Dear Dr. Zaehle,

We thank you and the reviewers for their comments and suggestions. These comments are very helpful for improving the presentation of our study. We have re-run the model after fixing a problem that leads to high wood C:N ratio (350 ~ 800) in the codes, and made a thorough revision of the paper.

We mainly did the following:

1. We added a new description of the allocation scheme of our model with analytical solution of allocation at each step.
2. We fixed a numerical error in the codes that leads to high wood C:N ratio and updated all the figures and results. The major patterns in new model runs are very similar with those in previous version.
3. We added discussion about the reality of simulated results in comparison with data from meta-analysis and FACE experiments. We also discussed emerging common patterns of allocation modeling in comparison with other models and implications of our research for ecosystem modeling and Earth system modeling studies.
4. We compiled a detailed description of our model and included it as Supplementary Information I. It includes photosynthesis model, respiration, demographic processes (reproduction, growth, and mortality), population dynamics, phenology, and soil biogeochemical processes. Most of them have been published in previous papers about LM3-PPA (Weng et al. 2015, Weng et al. 2017). We hope it make the readers of this paper easier to get the details of this model.
5. We also made a series of sensitivity runs with different parameters of soil nitrogen mineralization and alternative assumptions of extra carbon allocation at nitrogen limitation (suggested by editor) and found the simulated patterns are robust. We only included these results in this response letter.

Please see the detailed responses to reviewers' comments and revisions enclosed in this letter. Review comments are in italics and our responses are in normal.

Best,

Ensheng Weng on behalf of coauthors Ray Dybzinski, Caroline E. Farrior, and Stephen W. Pacala

Response to Referee #1

The current paper aims to compare the predictions of biomass allocation within a vegetation demographic model (VDM) ***with explicit competition versus a model without competition****, under elevated* CO_2 *across a nitrogen availability gradient. To this end, the authors use a derivation of an existing VDM, where the only process that varies is the biomass allocation. The authors then present comparisons between* ***the two model versions*** *at equilibrium for one site. The topic of predicting vegetation allocation pattern for different nutrient limitation states is an important one, and one that existing vegetation model often have trouble with. The approach of having one model with two different process representations is also very valuable as it can pinpoint model differences to the exact processes in question.*

However, the value of this study is largely obscured by the way the model is presented and discussed, making it very difficult for the reader to link between model assumptions, results and model implications.

Thanks for the comments. We have revised the manuscript following the comments and suggestions of all the three reviewers.

Major comments

It is unclear to me if this analysis actually shows ***a difference between a model with and one without competition or simply a difference between a model with fixed and one with flexible allocation****. As the authors themselves point out in the introduction, pool-based vegetation models often incorporate a flexible allocation scheme based on nutrient and water availability. It is currently unclear if a model with such a scheme would perform differently from the competition model included here.*

It is a model with monoculture PFT (no competition) vs. polyculture PFTs (with competition). We have clarified the model runs and changed the notations of the figures (from “fixed vs. comp.” to “mono. vs. multiple”).

One of the key assumptions of the model ***is the order of allocation*** *(l 245): first a fixed fraction allocated to the sapwood, then allocation to the leaves and roots, then if there is available C and N left, to sapwood and fruit. And, most importantly, any carbon left in excess because of N limitation is allocated to sapwood. This last step could have some interesting implications for light competition under N limitation, and can maybe explain the different wood allocation patterns observed for the competition models. This model assumption needs to be justified and discussed.*

We agree that our description of allocation scheme is confusing, and leads to misunderstanding of the simulation experiments. We used four steps to describe the technical implementation of the ideas of the allocation model in the codes. However, we failed to convey the major principles of the allocation scheme itself.

The allocation scheme is robust and has been used in many Perfect Plasticity Approximation model-based studies. The carbon assimilated by leaves via photosynthesis enters into the non-structural carbon (NSC) pool first and then is used for respiration, growth, and reproduction. The nitrogen absorbed by roots enters into the non-structural nitrogen (NSN) pool and then is allocated to plant pools (*i.e.*, leaves, fine roots, seeds, and sapwood) following plant growth. The partitioning of carbon and nitrogen into the plant pools is constrained by allometric equations, targets of leaves and fine roots, and the target C:N ratios of these plant pools. The plant growth (and therefore allocation) is simulated at two steps: 1) calculating the amount of carbon and nitrogen that can be used for plant growth at this time step (daily in this study); 2) allocating the available carbon and nitrogen to leaves, fine roots, seeds, and sapwood following a couple of rules based on allometric scaling and functional relationship. We let the plant growth follow the rules below as they are in the first version (Weng et al. 2015, Biogeosciences. carbon only model) and second version of LM3-PPA (Weng et al. 2017, Global Change Biology. Carbon-nitrogen model):

1. Plants maintain their leaves and fine roots as close as possible to their targets as defined by allometry equations during the growing season.
2. The ratio of fine root area to leaf area is constant (cf. pipe model) when there is no disturbance to abruptly change leaves and fine roots.
3. Plants must keep a certain level of carbon storage (i.e., NSC) for respiration (*i.e.*, they don't kill themselves by using up their NSC for tissue growth) and external risks.
4. C:N ratios of plant tissues must be close to their target C:N ratios, though they can have daily variations due to numerical issues in matching carbon and nitrogen allocation in daily growth.
5. Plants are able to use available carbon and nitrogen in the most efficient way from the perspective of competition.

We updated the whole section with a new description of the model (**Allocation and plant growth**).

"Empirical allometric equations relate woody biomass (including coarse roots, bole, and branches), crown area, and stem diameter. The individual-level dimensions of a tree, *i.e.*, height (Z), biomass (S), and crown area (A_{CR}) are given by empirical allometries (Dybzinski et al., 2011; Farrior et al., 2013):

$$Z(D) = \alpha_Z D^{\theta_Z}$$

$$S(D) = 0.25\pi\Lambda\rho_W\alpha_Z D^{2+\theta_Z} \qquad \text{(Eq. 2)}$$

$$A_{CR}(D) = \alpha_c D^{\theta_c}$$

where Z is tree height, D is tree diameter, 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}) (Table 1).

We set *targets* for leaf (L^*), fine root (FR^*), and sapwood cross-sectional area (A^*_{SW}) 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):

$$L^*(D,p) = l^* \cdot A_{CR}(D) \cdot \sigma \cdot p(t)$$

$$FR^*(D) = \varphi_{RL} \cdot l^* \cdot \frac{A_{CR}(D)}{\gamma} \qquad \text{(Eq. 3)}$$

$$A^*_{SW}(D) = \alpha_{CSA} \cdot l^* \cdot A_{CR}(D)$$

where L^* (D, p), $FR^*(D)$, and $A^*_{SW}(D)$ are the targets of leaf mass (kg C/tree), fine root biomass (kg C/tree), and sapwood cross sectional area (m^2/tree), respectively, at tree diameter D; l^* is the target leaf area per unit crown area of a given PFT; A_{CR}(D) is the crown area of a tree with diameter D; σ is PFT-specific leaf mass per unit area (LMA); and $p(t)$ is a PFT-specific function ranging from zero to one that governs leaf phenology (Weng et al., 2015); φ_{RL} is the target ratio of total root surface area to the total leaf area; γ is specific root area; and $\square_{CSA}$ is an empirical constant (the ratio of sapwood cross-sectional area to target leaf area). 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}. ”

“The partitioning of carbon and nitrogen into the plant pools (*i.e.*, leaves, fine roots, and sapwood) is limited by the allometric equations, targets of leaves, fine roots, and sapwood cross-sectional area, and the stoichiometry (i.e., C:N ratios) of these plant tissues. At a daily time step, the model calculates the amount of carbon and nitrogen that are available for growth according to the total NSC and NSN and current leaf and fine root biomass. Basically, the available NSC (G_C) is the summation of a small fraction (f_1) 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 (f_2) of NSC (Eq. 6.1). The available NSN (G_N) is analogous to that of the NSC and meets approximately the stoichiometrical requirement of plant tissues (Eq. 6.2).

$$G_C = \min\,(f_1NSC + L^* + FR^* - L - FR, f_2NSC\ ) \qquad \text{(Eq. 6.1)}$$

$$G_N = \min\,(f_1NSN + N^*_L + N^*_{FR} - N_L - N_{FR}, f_2NSN,) \qquad \text{(Eq. 6.2)}$$

where L^* and FR^* are the targets of leaves and fine roots, respectively (see Eq. 3); L and FR are current leaf and fine roots biomass, respectively; N^*_L and N^*_{FR} are nitrogen of leaves and fine roots at their targets according to their target C:N ratios. The parameter f_2 gives the daily availability of NSC during periods of leaf flush at the beginning of a growing season and f_1 normal growth of stems after plant leaves and fine roots approach their targets. Usually, parameter f_1 is much greater than f_2. We let f_1=0.02 and f_2= 1/(365x3) in this study.

The allocation of the available NSC (i.e., G_C) to wood (G_W), leaves (G_L), fine roots (G_{FR}), and seeds (G_F) follows the equations below (Eq. 7). These equations describe the mass growth of plant tissues with nitrogen effects on the carbon allocation between high-nitrogen tissues and low-nitrogen tissues (wood) for maximizing leaves and fine roots growth (G_L and G_{FR}, respectively), optimizing carbon usage at given nitrogen supply (G_N), and keeping the tissues at their target C:N ratios.

$$G_C \geq G_W + G_L + G_{FR} + G_F \quad \text{(Eq. 7.1)}$$

$$G_N \geq \frac{G_L}{CN_{L,0}} + \frac{G_{FR}}{CN_{FR,0}} + \frac{G_F}{CN_{F,0}} + \frac{G_W}{CN_{W,0}} \quad \text{(Eq. 7.2)}$$

$$\frac{(FR+G_{FR})\gamma}{(L+G_L)/\sigma} = \varphi_{RL} \quad \text{(Eq. 7.3)}$$

$$G_L + G_{FR} = Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} \cdot r_{S/D} \quad \text{(Eq. 7.4)}$$

$$G_F = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot v \cdot r_{S/D} \quad \text{(Eq. 7.5)}$$

$$G_W = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot (1 - v \cdot r_{S/D}) \quad \text{(Eq. 7.6)}$$

where, $CN_{L,0}$, $CN_{FR,0}$, $CN_{F,0}$, and $CN_{W,0}$ are the target C:N ratios of leaves, fine roots, seeds, and sapwood, respectively; γ is specific root area (m^2 kgC^{-1}); σ is leaf mass per unit area (kgC m^{-2}); $f_{LFR,max}$ is the maximum fraction of G_C for leaves and fine roots (0.85 in this study); v is the fraction of left carbon for seeds (0.1 in this study); $r_{S/D}$ is a nitrogen-limiting factor ranging from 0 (no nitrogen for leaves, fine roots, and seeds) to 1 (nitrogen available for full growth of leaves, fine roots, and seeds). The parameter $r_{S/D}$ controls the allocation of G_C and G_N to the four plant pools (Eq. 7.1). It can be analytically solved (Eqs. 8 and 9).

$$r_{S/D} = Min\left[1, Max\left(0, \frac{G_N - G_C/CN_W}{N_{demand} - G_C/CN_W}\right)\right] , \quad \text{(Eq. 8)}$$

where, N_{demand} is the potential N demand for plant growth at $r_{S/D}$=1 (i.e., no nitrogen limitation).

$$N_{demand} = \frac{\gamma\sigma\left[FR + Min\begin{pmatrix} L^{*} + FR^{*} - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \varphi_{RL} L}{(\gamma\sigma + \varphi_{RL}) CN_L} + \frac{\varphi_{RL}\left[L + Min\begin{pmatrix} L^{*} + FR^{*} - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \gamma\sigma L}{(\gamma\sigma + \varphi_{RL}) CN_{FR}} + \frac{v\left[G_C - Min\begin{pmatrix} L^{*} + FR^{*} - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_F} + \frac{(1-v)\left[G_C - Min\begin{pmatrix} L^{*} + FR^{*} - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_W}. \tag{Eq. 9}$$

When $G_N \geq N_{demand}$ ($r_{S/D} = 1$), there is no nitrogen limitation, and all the G_C will be used for plant growth and the allocation follows the rules of the carbon only model (Eqs 7.4~7.6 as $r_{S/D} = 1$). The excessive nitrogen ($G_N - N_{demand}$) will be returned to the NSN pool. When $G_C/CN_{W,0} < G_N < N_{demand}$ (i.e., $0 < r_{S/D} < 1$), all G_C and G_N will be used in new tissue growth; however, the leaves and fine roots cannot reach their targets at this step. When $G_N \leq G_C/CN_{W,0}$ ($r_{S/D} = 0$), all the G_N will be allocated to sapwood and the excessive carbon ($G_C - G_N CN_{W,0}$) will be returned to NSC pool. This is a very rare case since a low G_N leads to low leaf growth, reducing G_C before the case $G_N < G_C/CN_{W,0}$ happens. Therefore, in most cases, Eq. 7.1 is: $G_C = G_W + G_L + G_{FR} + G_F$.

Allocation to wood tissues (G_W) drives the growth of tree diameter, height, crown area, and thus increases the targets of leaves and fine roots (Eq. 3). By differentiating the stem biomass allometry in Eq. 2 with respect to time, using the fact that dS/dt equals the carbon allocated for wood growth (G_W), we have the diameter growth:

$$\frac{dD}{dt} = \frac{G_W}{0.25\pi\Lambda\rho_W\alpha_Z(2+\theta_Z)D^{1+\theta_Z}} \tag{Eq. 10}$$

This equation transforms the mass growth to structural changes in tree architecture. With an updated tree diameter, we can calculate the new tree height and crown area using allometry equations (Eq. 2) and targets of leaf and fine root biomass (Eq. 3) for the next step growth. Overall, this is a flexible allocation scheme and still follows the major assumptions in the previous version of LM3-PPA (Weng, et al., 2015, 2017). This allocation scheme prioritizes the allocation to leaves and fine roots, maintains a minimum growth rate of stems, keeps the constant area ratio of fine roots to leaves, and optimizes resource usage by maximizing leaf and fine root growth when nitrogen is abundant and increasing allocation to wood tissues when nitrogen is limited. When nitrogen is limited, plants allocate a larger portion of NPP to stems and thus lower down leaves and fine roots, reducing photosynthesis and carbon supply."

And, we also discussed this allocation scheme from its first principles to competition mechanisms (Section **4.1 Modeling of allocation and competition and their effects on model predictions**)

"In our model, the allocation of carbon and nitrogen within an individual tree is based on allometric scaling, functional relationships, and optimization of resource usage. Basically, the allometric scaling relationships define the maximum leaf and fine root growth at a given tree size and the functional relationships (pipe model) define the ratios of leaf area to sapwood cross-sectional area and fine root surface area. These rules are commonly used in ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). Overall, these rules lead to the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to stems after leaf and fine root growth).

We define a maximum leaf and fine root allocation, $f_{\mathrm{LFR,max}}$, to limit the maximum allocation to leaves and fine roots to maintain a relatively stable growth rate of wood in years of low productivity. The simulated wood growth patterns agree with real wood growth in temperate trees (Cuny et al., 2012; Michelot et al., 2012). Trees need to grow new wood tissues continuously (especially early in the growing season) to maintain their functions (Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots are the priority. Since allocation ratios to stems are around 0.4~0.7 in temperate forests (Curtis et al., 2002; Litton et al., 2007), with a value of 0.85, $f_{\mathrm{LFR,max}}$ only seldom affects the overall carbon allocation ratios of leaves, fine roots, and stems, and still maintains wood grow in years of low productivity. If $f_{\mathrm{LFR,max}} = 1$ (i.e., the highest priority for leaf and fine root growth), simulated trunk radial growth would have unreasonably high interannual variation because leaf and fine root growth would use all carbon to approach to their targets, leaving nothing for stems in some years of low productivity."

While I understand that this is a theoretical study, and such studies are valuable and note ***every study needs to show a comparison with data*****, *there is a complete lack of model reality checking*****. *Especially when the two model versions show contrasting allocation patterns, there should be a way to determine what the reality is. There is a wealth of data from FACE experiments, N addition experiments, long-term measurements, soil N gradients etc. I believe it would be very interesting to have a section in the discussion comparing the current model predictions with general observed trends.*

We agree with this comment. We have added three paragraphs in Discussion for reality checking of the model and discussing our simulation results.

"Our competitively-optimal predictions are generally consistent with observations of forest ecosystem production and allocation. For example, high nitrogen environments (i.e., productive environments) favor high wood allocation and low root allocation (Litton et al., 2007; Poorter et al., 2012) because the woody tissues are an unlimited sink for surplus carbon. Low nitrogen availability limits plant CO_2 responses (Norby et al. 2010) in the competition runs (polyculture) because of high root allocation. Our model predicts increased root allocation at all nitrogen levels in response to elevated [CO_2] in the competition runs. Data from free air CO_2

enhancement (FACE) forest experiments largely agree (Drake et al., 2011; Iversen et al., 2012; Jackson et al., 2009; Lukac et al., 2003; Nie et al., 2013; Pritchard et al., 2008; Smith et al., 2013). However, in ORNL-FACE, the increases in root production due to elevated CO_2 increase and then declined after 8 years of CO_2 enhancement (Iversen, 2010; Norby and Zak, 2011). Though there are no direct data available for quantitatively validating the patterns predicted by our model, especially for the long-term, competitive runs, a detailed modeling analysis can help to understand the varied patterns in the experiments and shed light on the modeling of allocation. ”

As it is, the discussion mostly contains comparisons with previous models from the same model family, which while I think is probably relevant to the authors for model development purposes, is of little interest to the general audience.

We have summarized the universal rules of this modeling approach and added a paragraph in discussion to compare with other model predictions.

“In our model, the allocation of carbon and nitrogen within an individual tree is based on allometric scaling, functional relationships, and optimization of resource usage. Basically, the allometric scaling relationships define the maximum leaf and fine root growth at a given tree size and the functional relationships (pipe model) define the ratios of leaf area to sapwood cross-sectional area and fine root surface area. These rules are commonly used in ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). Overall, these rules lead to the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to stems after leaf and fine root growth).”

We also discussed the emerging common principles for modeling allocation:

“As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014). Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences."

Detailed comments

L 52 I'm not sure there are any ESM's that just simulate the nitrogen cycle, this sentence might need rephrasing

We rephrased this sentence to "that simulate ecosystem biogeochemical cycles as lumped pools and fluxes …".

L85 the last sentence in this paragraph ("Competitively-optimal...") does not follow directly from the rest of the paragraph, there seems to be a logic jump. What is competitively-optimal? How does such a model result in allocation strategies?

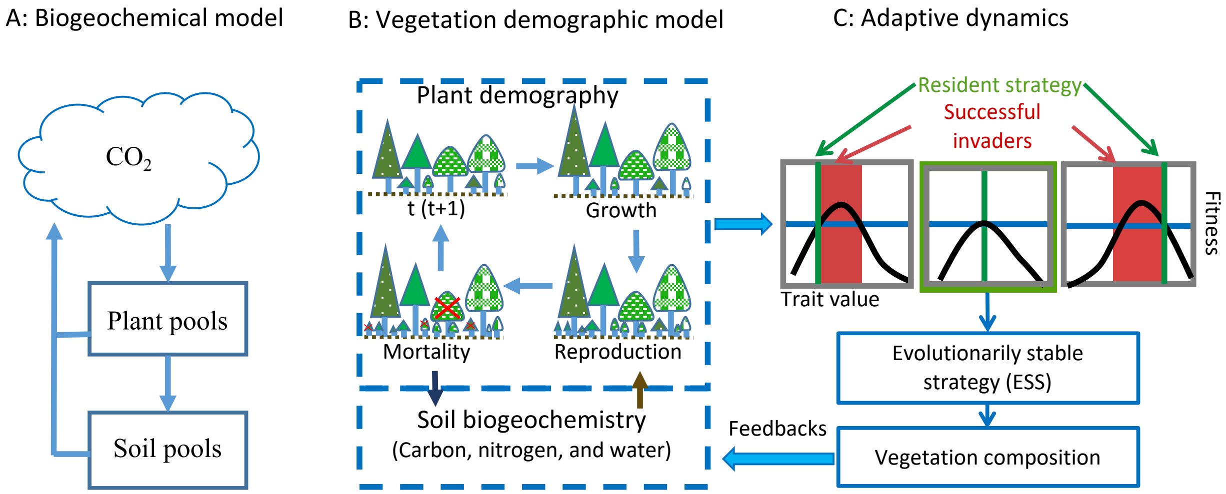
We reorganized these three paragraphs and add a couple of sentences (in a paragraph) to explain "competitively optimal strategy".

" 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, VDMs explicitly simulate demographic processes, such as plant reproduction, growth, and mortality, to generate the dynamics of populations (Fig. 1: B). To speed computations and minimize complexity, groups of individuals are usually modeled as cohorts. With multiple cohorts and PFTs, VDMs can bring plant functional diversity and adaptive dynamics into ESMs when explicitly simulating individual-based competition for different resources and vegetation succession and thus predict dominant plant traits changes with environmental conditions and ecosystem development (Scheiter et al., 2013; Scheiter and Higgins, 2009; Weng et al., 2015).

The combinations of plant traits represent the competition strategies at different stages of ecosystem development. Evolutionarily, a strategy that can outcompete all other strategies in the environment created by itself will be dominant. This strategy is called an evolutionarily stable strategy or a competitively-optimal strategy (McGill and Brown, 2007). In VDMs, competitively-optimal strategies can therefore be reasonably predicted based on the costs and benefits of different strategies (i.e., combinations of plant traits) through their effects on demographic processes (i.e., fitness) and ecosystem biogeochemical cycles (Fig. 1:C) (e.g., Farrior et al., 2015; Weng et al., 2015)."

L99 There is a lot of information packed into this equation which is not appropriately explained. Also I am not sure if this equation is relevant to the rest of the paper.

We removed this equation and added a figure (Fig. 1) to show the three levels of model processes in VDMs.



L111 The turnover of vegetation carbon pools is generally not only driven by mortality but also tissue senescence

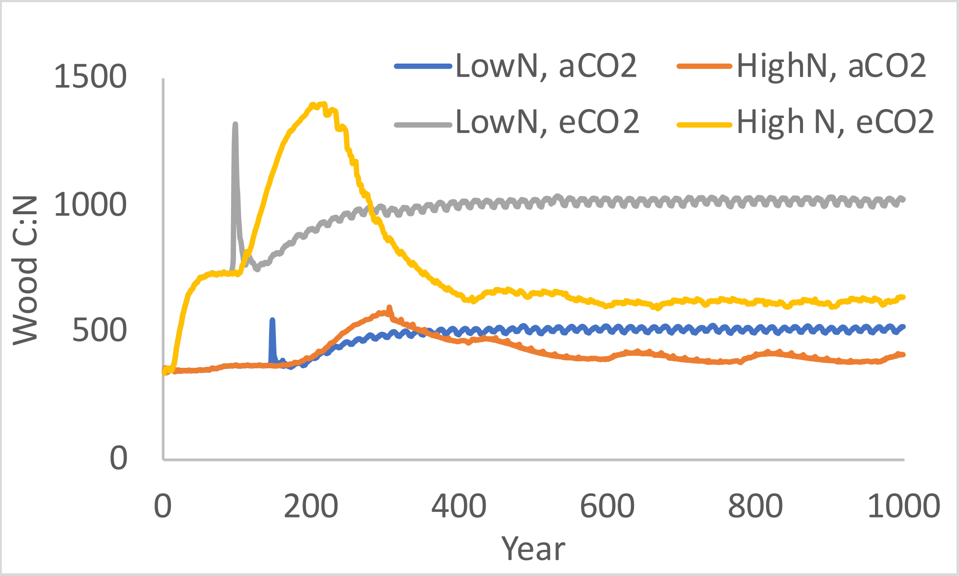
We rephrased this sentence to include senescence of leaves and turnover of fine roots.

"In addition, the turnover of vegetation carbon pools becomes a function of allocation, leaf longevity, fine root turnover, and tree mortality rates, which change with vegetation succession and the most competitive plant traits."

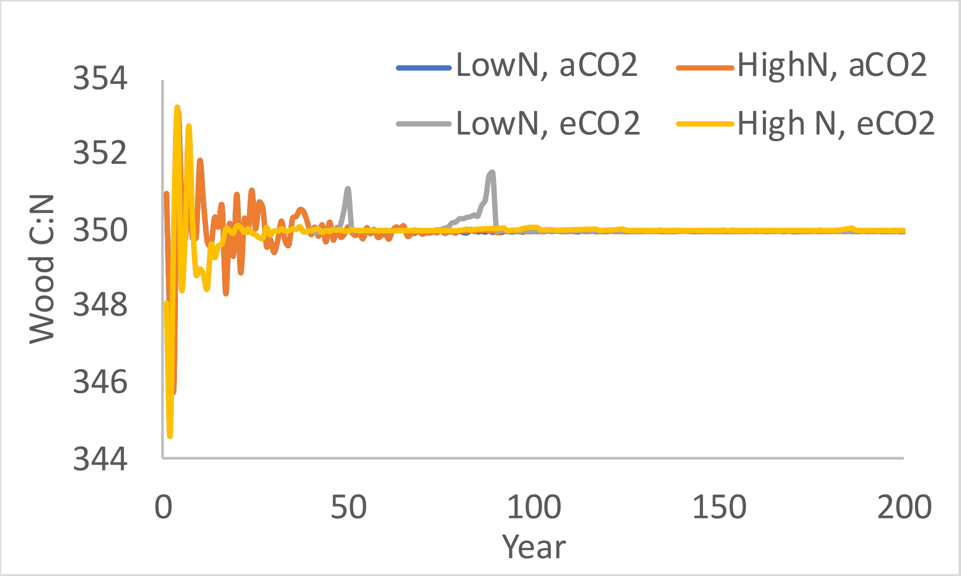
L 207 Are the C:N ratios of all pools considered fixed?

Only leaves and fine roots are strictly fixed. Wood C:N can be variable in numerically solving the allocation patterns for convenience, but the allocation scheme makes it only variates in a very small range.

However, we had a logical bug in our previous codes, making wood C/N ratio not constrained (see the figure below).



We fixed that problem and re-ran all the tests, and updated all the figures with new simulations. For the wood C:/N ratio, see the figure below:



L238, eq. 7 It would help here if the first term and the second term in the minimum function were explained in words - I think it is start of growing season available NSC and during growing season available NSC?

We have re-written this section and in revised manuscript, it is Eq. 6:

"the available NSC (G_C) is the summation of a small fraction (f_1) 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 (f_2) of NSC (Eq. 6.1). The available NSN (G_N) is analogous to that of the NSC and meets approximately the stoichiometrical requirement of plant tissues (Eq. 6.2).

$$G_C = \min\,(f_1 NSC + L^* + FR^* - L - FR, f_2 NSC\,) \qquad \text{(Eq. 6.1)}$$

$$G_N = \min\,(f_1 NSN + N_L^* + N_{FR}^* - N_L - N_{FR}, f_2 NSN,) \qquad \text{(Eq. 6.2)}$$

where L^* and FR^* are the targets of leaves and fine roots, respectively (see Eq. 3); L and FR are current leaf and fine roots biomass, respectively; N_L^* and N_{FR}^* are nitrogen of leaves and fine roots at their targets according to their target C:N ratios. The parameter f_2 gives the daily availability of NSC during periods of leaf flush at the beginning of a growing season and f_1 normal growth of stems after plant leaves and fine roots approach their targets. Usually, parameter f_1 is much greater than f_2. We let f_1=0.02 and f_2= 1/(365x3) in this study."

L245 I'm not sure I understand why step 1 is needed given eq 6c

We have re-written this section and we have a parameter $f_{\mathrm{LFR,max}}$ in the equations for partitioning available carbon and nitrogen into new tissues (i.e., allocation, Eq. 7). Step 1 means 1-$f_{\mathrm{LFR,max}}$, where $f_{\mathrm{LFR,max}}$ is the maximum fraction of available carbon used for leaf and fine root growth. We added a paragraph in Discussion to explain parameter $f_{\mathrm{LFR,max}}$:

"We define a maximum leaf and fine root allocation, $f_{\mathrm{LFR,max}}$, to limit the maximum allocation to leaves and fine roots to maintain a relatively stable growth rate of wood in years of low productivity. The simulated wood growth patterns agree with real wood growth in temperate trees (Cuny et al., 2012; Michelot et al., 2012). Trees need to grow new wood tissues continuously (especially early in the growing season) to maintain their functions (Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots are the priority. Since allocation ratios to stems are around 0.4~0.7 in temperate forests (Curtis et al., 2002; Litton et al., 2007), with a value of 0.85, $f_{\mathrm{LFR,max}}$ only seldom affects the overall carbon allocation ratios of leaves, fine roots, and stems, and still maintains wood grow in years of low productivity. If $f_{\mathrm{LFR,max}}$ = 1 (i.e., the highest priority for leaf and fine root growth), simulated trunk radial growth would have unreasonably high interannual variation because leaf and fine root growth would use all carbon to approach to their targets, leaving nothing for stems in some years of low productivity. "

L254 Does step 4 here imply that the sapwood has variable C:N? Can this increase indefinitely under N limitation?

Yes, sapwood has variable C:N ratio during the numerical iteration. However, it does not lead to indefinite increase in wood C:N because of reduced GPP and relatively stable supply of mineral nitrogen. However, we had a bug in the old codes, making the high equilibrium wood C:N ratio close to 900 (target is 350). We fixed it. Actually, the allocation equations can be analytically solved (please see Eqs. 8 and 9 in the main text, and also copied in response to the major comments).

L279 Is there a justification for the range of soil N availability?

We set this range according to the soil nitrogen content of Harvard Forest from Compton and Boone, 2000. We have updated the manuscript with description of soil nitrogen and references. "In forest sites, soil carbon is around 8 kgC m^{-2} and nitrogen 300 gN m^{-2} (Compton and Boone, 2000). "

L355 Generally, I would say 'hump-shaped' is a curve that goes up then down, which is not the case here.

We rephrased this sentence as "Fine root NPP does not significantly change with total nitrogen in polyculture runs".

L445 Are there no observational studies showing this behaviour?

This study (Dybzinski et al. 2019) is experimental. We added another observational study from Oyewole et al., 2017.

L482 Are there no measurements in the literature of fine root C:N ratios?

There are many measurements of root C:N. However, here, we were trying to talk about its ESS responses to ecosystem nitrogen. We removed this sentence in the revised manuscript since it is not necessary.

Response to Referee #2

This study presents a modeling comparison where a single model was altered with fixed allocation and competition-driven allocation scheme along a nitrogen availability gradient and under ambient and elevated CO_2. The competition scheme that the author considered are nutrient availability and light availability. The authors found that competition-driven allocation scheme predicted different fractional allocation to fine root and wood as compared to fixed-allocation scheme. While the results are generally supported by their study, I do have several issues that I would like to bring to author's attention.

The terms "fixed allocation scheme" is really confusing. It's a "fixed scheme" of allocation, while "allocation" is flexible. We will change to "mono vs. poly" in the revised version.

Major comments:

It appears that the allocation assumptions made in L 254 – 256 are key to their predicted results. In particular, it appears to me that the exact order of ***step 1 and step 2*** *may have a profound effect on the competition dynamics. I wonder what will happen if plant prioritize NSC allocation to leaf and root first, and chuck the remaining C to wood next? In the current text, I think the author did not provide sufficient discussion or justification to these potentially fundamental assumptions. Moreover, what happen if the extra C under step 4 is respired rather than allocated to wood? This could potentially match with some existing model treatment with the extra C, which deserves some discussion.*

We replace the whole section with a new description from the perspective of mathematics. It is in the section of "**Allocation and plant growth**" and copied in the response to the major comments of reviewer #1. We don't copy the whole section here for saving space.

Furthermore, while the results indicate a reversed fractional allocation pattern to fine- root and wood under competition-driven allocation scheme, there is no "data" to actually prove that this new allocation scheme is an improvement to the fixed allocation scheme. Many models already consider "dynamic" allocation based on nutrient avail- ability and water, but the author did not make any comparison against those model behaviors. I'd suggest the authors at least to bridge their modeling results with some observations to make a more convincing argument that their scheme has some advantages.

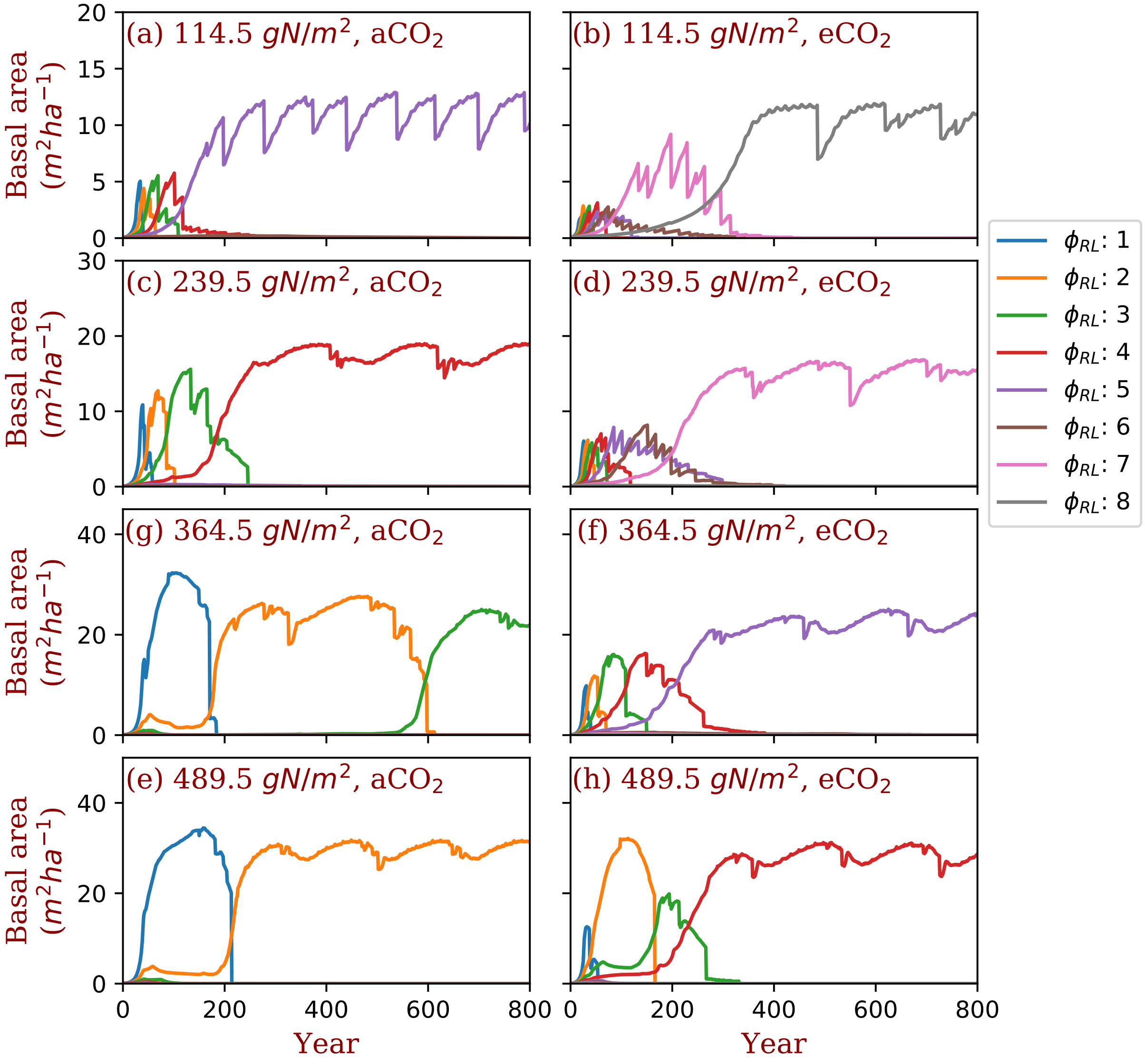
We added two paragraphs to discuss the reality of our simulations and bridge our modelling approach to modeling community.

"Our competitively-optimal predictions are generally consistent with observations of forest ecosystem production and allocation. For example, high nitrogen environments (i.e., productive environments) favor high wood allocation and low root allocation (Litton et al., 2007; Poorter et al., 2012) because the woody tissues are an unlimited sink for surplus carbon. Low nitrogen availability limits plant CO_2 responses (Norby et al. 2010) in the competition runs (polyculture) because of high root allocation. Our model predicts increased root allocation at all nitrogen levels in response to elevated [CO_2] in the competition runs. Data from free air CO_2 enhancement (FACE) forest experiments largely agree (Drake et al., 2011; Iversen et al., 2012; Jackson et al., 2009; Lukac et al., 2003; Nie et al., 2013; Pritchard et al., 2008; Smith et al., 2013). However, in ORNL-FACE, the increases in root production due to elevated CO_2 increase and then declined after 8 years of CO_2 enhancement (Iversen, 2010; Norby and Zak, 2011). Though there are no direct data available for quantitatively validating the patterns predicted by our model, especially for the long-term, competitive runs, a detailed modeling analysis can help to understand the varied patterns in the experiments and shed light on the modeling of allocation"

"As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014). Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences. "

Moreover, the author highlighted that competition for light and nutrient drives successional dynamics (e.g. L 46, 83, 105-107, etc.), which left me with the impression that successional dynamics is a key component of the paper. But in fact, it surprises me that the authors only included results on successional dynamics in the supplementary materials, and there's little discussion around this topic. I'd suggest tightening up Figure S4 and S5, and move them into the main text, with more thorough discussions around them.

We added a succession pattern figure (below) into the paper (Fig. 4 in revised manuscript).



Minor comments:

L 24-26: question: does this mean fixed allocation performs similarly in predicted NPP when compared to those based on competitive-allocation strategy? So the change in allocation pattern does not result in any changes in predicted NPP?

Yes, though NPP changes a little bit. Changes in allocation pattern mainly affect the relative allocation between stems and fine roots. Leaves' NPP is similar at the same nitrogen level.

L35-36. It's a bit unclear what the author trying to illustrate here.

We rephrased this sentence as "competition leads to higher plant biomass response to elevated [CO$_2$] with increasing nitrogen availability".

L38: "ecosystem-level predictions" of what? You indicated earlier that the predicted NPP was similar, right?

Yes, it's ecosystem carbon storage. Clarified in revised manuscript: "significantly different ecosystem-level predictions of carbon storage than those that use fixed strategies".

L230. The symbol φ_{RL} *was described here, which appears to be too late. Suggest to define it in its first appearance.*

We have moved it to the equation where it is used first time and reorganized this section.

Figure 2. The author showed how competition runs compared differently to the fixed allocation runs, based on $\varphi RL = 4$*. Since you are talking about succession and competition, it remains unclear what is the community response?*

We added the successional figures as Fig. 4 (copied above).

Figure 3. Missing unit on y-axis.

Added.

Response to Referee #3 (Dr. Benjamin Stocker)

This paper describes a model and its prediction for competitively optimal allocation (ratio of root to foliage surface area) and how it varies with a range of nitrogen levels and two CO2 levels. The same (or a similar version of the same? See point 12 below) model has been described and applied previously to investigate optimal phenological strategies in Weng et al. (2016, GCB, doi: 10.1111/gcb.13542) and a carbon only version was presented in Weng et al. (2015, BG, doi:10.5194/bg-12-2655-2015).

Thanks for the summary.

The present manuscript addresses allocation as a single variable parameter, although multiple traits affect plant functioning in the face of N availability and CO2 concentrations. However, the focus on allocation is justified, in my opinion, for two reasons: First, allocation warrants particular attention as it is a key process that is known to be responsive to changes in above and belowground resource availabilities and affects the carbon cycling in ecosystems when an allocation shifts occur between long-lived wood and short-lived foliage or fine roots. Second, most vegetation models simulate allocation either based on fixed parameters, or based on empirical relationships. However, as pointed out in the manuscript (l. 528), predicting allocation from first principles is key to realistically and robustly simulating vegetation changes in response to multiple changing environmental factors. The present model embodies a promising way forward to resolve this challenge, determining a competitively optimal allocation strategy, based on height-structured competition for light in the form of a Vegetation Demographics Modelling approach (cohort-based, not average individual-based as is common in Dynamic Vegetation Models). In this respect, the present model takes a pioneering path, that only less than a handful (or even less?) other models can follow.

Thanks for the comments.

I see two main weaknesses of the present study. ***First, predictions are not tested against observational data****. What data needs to be used as a test (see comment 10)? However, I don't expect much additional insight from a comparison to observational data at this stage, and consider the theoretical predictions to deserve to be presented as "naked predictions". However, for a paper that deals with just the theoretical side of the problem, some aspects may warrant additional attention (additional figures for results and extended discussion) in the manuscript (see comments 6, 8, 10, 11).* ***Second, the modelling approach with regards to the excess-C-sapwood allocation*** *(see l.245) raised some questions for me. Is it compatible with our understanding for what controls sapwood area (or what determines the Huber value, defined as the ratio of sapwood area: leaf area)? I worry that this model formulation may cause unrealistic* *model behaviour in some instances. Anyways, the conclusions need to be drawn carefully with regards to this aspect (see comment 5 below).*

I agree with Dr. Stocker. We have updated the description of allocation scheme (copied in response to a major comment of reviewer #1) and discussed the comparison of our simulations with observations and simulations of other models.

Specifically for the Huber value (sapwood area/leaf area), it is kept constant for a PFT, following Eq. 3 ($A_{SW}^{*}(D) = \alpha_{CSA} \cdot l^{*} \cdot A_{CR}(D)$) in the main text of the revised manuscript, where Huber value is a PFT-specific parameter (α_{CSA}). Since the allometry equations are correct (Eq. 2 in the main text) and the model doesn't have processes of plant hydraulics, Huber value is just used to differentiate sapwood and heartwood and does not affect the functions of the trees. We revised the description of this equation in the manuscript and also copied below:

"We set *targets* for leaf (L^{*}), fine root (FR^{*}), and sapwood cross-sectional area (A_{SW}^{*}) 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):

$$L^{*}(D,p) = l^{*} \cdot A_{CR}(D) \cdot LMA \cdot p(t)$$

$$FR^{*}(D) = \varphi_{RL} \cdot l^{*} \cdot \frac{A_{CR}(D)}{SRA} \qquad \text{(Eq. 3)}$$

$$A_{SW}^{*}(D) = \alpha_{CSA} \cdot l^{*} \cdot A_{CR}(D)$$

where L^{*} (D, p), $FR^{*}(D)$, and $A_{SW}^{*}(D)$ are the targets of leaf mass (kg C/tree), fine root biomass (kg C/tree), and sapwood cross sectional area (m^{2}/tree), respectively, at tree diameter D; l^{*} is the target leaf area per unit crown area of a given PFT; 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); φ_{RL} is the target ratio of total root surface area to the total leaf area; SRA is specific root area; and $\square_{\mathrm{CSA}}$ is an empirical constant (the ratio of sapwood cross-sectional area to target leaf area). 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}."

The "excess-C-sapwood allocation" is a numerical step to adjust the growth of leaves, fine roots, wood, and seeds according to available carbon and nitrogen. We have replaced the whole section with a new description of plant growth and allocation. And we also compiled a detailed description of the model in supplementary information I. Please see section "C. Plant growth and carbon allocation", where we have described the conversion from sapwood to heartwood in detail.

Copied below:

“**Conversion from sapwood to heartwood**

As trees grow, sapwood (SW) is transformed to heartwood (HW). This unidirectional process does not affect the size of the woody biomass C pool. We assume that if the actual sapwood cross-sectional area A_{SW} is larger than its target value, $A^*_{SW}(D)$, the excess portion of sapwood biomass is converted to heartwood. Thus, to determine the amount of sapwood converted to heartwood in a given time step (dHW), we simply calculate the difference between SW and the target sapwood C (SW^*) needed to balance L^* and FR^*:

$$dHW = \max(0, SW - SW^*) \tag{C19}$$

Using the equation for total tree biomass (main text Eq. 4), the target biomass of sapwood is:

$$SW^* = 0.25\pi\Lambda\rho_W\alpha_Z(D^{2+\theta_Z} - {D_{HW}}^{2+\theta_Z}) \tag{C20}$$

where D is the diameter of the trunk and D_{HW} is the heartwood diameter, which is given by:

$$D_{HW} = 2\sqrt{A_{HW}/\pi} \tag{C21}$$

where A_{HW} is the cross-sectional area of heartwood. Assuming A_{SW} is at its target value,

$$A_{HW} = A_t - A^*_{SW} \tag{C22}$$

The cross-sectional area of a trunk (A_t) is:

$$A_t = \pi\left(\frac{D}{2}\right)^2 \tag{C23}$$

And, according to Eq A2.1 and Eq A2.3, the target cross sectional area of sapwood is defined as:

$$A^*_{SW} = \alpha_{CSA}l^*A_{CR}(D) = \alpha_{CSA}l^*\alpha_C D^{\theta_C} \tag{C24}$$

”

In the “SPECIFIC POINTS” described below, I am suggesting some modifications in the description of the model and to improve readability, and some changes in the presentation to distill the most relevant points and most interesting insights from this research. GENERAL POINTS may warrant particular attention. The paper is generally written very well and the presentation of results is clear and clean. If these points can be addressed satisfactorily, I may recommend a revised version of this manuscript for publication in Biogeosciences.

GENERAL POINTS

1. Dynamic adaptation (adaptive plastic responses) of allocation occurs also within species. The present model embodies the assumption that species follow a fixed allocation strategy, and changes in allocation are induced by replacement of species with different allocation strategies. ***Please add a discussion for the assumption of fixed within-species allocation may affect results.***

Our allocation scheme itself is flexible and can change with environment even with one fixed scheme of allocation (i.e., fixed φ_{RL}) by numerically maximizing carbon usage at nitrogen limitation. The key step in solving this set of equations is to solve $r_{D/S}$ in each growth step (daily in this simulator). The parameter $r_{D/S}$ changes with relative nitrogen availability. When there is no nitrogen limitation, $r_{D/S}$ equals to 1 and the allocation follows the conditions defined by Eqs. 7.1~7.5 (carbon only model). When $r_{D/S}$ equals to 0, G_N does not meet the nitrogen demand even if all the G_C is allocated to wood tissues and the model has to return the excessive carbon to the NSC pool (this is a very rare case because of low carbon input long before $r_{D/S}$ approaches to 0 due to nitrogen limitation. However, our codes must be able to deal with all possible cases.). When $r_{D/S}$ is in between ($0< r_{D/S}<1$), the leaves and fine roots cannot reach to their targets after this step of growth (i.e., plants maintain a low LAI in low nitrogen environments). At low nitrogen availability, the parameter $r_{D/S}$ keeps a low LAI, a relatively constant NPP/GPP ratio, and a relatively stable NSC for each single PFT.

We have updated the section in the revised manuscript to give a detailed description mathematically (**Allocation and plant growth**).

We have added two paragraphs to discuss this allocation scheme following this suggestion in Discussion.

"In our model, the allocation of carbon and nitrogen within an individual tree is based on allometric scaling, functional relationships, and optimization of resource usage. Basically, the allometric scaling relationships define the maximum leaf and fine root growth at a given tree size and the functional relationships (pipe model) define the ratios of leaf area to sapwood cross-sectional area and fine root surface area. These rules are commonly used in ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). Overall, these rules lead to the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to stems after leaf and fine root growth).

We define a maximum leaf and fine root allocation, $f_{LFR,max}$, to limit the maximum allocation to leaves and fine roots to maintain a relatively stable growth rate of wood in years of low productivity. The simulated wood growth patterns agree with real wood growth in temperate trees (Cuny et al., 2012; Michelot et al., 2012). Trees need to grow new wood tissues continuously (especially early in the growing season) to maintain their functions (Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots are the priority. Since allocation ratios to stems are around 0.4~0.7 in temperate forests (Curtis et al., 2002; Litton et al., 2007), with a value of 0.85, $f_{LFR,max}$ only seldom affects the overall carbon allocation ratios of leaves, fine roots, and stems, and still maintains wood grow in years of low productivity. If $f_{LFR,max} = 1$ (i.e., the highest priority for leaf and fine root growth), simulated trunk radial growth would have unreasonably high interannual variation because leaf and fine root growth would use all carbon to approach to their targets, leaving nothing for stems in some years of low productivity."

2. A competitively optimal strategy is determined for stationary boundary conditions. Does this inhibit such a modelling approach to be applicable for global change simulations (transiently changing boundary conditions)? See also comment 11.

This study is not for directly application at global scale, but the succession patterns can be used to understand transient responses of vegetation to climate changes and the model formulations are being incorporated into an Earth system modeling framework (NASA GISS ModelE). Our analysis can help to understand model behavior at global scales.

We also added a paragraph in Section **4.3 Implications for Earth system modeling** to discuss the emerging principles of allocation modeling:

"As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014). Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences."

3. Allocation and the plant-level C and N budgets, assume fixed tissue C:N ratios and flexible allocation to sapwood to make C and N budgets work. ***This does not correspond to the known controls on sapwood area and may induce unwanted model behaviour.*** *However, it is difficult to think understand to what degree this affects the results and conclusions. See also comment 5.*

The allocation between fine roots plus leaves and wood does not affect the differentiation between sapwood and heartwood. We have a detailed description of the conversion from sapwood to heartwood in the appendix of Weng et al. 2015. The new tissues of wood are always counted as sapwood, and the oldest tissues are converted to heartwood. Actually, the differentiation between sapwood and heartwood does not affect model function in this model because we don't have plant hydraulics yet in this model. We included a supplementary material to describe the conversion from sapwood to heartwood. This section is copied in the response to General Points 1.

4. Total N that is circulating in the system is manipulated for the different simulations, with zero N loss and inputs. This sounds like a rather pragmatic than realistic solution. In reality, losses are never zero, and N levels are manipulated in experiments by fertilisation. Why is it not implemented like this? Would you expect any systematic differences between your implementation and one with non-zero losses and manipulated inputs?

The processes of nitrogen inputs and losses are complex, involving nitrogen deposition, fixation, soil nitrogen mineralization, root uptake efficiency, microbial immobilization, leaching, denitrification, etc.. However, at equilibrium state, the total ecosystem nitrogen is determined by relative rates of nitrogen input and nitrogen output. For example, a high nitrogen input and low output lead to high total ecosystem nitrogen level. In this study, we pack all these effects by setting different total N levels to represent implicitly relative nitrogen input and loss rates. For example, a high total ecosystem nitrogen level represents the ecosystems and edaphic conditions with relative high nitrogen input and low loss rates. By packing these processes into different total N levels, we can focus our study on allocation.

We did both nitrogen closed (with zero nitrogen input and loss) and nitrogen open (with non-zero nitrogen input and output) runs in a previous study (Weng et al. 2017, Global Change Biology). In both types of runs, the nitrogen level determines the competition of PFTs and the competitively optimal player since plants can only "feel" the nitrogen availability, and don't "care" how this availability is set (e.g., either by setting the total N or through complex input and output processes).

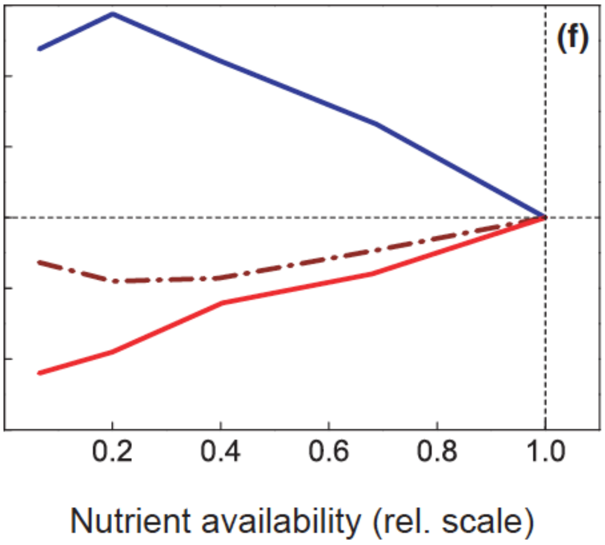
We explained the meaning of the different nitrogen levels in the section of simulation experiments.

"In all the simulation experiments, we assume the ecosystem has no nitrogen inputs and no outputs for convenience since we already have eight total nitrogen levels to represent the consequences of different nitrogen input and output processes at equilibrium state."

5. The abstract mentions "opposite fractional allocation to fine roots and wood" in competitive and fixed-allocation runs. ***Relatively more allocation to fine roots at high N levels in fixed allocation runs sounds like a result that runs counter to the common understanding of the controls on fine root allocation*** *(e.g. Poorter et al., 2012 New Phytologist, doi: 10.1111/j.1469-8137.2011.03952.x), and appears confusing in view of the fact that the model is based on a fixed* *root:leaf area ratio.* ***I suspect that the increase in relative root allocation at high N levels in the fixed-allocation run is a result of the excess-C-sapwood allocation in this model.*** *See also my comment 3. If this is indeed the case, I would recommend not to present results in the abstract that are contingent on this, arguably unrealistic, model behaviour. I guess the authors don't want to challenge the common understanding of fine root allocation controls with their results. It would suffice to point out that in the competition runs, relative fine root allocation de- creases with increasing N levels; and present this in the light of the common modelling approach whereby the root:leaf area ratios (and effective relative allocation ratios) are fixed.*

Thanks for the suggestion. High allocation to fine roots is resulted from "**excess-C-sapwood allocation**" in the allocation scheme for the individual growth (numerical solution of parameter $r_{D/S}$). The model solves two parameters in these model runs: $r_{D/S}$ (at each daily step for both single PFT runs and multi PFTs runs) and φ_{RL} (after more than a thousand years model runs with multiple PFTs).

Our results are consistent with Poorter et al. 2012 well (Fig. 1:f of Poorter et al. 2012), because their data should be compared with our multi-PFT, long-term simulation results (i.e., competitively optimal strategy in our Fig. 3). For a single PFT (fixed strategy and short-term responses to nitrogen addition), it should be compared with fertilization experiments (e.g., Lee & Jose 2003, Forest Ecology & Management).



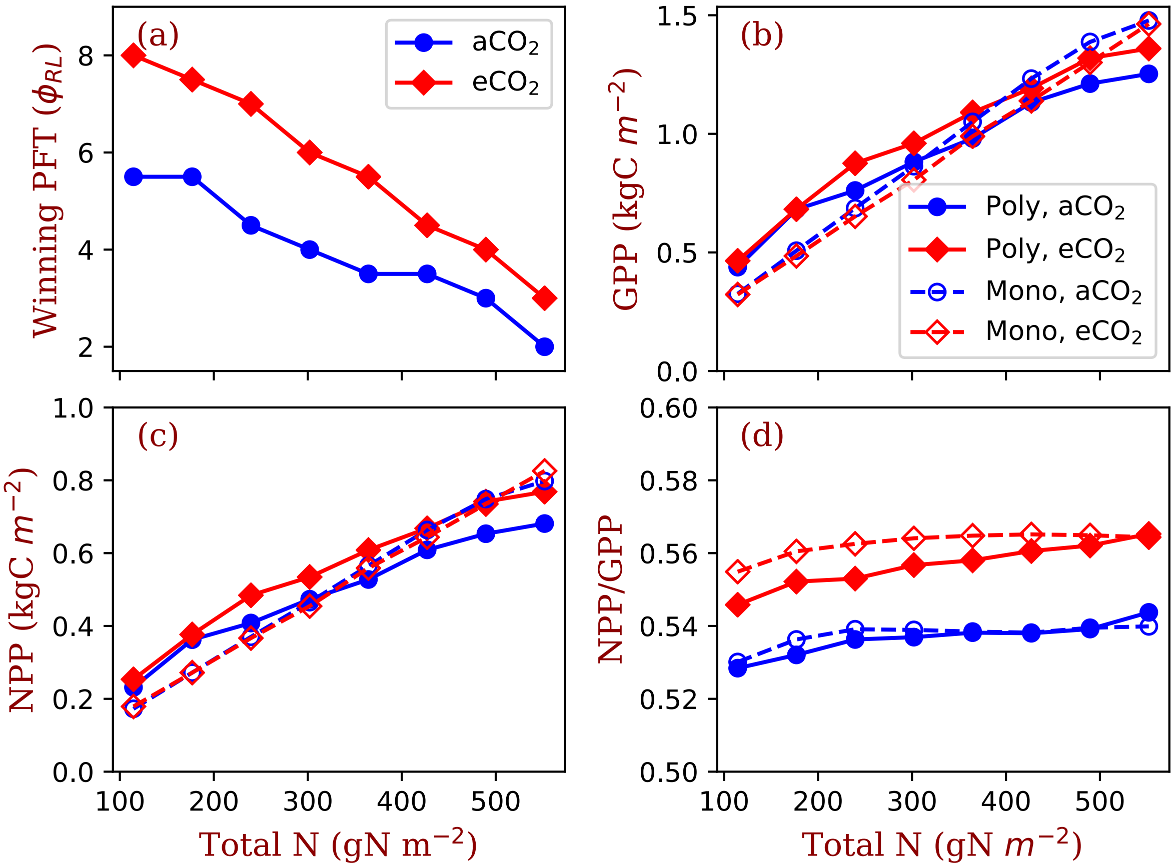
leaves (LMF; red line), stems (SMF; brown line) and roots (RMF; blue line)

We have added a paragraph in discussion to validate our simulation results.

"As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014). Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences."

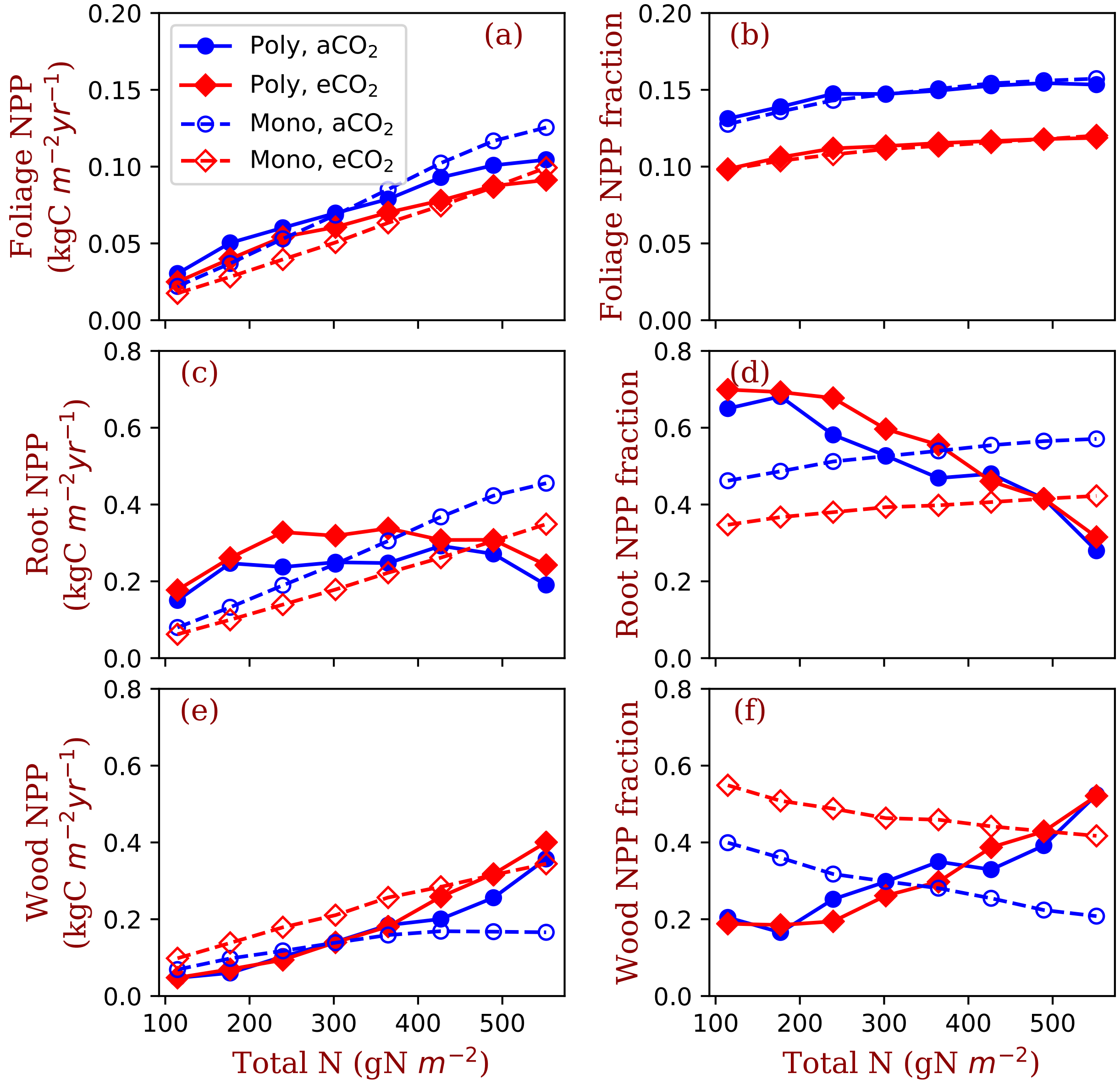
6. Presentation of results for a fixed φ: In my understanding, the essence of this research is to predict how stand-level relative allocation changes in response to N availability and CO2. The approach to predict it is to derive a competitively optimal allocation strategy at the individual-level. In view of the main aim (essence) of this research, I would expect as a (first) figure something that shows competitively optimal φ for each N/CO2 level, derived from the competition runs.

Thanks for the suggestion. We added a panel into Fig. 5 in revised manuscript (original Fig. 3) to show the winning strategy in polyculture runs, which shows the closest φ_{RL} to the competitively optimal. We also added two figures in supplementary material II (Fig. S4 and S5) to show the winning φ for each N and CO_2 level in polyculture runs II.



7. A question: Does each point in Fig. 3 show the wood/root/foliage NPP (fraction) for the competitively optimal φ at the respective N and CO2 levels (for the competition runs)? Comparing this to values from fixed-allocation runs with a pre-specified φ is maybe not the most interesting. This leads to the next point. . .

The left is absolute, and right is fraction. We have updated this figure (Fig. 6 in revised manuscript)



8. [see Addendum to this comment] In view of my comment 1 (dynamic adaptation of allocation also within species), readers may want to know ***if an optimality criterion that is defined for some instantaneous individual-level metric (like foliage NPP, or height growth, etc.) leads to the (qualitatively) same predictions as an optimality criterion that is funded in an evolutionarily stable strategy (ESS, like the one applied here)****. It might be interesting to evaluate the fixed-allocation runs to determine which φ maximises some optimality criterion (like foliage NPP, or height growth, etc.). A (first) figure could then compare this individual-level derived optimal φ to the ESS-derived optimal φ. Furthermore, points in Fig. 3 for the fixed-allocation runs could then be taken to represent the φ level that maximises the optimality criterion for each N/CO2 level respectively. This would also enable a direct comparison of the* *two optimality approaches (ESS vs. instantaneous). I understand if this suggestion is beyond the scope of this paper, or not feasible. Anyways, I would be interested to learn more about such a comparison. Addendum: I see now (upon reading the Discussion, l. 425), that this point is addressed by Supplementary figures S1 and S2. Maybe this is too much of my own personal interest, but I think to generally enhance this point in the presentation of the results (possibly with additional/modified figures as suggested above) would improve the manuscript.*

We explained the differences between optimal vs. competitively optimal in introduction following reviewer's suggestion. Basically, optimal strategy is not necessarily the competitively optimal. From Figures 1 and 2, you can see that low root allocation is optimal in many N levels. However, they cannot outcompete high root allocation strategies if invaded by them. That means, in the environment created by the optimal strategy individuals, another strategy can out compete the resident, though it may have low NPP or fitness in monoculture. The revision is copied below:

"The competitively optimal strategy is the one that can successfully exclude all others in the processes of competition and succession, but it is not necessarily the one that maximizes production in monoculture. For example, each φ_{RL} creates an environment of light profile and soil nitrogen in its monoculture. Other φ_{RL} PFTs may have higher fitness in this environment than the one who creates it. Only the competitively dominant strategy has the highest fitness in the environment it creates (Fig. 1: C)."

9. A description of how the competitively optimal allocation is determined (description of the algorithm), would be helpful. May be added before current Section 2.2.

We have added a description of competitively optimal strategy following this suggestion.

"The process of choosing a context-dependent competitively 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 competitively optimal strategy is the one that can successfully exclude all others in the processes of competition and succession, but it is not necessarily the one that maximizes production in monoculture. For example, each φ_{RL} creates an environment of light profile and soil nitrogen in its monoculture. Other φ_{RL} PFTs may have higher fitness in this environment than the one who creates it. Only the competitively dominant strategy has the highest fitness in the environment it creates (Fig. 1: C). "

10. The differences in predictions based on different allocation schemes are interesting, but the missing comparison to observational data prevents conclusions to be drawn about which is more realistic or leads to better model performance. The question is: What is the key observation that can be used to test predictions? And of course: What is the key prediction that authors want to test? In my view, it is a viable option to remain with theoretical predictions, not actually using *data from observations. However, this may require an extended discussion in the light of generally observed patterns with additional references to the literature. The challenge remains that the overproliferation in root growth predicted by the competitively-optimal allocation scheme may not directly be testable.* ***How much is over-proliferation in reality? What would be a suitable observation to evaluate this prediction?***

We added a paragraph in discussion to discuss the experimental results related to root overproliferation and proposed our expectation of what we want to get from new experiments.

"Root overproliferation is still controversial in experiments. For example, Gersani et al. (2001) and O'Brien (2005) found competing plants generate more roots than those planted isolated for pea and soybeans, respectively; whereas, McNickle and Brown (2014) found root growth follows the availability of soil nutrients and individuals growth with competitors have the same root growth as that predicted by the changed nutrient availability. Roots are far more adaptive and complex than those simulated in models at modifying their growth patterns in response to soil nutrient and water dynamics (Hodge, 2009). The root growth strategies in response to competition also vary with species (Belter and Cahill, 2015). The mechanisms of self-recognition of inter- and intra- roots also can lead to varied behavior of root growth (Chen et al., 2012). However, all of the aforementioned studies considered only *plastic* root overproliferation, where individuals produce more roots in the presence of other individuals than they do in isolation, analogous to stem elongation of crowded seedlings (Dudley and Schmitt, 1996). A portion of root overproliferation may also be *fixed*, analogous to trees that still grow tall even when grown in isolation. Dybzinski et al. (2019) showed that plant community nitrogen uptake rate was independent of fine root mass in seedlings of numerous species, suggesting a high degree of fixed fine root overproliferation. To improve root competition models, more detailed experiments that control root growth should be conducted to quantify the marginal benefits of roots in isolated, monoculture, and polyculture environments. "

11. Regarding implications for Earth system modelling: From reading this manuscript, it's not entirely clear whether the approach for determining the competitively-optimal allocation strategy is applicable for typical Earth system simulations, where boundary conditions change transiently. In my understanding, the approach chosen here determines a system steady state, formed by a monospecific stand with a certain allocation strategy, that cannot be invaded by any species with a different allocation strategy. As explained in the manuscript, this requires the model to be run into steady state for 1200 simulation years. How would this be implemented for a typical Earth system simulation setup? I think it would be very informative to complement Section 4.3 with a discussion on this point.

It is helpful for understanding model behavior and track competitively optimal strategy.

We are exploring one more layer of complexity, adaptive dynamics (or successional dynamics), on the top of the pool-flux dynamics and demographic dynamics. For a robust DGVM in Earth system models, it is necessary to analyze these processes and their effects on model performance in detail.

We added a paragraph in "**4.3 Implications for Earth system modeling**" to discuss the emerging common principles of allocation modeling:

"As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014). Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences."

12. The description of how the present model version differs from model versions used in Weng et al., 2016, 2015, could be made clearer.

We have compiled a full description of the model in a supplementary material I.

SPECIFIC POINTS

l.96: Should be a gap in 'trait (s)'?

We removed this equation following Reviewer 1's suggestion.

Eq. 2: To solve the model, ds/dt has to be set to zero, I guess. Shouldn't this be reflected in Eq. 2? Or how exactly is the competitively optimal strategy determined?

This equation is used to show the temporal dynamics of a plant trait in evolution, which, conceptually, is the numerical shifts of a plant trait approaching its ESS in simulations.

For analytically solve this equation, one needs to build up a fitness equation, such as:

$$Fitness(s_{\mathrm{I}}|s_{\mathrm{R}}) = Benefit(s_{\mathrm{I}}|s_{\mathrm{R}}) - Cost_{I,R}(s_{\mathrm{I}}|s_{\mathrm{R}}) - Cost_{I}(s_{\mathrm{I}})$$

where, s_I is invader's trait and s_R is residence. Let the derivative of the right side to be zero and according to the definition of ESS s_I=s_R. Then, it is possible to solve it analytically if you are lucky.

We removed this equation following Reviewer 1's suggestion. We agree with the Reviewer 1 that this equation is not very helpful here. We will add a paragraph to explain the processes of approaching ESS by succession in VDMs. Since the numerical simulations are complex, we don't want to complicate the paper with more discussions of this equation.

l.148: Apart from variations in across-species allocation patterns (e.g., oak species tending to invest more into roots), there are also clear patterns in within species and within-individuals (flexible adaptation) variations in allocation when subjected to shifts in resource availability. In my understanding, such fast allocation responses are not captured by the modelling approach here. This should be clarified. Connects to Comment 1 above.

They have to follow the same rules, otherwise they will be replaced by those who follow the rules. Actually, we used only one PFT, which only differs in fine root – leaf area ratio (φ_{RL}). If plants have enough plasticity in allocation, they will approach the ESS much quicker. We will make it clear in a revised manuscript.

l.159: The simulation experiments are described in the abstract and intro to be done along a "nitrogen availability gradient". How did you manipulate N? This is described at a later stage, but could already be made clear here.

We clarified it in the description of Simulation experiments, but did not mention those settings here because they are not part of the universal feature of the model.

"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}) by assigning the initial content of the slow SOM pool for our simulation experiments (Table 1). This range covers the soil nitrogen content at Harvard Forest (Compton and Boone, 2000; Melillo et al., 2011). The nitrogen cycles through the plant and soil pools and is redistributed among them via plant demographic processes, soil carbon transfers, and plant uptake. In all the simulation experiments, we assume the ecosystem has no nitrogen inputs and no outputs for convenience since we already have eight total nitrogen levels to represent the results of different nitrogen input and output processes at equilibrium state. "

Section 2.1: A separate paragraph on how CO2 assimilation is simulated, would be helpful.

We added a brief description of the photosynthesis model, which is the same as it in LM3-PPA and LM3.

“Plant growth and reproduction are driven by the carbon assimilation of leaves via photosynthesis, which is in turn dependent on water and nitrogen uptake by fine roots. The photosynthesis model is the same as it in LM3-PPA (Weng et al., 2015), which is a simplified version of Leuning model (Leuning et al., 1995). This model first calculates photosynthesis rate, stomatal conductance, and water demand of the leaves of each tree (cohort) in the absence of soil water limitation. Then, it calculates available water supply, and reduce the demand-based assimilation and stomatal conductance accordingly if water supply is less than water demand. Assimilated carbon enters into the NSC pool and is subsequently used for respiration, growth, and reproduction. (Please see Supplementary Information I-A for detail).”

Eq. 3: To be consistent with Fig. 1, I would suggest to use the symbol X_FR as the pool size (or C_FR in this case), distinguish community- and individual-level variables for example using a bar over the variable for the community-level, and use a separate letter for the parameter ‘Root_0’ (e.g., K_FR).

Done as suggested. (In revised manuscript, it Eq. 4)

Eq. 4: Should be clarified that this is the community-level total root biomass (if I am correct). Clarification is needed to understand Eq. 4.

Clarified. C_{FR}, total is the total roots in soil, with unit of kgC/m2 and CFR,tree is the total root carbon of a tree (in a cohort with identical trees) with unit of kgC/tree. This equation transforms nitrogen uptake rate from gN m-2 hour-1 to gN tree-1 hour-1. We also added a tale (Table 1) in the revised manuscript for the major parameters of this model.

Eq. 5: D is not defined. Diameter?

Yes, it is diameter. defined.

*l. 215: Add bracket: “. . . targets for leaf, fine root, and sapwood cross-sectional area (L*_k, FR*_k, and A*_SW)” here for a better overview of the description.*

Done as suggested.

Eq. 5/6: How is D incremented? The way the system is described now, the tree doesn’t grow in D or am I missing something?

We add a new equation to show diameter growth.

l. 238: Can you add f_1 and f_2 to the description in this sentence? E.g., “capped by a larger fraction of NSC (f_1)”?

Done as suggested. We switched the definition of f1 and f2 for convenience.

l. 241: Are Eq. 7 and its parameters f_1 and f_2 identical throughout the year? The description here suggests that something is different during leaf flush versus the period of "normal growth". Or maybe I'm just misunderstanding it the way it's formulated now.

They are constant over time. Generally, "f_1NSC" defines the maximum NSC availability at the beginning of a growing season when (L+FR)<<(L^*+FR^*); "f_2NSC"defines the normal growth of stems after (L+FR) is close to (L^*+FR^*) (i.e., normal growth during the growing season; "[(L^*+FR^*) -(L+FR)]" are the carbon for the new leaves and fine roots due to stem growth in last time step.

The term "f_1NSC" also prevents overspending of NSC when NSC is very low in some bad years.

l. 246: Units of 0.15? g C?

It's the fraction of NSC. Clarified. In revised manuscript, we define a parameter to cap the maximum fraction of available carbon allocated to leaves and fine roots, $f_{\mathrm{LFR,max}}$, as:

1 - 0.15 =0.85.

l. 254: Since sapwood production requires N as well (although relatively less than production of other tissues), and "excess C" sounds like this is the amount of NSC left, after NSN is used up (hence zero), I would assume that some iteration is necessary to perfectly match the use of NSC and NSN in the allocation procedure. How is this solved? Either more detail should be given here, or the description should be modified to avoid misunderstanding.

It can be analytically solved. In the codes, we numerically solve it by iterating at daily step and allowing the wood C:N ratio to variate from day to day. We clarified the whole allocation section it in the revised manuscript and added the analytical solution.

"The parameter $r_{\mathrm{S/D}}$ controls the allocation of G_{C} and G_{N} to the four plant pools (Eq. 7.1). It can be analytically solved (Eqs. 8 and 9).

$$r_{S/D} = Min\left[1, Max\left(0, \frac{G_N - G_C/CN_W}{N_{demand} - G_C/CN_W}\right)\right] , \qquad \text{(Eq. 8)}$$

where, N_{demand} is the potential N demand for plant growth at $r_{\mathrm{S/D}}$=1 (i.e., no nitrogen limitation).

$$N_{demand} = \frac{\gamma\sigma\left[FR+Min\begin{pmatrix}L^*+FR^*-L-FR,\\ f_{LFR,max}\,G_C\end{pmatrix}\right]-\varphi_{RL}L}{(\gamma\sigma+\varphi_{RL})CN_L} + \frac{\varphi_{RL}\left[L+Min\begin{pmatrix}L^*+FR^*-L-FR,\\ f_{LFR,max}\,G_C\end{pmatrix}\right]-\gamma\sigma L}{(\gamma\sigma+\varphi_{RL})CN_{FR}} + \frac{v\left[G_C-Min\begin{pmatrix}L^*+FR^*-L-FR,\\ f_{LFR,max}\,G_C\end{pmatrix}\right]}{CN_F} + \frac{(1-v)\left[G_C-Min\begin{pmatrix}L^*+FR^*-L-FR,\\ f_{LFR,max}\,G_C\end{pmatrix}\right]}{CN_W}. \qquad \text{(Eq. 9)}$$

When $G_N \geq N_{demand}$ ($r_{S/D} = 1$), there is no nitrogen limitation, and all the G_C will be used for plant growth and the allocation follows the rules of the carbon only model (Eqs 7.4~7.6 as $r_{S/D} = 1$). The excessive nitrogen ($G_N - N_{demand}$) will be returned to the NSN pool. When $G_C/CN_{W,0} < G_N < N_{demand}$ (i.e., $0 < r_{S/D} < 1$), all G_C and G_N will be used in new tissue growth; however, the leaves and fine roots cannot reach their targets at this step. When $G_N \leq G_C/CN_{W,0}$ ($r_{S/D} = 0$), all the G_N will be allocated to sapwood and the excessive carbon ($G_C - G_N CN_{W,0}$) will be returned to NSC pool. This is a very rare case since a low G_N leads to low leaf growth, reducing G_C before the case $G_N < G_C/CN_{W,0}$ happens. Therefore, in most cases, Eq. 7.1 is: $G_C = G_W + G_L + G_{FR} + G_F$."

l. 260: I would welcome a summarising sentence on the mechanisms determining C:N stoichiometry. The connection between sapwood allocation and the NSC:NSN budget implies that a plant that acquires relatively little N in comparison to assimilated C (in other words: an "N-limited tree") would produce relatively more sapwood. Does this mean that Eq. 6 (the A_SW sub-equation) is "over"-satisfied? What are the implications of this in the model? Does it affect the relationship between height growth vs. crown area expansion?

According to the allometry equation (Eq. 5 in the main text), tree height and crown area are functions of diameter. So, how to define sapwood does not affect anything in the current version of the model. The A_{SW} sub-equation Eq. 6 is used to separate sapwood from the whole trunk. As mentioned in the responses to General comment 2, it does not affect anything of the model. We did this because the model needs this variable. (We really need it when incorporating plant hydraulics.).

We have updated the whole section with a new description of the model's allocation scheme (Pages 10~16, and also copied in response to Reviewer #1's major comments). The partitioning of carbon and nitrogen into the plant pools is constrained by allometric equations, targets of leaves and fine roots, and the C:N ratios of these plant pools. The plant growth (and therefore allocation) is simulated at two steps: 1) calculating the amount of carbon and nitrogen that will be used for plant growth at this time step (which can be hourly, daily, weekly, etc.); 2) allocating the available carbon and nitrogen to leaves, fine roots, seeds, and sapwood following rules of first principles. We let the plant growth follow the rules below as they are in the first version (Weng et al. 2015, Biogeoscieces. carbon only model) and second version of LM3-PPA (Weng et al. 2017, Global Change Biology. carbon and nitrogen). Overall, this is a flexible allocation scheme and still follows the major assumptions in the previous versions of LM3-PPA (Weng, et al., 2015, 2017). It prioritizes the allocation to leaves and fine roots, maintains a minimum growth rate of stems at nitrogen limitation, keeps the constant area ratio of fine roots to leaves, and optimizes resource usage by relocating carbon and nitrogen to wood tissues when nitrogen is not sufficient for full growth of leaves and fine roots. When nitrogen is limited, leaves and fine roots are lower than their targets, reducing photosynthesis and carbon supply.

Section 2.1: A description of how the competitively optimal allocation is determined (description of the algorithm) would be helpful. May be added before current Section 2.2.

We have added a description of "competitively optimal" in the end of Section 2.1.

"The process of choosing a context-dependent competitively 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 competitively optimal strategy is the one that can successfully exclude all others in the processes of competition and succession, but it is not necessarily the one that maximizes production in monoculture. For example, each φ_{RL} creates an environment of light profile and soil nitrogen in its monoculture. Other φ_{RL} PFTs may have higher fitness in this environment than the one who creates it. Only the competitively dominant strategy has the highest fitness in the environment it creates (Fig. 1: C). "

l. 292: "Full factorial" suggests that all combinations of treatment factors are applied to force the runs. But here, this is a mix of a treatment factor (N levels) and model parameter (phi). I suggest to rephrase this.

We removed the word "factorial" and clarified the combinations of PFTs, N levels, and CO2 concentrations of the monoculture runs.

*Table 1: If i=(114.5, . . ., 552) g N m-2, then 4.5-0.5*i is a negative number. Is this correct? Maybe N levels in units of kg N m-2 are used here?*

Here, *i* takes the value of 1, 2, 3, 4, …, 8, following the order of the nitrogen levels from 114.5 to 552 gN m^{-2}. We clarified it.

"For each nitrogen level, we set eight PFTs with φ_{RL} that varied in a range 3.5 (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 (114.5 gN m^{-2}) and decreasing 0.5 per level of increase in ecosystem total N. Let i=1, 2, …, 8 denote the eight N levels from 114.5 to 552 gN m^{-2}, the φ_{RL} of the eight PFTs at each level are (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), 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. "

l. 362-364: The decrease in fractional allocation to fine roots with elevated CO2 at high N levels is surprising. May it be a result of the excess-C sapwood allocation approach implemented in this model? May warrant a brief discussion of this aspect.

In monoculture runs, the fractional allocation to fine roots decreases with elevated CO2 at all N levels because of high nitrogen limitation due to high carbon assimilation (photosynthesis) at elevated CO2. It is consistent with field observations that high production forests have high wood allocation (Litton et al. 2007). In polyculture runs, it only happens in high N levels, because the differences in competitive φRL between the two CO2 concentrations become small (Fig. 4:a), while GPP increases are high, which leads to high fractional allocation to wood.

l. ***386-388: In my reading, this is a main result and should be shown in*** *a separate figure, shown at the very beginning of the results section.*

We moved this paragraph in 390~406 to the beginning of the results section and the figure S1 to the main text as Figure 3.

l. 418-419: See my comment 5.

We removed "but decreases – the opposite qualitative response – under fixed strategy".

l.425: See my comment 8. This is an interesting point, but is dealt with rather briefly here. How is "maximising growth rate" implemented exactly? NPP? NPP of a specific pool? "Allocating very little" is vague. The crucial aspect is that for a given N level and uptake half-saturation constant, the plants allocate much less to fine roots in the best- performing (by what measure?) fixed-allocation run than in the competitively optimal- allocation run.

We removed this sentence because the pattern not so strong in the new simulations, and we discussed the competitively optimal strategy by outcompeting other strategies.

l. 430-433: Sentence is hard to follow. Is the height at transition into the canopy (reaching critical height) increasing or decreasing with increasing N?

We rephrased this sentence: "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." to:

"Increases in the critical height, which is the height of the shortest tree in canopy layer, from low nitrogen to high nitrogen indicates a shift from the importance of competition for soil nitrogen to the importance of competition for light as ecosystem nitrogen increases."

*l. 493 ("succession"): Discussing competitively optimal strategy shifts during succession confused me here. I understood, that the competitively optimal strategy is determined for a *steady-state*, and (based on my understanding from reading previous papers of this group of authors) an ESS is determined from competition upon invasion into a mono-specific stand. But now* ***I realise that the algorithm for determining competitive optimality has never been described in the present paper. A gap that should be filled (see also comments above).***

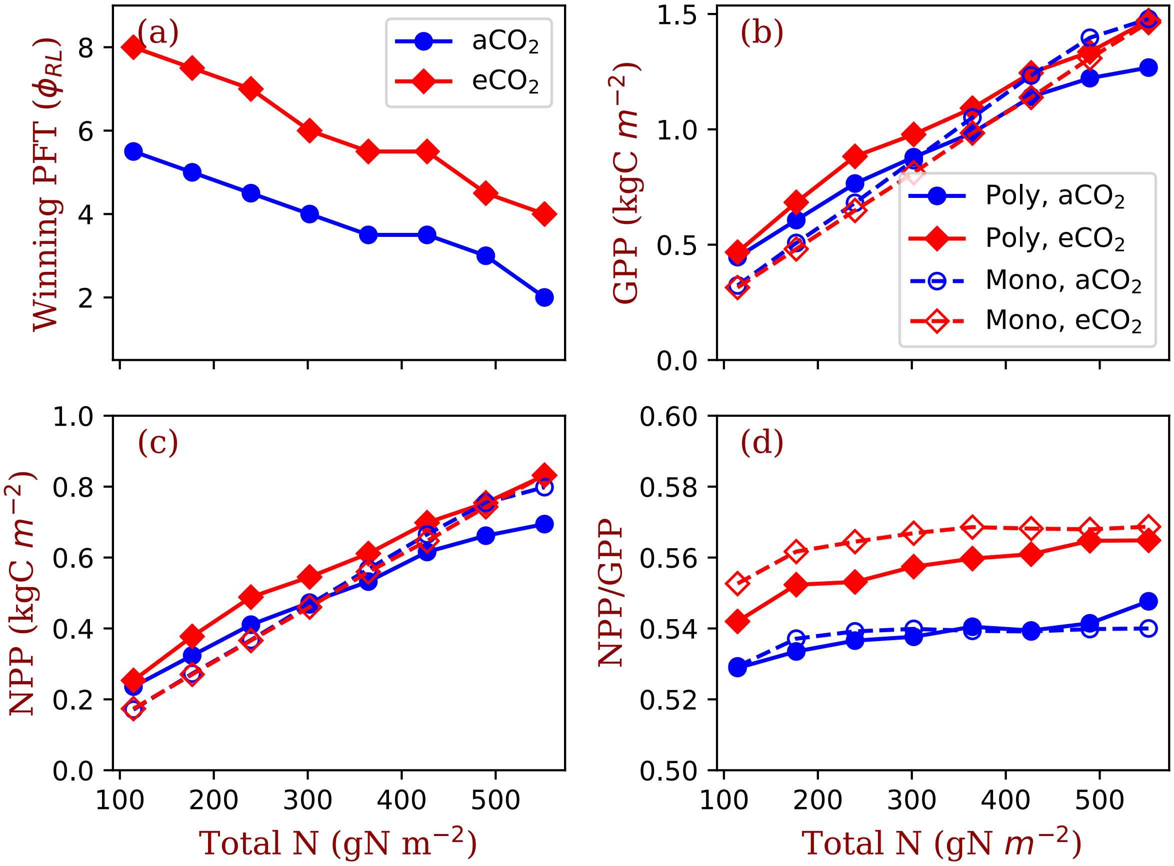
We have added a brief description of "competitively optimal strategy" in model description. In the simulations, the strategy closest to the competitively optimal is obtained by the polyculture runs (i.e., the one who survives 1800 years model run in competition with others).

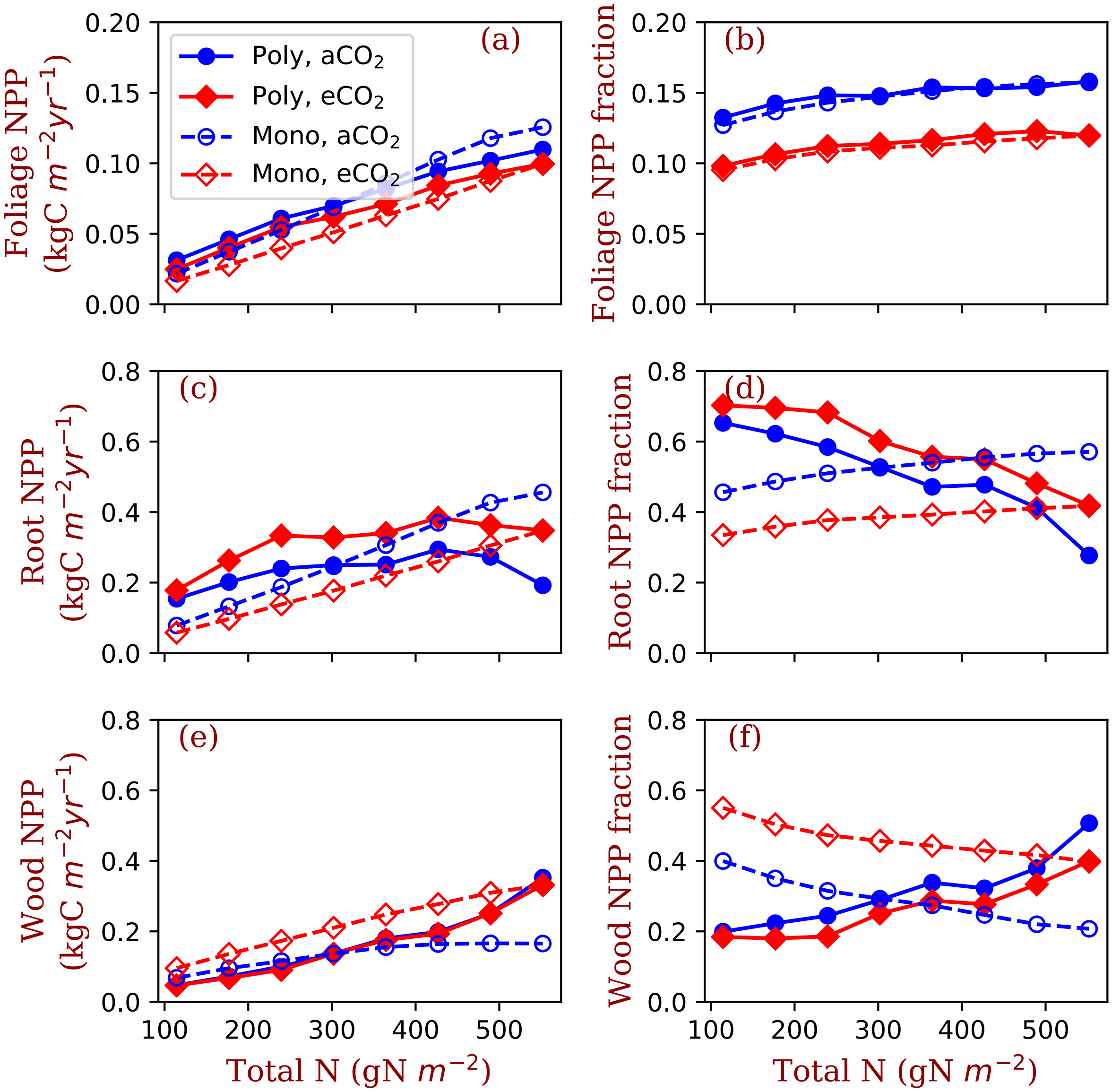
l. 569: I had a great laugh when I read the short description of that repository on github ("BiomeESS: for simulating multiple plant forms, on-going, unpublished, with ridiculous processes and many bugs.") Maybe the author wants to change that upon publication of this manuscript (and if necessary resolve some known bugs). If not, I appreciate the honesty.

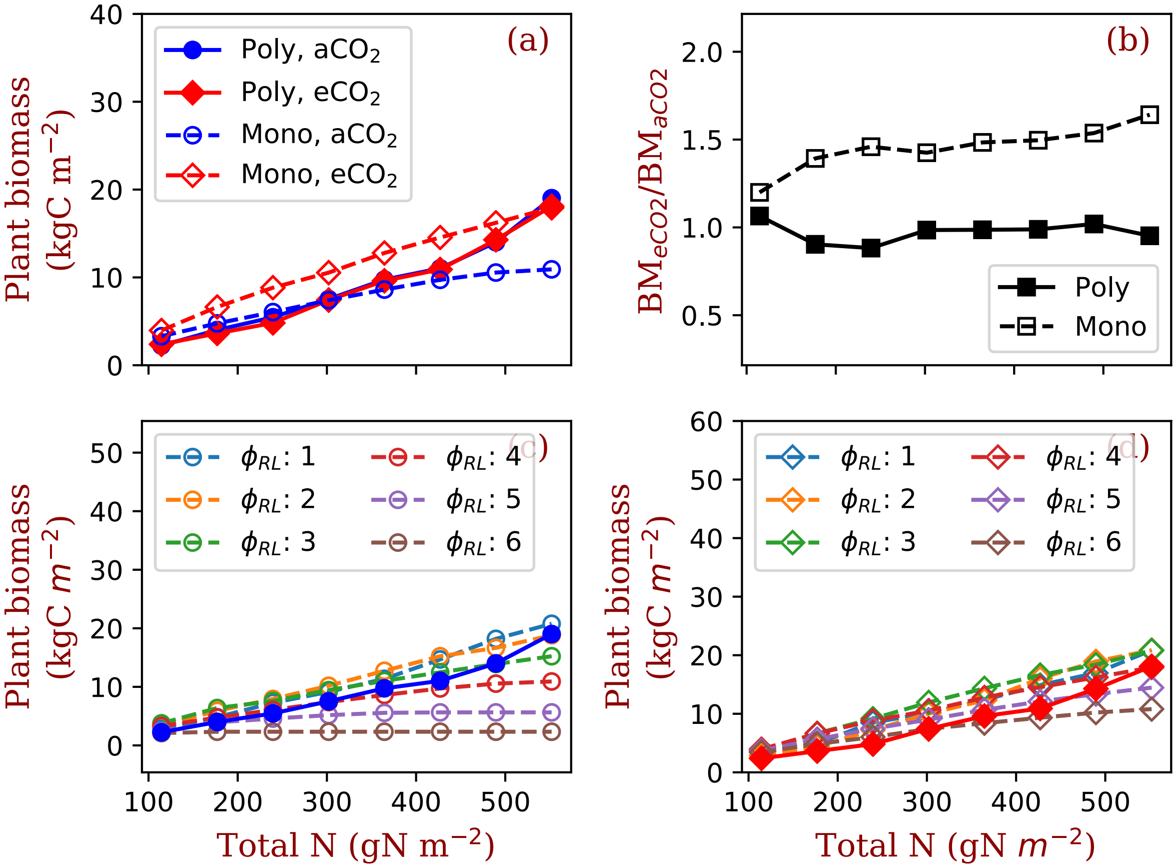
Thanks for taking a look! We have set a new branch for the version used in this paper and we will update the description upon accept of this paper. We also included a detailed description of the model as supplementary material of this paper.

Additional sensitivity tests

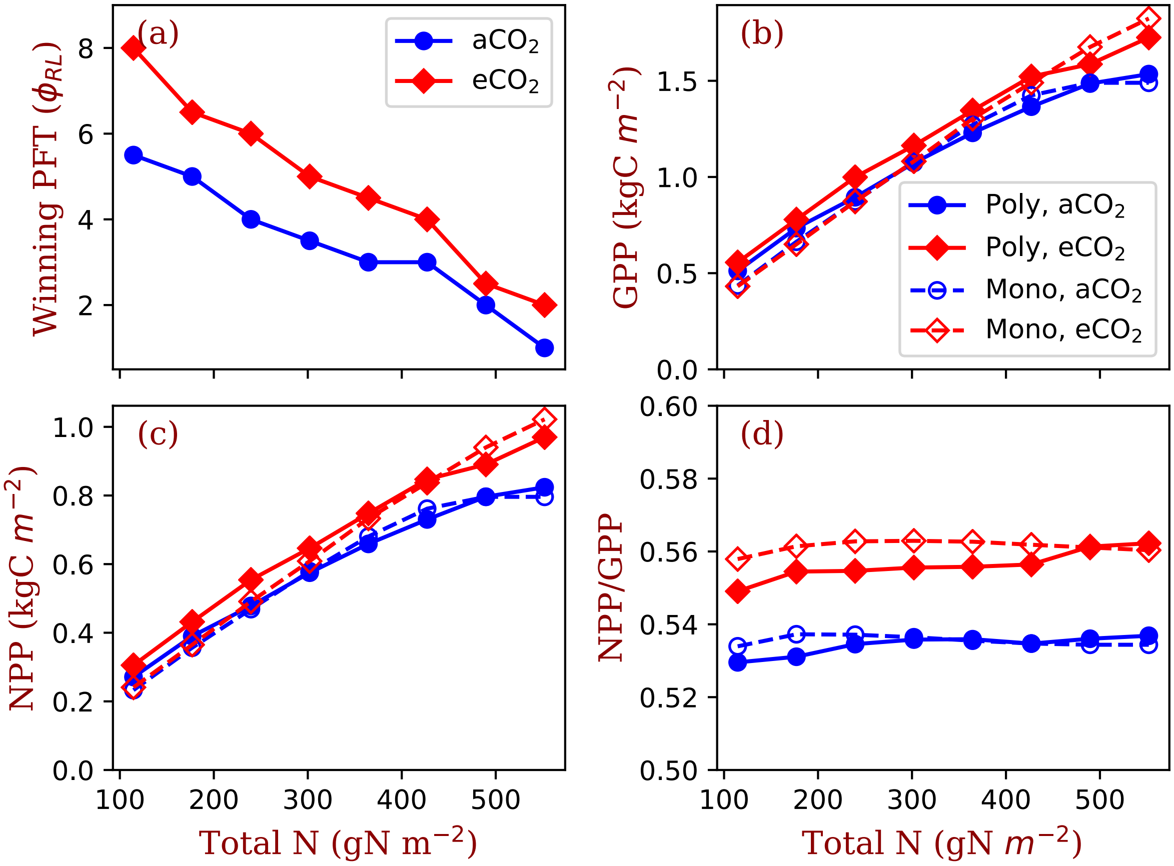
1. Extra carbon returned to non-structural pool when available nitrogen cannot meet the demand

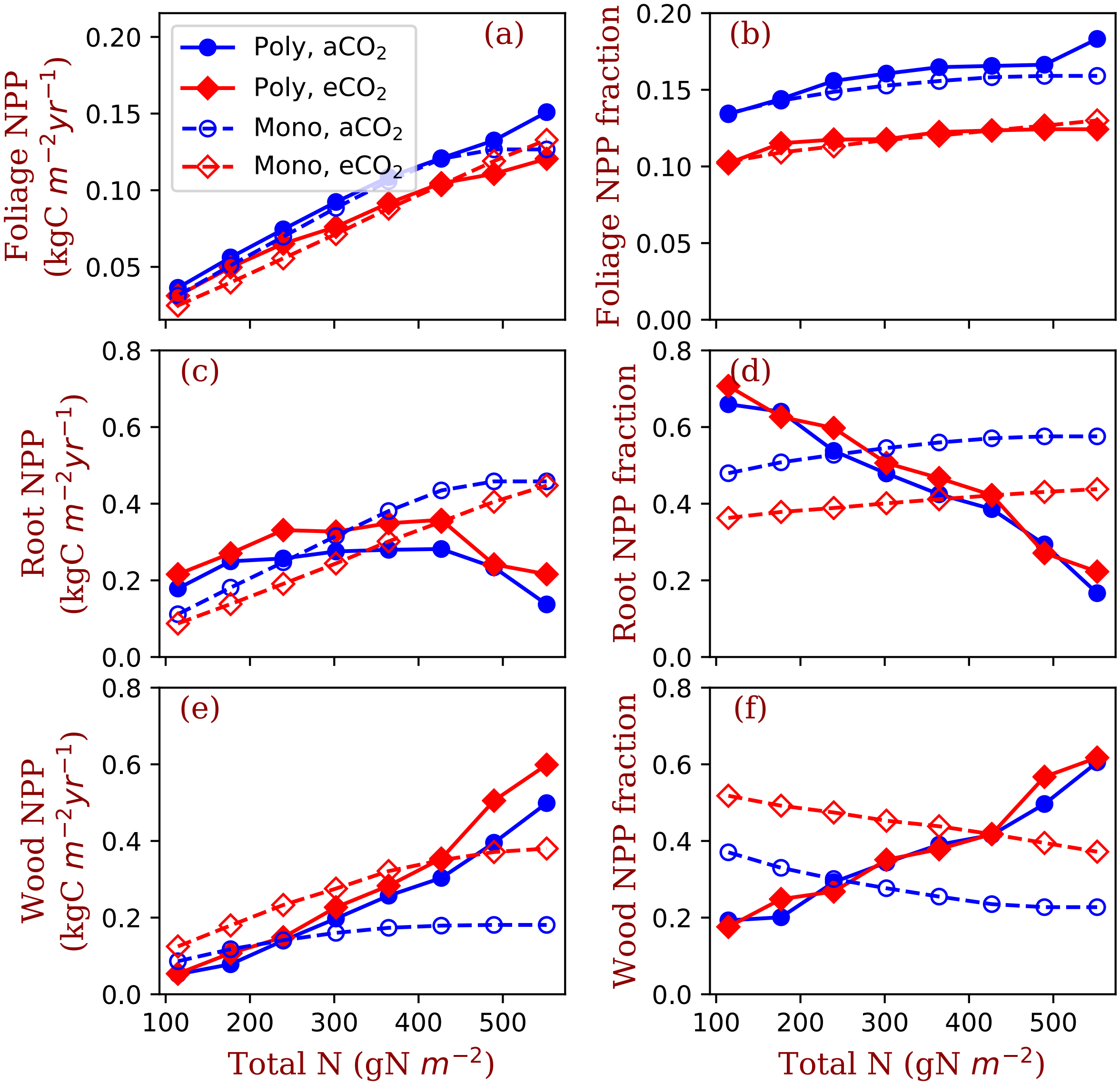



(a)
(b)
(c)
(d)
(e)
(f)
Poly, aCO$_2$
Poly, eCO$_2$
Mono, aCO$_2$
Mono, eCO$_2$
Foliage NPP (kgC $m^{-2}yr^{-1}$)
Foliage NPP fraction
Root NPP (kgC $m^{-2}yr^{-1}$)
Root NPP fraction
Wood NPP (kgC $m^{-2}yr^{-1}$)
Wood NPP fraction
Total N (gN m^{-2})
0.00
0.05
0.10
0.15
0.20
0.0
0.2
0.4
0.6
0.8
100
200
300
400
500

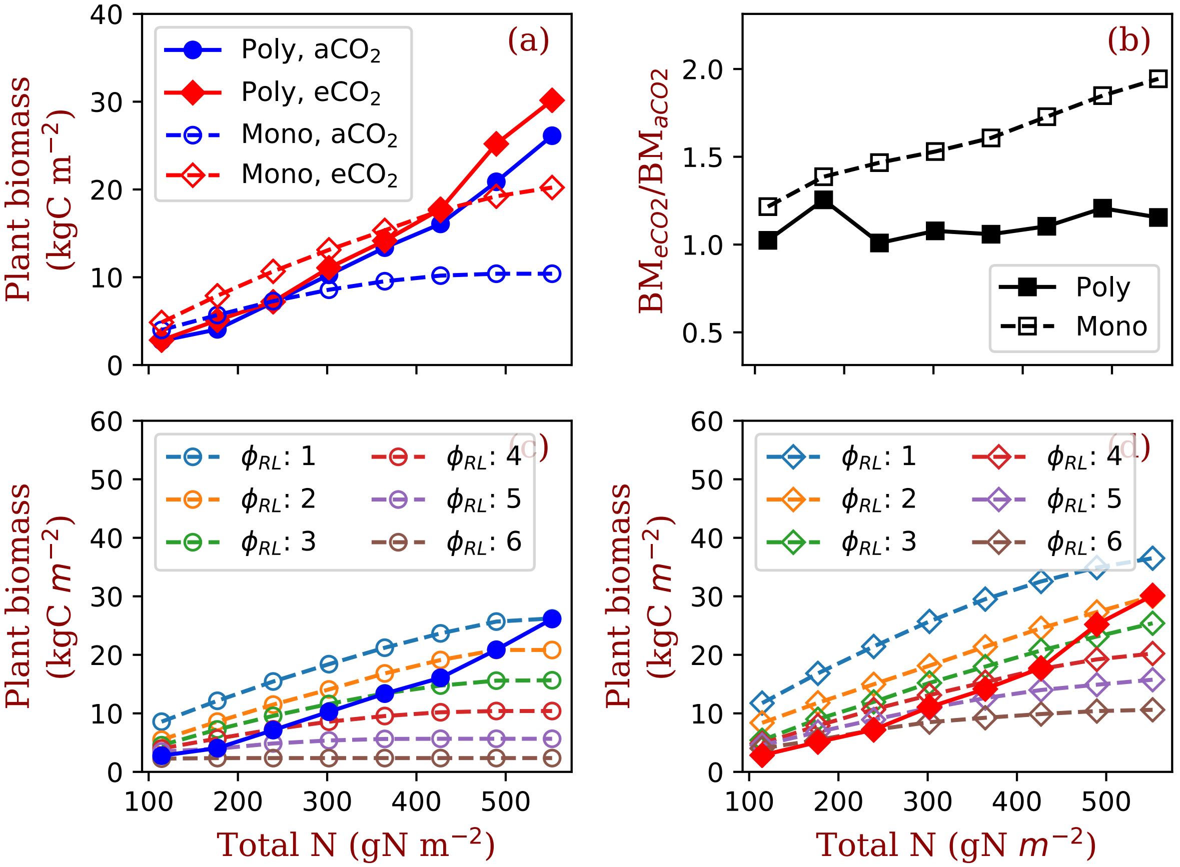

(a)
Plant biomass (kgC m^{-2})
Poly, aCO$_2$
Poly, eCO$_2$
Mono, aCO$_2$
Mono, eCO$_2$
0
10
20
30
40
(b)
BM$_{eCO2}$/BM$_{aCO2}$
0.5
1.0
1.5
2.0
Poly
Mono
(c)
Plant biomass (kgC m^{-2})
ϕ_{RL}: 1
ϕ_{RL}: 2
ϕ_{RL}: 3
ϕ_{RL}: 4
ϕ_{RL}: 5
ϕ_{RL}: 6
0
10
20
30
40
50
100
200
300
400
500
Total N (gN m^{-2})
(d)
Plant biomass (kgC m^{-2})
ϕ_{RL}: 1
ϕ_{RL}: 2
ϕ_{RL}: 3
ϕ_{RL}: 4
ϕ_{RL}: 5
ϕ_{RL}: 6
0
10
20
30
40
50
60
100
200
300
400
500
Total N (gN m^{-2})

2: Higher soil nitrogen mineralization rate





(a)
(b)
(c)
(d)
(e)
(f)
Poly, aCO_2
Poly, eCO_2
Mono, aCO_2
Mono, eCO_2
Foliage NPP ($kgC\ m^{-2}yr^{-1}$)
Foliage NPP fraction
Root NPP ($kgC\ m^{-2}yr^{-1}$)
Root NPP fraction
Wood NPP ($kgC\ m^{-2}yr^{-1}$)
Wood NPP fraction
Total N ($gN\ m^{-2}$)
Total N ($gN\ m^{-2}$)
0.05
0.10
0.15
0.20
0.00
0.0
0.2
0.4
0.6
0.8
100
200
300
400
500


(a)
Plant biomass (kgC m^{-2})
Poly, aCO$_2$
Poly, eCO$_2$
Mono, aCO$_2$
Mono, eCO$_2$
0
10
20
30
40
(b)
BM$_{eCO2}$/BM$_{aCO2}$
Poly
Mono
0.5
1.0
1.5
2.0
(c)
Plant biomass (kgC m^{-2})
ϕ_{RL}: 1
ϕ_{RL}: 2
ϕ_{RL}: 3
ϕ_{RL}: 4
ϕ_{RL}: 5
ϕ_{RL}: 6
0
10
20
30
40
50
60
100
200
300
400
500
Total N (gN m^{-2})
(d)
Plant biomass (kgC m^{-2})
ϕ_{RL}: 1
ϕ_{RL}: 2
ϕ_{RL}: 3
ϕ_{RL}: 4
ϕ_{RL}: 5
ϕ_{RL}: 6
Total N (gN m^{-2})

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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Key words: Allocation; Biome Ecological strategy simulator (BiomeE); Competitively-optimal strategy; Game theory; Nitrogen cycle

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 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 leads to higher plant biomass response to 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 allocation may generate significantly different ecosystem-level predictions of carbon storage than those that use fixed strategies.

Deleted: -

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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 biogeochemical cycles as lumped pools and fluxes of plant tissues and soil organic matter (Fig. 1: A) (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 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).

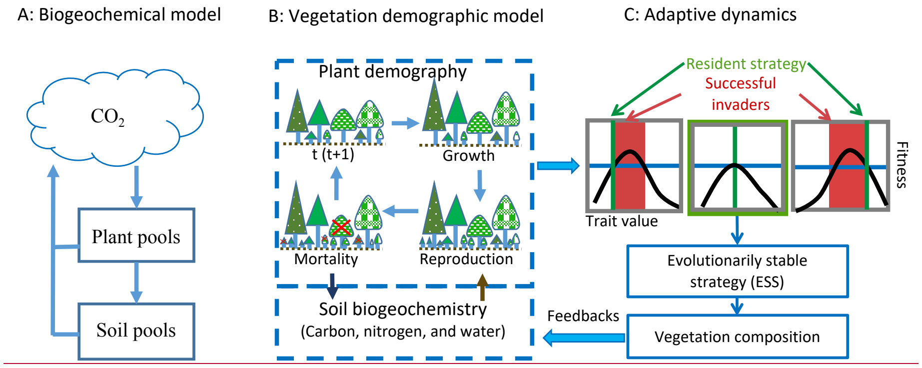

Figure 1 Hierarchical structure of vegetation models

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, VDMs explicitly simulate demographic processes, such as plant reproduction, growth, and mortality, to generate the dynamics of populations (Fig. 1: B). To speed computations and minimize complexity, groups of individuals are usually modeled as cohorts. With multiple cohorts and PFTs, VDMs can bring plant functional diversity and adaptive dynamics into ESMs when explicitly simulating individual-based competition for different resources and vegetation succession and thus predict dominant plant traits changes with environmental conditions and ecosystem development (Scheiter et al., 2013; Scheiter and Higgins, 2009; Weng et al., 2015).

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The combinations of plant traits represent the competition strategies at different stages of ecosystem development. Evolutionarily, a strategy that can outcompete all other strategies in the environment created by itself will be dominant. This strategy is called an evolutionarily stable strategy or a competitively-optimal strategy (McGill and Brown, 2007). In VDMs, competitively-optimal strategies can therefore be reasonably predicted based on the costs and benefits of different strategies (i.e., combinations of plant traits) through their effects on demographic processes (i.e., fitness) and ecosystem biogeochemical cycles (Fig. 1:C) (e.g., Farrior et al., 2015; Weng et al., 2015).

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The dynamics of plant traits can substantially change predictions of ecosystem biogeochemical dynamics since they change 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). Therefore, 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

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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, leaf longevity, fine root turnover, and tree 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.

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 mono- and polyculture model runs. In the monoculture 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 polyculture 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 single **fixed 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 overview

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). In this version, 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. 2). 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.

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Each tree consists of seven pools: leaves, fine roots, sapwood, heartwood, fecundity (seeds), and non-structural carbohydrates and nitrogen (NSC and NSN, respectively) (Fig. 2: 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 determined by the basal turnover rate together with soil temperature and moisture. The nitrogen mineralization rate is a function of decomposition rate and the C:N ratio of the SOM. Microbes must consume more carbon in the high C:N ratio SOM pool to get enough nitrogen and must release excessive nitrogen in the low C:N ratio SOM pool to get enough carbon for energy (Weng *et al*. 2017).

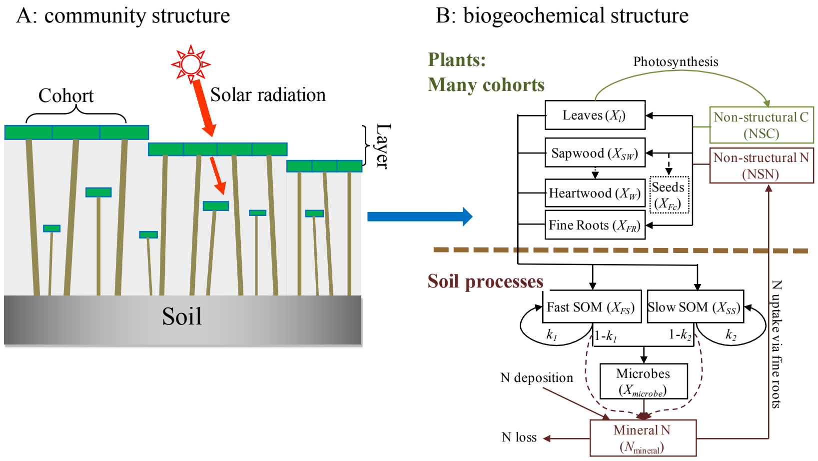

Figure 2. Model structure of BiomeE

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

Table 1 Model parameters

Symbol	Definition	Unit	Default value
α_Z	Parameter of tree height	$m\ m^{-0.5}$	36
θ_Z	Diameter exponent of tree height	-	0.5
Λ	Taper factor	-	0.75
ρ_W	Wood density	$kgC\ m^{-3}$	300
α_C	Parameter of crown area	$m\ m^{-1.5}$	150
θ_C	Diameter exponent of crown area	-	1.5
l^*	Target crown leaf area layers (crown leaf area index)	$m^2\ m^{-2}$	3.5
σ	Leaf mass per unit area	$kgC\ m^{-2}$	0.14
γ	Specific root area, calculated from root radius and density	$m^2\ kgC^{-1}$	34.5
φ_{RL}	Ratio of target fine root area to target leaf area	$m^2\ m^{-2}$	Vary with PFTs
α_{CSA}	ratio of target sapwood cross-sectional area to target leaf area	$m^2\ m^{-2}$	0.2E-4
$f_{U,max}$	Maximum mineral N absorption rate	$hour^{-1}$	0.5
K_{FR}	Root biomass at which the N-uptake rate is half of the maximum	$kgC\ m^{-2}$	0.3
$CN_{L,0}$	Target C:N ratio of leaves	$kgC\ kgN^{-1}$	76.5(Function of LMA)
$CN_{FR,0}$	Target C:N ratio of fine roots	$kgC\ kgN^{-1}$	60
$CN_{W,0}$	Target C:N ratio of wood	$kgC\ kgN^{-1}$	350
$CN_{F,0}$	Target C:N ratio of seeds	$kgC\ kgN^{-1}$	20
f_1	Supply rate of NSC and NSN	-	1/(3*365)
f_2	Maximum fraction of NSC and NSN used for growth in a day	-	0.02
$f_{LFR,max}$	Maximum fraction of available carbon allocated to leaves and fine roots	-	0.85
v	Fraction of carbon converted to seeds	-	0.1
$r_{D/S}$	Nitrogen-limiting factor	-	Solve by the model (Eqs 9 and 10)

Plant growth and reproduction are driven by the carbon assimilation of leaves via photosynthesis, which is in turn dependent on water and nitrogen uptake by fine roots. The photosynthesis model is identical to that of LM3-PPA (Weng et al., 2015), which is a simplified version of Leuning model (Leuning et al., 1995). This model first calculates photosynthesis rate, stomatal conductance, and water demand of the leaves of each tree (cohort) in the absence of soil water limitation. Then, it calculates available water supply and reduces the demand-based assimilation and stomatal conductance accordingly if water supply is less than water demand. Assimilated carbon enters into the NSC pool and is subsequently used for respiration, growth, and reproduction. (Please see Supplementary Information I for details of this model).

Empirical allometric equations relate woody biomass (including coarse roots, bole, and branches), crown area, and stem diameter. The individual-level dimensions of a tree, *i.e.*, height (Z), biomass (S), and crown area (A_{CR}) are given by empirical allometries (Dybzinski et al., 2011; Farrior et al., 2013):

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

where Z is tree height, D is tree diameter, S is total woody biomass carbon (including bole, coarse roots, and branches) of a tree, α_c and α_Z are PFT-specific constants, θc=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}) (Table 1).

We set *targets* for leaf (L^*), fine root (FR^*), and sapwood cross-sectional area (A^*_{SW}) 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):

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\begin{aligned}
L^*(D,p) &= l^* \cdot A_{CR}(D) \cdot \sigma \cdot p(t) \\
FR^*(D) &= \varphi_{RL} \cdot l^* \cdot \frac{A_{CR}(D)}{\gamma} \qquad \text{(Eq. 3)} \\
A^*_{SW}(D) &= \alpha_{CSA} \cdot l^* \cdot A_{CR}(D)
\end{aligned}
$$

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where $L^*(D, p)$, $FR^*(D)$, and $A^*_{SW}(D)$ are the targets of leaf mass (kg C/tree), fine root biomass (kg C/tree), and sapwood cross sectional area (m^2/tree), respectively, at tree diameter D; l^* is the target leaf area per unit crown area of a given PFT; $A_{CR}(D)$ is the crown area of a tree with diameter D; σ is PFT-specific leaf mass per unit area (LMA); and $p(t)$ is a PFT-specific function ranging from zero to one that governs leaf phenology (Weng et al., 2015); φ_{RL} is the target ratio of total root surface area to the total leaf area; γ is specific root area; and α_{CSA} is an empirical constant (the ratio of sapwood cross-sectional area to target leaf area). 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}. (Please see Supplementary Information I for details of the phenology model)

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Nitrogen uptake

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

$$U = f_{\text{U,max}} \cdot N_{\text{mineral}} \cdot \frac{C_{\text{FR,total}}}{C_{\text{FR,total}}+K_{FR}} \qquad \text{(Eq. 4)}$$

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

$$U_{\mathrm{tree}} = U \cdot \frac{C_{\mathrm{FR,tree}}}{C_{\mathrm{FR,total}}} \qquad \text{(Eq. 5)}$$

where, $C_{\mathrm{FR,tree}}$ is the fine root biomass of a tree (kgC tree^{-1}). The nitrogen absorbed by roots enters into the NSN pool and then is allocated to plant tissues through plant growth.

Allocation and plant growth

The partitioning of carbon and nitrogen into the plant pools (*i.e.*, leaves, fine roots, and sapwood) is limited by the allometric equations, targets of leaves, fine roots, and sapwood cross-sectional area, and the stoichiometry (i.e., C:N ratios) of these plant tissues. At a daily time step, the model calculates the amount of carbon and nitrogen that are available for growth according to the total NSC and NSN and current leaf and fine root biomass. Basically, the available NSC (G_{C}) is the summation of a small fraction (f_1) 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 (f_2) of NSC (Eq. 6.1). The available NSN (G_{N}) is analogous to that of the NSC and meets approximately the stoichiometrical requirement of plant tissues (Eq. 6.2).

$$G_C = \min\left(f_1 NSC + L^* + FR^* - L - FR, f_2 NSC\right) \qquad \text{(Eq. 6.1)}$$

$$G_N = \min\left(f_1 NSN + N_L^* + N_{FR}^* - N_L - N_{FR}, f_2 NSN,\right) \qquad \text{(Eq. 6.2)}$$

where L^* and FR^* are the targets of leaves and fine roots, respectively (see Eq. 3); L and FR are current leaf and fine roots biomass, respectively; N_L^* and N_{FR}^* are nitrogen of leaves and fine roots at their targets according to their target C:N ratios. The parameter f_2 gives the daily availability of NSC during periods of leaf flush at the beginning of a growing season and f_1

normal growth of stems after plant leaves and fine roots approach their targets. Usually, parameter f_1 is much greater than f_2. We let f_1=0.02 and f_2= 1/(365x3) in this study.

The allocation of the available NSC (i.e., G_C) to wood (G_W), leaves (G_L), fine roots (G_{FR}), and seeds (G_F) follows the equations below (Eq. 7). These equations describe the mass growth of plant tissues with nitrogen effects on the carbon allocation between high-nitrogen tissues and low-nitrogen tissues (wood) for maximizing leaves and fine roots growth (G_L and G_{FR}, respectively), optimizing carbon usage at given nitrogen supply (G_N), and keeping the tissues at their target C:N ratios.

$$G_C \geq G_W + G_L + G_{FR} + G_F \qquad \text{(Eq. 7.1)}$$

$$G_N \geq \frac{G_L}{CN_{L,0}} + \frac{G_{FR}}{CN_{FR,0}} + \frac{G_F}{CN_{F,0}} + \frac{G_W}{CN_{W,0}} \qquad \text{(Eq. 7.2)}$$

$$\frac{(FR+G_{FR})\gamma}{(L+G_L)/\sigma} = \varphi_{RL} \qquad \text{(Eq. 7.3)}$$

$$G_L + G_{FR} = Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} \cdot r_{S/D} \qquad \text{(Eq. 7.4)}$$

$$G_F = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot v \cdot r_{S/D} \qquad \text{(Eq. 7.5)}$$

$$G_W = \left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix} r_{S/D}\right] \cdot (1 - v \cdot r_{S/D}) \qquad \text{(Eq. 7.6)}$$

where, $CN_{L,0}$, $CN_{FR,0}$, $CN_{F,0}$, and $CN_{W,0}$ are the target C:N ratios of leaves, fine roots, seeds, and sapwood, respectively; γ is specific root area (m^2 kgC^{-1}); σ is leaf mass per unit area (kg C m^{-2}); $f_{LFR,max}$ is the maximum fraction of G_C for leaves and fine roots (0.85 in this study); v is the fraction of left carbon for seeds (0.1 in this study); $r_{S/D}$ is a nitrogen-limiting factor ranging from 0 (no nitrogen for leaves, fine roots, and seeds) to 1 (nitrogen available for full growth of leaves, fine roots, and seeds). The parameter $r_{S/D}$ controls the allocation of G_C and G_N to the four plant pools (Eq. 7.1). It can be analytically solved (Eqs. 8 and 9).

$$r_{S/D} = Min\left[1, Max\left(0, \frac{G_N - G_C/CN_W}{N_{demand} - G_C/CN_W}\right)\right]. \qquad \text{(Eq. 8)}$$

where, N_{demand} is the potential nitrogen demand for plant growth at $r_{S/D}=1$ (i.e., no nitrogen limitation).

$$N_{demand} = \frac{\gamma\sigma\left[FR + Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \varphi_{RL} L}{(\gamma\sigma + \varphi_{RL}) CN_L} + \frac{\varphi_{RL}\left[L + Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right] - \gamma\sigma L}{(\gamma\sigma + \varphi_{RL}) CN_{FR}} + \frac{v\left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_F} + \frac{(1-v)\left[G_C - Min\begin{pmatrix} L^* + FR^* - L - FR, \\ f_{LFR,max}\, G_C \end{pmatrix}\right]}{CN_W}. \qquad \text{(Eq. 9)}$$

When $G_N \geq N_{demand}$ ($r_{S/D} = 1$), there is no nitrogen limitation, and all the G_C will be used for plant growth and the allocation follows the rules of the carbon only model (Eqs 7.4~7.6 as $r_{S/D} = 1$). The excessive nitrogen ($G_N - N_{demand}$) will be returned to the NSN pool. When $G_C/CN_{W,0} < G_N < N_{demand}$ (i.e., $0 < r_{S/D} < 1$), all G_C and G_N will be used in new tissue growth; however, the leaves and fine roots cannot reach their targets at this step. When $G_N \leq G_C/CN_{W,0}$ ($r_{S/D} = 0$), all the G_N will be allocated to sapwood and the excessive carbon ($G_C - G_N CN_{W,0}$) will be returned to NSC pool. This is a very rare case since a low G_N leads to low leaf growth, reducing G_C before the case $G_N < G_C/CN_{W,0}$ happens. Therefore, in most cases, Eq. 7.1 is: $G_C = G_W + G_L + G_{FR} + G_F$.

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Allocation to wood tissues (G_W) drives the growth of tree diameter, height, and crown area and thus increases the targets of leaves and fine roots (Eq. 3). By differentiating the stem biomass allometry in Eq. 2 with respect to time, using the fact that dS/dt equals the carbon allocated for wood growth (G_W), we have the diameter growth:

$$\frac{dD}{dt} = \frac{G_W}{0.25\pi\Lambda\rho_W\alpha_Z(2+\theta_Z)D^{1+\theta_Z}} \qquad \text{(Eq. 10)}$$

This equation transforms the mass growth to structural changes in tree architecture. With an updated tree diameter, we can calculate the new tree height and crown area using allometry equations (Eq. 2) and targets of leaf and fine root biomass (Eq. 3) for the next growth step.

Overall, this is a flexible allocation scheme and still follows the major assumptions in the previous version of LM3-PPA (Weng, et al., 2015, 2017). This allocation scheme prioritizes the allocation to leaves and fine roots, maintains a minimum growth rate of stems, and keeps the constant area ratio of fine roots to leaves. Based on these allocation rules, the average allocation 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*. Note, here φ_{RL} is fixed for each PFT and will remain so for all the model runs.

The process of choosing a context-dependent competitively 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 competitively optimal strategy is the one that can successfully exclude all others in the processes of competition and succession, but it is not necessarily the one that maximizes production in monoculture. For example, each φ_{RL} creates an environment of light profile and soil nitrogen in its monoculture. Other φ_{RL} PFTs may have higher fitness in this environment than the one that creates it. Only the competitively dominant strategy has the highest fitness in the environment it creates (Fig. 1: C).

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. In forest sites, soil carbon is around 8 kg C m^{-2} and nitrogen 300 g N m^{-2} (Compton and Boone, 2000). 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-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 g N m^{-2} to 552 g N m^{-2} at the interval of 62.5 g N m^{-2}) by assigning the initial content of the slow SOM pool for our simulation experiments (Table 2). This range covers the soil nitrogen content at Harvard Forest (Compton and Boone, 2000; Melillo et al., 2011). The nitrogen cycles through the plant and soil pools and is redistributed among them via plant demographic processes, soil carbon transfers, and plant uptake. In all the simulation experiments, we assume the ecosystem has no nitrogen inputs and no outputs for convenience since we already have eight total nitrogen levels to represent the consequences of different nitrogen input and output processes at an equilibrium state. The PFTs were based on an evergreen needle-leaved tree PFT with different leaf to fine root area ratios, φ_{RL}, in the range from 1 to 8 (Table 2). 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 "monoculture 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 "polyculture 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 monoculture runs and two sets of polyculture runs (Table 2).

Table 2 Simulation experiments

Type	Model runs	Initial PFT(s) φ_{RL}	Ecosystem total nitrogen levels	CO_2 concentration [CO_2]
Monoculture 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},	Ambient: 380 ppm Elevated: 580 ppm
Polyculture runs I	One model run per combination of nitrogen level and CO_2 concentration	All the PFTs (φ_{RL}= 1~ 8) used in the monoculture runs		
Polyculture runs II	One model run per combination of nitrogen level and CO_2 concentration	Eight PFTs with φ_{RL} ranging from 4.5-0.5i to 8.5-0.5i at the interval of 0.5, where i denotes the eight nitrogen		

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	levels from 114.5 to 552 gN m^{-2}.	552 g N m^{-2}	

In the monoculture runs, we run the full combinations of eight PFTs with root/leaf area ratios (φ_{RL}) from 1 to 8, eight ecosystem total nitrogen levels, and two CO_2 concentrations [CO_2] (380 ppm and 580 ppm) (Table 2). For the eight PFTs, 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 φ_{RL}>6. The monoculture runs are for exploring the model predictions of gross primary production (GPP), net primary production (NPP), allocation, and biomass at equilibrium with fixed φ_{RL} and ecosystem total nitrogen levels, analogous to the functional relationship schemes used in many ecosystem models (e.g., De Kauwe et al., 2014).

In polyculture runs I, we used the same PFTs as in the monoculture 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 monoculture runs (Table 2). This set of polyculture 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.

To achieve greater resolution in our competition predictions, we designed the polyculture runs II using a dynamic PFT combination scheme according to the ranges of φ_{RL} obtained from the polyculture runs I that could survive at a particular nitrogen level at both CO_2 concentrations. For each nitrogen level, we set eight PFTs with φ_{RL} that varied in a range 3.5 (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 (114.5 g N m^{-2}) and decreasing 0.5 per level of increase in ecosystem total N. Let i=1, 2, …, 8 denote the eight N

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Table 1 Simulation experiments¶
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levels from 114.5 to 552 g N m^{-2}, the φ_{RL} of the eight PFTs at each level are (5.0-0.5*i*, 5.5-0.5*i*, …, 8.5-0.5*i*) (Table 2). For example, at the nitrogen of 114.5 g N m^{-2} ($i = 1$), the φ_{RL} of the eight PFTs are 4.5, 5.0, …, 8.0 and at 177 g N m^{-2} ($i = 2$), they are 4.0, 4.5, …, 7.5.

For both monoculture and polyculture runs, visual inspection indicated that stands had reached equilibrium after ~1200 years. To be conservative, we present equilibrium data by averaging model properties between years 1400 and 1800. We compared simulated equilibrium gross primary production (GPP), net primary production (NPP), allocation (both absolute amount of carbon and fractions of the total NPP), and plant biomass of the polyculture runs II with those from the monoculture runs. We used the results from one PFT (φ_{RL}=4) to highlight the differences of plant responses with competitively optimal allocation strategies obtained from the polyculture runs II.

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3 Results

In the monoculture 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 (Fig. 3) and elevated [CO$_2$] (Figs. S1). 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. 3: a and b) when φ_{RL} is in the range that allows plants to grow normally (1~5 in the case of ambient [CO$_2$]). As prescribed by the definition of φ_{RL}, allocation of NPP to fine roots increases with φ_{RL} in monoculture runs (Fig. 3: c). As a consequence, allocation of NPP to wood decreases as φ_{RL} increases (Fig. c: d). Allocation to leaves does not change much with φ_{RL}. (Fig. 3: e, note differences in scale). Correspondingly, plant biomass at equilibrium decreases with φ_{RL} (Fig. 3: f). The effects of

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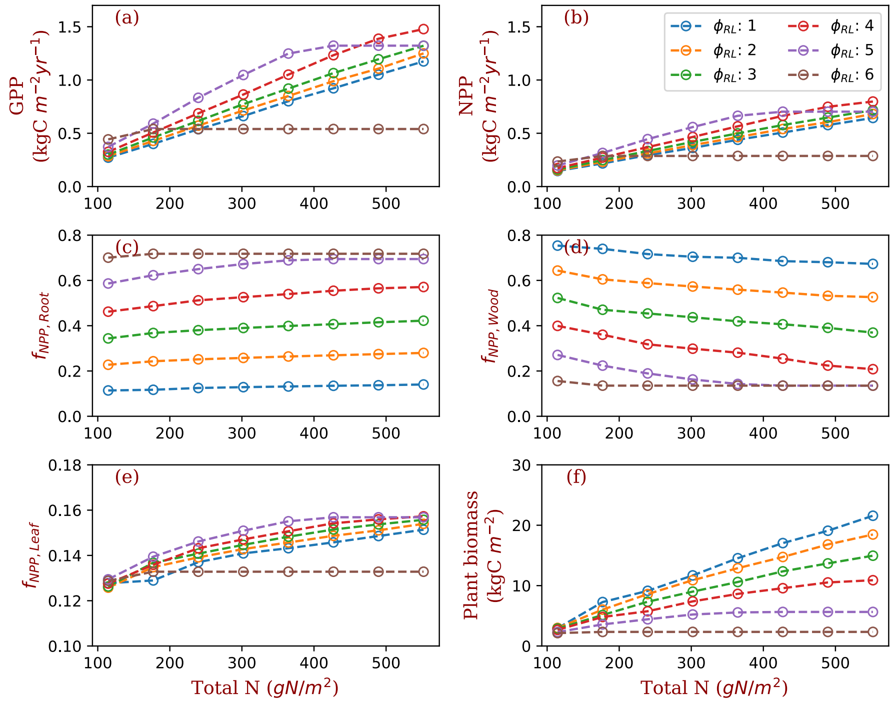

Figure 3. GPP, NPP, Allocation and Plant biomass at equilibrium state simulated by monoculture runs. GPP: Gross primary production; NPP: Net primary production; $f_{NPP,x}$: the fraction of NPP allocated to *x*, where *x* is Root (fine roots), Leaf (leaves in crown), or Wood (including tree trunk, stems, and coarse roots). The data are from the averages of the model run

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years from 1400 and 1800. Each model run is initiated with one PFT with fixed ratio of fine root area to leaf area (φ_{RL}).

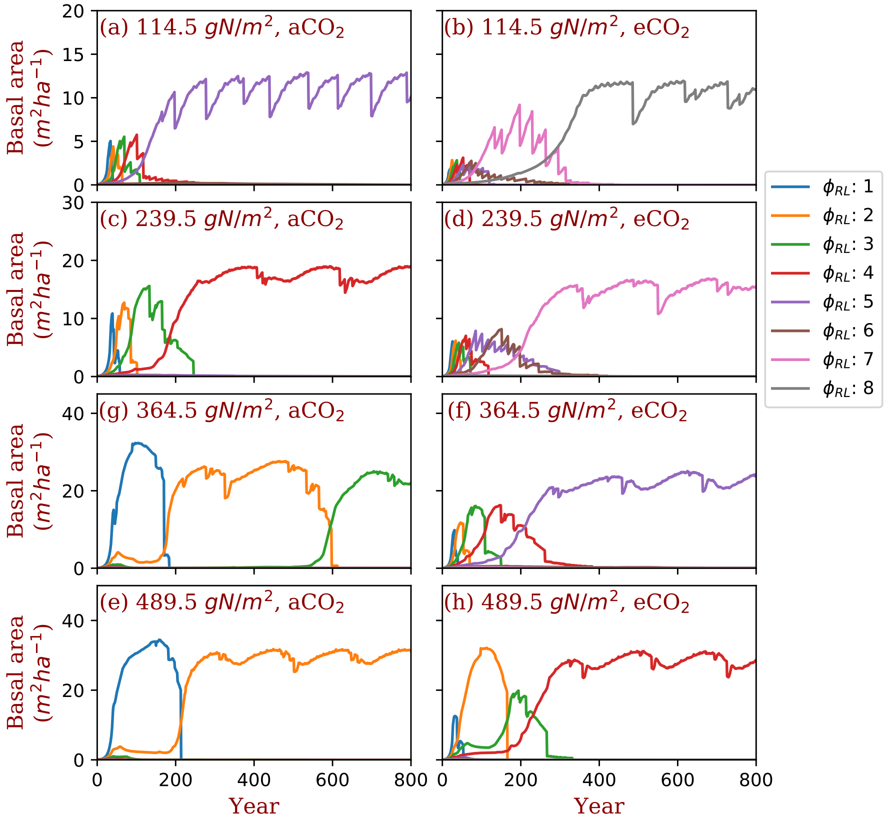

Figure 4 Successional patterns of polyculture runs I at ambient and elevated CO2 concentrations.

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We used two sets of polyculture runs to look for the φ_{RL} that is closest to the competitively optimal (i.e., evolutionarily stable strategy). In the polyculture runs I, where φ_{RL} ranges from 1 to

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8 at all nitrogen levels, the winning strategy (φ_{RL}) increases from 5 to 2 as the total nitrogen increases from 114.5 g N m^{-2} to 489.5 g N m^{-2} at ambient CO$_2$ (380 ppm) (Fig. 4: a, c, g, e). Elevated CO$_2$ (580 ppm) shifts the winning strategy to higher (φ_{RL}) at all the total nitrogen levels. As shown in Fig. 4, the winning strategy shifts from φ_{RL}=5 to φ_{RL}=8 at 114.5 g N m^{-2} and from φ_{RL} =2 to φ_{RL}=4 at 489.5 g N m^{-2}.

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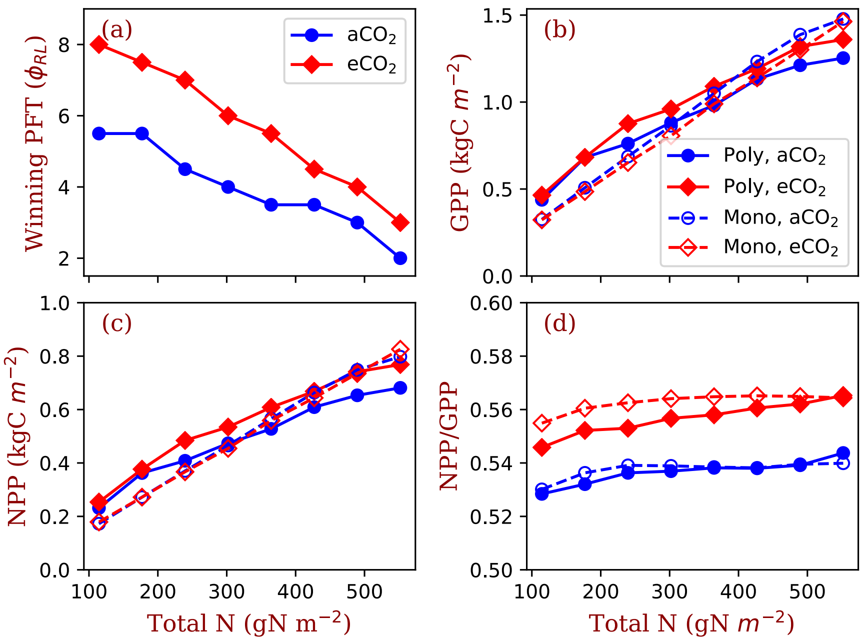

Figure 5 Winning PFTs (φ_{RL}, a) in polyculture runs II and equilibrium Gross Primary Production (GPP, b), Net Primary Production (NPP, c), and Carbon Use Efficiency (NPP/GPP, d). The closed symbols with solid line represent polyculture runs. The open symbols with dashed lines represent monoculture runs (only φ_{RL}=4 shown in this figure).

Based on the shifts of the winning φ_{RL} from aCO_2 to eCO_2 at the eight nitrogen levels, we designed the polyculture runs II with high resolution of φ_{RL} and calculated their GPP, NPP, allocation, and plant biomass at equilibrium state. The of φ_{RL} of the winning PFTs decreases from 5.5 to 2 at ambient [CO_2] and from 8.0 to 3.0 at elevated [CO_2] as total N increases from 114.5 gN m^{-2} to 552.0 gN m^{-2}. The equilibrium GPP and NPP increase with total nitrogen at values similar to those of the monoculture runs (Fig. 5: b and c). However, the CO_2 stimulation of NPP increases with total nitrogen in the polyculture runs more than it in the monoculture runs. Elevated [CO_2] increases carbon use efficiency (defined as the ratio of NPP to GPP in this study, NPP/GPP) in both the monoculture and polyculture runs (Fig. 5: d). Also, the dependence of NPP:GPP ratio on nitrogen is higher in the polyculture runs than it in the monoculture runs (Fig. 5:c).

Allocation of NPP to leaves increases with total nitrogen in all conditions, i.e. both competition and monoculture at both ambient [CO_2] and elevated [CO_2] (Fig. 6: a). Foliage NPP is similar in these four model runs when N is low. At high nitrogen (>400 g N m^{-2}), polyculture runs have higher foliage NPP than the monoculture runs generally. Allocation to leaves is relatively stable across the nitrogen gradient at the two CO_2 concentration levels (Fig. 6: b). The fraction of NPP allocated to leaves changes little with nitrogen (Fig. 6: b) and it is universally higher at ambient [CO_2] than at elevated [CO_2].

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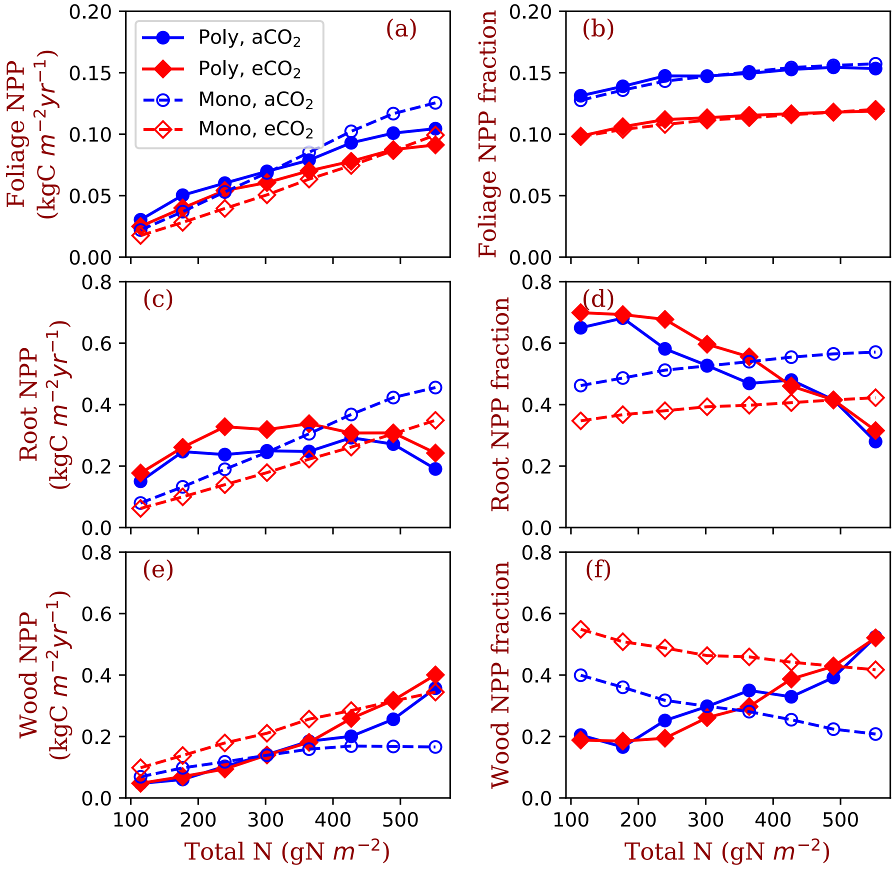

Figure 6 Allocation to leaves, fine roots, and wood tissues of the competition and monoculture runs at the eight total nitrogen levels and two CO_2 concentrations. The panels a, c, and e show the NPP allocated to the tissues and the panels b, d, and f show the fractions of the allocation in total NPP. The closed symbols with solid line represent polyculture runs (poly.). The open symbols with dashed lines represent monoculture runs (only φ_{RL}=4 shown in this figure).

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Fine root NPP does not significantly change with total nitrogen in polyculture runs, whereas it increases monotonically with increasing nitrogen in monoculture runs (Fig. 6: c). Elevated [CO$_2$] increases fine root allocation at low nitrogen in polyculture runs but decreases root allocation irrespective of nitrogen in monoculture runs (Fig. 6: c). The fraction of NPP allocated to fine roots decreases with nitrogen at both CO$_2$ concentrations in polyculture runs but it increases slightly in monoculture runs (Fig. 6: d). In monoculture runs, elevated CO$_2$ reduces the fraction of NPP allocated to fine roots at all nitrogen levels. In polyculture runs, fractional allocation to fine roots increases at elevated [CO$_2$] when ecosystem total nitrogen is low (e.g., 114.5 - 302 g N m^{-2}) and decrease at elevated [CO$_2$] when ecosystem total nitrogen is high (e.g., 364-552 g N m^{-2}).

In the reverse of the fine root response, NPP allocation to woody tissues increases with total nitrogen in both competition and monoculture runs (Fig. 6: e). In polyculture runs, the fraction of allocation to woody tissues decreases at elevated [CO$_2$] when ecosystem total nitrogen is low (e.g., 114 – 245 g N m^{-2}) and increases at elevated [CO$_2$] when ecosystem total nitrogen is high (e.g., 302 – 552 g N m^{-2}).

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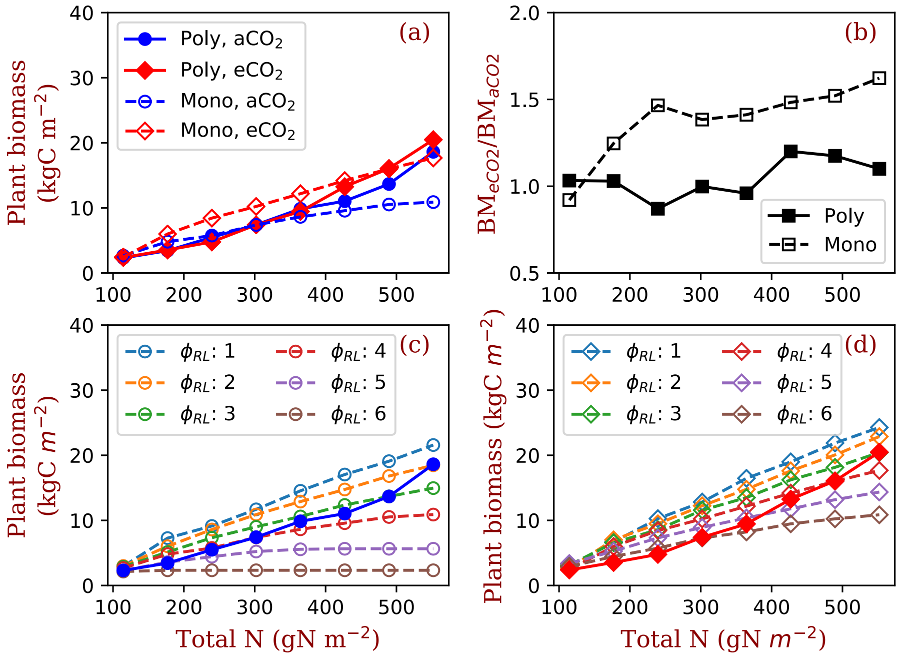

Figure 7 Plant biomass responses to elevated [CO$_2$] and nitrogen

Panel a shows the equilibrium plant biomass (means of simulated plant biomass from model run year 1400 to 1800) in polyculture runs and monoculture 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 monoculture runs. Panels c and d show the comparisons with monoculture runs with φ_{RL} increasing from 1 to 6 at ambient (c) and elevated [CO$_2$] (d). The closed symbols with solid line represent polyculture runs. The open symbols with dashed lines represent monoculture runs (φ_{RL} ranges from 1 to 6).

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As a result of the changes in competitively-optimal φ_{RL}, plant biomass increases dramatically with ecosystem nitrogen in polyculture runs compared with that in monoculture runs (Fig. 7: a). The effects of elevated [CO_2] on plant biomass increase with nitrogen in polyculture runs but are constant overall in monoculture runs (Fig. 7: b). Compared with the full spread of monoculture runs with φ_{RL} ranging from 1 to 6, polyculture 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. 7: c and d).

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4 Discussion

Our competitively-optimal predictions are generally consistent with observations of forest ecosystem production and allocation. For example, high nitrogen environments (i.e., productive environments) favor high wood allocation and low root allocation (Litton et al., 2007; Poorter et al., 2012) because the woody tissues are an unlimited sink for surplus carbon. Low nitrogen availability limits plant CO_2 responses (Norby et al. 2010) in the competition runs (polyculture) because of high root allocation. Our model predicts increased root allocation at all nitrogen levels in response to elevated [CO_2] in the competition runs. Data from free air CO_2 enhancement (FACE) forest experiments largely agree (Drake et al., 2011; Iversen et al., 2012; Jackson et al., 2009; Lukac et al., 2003; Nie et al., 2013; Pritchard et al., 2008; Smith et al., 2013). However, in ORNL-FACE, the increases in root production due to elevated CO_2 increase and then declined after 8 years of CO_2 enhancement (Iversen, 2010; Norby and Zak, 2011). Though there are no direct data available for quantitatively validating the patterns predicted by our model, especially for the long-term, competitive runs, a detailed modeling analysis can help to understand the varied patterns in the experiments and shed light on the modeling of allocation.

4.1 Modeling of allocation and competition and their effects on model predictions

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In our model, the allocation of carbon and nitrogen within an individual tree is based on allometric scaling, functional relationships, and optimization of resource usage. Basically, the allometric scaling relationships define the maximum leaf and fine root growth at a given tree size and the functional relationships (pipe model) define the ratios of leaf area to sapwood cross-sectional area and fine root surface area. These rules are commonly used in ecosystem models (Franklin et al., 2012) and have been shown to generate reasonable predictions (De Kauwe et al., 2014; Valentine and Mäkelä, 2012). Overall, these rules lead to the priority of allocation to leaves and fine roots but allow for structurally-unlimited stem growth when resources (carbon and nitrogen in this study) are available (i.e., the remainder goes to stems after leaf and fine root growth).

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We define a maximum leaf and fine root allocation, $f_{\mathrm{LFR,max}}$, to limit the maximum allocation to leaves and fine roots to maintain a relatively stable growth rate of wood in years of low productivity. The simulated wood growth patterns agree with real wood growth in temperate trees (Cuny et al., 2012; Michelot et al., 2012). Trees need to grow new wood tissues continuously (especially early in the growing season) to maintain their functions (Plomion et al., 2001). This parameter does not change the fact that leaves and fine roots are the priority. Since allocation ratios to stems are around 0.4~0.7 in temperate forests (Curtis et al., 2002; Litton et al., 2007), with a value of 0.85, $f_{\mathrm{LFR,max}}$ only seldom affects the overall carbon allocation ratios of leaves, fine roots, and stems, and still maintains wood grow in years of low productivity. If

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$f_{\mathrm{LFR,max}}$ = 1 (i.e., the highest priority for leaf and fine root growth), simulated trunk radial growth would have unreasonably high interannual variation because leaf and fine root growth would use all carbon to approach to their targets, leaving nothing for stems in some years of low productivity.

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 a fixed strategy (Fig. 6: f). Consequently, equilibrium plant biomass is predicted to increase much more with increasing nitrogen availability under a competitive strategy than under a fixed 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.

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Although the strategy that maximizes the growth rate in a fixed-allocation strategy allocates very little to fine roots (Figs. 3 and S1), the competitively optimal strategy allocates more carbon to fine roots to compete for nitrogen, a competitive effect termed “fine-root overproliferation" (Gersani et al., 2001; McNickle and Dybzinski, 2013; O'Brien et al., 2005). Elevated [CO_2] increases the carbon gain of leaves, making more carbon available for roots to compete for nitrogen and thus exacerbating the fine-root overproliferation (Dybzinski et al., 2015). Because most nitrogen uptake is via mass flow and diffusion (Oyewole et al., 2017) 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; Kulmatiski et al., 2017). Thus, 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). 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.

Root overproliferation is still controversial in experiments. For example, Gersani et al. (2001) and O'Brien (2005) found competing plants generate more roots than those planted isolated for pea and soybeans, respectively; whereas, McNickle and Brown (2014) found root growth follows the availability of soil nutrients and individuals growth with competitors have the same root growth as that predicted by the changed nutrient availability. Roots are far more adaptive and complex than those simulated in models at modifying their growth patterns in response to soil nutrient and water dynamics (Hodge, 2009). The root growth strategies in

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response to competition also vary with species (Belter and Cahill, 2015). The mechanisms of self-recognition of inter- and intra- roots also can lead to varied behavior of root growth (Chen et al., 2012). However, all of the aforementioned studies considered only *plastic* root overproliferation, where individuals produce more roots in the presence of other individuals than they do in isolation, analogous to stem elongation of crowded seedlings (Dudley and Schmitt, 1996). A portion of root overproliferation may also be *fixed*, analogous to trees that still grow tall even when grown in isolation. Dybzinski et al. (2019) showed that plant community nitrogen uptake rate was independent of fine root mass in seedlings of numerous species, suggesting a high degree of fixed fine root overproliferation. To improve root competition models, more detailed experiments that control root growth should be conducted to quantify the marginal benefits of roots in isolated, monoculture, and polyculture environments.

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 (fine roots vs. stems) can be observed in our model predictions as a shift from fine root allocation to wood allocation as soil nitrogen increases. The increases in the critical height, which is the height of the shortest tree in canopy layer, from low nitrogen to high nitrogen indicates a shift from the importance of competition for soil nitrogen to the importance of competition for light as ecosystem nitrogen increases (Fig. S6). Because the most competitive type shifts from high fine root allocation to low fine root allocation as ecosystem total nitrogen increases, increases in NPP and plant biomass across the nitrogen gradient are greater than the increases in NPP and plant biomass under the fixed strategy (Fig. 3). This greatly reduces the carbon cost of belowground competition. The slight decrease in the fraction of NPP allocated to

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leaves at elevated [CO_2] occurs because of increases in total NPP and constant absolute NPP allocation to foliage. It is consistent with FACE experiments that show leaf area index (LAI) in closed-canopy forests is not responsive to elevated [CO_2] (Norby et al., 2003).

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

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and understand this discrepancy highlights the utility of deploying closely-related analytical and simulation models (Weng et al., 2017).

4.2 Model complexity and uncertainty

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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 more layers of complexity. The first 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 is the simulated shift in dominant plant traits during succession due to the shifting of 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.

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Together, these mechanisms may alter long-term predictions of terrestrial carbon cycling due to changes in PFT-based parameters (Dybzinski et al., 2011; Farrior et al., 2013; Weng et al., 2015). As described in the Introduction, current pool-based models can be described by a linear system of equations characterized by the key parameters of allocation, residence time, and transfer coefficients (Eq. 1) with the rigid assumption of unchangeable plant types (Luo et al., 2012; Xia et al., 2013). In VDMs however, allocation, residence time, leaf traits, phenology, mortality, plant forms, and their responses to climate change are all strategies of competition whose success varies with the environmental conditions and the traits of the individuals they are competing against. To make predictions of carbon cycle responses to the novel conditions of climate change, we must understand what determines the most competitive strategy, how the most competitive strategy changes with conditions, and how the most competitive strategy impacts the carbon cycle.

Many trade-offs between plant traits can shift in response to environmental and biotic changes, limiting the applicability of varying a single trait, as we have in this study. For example, allocation, leaf traits, mycorrhizal types, and nitrogen fixation can all change with ecosystem nitrogen availability (Menge et al., 2017; Ordoñez et al., 2009; Phillips et al., 2013; Vitousek et al., 2013). The unrealistic effects of model simplification can be corrected by adding important tradeoffs that are missing. For example, the positive feedback between root allocation and SOM decomposition plays a role in mitigating the effects of tragedies of the commons of root over-proliferation (e.g., Gersani et al., 2001; Zea-Cabrera et al., 2006) due to a negative feedback induced by root turnover. High root allocation increases the decomposition rate of SOM and the supply of mineral nitrogen because of the high turnover rate of root litter, which favors a strategy 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

As shown in model inter-comparison studies, the mechanisms of modeling allocation differ very much, leading to high variation in their predictions (e.g., De Kauwe et al. 2014).

Calibrating model parameters to fit data may not increase model predictive skill because data are often also highly variable. Franklin et al. (2012) suggest that in order to build realistic and predictive allocation models, we should correctly identify and implement fundamental principles. Our model predicts similar patterns to those of Valentine and Mäkelä (2012), which are very different in their details but share fundamental principles, including 1) evolutionary- or competitive-optimization, 2) capped leaves and fine roots, 3) structurally unlimited stem allocation (i.e., for optimizing carbon use), and 4) height-structure competition for light and root-mass-based competition for soil resources. The principles 2 and 3 are commonly used in models (De Kauwe et al., 2014; Jiang et al., 2019). However, the different rules of implementing them (e.g., allometric equation, functional relationships, etc.) lead to highly varied predictions (as shown in De Kauwe et al., 2014), though the formulations may be very similar. In competitively-optimal models, such as this study and also Valentine and Mäkelä (2012), the competition processes generate similar emergent patterns by selecting those that can survive in competition, regardless the details of those differences.

In this study, similar as in Valentine and Mäkelä (2012), there is a hypothesis for the tradeoffs between light capture and nitrogen uptake via allocation based on insights gained from simpler models (e.g., Dybzinski et al., 2015; Mäkelä et al., 2008) for predicting 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. With these first principles, the models can produce reasonable predictions, though the details of physiological and demographic processes vary among models. For vegetation models designed to predict the effects of climate change, the important operational distinction is that the fundamental rules cannot or will not

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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

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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 monoculture runs are opposite to those in competitive-allocation runs. For example, in monoculture 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 calibrating against short-term observational data may improve the agreements with observations but would not change model predictions because these results emerge from the fundamental assumptions of the models. An updated model benchmarking system should have the metrics of competitive plant traits during the development of ecosystems and their responses to changes in climate.

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5 Conclusions

Our study illustrates that including the competition processes for light and soil resources in a game-theoretic vegetation demographic model can substantially change the prediction of the contribution of ecosystems to the global carbon cycle. Allowing the model to track the competitive allocation strategies can generate significantly different ecosystem-level predictions (e.g., biomass and ecosystem carbon storage) than those of fixed strategies. Building such a

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model requires differentiating between the unbreakable tradeoffs of plant traits and ecological processes from the emergent properties of ecosystems. Drawing on insights from closely-related analytical models to develop and understand more complicated simulation models seems, to us, indispensable. Evaluating these models also requires an updated model benchmarking system that includes the metrics of competitive plant traits during the development of ecosystems and their responses to climate changes.

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Codes and data availability

The codes of the BiomeE model are available at GitHub:

https://github.com/wengensheng/BiomeESS

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

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