Wang Bin (Orcid ID: 0000-0003-0453-458X)
Ricciuto Daniel (Orcid ID: 0000-0002-3668-3021)
Iversen Colleen M (Orcid ID: 0000-0001-8293-3450)

Embracing fine-root system complexity in terrestrial ecosystem modelling

Running title: Embracing fine-root system complexity

Bin Wang[1]* (0000-0003-0453-458X),

M. Luke McCormack[2] (0000-0002-8300-5215),

Daniel M. Ricciuto[1] (0000-0002-3668-3021),

Xiaojuan Yang[1] (0000-0002-2686-745X), and

Colleen M. Iversen[1] (0000-0001-8293-3450)

1 Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee

37830 USA

2 Center for Tree Science, The Morton Arboretum, Lisle, Illinois 60532 USA

*Correspondence: Bin Wang (wangb@ornl.gov or wbwenwu@gmail.com)

Abstract

Projecting the dynamics and functioning of the biosphere requires a holistic consideration of whole-ecosystem processes. However, biases towards leaf, canopy, and soil modelling since the 1970s have constantly left fine-root systems being rudimentarily treated. As accelerated empirical advances in the last two decades establish clearly functional differentiation conferred by the hierarchical structure of fine-root orders and associations with mycorrhizal fungi, a need emerges to embrace this complexity to bridge the data-model gap in still extremely uncertain models. Here, 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. Emerging from a conceptual shift away from arbitrary homogenization, TAM builds upon theoretical and empirical foundations as an effective and efficient approximation that balances realism and simplicity. A proof-of-concept demonstration of TAM in a big-leaf model both conservatively and radically shows robust impacts of differentiation within fine-root systems on simulating carbon cycling in temperate forests. Theoretical and quantitative support warrants exploiting its rich potentials across ecosystems and models to confront uncertainties and challenges for a predictive understanding of the biosphere. Echoing a broad trend of embracing ecological complexity in integrative ecosystem modelling, TAM may offer a consistent framework where modelers and empiricists can work together towards this grand goal.

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

1. Introduction

Earth System Models (ESMs; **Box 1**) grapple with low confidence in projecting the dynamics and functioning of the biosphere within the Earth System. 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 aboveground leaf and canopy processes (e.g., Sinclair et al., 1976; Friend et al. 2014; Lovenduski and Bonan 2017) and belowground soil biogeochemistry (e.g., Allison et al. 2010; Todd-Brown et al. 2013). Meanwhile, plant roots, integral to the evolution of plant forms and functions (e.g., Raven and Edwards 2001; Matthew et al. 2022), sit at the nexus of plant-microbe-soil interactions (e.g., Bardgett et al. 2014; Freschet et

al. 2021). However, fine-root systems—the ephemeral portion of the root system in association with microbiomes (**Box 1**)—have been consistently treated rudimentarily. Such a modelling bias against fine-root systems has been argued to contribute largely to the poor representation within ESMs of feedbacks of terrestrial ecosystems to global changes (e.g., Warren et al. 2015; Bonan and Doney 2018). Reducing this bias is therefore expected to contribute to enhancing reliability of ESMs projections.

However, the gap arising from this bias becomes even larger as accelerated empirical progress over the past two decades reveals structural and functional differentiation within fine-root systems. An order-based branching structure view of plant root systems has been argued since the 1980s (Fitter 1982). In the 2000s, experimental measurements revealed unique morphological, anatomical, chemical, physiological, and demographic properties among root branching orders (e.g., Pregitzer et al. 2002; Guo et al., 2008; Atucha et al. 2021), as well as varying microbial associations with both mycorrhizal fungi and bacteria (e.g., Sen and Jenik 1962; Phillips et al. 2013; King et al. 2021). These structural differences support functional differentiation within fine-root systems: only finer and more distal roots in symbiosis with mycorrhizal fungi are responsible for nutrient and water acquisition from soils, while fine roots of higher orders are primarily responsible for transport (e.g., Hishi & Takeda 2005; McCormack et al. 2015a; Wang et al. 2022). This internal heterogeneity within a fine-root system, and degree of coordination with the aboveground, change with species and habitat, shaping fine-root system complexity and forming diverse whole-plant strategies (e.g., McShea and Brandon 2010; McCormack and Iversen 2019; Weigelt et al. 2021).

By contrast, ecosystem models remain casual in treating structural and functional heterogeneity in fine-root systems. The prevailing option in terrestrial ecosystem modelling

remains a single fine-root pool (e.g., Kleidon & Heimann 1998; Zeng 2001; Warren et al. 2015; Burrows et al. 2020). Although empiricists have advocated for specifically representing arbuscular mycorrhizal fungi (Treseder 2016) and modelers have even already incorporated mycorrhizal fungi into models either implicitly (e.g., Woodward and Smith 1994; Brzostek et al. 2014) or explicitly (e.g., Hunt et al. 1991; Orwin et al. 2011; Sulman et al. 2018), no efforts yet holistically integrate the complexity of the fine-root system with a balanced perspective of both fine roots and mycorrhizal fungi. This structural simplification of fine-root systems fundamentally limits accurate representation of their functioning (e.g., Smithwick et al. 2014; Warren et al. 2015) and shapes biased model development towards photosynthesis and canopy processes that imparts a further structural limit on improvements to whole model performance. For instance, this bias has led to the prevailing assumption in current models of fine-root and fungal seasonal dynamics being dictated by leaf phenology (e.g., Burrows et al. 2020; but see Thum et al. 2019). Although there are individual-level crop models explicitly simulating root structures (e.g., Pointurier et al. 2021), empirical advances in fine-root system complexity are not reflected in more challenging ecosystem modelling.

Such a large observation-model discrepancy raises the question of whether models can improve performance (in a broad sense not narrowly limited to predictability) with an appreciation of fine-root system complexity. By analogy, the core of this question mirrors the debates on one layer versus multilayer modelling of forest canopies (e.g., Raupach and Finnigan 1988), on individual-based versus various functional groups in vegetation 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 led to the conclusion that

land surface models should move beyond the useful but incorrect paradigm of a 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 single fine-root model ELM revealed large prediction uncertainty arising from uncertainty in root-related parameters and processes (Ricciuto et al. 2018). Constraining uncertainty requires a model structure with parameterization and prediction informed and validated by empirical data. Furthermore, improving fine-root systems may systematically improve model performance by identifying closely coupled but deficient components. Therefore, dedicated efforts to embrace fine-root system complexity are warranted to explore alternatives to the current homogenization in ecosystem models.

To this end, we propose a generalized 3-pool structure including Transport and Absorptive fine roots with Mycorrhizal fungi (TAM; **Fig.1**) to represent fine-root systems in ecosystem models across organizational and spatio-temporal scales in the terrestrial biosphere. TAM is intended to approximate both structurally and functionally the high-dimensional heterogeneity within the hierarchical branching of fine-root systems in associations with mycorrhizal fungi. The overarching objective of this opinion is to argue for this approximation as a quantitative keystone of the bridge between empiricists and modelers. After elaborating in detail on the conceptual, theoretical, and empirical foundations, we offer a quantitative demonstration by realizing TAM under the guidance of a high-level framework of partitioning, phenology, and distribution to simulate dynamically and vertically resolved fine-root systems. For a proof-of-concept purpose the focus of this demonstration is showing impacts of TAM both analytically and descriptively by using a model representative of the relatively simplest big-leaf paradigm to simulate two different temperate forest types (deciduous and evergreen forests) across the Eastern United States.

Although TAM echoes a trend of embracing biological and ecological complexity in ecosystem modelling (in a philosophical sense), we do not intend to claim that at this stage this structure improves model predictability, which is too big a topic to address in a proof-of-concept work. Rather, we hope that TAM can serve as a consistent structure around which new observations and ideas from both modelers and empiricists can be assembled and discussed, which, we anticipate, will eventually contribute to improving predictability of ecosystem models across spatial-temporal scales. Accordingly, we identify uncertainties and challenges to exploit more broadly its potential in different ecosystems and vegetation modelling paradigms. We conclude by pointing out potential implications of TAM for guiding empirical research, understanding ecosystem functioning, and improving prognosis of ESMs.

Box 1 Terminology

Fine-root system: Root-microbe association at the individual plant level comprising fine roots of different orders and associated microbiome (mycorrhizal fungi in this study).

TAM: An approach argued for in this study 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; hyphae in practice).

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 of 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 surface 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-leaves' model).

ELM: A land model using the 'two big-leaves' approach with a single fine-root pool in the Energy Exascale Earth System Model (E3SM), a state-of-the-art ESM developed by the US Department of Energy (Golaz et al. 2019).

Demography model: Terrestrial ecosystem models that can simulate dynamics of vegetation pattern (e.g., forested mosaic of gaps) with demographic processes of growth, mortality, and reproduction.

Demand-driven approach: An approach for formulating plant and microbial nutrient uptake based exclusively on the nutrient demands determined by their potential growth rates, organic matter decomposition rates, and chemical stoichiometry (i.e., individual fine roots and mycorrhizal fungi do not explicitly acquire nutrients from the soil using this approach). The competition between plants and microbes for nutrients is resolved by comparing their demands, and this solution is thus referred to as the relative-demand approach (Thornton et al. 2007; Yang et al. 2014).

Trait divergence: Trait variability or heterogeneity where a 3-pool TAM model allows for unique trait values for each pool while a 1-pool fine-root model only allows a single value to represent the fine-root system.

Preservation: A procedure to keep the same bulk fine-root system property (e.g., C/N in this study) while capturing trait divergence from a 1-pool to 3-pool TAM structure.

Partitioning: The allocation of plant photosynthates (including storage) to one of the TAM pools.

Vertical Distribution: The explicit vertical distribution of photosynthates in a soil profile partitioned to one of the TAM pools.

2. Conceptual, theoretical, and empirical foundations

Originating from fine-root system complexity, TAM emerges directly from a conceptual shift in our understanding of fine-root systems. Traditionally, different fine-root orders narrower than the 2-mm diameter threshold are arbitrarily homogenized and measured as functionally equivalent units. Instead, the empirical progress stimulated a new conceptualization by McCormack et al (2015a) that treats coarser, high-order fine roots as transport roots, and finer, low-order fine roots absorption roots with facilitation by colonizing mycorrhizal fungi. This reconceptualization is the very foundation for our aggregation of fine-root systems of different orders and associations with mycorrhizal fungi into three functional groups comprising transport roots, absorptive roots, and mycorrhizal fungi (**Fig.1**). Such a grouping follows 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). Inheriting this long history and grounded on a reconceptualization, TAM is expected to be effective theoretically and efficient empirically in modelling above- and below-ground processes in ecosystems across scales.

In principle, a 3-pool TAM in ecosystem models is an effective approximation that offers a parsimonious but balanced representation of fine roots and mycorrhizal fungi. A single fine-root pool without symbiotic associations with mycorrhizal fungi oversimplifies fine-root systems.

Recognizing the importance of mycorrhizal fungi, some plant-centric models account for these fine-root partners as an implicit component (e.g., Koide and Elliot 1989; Kirschbaum and Paul 2002; Brzostek et al. 2014). Though improving simulations of plant nutrient uptake and soil organic matter decomposition overall, missing a pool of mycorrhizal fungi with certain autonomy thwarts a balanced perspective of plant and mycorrhizal fungi. However, when an explicit mycorrhizal fungal pool is included (e.g., Hunt et al. 1991; Orwin et al. 2011; Sulman et al. 2019), the homogenization of fine roots misses the differentiation of transport versus absorptive fine roots. Undoubtedly, a discretized 3-pool structure cannot yet fully capture the high-dimensional variations in fine-root systems. However, an explicitly order-based continuous treatment of individual fine-root orders may be more suitable for individual-level plant models (e.g., crop modelling; Couvreur et al. 2012; Pointurier et al. 2021). Instead, TAM attempts to balance biological and ecological complexity with model simplicity in the ecosystem modelling setting to avoid a parameterization challenge that may overwhelm model improvement (e.g., Prentice et al. 2015; Transtrum et al. 2015).

Parameterization of a 3-pool TAM structure has high empirical feasibility. This feasibility is even higher than models simply homogenizing the fine-root systems. For instance, instead of aggregating distinctive turnover rates (ranging from less than a year to more than a decade) into one homogeneous pool (with one-year lifespan), TAM can efficiently capture this heterogeneity. TAM confers generality across organizational levels of ecosystems from individual- to community-level over spatial-temporal scales by enabling easily adaptable and aggregate pools. While T and A capture widespread functional differentiation between transport and absorption, they can be effectively re-aggregated to accommodate species without such a clear differentiation (e.g., some grasses; McCormack et al. 2015a). The M pool, in practice, can be largely informed

by measurements of hyphal mycelium of arbuscular (AM), ericoid fungi, and/or ectomycorrhizal (ECM), depending on the geographic context and local environment and organismal composition (e.g., Read 1991; Soudzilovskaia et al. 2019). In addition, TAM still allows aggregation of individual- or species-based measurements to parameterize lower resolutions of vegetation composition using different Plant Functional Types (PFTs; **Fig.2**). Such empirical feasibility is facilitated further by availability of trait databases. In the context of a belowground data revolution, databases of explicit fine-root traits and fungal traits aggregated from either function- or order-based measurement increase with spatial resolution and extent [see a synthesis by Iversen and McCormack (2021)]. Notably, the Fine-Root Ecology Database (FRED) houses root trait observations from across c. 4600 unique plant species and continues to grow (Iversen et al. 2017; Iversen and McCormack 2021). With these compelling arguments for TAM from conceptual to theoretical to empirical, we sought further quantitative support by realizing and demonstrating TAM in terrestrial ecosystem models.

3. Realizing TAM in terrestrial ecosystem models

To realize TAM in terrestrial ecosystem models, we first propose a high-level framework of partitioning, phenology, and distribution to encapsulate the multiple interrelated processes towards simulating a temporally and vertically resolved 3-pool fine-root system (**Fig.1**). Partitioning (**Box 1**) 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 the changes in biotic and abiotic environment such as edaphic factors (e.g., nutrient and water availability) and atmospheric changes (e.g., elevated CO_2) (e.g., Mooney 1972; Kothari et al., 1990; Béguiristain and Lapeyrie 1997; Chapin et al. 2009; Drigo et al. 2010; Gorka et al. 2019;

Ouimette et al. 2020). Phenology then controls the timing of partitioning. Here, we spotlight phenology because of recurring observations of above- and below-ground phenological asynchronicity (e.g., Steinaker et al. 2010; Abramoff and Finzi 2015; McCormack et al. 2015b; Radville et al. 2016; Iversen et al. 2018). In addition to variations among the TAM structures, phenology varies with soil depth (e.g., Fernandez & Caldwell 1975; Maeght et al. 2015). This vertical variability makes it essential to capture accurately the vertical distribution (**Box 1**) within the soil profile of carbon and nutrients partitioned to TAM pools (e.g., Tumber-Dávila et al. 2022). Moreover, properties of fine roots and mycorrhizal fungi change vertically (e.g., McElrone et al. 2004; Robin et al. 2019), which feeds back to influence partitioning. Therefore, these three components are interrelated in such a way that requires a close coupling of dynamic partitioning with phenology temporally and distribution vertically. These components and their interactions can be integrated into existing models by coupling with upstream photosynthesis and allocation and with downstream soil biogeochemistry.

Starting this integration from a simple model structure is practical for proof of concept while paving the way for TAM in more complex model structures. Existing models, built with different perspectives and assumptions for different purposes, vary in their structural realism of capturing vegetation pattern and process under three different paradigms (**Fig.2**). 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: 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. Integrating TAM into models under these paradigms can incorporate different organizational levels across spatial-temporal scales, but trades off with feasibility in terms of formulation, parameterization, and evaluation. Given its high feasibility, the big-leaf paradigm, albeit with low ecological realism, offers a gateway to identifying both opportunities and challenges to realize TAM under structurally more realistic paradigms.

Accordingly, we explicate realizing TAM in the context of the big-leaf model ELM. ELM, as the land model of the Energy Exascale Earth System Model (E3SM; Golaz et al. 2019; Burrows et al. 2020), assumes a single fine-root pool without mycorrhizal fungi under the traditional scheme of representing global plant diversity with a few PFTs. This structural assumption in ELM is broadly representative of existing land models, albeit varying in specific processes (Bonan and Doney 2018). Also, ELM has been extensively applied to simulating land-atmosphere interactions both regionally and globally (e.g., Golaz et al. 2019; Burrows et al. 2020), but a comprehensive sensitivity analysis pointed large prediction uncertainty to deficiencies in root-related parameters and processes (Ricciuto et al. 2018). Moreover, ELM uses the relative-demand approach (**Box 1**) as a default configuration to simplify plant-microbe competition for nutrients without requiring explicit fine-root and fungal functions (e.g., Thornton et al. 2007; Yang et al. 2014). Such formulations, plus its representativeness, transferability across models, and wide usage, make ELM feasible and practical for introducing changes to demonstrate TAM for a proof-of-concept purpose.

In the context of ELM, we introduce a series of specific changes within the above high-level framework to realize a 3-pool TAM structure. In contrast to the brute homogenization of a

single-pool structure, TAM allows trait divergence (**Box 1**) among the fine-root and fungal pools with respect to the ratio of carbon to nitrogen (C/N), longevity, and chemical composition, as well as respiration (**Table 1**), following observations of trait variability within fine-root systems [see the synthesis by 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 allocation of photosynthates to leaves and fine roots (but see Thum et al. 2019). These fractions together with C/N of the three TAM pools determine the C/N of bulk fine-root system (**Eq. 1** in **Supporting Information**), 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 belowground TAM pools from aboveground 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 a changing vertical 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 with a relative higher availability of nitrogen. See section TAM Realization in **Supporting Information** for details.

4. Impacts of TAM in forest ecosystems: an example demonstration

By implementing the specific changes as introduced above, we illustrated TAM impacts against the single-pool structure in ELM. We chose two representative sites for illustrative purposes: a deciduous forest of the central US and an evergreen forest of the northeastern US in the temperate forest biome of North America (see section Parameterization and Simulation in the **Supporting Information** for details). Accounting for parameter (by considering measurement uncertainty; **Table S1**) and structural uncertainties (by implementing those changes to different extents), we examined impacts of TAM against ELM with two complimentary cases: a conservative case and a radical case. The conservative case, by preserving bulk fine-root stoichiometry, was intended to see whether differentiation of TAM traits alone affects key carbon cycling processes. The radical case, which implemented all of the above changes without this stoichiometry constraint (that is why we dub it radical), was intended to show implications of TAM differentiation for ecosystem-level functioning. See Uncertainty and Sensitivity Analysis in **Supporting Information** for more details.

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 gave us a conservative 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 for using existing field observations of bulk fine-root C/N to constrain the model. We acknowledge that in principle other properties (e.g., fractions of carbon compounds) could also be preserved. However, with a demand-driven approach (**Box 1**) 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 plant nutrient uptake capability as the single-pool model while capturing the divergence in C/N among TAM pools. The preservation was achieved via pairing a set of C/N values with a set of partitioning fractions of TAM (**Eq. 7** in **Supporting Information**). To capture the wide spectrum of plant partitioning variability among different belowground sinks, we considered 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). Keeping the same synchronous phenology as in ELM, we compared conservative 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, significant partitioning-dependent impacts of TAM compared against the single-pool model can be attributed to changes in turnover and litter inputs. These changes arose from explicit low to high turnover rates and high to low C/N moving from T through M pools, since both the stoichiometry and the phenology are the same. The impacts were 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 slightly dampened responses (relative to the

descending pattern) were seen under the ascending pattern, as there was relatively more carbon partitioned 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 litter inputs from the fine-root systems 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 as nutrient limitation did not become dominant (**Fig. S1**).

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 GPP (**Fig. 3b, f**) and soil respiration (**Fig.3c, g**) but with a net effect of soil carbon stock decline under both patterns (**Fig. 3d, h**). However, fine-root biomass experienced continued increases in the evergreen forest compared to pauses in the deciduous forest because relatively more biomass accumulated in deeper soils with slower turnover rates in the evergreen than in the deciduous forest (**Fig. 3a, e**). These new changes under dynamic distribution highlight the role of vertical variability of TAM in influencing plant-soil interactions. In short, a conservative TAM had significant impacts on simulating carbon cycling in forests, which shows convincingly the necessity of capturing differentiation and thus favors testing a radical TAM without the restraint of preservation.

4.2 Radical TAM dampens forest productivity and carbon stocks

Implementing a radical TAM consistently resulted in reduced ecosystem productivity and carbon stocks compared to the single-pool model regardless of forest type. With a full accounting

of parameter uncertainty informed by measurements (see Uncertainty and Sensitivity Analysis in **Supporting Information**), on average annual GPP was reduced by 20.3 % and 36.3 % in the evergreen and deciduous forest, respectively (**Fig. 4**). These reductions in equilibrium originated from asynchronous phenology, changing allocation (different C/N), and explicit fine-root system turnover (different longevity), as indicated by the peak-shifting and increased (though not seasonally consistent) fine-root system biomass in equilibrium **(Fig. S2)**. Over time these changes, though with dynamical distribution, led to aggravated nutrient limitation (**Fig. S3**), together with decreased leaf area, contributing to declines in GPP (**Fig. 4a, b**). Such GPP reductions eventually resulted in decreased respiration (by 21.8 % and 32.6 % in the evergreen and deciduous forest, respectively) and a net decline of carbon stock (by 6.2 % and 10.6 %, respectively; **Fig. 4a, b**). These robust changes are in line with the general notion of a lack of accurate sink-limited growth leading to an overestimation of land carbon sink (e.g., Fatichi et al. 2019; Cabon et al. 2022). In fact, comparisons with field-based accounting of whole ecosystem carbon did show TAM has a better agreement (**Fig. S4**). In summary, a radical TAM suggests that models homogenizing fine-root systems may overestimate forest productivity and carbon stocks and that capturing fine-root system complexity may contribute to simulating sink-limited growth more accurately.

4.3 TAM impacts echo embracing complexity in ecosystem modelling

Echoing a trend of embracing complexity in ecosystem modelling, the above results from conservative to radical provide quantitative support for TAM. Accounting for structural and parametric uncertainties, the two cases together demonstrate robust impacts of TAM against a homogeneous single-pool structure: the conservative case with stoichiometry preservation is compelling by itself in showing the impacts of differentiation enabled by TAM, while the radical

case reveals potential implications of the differentiation by showing consistent reductions of productivity and carbon stocks. Such impacts arising from a shift from implicit to explicit reflect a broad trend of embracing biological and ecological complexity in ecosystems from above- to below-ground to improve performance. A notable aboveground shift in vegetation structure is from the big-leaf approach using a single-layer canopy to explicitly modeling multi-layer canopy structures (e.g., Sinclair et al., 1976; Norman, 1993; Yan et al. 2017; Bonan et al. 2021), and further to a paradigm simulating vegetation dynamics in the spatial and vertical structuring by age and size (e.g., Shugart 1984; Kohyama 1993; Moorcroft et al. 2001; Wang et al. 2016; Shugart et al. 2018; Fisher et al. 2018). A similar belowground example is the shift from simulating the tremendously complex soil microbiomes first implicitly (e.g., Parton et al. 1987), then as a 'big microbe' (e.g., Allison et al. 2010), and more recently as a constellation of a few discrete functional groups (e.g., Wieder et al. 2015) or of even continuous hypothetical individuals using a trait-based approach (Wang and Allison 2022) in a structurally explicit soil environment (Wang et al. 2019). Resonating with this trend of complexity, our demonstration added quantitative support to the conceptual, theoretical, and empirical arguments for TAM. Though compelling theoretically and quantitatively, this demonstration, admittedly, was limited in scope to just two forest sites using only one model under the big-leaf paradigm; therefore, we do not yet claim that TAM has improved model predictivity. Rather, the door is now opened wide by this demonstration to working toward this objective by empiricists and modelers together under a consistent framework. However, exploiting TAM more deeply and extensively across ecosystems and models needs to confront a series of challenges as implied by the prevailing model assumptions and lingering uncertainties in this example realization.

5. Challenges in exploiting the TAM structure

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 Uncertainty and Sensitivity Analysis in **Supporting Information**) show the parameters controlling partitioning are among the most sensitive ones (**Fig. S5**). 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 detailed 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 might offer such a unified framework, but they still face 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, a holistic understanding of phenology and vertical distribution of fine roots and mycorrhizal fungi is in its 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 mycorrhizal fungi with spore dormancy (e.g., Gianinazzi-Pearson et al., 1989; Bago et al. 2000; Defrenne et al. 2021). TAM variability in phenology is far from being robust as it cannot yet account for all relevant abiotic factors. However, an independent treatment of TAM initiation and mortality allowing for asynchronous phenology between leaves and fine-root systems represents a substantial improvement. Still, the lack of asynchronous TAM phenology vertically means that the timing of partitioning at each depth is not fully realistic. Also, dynamic distribution, though constrained by dynamic nutrient availability in the soil profile, needs to account for other important factors (e.g., soil moisture and temperature). Addressing these interrelated processes under an optimization framework requires explicit seasonal observations within soil profiles of fine-root system dynamics across root orders and mycorrhizal fungi to disentangle environmental controls. Meanwhile, we must go beyond the demand-driven approach to improve modelling of root nutrient demand and uptake and explicitly connect them to TAM.

5.2 Connecting TAM with fine-root and mycorrhizal fungal functions

Relaxing the assumption of demand-driven nutrient uptake and competition entails an explicit formulation of the different functions of TAM pools and their interactions with soils. Incorporating explicit TAM functioning with respect to nutrient and water uptake will require explicit absorptive root and mycorrhizal fungi traits (**Table 1**) related to uptake of nutrients in various forms of nitrogen and phosphorous (e.g., Yang et al. 2014; 2019) and water (e.g., Polverigiani et al. 2011; Jackisch et al. 2020; Mackay et al. 2020; Kakouridis et al. 2022)**.** Notably, mycorrhizal fungi in TAM, especially ectomycorrhiza and ericoid mycorrhiza, can directly mediate litter and soil organic matter decomposition by exuding enzymes and taking up organic nitrogen (e.g., Gadgil and Gadgil 1971; Frey 2019). Therefore, once TAM incorporates explicit

root and mycorrhizal functions, it becomes highly necessary to make a concomitant change to microbially-explicit organic matter decomposition with exoenzymes instead of the first-order decomposition assumed in ELM. A microbially-explicit decomposition model then needs to accommodate fine-root system exudates while handling explicit litter decomposition arising from the explicit turnover of TAM components, especially with fungal necromass (e.g., Matamala et al, 2003; Strand et al. 2008; Fernandez et al. 2018; Sun et al. 2018). These aspects can be addressed by combining a microbially-explicit organic matter decomposition model interacting with the functioning of fine-root systems (e.g., Sulman et al. 2018; Wang and Allison 2019) with the existing approach of resolving plant-microbe competition for nutrient uptake based on the Equilibrium Chemistry Approximation theory (Zhu et al. 2017; Wang and Allison 2019). However, to capture the variability in these processes and their interactions arising from biological diversity, we need to move beyond the big-leaf paradigm.

5.3 Realizing TAM in demography models

Moving beyond the big-leaf paradigm to realizing TAM in demography models will require efforts to better capture patterns and processes belowground. Simulating the mosaic of forested landscapes in demography models has so far only emphasized the aboveground, making a TAM-based belowground mosaic particularly challenging (**Fig.2**). One outstanding issue towards this belowground mosaic is to simulate age- and/or size-related changes in TAM in the context of complete life cycles of growth, mortality, and reproduction for diverse individuals with frequent disturbances. For instance, evidence has indicated roles of mycorrhizal fungi change with plant community succession stage (e.g., Pankow et al. 1991; Read 1991; Nara 2006). One strategy of simulating age- and size-related changes would be conditioning TAM on a dynamic rooting

depth of coarse roots (constrained by, for example, maximum rooting depth; **Fig.1; Table 1**), instead of using a constant value as widely assumed in current models. This change in rooting depth should involve geometric and allometric relationships with aboveground structural tissues (e.g., Eshel and Grünzweig 2013; Brum et al. 2019; Tumber-Dávila et al. 2022) while accounting for direct influences from, for example, soil hydrological conditions (e.g., Stone and Kalisz 1991; Fan et al. 2007). Addressing these aspects requires long-term observations of successional dynamics of not only the aboveground but also the belowground (e.g., Rees et al. 2001).

6. Implications for root ecology, ecosystem dynamics and functioning, and ESMs

Confronting those challenges above to exploit TAM potentials holds promise to stimulate empirical ecology of fine-root systems, to drive theory-driven explorations of hypotheses of fine-root system roles in ecosystem functioning, and to eventually improve the prognostic capability of ESMs. First, adopting this structure would stimulate more targeted efforts at an increasing resolution of empirical investigations into fine roots and mycorrhizal fungi as discussed above about challenges (**Table 1**). The proposal of TAM is largely fueled by the belowground trait data revolution, especially with tremendous empirical progress in collecting function- and/or order-based fine-root traits including microbial associations (e.g., McCormack et al. 2017; Iversen 2017; Iversen and McCormack 2017; Tedersoo et al. 2021). Building on standardized measurement protocols (Freschet et al. 2021), TAM may also stimulate further technical research and possible advances in, for example, neutron imaging (e.g., Warren et al. 2013), remote sensing (e.g., Sousa et al. 2021), and machine learning in image recognition (e.g., Han et al. 2021) to speed up characterization and classification of functional 'roots' within fine-root systems. Undoubtedly,

new measurements and causal relationships revealed will help improve formulation, parameterization, and evaluation of TAM in models of increasing complexity (**Fig. 2**).

Then, theory-driven modelling studies can be conducted with explicit TAM-based demography models to explore hypotheses of root-associated community-level processes underlying ecosystem functioning. One of the major motivations for demography models is that community-level processes are integral to modelling ecosystem dynamics and functioning responding to various disturbances (e.g., Wang et al. 2016; Fisher et al. 2018). Although increasing empirical and theoretical studies have indicated an equally (if not more) important role of belowground interactions in shaping plant community dynamics (e.g., Gersani et al. 2001; Ljubotina and Cahill 2019; Cabal et al. 2020; Sauter et al. 2021), community-level processes involving diverse plants and diverse mycorrhizal fungi and consequences for ecosystem functioning remain challenging to experimentally track in the field (e.g., Helgason and Fitter 2009). Instead, TAM-based demography models enable these explorations theoretically and inform empirical investigations.

We anticipate that these empirical and theoretical efforts prompted by TAM would eventually contribute to improving ESMs both directly and indirectly. TAM-based fine-root systems across ecosystems over different temporal scales may be directly incorporated into land models with different vegetation structures, as implied by the example realization in temperate forest systems. However, we would not exclude the possibility that a simplified (relative to TAM) but effective (relative to current homogenization) approach might emerge from TAM to simulate fine-root systems dynamics and functioning in land models. Indirect benefits accompanying TAM and root improvement would also likely follow by helping to identify sources of deficiencies in other components. This indirect avenue is both promising and exciting, considering the historical

dominance of top-down thinking in ESMs development (e.g., Sellers et al. 1986). For instance, one foundational aspect would be to stimulate efforts to improve the scheme of global plant functional type classification by systematically integrating fine-root and fungal traits. These direct and indirect consequences together would improve the prognostic capability of ESMs in simulating biosphere-atmosphere interactions.

7. Conclusions

Accelerated empirical progress over the past two decades has revealed clearly fine-root system complexity. However, a bias against fine-root systems lingers in ecosystem modelling across spatial-temporal scales. Dedicated efforts are warranted to explore ways to embrace fine-root system complexity. In this study, we propose TAM (Transport and Absorptive fine roots with Mycorrhizal fungi) as a structure-based, function-oriented framework to approximate the high-dimensional structural and functional variations within fine-root systems. Originating from a conceptual shift, TAM emerges from theoretical and empirical foundations of balancing fine roots and mycorrhizal fungi and holding high parameterization feasibility as a tradeoff between realism and simplicity. We quantitatively confirm the significance of TAM for simulating temperate forest ecosystem functioning using a big-leaf land surface model. This proof-of-concept work opens the door for exploiting its potential across ecosystems and modelling paradigms in guiding empirical research, understanding ecosystem functioning, and improving prognosis of ESMs. Though uncertainties and challenges remain, our study overall supports TAM as a quantitative keystone of the bridge between empiricists and modelers to embrace fine-root system complexity.

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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.

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Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.7678851. The database FRED is accessible at https://roots.ornl.gov/. These data are outputs from the simulations of the simple_ELM model accessible at https://github.com/dmricciuto/simple_ELM/tree/rootcomplexity. The Jupyter Notebooks analyzing and visualizing (in Python) these outputs are available at https://github.com/bioatmosphere/TAM.

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.

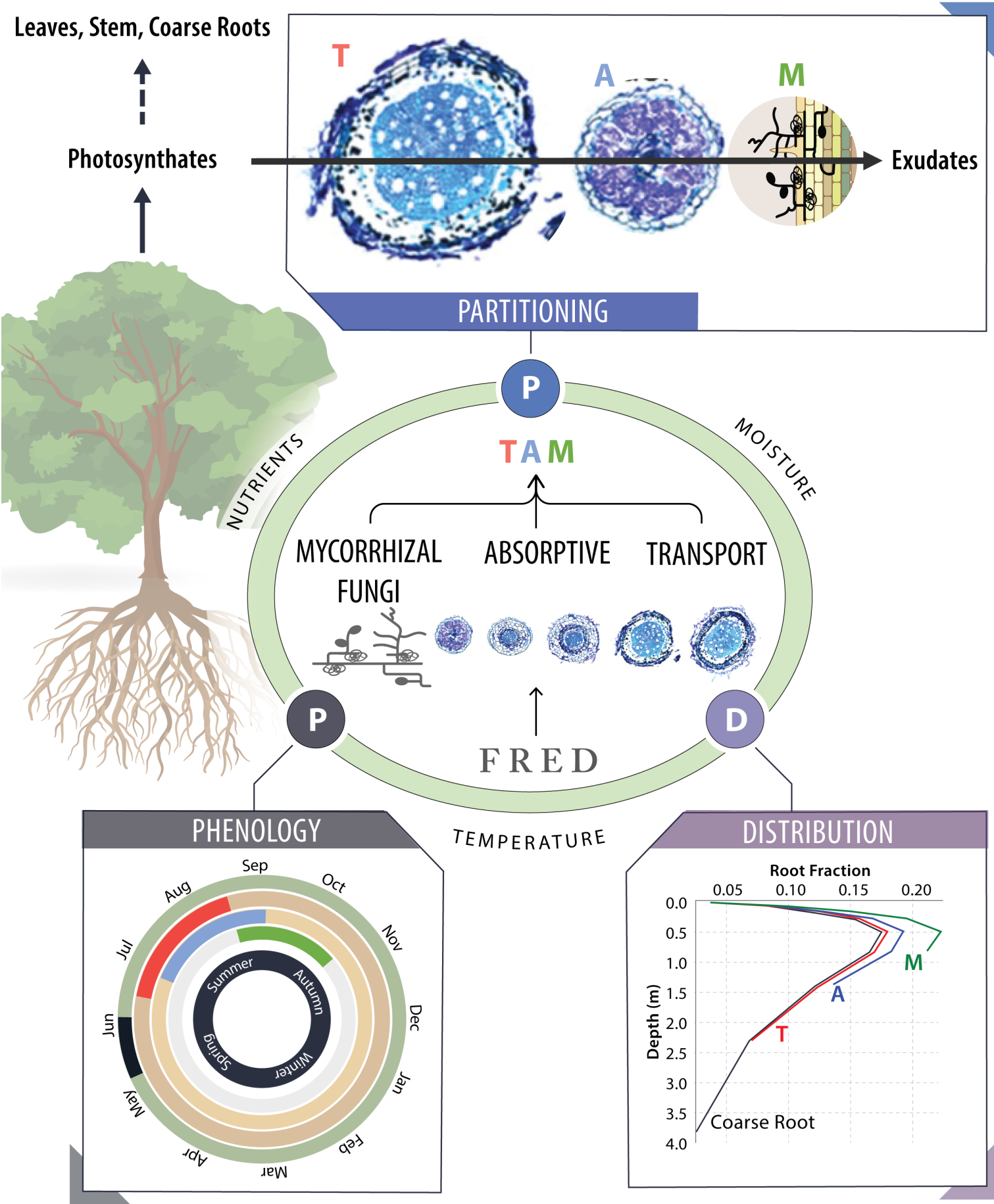| Category	Trait	T	A	M	Database
chemistry	**stoichiometry**				FRED
	chemical composition				FRED
demography	**longevity**				FRED
	phenology				
morphology	diameter				FRED
	tissue density				FRED
	specific root length				FRED
physiology/metabolism	**respiration rate**				FRED
	temperature sensitivity of respiration (Q_{10})				
	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 study, 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). The RSIP (Root Systems of Individual Plants; Tumber-Dávila et al. 2022) database is a primary source for root system size. See Iversen and McCormack (2021) for a synthesis of available databases of fine-root and mycorrhizal fungi traits.

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 (exemplified by FRED). Partitioning of photosynthates to exudates (i.e., loss from the fine-root system) 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 coarse-root distribution) is for an illustrative purpose only; distribution of new carbon is still assumed to be the same across TAM pools though with different turnover rates. The image of cross sections of 5 fine-root orders appears in McCormack et al. 2015a (Image courtesy of Marcin Zadworny, Faculty of Forestry and Wood Technology, Poznan University of Life Sciences).
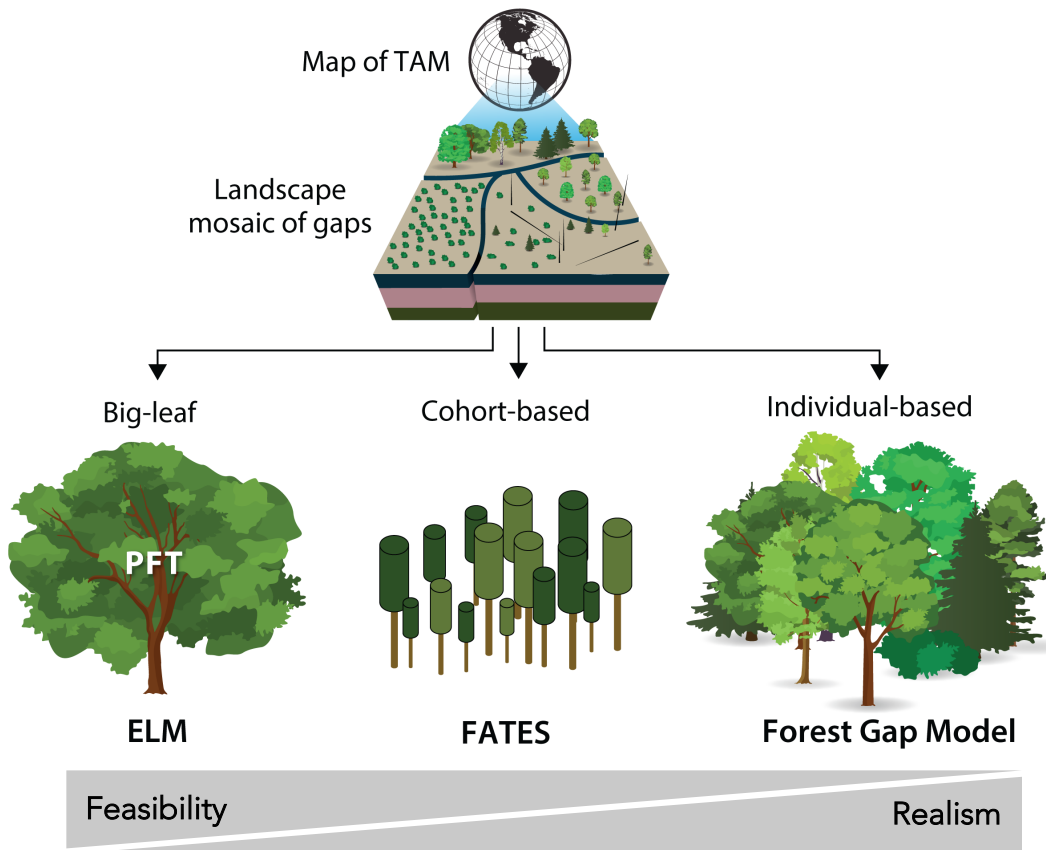
Fig. 2 Realizing TAM with a feasibility-realism tradeoff in terrestrial ecosystem models under three paradigms of vegetation structure. The landscape of vegetation, especially forests, is viewed as a mosaic of gaps (or patches) at different successional stages under exogeneous and endogenous disturbances, 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 from the simplest big-leaf paradigm (e.g., ELM) to the cohort-based paradigm (e.g., FATES: Functionally Assembled Terrestrial Ecosystem Simulator) to the relatively most realistic individual-based paradigm (e.g., forest gap models).

Fig. 3 Conservative TAM impacts against the 1-pool fine-root model on temperate evergreen (a-d) and deciduous forests (e-h). The preservation was differentiated between two partitioning patterns: TAM_descend (increasingly less photosynthates partitioned to mycorrhizal fungi) and TAM_ascend (increasingly more partitioned to the mycorrhizal fungi), on top of which comparisons were made by further adding dynamic distribution (TAM_descend_dd and TAM_ascend_dd). The variance (95% confidence interval) arose from parameterization uncertainty with respect to longevity and chemistry. TAM Biomass: total biomass of transport and absorptive roots and mycorrhizal fungi; Rh: heterotrophic respiration excluding mycorrhizal fungi. See **Fig. S1** in **Supporting Information** for seasonal dynamics of GPP, fine-root system, and leaf biomass.

Fig. 4 Impacts of radical TAM on GPP, R_{ECO} (ecosystem respiration), and C_{ECO} (ecosystem carbon stock) quantified by changes relative to the 1-pool fine-root model. Both GPP and R_{ECO} were based on annual fluxes. Variance (95% confidence intervals) arose from uncertain parameterization (**Table S1**).

Leaves, Stem, Coarse Roots

Photosynthates

PARTITIONING

T   A   M

Exudates

P

T A M

MYCORRHIZAL FUNGI   ABSORPTIVE   TRANSPORT

FRED

P   D

NUTRIENTS

MOISTURE

TEMPERATURE

PHENOLOGY

Sep
Aug   Oct
Jul   Nov
Summer   Autumn
Jun   Dec
Spring   Winter
May   Jan
Apr   Feb
Mar

DISTRIBUTION

Root Fraction
0.05   0.10   0.15   0.20

M
A
T

Coarse Root

Depth (m)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

GCB_16659_Fig1.png

Map of TAM

Landscape
mosaic of gaps

Big-leaf

PFT

ELM

Cohort-based

FATES

Individual-based

Forest Gap Model

Feasibility   Realism

Evergreen

Deciduous

Legend: TAM_descend_dd, TAM_descend, ELM, TAM_ascend, TAM_ascend_dd