types (PFTs) or trait clusters, which could then be combined with nutrient acquisition types to improve tropical plant representation in vegetation models.



For nutrient acquisition, aboveground–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; Brzostek *et al.*, 2014; Shi *et al.*, 2016; 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 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 aboveground–belowground resource strategies: *avenues for model improvement* Integrating more of the hydraulic function of fine and coarse roots into existing aboveground–belowground hydraulic PFTs is an important next step for model development (Fig. 1). In particular, aboveground–belowground linkages for plant hydraulics could be expanded, including the hydraulic function of coarse roots, which is rare in vegetation models, present 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 trade-off 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 trade-off can emerge from variable rooting depth and trade-offs with P50 and deciduousness (Langan *et al.*, 2017). Given the empirical support for this three-way trade-off, 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. A focused collection of data on root hydraulics, such as root embolism resistance, would help to clarify the aboveground–belowground coordination of this three-way trade-off for tropical forests with periodic moisture scarcity.

For aboveground–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 trade-off between C expenditure above vs 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 PTFs? Investigations into these types of aboveground–belowground nutrient acquisition questions could then be combined with hydraulic aboveground–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 included as follows: 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).

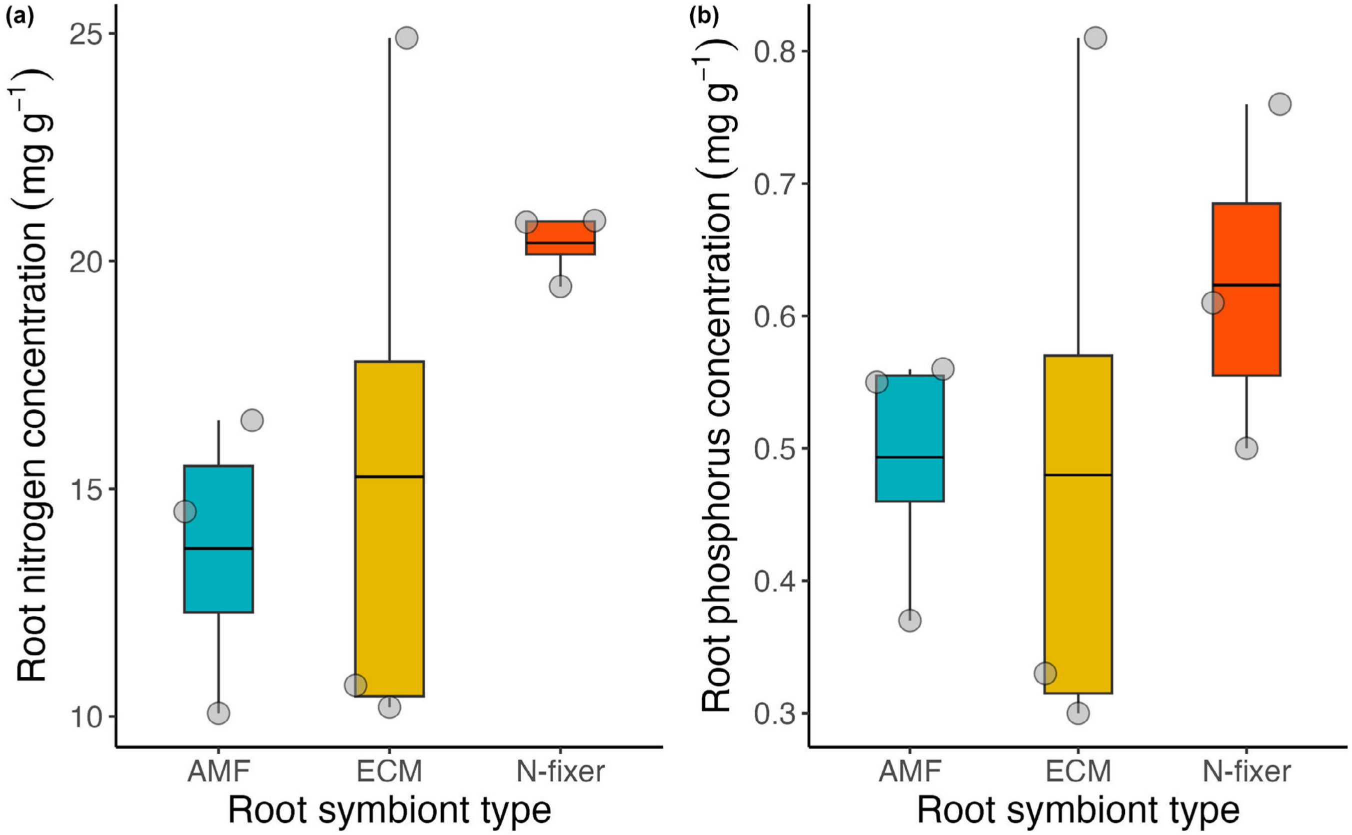
Recently, an expanded global database including root C : N : P and morphology was published as the Global Root Trait (GRooT) database (Guerrero-Ramirez *et al.*, 2021; Fig. 2), which may be useful for further exploration of functional linkages to stoichiometry. To increase the functional utility of this 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 whether 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, and branching) for 1467 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

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 data are relatively more available than functional trait measurements like nutrient uptake (Fig. 2).

However, there remains a knowledge gap linking tropical 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 content (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 stoichiometry across these three functional types. Figure shows means and quantiles for nine tree species ($n = 3$ individuals per functional type); data are shown in gray points; no letters indicate no significant differences among groups using Tukey HSD tests. Details on species used and methods are in Notes S1, and data for each tree species are provided as Dataset S6. These data highlight the uncertainty of 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).



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 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 2 and Notes S1). 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 (Tables 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 and water transport by coarse roots). (4) Functional characterization of fine roots is often different in models vs 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 *c.* 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 with P uptake rates, 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 (following Fleischer *et al.*, 2019; Koven *et al.*, 2020; Caldararu *et al.*, 2023). New experiments could also test model-derived hypotheses before the inclusion of a new process in models. For example, the Amazon-FACE 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 US Department of Energy Next Generation Ecological Experiments–Tropics (NGEE-Tropics, https://ngee-tropics.lbl.gov/), the Amazon-FACE, 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.

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Competing interests

None declared.

Author contributions

DFC, BC, RN, CSM, KMA, AC, SJW, NG-R, LFL, LM, MS, KF, CD, LT, CF, SB, MW and LF contributed via the in-person workshop with discussions and idea development. BC, DFC, SJW and CF compiled and created the tables. DFC, NG-R, LFL, CD, LT, LM, MS and AC contributed to the figure design and finalization. DFC, ALC, KMA, CSM and DY contributed to the data contributions for the boxes. DFC, ALC, RN, SJW and KMA led funding acquisition and coordination. All authors contributed initial ideas, text, and final edits to the manuscript.

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Data availability

Data presented in Boxes 1–4 are available in the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Raw data for Panama roots used in Box 1.

Dataset S2 Raw data for Puerto Rico roots used in Box 1.

Dataset S3 Raw data for Panama roots used in Box 2.

Dataset S4 Raw data for Singapore roots referenced in Box 2 and in Notes S1.

Dataset S5 Raw data for Costa Rica roots used in Box 3.

Dataset S6 Raw data for Panama root stoichiometry used in Box 4.

Notes S1 Methodological details and results in the main text and boxes.

Key words: ecosystem vegetation models, fine roots, hydraulics, nutrient acquisition, phosphorus uptake, plant functional types, root trait clusters, tropical forests.

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