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Competition alters predicted forest carbon cycle responses to nitrogen availability and elevated CO_2: simulations using an explicitly competitive, game-theoretic vegetation demographic model

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Abstract: Competition is a major driver of carbon allocation to different plant tissues (e.g. wood, leaves, fine roots), and allocation, in turn, shapes vegetation structure. To improve their modeling of the terrestrial carbon cycle, many Earth system models now incorporate vegetation demographic models (VDMs) that explicitly simulate the processes of individual-based competition for light and soil resources. Here, in order to understand how these competition processes affect predictions of the terrestrial carbon cycle, we simulate forest responses to elevated CO_2 along a nitrogen availability gradient using a VDM that allows us to compare fixed allocation strategies versus competitively-optimal allocation strategies. Our results show that competitive- and fixed-allocation strategies predict opposite fractional allocation to fine roots and wood, though they predict similar changes in total NPP along the nitrogen gradient. The competitively-optimal allocation strategy predicts decreasing fine root and increasing wood allocation with increasing nitrogen, whereas the fixed allocation strategy predicts the opposite. Although simulated plant biomass at equilibrium increases with nitrogen due to increases in photosynthesis for both allocation strategies, the increase in biomass with nitrogen is much steeper for competitively-optimal allocation due to its increased allocation to wood. The qualitatively opposite fractional allocation to fine roots and wood of the two strategies also impacts the effects of elevated [CO_2] on plant biomass. Whereas the fixed allocation strategy predicts an increase in plant biomass under elevated [CO_2] that is approximately independent of nitrogen availability, competition's effect on wood allocation amplifies plant biomass under elevated [CO_2] with increasing nitrogen availability. Our results indicate that the VDMs that explicitly include the effects of competition for light and soil resources on plant strategies may generate significantly different ecosystem-level predictions than those that use fixed allocation strategies.

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1 Introduction

Allocation of assimilated carbon to different plant tissues is a fundamental aspect of plant growth and profoundly affects terrestrial ecosystem biogeochemical cycles (Cannell and Dewar, 1994; Lacointe, 2000). Ecologically, allocation represents an evolutionarily-honed "strategy" of plants that use limited resources and compete with other individuals and consequently drives successional dynamics and vegetation structure (De Kauwe et al., 2014; DeAngelis et al., 2012; Haverd et al., 2016; Tilman, 1988). Biogeochemically, allocation links plant physiological processes, such as photosynthesis and respiration, to biogeochemical cycles and carbon storage of ecosystems (Bloom et al., 2016; De Kauwe et al., 2014). Thus, correctly modeling allocation patterns is critical for correctly predicting terrestrial carbon cycles and Earth system dynamics.

In current Earth System Models (ESMs), the terrestrial carbon cycle is usually simulated by pool-based compartment models that simulate ecosystem carbon and/or nitrogen cycles as lumped pools and fluxes of plant tissues and soil organic matter (Emanuel and Killough, 1984; Eriksson, 1971; Parton et al., 1987; Randerson et al., 1997; Sitch et al., 2003). In these models, the dynamics of carbon can be described by a linear system of equations (Koven et al., 2015; Luo et al., 2001; Luo and Weng, 2011; Sierra and Mueller, 2015; Xia et al., 2013):

$$\frac{dX}{dt} = AX + BU \qquad \text{(Eq. 1)}$$

where X is a vector of ecosystem carbon pools, U is carbon input (i.e., Gross Primary Production, GPP), B is the vector of allocation parameters to autotrophic respiration and plant carbon pools (e.g., leaves, stems, and fine roots), and A is a matrix of carbon transfer and turnover. In this system, carbon dynamics are defined by carbon input (U), allocation (B), and residence time and transfer coefficients (A). The allocation schemes (B) are thus embedded in a linear system, or

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quasi-linear system if the allocation parameters in B are a function of carbon input (U) or plant carbon pools (X).

The modeling of allocation in this system (i.e., the parameters in vector B) is usually based on plant allometry, biomass partitioning, and resource limitation (De Kauwe et al., 2014; Montané et al., 2017). The allocation parameters are either fixed ratios to leaves, stems, and roots, which may vary among plant functional types (e.g., CENTURY, Parton et al., 1987; TEM, Raich et al., 1991; CASA, Randerson et al., 1997) or are responsive to climate and soil conditions as a way to phenomenologically mimic the shifts in allocation that are empirically observed or hypothesized (e.g., CTEM, Arora and Boer, 2005; ORCHIDEE, Krinner et al., 2005; LPJ, Sitch et al., 2003). These modeling approaches either assume that vegetation is equilibrated (fixed ratios) or average the responses of plant types to changes in environmental conditions as a collective behavior. Thus, the carbon dynamics in these models can be constrained by selecting appropriate parameters of allocation, turnover rates, and transfer coefficients to fit the observations (Friend et al., 2007; Hoffman et al., 2017; Keenan et al., 2013).

To predict transient changes in vegetation structure and composition in response to climate change, vegetation demographic models (VDMs) that are able to simulate transient population dynamics are incorporated into ESMs (Fisher et al., 2018; Scheiter and Higgins, 2009). Generally, these VDMs explicitly simulate plant reproduction, growth, and mortality to generate the dynamics of populations. To speed computations and minimize complexity, groups of individuals are usually modeled as cohorts. These models may also simulate the competition between individuals for light and soil resources to drive vegetation succession and thus changes in the combinations of plant traits that represent competition strategies at different stages (Scheiter et al., 2013; Scheiter and Higgins, 2009; Weng et al., 2015). Competitively-optimal

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allocation strategies can therefore be reasonably predicted based on the costs and benefits of allocation strategies through their effects on demographic processes (i.e., fitness) and ecosystem biogeochemical cycles (Farrior et al., 2015; Weng et al., 2015).

The processes of VDMs (e.g., demographic processes, individual-based competition for different resources, and community assembly) can be used to bring plant functional diversity and adaptive dynamics into ESMs, causing dominant plant traits to change in response to plant competition, environmental conditions, and ecosystem development. The dynamic response of plant traits can substantially change predictions of ecosystem biogeochemical dynamics of current ESMs since it changes the key parameters of vegetation physiological processes and soil organic matter decomposition (e.g., Dybzinski et al., 2015; Farrior et al., 2015; Weng et al., 2017). Using the methodology of adaptive dynamics, the dynamics of plant trait(s) in succession can be described by a canonical equation in a simple and continuous case (Dieckmann et al., 2007):

$$\frac{ds}{dt} = \frac{1}{2}\mu(s)\sigma^2(s)N(s)\frac{\partial W(s',s)}{\partial s'} \qquad \text{(Eq. 2)}$$

where, μ is the mutation rate, σ^2 is the variance of mutation distribution, N is the population size at equilibrium, and $\frac{\partial W(s',s)}{\partial s'}$ is the selection gradient. $W(s', s)$ is the fitness function, measured as the fitness of a rare individual with trait value s' (*i.e.*, a "mutant," "novel colonist," "invader," or "challenger") in an environment created by a population of individuals with trait value s (the "resident").

With such a model, the carbon dynamics of an ecosystem are the emergent result of competition among different strategies as represented by plant traits, and the most competitive strategies may shift with community composition during succession. The key parameters that are used to estimate carbon dynamics in the linear system model (Eq. 1), such as allocation (B) and

residence times in different carbon pools (matrix A, which includes coefficients of carbon transfer and turnover time) become functions of competition strategies that vary with environment and carbon input. In addition, the turnover of vegetation carbon pools becomes a function of allocation and mortality rates, which change with vegetation succession and the most competitive plant traits. These changes make the system nonlinear and can lead to large biases within the framework of the compartmental pool-based models as represented by Eq. (1) (Sierra et al., 2017; Sierra and Mueller, 2015). Because of the high complexity associated with demographic and competition processes, the model predictions are usually sensitive to the parameters in these processes and are of high uncertainty (e.g., Pappas et al., 2016).

In contrast to their implementation in the more complicated VDMs discussed above, models of competitively-dominant plant strategies using much simpler model structures and assumptions can sometimes be solved analytically (Dybzinski et al., 2011, 2015; Farrior et al., 2013, 2015). Although simplified, such models can pin-point the key processes that improve the predictive power of simulation models (Dybzinski et al., 2011; Farrior et al., 2013, 2015), allowing them to help researchers formulate model processes and understand the simulated ecosystem dynamics in ESMs. For example, the analytical model derived by Farrior et al. (2013) that links interactions between ecosystem carbon storage, allocation, and water stress at elevated CO_2 sheds light on the otherwise inscrutable processes leading to varied soil water dynamics in a land model coupled with an VDM (Weng et al., 2015). Recognizing the benefit, Weng et al. (2017) included both a simplified analytical model and a more complicated VDM to understand competitively optimal leaf mass per area, competition between evergreen and deciduous plant functional types, and the resulting successional patterns.

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In this study, we use a stand-alone simulator derived from the LM3-PPA model (Weng et al., 2017, 2015) to show how forests respond to elevated CO_2 and nitrogen availability via different competitively-optimal allocation strategies. The model is an individual-based vegetation demographic model, whose vegetation demographic scheme has been coupled into the land model of the Geophysical Fluid Dynamical Laboratory's Earth System Model (Shevliakova et al., 2009; Weng et al., 2015) and NASA Goddard Institute for Space Study's Earth system model, ModelE (Schmidt et al., 2014). Using this model, we simulate the shifts in competitively optimal allocation strategies in response to elevated CO_2 at different nitrogen levels based on insights from the analytical model derived by Dybzinski et al. (2015). Dybzinski et al.'s (2015) model predicts that increases in carbon storage at elevated CO_2 relative to storage at ambient CO_2 are largely independent of total nitrogen because of an increasing shift in carbon allocation from long-lived, low-nitrogen wood to short-lived, high-nitrogen fine roots under elevated CO_2 with increasing nitrogen availability. Here, we analyze the simulated ecosystem carbon cycle variables (gross and net primary production, allocation, and biomass) of separate fixed-allocation and competitively-optimal allocation model runs. In the fixed-allocation runs, ecosystem properties are the result of the prescribed allocation strategies of a given PFT, analogous to the fixed allocation schemes of most VDMs (see above). In the competitively-optimal allocation runs, competition between the different allocation strategies results in succession and the eventual dominance of the most competitive allocation strategy for a given nitrogen availability and CO_2 level. Since everything else in the model is identical, we are able to compare the predictions of fixed-allocation strategies with competitively-optimal allocation strategies by comparing the ecosystem properties of these two types of runs.

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2 Methods and Materials

2.1 BiomeE Model

We used a stand-alone ecosystem simulator (Biome Ecological strategy simulator, BiomeE) to conduct simulation experiments. BiomeE is derived from the version of LM3-PPA used in Weng *et al*. (2017). We simplified the processes of energy transfer and soil water dynamics of LM3-PPA (Weng et al., 2015) but still retained the key features of plant physiology and individual-based competition for light, soil water, and, via the decomposition of soil organic matter, nitrogen (Fig. 1). In this model, individual trees are represented as sets of *cohorts* of similar size trees and are arranged in different vertical canopy layers according to their height and crown area following the rules of the Perfect Plasticity Approximation (PPA) model (Strigul et al., 2008). Sunlight is partitioned into these canopy layers according to Beer's law. Thus, a key parameter for light competition, critical height, is defined; all the trees above this context-dependent height get full sunlight and all trees below this height are shaded by the upper layer trees. Plant growth, reproduction, and mortality are driven by the carbon assimilation of leaves, which is in turn dependent on water and nitrogen uptake by fine roots.

Each tree consists of seven pools: leaves, fine roots, sapwood, heartwood, fecundity (seeds), and non-structural carbohydrates and nitrogen (NSC and NSN, respectively) (Fig. 1: b). The carbon and nitrogen in plant pools enter the soil pools with the mortality of individual trees and the turnover of leaves and fine roots. There are three soil organic matter (SOM) pools for carbon and nitrogen: fast-turnover, slow-turnover, and microbial pools, along with a mineral nitrogen pool for mineralized nitrogen in soil. The simulation of SOM decomposition and nitrogen mineralization is based on the models of Gerber *et al*. (2010) and Manzoni *et al*. (2010) and described in detail in Weng et al. (2017). The decomposition rate of a SOM pool is

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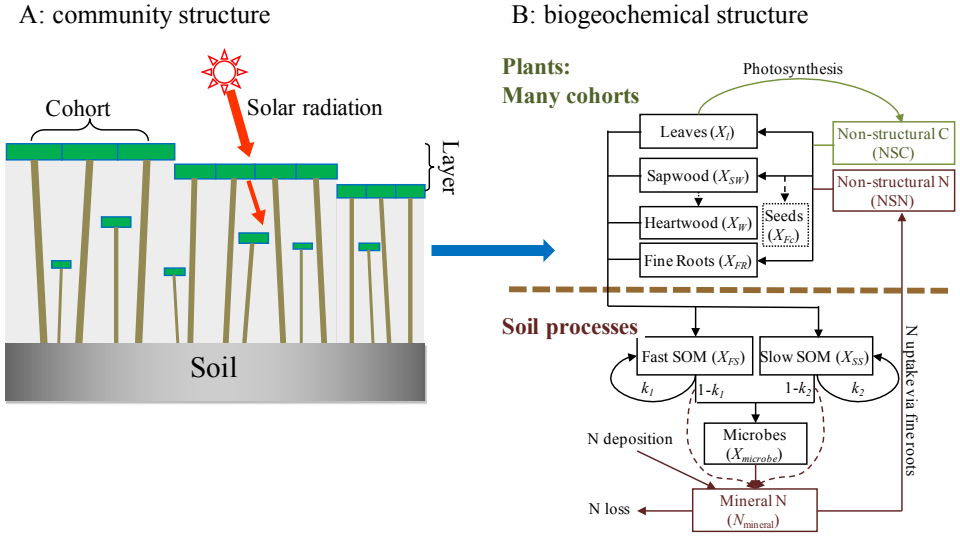
176 determined by the basal turnover rate together with soil temperature and moisture. The nitrogen
177 mineralization rate is a function of decomposition rate and the C:N ratio of the SOM. Microbes
178 must consume more carbon in the high C:N ratio SOM pool to get enough nitrogen and must
179 release excessive nitrogen in the low C:N ratio SOM pool to get enough carbon for energy
180 (Weng *et al*. 2017).
181



182

183 **Figure 1. Model structure of BiomeE**

184 Panel A: vegetation structure: trees organize their crowns into canopy layers according to both
185 their height and their crown area following the rules of the PPA model, which mechanistically
186 models light competition. Panel B: Biogeochemical structure and compartmental pools. The
187 green, brown, and black lines are the flows of carbon, nitrogen, and coupled carbon and nitrogen,
188 respectively. The green box is for carbon only. The brown boxes are N pools. The black boxes
189 are for both carbon and nitrogen pools, where *X* can be C (carbon) and N (nitrogen). The C:N
190 ratios of leaves, fine roots, seeds, and microbes are fixed. The C:N ratios of woody tissues, fast
191 soil organic matter (SOM), and slow SOM are flexible. Only one tree's C and N pools are shown
192 in this figure. The model can have multiple cohorts of trees, which share the same pool structure.
193 The dashed line separates the plant and soil processes.

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195 **Nitrogen uptake** The rate of nitrogen uptake (U, g N m^{-2} hour^{-1}) from the soil mineral
196 nitrogen pool is an asymptotically increasing function of fine root biomass density ($Root_{\text{total}}$, kgC
197 m^{-2}), following McMurtrie *et al.* (2012)

$$U = f_{\text{U,max}} \cdot N_{\text{mineral}} \cdot \frac{Root_{\text{total}}}{Root_{\text{total}} + Root_0}, \quad \text{(Eq. 3)}$$

198 where, N_{mineral} is the mineral N in soil (g N m^{-2}), $f_{\text{U,max}}$ is the maximum rate of nitrogen
199 absorption per hour when $Root_{\text{total}}$ approaches infinity, $Root_0$ is a constant of root biomass (kg C
200 m^{-2}) at which the nitrogen uptake rate is half of the parameter $f_{\text{U,max}}$. The nitrogen uptake rate
201 of an individual tree (U_{tree}, g N hour^{-1} tree^{-1}) is calculated as follows:

$$U_{\text{tree}} = U \cdot \frac{Root_{\text{tree}}}{Root_{\text{total}}}, \quad \text{(Eq. 4)}$$

202 where, $Root_{\text{tree}}$ is the fine root biomass of a tree (kg C tree^2). The N absorbed by roots enters into
203 the NSN pool and then is allocated to plant tissues through plant growth following carbon flows.
204 **Allocation** Carbon assimilated by leaves via photosynthesis enters into the NSC pool first
205 and is subsequently used for respiration, growth, and reproduction. The partitioning of carbon
206 and nitrogen into the plant pools (*i.e.*, leaves, fine roots, and sapwood) is limited by a set of
207 allometric equations and the C:N ratios of these pools. Empirical allometric equations relate
208 woody biomass (including coarse roots, bole, and branches), crown area, and stem diameter. The
209 individual-level dimensions of a tree, *i.e.*, height (Z), biomass (S), and crown area (A_{CR}) are
210 given by empirical allometries (Dybzinski et al., 2011; Farrior et al., 2013):

$$\begin{aligned} Z(D) &= \alpha_Z D^{\theta_Z} \\ S(D) &= 0.25\pi\Lambda\rho_W\alpha_Z D^{2+\theta_Z} \\ A_{CR}(D) &= \alpha_c D^{\theta_c} \end{aligned} \quad \text{(Eq. 5)}$$

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where Z is tree height, S is total woody biomass carbon (including bole, coarse roots, and branches) of a tree, α_c and α_Z are PFT-specific constants, θ_c=1.5 and θ_Z=0.5 (Farrior et al., 2013) (although they could be made PFT-specific if necessary), π is the circular constant, Λ is a PFT-specific taper constant, and ρ_W is PFT-specific wood density (kg C m^{-3}) .

We set *targets* for leaf, fine root, and sapwood cross-sectional area that govern plant allocation of non-structural carbon and nitrogen during growth. These *targets* are related by the following equations based on the assumption of the pipe model (Shinozaki, Kichiro et al., 1964):

$$L_k^*(D,p) = l_k^* \cdot A_{CR}(D) \cdot LMA \cdot p(t)$$
$$FR_k^*(D) = \varphi_{RL} \cdot l_k^* \cdot \frac{A_{CR}(D)}{SRA} \quad \text{(Eq. 6)}$$
$$A_{SW,k}^*(D) = \alpha_{CSA} \cdot l_k^* \cdot A_{CR}(D)$$

where $L_k^*(D, p)$ is the target leaf mass of canopy-level k at given stem diameter (D), l_k^* is the target leaf area per unit crown area of a given PFT at canopy-level k, A_{CR}(D) is the crown area of a tree with diameter D, LMA is PFT-specific leaf mass per unit area, and p(t) is a PFT-specific function ranging from zero to one that governs leaf phenology (Weng et al., 2015). Note, here φ_{RL} is fixed for each PFT and will remain so for the fixed allocation strategies and the competitive allocation strategies. The process of choosing a context-dependent competitive dominant φ_{RL} will take place after finding the fitness of each φ_{RL} in monoculture and in competition with other PFTs (*i.e.*, different values of φ_{RL}). The phenology function p(t) takes values 0 (non-growing season) or 1 (growing season) following the phenology model of LM3-PPA (Weng et al., 2015). The onset of a growing season is controlled by two variables, growing degree days (GDD), and a weighted mean daily temperature (T_{pheno}), while the end of a growing season is controlled by T_{pheno}. $FR_k^*(D)$ is the target fine root biomass at tree diameter D and canopy-level k, φ_{RL} is the target ratio of total root surface area to the total leaf area, SRA is

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specific root area, $A^*_{SW,k}(D)$ is the target cross sectional area of sapwood at canopy-level k, and α_{CSA} is an empirical constant (the ratio of sapwood cross-sectional area to target leaf area).

In the model simulation, plant growth is updated at a daily time step. For each simulated day, the model calculates the amount of carbon and nitrogen that are available for growth (i.e., building new tissues) according to the total NSC and NSN and current leaf and fine root biomass. Basically, the available NSC (NSC_g) is the summation of a small fraction of the total NSC in an individual plant and the differences between the targets of leaf and fine roots and their current biomass capped by a larger fraction of NSC (Eq. 7).

$$NSC_g = min\left(f_1 NSC, f_2 NSC + L^* + FR^* - L - FR\right), \quad \text{(Eq. 7)}$$

where L^* and FR^* are the targets of leaves and fine roots, respectively, and functions of plant size (see Eq. 6); L and FR are current leaf and fine roots biomass. The parameters f_1 and f_2 give the daily availability of NSC during periods of leaf flush at the beginning of a growing season and normal growth after plant leaves and fine roots approach their targets. Usually, parameter f_1 is much greater than f_2. We let f_1=0.05 and f_2= 1/(365x3) in this study. The equation for available NSN is analogous.

The allocation of the available NSC and NSN to wood, leaves, fine roots, and seeds is calculated in four steps. 1) First, the model allocates a small fraction of the available NSC (0.15 in this study) for sapwood growth. 2) Then it allocates to leaves and fine roots by tracking PFT-specific targets for leaf area per unit crown area (l^*) and the ratio of fine root area per to leaf area (φ_{RL}). As long as there are sufficient available NSC and NSN, plants allocate them to new leaves and fine roots to close the gap between their current and target areas. 3) If there are extra available NSC and NSN left after the leaves and fine roots reached their targets, they will be

allocated to sapwood and seeds. Since the C:N ratios of leaves, fine roots, and seeds are fixed in this model, the nitrogen used to construct these tissues is simply the carbon allocated from NSC to them divided by their leaf C:N ratio, respectively. 4) When the available NSN cannot meet the demand, the excess carbon is re-allocated to sapwood because sapwood requires less nitrogen than those of leaves, fine roots, and seeds at the same supply of carbon.

Based on these allocation rules, the mean of allocations of carbon and nitrogen to leaves, fine roots, and wood over a growing season are governed by the targets for the leaf area per unit crown area (i.e., crown leaf area index, l^*) and fine root area per unit leaf area (φ_{RL}). Since the crown leaf area index, l^*, is fixed in this study, φ_{RL} is the key parameter determining the relative allocation of carbon to fine roots and stems. A high φ_{RL} means a high relative allocation to fine roots and therefore low relative allocation to stems, and *vice versa*.

2.2 Site and Data

Data pertaining to vegetation, climate, and soil at Harvard Forest (Aber et al., 1993; Hibbs, 1983; Urbanski et al., 2007) were used to design the plant functional types (PFTs) and ecosystem nitrogen levels used in the simulation experiments, to drive the model, and to calibrate model parameters. Harvard Forest is located in Massachusetts, USA (42.54°, -72.17°). The climate of Harvard Forest is cool temperate with annual precipitation 1050 mm, distributed fairly evenly throughout the year. The annual mean temperature is 8.5 °C with a high monthly mean temperature of 20°C in July and a low of -7°C in January. The soils are mainly sandy loam with average depth around 1 m and are moderately well drained in most areas. The vegetation is deciduous broadleaf/mixed forest with major species red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta*), white pine (*Pinus strobus*), and hemlock (*Tsuga canadensis*) (Compton and Boone, 2000; Savage et al., 2013). The data used to drive our model runs are gap-

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filled hourly meteorological data at Harvard Forest from 1991 to 2006, obtained from North American Carbon Program (NACP) Site-Level Synthesis datasets (Barr et al., 2013).

2.3 Simulation experiments

We set two atmospheric CO_2 concentration ($[CO_2]$) levels: 380 ppm and 580 ppm, and eight ecosystem total nitrogen levels (ranging from 114.5 gN m^{-2} to 552 gN m^{-2} at the interval of 62.5 gN m^{-2}) for our simulation experiments (Table 1). In all the simulation experiments, we assume there are no nitrogen inputs or outputs to the system. The nitrogen cycles through the plant and soil pools and is redistributed among them via plant demographic processes, soil carbon transfers, and plant uptake. The PFTs were based on a PFT of an evergreen needle-leaved tree with different leaf to fine root area ratios, φ_{RL}, in the range from 1 to 8 (Table 1). Simply stated, the PFTs we investigate only differ in parameter φ_{RL}.

We define the model runs initialized with only one fixed-φ_{RL} PFT as "fixed-allocation runs" although the actual allocation of carbon to different plant tissues varies with $[CO_2]$ concentration and ecosystem nitrogen availability. We define the model runs initialized with multiple PFTs as "competition runs" (eight PFTs with different φ_{RL} at the beginning, although many are driven to extinction during a given model run). We conducted one set of fixed-allocation runs and two sets of competition runs (Table 1).

In the fixed-allocation runs, we run the full factorial combinations of the eight PFTs with root/leaf area ratios (φ_{RL}) from 1 to 8 and the eight ecosystem total nitrogen levels (Table 1), but only those with φ_{RL} <=6 survived at ambient CO_2 (380 ppm) because the carbon consumed by fine roots exceeded what leaves provided at high φ_{RL}. The fixed allocation runs are for exploring the model predictions of gross primary production (GPP), net primary production (NPP),

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allocation, and biomass at equilibrium with fixed root/leaf area ratios (φ_{RL}) and ecosystem total nitrogen levels, analogous to the fixed allocation schemes used in many VDMs.

Table 1 Simulation experiments

Type	Model runs	Initial PFT(s) φ_{RL}	Ecosystem total nitrogen levels	CO_2 concentration [CO_2]
Fixed-allocation runs	One model run per combination of PFT (φ_{RL}), nitrogen level, and CO_2 concentration	One of the following PFTs: φ_{RL}= 1, 2, 3, 4, 5, 6, 7, or 8	Eight levels ranging from 114.5 g N m^{-2} to 552 g N m^{-2} at the interval of 62.5 g N m^{-2}: 114.5 g N m^{-2}, 177 g N m^{-2}, 239.5 g N m^{-2}, 302 g N m^{-2}, 364.5 g N m^{-2}, 427 g N m^{-2}, 489.5 g N m^{-2}, 552 g N m^{-2}	Ambient: 380 ppm Elevated: 580 ppm
Competition runs I	One model run per combination of nitrogen level and CO_2 concentration	All the PFTs (φ_{RL}= 1~ 8) used in the fixed-allocation runs		
Competition runs II	One model run per combination of nitrogen level and CO_2 concentration	Eight PFTs with φ_{RL} ranging from 4.5-0.5*i* to 8.5-0.5*i* at the interval of 0.5, where *i* denotes the eight nitrogen levels from 114.5 to 552 gN m^{-2}.		

In competition runs I, we used the same PFTs as in the fixed-allocation runs, where their φ_{RL} varies from 1 to 8 at the interval of 1.0 and the ecosystem total nitrogen levels are the same as those used in the fixed-allocation runs (Table 1). This set of competition runs was used to explore successional patterns at both ambient and elevated CO_2 concentrations (380 ppm and 580 ppm, respectively). However, this set of model runs could not show the details of equilibrium plant biomass and allocation patterns along the nitrogen gradient because of the large intervals between the φ_{RL} values.

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309 To achieve greater resolution in our competition predictions, we designed the competition
310 runs II using a dynamic PFT combination scheme according to the ranges of φ_{RL} obtained from
311 the competition runs I that could survive at a particular nitrogen level at both CO_2
312 concentrations. For each nitrogen level, we set eight PFTs with φ_{RL} that varied in a range 3.5
313 (e.g., $x \sim x+3.5$) at the interval of 0.5, starting with the highest φ_{RL} of 8.0 at the lowest N level
314 (114.5 gN m^{-2}) and decreasing 0.5 per level of increase in ecosystem total N. Let i=1, 2, …, 8
315 denote the eight N levels from 114.5 to 552 gN m^{-2}, the φ_{RL} of the eight PFTs at each level are
316 (5.0-0.5i, 5.5-0.5i, …, 8.5-0.5i) (Table 1). For example, at the nitrogen of 114.5 gN m^{-2} (i = 1),
317 the φ_{RL} of the eight PFTs are 4.5, 5.0, …, 8.0 and at 177 gN m^{-2} (i = 2), they are 4.0, 4.5, …, 7.5.
318 For both fixed-allocation and competition runs, visual inspection indicated that stands had
319 reached equilibrium after ~1200 years. To be conservative, we present equilibrium data by
320 averaging model properties between years 1400 and 1800. We compared simulated equilibrium
321 gross primary production (GPP), net primary production (NPP), allocation (both absolute amount
322 of carbon and fractions of the total NPP), and plant biomass of the competition runs II with those
323 from the fixed-allocation runs. We used the results from one PFT (φ_{RL}=4) to highlight the
324 differences of plant responses with competitively optimal allocation strategies. The complete
325 results from the fixed-allocation runs are shown in the Figures S1 and S2 in supplementary
326 materials.

327 **3 Results**

328 In the competition runs, the equilibrium GPP and NPP increase with total nitrogen at values
329 similar to those of the fixed-allocation runs (Fig. 2: a and b). However, the CO_2 stimulation of
330 NPP increases with total nitrogen in competition runs more than it in the fixed-allocation runs.
331 Elevated [CO_2] increases carbon use efficiency (defined as the ratio of NPP to GPP in this study,

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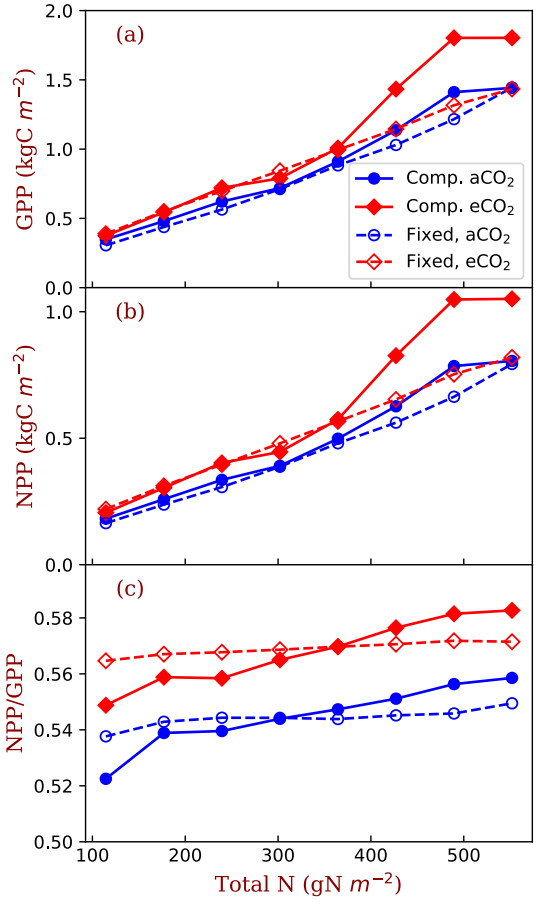
332 NPP/GPP) in both the fixed-allocation and competition runs (Fig. 2: c). Also, the dependence of
333 NPP/GPP on nitrogen is higher in the competition runs than it in the fixed-allocation runs.

334



335

336 **Figure 2 Equilibrium Gross Primary Production (GPP, a), Net Primary Production (NPP,**
337 **b), and Carbon Use Efficiency (NPP/GPP, c).** The closed symbols with solid line represent
338 competition runs (comp.). The open symbols with dashed lines represent fixed-allocation runs
339 (only φ_{RL} =4 shown in this figure).

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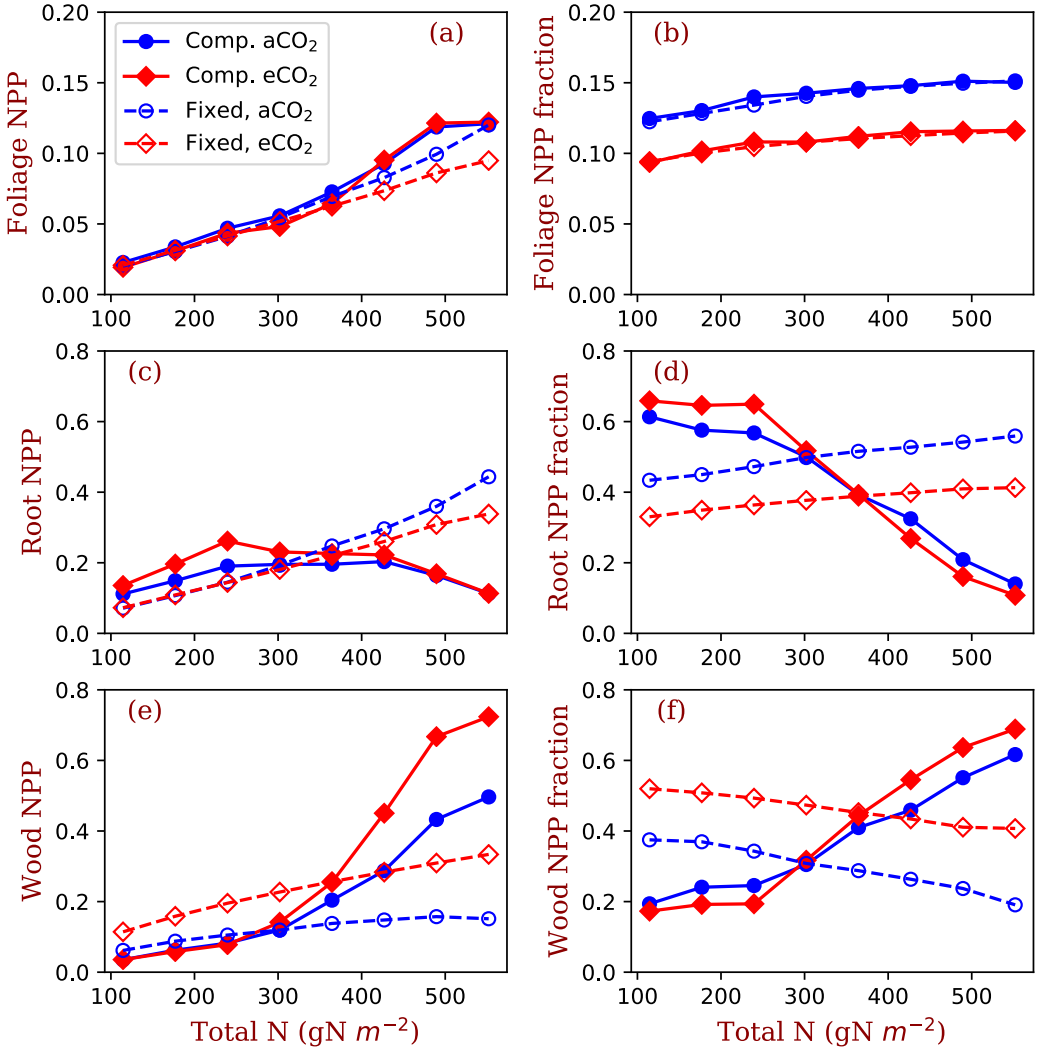

Figure 3 Allocation to leaves, fine roots, and wood tissues of the competition and fixed-allocation runs at the eight total nitrogen levels and two CO_2 concentrations. The panels a, c, and e show the NPP allocated to the tissues and the panels b, d, and f show the fractions of the allocation in total NPP. The closed symbols with solid line represent competition runs (comp.). The open symbols with dashed lines represent fixed-allocation runs (only φ_{RL}=4 shown in this figure).

348 Allocation of NPP to leaves increases with total nitrogen in all conditions, i.e. both
349 competition and fixed-allocation at both ambient [CO_2] and elevated [CO_2] (Fig. 3: a). Foliage
350 NPP is similar in these four model runs when N is low. At high nitrogen (>400 g N m^{-2}),
351 competition runs have higher foliage NPP than the fixed-allocation runs generally. Allocation to
352 leaves is relatively stable across the nitrogen gradient at the two CO_2 concentration levels (Fig. 3:
353 b). The fraction of NPP allocated to leaves changes little with nitrogen (Fig. 3: b) and it is
354 universally higher at ambient [CO_2] than at elevated [CO_2].

355 Allocation of NPP to fine roots is hump-shaped with increasing nitrogen in competition
356 runs, whereas it increases monotonically with increasing nitrogen in fixed-allocation runs (Fig. 3:
357 c). Elevated [CO_2] increases fine root allocation at low nitrogen in competition runs but
358 decreases root allocation irrespective of nitrogen in fixed-allocation runs (Fig. 3: c). The fraction
359 of NPP allocated to fine roots decreases with nitrogen at both CO_2 concentrations in competition
360 runs but it increases slightly in fixed-allocation runs (Fig. 3: d). In fixed-allocation runs, elevated
361 CO_2 reduces the fraction of NPP allocated to fine roots at all nitrogen levels. In competition runs,
362 fractional allocation to fine roots increases at elevated [CO_2] when ecosystem total nitrogen is
363 low (e.g., 114.5 - 302 g N m^{-2}) and decrease at elevated [CO_2] when ecosystem total nitrogen is
364 high (e.g., 364-552 g N m^{-2}).

365 In the reverse of the fine root response, NPP allocation to woody tissues increases with
366 total nitrogen in both competition and fixed-allocation runs (Fig. 3: e). In competition runs, the
367 fraction of allocation to woody tissues decreases at elevated [CO_2] when ecosystem total
368 nitrogen is low (e.g., 114 – 245 g N m^{-2}) and increases at elevated [CO_2] when ecosystem total
369 nitrogen is high (e.g., 302 – 552 g N m^{-2}).

370

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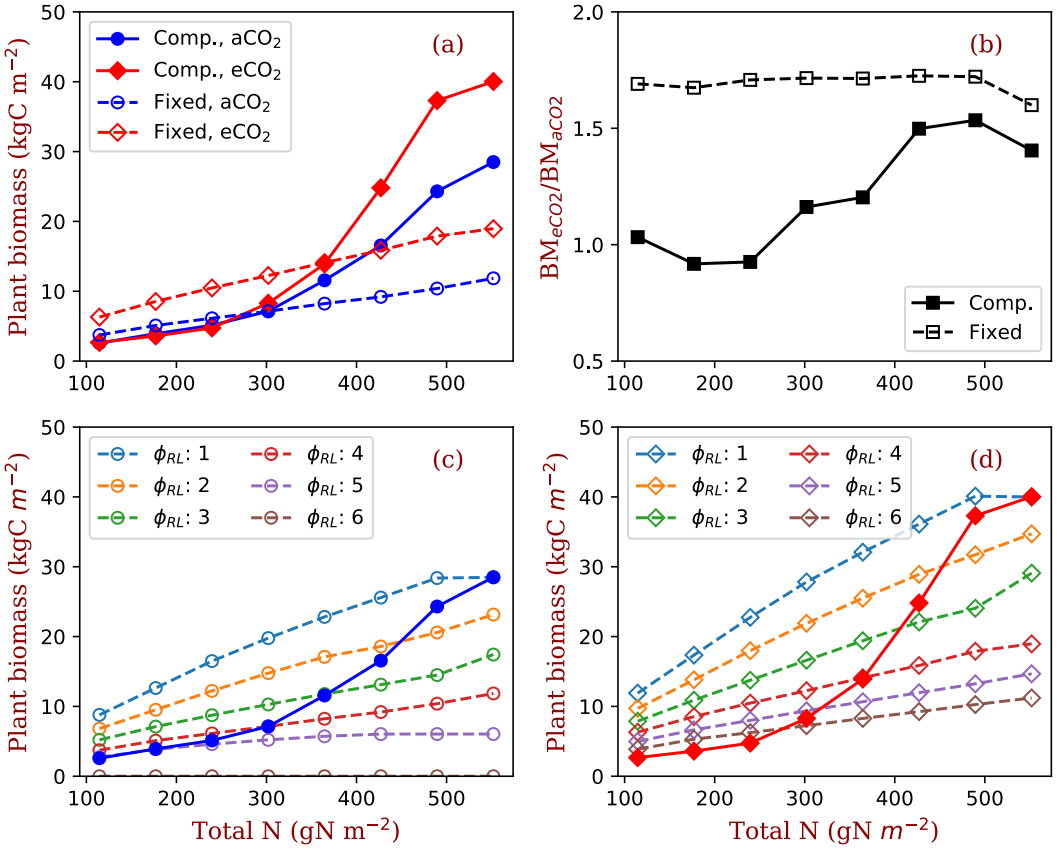

Figure 4 Plant biomass responses to elevated [CO_2] and nitrogen

Panel a shows the equilibrium plant biomass (means of simulated plant biomass from model run year 1400 to 1800) in competition runs and fixed-allocation runs (φ_{RL}=4). Panel b shows the ratio of simulated plant biomass at elevated [CO_2] to ambient [CO_2] for both competition and fixed-allocation runs. Panels c and d show the comparisons with fixed-allocation runs with φ_{RL} from 1 to 6 at ambient (c) and elevated [CO_2] (d). The closed symbols with solid line represent competition runs. The open symbols with dashed lines represent fixed-allocation runs (φ_{RL} ranges from 1 to 6).

As a result of the changes in competitively-optimal allocation, plant biomass increases dramatically with ecosystem nitrogen in competition runs compared with that in fixed-allocation runs (Fig. 4: a). The effects of elevated [CO_2] on plant biomass increase with nitrogen in competition runs but are constant overall in fixed-allocation runs (Fig. 4: b). Compared with the full spread of fixed-allocation runs with φ_{RL} ranging from 1 to 6, competition runs have high root allocation at low nitrogen and low root allocation at high nitrogen due to changes in the dominant competitive allocation strategy, which amplifies plant biomass responses to elevated [CO_2] with increasing nitrogen (Fig. 4: c and d).

Generally, in the fixed-allocation runs, GPP and NPP increase by a factor of three along the gradient of nitrogen used in this study (114.5 - 552 g N m^{-2}) at both ambient and elevated [CO_2] (Figs. S1 and S2). As φ_{RL} increases (i.e. more fine roots per unit leaf), GPP and NPP decrease at all the nitrogen levels overall, though not monotonically. The magnitude of differences in GPP and NPP due to differences in fixed allocation within a given nitrogen level is comparable to the magnitude of differences in GPP and NPP due to nitrogen level within a given fixed allocation strategy (Fig. S1: a and b) when φ_{RL} is in the range that allows plants to grow normally (1~5 in the case of ambient [CO_2]). At φ_{RL}=6, the simulated trees just barely survive with very limited growth, and their GPP and NPP are close to zero. As prescribed by the definition of φ_{RL}, allocation of NPP to fine roots increases with φ_{RL} in fixed-allocation runs (Fig. S1: c). As a consequence, allocation of NPP to wood decreases as φ_{RL} increases (Fig. S1: d). Allocation to leaves does not change much with φ_{RL}. (Fig. S1: e, note differences in scale). Correspondingly, plant biomass at equilibrium decreases with φ_{RL} and almost falls to zero at φ_{RL}=6. Total nitrogen affects the allocation to fine roots and wood (Fig. S1: d) because extra carbon is diverted to woody tissues in our model when nitrogen is limited. However, the

amplitude of changes in GPP and NPP induced by nitrogen availability is lower than the amplitude of changes resulting from different values of φ_{RL} in the fixed-allocation runs.

4 Discussion

4.1 Mechanisms of model predictions

In our model, the simulation of competition for light and soil resources is based on two fundamental mechanisms: 1) competition for light is based on the height of trees according to the rules of the PPA model (Strigul et al., 2008); and 2) individual nitrogen uptake is linearly dependent on the fine root surface area of an individual tree relative to that of its neighbors (Dybzinski et al., 2019; McMurtrie et al., 2012; Weng et al., 2017). These two mechanisms define an allocational tradeoff between wood and fine roots for carbon and nitrogen investment in different [CO_2] and nitrogen environments. Allowing competition for these resources to determine the dominant traits results in very different predicted allocation patterns – and thus ecosystem level responses – than those of fixed allocation strategies. For example, fractional wood allocation increases with increasing nitrogen availability under competitive allocation but decreases – the opposite qualitative response – under fixed allocation (Fig. 3: f). Consequently, equilibrium plant biomass is predicted to increase much more with increasing nitrogen availability under a competitive- than under a fixed-allocation strategy (Fig. 4: c, d). In nature, the effects of competition on dominant plant traits may occur through species replacement or community assembly (akin to the mechanism in our model), but it may also occur through adaptive plastic responses or in-place sub-population evolution of ecotypes.

Although the strategy that maximizes the growth rate in a fixed-allocation strategy allocates very little to fine roots (Figs. S1 and S2), the competitively optimal strategy allocates more carbon to fine roots to compete for nitrogen, a competitive effect termed “fine-root

overproliferation" (McNickle and Dybzinski, 2013). Elevated [CO_2] increases the carbon gain of leaves, making more carbon available for nitrogen competition and thus exacerbating the fine-root overproliferation (Dybzinski et al., 2015). Changes in the height at which understory trees transition to the canopy from low nitrogen to high nitrogen indicate a shift from the importance of competition for soil nitrogen to the importance of competition for light as ecosystem nitrogen increases (Fig. S3).

Under competitive allocation, increases in NPP and plant biomass across the nitrogen gradient are greater than the increases in NPP and plant biomass under fixed allocation (Fig. S1) because the most competitive type shifts from high fine root allocation to low fine root allocation as ecosystem total nitrogen increases from 117 to 552 g N m^{-2} (Figs. S4 and S5). This greatly reduces the carbon cost of belowground competition. The slight decrease in the fraction of NPP allocated to leaves at elevated [CO_2] occurs because of increases in total NPP and constant absolute NPP allocation to foliage. It is consistent with free air CO_2 enhancement (FACE) experiments that show leaf area index (LAI) in closed-canopy forests is not responsive to elevated [CO_2] (Norby et al., 2003).

Because most nitrogen uptake is via mass flow and diffusion and because both of these mechanisms depend on sink strength, individuals with *relatively* greater fine root mass than their neighbors take a greater share of nitrogen, as was recently demonstrated empirically (Dybzinski et al., 2019). This is consistent with the idea mentioned above that fine roots may overproliferate for competitive reasons relative to lower optimal fine root mass in the hypothetical absence of an evolutionary history of competition (Craine, 2006; McNickle and Dybzinski, 2013). The increased fitness (*i.e.*, reproductive success) of the *relatively* greater strategy increases the *absolute* fine root mass. But again, individuals with even *relatively* greater fine root mass take a

greater share of nitrogen, leading to what has been termed a "tragedy of the commons" (Gersani et al., 2001). At high soil nitrogen, height-structured competition for light (also a game-theoretic tragedy of the commons, Falster and Westoby, 2003; Givnish, 1982) prevails, and trees with greater *relative* allocation to trunks prevail. The balance between these two competitive priorities can be observed in our model predictions as a shift from fine root allocation to wood allocation as soil nitrogen increases. This may also explain why root C:N ratio is highly variable (Dybzinski et al., 2015; Luo et al., 2006; Nie et al., 2013): a high density of fine roots in soil may be more important than the high absorption ability of a single root in competing for soil nitrogen in the usually low mineral nitrogen soils.

Our model predicts that the ratio of plant biomass under elevated [CO_2] relative to plant biomass under ambient [CO_2] should increase with increasing nitrogen due to the shift of carbon allocation from fine roots to woody tissues. In contrast, the analytic model of Dybzinski *et al.* (2015) predicts that the ratio of plant biomass under elevated [CO_2] relative to plant biomass under ambient [CO_2] should be largely independent of total nitrogen because of an increasing shift in carbon allocation from long-lived, low-nitrogen wood to short-lived, high-nitrogen fine roots under elevated [CO_2] and with increasing nitrogen. This significant difference between these two predictions traces back to differences in how fine root stoichiometry is handled in the two models. In the model of Dybzinski *et al.* (2015), the fine root C:N ratio is flexible and the marginal nitrogen uptake capacity per unit of carbon allocated to fine roots depends on its nitrogen concentration. Like the model presented here, the model of Dybzinski *et al.* (2015) predicts decreasing fine root mass with increasing nitrogen availability. *Unlike* the model presented here (which has constant fine root nitrogen concentration), the model of Dybzinski et al. (2015) predicts increasing fine root nitrogen concentration with increasing nitrogen

availability. As a result, there is less nitrogen to allocate to wood as nitrogen increases in the model of Dybzinski *et al*. (2015) than there is in the model presented here. These countervailing factors even out the ratio of plant biomass under elevated [CO_2] relative to plant biomass under ambient [CO_2] across the nitrogen gradient in Dybzinski *et al*. (2015), whereas their absence amplifies this ratio with increasing nitrogen in the model presented here. Our ability to diagnose and understand this discrepancy highlights the utility of deploying closely-related analytical and simulation models (Weng et al., 2017). It also points to a critical empirical research gap: which model's fine root (and strictly speaking, active root, McCormack et al., 2017) assumptions about stoichiometry are closer to the truth?

4.2 Model complexity and uncertainty

Compared with the conventional pool-based vegetation models that use pools and fluxes to represent plant demographic processes at a land simulation unit (e.g., grid or patch), VDMs add two new mechanisms. The first mechanism is the inclusion of stochastic birth and mortality processes of individuals (i.e., demographic processes). These processes allow the models to predict population dynamics and transient vegetation structure, such as size-structured distribution and crown organization (e.g., Moorcroft et al., 2001; Strigul et al., 2008). With changes in vegetation structure, allocation and mortality rates can change, generating a different carbon storage accumulation curve compared with those predicted by pool-based models where vegetation structure is not explicitly represented (e.g., Weng et al., 2015). The second new mechanism is the simulated shift in dominant plant traits during succession due to shifting competitive outcomes among different PFTs, which changes the allocation between fast- and slow-turnover pools and thus the parameters of allocation and the residence time of carbon in the ecosystem.

497 Together, these mechanisms may alter long-term predictions of terrestrial carbon cycling
498 due to changes in PFT-based parameters (Dybzinski et al., 2011; Farrior et al., 2013; Weng et al.,
499 2015). As described in the Introduction, current pool-based models can be described by a linear
500 system of equations characterized by the key parameters of allocation, residence time, and
501 transfer coefficients (Eq. 1) with the rigid assumption of unchangeable plant types (Luo et al.,
502 2012; Xia et al., 2013). In VDMs however, allocation, residence time, leaf traits, phenology,
503 mortality, plant forms, and their responses to climate change are all strategies of competition
504 whose success varies with the environmental conditions and the traits of the individuals they are
505 competing against. To make predictions of carbon cycle responses to the novel conditions of
506 climate change, we must understand what determines the most competitive strategy, how the
507 most competitive strategy changes with conditions, and how the most competitive strategy
508 impacts the carbon cycle.
509 Many trade-offs between plant traits can shift in response to environmental and biotic
510 changes, limiting the applicability of varying a single trait, as we have in this study. For example,
511 allocation, leaf traits, mycorrhizal types, and nitrogen fixation can all change with ecosystem
512 nitrogen availability (Menge et al., 2017; Ordoñez et al., 2009; Phillips et al., 2013; Vitousek et
513 al., 2013). The unrealistic effects of model simplification can be corrected by adding important
514 tradeoffs that are missing. For example, the positive feedback between root allocation and SOM
515 decomposition plays a role in mitigating the effects of tragedies of the commons of root over-
516 proliferation (e.g., Gersani et al., 2001; Zea-Cabrera et al., 2006) due to a negative feedback
517 induced by root turnover. High root allocation increases the decomposition rate of SOM and the
518 supply of mineral nitrogen because of the high turnover rate of root litter, which favors a strategy
519 of high wood allocation and reduces the competitive optimal fine root allocation. This negative

feedback indicates that the model structure is flexible and that we can incorporate correct mechanisms step by step to improve model prediction skills. Testing single strategies is still a necessary step to improving our understanding of the system and prediction skills of the models, though it could lead to unrealistic responses sometimes.

4.3 Implications for Earth system modeling

In this study, we set forth a hypothesis for the tradeoffs between light competition and nitrogen uptake via allocation based on insights gained from the simpler model of Dybzinski et al. (2015) to predict allocation as an emergent property of competition. One advantage of building a model in this way is that the vegetation dynamics are predicted from first principles, rather than based on the correlations between vegetation properties and environmental conditions. For vegetation models designed to predict the effects of climate change, the important operational distinction is that the fundamental rules cannot or will not change as climate changes. Nor, presumably, will the underlying ecological and evolutionary processes change as climate changes. The emergent properties can change as climate changes however, and the models built on the "scale-appropriate" unbreakable constraints and ecological and evolutionary processes will be able to accurately predict changes in emergent ecosystem properties.

This modeling approach also demands improvement in model validation and benchmarking systems (Collier et al., 2018; Hoffman et al., 2017). As shown in this study, allocation responses to elevated CO_2 at different nitrogen levels in fixed-allocation runs are opposite to those in competitive-allocation runs. For example, in fixed-allocation runs, elevated [CO_2] increases wood allocation and decreases fine root allocation at low nitrogen; whereas in competitive-allocation runs elevated [CO_2] leads to low wood allocation and high fine root allocation. Simply

543 calibrating against short-term observational data may improve the agreements with observations
544 but would not change model predictions because these results emerge from the fundamental
545 assumptions of the models. An updated model benchmarking system should have the metrics of
546 competitive plant traits during the development of ecosystems and their responses to changes in
547 climate.

548 **5 Conclusions**

549 Overall, our study illustrates that including the competition processes for light and soil
550 resources in a game-theoretic vegetation demographic model can substantially change the
551 prediction of the contribution of ecosystems to the global carbon cycle. Allowing the model to
552 track the competitive allocation strategies can generate significantly different ecosystem-level
553 predictions than those of fixed allocation strategies. Building such a model requires
554 differentiating between the unbreakable tradeoffs of plant traits and ecological processes from
555 the emergent properties of ecosystems. Drawing on insights from closely-related analytical
556 models to develop and understand more complicated simulation models seems, to us,
557 indispensable. Evaluating these models also requires an updated model benchmarking system
558 that includes the metrics of competitive plant traits during the development of ecosystems and
559 their responses to climate changes.

560

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566

567 **Codes and data availability**

568 The codes of the BiomeE model are available at GitHub:

569 https://github.com/wengensheng/BiomeESS

570 The simulated data from simulation experiments and Python scripts used in this study will be
571 made publicly available at the publish of this paper.

572

Reference

Aber, J. D., Magill, A., Boone, R., Melillo, J. M. and Steudler, P.: Plant and Soil Responses to Chronic Nitrogen Additions at the Harvard Forest, Massachusetts, Ecol. Appl., 3(1), 156–166, doi:10.2307/1941798, 1993.

Arora, V. K. and Boer, G. J.: A parameterization of leaf phenology for the terrestrial ecosystem component of climate models, Glob. Change Biol., 11(1), 39–59, doi:10.1111/j.1365-2486.2004.00890.x, 2005.

Barr, A. G., Ricciu, D. M., Schaefer, K., Richarson, A., Agarwal, D., Thornton, P. E., Davis, K., Jackson, B., Cook, R. B., Hollinger, D. Y., Van Ingen, C., Amiro, B., Andrews, A., Arain, M. A., Baldocchi, D., Black, T. A., Bolstad, P., Curtis, P., Desai, A., Dragoni, D., Flanagan, L., Gu, L., Katul, G., Law, B. E., Lafleur, P. M., Margolis, H., Matamala, R., Meyers, T., McCaughey, J. H., Monson, R., Munger, J. W., Oechel, W., Oren, R., Roulet, N. T., Torn, M. and Verma, S. B.: NACP Site: Tower Meteorology, Flux Observations with Uncertainty, and Ancillary Data, , doi:10.3334/ornldaac/1178, 2013.

Bloom, A. A., Exbrayat, J.-F., van der Velde, I. R., Feng, L. and Williams, M.: The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times, Proc. Natl. Acad. Sci., 113(5), 1285–1290, doi:10.1073/pnas.1515160113, 2016.

Cannell, M. G. R. and Dewar, R. C.: Carbon Allocation in Trees: a Review of Concepts for Modelling, in Advances in Ecological Research, vol. 25, pp. 59–104, Elsevier., 1994.

Collier, N., Hoffman, F. M., Lawrence, D. M., Keppel-Aleks, G., Koven, C. D., Riley, W. J., Mu, M. and Randerson, J. T.: The International Land Model Benchmarking (ILAMB) System: Design, Theory, and Implementation, J. Adv. Model. Earth Syst., 10(11), 2731–2754, doi:10.1029/2018MS001354, 2018.

Compton, J. E. and Boone, R. D.: Long-Term Impacts of Agriculture on Soil Carbon and Nitrogen in New England Forests, Ecology, 81(8), 2314, doi:10.2307/177117, 2000.

Craine, J. M.: Competition for Nutrients and Optimal Root Allocation, Plant Soil, 285(1–2), 171–185, doi:10.1007/s11104-006-9002-x, 2006.

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y.-P., Luo, Y., Jain, A. K., El-Masri, B., Hickler, T., Wårlind, D., Weng, E., Parton, W. J., Thornton, P. E., Wang, S., Prentice, I. C., Asao, S., Smith, B., McCarthy, H. R., Iversen, C. M., Hanson, P. J., Warren, J. M., Oren, R. and Norby, R. J.: Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO_2 enrichment sites, New Phytol., 203(3), 883–899, doi:10.1111/nph.12847, 2014.

DeAngelis, D. L., Ju, S., Liu, R., Bryant, J. P. and Gourley, S. A.: Plant allocation of carbon to defense as a function of herbivory, light and nutrient availability, Theor. Ecol., 5(3), 445–456, doi:10.1007/s12080-011-0135-z, 2012.

Dieckmann, U., Brannstrom, A., HilleRisLambes, R. and Ito, H. C.: The Adaptive Dynamics of Community Structure, in Mathematics for Ecology and Environmental Sciences, edited by Takeuchi, Yasuhiro, Iwasa, Yoh, and Sato, Kazunori, pp. 145–177, Springer., 2007.

614 Dybzinski, R., Farrior, C., Wolf, A., Reich, P. B. and Pacala, S. W.: Evolutionarily Stable
615 Strategy Carbon Allocation to Foliage, Wood, and Fine Roots in Trees Competing for
616 Light and Nitrogen: An Analytically Tractable, Individual-Based Model and Quantitative
617 Comparisons to Data, Am. Nat., 177(2), 153–166, doi:10.1086/657992, 2011.

618 Dybzinski, R., Farrior, C. E. and Pacala, S. W.: Increased forest carbon storage with increased
619 atmospheric CO2 despite nitrogen limitation: a game-theoretic allocation model for trees
620 in competition for nitrogen and light, Glob. Change Biol., 21(3), 1182–1196,
621 doi:10.1111/gcb.12783, 2015.

622 Dybzinski, R., Kelvakis, A., McCabe, J., Panock, S., Anuchitlertchon, K., Vasarhelyi, L., Luke
623 McCormack, M., McNickle, G. G., Poorter, H., Trinder, C. and Farrior, C. E.: How are
624 nitrogen availability, fine-root mass, and nitrogen uptake related empirically?
625 Implications for models and theory, Glob. Change Biol., doi:10.1111/gcb.14541, 2019.

626 Emanuel, W. R. and Killough, G. G.: Modeling terrestrial ecosystems in the global carbon cycle
627 with Shifts in carbon storage capacity by land-use change, Ecology, 65(3), 970–983,
628 doi:10.2307/1938069, 1984.

629 Eriksson, E.: Compartment Models and Reservoir Theory, Annu. Rev. Ecol. Syst., 2(1), 67–84,
630 doi:10.1146/annurev.es.02.110171.000435, 1971.

631 Falster, D. and Westoby, M.: Plant height and evolutionary games, TRENDS Ecol. Evol., 18(7),
632 337–343, doi:10.1016/S0169-5347(03)00061-2, 2003.

633 Farrior, C. E., Dybzinski, R., Levin, S. A. and Pacala, S. W.: Competition for Water and Light in
634 Closed-Canopy Forests: A Tractable Model of Carbon Allocation with Implications for
635 Carbon Sinks, Am. Nat., 181(3), 314–330, doi:10.1086/669153, 2013.

636 Farrior, C. E., Rodriguez-Iturbe, I., Dybzinski, R., Levin, S. A. and Pacala, S. W.: Decreased
637 water limitation under elevated CO2 amplifies potential for forest carbon sinks, Proc.
638 Natl. Acad. Sci. U. S. A., 112(23), 7213–7218, doi:10.1073/pnas.1506262112, 2015.

639 Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C.
640 E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M.,
641 Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato,
642 H., Shuman, J. K., Smith, B., Trugman, A. T., Viskari, T., Verbeeck, H., Weng, E., Xu,
643 C., Xu, X., Zhang, T. and Moorcroft, P. R.: Vegetation demographics in Earth System
644 Models: A review of progress and priorities, Glob. Change Biol., 24(1), 35–54,
645 doi:10.1111/gcb.13910, 2018.

646 Friend, A. D., Arneth, A., Kiang, N. Y., Lomas, M., Ogee, J., Roedenbeckk, C., Running, S. W.,
647 Santaren, J.-D., Sitch, S., Viovy, N., Woodward, F. I. and Zaehle, S.: FLUXNET and
648 modelling the global carbon cycle, Glob. Change Biol., 13(3), 610–633,
649 doi:10.1111/j.1365-2486.2006.01223.x, 2007.

650 Gersani, M., Brown, J. s., O'Brien, E. E., Maina, G. M. and Abramsky, Z.: Tragedy of the
651 commons as a result of root competition, J. Ecol., 89(4), 660–669, doi:10.1046/j.0022-
652 0477.2001.00609.x, 2001.

653 Givnish, T. J.: On the Adaptive Significance of Leaf Height in Forest Herbs, Am. Nat., 120(3),
654 353–381, doi:10.1086/283995, 1982.

Haverd, V., Smith, B., Raupach, M., Briggs, P., Nieradzik, L., Beringer, J., Hutley, L., Trudinger, C. M. and Cleverly, J.: Coupling carbon allocation with leaf and root phenology predicts tree–grass partitioning along a savanna rainfall gradient, Biogeosciences, 13(3), 761–779, doi:10.5194/bg-13-761-2016, 2016.

Hibbs, D. E.: Forty Years of Forest Succession in Central New England, Ecology, 64(6), 1394–1401, doi:10.2307/1937493, 1983.

Hoffman, F. M., Koven, C. D., Keppel-Aleks, G., Lawrence, D. M., Riley, W. J., Randerson, J. T., Ahlström, A., Abramowitz, G., Baldocchi, D. D., Best, M. J., Bond-Lamberty, B., De Kauwe, M. G., Denning, A. S., Desai, A. R., Eyring, V., Fisher, J. B., Fisher, R. A., Gleckler, P. J., Huang, M., Hugelius, G., Jain, A. K., Kiang, N. Y., Kim, H., Koster, R. D., Kumar, S. V., Li, H., Luo, Y., Mao, J., McDowell, N. G., Mishra, U., Moorcroft, P. R., Pau, G. S. H., Ricciuto, D. M., Schaefer, K., Schwalm, C. R., Serbin, S. P., Shevliakova, E., Slater, A. G., Tang, J., Williams, M., Xia, J., Xu, C., Joseph, R. and Koch, D.: 2016 International Land Model Benchmarking (ILAMB) Workshop Report., 2017.

Keenan, T. F., Davidson, E. A., Munger, J. W. and Richardson, A. D.: Rate my data: quantifying the value of ecological data for the development of models of the terrestrial carbon cycle, Ecol. Appl., 23(1), 273–286, doi:10.1890/12-0747.1, 2013.

Koven, C. D., Chambers, J. Q., Georgiou, K., Knox, R., Negron-Juarez, R., Riley, W. J., Arora, V. K., Brovkin, V., Friedlingstein, P. and Jones, C. D.: Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth System Models, Biogeosciences, 12(17), 5211–5228, doi:10.5194/bg-12-5211-2015, 2015.

Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S. and Prentice, I. C.: A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, Glob. Biogeochem. Cycles, 19(1), doi:10.1029/2003GB002199, 2005.

Lacointe, A.: Carbon allocation among tree organs: A review of basic processes and representation in functional-structural tree models, Ann. For. Sci., 57(5), 521–533, doi:10.1051/forest:2000139, 2000.

Luo, Y. and Weng, E.: Dynamic disequilibrium of the terrestrial carbon cycle under global change, Trends Ecol. Evol., 26(2), 96–104, doi:10.1016/j.tree.2010.11.003, 2011.

Luo, Y., Hui, D. and Zhang, D.: Elevated CO2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis, Ecology, 87(1), 53–63, 2006.

Luo, Y. Q., Wu, L. H., Andrews, J. A., White, L., Matamala, R., Schafer, K. V. R. and Schlesinger, W. H.: Elevated CO2 differentiates ecosystem carbon processes: Deconvolution analysis of Duke Forest FACE data, Ecol. Monogr., 71(3), 357–376, doi:10.1890/0012-9615(2001)071[0357:ECDECP]2.0.CO;2, 2001.

Luo, Y. Q., Randerson, J. T., Abramowitz, G., Bacour, C., Blyth, E., Carvalhais, N., Ciais, P., Dalmonech, D., Fisher, J. B., Fisher, R., Friedlingstein, P., Hibbard, K., Hoffman, F., Huntzinger, D., Jones, C. D., Koven, C., Lawrence, D., Li, D. J., Mahecha, M., Niu, S. L., Norby, R., Piao, S. L., Qi, X., Peylin, P., Prentice, I. C., Riley, W., Reichstein, M., Schwalm, C., Wang, Y. P., Xia, J. Y., Zaehle, S. and Zhou, X. H.: A framework for

benchmarking land models, Biogeosciences, 9(10), 3857–3874, doi:10.5194/bg-9-3857-2012, 2012.

McCormack, M. L., Guo, D., Iversen, C. M., Chen, W., Eissenstat, D. M., Fernandez, C. W., Li, L., Ma, C., Ma, Z., Poorter, H., Reich, P. B., Zadworny, M. and Zanne, A.: Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes, New Phytol., 215(1), 27–37, doi:10.1111/nph.14459, 2017.

McMurtrie, R. E., Iversen, C. M., Dewar, R. C., Medlyn, B. E., Näsholm, T., Pepper, D. A. and Norby, R. J.: Plant root distributions and nitrogen uptake predicted by a hypothesis of optimal root foraging, Ecol. Evol., 2(6), 1235–1250, doi:10.1002/ece3.266, 2012.

McNickle, G. G. and Dybzinski, R.: Game theory and plant ecology, edited by J. Klironomos, Ecol. Lett., 16(4), 545–555, doi:10.1111/ele.12071, 2013.

Menge, D. N. L., Batterman, S. A., Hedin, L. O., Liao, W., Pacala, S. W. and Taylor, B. N.: Why are nitrogen-fixing trees rare at higher compared to lower latitudes?, Ecology, 98(12), 3127–3140, doi:10.1002/ecy.2034, 2017.

Montané, F., Fox, A. M., Arellano, A. F., MacBean, N., Alexander, M. R., Dye, A., Bishop, D. A., Trouet, V., Babst, F., Hessl, A. E., Pederson, N., Blanken, P. D., Bohrer, G., Gough, C. M., Litvak, M. E., Novick, K. A., Phillips, R. P., Wood, J. D. and Moore, D. J. P.: Evaluating the effect of alternative carbon allocation schemes in a land surface model (CLM4.5) on carbon fluxes, pools, and turnover in temperate forests, Geosci. Model Dev., 10(9), 3499–3517, doi:10.5194/gmd-10-3499-2017, 2017.

Moorcroft, P. R., Hurtt, G. C. and Pacala, S. W.: A method for scaling vegetation dynamics: The ecosystem demography model (ED), Ecol. Monogr., 71(4), 557–585, doi:10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2, 2001.

Nie, M., Lu, M., Bell, J., Raut, S. and Pendall, E.: Altered root traits due to elevated CO2: a meta-analysis: Root traits at elevated CO2, Glob. Ecol. Biogeogr., 22(10), 1095–1105, doi:10.1111/geb.12062, 2013.

Norby, R. J., Sholtis, J. D., Gunderson, C. A. and Jawdy, S. S.: Leaf dynamics of a deciduous forest canopy: no response to elevated CO 2, Oecologia, 136(4), 574–584, doi:10.1007/s00442-003-1296-2, 2003.

Ordoñez, J. C., van Bodegom, P. M., Witte, J.-P. M., Wright, I. J., Reich, P. B. and Aerts, R.: A global study of relationships between leaf traits, climate and soil measures of nutrient fertility, Glob. Ecol. Biogeogr., 18(2), 137–149, doi:10.1111/j.1466-8238.2008.00441.x, 2009.

Pappas, C., Fatichi, S. and Burlando, P.: Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter?, New Phytol., 209(1), 137–151, doi:10.1111/nph.13590, 2016.

Parton, W., Schimel, D., Cole, C. and Ojima, D.: Analysis of factors controlling soil organic matter levels in Great Plains grasslands, Soil Sci. Soc. Am. J., 51(5), 1173–1179, doi:10.2136/sssaj1987.03615995005100050015x, 1987.

Phillips, R. P., Brzostek, E. and Midgley, M. G.: The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests, New Phytol., 199(1), 41–51, doi:10.1111/nph.12221, 2013.

Raich, J., Rastetter, E. B., Melillo, J. M., Kicklighter, D. W., Steudler, P. A., Peterson, B. J., Grace, A., Moore, B. and Vorosmary, C. J.: Potential Net Primary Productivity in South America: Application of a Global Model, Ecol. Appl., 1(4), 399–429, doi:10.2307/1941899, 1991.

Randerson, J., Thompson, M., Conway, T., Fung, I. and Field, C.: The contribution of terrestrial sources and sinks to trends in the seasonal cycle of atmospheric carbon dioxide, Glob. Biogeochem. Cycles, 11(4), 535–560, doi:10.1029/97GB02268, 1997.

Savage, K. E., Parton, W. J., Davidson, E. A., Trumbore, S. E. and Frey, S. D.: Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest, Glob. Change Biol., 19(8), 2389–2400, doi:10.1111/gcb.12224, 2013.

Scheiter, S. and Higgins, S. I.: Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach, Glob. Change Biol., 15(9), 2224–2246, doi:10.1111/j.1365-2486.2008.01838.x, 2009.

Scheiter, S., Langan, L. and Higgins, S. I.: Next-generation dynamic global vegetation models: learning from community ecology, New Phytol., 198(3), 957–969, doi:10.1111/nph.12210, 2013.

Schmidt, G. A., Kelley, M., Nazarenko, L., Ruedy, R., Russell, G. L., Aleinov, I., Bauer, M., Bauer, S. E., Bhat, M. K., Bleck, R., Canuto, V., Chen, Y.-H., Cheng, Y., Clune, T. L., Del Genio, A., de Fainchtein, R., Faluvegi, G., Hansen, J. E., Healy, R. J., Kiang, N. Y., Koch, D., Lacis, A. A., LeGrande, A. N., Lerner, J., Lo, K. K., Matthews, E. E., Menon, S., Miller, R. L., Oinas, V., Oloso, A. O., Perlwitz, J. P., Puma, M. J., Putman, W. M., Rind, D., Romanou, A., Sato, M., Shindell, D. T., Sun, S., Syed, R. A., Tausnev, N., Tsigaridis, K., Unger, N., Voulgarakis, A., Yao, M.-S. and Zhang, J.: Configuration and assessment of the GISS ModelE2 contributions to the CMIP5 archive, J. Adv. Model. Earth Syst., 6(1), 141–184, doi:10.1002/2013MS000265, 2014.

Shevliakova, E., Pacala, S. W., Malyshev, S., Hurtt, G. C., Milly, P. C. D., Caspersen, J. P., Sentman, L. T., Fisk, J. P., Wirth, C. and Crevoisier, C.: Carbon cycling under 300 years of land use change: Importance of the secondary vegetation sink, Glob. Biogeochem. Cycles, 23, GB2022, doi:10.1029/2007GB003176, 2009.

Shinozaki, Kichiro, Yoda, Kyoji, Hozumi, Kazuo and Kira, Tatuo: A quantitative analysis of plant form – the pipe model theory. I. Basic analyses, Jpn. J. Ecol., 14(3), 97–105, 1964.

Sierra, C. A. and Mueller, M.: A general mathematical framework for representing soil organic matter dynamics, Ecol. Monogr., 85(4), 505–524, doi:10.1890/15-0361.1, 2015.

Sierra, C. A., Muller, M., Metzler, H., Manzoni, S. and Trumbore, S. E.: The muddle of ages, turnover, transit, and residence times in the carbon cycle, Glob. Change Biol., 23(5), 1763–1773, doi:10.1111/gcb.13556, 2017.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., Sykes, M. T., Thonicke, K. and Venevsky, S.: Evaluation of ecosystem

778 dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global
779 vegetation model, Glob. Change Biol., 9(2), 161–185, doi:10.1046/j.1365-
780 2486.2003.00569.x, 2003.

781 Strigul, N., Pristinski, D., Purves, D., Dushoff, J. and Pacala, S.: Scaling from trees to forests:
782 tractable macroscopic equations for forest dynamics, Ecol. Monogr., 78(4), 523–545,
783 doi:10.1890/08-0082.1, 2008.

784 Tilman, D.: Plant strategies and the dynamics and structure of plant communities, Princeton
785 University Press, Princeton, N.J., 1988.

786 Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., McKain, K., Fitzjarrald,
787 D., Czikowsky, M. and Munger, J. W.: Factors controlling CO2 exchange on timescales
788 from hourly to decadal at Harvard Forest, J. Geophys. Res. - Biogeosciences, 112(G2),
789 doi:10.1029/2006JG000293, 2007.

790 Vitousek, P. M., Menge, D. N. L., Reed, S. C. and Cleveland, C. C.: Biological nitrogen fixation:
791 rates, patterns and ecological controls in terrestrial ecosystems, Philos. Trans. R. Soc. B
792 Biol. Sci., 368(1621), 20130119–20130119, doi:10.1098/rstb.2013.0119, 2013.

793 Weng, E., Farrior, C. E., Dybzinski, R. and Pacala, S. W.: Predicting vegetation type through
794 physiological and environmental interactions with leaf traits: evergreen and deciduous
795 forests in an earth system modeling framework, Glob. Change Biol., 23(6), 2482–2498,
796 doi:10.1111/gcb.13542, 2017.

797 Weng, E. S., Malyshev, S., Lichstein, J. W., Farrior, C. E., Dybzinski, R., Zhang, T.,
798 Shevliakova, E. and Pacala, S. W.: Scaling from individual trees to forests in an Earth
799 system modeling framework using a mathematically tractable model of height-structured
800 competition, Biogeosciences, 12(9), 2655–2694, doi:10.5194/bg-12-2655-2015, 2015.

801 Xia, J., Luo, Y., Wang, Y.-P. and Hararuk, O.: Traceable components of terrestrial carbon
802 storage capacity in biogeochemical models, Glob. Change Biol., 19(7), 2104–2116,
803 doi:10.1111/gcb.12172, 2013.

804 Zea-Cabrera, E., Iwasa, Y., Levin, S. and Rodríguez-Iturbe, I.: Tragedy of the commons in plant
805 water use, Water Resour. Res., 42(6), W06D02, doi:10.1029/2005WR004514, 2006.

806