

4 **Embracing fine-root system complexity in terrestrial ecosystem modelling**

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15 **1 Realization of TAM**

16 sELM is a simplified version of the Energy Exascale Earth System Model (E3SM) Land
17 Model ELM, a state-of-the-art land surface model developed by Department of Energy, United
18 States (Golaz et al. 2019; Burrows et al. 2020). ELM is traced back to the original CLM4.5 (Oleson
19 et al. 2013) and the later version E3SM Land Model (ELM). sELM simplifies ELM by keeping
20 only essential components simulating natural ecosystems in North America including vegetation
21 and soil biogeochemistry (Lu and Ricciuto 2019). Following the same global PFT classification
22 scheme as ELM, vegetation has the same structural pools (with a single fine-root pool) as ELM
23 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. Changes introduced to realize TAM are described below in detail following the PPD(Partitioning-Phenology-Distribution) framework.

1.1 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:

$$\begin{cases} Callom = (1 + g_1)[1 + a_1 + a_3(1 + a_2)] \\ Nallom = \frac{1}{CN_{leaf}} + a_1 \sum_{i=1}^3 \frac{frootpar_i}{frootcn_i} + \frac{a_3 a_4 (1 + a_2)}{CN_{livewood}} + \frac{a_3 (1 - a_4) (1 + a_2)}{CN_{deadwood}} \end{cases} \quad (1)$$

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 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., $f_{cur} = 1$), 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 GDD_{sum} (growing degree days with a 0-degree base) relative to a threshold value, $GDD_{froot_sum_crit}$:

$$GDD_{froot_sum_crit} = GDD_{leaf_sum_crit} + \Delta GDD_{froot_leaf} \quad (2)$$

where ΔGDD_{leaf_froot} is the difference between leaf and fine root threshold of GDD. Once $GDD_{sum} > GDD_{froot_sum_crit}$, 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 2.4** on TAM mortality.

1.3 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:

$$r_{croot_i} = \begin{cases} 0.5[\exp(-r_a z_{h,i-1}) + \exp(-r_b z_{h,i-1}) - \exp(-r_a z_{h,i}) - \exp(-r_b z_{h,i})], & \text{for } 1 \leq i < N_{levsoi} \\ 0.5[\exp(-r_a z_{h,i-1}) + \exp(-r_b z_{h,i-1})], & \text{for } i = N_{levsoi} \end{cases} \quad (4)$$

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:

$$r_{froot_i} = \frac{r_{croot_ifn_ifm_i}}{\sum_{i=1}^{nlevsoi} r_{croot_ifn_ifm_i}} \quad (5)$$

where fn_i and fm_i are the relative availability of nutrients and the relative availability of water at soil layer i , respectively, which are calculated by dividing nutrient or water availability in each layer by the total amount across the whole soil profile. 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.

1.4 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:

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$$138 \quad \begin{cases} Mr_{i,j} = \frac{1}{froot_long_i} \alpha_j \\ \alpha_j = e^{-\frac{dz_j}{mort_depth_efolding}} \end{cases} \quad (6)$$

139

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

143 Mortality of the T, A, and M pools are parameterized with different but decreasing
 144 lifespans based on relatively easy-to-make observations in shallow soil depths (**Table S1**). This
 145 pattern is based on field observations of a dramatic increase in survivorship with diameter even
 146 within a very narrow range (e.g., ≤ 0.5 mm) (e.g., Reid et al., 1993; Hendrick & Pregitzer 1993;
 147 Tierney & Fahey 2002; Edwards et al. 2004; Joslin et al. 2006; Espeleta et al. 2009; Riley et al.
 148 2009; Xia et al. 2010) and direct observations of lifespan and turnover in fungal tissues (Allen and
 149 Kitajima 2013; McCormack et al. 2010). The depth-correction term (α) further corrects the fine
 150 root and fungi longevity (**froot_long**) for increasing lifespan with soil depth (e.g., Baddeley and
 151 Waston 2005; Iversen et al. 2008; McCormack et al. 2012; Germon et al 2015; Gu et al. 2017).
 152 This depth-based correction partly accounts for the plasticity of fine-root systems in response to
 153 vertical variability in soil resource availability (e.g., Pregitzer et al. 1993; Eissenstat and Yanai,
 154 1997).

155 An explicit turnover of fine-root systems means explicit production of litters from the three
 156 pools. The TAM structure is coupled with existing litter decomposition model simply by
 157 aggregating litters across the 3 pools and depositing them in the three vertically resolved soil litter
 158 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 (**Table S1**). 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.

2 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 (**Table S1**). Simulation at each site was driven by forcings including daily radiation, maximum and minimum temperature, precipitation, day length, and a constant CO₂ level (cycled 6 times).

3 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 conservative 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**):

$$\begin{cases} \sum_{i=1}^3 \frac{frootcn_i}{frootpar_i} = 42 \\ frootcn_t > frootcn_a > frootcn_m \\ frootpar_i = [0.5, 0.3, 0.2] \text{ or } [0.2, 0.3, 0.5] \end{cases} \quad (7)$$

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 radical case with 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*] (**Table S1**). 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 (**Table S2**). 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>).

Table S1. List of introduced parameters and their uncertainty ranges.

Parameter	Description	Unit	Range(evergreen/deciduous)	Reference
<i>frootcn_t</i>	C/N of T root	-	[20,184]/[19, 116]	FRED v3
<i>frootcn_a</i>	C/N of A root	-	[11,119]/[9, 81]	FRED v3
<i>frootcn_m</i>	C/N of M root	-	[7,25]/[7, 25]	Zanne et al. 2019
<i>frootpar_t</i>	Fraction of total allocation to T	-	[0.05, 0.95]	
<i>frootpar_a</i>	Fraction to total allocation to A	-	[0.05, 0.95]	
<i>frootpar_m</i>	Fraction to total allocation to M	-	[0.05, 0.95]	
<i>frootlong_t</i>	Longevity of T	year	[3, 10]	Matamala et al. 2003; Xia et al. 2010
<i>frootlong_a</i>	Longevity of A	year	[0.5, 4]	Matamala et al. 2003; Xia et al. 2010
<i>frootlong_m</i>	Longevity of M	year	[0.13, 1]	Pepe et al. 2018
<i>fr_flab_t</i>	Fraction of labile carbon in T	-	[0.125, 0.375]	± 50% of default value
<i>fr_flab_a</i>	Fraction of labile carbon in A	-	[0.125, 0.375]	± 50% of default value
<i>fr_flab_m</i>	Fraction of labile carbon in M	-	[0.125, 0.375]	± 50% of default value
<i>fr_flg_t</i>	Fraction of lignin carbon in T	-	[0.125, 0.375]	± 50% of default value
<i>fr_flg_a</i>	Fraction of lignin carbon in A	-	[0.125, 0.375]	± 50% of default value
<i>fr_flg_m</i>	Fraction of lignin carbon in M	-	[0.125, 0.375]	± 50% of default value
<i>fr_fcel_t</i>	Fraction of cellulose/hemicellulose C in T	-	[0.25, 0.75]	± 50% of default value
<i>fr_fcel_a</i>	Fraction of cellulose/hemicellulose C in A	-	[0.25, 0.75]	± 50% of default value
<i>fr_fcel_m</i>	Fraction of cellulose/hemicellulose C in M	-	[0.25, 0.75]	± 50% of default value
<i>mort_depth_efolding</i>	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
<i>gdd_crit_gap</i>	Difference in GDD between root and leaf onset	°C *day	[-300, 300]	Expert judgement

Table S2. List of existing parameters of interest in ELM and their uncertainty ranges.

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

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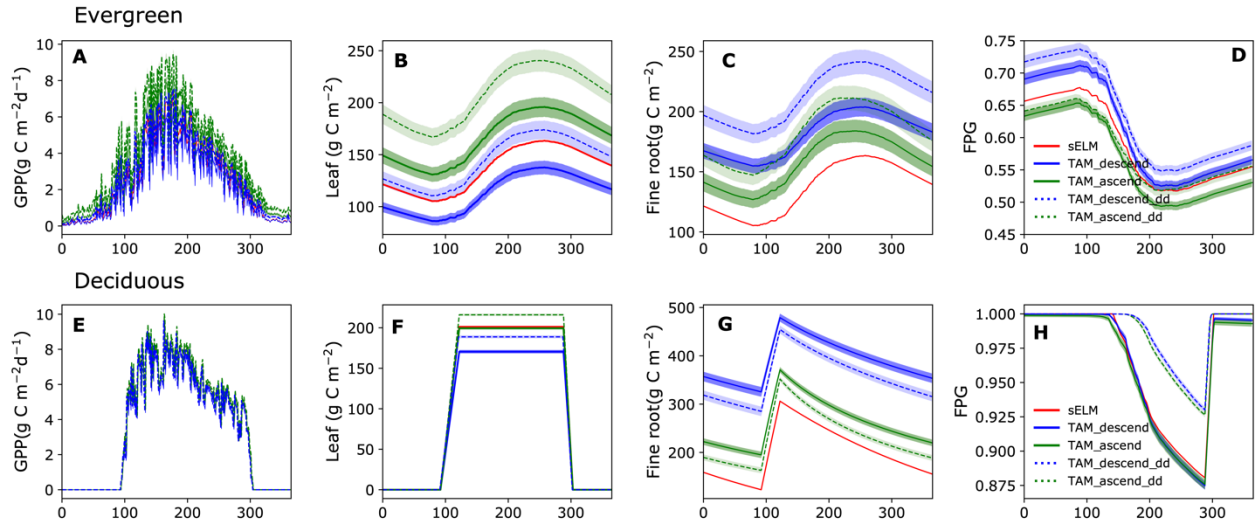


Fig. S1 Annual cycle of GPP, leaf mass, and fine-root system mass, as well as FPG (Fraction of Potential Growth) of TAM against the 1-pool structure of ELM (i.e., sELM) under preservation of fine-root system stoichiometry.

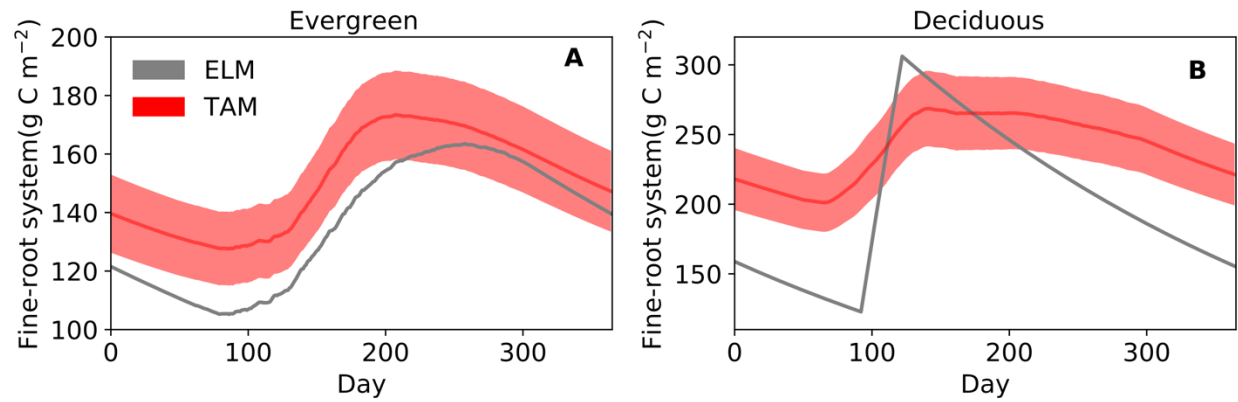


Fig. S2 Seasonal variation in fine-root system biomass of radical TAM corresponding to Fig.4 in the main text.

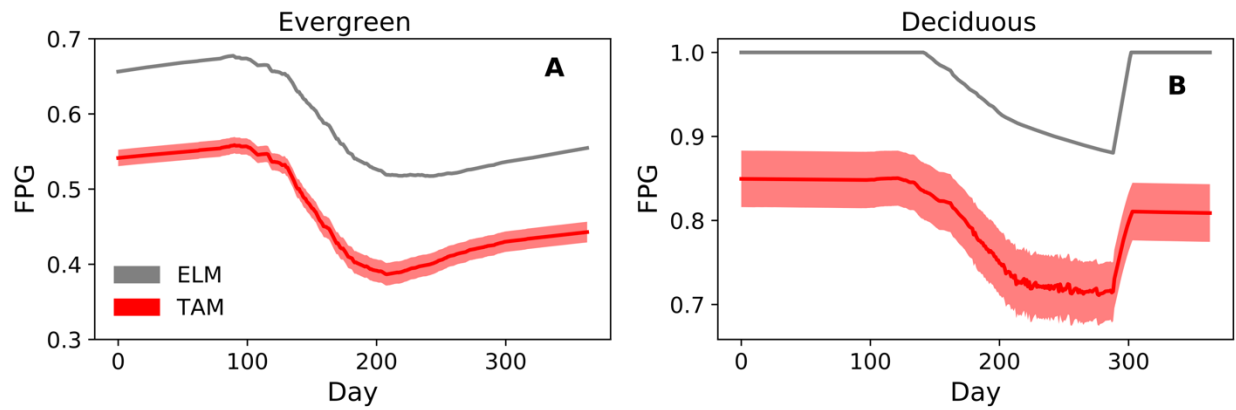


Fig. S3 Seasonal variation in FPG (Fraction of Potential Growth) under a full implementation of TAM corresponding to Fig.4 in the main text.

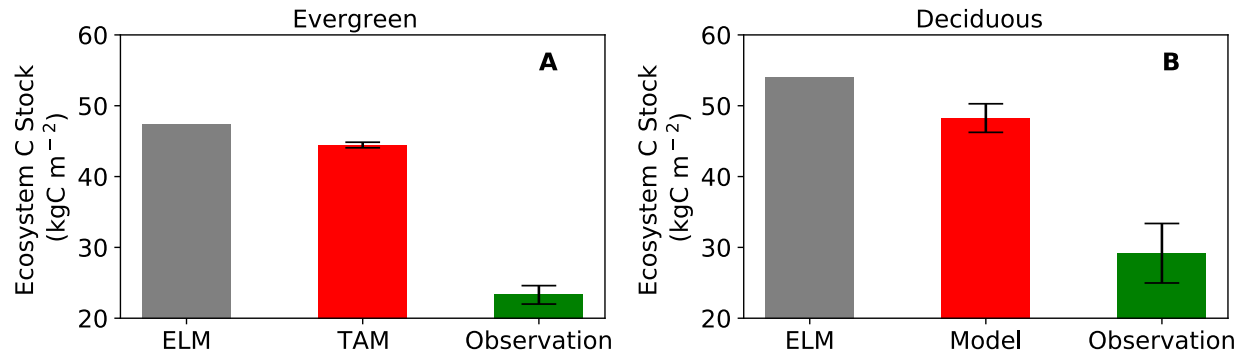


Fig. S4 Radical TAM brings simulated total ecosystem carbon stocks closer to observations.

Observation in the evergreen forest is based on Hollinger et al. (2021), while the observation in the deciduous forest per Chen et al. (2015). Error bars represent 95% confidence intervals.

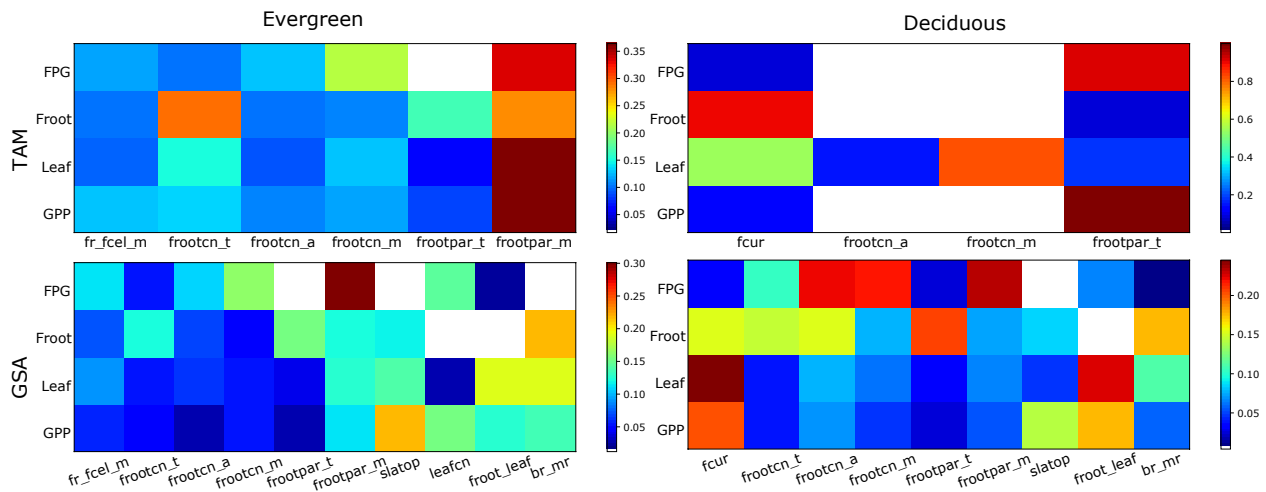


Fig. S5 Attribution of TAM and global uncertainty with the main effect sensitivity index for the two sites. The TAM sensitivity corresponds to the conservative case of **Fig. 3** in the main text. The Global Sensitivity Analysis (GSA) also includes some of existing parameters (**Table S2**). Only the 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.

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