Embracing fine-root system complexity to improve the predictive understanding of ecosystem functioning

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Abstract

Projecting the functioning of the biosphere requires a holistic consideration of whole-ecosystem processes. Although improving leaf and canopy processes has been the focus of ecosystem model development since the 1970s, the arbitrary homogenization of fine-root systems into a single pool is at odds with observations. This discrepancy has increased in the last two decades as accelerated conceptual and empirical advances have revealed functional differentiation and cooperation

conferred by the hierarchical structure of fine-root orders and associations with mycorrhizal fungi in fine-root systems. To close this model-data gap, we propose a 3-pool structure comprising Transport and Absorptive fine roots with Mycorrhizal fungi (TAM) to model vertically resolved fine-root systems across organizational and spatial-temporal scales. A comparison of TAM to the single fine-root structure in a state-of-the-art Earth System Model using the 'big-leaf' approach demonstrates robust impacts on carbon cycling in temperate forests, lending further quantitative support to the empirical and theoretical basis for TAM. Strong support in both theory and practice therefore suggests a move beyond the useful but incorrect paradigm of single-pool homogenization, echoing a broad trend of embracing ecological complexities in terrestrial ecosystem modelling. Although challenges lay ahead towards realizing TAM in ecologically realistic demography models simulating emergent functioning from pattern and diversity, adoption of TAM by both modelers and empiricists holds promise to build a better predictive understanding of ecosystem functioning in the context of global change.

Key words: ecosystem model, complexity, fine root, mycorrhiza, TAM, partitioning, phenology, demography

1. Introduction

Earth System Models (ESMs) grapple with low confidence in projecting the functioning of the biosphere within the Earth System across space and over time. Many efforts have been made to improve predictability regarding the structure and functions of terrestrial ecosystems since the 1970s, though this work has mostly focused on the aboveground leaf and canopy processes (e.g., **Sinclair et al., 1976; Friend et al. 2014**; **Lovenduski and Bonan 2017**). Meanwhile, plant roots

have been integral to the evolution of plant form and function (e.g., **Raven and Edwards 2001**) and sit at the nexus of plant-microbe-soil interactions in the biosphere, linking the atmosphere and pedosphere (e.g., **Bardgett et al. 2014; Freschet et al. 2021**). However, current models treat fine-root systems—the ephemeral portion of the root system responsible for water and nutrient acquisition—rudimentarily, and more importantly, lag behind empirical and theoretical advances with regard to fine-root system complexity (e.g., **Fitter 1982; Pregitzer 2002; Phillips et al. 2013; McCormack et al. 2015a**). This model-data discrepancy likely contributes to the poor representation of terrestrial ecosystem feedbacks to increasing CO_2 within ESMs (e.g., **Warren et al. 2014; Bonan and Doney 2018**). Therefore, embracing fine-root system complexity to improve structural realism is expected to increase the prognostic capability of terrestrial ecosystem models in biosphere-atmosphere interactions.

Over the past two decades belowground ecologists have made tremendous progress in revealing the heterogeneity within fine-root systems. Within a fine-root system, plants have evolved roots with unique morphological, anatomical, chemical, and physiological features that differ among root branching orders (e.g., **Pregitzer et al. 2002; Atucha et al. 2021**), as well as varying microbial associations with both mycorrhizal fungi and bacteria (e.g., **Sen and Jenik 1962; King et al. 2021**). These structural differences support both functional differentiation and cooperation within fine-root systems; fine roots of higher orders are primarily responsible for transport of water and nutrients to the rest of the plant, while finer and more distal roots in cooperation with mycorrhizal fungi are responsible for nutrient and water absorption (e.g., **Hishi & Takeda 2005; McCormack et al. 2015a; Wang et al. 2022**). This heterogeneity, and degree of coordination with aboveground plant activities, changes with species and habitat, forming

69 diverse whole-plant strategies across biomes under physical and functional constraints (e.g.,
70 **McCormack and Iversen 2019; Weigelt et al. 2021**).

71 By contrast, fine-root systems in ecosystem models are often treated without accounting
72 for their structural and functional heterogeneity. Currently, the prevailing option in terrestrial
73 ecosystem modelling remains a single fine-root pool (e.g., **Kleidon & Heimann 1998**; **Zeng 2001;**
74 **Warren et al. 2015; Burrows et al. 2020**). Although empiricists have advocated for specifically
75 representing arbuscular mycorrhizal fungi traits and function (**Treseder 2016**) and modelers have
76 even already incorporated impacts of mycorrhizal fungi into models either implicitly (e.g.,
77 **Woodward and Smith 1994; Brzostek et al. 2014**) or explicitly (e.g., **Hunt et al. 1991; Orwin**
78 **et al. 2011; Sulman et al. 2018**), no efforts yet holistically integrate the complexity of fine-root
79 system with a balanced perspective of both fine roots and mycorrhizal fungi. This
80 oversimplification of fine-root system structure fundamentally limits accurate representation of its
81 functioning and hence above- and below-ground interactions (e.g., **Smithwick et al. 2014*;***
82 **Warren et al. 2015**). In addition, such a simplification forms an asynchronous development in
83 terrestrial ecosystem models relative to other components (notably photosynthesis and canopy
84 processes) that likely imparts a structural limit on improvements to whole model performance. For
85 instance, fine-root dynamics are normally assumed to follow leaf phenology closely (e.g.,
86 **Burrows et al. 2020**). Of course, there are individual-level plant models, especially for crops,
87 simulating explicit root structures (e.g., **Pointurier et al. 2021**). However, it has been a challenge
88 to integrate theoretical and empirical advances at scales relevant for ecosystem models while
89 balancing model simplicity and realism.

90 Such a large model-theory discrepancy raises the question of whether models can improve
91 performance with an appreciation of fine-root system complexity. The core of this question about

a single pool versus a more explicit treatment, by analogy, mirrors the debates in vegetation modelling on one layer versus multilayer canopy modelling (e.g., **Raupach and Finnigan 1988**), on individual-based versus various functional group modelling (e.g., **Smith et al. 1997; Shugart et al. 2018**), and on different lumping approaches in modelling various complex physical, chemical, and biological systems more generally (e.g., **Okino and Mavrovouniotis 1998)**. For example, comparisons of one- versus multi-layer canopy simulations have led to the conclusion that land surface models should move beyond the useful but incorrect paradigm of single-layer canopy scheme to help resolve uncertainties in canopy processes (**Bonan et al. 2021**). Similarly, current models show large uncertainties related to belowground processes; for example, a comprehensive sensitivity analysis of the ELM (**Box 1**) revealed large prediction uncertainty arising from uncertainty in root-related parameters and processes (**Ricciuto et al. 2018**). Constraining model uncertainty requires a model structure that can predict measurable quantities in real fine-root systems. Furthermore, improving the representation of fine roots may help model performance by identifying other coupled but deficient components. Therefore, dedicated efforts are warranted to explore alternatives to the single fine-root pool in current terrestrial ecosystem models. Meanwhile, the increasingly available data on fine-root traits (FRED; **Iversen et al. 2017; Box 1**) and fungal traits (e.g., **Zanne et al. 2020; Iversen and McCormack 2021**) can facilitate these efforts.

To this end, we propose a generalized 3-pool structure including Transport and Absorptive fine roots as well as Mycorrhizal fungi (TAM) to represent fine-root systems across organizational and spatio-temporal scales in terrestrial ecosystem models. This function-based TAM structure is intended to approximate the high-dimensional heterogeneity within the hierarchical branching fine-root systems and to serve as an explicit but tractable approach to model fine-root system

115 functioning. The overarching objective of this viewpoint is to argue for adoption of this structure
116 as the quantitative keystone of the bridge between modelers and empiricists. To achieve this
117 objective, we evaluate this TAM structure both theoretically and quantitatively. After elaborating
118 on the conceptual, theoretical, and empirical bases of TAM, we specifically address the following
119 three questions: First, how to realize TAM in ecosystem models? Second, how does this new
120 structure alter simulations of major ecosystem carbon fluxes (e.g., productivity and soil
121 respiration) and pools (e.g., fine-root biomass and soil carbon storage)? Third, what are the
122 uncertainties and challenges in broadly adopting this TAM structure?

123 We answer the first question by proposing a high-level framework of carbon partitioning,
124 the phenological patterns of root and fungal birth, growth, and death, and the vertical distribution
125 of fine roots and fungi throughout the soil profile that can be integrated into existing modelling
126 paradigms of varying complexity in terms of vegetation structure. Starting with the relatively
127 simple big-leaf modeling paradigm, we then answer the second question with an example
128 implementation in the context of a representative big-leaf model with a single fine-root pool—
129 ELM—in two different temperate forest types (deciduous and evergreen forests) across the Eastern
130 United States. For a proof-of-concept purpose the focus of this example is mostly descriptive rather
131 than analytical. By showing significant impacts of TAM in a relatively simple model structure we
132 do not fully address the question of whether TAM really improves model predictability. Rather,
133 we believe a combination of the conceptual, theoretical, and empirical bases and an initial
134 demonstration in this viewpoint lays the groundwork for broad adoption and evaluation of TAM
135 in different modelling paradigms against observations at varying scales. Accordingly, we answer
136 the third question by discussing uncertainties and challenges to fully exploit its potential. We

conclude by pointing out potential implications of TAM for guiding empirical research, understanding ecosystem functioning, and improving ESMs prognosis.

Box 1 Terminology

Fine-root system: Root-mycorrhizal association at the individual plant level comprising fine roots of different orders and associated mycorrhizal fungi.

TAM: An approach argued for in this viewpoint to abstract fine-root systems with two pools representing the traits and function of fine roots—transport roots (T) and absorptive roots (A)—as well as mycorrhizal fungi (M).

FRED (Fine Root Ecology Database): a database conceived and built by **Iversen et al. (2017)** that houses fine-root trait observations from across the world (https://roots.ornl.gov/).

ESM (Earth System Model): A coupled-climate model that explicitly simulates the atmosphere, the ocean, and the land surface in the Earth system, of which the land component is usually referred to as the land model.

Terrestrial Ecosystem Model: Models that simulate ecosystems across spatial-temporal scales in the terrestrial biosphere, which is synonymous with land model, terrestrial biosphere model, or ecosystem model in this study.

Big-leaf model: Terrestrial ecosystem models that represent vegetation using prescribed, static fractional coverage of different Plant Functional Types (an approach to aggregate and simplify global plant diversity) with either a single canopy layer (i.e., one big-leaf model) or sun and shaded layers (i.e., two big-leaf model).

158 **ELM**: The land model using the big-leaf approach with a single fine-root pool in the Energy
159 Exascale Earth System Model (E3SM), a state-of-the-art ESM developed by the US Department
160 of Energy (**Golaz et al. 2019)**.
161 **Demography model**: Terrestrial ecosystem models that can simulate dynamics of vegetation
162 pattern (e.g., forested mosaic of gaps) with demographic processes of growth, mortality, and
163 reproduction.
164 **Demand-driven approach**: An approach for formulating nutrient uptake by fine-root systems of
165 plants or heterotrophic microbes based exclusively on their nutrient demands determined by their
166 potential growth or decomposition rates. The competition between plants and microbes for
167 nutrients is resolved by comparing their demands, which is thus referred to as relative-demand
168 approach.
169 **Trait divergence**: Trait variability or heterogeneity where a 3-pool TAM model allows for unique
170 trait values for each pool while a 1-pool fine-root model only allows a single value to represent
171 the fine-root system.
172 **Preservation**: A procedure to keep the same whole bulk fine-root system property (e.g., C/N in
173 this study) while capturing trait divergence from a 1-pool to 3-pool TAM structure.
174 **Partitioning**: The division of plant photosynthates allocated to one of the TAM pools.
175 **Distribution**: The explicit vertical representation of photosynthates in a soil profile partitioned to
176 one of the TAM pools.
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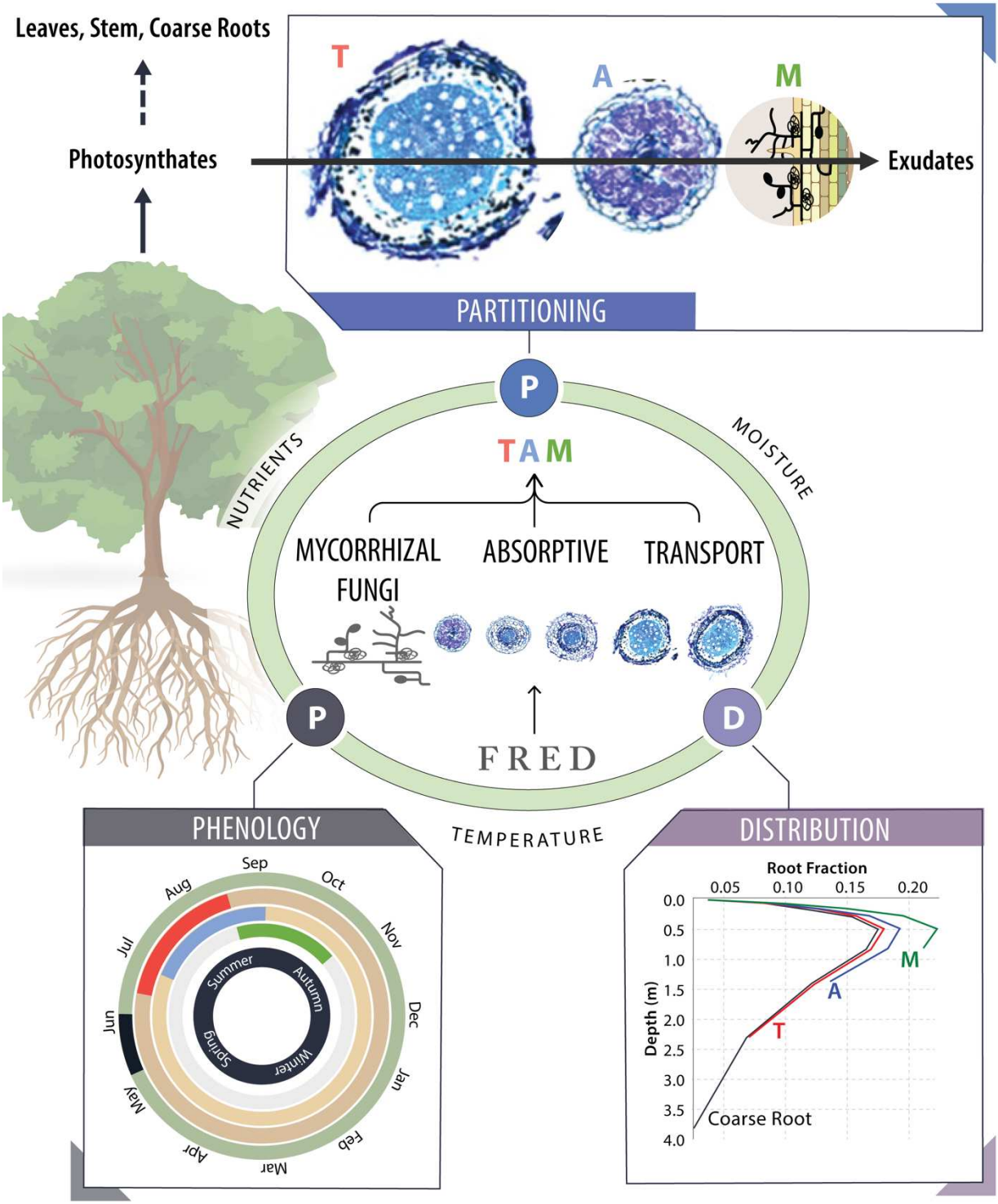

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Fig. 1 Schematic of the 3-pool TAM structure governed by interrelated processes of partitioning, phenology, and distribution under environmental constraints. TAM is conceived to be informed by order- or function-based explicit measurements of fine-root and mycorrhizal fungal traits as compiled in various databases, e.g., FRED. Partitioning of photosynthates to the outside of fine-root systems as exudates is also indicated, though not yet explicitly treated in the current study. Asynchronous phenology within TAM and with leaf phenology is illustrated with approximate periods of production (indicated by colored bands) for leaves, T, A, and M pools based on a *Quercus alba* Plot at The Morton Arboretum, USA in 2019. In addition, the different vertical distribution of TAM (in reference to the coarse root distribution) is for an illustrative purpose only; distribution of new carbon still assumed to be the same across TAM pools though with different turnover rates. The cross sections of 5 fine-root orders are reproduced from **McCormack et al. (2015a)**.

2. Conceptual, theoretical, and empirical basis of the TAM structure

TAM arises from a conceptual shift of fine-root systems. Fine-root systems develop structural and functional differentiation within an individual plant and express substantial variation among individuals, across species, and across biomes (e.g., **Weigelt et al. 2021**). Structurally, fine-root systems bear a hierarchical branching structure with different orders; each order displays different properties in its anatomy, morphology, chemistry, physiology, lifespan, and fungal colonization (e.g., **Pregitzer et al. 2002**; **Guo et al., 2008; McCormack et al., 2017; Klimešová & Herben 2021; Zhou et al. 2022**). This structural variation underlies distinct functional differentiation within fine-root systems. Therefore, an arbitrary homogenization of such differentiation below the 2-mm diameter threshold as functionally equivalent fine roots is

problematic. Instead, a new conceptualization of functional differentiation is argued in terms of transport (coarser, high-order fine roots), absorption (finer, low-order fine roots), and facilitation by colonizing mycorrhizal fungi (**McCormack et al 2015a**). Therefore, following a long tradition of function-based lumping of objects in both empirical and quantitative ecology (e.g., **Raunkiaer 1934; Root 1967; Grime 1974; Smith et al. 1997**), we aggregate fine-root systems of different orders and associations with mycorrhizal fungi into three functional pools that comprise transport roots, absorptive roots, and mycorrhizal fungi—TAM (**Fig.1**).

Theoretically, this 3-pool TAM structure allows a balanced perspective of fine roots and fungi in ecosystem models while capturing both functional differentiation and cooperation within the fine-root systems. A single fine-root pool oversimplifies fine-root systems and misses important symbiotic associations with mycorrhizal fungi. Recognizing the importance of mycorrhizal fungi, some models have accounted for these fine-root partners as an implicit component (e.g., **Koide and Elliot 1989; Kirschbaum and Paul 2002**; **Brzostek et al. 2014**). While these efforts have contributed to more accurate simulations of vegetation nutrient uptake and soil organic matter decomposition in general, these plant-centric models do not include an active mycorrhizal pool that enables a balanced perspective of plant and mycorrhizal fungi. However, even when an explicit mycorrhizal fungal pool is included (e.g., **Hunt et al. 1991; Orwin et al. 2011; Sulman et al. 2019**), a homogenous treatment of fine roots still misses the structural and functional differentiation arising from fine-root orders (**Fig.1**). Of course, a discretized 3-pool structure cannot fully capture the high-dimensional fine-root system heterogeneity (typically five or more root orders plus mycorrhizal fungal colonization, e.g., **Pregitzer et al. 2002; Guo et al. 2008**). Individual-level plant models, especially for crops, may be suitable for an order-based continuous treatment (e.g., **Couvreur et al. 2012; Pointurier et al.**

226 **2021**), whereas ecosystem models often need to balance biological and ecological complexity with
227 computational efficiency. Further increasing complexity by having more pools to account for each
228 fine-root order would likely fall into the trap of diminishing returns in performance with an
229 increasing parameterization challenge (e.g., **Transtrum et al. 2015**).

230 Parameterization of a 3-pool TAM structure has empirical support across organizational
231 and spatial-temporal scales in the biosphere. TAM confers generality across scales by enabling
232 adaptable fine-root pools. While T and A capture widespread functional differentiation between
233 transport and absorption, they can be effectively reduced to one pool to accommodate rare species
234 without such a clear differentiation (**McCormack et al. 2015a**). Also, the M pool, in practice, can
235 be attributed to hyphal mycelium of arbuscular (AM), ectomycorrhizal (ECM), and/or ericoid
236 fungi, depending on the specific site and/or geographic context (e.g., **Read 1991; Soudzilovskaia**
237 **et al. 2015**). Besides this adaptability, the empirical support is facilitated by availability of trait
238 databases. In the context of a belowground data revolution [see a synthesis by **Iversen and**
239 **McCormack (2021)**], databases with increasing spatial coverage of explicit fine-root traits and
240 fungal traits aggregated from either function- or order-based measurement make it feasible to
241 parameterize TAM across scales in terrestrial ecosystem models. Notably, the Fine-Root Ecology
242 Database (FRED), houses root trait observations from across c. 4600 unique plant species and
243 continues to grow (**Iversen et al. 2017; Iversen and McCormack 2021**). Such an empirical
244 support warrants realizing and testing TAM in terrestrial ecosystem models.
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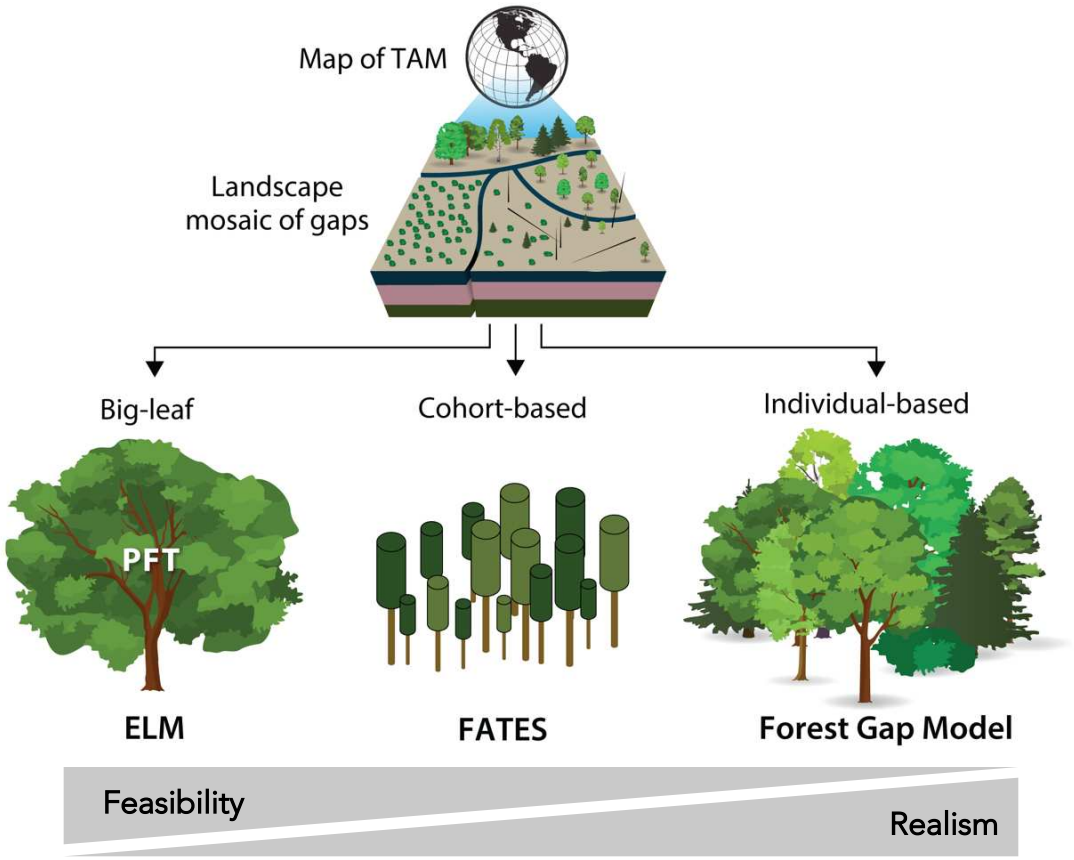


Fig. 2 Realizing TAM with a feasibility-realism tradeoff in terrestrial ecosystem models under three paradigms of vegetation structure. The landscape of vegetation, particularly forests, is a mosaic of gaps (or patches) at different successional stages under exogeneous and endogenous disturbances, structuring vegetation dynamics both vertically by size and horizontally by age (e.g., **Watt 1947; Bormann and Likens 1979**). The three paradigms capture such pattern and process of vegetation to different extents. Big-leaf models (e.g., ELM), representing global vegetation in fractional coverage using a few PFTs, do not capture local plant diversity and cannot predict structural dynamics. By contrast, in capturing the vertical and spatial structure of forests, individual-based forest gap models explicitly simulate growth, mortality, and reproduction of very single individual in an array of gaps (e.g., **Shugart 1984; Shugart et al. 2018**). By approximating

the spatial and vertical structuring of vegetation without an explicit parameterization of different individuals (e.g., **Kohyama 1993**), cohort-based models [e.g., FATES: Functionally Assembled Terrestrial Ecosystem Simulator (**Fisher et al. 2018**) and ED: Ecosystem Demography model (**Moorcroft et al. 2001**)] simplify individual-based gap models by utilizing cohorts of like-sized plants under the traditional PFT scheme. Models under these paradigms assume a single fine-root pool; realizing TAM in these models can capture different organizational levels across spatio-temporal scales in the biosphere. ELM, as a representative of the relatively simplest big-leaf model, is taken as an example for TAM demonstration in this viewpoint.

3. Realizing the TAM structure in terrestrial ecosystem models

To realize TAM in terrestrial ecosystem models, we propose a high-level framework of partitioning, phenology, and distribution to encapsulate processes towards simulating a temporally and vertically resolved 3-pool fine-root system (**Fig.1**). Partitioning is responsible for determining the magnitude of carbon allocated from recent photosynthates or storage to the T, A, and M pools, which is dynamic in nature arising from changes in biotic and abiotic environment from edaphic factors (e.g., nutrient availability) to atmospheric changes (e.g., elevated CO_2) (**Mooney 1972; Chapin et al. 2009; Drigo et al. 2010; Gorka et al. 2019; Ouimette et al. 2020; Prescott et al. 2020**). Phenology then controls the timing of partitioning. Here, we are highlighting phenology as an essential component because of recurring observations of above- and below-ground phenological asynchronicity (e.g., **Steinaker et al. 2010; Abramoff & Finzi 2015**; **McCormack et al. 2015b; Radville et al. 2016; Iversen et al. 2018**). In addition to variations in phenology among the TAM structures, phenology varies with soil depth (e.g., **Maeght et al. 2015**). This vertical variability makes it essential to represent the vertical distribution within the soil profile of

281 carbon and nutrients partitioned to TAM pools at each time-step (e.g., **Tumber-Dávila et al.**
282 **2022**). Moreover, traits of fine roots and mycorrhizal fungi vary vertically (e.g., **McElrone et al.**
283 **2004; Robin et al. 2019**). This vertical variability feeds back to influence partitioning. Therefore,
284 these three components are interrelated in such a way that requires a close coupling of dynamic
285 partitioning with phenology temporally and distribution vertically. These components and their
286 interactions can be integrated into existing models by coupling with upstream photosynthesis and
287 allocation and with downstream soil biogeochemistry.

288 Starting this integration from a simple model structure is practical in the sense of observing
289 impacts of TAM while paving the way for realization and evaluation in more complicated model
290 structures (**Fig.2**). Existing models, built with different assumptions for different purposes, vary
291 in their structural realism of representing vegetation pattern and process under three different
292 paradigms. Integrating TAM into models under these paradigms can incorporate different
293 organizational levels across spatial-temporal scales, which, though exciting, trades off with
294 feasibility in terms of formulation, parameterization, and evaluation. Testing proof-of-concept
295 impacts of TAM under the relatively simple big-leaf paradigm is expected to help identify both
296 opportunities and challenges to realize TAM under structurally more realistic vegetation
297 paradigms.

298 Therefore, we examine impacts of TAM in the context of the state-of-the-art Energy
299 Exascale Earth System Model Land Model, ELM. ELM is a typical big-leaf model with a single
300 fine-root pool based on the traditional scheme of representing global plant diversity using
301 relatively few PFTs, which has been extensively used for land-atmosphere interactions regionally
302 and globally (e.g., **Golaz et al. 2019; Burrows et al. 2020**). Moreover, ELM uses the relative-
303 demand approach as a default configuration for plant-microbe nutrient competition (**Box 1**), which

304 does not require an explicit representation of fine-root and fungal functions and remains a
305 prevailing approach in earth system modelling as a simplification of plant-microbe competition
306 for nutrients (e.g., **Thornton et al. 2007; Yang et al. 2014**). Such formulations of ELM make it
307 feasible for building and testing the TAM structure for a proof-of-concept purpose.

Table 1 Measured traits used to parameterize TAM in the example realization and expected to be used to directly parameterize a functionally explicit TAM in terrestrial ecosystem models.

Category	Trait	T	A	M	Database
chemistry	**stoichiometry**				FRED
	chemical composition				FRED
demography	**longevity**				FRED
	phenology				
morphology	diameter				FRED
	tissue density				FRED
	specific root length				FRED
physiology/metabolism	**respiration rate**				FRED
	temperature sensitivity of respiration (*Q10*)				
	transporter enzyme production rate				
	exoenzyme production rate				
nutrient acquisition	transporter enzyme kinetics (*Km* & *Vmax*)				
	exoenzyme degradation kinetics (*Km* & *Vmax*)				
water uptake	hydraulic conductivity				FRED
	water uptake				
profile	max rooting depth				FRED, RSIP

Note that the traits listed above are those that can directly inform TAM parameterization. Many of the measurements listed in databases (e.g., FRED) are emergent properties and could instead be used for model validation. Bolded traits are used for demonstration in this viewpoint, while grey cells indicate applicability of the traits to TAM. Database indicates coverage of the traits by FRED (which does not necessarily mean a full coverage of all TAM structures) or not (which clearly suggest targets of more empirical efforts). RSIP (Root Systems of Individual Plants) database is a primary source for root system size. See **Iversen and McCormack (2022)** for a synthesis of available databases of fine-root and mycorrhizal fungi traits.

4. Impacts of TAM on forest ecosystems: an example realization

We introduced a series of specific changes within the above framework to realize a 3-pool TAM structure and examined its impacts against the 1-pool structure in ELM. In contrast to the constraint of a single-pool structure, TAM allows trait divergence (**Box 1**) among the fine-root and fungal pools with respect to carbon to nitrogen ratio (C/N), longevity, and chemical composition, as well as respiration (**Table 1**), following observed trait variability within fine-root systems [see the synthesis of **McCormack et al. (2015a)**]. To partition the carbon fixed by a plant to each of the TAM pools, we introduced three parameters—fractions of the total allocation to a fine-root system determined by the prevailing assumption of a 1:1 allometry between leaf and fine-root system. These fractions together with C/N of the three TAM pools determine the C/N of bulk fine-root system (**Eq. 1** in the **Appendix**), which, in combination with other structural tissues (leaf, stem, and coarse-root), determine whole-plant stoichiometry and thus dictate nitrogen demand and uptake under the demand-driven approach. We then decoupled the timing of partitioning to TAM pools from leaf phenology, enabling an independent control on initiation (as a function of growing degree days) and turnover (determined by prescribed longevity) of TAM for both deciduous and evergreen PFTs. The turnover is further constrained by a depth-correction term to capture the widely observed pattern of decreasing turnover with soil depth (e.g., **Baddeley and Waston 2005; McCormack et al. 2012; Gu et al. 2017**). To vertically distribute the carbon partitioned to TAM pools within the soil profile we introduced a formulation of dynamic distribution based on changing profile of nutrient availability instead of the prevailing static assumption (e.g., **Zeng 2001; Drewniak 2019**). This nutrient-based dynamic distribution allows more of the partitioning to go to the depth where the relative availability of nitrogen is higher. We implemented these changes to different extents to examine structural uncertainty while accounting for parameter

uncertainty in a deciduous forest and an evergreen forest in the temperate forest biome of North America only for an illustration of impacts of TAM against ELM (see **Methods** in the **Appendix** for details).

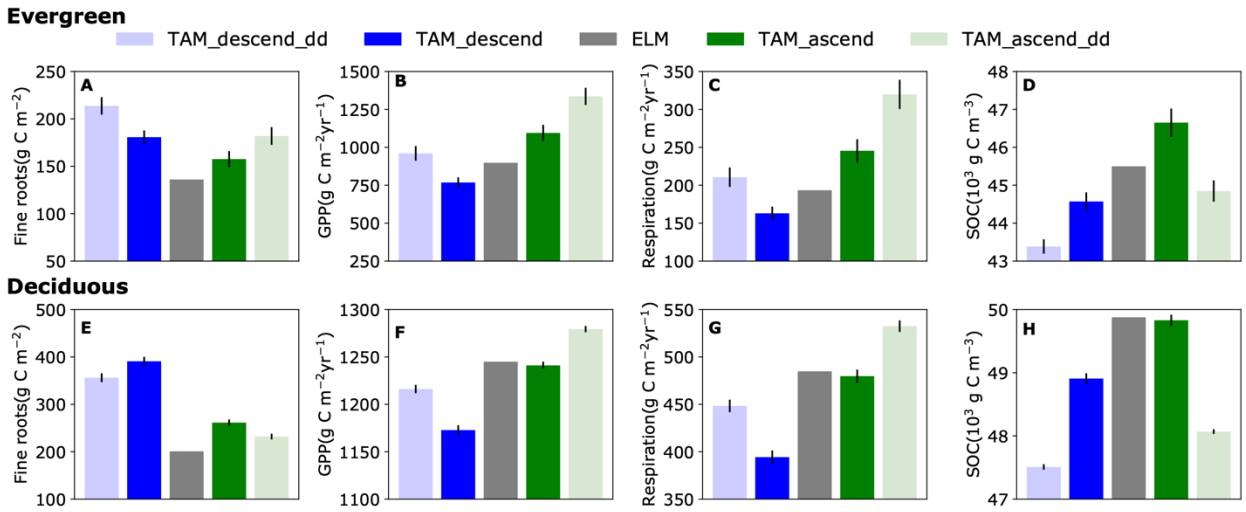


Fig. 3 TAM impacts against the 1-pool fine-root model on temperate evergreen (A-D) and deciduous forests (E-H) under preservation of the bulk fine-root C/N. The preservation is differentiated between two partitioning patterns: TAM_descend (increasingly less partitioned to mycorrhizal fungi) and TAM_ascend (increasingly more partitioned to the mycorrhizal fungi), on top of which comparisons are made by further adding dynamic distribution (TAM_descend_dd and TAM_ascend_dd). Note these comparisons were made under an assumption of the same phenology between TAM and ELM. Fluxes of GPP (**B, F**) and heterotrophic respiration (**C, G**) are aggregated annual values, while pools of fine-root mass and SOC are mean daily values. The variance (95% confidence interval) arises from parameter uncertainty with respect to longevity and fine-root chemistry. Note different y-axis scales across panels are for distinguishing between different scenarios. See seasonal dynamics of GPP and fine roots, as well as leaf biomass in **Supplementary Fig. 1** in the **Appendix**.

4.1 TAM impacts under preservation of bulk fine-root stoichiometry

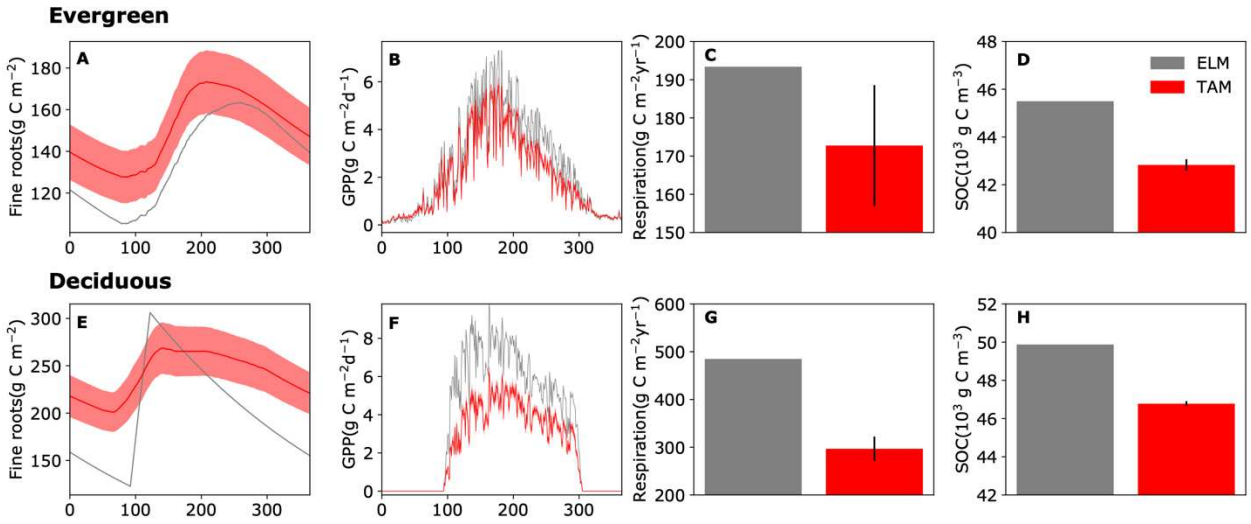
First, changing the structure from 1 to 3 pools but preserving the C/N of bulk fine-root system can give us a parsimonious view of impacts arising from trait divergence in TAM. A direct reason of preservation (**Box 1**) is that C/N of the bulk fine-root system, in principle, should be the same irrespective of the number of pools used in model representation. Keeping the same C/N is also useful in the sense of using existing field observations of bulk fine-root C/N to constrain the model. More importantly, with a demand-driven approach in ELM, C/N of the bulk fine-root system instead of C/N of any of the TAM components dictates plant nitrogen demand and uptake. Therefore, a preservation provides two benefits: it keeps the same nutrient uptake capability as the single-pool model while capturing the divergence in C/N among TAM pools. The preservation is achieved via pairing a set of C/N values with a set of partitioning fractions of TAM (see **Methods** in the **Appendix**). To capture the wide spectrum of plant partitioning variability among different belowground sinks, we consider two sets of partitioning fractions forming two contrasting partitioning patterns: a descending pattern (i.e., increasingly less carbon partitioned to the mycorrhizal fungi) and an ascending pattern (i.e., increasingly more carbon partitioned to the mycorrhizal fungi). Under both patterns, the tissue C/N decreases while turnover increases from T, to A, and then to the M pool; the M has the lowest C/N and fastest turnover, reflecting their consistently lower C/N and short lifespans (**Allen and Kitajima 2013; Zanne et al. 2020**). Under the same phenology, we compared TAM under the two partitioning patterns against ELM first by assuming the same fixed vertical distribution and then by adding dynamic vertical distribution contingent on relative nutrient availability (**Fig. 3**).

With the same static distribution, since both the stoichiometry and the phenology are the same, significant partitioning-dependent impacts of TAM compared against the 1-pool model can

be attributed to changes in turnover and litter inputs arising from explicit low to high turnover rates and high to low C/N moving from T through M pools. The impacts are directly reflected in changes in fine-root biomass (including mycorrhizal hyphae biomass). When reaching equilibrium in both the evergreen and deciduous forest, under the descending partitioning pattern total fine-root biomass increased relative to the single-pool model owing to the lowest turnover rate of T roots (**Fig. 3A, E**). Similar, but somewhat dampened responses, were seen under the ascending pattern as there was relatively more carbon portioned to the M pool which has the highest turnover rate and resulted in less total standing biomass. These changes under equilibrium also came from feedbacks associated with changing temporal patterns of fine-root litter inputs and subsequent changes in GPP (**Fig. 3B, F**), soil heterotrophic respiration (**Fig. 3C, G**), and soil organic carbon storage (**Fig. 3D, H**), although these shifts were insignificant for the deciduous forest under the ascending pattern.

Enabling the dynamic vertical distribution further enhanced the effects of changing turnover of fine-root systems and hence litter inputs according to soil nutrient availability. Because this dynamic distribution increased inputs of fine-root and mycorrhizal fungal litters into soil layers where N availability was relatively higher, a reduction in N limitation led to increased soil respiration and GPP (**Fig. 3D, H**) but with a net effect of soil carbon stock decline under both patterns (**Fig. 3C, G**). However, fine-root biomass experienced a continued increase in the evergreen forest compared to a pause in the deciduous forest because relatively more biomasses accumulated in deeper soils with slower turnover rates in evergreen forest than in the deciduous forest (**Fig. 3D, H**). These new changes under dynamic distribution highlight the role of vertical variability of TAM in influencing plant-soil interactions. In short, even parsimonious TAM has

394 important implications for carbon cycling under stoichiometry preservation while capturing
395 observed differentiation within fine-root systems.
396



397

398 **Fig. 4 TAM impacts against the 1-pool fine-root model on temperate evergreen (A-D) and**
399 **deciduous forests (E-H) without the restraint of preservation**. Respiration is aggregated annual
400 values (**C, G**) and SOC is averaged across a whole year (**D, H**). The variance (95% confidence
401 interval) arose from accounting for all uncertain parameters introduced to realize TAM (see
402 **Supplementary Table 1**).
403

404 **4.2 TAM dampens forest productivity and soil carbon storage**

405 Implementing TAM without the constraint of stoichiometry preservation consistently
406 resulted in reduced ecosystem productivity and soil carbon stock regardless of forest type
407 compared to the 1-pool model (**Fig. 4**). With a full accounting of parameter uncertainty informed
408 by observations (see **Methods** in **Appendix** for details), on average annual GPP was reduced by
409 20.3 % and 36.3 % while soil organic carbon was reduced by 5.9 % and 6.2 % in the evergreen
410 and deciduous forests, respectively. These reductions in equilibrium originated from changing

411 allocation (different C/N of fine-root systems) and explicit fine-root turnover, as indicated by the
412 increased, though not seasonally consistent, fine-root biomass in equilibrium **(Fig. 4A, E)**. Over
413 time these changes led to aggravated nutrient limitation (**Supplementary Fig. 2**), together with
414 decreased leaf area, contributing to declines in GPP (**Fig. 4B, F**). Such a GPP reduction eventually
415 resulted in decreased heterotrophic respiration and a net decline of soil organic carbon (**Fig. 4D,**
416 **H**). These robust changes arising from TAM suggest that 1-pool models may overestimate forest
417 productivity and soil carbon storage, which is in line with the general notion of a lack of accurate
418 sink-limited growth in current terrestrial ecosystem models leading to an overestimation of land
419 carbon sink (e.g., **Cabon et al. 2022**). In summary, the improved realism of TAM informed by
420 empirical trait divergence can show robust impacts while accounting for parameter uncertainty.
421
422 **4.3 TAM echoes embracing complexity in ecosystem modelling in general**
423 These results provide strong quantitative support for TAM. The examples above
424 demonstrate significant impacts of the explicit TAM structure against a homogeneous single-pool
425 structure while accounting for structural and parameter uncertainty, especially considering the case
426 of parsimonious stoichiometry preservation. Admittedly, this demonstration is based on only one
427 simplified, though generally representative, vegetation modelling scheme, and it remains
428 premature to claim that this TAM structure has improved model predictability without testing
429 TAM across a broader range of sites in demography models (**Fig.2**). However, such a shift from
430 implicit to explicit reflects a broad notion of embracing biological and ecological complexity in
431 ecosystems from above- to below-ground to improve model performance. A notable aboveground
432 shift in vegetation structure is from the big-leaf approach using a single-layer canopy to explicitly
433 modeling multi-layer canopy structures (e.g., **Sinclair et al., 1976; Norman, 1993; Yan et al.**

434 **2017; Bonan et al. 2021**), and further to a paradigm simulating vegetation dynamics in the spatial
435 and vertical structuring by age and size (e.g., **Shugart 1984; Kohyama 1993; Moorcroft et al.**
436 **2001; Wang et al. 2016; Shugart et al. 2018; Fisher et al. 2018**). A similar belowground example
437 is the shift from simulating the tremendously complex soil microbiomes first implicitly (e.g.,
438 **Parton et al. 1987**), then as a 'big microbe (e.g., **Allison et al. 2010**), and more recently as a
439 constellation of a few discrete functional groups (e.g., **Wieder et al. 2015**) or even of continuous
440 hypothetical individuals using a trait-based approach (**Wang and Allison 2022**) in a structurally
441 explicit soil environment (**Wang et al. 2019**). Echoing this trend of effectively embracing
442 ecological complexity, we present empirical and theoretical bases for the TAM structure and
443 demonstrate its impacts, arguably suggesting a move beyond the single fine-root pool paradigm in
444 terrestrial ecosystem modelling, which, however, still needs to confront a myriad of uncertainties
445 and challenges.
446
447 **5. Uncertainties and challenges in realizing the TAM structure**
448 Lingering uncertainties and challenges are closely tied to prevailing model assumptions as
449 exemplified in the example realization. First, parameter uncertainties point us to a challenge of
450 constraining partitioning while improving the representations of phenology and distribution in
451 general. Second, going beyond the simplistic demand-driven nutrient acquisition assumption to
452 integrate fine-root and mycorrhizal fungal functions with TAM will necessitate significant
453 theoretical explorations and empirical investigations for model formulation, parameterization, and
454 validation. However, to eventually realize TAM in ecologically realistic demography models
455 (**Fig.2**), new challenges will emerge regarding age- and size-based changes in TAM that the big-
456 leaf paradigm neglects, especially in ecosystems of high biological diversity.

5.1 A unified framework to simulate partitioning, phenology, and distribution

Partitioning, a key component in realizing a 3-pool TAM structure, is the most outstanding uncertainty. Sensitivity analyses (see **Methods** in the **Appendix**) show the parameters controlling partitioning are among the most sensitive ones (**Supplementary Fig. 3**). A direct reason for this sensitivity to partitioning is trait divergence from 1 to 3 pools with respect to, e.g., C/N, longevity, and chemical composition, as well as vertical differentiation in turnover time (**Table 1**). In addition to more constrained parameterizations of these traits, more accurate partitioning is essential for uncertainty reduction. Constraining the uncertainty of partitioning, however, is not as straightforward as simply improving parameterization of TAM traits, which can be informed by more field measurements. Instead, the interactive nature among partitioning, phenology, and vertical distribution, as indicated in **Section 3**, calls for a unified framework to simulate dynamic partitioning while accurately treating phenology and distribution to reduce the associated uncertainties.

Optimization techniques may offer such a unified framework, but it still faces a few immediate challenges. First, finding appropriate objectives for optimization with a balanced perspective of both plant and mycorrhizal fungi is non-trivial (e.g., **Bloom et al. 1985**; **Koide and Elliot 1989**). In addition, understanding of both phenology and distribution of TAM are in their infancy. Phenology is influenced by a plethora of factors including endogenous cues (**Joslin et al. 2001; Tierney et al. 2003**) and exogenous, abiotic cues (e.g., **Radville et al. 2016**), as well as microbial processes in the soil [see the review by **O'Brien et al. (2021)**]. This complex regulation is evident from mounting observations of variability in numbers of fine-root growth peaks (e.g., **Steinaker et al. 2010; McCormack et al. 2015b**) and of complex life history strategies of

480 mycorrhizal fungi with spore dormancy (e.g., **Gianinazzi-Pearson et al., 1989; Bago et al. 2000**;
481 **Defrenne et al. 2021**). TAM variability in phenology is far from being robust as it cannot yet
482 account for all relevant abiotic factors. However, an independent treatment of TAM initiation and
483 mortality allowing for asynchronous phenology between leaves and fine-root systems represents a
484 substantial improvement. Still, the lack of asynchronous TAM phenology vertically means that the
485 timing of partitioning at each depth is not fully accurate. Also, dynamic distribution, though
486 constrained by dynamic nutrient availability in the soil profile, needs to account for other important
487 factors (e.g., soil moisture and temperature). Addressing these interrelated processes under an
488 optimization framework requires not only explicit seasonal observations of fine-root system
489 dynamics across root orders and mycorrhizal fungi within soil profiles to disentangle
490 environmental controls but requires explicit TAM functioning that goes beyond the demand-driven
491 approach.
492
493 **5.2 Connecting TAM with fine-root and mycorrhizal fungal functions**
494 Relaxing the assumption of demand-driven nutrient uptake and competition entails an
495 explicit formulation of the different functions of T, A and M pools and their interactions with soils.
496 Incorporating explicit TAM functioning with respect to nutrient and water uptake will require
497 explicit absorptive root and mycorrhizal fungi traits (**Table 1**) related to uptake of nutrients in
498 various forms of nitrogen and phosphorous (e.g., **Yang et al. 2014; 2019**) and water (e.g.,
499 **Polverigiani et al. 2011; Jackisch et al. 2020; Kakouridis et al. 2020; Mackay et al. 2020).**
500 Notably, mycorrhizal fungi in TAM, especially ectomycorrhiza and ericoid mycorrhiza, can
501 directly mediate litter and soil organic matter decomposition by exuding enzymes and taking up
502 organic nitrogen (e.g., **Gadgil and Gadgil 1971; Frey 2019**). Therefore, once TAM incorporates

503 explicit root and mycorrhizal functions, it becomes highly necessary to make a concomitant change
504 to microbially-explicit organic matter decomposition with exoenzymes instead of the first-order
505 decomposition assumed in ELM. A microbially explicit decomposition model then needs to
506 accommodate fine-root system exudates while handling explicit litter decomposition arising from
507 the explicit turnover of TAM components, especially with fungal necromass (e.g., **Matamala et**
508 **al, 2003; Strand et al. 2008; Fernandez et al. 2013; Sun et al. 2018**). These aspects can be
509 addressed by combining a microbially explicit organic matter decomposition model interacting
510 with the functioning of fine-root systems (e.g., **Sulman et al. 2018; Wang and Allison 2019**) with
511 the existing approach of resolving plant-microbe competition for nutrient uptake based on the
512 Equilibrium Chemistry Approximation theory (**Zhu et al. 2017; Wang and Allison 2019**).
513 However, to capture the variability in these processes and their interactions arising from biological
514 diversity, we need to move beyond the big-leaf paradigm.
515
516 **5.3 Realizing TAM in demography models**
517 Moving forward from the big-leaf structure to realizing TAM in demography models will
518 require creative efforts to best capture patterns and processes belowground. The mosaic of forested
519 landscapes so far has only been emphasized aboveground, and while previous studies have
520 documented high heterogeneity in belowground processes, our example realization of TAM using
521 the big-leaf approach circumvents this challenge (**Fig.2**). One outstanding issue towards this end
522 is to simulate age- and size-related changes in TAM in the context of complete life cycles of
523 growth, mortality, and reproduction for many different individuals under disturbances. For
524 instance, evidence has indicated roles of mycorrhizal fungi change with plant community
525 succession stage (e.g., **Pankow et al. 1991; Read 1991; Nara 2006**). One strategy of simulating

526 age- and size-related changes would be conditioning TAM on a dynamic rooting depth of coarse
527 roots (constrained by, for example, maximum rooting depth; **Fig.1; Table 1**), instead of using a
528 constant value as widely assumed in current models. This change in rooting depth should involve
529 geometric and allometric relationships with aboveground structural tissues (e.g., **Eshel and**
530 **Grünzweig 2013; Brum et al. 2019; Tumber-Dávila et al. 2022**) while accounting for direct
531 influences from, for example, soil hydrological conditions (e.g., **Stone and Kalisz 1991**; **Fan et**
532 **al. 2007**). Addressing these aspects requires long-term observations of successional dynamics of
533 not only the aboveground but also the belowground (e.g., **Rees et al. 2001; "We must get a grip**
534 **on forest science — before it's too late", 2022**).
535
536 **6. Implications of TAM for root ecology, ecosystem functioning, and ESMs**
537 Confronting those above challenges holds promise to stimulate empirical ecology of fine-
538 root systems, to drive theory-driven explorations of hypotheses of fine-root systems' roles in
539 ecosystem functioning, and to improve the prognostic capability of ESMs. First, adopting this
540 structure would stimulate more targeted efforts at an increasing resolution of empirical research of
541 fine roots and mycorrhizal fungi as discussed above on challenges (**Table 1**). The proposal of
542 TAM is largely fueled by the belowground trait data revolution, especially with tremendous
543 empirical progress in collecting function- and/or order-based fine-root traits including microbial
544 associations (e.g., **McCormack et al. 2017; Iversen 2017; Iversen and McCormack 2017;**
545 **Freschet et al. 2021**; **Tedersoo et al. 2021**). Building on standardized measurement protocols
546 (**Freschet et al. 2021**), TAM may also stimulate further technical research and possible advances
547 in, for example, neutron imaging (e.g., **Warren et al. 2013**), remote sensing (e.g., **Sousa et al.**

548 **2021**), and machine learning in image recognition (e.g., **Han et al. 2021**), to speed up
549 characterization and classification of functional 'roots' within fine-root systems.

550 Undoubtedly, new measurements and causal relationships revealed by empiricists will
551 improve formulation, parameterization, and validation of TAM in models of increasing complexity
552 (**Fig. 2**). It is noteworthy that one of the major motivations for demography models is that local
553 community-level processes are essential in modelling ecosystem functioning responding to various
554 disturbances (e.g., **Wang et al. 2016; Fisher et al. 2018**). Increasing empirical and theoretical
555 studies have indicated that root competition may even be more important than aboveground
556 competition in shaping a plant community (e.g., **Gersani et al. 2001; Ljubotina and Cahill 2019;**
557 **Cabal et al. 2020; Sauter et al. 2021**). With this explicit structure of fine-root systems in
558 demography models of varying complexity, we can conduct theory-driven modelling studies to
559 explore hypotheses of root-associated community-level processes underlying ecosystem
560 functioning, which is otherwise challenging to experimentally track in the field.

561 We anticipate that all these empirical and theoretical advances arising from TAM
562 eventually will contribute to improving ESMs both directly and indirectly. A more accurate and
563 effective representation of fine-root systems across ecosystems may be directly incorporated into
564 terrestrial ecosystem models with different vegetation structures, as implied by the example
565 realization in temperate forest systems. Indirect benefits accompanying root improvement would
566 also likely follow by helping to identify sources of uncertainty in components of aboveground and
567 soil processes. One fundamental aspect might be to stimulate efforts to improve the scheme of
568 global plant functional type classification by systematically integrating belowground traits (e.g.,
569 **Smith et al. 1997; Phillips et al. 2013**). This indirect avenue is particularly promising considering
570 the historical dominance of top-down thinking in ESMs development (e.g., **Sellers et al. 1986**).

These direct and indirect effects together will improve the prognostic capability of ESMs to evaluate biosphere-atmosphere interactions in the Earth system.

7. Conclusions

Uncertain terrestrial ecosystem models still contain a huge data-model discrepancy with respect to fine-root system complexity. We speculate that closing this model-data gap will improve the prognostic capability of models across scales. To effectively simulate this complexity, we propose a function-based, 3-pool TAM structure representing transport and absorptive fine roots and mycorrhizal fungi to approximate the high-dimensional structural and functional variations within fine-root systems. Building upon theoretical and empirical bases of TAM as a balanced approximation between realism and simplicity, we quantitatively confirmed the significance of TAM for pools and fluxes of temperate forests arising from capturing the structural and functional differentiation within fine-root systems in a big-leaf land surface model. Though uncertainties and challenges remain towards realizing TAM in explicit demography models, TAM opens the door for more realistically and effectively capturing fine-root systems complexity underlying their functioning to eventually contribute to uncertainty reduction in ESMs.

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Author Contributions

BW, MLM, DMR, XY, and CMI designed the research. BW performed the research, analyzed data, and wrote the first manuscript draft. MLM, DMR, XY, and CMI contributed to results interpretation and manuscript editing.

Data Availability

The code of simple_ELM in Python is accessible at https://github.com/dmricciuto/simple_ELM/tree/rootcomplexity. Outputs from the simulations and code of analysis and visualization in Python are available at https://github.com/bioatmosphere/TAM. The database FRED is accessible at https://roots.ornl.gov/.

References

Abramoff, R. Z., & Finzi, A. C. (2015). Are above-and below-ground phenology in sync? New Phytologist, 205, 1054-1061.

Allen, M. F., & Kitajima, K. (2013). In situ high-frequency observations of mycorrhizas. New Phytologist, 200, 222-228.

Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience, 3, 336-340.

Atucha, A., Workmaster, B. A., & Bolivar-Medina, J. L. (2021). Root growth phenology, anatomy, and morphology among root orders in *Vaccinium macrocarpon Ait.* Botany, 99, 209-219.

Baddeley, J. A., & Watson, C. A. (2005). Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant and Soil, 276, 15-22.

Bago, B., Pfeffer, P. E., & Shachar-Hill, Y. (2000). Carbon metabolism and transport in arbuscular mycorrhizas. Plant Physiology, 124, 949-958.

Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: root traits as drivers of ecosystem processes. Trends in Ecology & Evolution, 29, 692-699.

Bloom, A. J., Chapin, F. S., & Mooney, H. A. (1985). Resource limitation in plants--an economic analogy. Annual review of Ecology and Systematics, 363-392.

Bormann, F. H., & Likens, G. E. (1979). Catastrophic disturbance and the steady state in northern hardwood forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. American Scientist, 67, 660-669.

640 Bonan, G. B., Patton, E. G., Finnigan, J. J., Baldocchi, D. D., & Harman, I. N. (2021). Moving
641 beyond the incorrect but useful paradigm: reevaluating big-leaf and multilayer plant canopies to
642 model biosphere-atmosphere fluxes–a review. Agricultural and Forest Meteorology, 306, 108435.
643
644 Bonan, G. B., & Doney, S. C. (2018). Climate, ecosystems, and planetary futures: The challenge
645 to predict life in Earth system models. SCIENCE, 359(6375).
646
647 Brum, M., Vadeboncoeur, M. A., Ivanov, V., Asbjornsen, H., Saleska, S., Alves, L. F., ... &
648 Oliveira, R. S. (2019). Hydrological niche segregation defines forest structure and drought
649 tolerance strategies in a seasonal Amazon forest. Journal of Ecology, 107, 318-333.
650
651 Brzostek, E. R., J. B. Fisher, and R. P. Phillips (2014), Modeling the carbon cost of plant nitrogen
652 acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of
653 retranslocation. J. Geophys. Res. Biogeosci., 119, 1684–1697
654
655 Burrows, S. M., Maltrud, M., Yang, X., Zhu, Q., Jeffery, N., Shi, X., ... & Leung, L. R. (2020).
656 The DOE E3SM v1.1 biogeochemistry configuration: Description and simulated ecosystem-
657 climate responses to historical changes in forcing. Journal of Advances in Modeling Earth
658 Systems, 12, e2019MS001766.
659
660 Cabal, C., Martínez-García, R., de Castro Aguilar, A., Valladares, F., & Pacala, S. W. (2020). The
661 exploitative segregation of plant roots. Science, 370, 1197-1199.
662

663 Cabon, A., Kannenberg, S. A., Arain, A., Babst, F., Baldocchi, D., Belmecheri, S., ... & Anderegg,
664 W. R. (2022). Cross-biome synthesis of source versus sink limits to tree growth. Science, 376,
665 758-761.
666
667 Defrenne, C. E., Childs, J., Fernandez, C. W., Taggart, M., Nettles, W. R., Allen, M. F., ... &
668 Iversen, C. M. (2021). High-resolution minirhizotrons advance our understanding of root-fungal
669 dynamics in an experimentally warmed peatland. Plants, People, Planet, 3, 640-652.
670
671 Chapin III, S. F., McFarland, J., David McGuire, A., Euskirchen, E. S., Ruess, R. W., & Kielland,
672 K. (2009). The changing global carbon cycle: linking plant–soil carbon dynamics to global
673 consequences. Journal of Ecology, 97, 840-850.
674
675 Couvreur, V., Vanderborght, J., & Javaux, M. (2012). A simple three-dimensional macroscopic
676 root water uptake model based on the hydraulic architecture approach. Hydrology and Earth
677 System Sciences, 16, 2957-2971.
678
679 Drewniak, B. A. (2019). Simulating dynamic roots in the energy exascale earth system land model.
680 Journal of Advances in Modeling Earth Systems, 11, 338-359.
681
682 Drigo, B., Pijl, A. S., Duyts, H., Kielak, A. M., Gamper, H. A., Houtekamer, M. J., ... &
683 Kowalchuk, G. A. (2010). Shifting carbon flow from roots into associated microbial communities
684 in response to elevated atmospheric CO_2. Proceedings of the National Academy of Sciences, 107,
685 10938-10942.

Eshel, A., & Grünzweig, J. M. (2013). Root–shoot allometry of tropical forest trees determined in a large-scale aeroponic system. Annals of botany, 112, 291-296.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B., & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. Proceedings of the National Academy of Sciences, 114, 10572-10577.

Fernandez, C. W., & Kennedy, P. G. (2018). Melanization of mycorrhizal fungal necromass structures microbial decomposer communities. Journal of Ecology, 106, 468-479.

Fisher, R. A., Koven, C. D., Anderegg, W. R., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., ... & Moorcroft, P. R. (2018). Vegetation demographics in Earth System Models: A review of progress and priorities. Global Change Biology, 24, 35-54.

Fitter, A. H. (1982). Morphometric analysis of root systems: application of the technique and influence of soil fertility on root system development in two herbaceous species. Plant, Cell & Environment, 5, 313-322.

Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. Annual Review of Ecology, Evolution, and Systematics, 50(1).

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., ... & Woodward, F. I. (2014). Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proceedings of the National Academy of Sciences, 111, 3280-3285.

Gadgil, R., Gadgil, P. (1971). Mycorrhiza and Litter Decomposition. Nature **233,** 133. https://doi.org/10.1038/233133a0

Gersani, M., Brown, J. S., O'Brien, E. E., Maina, G. M., & Abramsky, Z. (2001). Tragedy of the commons as a result of root competition. Journal of Ecology, 89, 660-669.

Gianinazzi-Pearson, V., B. Branzanti, and S. Gianinazzi. 1989. In vitro enhancement of spore germination and early hyphal growth of a vesicular-arbuscular mycorrhizal fungus by host root exudates and plant flavonoids. Symbiosis 7, 243–255.

Gorka, S., Dietrich, M., Mayerhofer, W., Gabriel, R., Wiesenbauer, J., Martin, V., ... & Kaiser, C. (2019). Rapid transfer of plant photosynthates to soil bacteria via ectomycorrhizal hyphae and its interaction with nitrogen availability. Frontiers in Microbiology, 10, 168.

Grime, J. P. (1974). Vegetation classification by reference to strategies. Nature 250, 26–31.

729 Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., & Wang, Z. (2008). Anatomical traits associated
730 with absorption and mycorrhizal colonization are linked to root branch order in twenty-three
731 Chinese temperate tree species. New Phytologist, 180, 673-683.
732
733 Han, Eusun, Abraham George Smith, Roman Kemper, Rosemary White, John A Kirkegaard,
734 Kristian Thorup-Kristensen, Miriam Athmann. (2021). Digging roots is easier with AI. Journal of
735 Experimental Botany, 13, 4680–4690
736
737 Hishi, T., & Takeda, H. (2005). Dynamics of heterorhizic root systems: protoxylem groups within
738 the fine-root system of *Chamaecyparis obtusa*. New Phytologist, 167, 509-521.
739 Hunt, H. W., Trlica, M. J., Redente, E. F., Moore, J. C., Detling, J. K., Kittel, T. G. F., ... & Elliott,
740 E. T. (1991). Simulation model for the effects of climate change on temperate grassland
741 ecosystems. Ecological Modelling, 53, 205-246.
742
743 Iversen, C. M. et al. (2017). A global Fine-Root Ecology Database to address below-ground
744 challenges in plant ecology. New Phytologist, 215, 15–26.
745
746 Iversen, C.M., Childs, J., Norby, R.J. et al. (2018). Fine-root growth in a forested bog is seasonally
747 dynamic, but shallowly distributed in nutrient-poor peat. Plant and Soil 424, 123–143.
748
749 Iversen, C. M., & McCormack, M. L. (2021). Filling gaps in our understanding of belowground
750 plant traits across the world: an introduction to a Virtual Issue. New Phytologist, 231, 2097-2103.
751

752 Jackisch, C., Knoblauch, S., Blume, T., Zehe, E., & Hassler, S. K. (2020). Estimates of tree root
753 water uptake from soil moisture profile dynamics. Biogeosciences, 17, 5787-5808.
754
755 Joslin, J. D., Gaudinski, J. B., Torn, M. S., Riley, W. J., & Hanson, P. J. (2006). Fine-root turnover
756 patterns and their relationship to root diameter and soil depth in a ^{14}C-labeled hardwood forest.
757 New Phytologist, 172, 523-535.
758
759 Kakouridis, A., Hagen, J. A., Kan, M. P., Mambelli, S., Feldman, L. J., Herman, D. J., ... &
760 Firestone, M. K. (2020). Routes to roots: direct evidence of water transport by arbuscular
761 mycorrhizal fungi to host plants. https://doi.org/10.1111/nph.1828
762
763 Koide, R. & Elliot, G. (1989). Cost, benefit, and efficiency of the vesicular-arbuscular mycorrhizal
764 symbiosis. Functional Ecology 3, 252-255.
765
766 Kenrick, P., & Strullu-Derrien, C. (2014). The origin and early evolution of roots. Plant
767 Physiology, 166, 570-580.
768
769 King, W.L., Yates, C.F., Guo, J. et al. (2021). The hierarchy of root branching order determines
770 bacterial composition, microbial carrying capacity and microbial filtering. Communication
771 Biology 4, 483.
772
773 Kirschbaum, M. U., & Paul, K. I. (2002). Modelling C and N dynamics in forest soils with a
774 modified version of the CENTURY model. Soil Biology and Biochemistry, 34, 341-354.

Kleidon, A., & Heimann, M. (1998). Optimised rooting depth and its impacts on the simulated climate of an atmospheric general circulation model. Geophysical research letters, 25, 345-348.

Klimešová, J., & Herben, T. (2021). The hidden half of the fine root differentiation in herbs: nonacquisitive belowground organs determine fine-root traits. Oikos. doi: 10.1111/oik.08794

Kohyama, T. (1993). Size-structured tree populations in gap-dynamic forest--the forest architecture hypothesis for the stable coexistence of species. Journal of Ecology, 81, 131-143.

Ljubotina MK, Cahill Jr JF. 2019 Effects of neighbour location and nutrient distributions on root foraging behaviour of the common sunflower. Proc. R. Soc. B 286: 20190955.

Lovenduski, N. S., & Bonan, G. B. (2017). Reducing uncertainty in projections of terrestrial carbon uptake. Environmental Research Letters, 12, 044020.

Mackay, D. S., Savoy, P. R., Grossiord, C., Tai, X., Pleban, J. R., Wang, D. R., ... & Sperry, J. S. (2020). Conifers depend on established roots during drought: results from a coupled model of carbon allocation and hydraulics. New Phytologist, 225, 679-692.

Maeght, J. L., Gonkhamdee, S., Clement, C., Isarangkool Na Ayutthaya, S., Stokes, A., & Pierret, A. (2015). Seasonal patterns of fine root production and turnover in a mature rubber tree (*Hevea*

797 *brasiliensis Müll. Arg.*) stand-differentiation with soil depth and implications for soil carbon
798 stocks. Frontiers in Plant Science, 6, 1022.
799
800 Matamala, R., Gonzalez-Meler, M. A., Jastrow, J. D., Norby, R. J., & Schlesinger, W. H. (2003).
801 Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science, 302, 1385-
802 1387.
803
804 McCormack, M.L., Adams, T. S., Smithwick, E. A., & Eissenstat, D. M. (2012). Predicting fine
805 root lifespan from plant functional traits in temperate trees. New Phytologist, 195, 823-831.
806
807 McCormack, M. L., I. A. Dickie, D. M. Eissenstat, T. J. Fahey, C. W. Fernandez, D. Guo, H.-S.
808 Helmisaari, E. A. Hobbie, C. M. Iversen, R. B. Jackson, J. Leppälammi-Kujansuu, R. J. Norby, R.
809 P. Phillips, K. S. Pregitzer, S. G. Pritchard, B. Rewald, M. Zadworny (2015a). Redefining fine
810 roots improves understanding of below-ground contributions to terrestrial biosphere processes.
811 New Phytologist. 207, 505–518.
812
813 McCormack, M. L., Gaines, K. P., Pastore, M., & Eissenstat, D. M. (2015b). Early season root
814 production in relation to leaf production among six diverse temperate tree species. Plant and Soil,
815 389, 121-129.
816
817 McCormack, M. L., Guo, D., Iversen, C. M., Chen, W., Eissenstat, D. M., Fernandez, C. W., ... &
818 Zanne, A. (2017). Building a better foundation: Improving root-trait measurements to understand
819 and model plant and ecosystem processes. New Phytologist, 215, 27-37.

McCormack, M. L., & Iversen, C. M. (2019). Physical and functional constraints on viable belowground acquisition strategies. Frontiers in Plant Science, 1215.

McElrone, A. J., Pockman, W. T., Martínez-Vilalta, J., & Jackson, R. B. (2004). Variation in xylem structure and function in stems and roots of trees to 20 m depth. New phytologist, 163, 507-517.

Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecological Monographs, 71, 557-586.

Nara, K. (2006). Ectomycorrhizal networks and seedling establishment during early primary succession. New Phytologist, 169, 169-178.

Norman, J.M., 1993. Scaling processes between leaf and canopy levels. In: Ehleringer, J. R., Field, C.B. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, New York, pp. 41–76.

O'Brien, A. M., Ginnan, N. A., Rebolleda-Gómez, M., & Wagner, M. R. (2021). Microbial effects on plant phenology and fitness. American Journal of Botany, 108, 1824-1837.

Okino, M. S., & Mavrovouniotis, M. L. (1998). Simplification of mathematical models of chemical reaction systems. Chemical Reviews, 98, 391-408.

843 Orwin, K. H., Kirschbaum, M. U., St John, M. G., & Dickie, I. A. (2011). Organic nutrient uptake
844 by mycorrhizal fungi enhances ecosystem carbon storage: a model-based assessment. Ecology
845 Letters, 14, 493-502.
846
847 Ouimette, A.P., Ollinger, S.V., Lepine, L.C. et al. (2020). Accounting for Carbon Flux to
848 Mycorrhizal Fungi May Resolve Discrepancies in Forest Carbon Budgets. Ecosystems 23, 715–
849 729.
850
851 Pankow, W., Boller, T., & Wiemken, A. (1991). The significance of mycorrhizas for protective
852 ecosystems. Experientia, 47, 391-394.
853
854 Parton, W. J., Schimel, D. S., Cole, C. V., & Ojima, D. S. (1987). Analysis of factors controlling
855 soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal, 51,
856 1173-1179.
857
858 Phillips, R. P., Brzostek, E., & Midgley, M. G. (2013). The mycorrhizal-associated nutrient
859 economy: a new framework for predicting carbon–nutrient couplings in temperate forests. New
860 Phytologist, 199, 41-51.
861
862 Pointurier, O., Moreau, D., Pagès, L., Caneill, J., & Colbach, N. (2021). Individual-based 3D
863 modelling of root systems in heterogeneous plant canopies at the multiannual scale. Case study
864 with a weed dynamics model. Ecological Modelling, 440, 109376.
865

Polverigiani, S., McCormack, M. L., Mueller, C. W., & Eissenstat, D. M. (2011). Growth and physiology of olive pioneer and fibrous roots exposed to soil moisture deficits. Tree Physiology, 31, 1228-1237.

Pregitzer, K. S. (2002). Fine roots of trees–a new perspective. New Phytologist, 154, 267-270.

Pregitzer, K. S., DeForest, J. L., Burton, A. J., Allen, M. F., Ruess, R. W., & Hendrick, R. L. (2002). Fine root architecture of nine North American trees. Ecological Monographs, 72, 293-309.

Prescott, C. E., Grayston, S. J., Helmisaari, H. S., Kaštovská, E., Körner, C., Lambers, H., ... & Ostonen, I. (2020). Surplus carbon drives allocation and plant–soil interactions. Trends in Ecology & Evolution, 35, 1110-1118.

Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a changing climate. Journal of Experimental Botany, 67, 3617-3628.

Raunkiaer, C.C. 1934. The Life Forms of Plants and Statistical Plant Geography. Clarendon Press, Oxford

Raupach, M.R., Finnigan, J.J., 1988. 'Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multilayer models are correct but useless'. Discuss. Aust. Journal Plant Physiol. 15, 705–716.

889 Raven, J. A., & Edwards, D. (2001). Roots: evolutionary origins and biogeochemical significance.
890 Journal of Experimental Botany, 52, 381-401.
891
892 Read, D. J. (1991). Mycorrhizas in ecosystems. Experientia, 47, 376-391.
893
894 Rees, M., Condit, R., Crawley, M., Pacala, S., & Tilman, D. (2001). Long-term studies of
895 vegetation dynamics. SCIENCE, 293, 650-655.
896
897 Ricciuto, D., Sargsyan, K., & Thornton, P. (2018). The impact of parametric uncertainties on
898 biogeochemistry in the E3SM land model. Journal of Advances in Modeling Earth Systems, 10,
899 297–319.
900
901 Robin, A., Pradier, C., Sanguin, H. et al. (2019). How deep can ectomycorrhizas go? A case study
902 on Pisolithus down to 4 meters in a Brazilian eucalypt plantation. Mycorrhiza 29, 637–648.
903
904 Root, R. B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. Ecological
905 Monographs 37, 317–350.
906
907 Sauter, F., Albrecht, H., Kollmann, J., & Lang, M. (2021). Competition components along
908 productivity gradients–revisiting a classic dispute in ecology. Oikos. 130, 1326-1334.
909
910 Sellers, P. J., Mintz, Y. C. S. Y., Sud, Y. E. A., & Dalcher, A. (1986). A simple biosphere model
911 (SiB) for use within general circulation models. Journal of the Atmospheric Sciences, 43, 505-531.

Sen, D. N., & Jenik, J. (1962). Root ecology of *Tilia europaea L.*: anatomy of Mycorrhizal roots. Nature, 193, 1101-1102.

Shugart, H. H. A Theory of Forest Dynamics (Springer, 1984).

Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., ... & Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. Environmental Research Letters, 13, 033001.

Sinclair, T.R., Murphy, C.E., Knoerr, K.R., 1976. Development and evaluation of simplified models for simulating canopy photosynthesis and transpiration. J. Appl. Ecol 13, 813–829.

Smith et al. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. (1997). United Kingdom: Cambridge University Press.

Smithwick, E. A., Lucash, M. S., McCormack, M. L., & Sivandran, G. (2014). Improving the representation of roots in terrestrial models. Ecological Modelling, 291, 193-204.

Sousa, D., Fisher, J. B., Galvan, F. R., Pavlick, R. P., Cordell, S., Giambelluca, T. W., et al. (2021). Tree canopies reflect mycorrhizal composition. Geophysical Research Letters, 48, e2021GL092764.

935 Steinaker DF, Wilson SD, Peltzer DA. 2010. Asynchronicity in root and shoot phenology in
936 grasses and woody plants. Global Change Biology 16, 2241–2251.
937
938 Stone, E. L., & Kalisz, P. J. (1991). On the maximum extent of tree roots. Forest ecology and
939 management, 46, 59-102.
940
941 Sun, T., Hobbie, S. E., Berg, B., Zhang, H., Wang, Q., Wang, Z., & Hättenschwiler, S. (2018).
942 Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition.
943 Proceedings of the National Academy of Sciences, 115, 10392-10397.
944
945 Thornton, P. E., Lamarque, J. F., Rosenbloom, N. A., & Mahowald, N. M. (2007). Influence of
946 carbon-nitrogen cycle coupling on land model response to CO2 fertilization and climate
947 variability. Global biogeochemical cycles, 21(4).
948
949 Tierney, G. L., Fahey, T. J., Groffman, P. M., Hardy, J. P., Fitzhugh, R. D., Driscoll, C. T., &
950 Yavitt, J. B. (2003). Environmental control of fine root dynamics in a northern hardwood forest.
951 Global Change Biology, 9, 670-679.
952
953 Transtrum, M. K., Machta, B. B., Brown, K. S., Daniels, B. C., Myers, C. R., & Sethna, J. P.
954 (2015). Perspective: Sloppiness and emergent theories in physics, biology, and beyond. The
955 Journal of Chemical Physics, 143(1), 07B201_1.
956

957 Treseder, K. K. (2016). Model behavior of arbuscular mycorrhizal fungi: predicting soil carbon
958 dynamics under climate change. Botany, 94, 417-423.
959
960 Tumber-Dávila, S. J., Schenk, H. J., Du, E., & Jackson, R. B. (2022). Plant sizes and shapes above
961 and belowground and their interactions with climate. New Phytologist, 235, 1032-1056
962
963 Wang, B., Shugart, H. H., Shuman, J. K., & Lerdau, M. T. (2016). Forests and ozone: Productivity,
964 carbon storage and feedbacks. Scientific Reports, 6, 1-7.
965
966 Wang, B., and Allison, S. D. (2019). Emergent properties of organic matter decomposition by soil
967 enzymes. Soil Biology and Biochemistry, 136, 107522.
968
969 Wang, B., and Allison, S.D. (2022). Climate-driven legacies in simulated microbial communities
970 alter litter decomposition rates. Frontiers in Ecology and Evolution, 10, 841824.
971
972 Wang, B., Brewer, P. E., Shugart, H. H., Lerdau, M. T., & Allison, S. D. (2019). Building bottom-
973 up aggregate-based models (ABMs) in soil systems with a view of aggregates as biogeochemical
974 reactors. Global Change Biology, 25, e6-e8.
975
976 Wang, Q., Zhang, Z., Zhu, X., Liu, Z., Li, N., Xiao, J., ... & Yin, H. 2022. Absorptive roots drive
977 a larger microbial carbon pump efficacy than transport roots in alpine coniferous forests. Journal
978 of Ecology. https://doi.org/10.1111/1365-2745.13899
979

980 Warren JM, Bilheux H, Kang M, Voisin S, Cheng C-L, Horita J, Perfect E. 2013. Neutron imaging
981 reveals internal plant water dynamics. Plant and Soil 366, 683–693.
982
983 Warren, J. M., Hanson, P. J., Iversen, C. M., Kumar, J., Walker, A. P., & Wullschleger, S. D.
984 (2015). Root structural and functional dynamics in terrestrial biosphere models–evaluation and
985 recommendations. New Phytologist, 205, 59-78.
986
987 Watt, A. S. (1947). Pattern and process in the plant community. Journal of Ecology, 35, 1-22.
988
989 Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., ... &
990 McCormack, M. L. (2021). An integrated framework of plant form and function: The belowground
991 perspective. New Phytologist, 232, 42-59.
992
993 We must get a grip on forest science—before it's too late. (2022). Nature 608, 449.
994 https://doi.org/10.1038/d41586-022-02182-0
995
996 Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G., & Bonan, G. B. (2015).
997 Representing life in the Earth system with soil microbial functional traits in the MIMICS model.
998 Geoscientific Model Development, 8, 1789-1808.
999
1000 Woodward, F. I., & Smith, T. M. (1994). Global photosynthesis and stomatal conductance:
1001 Modelling the controls by soil and climate. In Advances in Botanical Research (Vol. 20, pp. 1-41).
1002 Academic Press.

Yan, H., Wang, S. Q., Yu, K. L., Wang, B., Yu, Q., Bohrer, G., ... & Shugart, H. H. (2017). A novel diffuse fraction-based two-leaf light use efficiency model: An application quantifying photosynthetic seasonality across 20 AmeriFlux flux tower sites. Journal of Advances in Modeling Earth Systems, 9, 2317-2332.

Yang, X., Ricciuto, D. M., Thornton, P. E., Shi, X., Xu, M., Hoffman, F., & Norby, R. J. (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, X., Thornton, P. E., Ricciuto, D. M., & Post, W. M. (2014). The role of phosphorus dynamics in tropical forests–a modeling study using CLM-CNP. Biogeosciences, 11, 1667-1681.

Zanne, A. E., Abarenkov, K., Afkhami, M. E., Aguilar-Trigueros, C. A., Bates, S., Bhatnagar, J. M., ... & Treseder, K. K. (2020). Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. Biological Reviews, 95, 409-433.

Zeng, X. (2001). Global vegetation root distribution for land modeling. Journal of Hydrometeorology, 2, 525-530.

1024 Zhou, M., Guo, Y., Sheng, J., Yuan, Y., Zhang, W. H., & Bai, W. (2022). Using anatomical traits
1025 to understand root functions across root orders of herbaceous species in temperate steppe. New
1026 Phytologist. https://doi.org/10.1111/nph.17978
1027
1028 Zhu, Q., W. J. Riley, and J.Y. Tang (2017) A new theory of plant–microbe nutrient competition
1029 resolves inconsistencies between observations and model predictions, Ecological Applications, 27,
1030 875–886

Appendix

Embracing fine-root system complexity to improve the predictive understanding of ecosystem functioning

1. Methods

1.1 Simple ELM (sELM)

sELM is a simplified version of the Energy Exascale Earth System Model (E3SM) Land Model ELM, a state-of-the-art land surface model developed by Department of Energy, United States (**Golaz et al. 2019; Burrows et al. 2020**). ELM is traced back to the original CLM4.5 (**Oleson et al. 2013)** and the later version E3SM Land Model (ELM). sELM simplifies ELM by keeping only essential components simulating natural ecosystems in North America including vegetation and soil biogeochemistry (**Lu and Ricciuto 2019**). Following the same global PFT classification scheme as ELM, vegetation has the same structural pools (with a single fine-root pool) as ELM using the big-leaf approach. Although photosynthesis and GPP are replaced by a neural network surrogate built from ELM simulations, the whole scheme of allocation of photosynthates remains the same. Soil system, except for the lack of hydrology, is the same as the ELM with a 10-layer profile of 3.8018 m deep. Litter and soil organic matter decomposition follow the CTC (Converging Trophic Cascade) framework (**Oleson et al. 2013; Burrows et al. 2020**). Plant-microbe competition for mineral nitrogen is achieved via the relative demand approach without further differentiating between nitrogen forms (i.e., NH_4 and NO_3). Such a simplified model, in a more formal sense, is a high-fidelity mechanistic surrogate; by omitting irrelevant

processes but keeping all essential components, it eases modifications of structures and processes and reduces computational burden for analyses of uncertainty and sensitivity, contributing to an acceleration of the development-evaluation-application cycle for Earth System Models in particular.

1.2 Realization of TAM

1.2.1 Partitioning

We directly introduce three parameters (***frootpar_i***, where *i* indexes the three fine root pools of T, A, and M) to determine the spreading of allocation to a fine-root system (from either photosynthates or storage) among TAM pools. This approach simplifies the partitioning without considering explicitly the processes of movement of carbohydrates across the branching structure. With known partitioning (***frootpar_i***) and fine root C/N (***frootcn_i***), allocation allometry (ratio of allocation to total new growth to allocation to new leaf, *Callom/Nallom*) can be determined following:

$$\begin{cases} Callom = (1+g1)[1+a1+a3(1+a2)] \\ Nallom = \frac{1}{CN_{leaf}} + a_1 \sum_{i=1}^{3} \frac{frootpar\_i}{frootcn\_i} + \frac{a3a4(1+a2)}{CN_{livewood}} + \frac{a3(1-a4)(1+a2)}{CN_{deadwood}} \end{cases} \quad (1)$$

where ***a1*** through ***a4*** are allometric parameters that relate allocation between various tissue types, among which ***a1*** is the ratio of new fine root to new leaf carbon allocation (i.e., ***froot_leaf***), ***a2*** ratio of new coarse root to new stem carbon allocation, ***a3*** ratio of new stem to new leaf carbon allocation, ***a4*** ratio new live wood to new total wood allocation, and ***g1*** allocation ratio of growth respiration carbon to new growth carbon, as well as C/N of both live wood and dead wood. TAM

pools are parameterized with different C/N ratios based on consistent observations of descending C/N while fine-root systems branching out (e.g., **Pregitzer et al. 1997; McCormack et al. 2015**).

1.2.2 Phenology

In ELM, fine-root production is temporally controlled by leaf phenology in moving carbon from two direct sources: recent photosynthate and storage, making leaf and root production perfectly synchronous. These two sources, though ultimately originating from photosynthesis, can also be referred to as direct and indirect allocation, respectively. The allocation from leaf photosynthates to the fine-root system is based on an allometric relationship between leaves and fine roots (***froot_leaf*** = 1). This allocation is divided between direct allocation to the currently displayed fine-root system (***fcur***) and a storage pool to supply future growth for the whole fine-root system (i.e., indirect allocation; 1 - ***fcur***). This storage-based indirect allocation is also controlled by leaf phenology. Such a totally synchronous treatment between leaf and fine-root production is the case across all current ecosystem models, which, however, does not reflect the increasingly rich evidence that shoot and root phenology are not synchronous (e.g., **Perry 1971**; **Steinaker and Wilson 2008**; **Steinaker et al. 2010**; **McCormack et al. 2015b; Abramoff & Finzi 2015; Radville et al. 2016**). We make the following 3-step changes to decouple the phenological control of shoot and TAM in both deciduous and evergreen systems.

First, we make evergreen PFTs have the two-source structure of storage and recent photosynthate. In the current ELM, this two-source structure only applies to deciduous PFTs. Evergreen PFTs do not accumulate carbon and nitrogen in the storage pools for fine-root systems; instead, root production is solely determined by direct allocation of new photosynthates (i.e., ***fcur* = 1**), an assumption that lacks empirical support (e.g., **Huang et al. 2021**). Therefore, this treatment is changed for evergreen PFTs to have the same two-source structure as deciduous PFTs.

This structure enables storage-based production of (or indirect allocation to) fine-root systems controlled by TAM phenology.

Then, we decouple TAM phenology from leaf phenology for both deciduous and evergreen PFTs (**Fig.1**). In the current ELM, storage-based initiation of fine roots is synchronous with leaf-based control of unfolding (triggered by a growing degree threshold) and shedding (triggered by a critical day length). This synchronous treatment is changed to allow TAM initiation to behave independently in both deciduous and evergreen systems, which are determined by ***GDDsum*** (growing degree days with a 0-degree base) relative to a threshold value, ***GDDfroot_sum_crit***:

$$GDD_{froot\_sum\_crit} = GDD_{leaf\_sum\_crit} + \Delta GDD_{froot\_leaf} \quad (2)$$

where $\boldsymbol{\Delta GDD_{leaf\_froot}}$ is the difference between leaf and fine root threshold of GDD. Once $\boldsymbol{GDDsum > GDD_{froot\_sum\_crit}}$, TAM initiation is triggered, and fluxes of carbon and nitrogen begin to move from storage pools (CS_{froot_stor}) to the fine-root system. This occurs via transfer pools ($CF_{froot\_stor,froot\_xfer}$) calculated following:

$$CF_{froot\_stor,froot\_xfer} = f_{stor,xfer} CS_{froot\_stor} \quad (3)$$

where $f_{stor,xfer}$ = 0.5, the fraction of current storage pool moved into the transfer pool for display over the incipient onset period (**Oleson et al. 2013**).

Finally, we make TAM turnover of deciduous PFTs dependent on pool-specific mortality. For deciduous PFTs in the current ELM, the shedding of fine roots is synchronous with leaf shedding, which lacks empirical support. This synchronous treatment is thus changed to allow

deciduous fine-root mortality to behave independently in deciduous systems in the same way as the fine roots of evergreen PFTs. See **Section 1.2.4** on TAM mortality.

1.2.3 Distribution

In ELM and other land surface models, the prevailing option assumes that fine roots and coarse roots follow the same distribution as determined by prescribed fixed rooting and soil depths following:

$$r_{croot\_i} = \begin{cases} 0.5\left[\exp\left(-r_a z_{h,i-1}\right) + \exp\left(-r_b z_{h,i-1}\right) - \exp\left(-r_a z_{h,i}\right) - \exp\left(-r_b z_{h,i}\right)\right], & for\ 1 \le i\ < N_{levsoi} \\ 0.5\left[\exp\left(-r_a z_{h,i-1}\right) + \exp\left(-r_b z_{h,i-1}\right)\right], & for\ i = N_{levsoi} \end{cases} \quad (4)$$

where ***ra*** and ***rb*** are PFT-dependent root distribution parameters. Because of the dynamic nature of fine-root systems, the vertical profile is modelled dynamically by assuming horizontal homogenization of TAM (that is, the same distribution profile across T, A, and M) constrained by nutrient and water availability:

$$r_{froot\_i} = \frac{r_{croot\_i} f_{n\_i} f_{m\_i}}{\sum_{i=1}^{nlevsoi} r_{croot\_i} f_{n\_i} f_{m\_i}} \quad (5)$$

where ***fn_i*** and ***fm_i*** are the relative availability of nutrients and the relative availability of water at soil layer i, respectively. This nutrient constraint means that relatively more of the allocation goes to the depth where the relative nutrient availability is high; that is, a plant can direct allocation

and distribution to the place where the nutrients are relatively richer. Note that root-water interactions are beyond the scope of this study and are not included in the analysis below. Such a realization of a dynamic profile contingent on a fixed coarse root profile partly accounts for the notion that coarser roots provide a structural constraint for potential fine-root system distribution dictated by the hierarchical branching structure of root systems.

1.2.4 Mortality and litter input

With a 3-pool structure, turnover of the fine-root system is modelled explicitly in a vertically resolved way by introducing a mortality term. Mortality of fine roots and mycorrhizal fungi is endogenously controlled but subject to exogenous influences (e.g., **Eissenstat & Yanai 1997; Hendrick and Pregitzer 1997**). Therefore, consistent with the current approach in ELM modelling turnover using a mortality parameter in general, TAM mortality in each time step is determined by longevity distinguished among T, A, and M (***froot_long***) and constrained by a depth-correction term (α) as follows:

$$\begin{cases} Mr_{i,j} = \frac{1}{froot\_long\_i}\,\alpha_j \\ \alpha_j = e^{-\frac{dzj}{mort\_depth\_efolding}} \end{cases} \quad (6)$$

where ***froot_long_i*** is longevity of the three TAM pools near the soil surface, ***mort_depth_efolding*** is a constant of mortality rate decrease with depth, and ***dzj*** is depth of soil layer *j*.

Mortality of the T, A, and M pools are parameterized with different but decreasing lifespans based on relatively easy-to-make observations in shallow soil depths (**Supplementary**

Table 1). This pattern is based on field observations of a dramatic increase in survivorship with diameter even within a very narrow range (e.g., ≤ 0.5 mm) (e.g., **Reid et al., 1993**; **Hendrick & Pregitzer 1993; Tierney & Fahey 2002; Edwards et al. 2004; Joslin et al. 2006; Espeleta et al. 2009**; **Riley et al. 2009; Xia et al. 2010**) and direct observations of lifespan and turnover in fungal tissues (**Allen and Kitajima 2013; McCormack et al. 2010**). The depth-correction term (α) further corrects the fine root and fungi longevity (***froot_long***) for increasing lifespan with soil depth (e.g., **Baddeley and Waston 2005; Iversen et al. 2008; McCormack et al. 2012; Germon et al 2015; Gu et al. 2017)**. This depth-based correction partly accounts for the plasticity of fine-root systems in response to vertical variability in soil resource availability (e.g., **Pregitzer et al. 1993; Eissenstat and Yanai, 1997**).

An explicit turnover of fine-root systems means explicit production of litters from the three pools. The TAM structure is coupled with existing litter decomposition model simply by aggregating litters across the 3 pools and depositing them in the three vertically resolved soil litter pools—labile, cellulose/hemicellulose, and lignin (**Oleson et al. 2013**). Each of the three fine-root pools is parameterized with fractions of these three different groups in terms of C (**Supplementary Table 1**). Nitrogen fluxes to the three litter pools from each of the three fine root pools are determined using the same fractions as used for carbon fluxes and their C/N ratios.

Additionally, maintenance and growth respiration follow the current ELM implementation (**Oleson et al. 2013**). Maintenance respiration rate is related to temperature and tissue N content without further differentiating intrinsic respiration rate and temperature sensitivity among TAM roots; varying N content differentiates respiration among TAM roots. Growth respiration is still calculated as a factor of 0.3 (***grperc***) times the total carbon in new growth including the fine-root system.

1.3 Parameterization and simulation

We implemented the changes as detailed above to realize the TAM structure in sELM. This implementation is referred to as TAM model (or TAM in short), while the original version is referred to as ELM. For an illustration purpose, we parameterized TAM and ELM for 2 temperate forests across the East US: Howland Forest (https://ameriflux.lbl.gov/sites/siteinfo/US-Ho1; **Hollinger et al. 2021;** a single temperate evergreen needleleaf PFT) and Ozark (https://ameriflux.lbl.gov/sites/siteinfo/US-MOz; a single temperate deciduous broadleaf PFT; **Gu et al. 2016**). We used FRED (v3.0), a global Fine-Root Ecology Database to address below-ground challenges in plant ecology (https://roots.ornl.gov/; **Iversen et al. 2017; Iversen and McCormack 2021**), FunFun, a fungal trait database (**Zanne et al. 2020**), and published literature to derive PFT-specific parameter values/ranges for TAM (**Supplementary Table 1**). Simulation at each site was driven by forcings including daily radiation, maximum and minimum temperature, precipitation, day length, and a constant CO_2 level (cycled 6 times).

1.4 Uncertainty and sensitivity analysis

TAM was compared with ELM (with default parameterization) by accounting for structural and parameter uncertainties introduced by the novel 3-pool structure. These comparisons involved outputs of interest including fluxes of GPP and heterotrophic respiration and pools of leaf and fine-root system TAM, as well as the nitrogen limitation factors for plant growth (i.e., Fraction of Potential Growth, $FPG = F_{plant\_uptake}/F_{plant\_demand}$).

First, one case of preserving the fine-root system C/N of ELM in TAM was examined to see impacts of this structural shift and its associated uncertainties. To preserve the fine-root system

C/N in TAM (i.e., the default parameterization of C/N = 42), two specific scenarios were derived by solving the following equation, **Eq.7**, conditioned on the observed pattern of ascending C/N across the hierarchical branching orders within fine-root systems (e.g., **McCormack et al. 2015a**) and on prescribing one case of descending allocation from T through A (**TAM_descend**) and one case of ascending allocation (**TAM_ascend**):

$$\begin{cases} \sum_{i=1}^{3} \frac{frootcn\_i}{frootpar\_i} = 42 \\ frootcn\_t > frootcn\_a > frootcn\_m \\ frootpar\_i = [0.5,0.3,0.2] \; or \; [0.2,03,0.5] \end{cases} \quad (7)$$

By prescribing two alternatives of partitioning fraction vector, the equation has two corresponding closed solutions of ***frootcn_i*****:** [60,42,24] or [72,42,36]. In other words, by preserving the fine-root system C/N and keeping the same phenology and distribution between ELM and TAM, the uncertainty of the TAM structure for these two scenarios potentially arose from parameters of only chemistry and longevity. On top of these two cases, a structural uncertainty arising from nitrogen-constrained dynamic vertical distribution of new allocation was also examined, which were referred to as **TAM_descend_dd** and **TAM_ascend_dd**, respectively.

Next, without preserving the C/N ratio, a full implementation of TAM (including phenology) was compared with ELM. This comparison, relative to the above case, accounted for uncertainty arising from parameters including C/N and partitioning (6 parameters) and phenology-related parameters [3 parameters: ***gdd_crit*** (for evergreen PFT only)***, gdd_crit_gap, fcur***] **(Supplementary Table 1)**. That is, varying the partitioning and C/N parameters freely and phenology-related parameters under a full implementation of the proposed implementation of

TAM, changes relative to ELM and their uncertainty were attributed to these newly introduced parameters.

Finally, a global sensitivity analysis of TAM was performed with 8 (7 for evergreen PFT which does not have ***crit_dayl***) more existing parameters in ELM (**Supplementary Table 2**). All parameter uncertainty was quantified by 1080 ensemble runs from Monte-Carlo sampling from parameters' uniform uncertainty ranges and uncertainty propagation through the model. Attribution of TAM uncertainty was then achieved via variance-based sensitivity analysis with Sobol's sensitivity indices (**Sobol 2003; Ricciuto et al. 2018**). The Sobol's sensitivity indices were indirectly derived from a polynomial chaos expansion of the outputs via a new Weighted Iterative Bayesian Compressive Sensing (WIBCS) algorithm using the Uncertainty Quantification Toolkit (**UQTk v3.0.2**; https://github.com/sandialabs/UQTk).

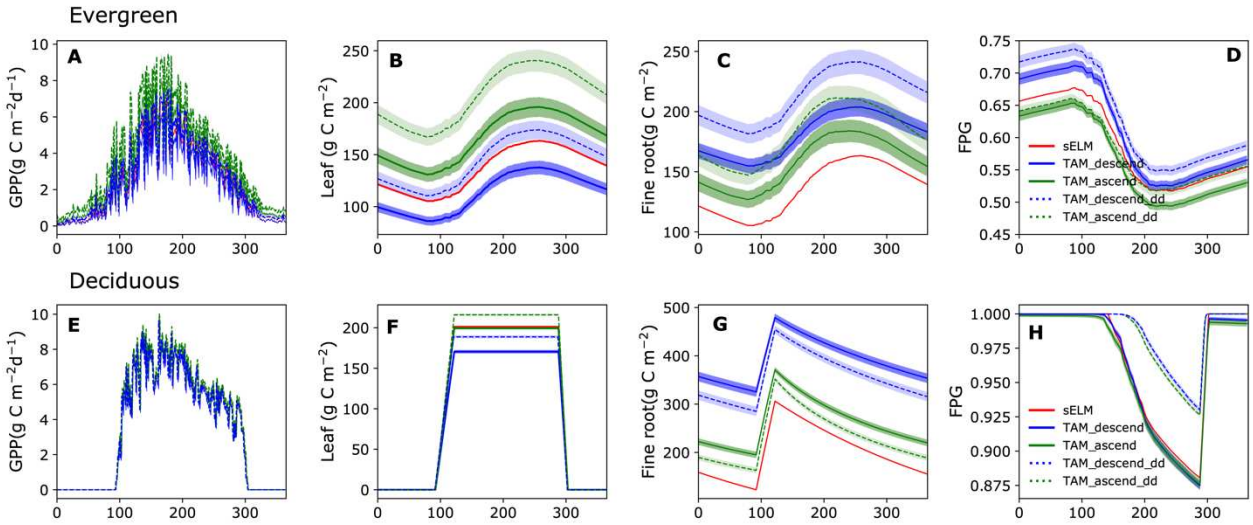
Supplementary Table 1. **List of introduced parameters and their uncertainty ranges.**

Parameter	Description	Unit	Range(evergreen/deciduous)	Reference
frootcn_t	C/N of T root	-	[20,184]/[19, 116]	FRED v3
frootcn_a	C/N of A root	-	[11,119]/[9, 81]	FRED v3
frootcn_m	C/N of M root	-	[7,25]/[7, 25]	Zanne et al. 2019
frootpar_t	Fraction of total allocation to T	-	[0.05, 0.95]	
frootpar_a	Fraction to total allocation to A	-	[0.05, 0.95]	
frootpar_m	Fraction to total allocation to M	-	[0.05, 0.95]	
frootlong_t	Longevity of T	year	[3, 10]	Matamala et al. 2003; Xia et al. 2010
frootlong_a	Longevity of A	year	[0.5, 4]	Matamala et al. 2003; Xia et al. 2010
frootlong_m	Longevity of M	year	[0.13, 1]	Pepe et al. 2018
fr_flab_t	Fraction of labile carbon in T	-	[0.125, 0.375]	± 50% of default value
fr_flab_a	Fraction of labile carbon in A	-	[0.125, 0.375]	± 50% of default value
fr_flab_m	Fraction of labile carbon in M	-	[0.125, 0.375]	± 50% of default value
fr_flig_t	Fraction of lignin carbon in T	-	[0.125, 0.375]	± 50% of default value
fr_flig_a	Fraction of lignin carbon in A	-	[0.125, 0.375]	± 50% of default value
fr_flig_m	Fraction of lignin carbon in M	-	[0.125, 0.375]	± 50% of default value
fr_fcel_t	Fraction of cellulose/hemicellulose C in T	-	[0.25, 0.75]	± 50% of default value
fr_fcel_a	Fraction of cellulose/hemicellulose C in A	-	[0.25, 0.75]	± 50% of default value
fr_fcel_m	Fraction of cellulose/hemicellulose C in M	-	[0.25, 0.75]	± 50% of default value
mort_depth_efolding	Rate of mortality decrease with depth	-	[187.15e-3,935.75e-3]	Iversen et al. 2008; McCormack et al. 2012; Germon et al 2015; Gu et al. 2017
gdd_crit_gap	Difference in GDD between root and leaf onset	℃ *day	[-300, 300]	Expert judgement

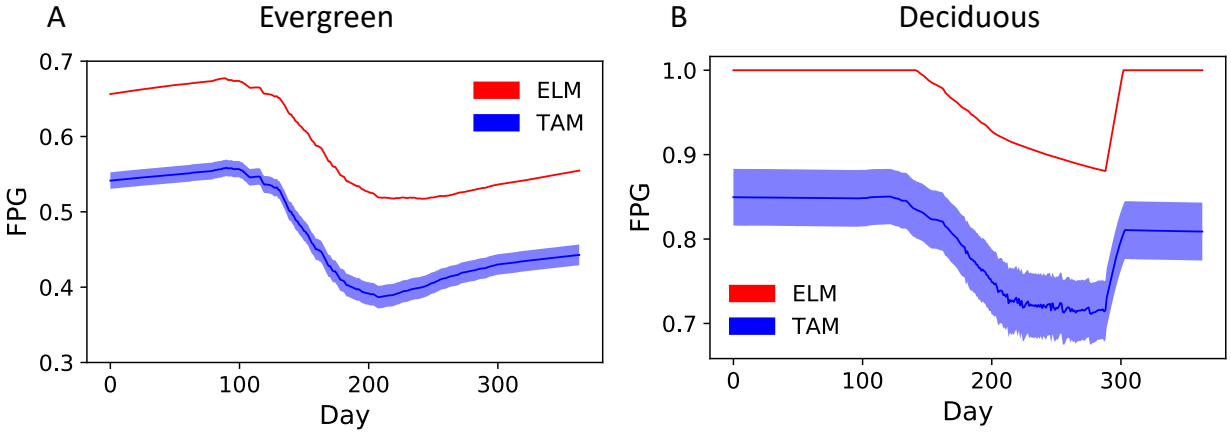
Supplementary Table 2. List of existing parameters of interest in ELM and their uncertainty ranges.

Parameter	Description	Unit	Range(evergreen/deciduous)
gdd_crit	Leaf onset GDD	℃ *day	150, 750
fcur	fraction of root allocation to display in current time step	-	[0.5, 1.0]/[0, 1]
froot_leaf	ratio of new fine root to new leaf carbon allocation	-	[0.5, 1.5]
slatop	Specific leaf area at canopy top	m2 gC-1	[0.005,0.015]/[0.015,0.045]
crit_dayl	Critical day length for leaf senescence in deciduous	Seconds	[36000, 43000]
leafcn	leaf C/N	-	[17.5, 52.5]/[12.5, 37.5]
roota_par	Rooting depth distribution parameter	m-1	[1.5,4.5]/[3, 9]
rootb_par	Rooting depth distribution parameter	m-1	[0.625, 1.875]/[1, 3]
br_mr	Base rate for maintenance respiration (MR)	umol m-2 s-1	[1.26e-06, 3.78e-06]
q10_mr	Temperature sensitivity for MR	-	[0.75, 2.25]

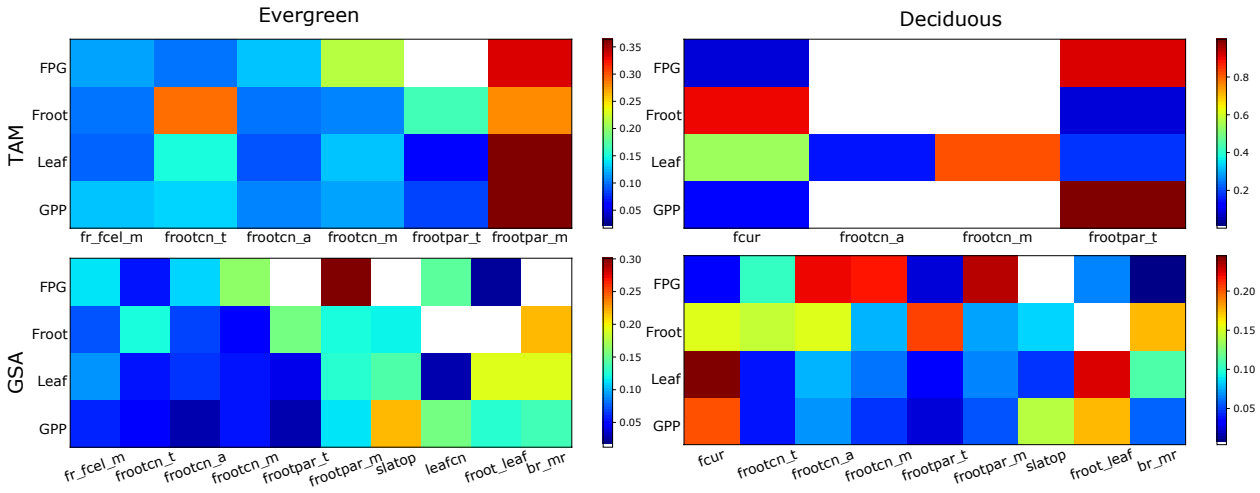
2. Results



Supplementary Fig. 1 Seasonal dynamics of GPP, leaf mass, and fine-root mass, as well as FPG (Fraction of Potential Growth) of TAM against the 1-pool structure of sELM under preservation of bulk fine-root system stoichiometry.



Supplementary Fig. 2 Seasonal variation in FPG (Fraction of Potential Growth) under a full implementation of TAM corresponding to **Fig.4** in the main text.



Supplementary Fig. 3 Attribution of TAM and global uncertainty with the main effect sensitivity index for the two sites. The TAM sensitivity corresponds to **Fig.3** in the main text. The global sensitivity analysis also includes some of existing parameters (**Supplementary Table 2**). Only the most relevant input parameters for each forest site are shown. The color code for each row is scaled according to the highest contributor to improve visibility.

References

Abramoff, R. Z., & Finzi, A. C. (2015). Are above-and below-ground phenology in sync? New Phytologist, 205, 1054-1061.

Allen, M. F., & Kitajima, K. (2013). In situ high-frequency observations of mycorrhizas. New Phytologist, 200, 222-228.

Baddeley, J. A., & Watson, C. A. (2005). Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant and Soil, 276, 15-22.

Burrows, S. M., Maltrud, M., Yang, X., Zhu, Q., Jeffery, N., Shi, X., ... & Leung, L. R. (2020). The DOE E3SM v1.1 biogeochemistry configuration: Description and simulated ecosystem-climate responses to historical changes in forcing. Journal of Advances in Modeling Earth Systems, 12, e2019MS001766.

Edwards, E. J., Benham, D. G., Marland, L. A., & Fitter, A. H. (2004). Root production is determined by radiation flux in a temperate grassland community. Global Change Biology 10, 209-227.

Eissenstat, D. M., & Yanai, R. D. (1997). The ecology of root lifespan. Advances in Ecological Research 27, 1-60.

Espeleta, J. F., West, J. B., & Donovan, L. A. (2009). Tree species fine-root demography parallels habitat specialization across a sandhill soil resource gradient. Ecology 90, 1773-1787.

Germon, A., Cardinael, R., Prieto, I. et al. (2016). Unexpected phenology and lifespan of shallow and deep fine roots of walnut trees grown in a silvoarable Mediterranean agroforestry system. Plant Soil 401, 409–426.

Golaz, J.-C., Caldwell, P. M., Van Roekel, L. P., Petersen, M. R., Tang, Q., Wolfe, J. D., et al. (2019). The DOE E3SM coupled model version 1: Overview and evaluation at standard resolution. Journal of Advances in Modeling Earth Systems, 11, 2089–2129.

Gu, L., Pallardy, S. G., Yang, B., Hosman, K. P., Mao, J., Ricciuto, D., ... & Sun, Y. (2016). Testing a land model in ecosystem functional space via a comparison of observed and modeled ecosystem flux responses to precipitation regimes and associated stresses in a Central US Forest. Journal of Geophysical Research: Biogeosciences 121, 1884-1902.

Gu, J., Wang, Y., Fahey, T.J. et al. (2017). Effects of root diameter, branch order, soil depth and season of birth on fine root life span in five temperate tree species. European Journal of Forest Research 136, 727-738.

Hendrick, R. L., & Pregitzer, K. S. (1993). Patterns of fine root mortality in two sugar maple forests. Nature 361, 59-61.

Hendrick, R. L., & Pregitzer, K. S. (1997). The relationship between fine root demography and the soil environment in northern hardwood forests. Ecoscience, 4, 99-105.

Hollinger, D. Y., Davidson, E. A., Fraver, S., Hughes, H., Lee, J. T., Richardson, A. D., ... & Teets, A. Multi-Decadal Carbon Cycle Measurements Indicate Resistance to External Drivers of Change at the Howland Forest AmeriFlux Site. Journal of Geophysical Research: Biogeosciences e2021JG006276.

1326 Huang, J., Hammerbacher, A., Gershenzon, J., van Dam, N. M., Sala, A., McDowell, N. G., ... &
1327 Hartmann, H. (2021). Storage of carbon reserves in spruce trees is prioritized over growth in the
1328 face of carbon limitation. Proceedings of the National Academy of Sciences 118, e2023297118
1329
1330 Iversen, C. M., Ledford, J., & Norby, R. J. (2008). CO_2 enrichment increases carbon and nitrogen
1331 input from fine roots in a deciduous forest. New Phytologist, 179, 837-847.
1332
1333 Iversen, C. M. et al. (2017). A global Fine-Root Ecology Database to address below-ground
1334 challenges in plant ecology. New Phytologist, 215, 15–26.
1335
1336 Joslin, J. D., Gaudinski, J. B., Torn, M. S., Riley, W. J., & Hanson, P. J. (2006). Fine-root turnover
1337 patterns and their relationship to root diameter and soil depth in a ^{14}C-labeled hardwood forest.
1338 New Phytologist, 172, 523-535.
1339
1340 Levine, E. R., Knox, R. G., & Lawrence, W. T. (1994). Relationships between soil properties and
1341 vegetation at the Northern Experimental Forest, Howland, Maine. Remote Sensing of Environment
1342 47, 231-241.
1343
1344 Lu, D. and Ricciuto, D. (2019) Efficient surrogate modeling methods for large-scale Earth system
1345 models based on machine-learning techniques. Geoscientific Model Development 12, 1791-1807
1346

McCormack, M. L., Pritchard, S. G., Breland, S., Davis, M. A., Prior, S. A., Brett Runion, G., ... & Rogers, H. H. (2010). Soil fungi respond more strongly than fine roots to elevated CO_2 in a model regenerating longleaf pine-wiregrass ecosystem. Ecosystems, 13, 901-916.

McCormack, M.L., Adams, T. S., Smithwick, E. A., & Eissenstat, D. M. (2012). Predicting fine root lifespan from plant functional traits in temperate trees. New Phytologist 195, 823-831.

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

McCormack, M. L., Gaines, K. P., Pastore, M., & Eissenstat, D. M. (2015b). Early season root production in relation to leaf production among six diverse temperate tree species. Plant and Soil, 389, 121-129.

Oleson, K., Lawrence, D., Bonan, G., Drewniak, B., Huang, M., Koven, C., ... & Yang, Z. (2013). Technical description of version 4.5 of the Community Land Model (CLM), NCAR. National Center for Atmospheric Research (NCAR) Boulder, Colorado.

Perry, T. O. (1971). Dormancy of Trees in Winter: Photoperiod is only one of the variables which interact to control leaf fall and other dormancy phenomena. Science, 171, 29-36.

Pregitzer, K. S., Kubiske, M. E., Yu, C. K., & Hendrick, R. L. (1997). Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia, 111, 302-308.

Pregitzer, K. S., Hendrick, R. L., & Fogel, R. (1993). The demography of fine roots in response to patches of water and nitrogen. New Phytologist, 125, 575-580.

Radville, L., McCormack, M. L., Post, E., & Eissenstat, D. M. (2016). Root phenology in a changing climate. Journal of Experimental Botany, 67, 3617-3628.

Reid, J. B., Sorensen, I., & Petrie, R. A. (1993). Root demography in kiwifruit (*Actinidia deliciosa*). Plant, Cell & Environment, 16, 949-957.

Ricciuto, D., Sargsyan, K., & Thornton, P. (2018). The impact of parametric uncertainties on biogeochemistry in the E3SM land model. Journal of Advances in Modeling Earth Systems, 10, 297–319.

Riley, W. J., Gaudinski, J. B., Torn, M. S., Joslin, J. D., & Hanson, P. J. (2009). Fine-root mortality rates in a temperate forest: estimates using radiocarbon data and numerical modeling. New Phytologist, 184, 387-398.

Sobol, I. M. (2003). Theorems and examples on high dimensional model representation. Reliability Engineering and System Safety, 79, 187–193.

Steinaker DF, Wilson SD. 2008. Phenology of fine roots and leaves in forest and grassland. Journal of Ecology, 96, 1222–1229.

Steinaker DF, Wilson SD, Peltzer DA. 2010. Asynchronicity in root and shoot phenology in grasses and woody plants. Global Change Biology 16, 2241–2251.

Tierney, G. L., & Fahey, T. J. (2002). Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. Canadian Journal of Forest Research, 32, 1692-1697.

Xia, M., Guo, D., & Pregitzer, K. S. (2010). Ephemeral root modules in *Fraxinus mandshurica*. New Phytologist, 188, 1065-1074.

Zanne, A. E., Abarenkov, K., Afkhami, M. E., Aguilar-Trigueros, C. A., Bates, S., Bhatnagar, J. M., ... & Treseder, K. K. (2020). Fungal functional ecology: bringing a trait-based approach to plant-associated fungi. Biological Reviews 95, 409-433.