Responses to reviewers' comments on Weng et al. manuscript (LM3-PPA model)

Dear Dr. van Bodegom,

Thank you for the reviews of our paper. We have thoroughly revised the manuscript according to reviewers' comments and concerns.

All four reviewers agree that our work represents an important modelling advance, but several reviewers were concerned that the applications in our paper are restricted to temperate forest. We agree with reviewer Fisher on this issue: (1) the title of the previous manuscript was perhaps misleading, because the paper does not present global-scale simulations; but (2) developing and testing a model like LM3-PPA, even for one grid cell, is a major undertaking and a significant step towards global applications. Despite the limited geographic scope of the paper, we suggest that the scientific scope of the paper is quite broad: (1) we have developed and tested ESM code (including all of the biophysical feedbacks needed for coupled land-atmosphere simulations), although we have yet to deploy the model at a global scale; and (2) we have presented a detailed and novel exploration of how competition among species or PFTs affects terrestrial C storage in an ESM modelling context. To address reviewer comments on this issue, we have (1) modified the title to make it consistent with the geographic scope of the work; (2) edited the main text to clarify why the work is important, despite its limited geographic scope to date; and (3) added a new Discussion section (4.6 Future challenges) that explains how the model can be applied at the global scale in future applications. The details of these changes, and our response to other reviewer comments, are explained below.

We also updated the transpiration and runoff plus evaporation in Figure 11, because in this figure the transpiration was represented by only one cohort's transpiration and evaporation was calculated as total evapotranspiration minus transpiration. We recalculated the total transpiration of all cohorts in a tile and the total evaporation in the new Fig. 11. The text is also changed accordingly. This correction doesn't change the conclusions drawn from the old Figure 11 (Please see attached figures in this letter).

We thank the reviewers for their thoughtful suggestions and comments, which were extremely helpful in guiding us to a revised paper that more clearly communicates the scope of the work and its importance. Our responses to reviewer comments are enclosed in this letter. Reviewer comments are in italics, and our responses are in roman.

Thank you for your consideration,

Authors of bgd-11-17757-2014

M. Smith (Referee)
Matthew.Smith@Microsoft.com

I congratulate the authors on a thorough piece of work that must have taken a lot of effort. In their study the Authors assess and provide evidence that they have successfully coupled their DGVM to an Earth System Model. On the basis of the evidence it appears as though they have been successful, although that evidence is presented for only one type of vegetation.

The introduction lays the foundations well and the program of work undertaken is important to establishing whether the LM3-PPA coupling works – however I was left feeling disappointed as I read the results and discussion that the results being presented were so limited, in terms of rigor of assessment for deciduous Northeastern US forests and in terms of vegetation globally. While "The model is formulated to be the land surface component of an Earth System Model" I would expect that the present analysis falls far short of establishing the LM3-PPA as being adequate for that purpose. Though the authors are very open in terms of the scope of the present analysis. Overall I recommend that the paper is published with minor revisions because it requires a different study to establish global performance.

Larger recommendations:

a) On the subject of using the PPA globally – my understanding is that PPA works fine when you have closed canopy forests, but that precisely what to do when that is not the case, and how it works when LAI<1, is not well established. It would be disingenuous to imply that extending the PPA to work globally would be straightforward when its not clear how it should be applied in nonclosed canopy forests. That said, if it genuinely would be straight forward then I have no problem with this point not being mentioned.

We have added a new Discussion section (4.6 Future challenges) to address this concern. To summarize: (1) we are working on extending the PPA to non-tree vegetation types; and (2) the main challenge to deploying LM3-PPA at the global scale involves the parameterization of a suitable global plant functional diversity scheme, rather than the need to incorporate new processes into the model. These points are explained in the new Section 4.6.

Also, by "LAI<1", we presume that the reviewer means that the canopy is not closed because the sum of the area of all tree crowns is less than the land area (note that the PPA algorithm applies to the horizontal arrangement of crown area, not leaf area). Such cases are well understood. They occur at equilibrium of the model presented in the paper when water becomes sufficiently limiting. The relevant mathematical results can be found in Farrior et al. (2013), which is cited in the paper.

b) Methods – it is unknown to me why you restrict your analysis to a maximum of 3 tree species. I understand your experiments to establish competitive dominance and evolutionary optima etc.. but is a maximum of 3 species how you'd propose to model stand dynamics for northeastern deciduous forests? If not then you're not even showing how you'd model these forests in an ESM.

The three-species simulations are not intended as a functional diversity scheme for ESMs, but rather to evaluate certain aspects of model performance at a single site (Willow Creek). Even at this site, we make no assumptions about the adequacy of the three-species approach, but rather present it as a contrast to the more typical ESM approach that lacks any successional tree diversity. In our view, the competition experiments with multiple allocational types (as opposed to species-level approaches) that are presented later in the paper are more relevant to ESM applications. We have re-written the first paragraph of Section 2.2.1 to clarify all of these points.

c) Results: It is unclear to me what, of what you have found out, is novel compared to the previous work. I have seen PPA outputs for different forests throughout the US and the core formulation has been established for some time. So what new does this paper bring to the table? What specific things did you learn about how to model stand dynamics when moving form a presumably uncoupled PPA to an ESM coupled PPA? If it is to just report that you have successfully coupled it to an earth system model then that is not a scientific paper – it's a technical report (and maybe should be published in a different journal). Now, of course, you do show this coupled model working, to the extent you declare at the end of your introduction – and I agree that should be published on that basis – but there is a big difference between the grandeur of what is raised in the introduction and what is delivered in the results.

We have added a new "Overview" section (4.1 in the revised MS) at the beginning of Discussion to clarify the novel aspects of our work. We agree that although the technical aspects of our work are formidable, this alone would not warrant publication in a top scientific journal. The novel scientific aspects of our paper largely concern the novel predictions about how competition may affect plant carbon allocation to wood (a long-lived C pool) vs. fine roots (a short-lived C pool), and showing how these predictions can be understood in the context of a mathematically tractable version of the PPA model. To our knowledge, the linkage we present between an ESM land-model component and a mathematically tractable forest dynamics model (that includes a representation of height-structured competition for light) is the first of its kind, and has important implications for the global modeling community.

Smaller corrections

1) P17759, L20: It's not clear to me what you mean by "Empirical rules". Empirical relationships? It's the "rules" part that causes me to wonder.

"Empirical rules" was meant to indicate that allocation and PFT distributions in most DGVMs are determined by a set of "top down" rules that prescribe model outcomes so as to match (at least crudely) empirical patterns. We changed this to the following (Lines 74~75 of revised MS): "Model-specific rules (often empirically derived) are used to allocate C to the different pools, …" We hope this is more clear.

2) P17760 L12: Add citation

Added (Friedlingstein et al., 2006)

3) P17761 L9: "around half" -> "equivalent to around half"

Done.

4) P17765 L9: SD undefined

Here and elsewhere, we changed "SD" to "standard deviation". (Our original MS had "standard deviation", but this was changed to "SD" by the journal when the formatted online version was produced.)

5) P17770 L9: I think 1-neta would read better if it had an additional set of parentheses around it e.g. ([1-neta] times: : :

Done.

6) P17771 L2: matters->matter

Done.

7) P17782 L7: large-> larger

Done.

8) P17783 L15: space needed

Done.

9) P17786-17787: The statements at the start of this discussion after the numbered list are not discussion – they are a statement of facts from the past and assertions. They should really be in the introduction with citations, although I suspect most of this text is not necessary at all.

We deleted this paragraph, and we also moved the numbered list to the Introduction to make the Discussion more focused on discussing the results and future directions.

10) Discussion. I encourage you to focus on discussing the findings and insights that are genuinely new. It's not a surprise, for example, that root and leaf carbon equilibrate quickly compared to wood – I don't think that should even be discussed – it is of no use to the reader beyond what is already published elsewhere. If you focus on discussing the genuinely novel findings then it'll be of more use to the reader.
As noted above, we inserted a new "Overview" section at the beginning of Discussion to clarify what aspects of the paper are novel, and we removed some extraneous text from Discussion.

11) P17789 L8: I don't think it's true that "Trees in the baseline LM3–PPA model (version H0 in Table 2) currently do not senesce" – it's just that they don't senesce quickly enough when they're getting really old.
By "do not senesce", we meant that mortality rates remain constant (rather than increase) with age. To avoid confusion, we have removed the word "senesce", and the text now reads (Lines 853~854 in the revised MS): "In the baseline LM3-PPA model (H0 in Table 2), canopy tree mortality rates are constant and independent of tree size and age, …"

12) P17798: "When consider leaf only" – grammar
We decided this phrase was unnecessary, so we deleted it. The sentence (which occurs just before Eq A2.7 in Appendix A) now begins "The dynamics of leaf biomass…"

13) Table C1 and C2 legend – needs to be improved.
We updated the legends of N, L, FR, SW, HW, L^*, FR^*, SW^*, Λ, τ_C, Ps, μ, f_{WF}, f_{LFR}, GDD_{crit} and T_{crit} in Table C1, q_c, $[O_2]$, α_{LUE}, P_{ref}, and SRA in Table C2, Λ, l^*, q, μ_{C0} and μ_{U0} in Table C3, making them consistent with those in Table C1. We also deleted some unnecessary symbols related to Soil Water Budget from Table 2.

R. Fisher (Referee)
rfisher@ucar.edu

This paper is quite clearly an exceptional study, summarizing a huge quantity of model development effort. I suspect it will become an important part of the dynamic vegetation modeling literature going forwards. The authors report the initial single-point testing of the coupling of the PPA model within the GFDL Earth system model, specifically including the fine-scale and biogeochemical processes from LM3 into the 'mathematically tractable' Perfect Plasticity Approximation model, the properties of which, regarding the elucidation of competitive and evolutionarily stable strategies, have previously been discussed by Farrior et al. (2013, in review).

Here, Weng at al. show for a site in the Eastern United states, that the model is capable of simulating carbon uptake, biogeochemical processes and succession all with some skill. They also describe a set of experiments that illustrate that the model can distinguish, by virtue of its competitive interactions driven by campy light interception, that it predicts different outcomes for polyculture/competition than for the species that maximizes productivity in isolation. This is an important result, as it further demonstrates, I think, that the use of 'many monocultures' in traditional DGVMs does not necessarily produce the correct competitive outcome.

The paper is extremely well written, and the explanations of emergent ecological phenomena are some of the best that I have come across, despite the often complex nature of the subject matter. I have few if any major objections to this paper and think it could be published in its present form. My main points are mostly suggestions that might increase the clarity of the text.

I do not agree with one other referee that the introduction is overly grandiose, since it is made quite clear at the end that this paper does not pertain to global simulations and is in fact a first step towards them. I do agree somewhat that the use of 'Earth System Model' in the title rather implies that the ESM capabilities have somehow been deployed in this paper. Clearly, implementation of the model within the code of the ESM is a hugely challenging task, and should be acknowledged somehow. Maybe "A mathematically tractable method for scaling individual trees to ecosystems within Earth System Models" would work? Or something along those lines.

We changed the title to "Scaling from individual trees to forests in an Earth system modeling framework using a mathematically tractable model of height-structured competition". The key changes in the title are:
"individuals to ecosystems" is now "individual trees to forests" to clarify that the paper focuses on forests
"Earth system model" changed to "Earth system modelling framework" to highlight that we have developed an approach, but have not yet deployed the new ESM. We realize that this point may

still not be 100% clear from the title, but we have now clarified this point in several places in the paper to minimize the potential for confusion.

Generally, given that the PPA uses a more empirical information in the parameterization of, for example, its canopy and understorey mortality rates, than a standard BGC model might, I was often left wondering which elements of the model testing process were genuine tests of the emergent properties of the model, and which derived from the model being 'told' the answer in advance. I think that a greater transparency (or maybe, just illustration) of this to the reader wold be helpful, since I do not think that the specific outcomes of the simulations for the Eastern US are the main interesting feature of this paper, given that all such models are prone to extreme parametric uncertainty, which would most likely comprise the main difficulty in scaling up to larger regions or the entire globe.

We added two paragraphs to Section 2.2 (Model evaluation and simulation tests), to clarify how we tested the model, and which aspects of model behavior were tuned. In brief, we tuned several physiological parameters related to photosynthesis and respiration to yield realistic predictions of NPP, mortality rates of trees smaller than 0.1 m diameter, and a single taper constant that affected the diameter growth rates of all trees. However, we did not tune tree size distributions, successional dynamics, or variation in tree growth rates among species or canopy layers. Thus, these latter types of data all provide tests of emergent model behaviors that were not tuned. These points are now explained in detail in the first two paragraphs of Section 2.2. In addition, we also added a sentence to the first paragraph of Section 4.2 (Model evaluation) in the Discussion (Lines 802~804 in revised MS): "These comparisons must be evaluated in light of the tuning of the physiological model to produce observed NPP, the tuning of a single parameter affecting diameter growth, and the tuning of the elevated mortality of seedlings and small saplings."

Specific Comments and Questions

17770 L3: While it is clear that the flat top assumption is very beneficial from a simplifying perspective and therefore appears justifiable, it is of course not physically realistic. What do you lose, in theory, by adopting it? Are there any downsides that might be considered, with regard to simulating co-existence, etc., that might cause this assumption to be revisited in future versions?

We agree that the assumption of flat crown tops seems unrealistic, but it has worked well in previous empirical tests of the PPA model (see Lines 330~336 of revised MS), and it greatly simplifies calculations and speeds computation. However, incorporating the PPA into LM3 did reveal a potential problem related to the flat top assumption, which we have now made this clear on Lines 342~350:

"In LM3-PPA, the assumption of flat-topped crowns introduces a potential problem that does not occur in simpler versions of the PPA model that lack physiological mechanisms. Specifically, the NSC pool can, in some cases, be quickly consumed when a tree enters the upper canopy layer from the understory because of the sudden increase in target leaf and fine root biomasses. This increase would be more gradual with other crown shapes (e.g., rounded). To address this problem (which we view as a model artifact), we introduced a parameter to limit the rate of increase of target leaf mass (and therefore fine-root mass, given the pipe-model constraint) for cohorts that recently entered the upper canopy (see Equation A6 in Appendix A)."

17772 L17: Does the NSC target scale with biomass, leaf area, etc?
The NSC target scales with target leaf mass (crown area * target crown LAI * LMA), as specified in Eq A2.4 in Appendix A. To make this clear in the main text, we added the following on Lines 401~403: "…and a species- or PFT-specific NSC target, which scales with target leaf area and tracks a plant's phenological state (Eq A2.4 in Appendix A)." We also added additional clarifying text below Eq A2.4 in Appendix A.

17773 L7: Does mortality of the entire cohort occur immediately if the average NSC for that cohort drops below zero, and if so does that not cause unrealistically 'thresholdy' behavior in the model? Perhaps the cohorts are large enough in number that killing a whole cohort does not produce a large deviation to the model state? Otherwise, I would imagine that some kind of continuous function relating NSC to mortality might be appropriate.
Yes, the cohorts will immediately die if their NSC approaches zero. But this rarely happens in LM3-PPA in its current form, except under prolonged drought (which was not simulated in the current paper). Even in the understory, we rarely observed starvation mortality in our simulations, which may simply reflect our parameterization of mortality, which attributes high rates of mortality in small size classes to "background mortality" (Fig. 1a), with "starvation mortality" occurring in our model only if NSCs drop to zero.

In our parameterization, target NSC (NSC*) is around 3-4 times the size of the combined target leaf and fine-root masses (Eq A2.4). So, trees usually have sufficient NSC to produce their target amounts of leaves and fine roots (Eq A2.6). When actual NSC is lower than NSC*, stems stop growing (Eq A2.10), and the NSC is only consumed by maintenance respiration. If a tree doesn't have carbon to sustain maintenance respiration (NSC = 0), it will die. This is the logic of the model formulation behind these equations. In our simulations, starvation (NSC=0) is restricted to the most-suppressed understory cohorts. Because these inevitably have small biomass and do not shade taller cohorts, the loss of an entire heavily-suppressed cohort has little effect on other predictions of the model. We inserted the following (Line 418~422 in the revised MS) to briefly clarify these points: "Because the target size of the NSC pool is assumed to be several times the size of the combined target leaf and fine-root masses (see Eq A2.4 in Appendix A), trees rarely die of carbon starvation unless they experience prolonged drought (which was not simulated in the current study) or have chronic negative carbon balance due to shading."

17773 L22: Does the PPA apply to all the vegetated areas, including cropland and pasture? It isn't clear here.

In this paper, we only include trees, although we have developed parameterizations for grasses, forbs and shrubs that will be published in forthcoming papers on a global implementation of the model. We explain these points in a new Discussion section: “4.6 Future challenges”.

Although beyond the scope of this paper, the model can currently be run with the old LM3 structure for croplands and pastures and the new multi-cohort structure in non-agricultural tiles. The final version will have the multi-cohort structure in all tiles, but this will have no effect in croplands which actually have only one cohort.

17773 L10: How is mortality a function of size in the understorey? I think this needs fleshing out or deferring to the appendix.
We added text in the Mortality and Disturbance section that explains this and gives the equation (see Lines 426~429 in revised MS). This equation was in Table 2 (the column of μ_{U0}). We deleted this column and put this equation here.

17766 L30: This paper does a very good job of carefully explaining the theory behind the PPA, but I think that, as written, this particular section risks alienating large fractions of its potential readership, and will decrease its impact accordingly. The ED model code -actually- discretizes the cohort and patch properties, and thus is realized as a relatively simple set of differential equations determining the growth of different biomass pools and mortality of the different cohorts, etc. It is therefore much easier to understand than the more abstract descriptions of this theory that exist in the literature.
This is something of a style point, but I find that the use of this type of language in model description papers, borrowed from more physical disciplines, does more harm than anything else in making demographic model theory less accessible to those who might wish to understand it. This barrier of understanding is a genuine problem, and is most acute when trying to communicate how models abstract the real world to scientists from fields that do not make use of such principles and to land surface scientists who do not habitually conceptualize ecological processes in this way. Is it possible to rephrase this section to reduce the likelihood of losing the audience at this rather critical point?
We added considerable text to the Population Dynamics sub-section in Section 2.1 (Lines 253~261) to make it more user-friendly. The text was obviously unclear before because the algorithmic simplicity that the reviewer describes in the ED model is precisely what is specified in the three population dynamics equations (1-3). We do feel strongly that these three equations need to be in the main text, because they are the foundation of the method.

17774 L8: Given that this paper doesn’t pertain to managed forests, this seems like a little too much detail, and also raises the question of why age-since-disturbance dynamics are operational for managed forests and not for the natural vegetation (my interpretation of how this operates at present). I think discussing the managed forest component is confusing if it isn’t presented at all in the simulations.

We moved this most of this section (**Subgrid-scale heterogeneity**) and the subsequent section (**Land use change and ED gap approximation**) to Appendix A and added a brief explanation of the tile dynamics to the main text (Lines 438~444 of the revised MS): “Like LM3, LM3-PPA model is implemented on a flexible grid, whose cell size can be specified independently of the atmospheric model’s grid. LM3-PPA also includes LM3’s dynamic tiling scheme for land use, stand-level disturbance, and subgrid-scale heterogeneity (Shevliakova et al., 2009). As explained in Appendix A, the tiling scheme can be used to implement the ED approximation for canopy gap dynamics (Moorcroft et al., 2001), but this feature was not used in the simulations presented in the current paper.”

17775 L15: In this discussion of ED, I think it would be good to state more clearly what is happening in the PPA at present - i.e. ‘we assume that there are no stand replacing disturbances’, or that ‘we do not run the model to old-growth equilibrium, on account of the absence of disturbance dynamics’. Otherwise it isn’t clear what once might stand to gain from adding in ED-like dynamics. Also, why does this section only seem to propose using gap-phase disturbance dynamics for secondary vegetation and not for primary vegetation?
We removed this section from the main text to avoid confusion because these issues do not affect the model presented in this paper. However, we include the discussion of ED in Section 5 of Appendix A because the design of any model intended for an ESM is constrained by the need to address issues of sub-grid-scale heterogeneity. We have now clarified in the revised MS that in the current work, we do not implement stand-level disturbances (Lines 435~437) or the ED gap approximation (Lines 441~444). In addition to the main text, we have also clarified these points in the new Section 5 of Appendix A.

We did not mean to imply that gap-phase was relevant for secondary but not primary vegetation. The tiling scheme can be used to implement land use and various forms of disturbance, including the ED gap approximation (see response to previous comment, above). We believe that the ED gap approximation would likely make the biggest difference when modeling old-growth forests (Lines 932~946 and 547~550 of the revised MS).

17775 L18: Why choose these N American species in particular? What is the general purpose of this illustration?
The Wisconsin, USA site was chosen because there are multiple data sources in the region that facilitate model calibration and testing; and because there are clear, well-understood patterns of succession in this region among the three selected species, which allows us to evaluate (as a proof of concept) if LM3-PPA can correctly predict forest succession. We have added two paragraphs at the beginning of Section 2.2 (Lines 455~480) to explain the rationale of the model evaluation, including the choice of region and focal species.

17777 L20: It isn’t clear to me here where the extra carbon goes, if it is not allocated to dbh increment, does it go into roots, or storage, etc?

As a result of parameterization of allometry and allocation, the growth rate of DBH is independent of DBH when crown area is proportional to DBH$^{1.5}$. In experiment H2, we stop the expansion of crown area when DBH exceeds a critical value (0.8m), but we maintain the same rules of allocation of NPP and the same allometry of DBH vs. wood biomass. Thus, carbon in excess of maintenance goes exclusively to stem growth and reproduction. Because the GPP of a tree is proportional to its crown area, GPP in experiment H2 no longer increases with DBH beyond a DBH of 0.8 m. As the tree continues to grow, the same GPP must be “stretched” around an ever-growing stem, and so the DBH growth increment must decrease as DBH increases beyond 0.8 m.

17778 L12: I think you should state the purpose of this comparison with the BGC models here? Is the intention to have the BGC processes mirrored exactly, or to more generally test the implications of modeling succession on carbon accumulation?
We added text to the beginning of Section 2.2.3 (Lines 560~563) to clarify the purpose of the comparison. The first sentence of this section now reads: “To explore how incorporating individual-level competition and successional diversity into land models affects carbon accumulation in vegetation and soil, we compared the LM3-PPA predictions to those of a CENTURY-like standard biogeochemical (BGC) model…”

17781 L24: Is the understorey aspen mortality parameterized, or emergent from the properties of the carbon starvation model?
Carbon starvation rarely occurred in our simulations, perhaps because of the way we partitioned mortality between starvation (NSC = 0) and “background” (i.e., high mortality rates in small size classes are attributed to “background mortality” in our parameterization; Fig. 1a). High understory mortality of aspen in our simulations is due to a combination of (1) its high background per-capita mortality rate (which is parameterized: see Table 1 and Eq 8 in the revised MS); and (2) growth suppression due to shading, which is an emergent property of the dynamics of size structure in the model, and which maintains understory cohorts in small size classes where they suffer high rates of mortality rates. We have clarified these points on Lines 645-652 of the revised MS.

17792 L20: What is the difference implied here between computational and mathematical tractability? If alternatives are computationally intractable, that implies that they are impossible to compute with given computational resources, which would be hard to demonstrate. Maybe computational efficiency rather than absolute tractability per-se, might be a better term to use?
We agree with the reviewer’s suggestion, and the new version of this sentence now reads: “Because of the tractability of the PPA, the coupled LM3-PPA model is computationally efficient (relative to existing alternatives to modeling height-structured, individual-level competition within ESMs) and retains close linkages to mathematically tractable special cases (e.g., constant climate).”

B. Poulter (Referee)
benjamin.poulter@montana.edu

The manuscript by Weng et al. describes the implementation of a size-structured approach to model forest dynamics in the LM3 DGVM by using the perfect plasticity assumption (PPA). The authors argue that the approach provides a mathematically tractable solution for modeling vegetation dynamics, i.e., where stochastic simulations and/or non-linear dynamics can be solved deterministically. The model is applied to a temperate broadleaf forest in northeastern USA to demonstrate how the approach can be used to analyze optimal allocation strategies and their evolution under elevated CO2 concentrations, which lead to competitive exclusion.

The technical accomplishment presented here, where PPA is implemented in LM3, represents a very important scientific advance in the field of dynamic global vegetation modeling. The paper articulates this point very clearly and provides sufficient information to follow most of the work in some detail. The challenge of efficiently representing light competition is very elegantly solved by PPA and the coupling of PPA to LM3 opens up many opportunities for studying forest dynamics.

My main concern is that the authors make the point that this development is for Earth System Modeling (ESM) and that the approach now makes ESM solutions tractable at the global scale. However, the example simulation is made for just one location and for just a handful of the tree species that co-exist at that location. The tractability of the modeling approach thus seems limited for grasslands, savannas, systems experiencing gap dynamics, and this is not fully covered in the paper. Beyond the technical presentation of the paper, which is superb, it would be more convincing to see a global simulation performed.

As explained in the cover letter, we would argue that the scientific scope of the paper is quite broad, even if the geographic of the model evaluation is limited. We have added an Overview section at the beginning of Discussion (Section 4.1 in the revised MS) that highlights the novel aspects of our analysis. For example, the last sentence of the new Section 4.1 states: "Our paper is novel because we present novel land-model predictions of how resource competition affects allocation to wood (a long-lived C pool) vs. fine roots (a short-lived C pool) at different CO2 levels, and because we show how these land-model predictions can be understood in the context of analytical predictions derived from a mathematically tractable version of the PPA model." The novel features of the LM3-PPA model are also highlighted on Lines 183~195 of Introduction, and the novel results are explored in detail in Discussion Section 4.5.

In addition to clarifying what is scientifically novel about the work presented, we also now include a new Discussion section (4.6) that addresses the challenges of extending our formalism to the entire globe. This section also states that the formalism does indeed extend to grasslands, savannas, and systems experiencing gap dynamics. The PPA was developed for forests as a way to deal with gap dynamics. Strigul et al. (2008) show many examples in which the PPA predicts stochastic gap simulator results. Farrior et al. (2013) and Dybzinski et al. (2011) derive conditions for systems with open canopies, and systems in which competition for water obviates competition for light. Finally, as mentioned in Section 4.6, we have developed parameterizations for shrubs, forbs and grasses.

Please find my more detailed comments below:

1. The compute times for the single grid cell, three species simulation for one year would be appreciated. Obviously a key limitation in DGVM development has been computational constraints – how fast does LM3-PPA run?
A 500-year run for three species on a single processor (~3GHz) takes about 6 hours.

2. P17762, line 5: spell out the LM3 acronym
Done as suggested: inserted "land model version 3"

3. P17762, line 15: the idealized conditions are mentioned here and then once in the Discussion. Some more detail on what the idealized conditions refers to would be very helpful.
The "idealized conditions" mean constant climate (i.e. every day the same). We have now clarified this on Lines 149 and 179~180.

4. P17765, line 9: need to define SD
Done. We have changed it to standard deviation.

5. P17773, 2.1.5: currently, the model has mortality from the non-structural carbohydrate pool being in deficit, and the authors point out that disturbance (insect, windstorms, etc..) are not included. Please can you define then what sort of mortality 'background mortality' refers to?
The version of the model implemented in this paper divides mortality into two sources: carbon starvation mortality and background mortality. Mortality due to carbon starvation happens if NSC pools cannot meet maintenance demand. This can occur noncompetitively (say due to drought), but it is most likely to occur in heavily shaded forest understory, where "self-thinning" is well documented. In contrast, background mortality includes all non-competitive sources that create single-tree gaps, including windthrow and insect attack. These sources of mortality are described in the rewritten section on mortality, beginning on Line 415. Although the simulations in this paper do not include stand-level disturbances, a new Discussion section (4.6) and Section 5 in Appendix A explain that LM3 already included the ability to simulate stand-level disturbance, which LM3-PPA inherits. This capability, and that fact that it was not implemented in the current work, is also highlighted in several additional parts of the revised MS: 435-437., and Lines 441-444.

6. P17774, line 11: what does 'sufficiently similar' refer to? Please define this in a quantitative way, presumably as implemented in the model.

This whole section is moved to Section 5 of Appendix A since the tile dynamics is not used in this study. The details of tile dynamics can be found in Shevliakova et al., 2009, which is cited in the main text (Line 441) and appendix A.

7. P17812, line 16: Medvigy reference is missing in References section

Added and we also corrected the citation to this paper in the main text.

8. P17788, line 9: If I understand correctly, the macroscopic equations are coming from ED? Throughout the paper, the approximation offered by ED (used by LM3) and the tractable solution to size structured population modeling (PPA) gets confusing. At this point, it would be helpful to distinguish the two.

The macroscopic equations are from Strigul et al. (2008) for deriving the analytical solution of the spatial stochastic processes that are simulated by individual-based forest simulators (e.g., SORTIE). We added a citation to Strigul et al. (2008) after this sentence to indicate the origination of the macroscopic equations.

The ED model represents another way to produce macroscopic equations from an individual-based forest simulator, but one that does not produce mathematically tractable equations. The main text previously contained a description about how the tiling scheme in LM3 could be used to include the fundamental approximation in the ED model (in the old section entitled: **Land use change and ED gap approximation**). Several reviewers objected to this section, or seemed to be confused by it, so we removed it from the main text.

The relationship between ED and LM3 was part of an earlier version of the paper, but we removed it before submission because the issue is complex, takes a lot of space, and is peripheral to what is new in this paper. But, just for your interest, we originally developed LM3 from the ED code by *removing* ED's fundamental approximation, because we were concerned that we would never get a global version running when we could not interrogate the macroscopic equations analytically. This is why we eventually developed a tractable approximation and are now extending it to the globe as LM3-PPA.

9. Equation B17: should variabl qc be qa, there seems to be an error here.

Corrected. Thanks.

T. Kohyama (Referee)
kohyama@ees.hokudai.ac.jp

*This article presents full description of the new LM3-PPA model that integrates tree population processes in height-structured forest (PPA), physiological and allocation properties of trees, and biogeochemical processes of forest ecosystems. The key assumption of PPA is that the condition of foliage crown position of a tree in vertically structured forest patch is determined by its relative height in dynamic k layers divided by threshold heights (Z*_k), and each layer (from the top layer-1 downwards) is determined by the sum of crown areas from the highest tree of the layer to cover the entire area of forest patch. Under conditions that a forest has only one closed layer of top canopy (k < 2 with Z*_1 height) and that physiological properties are in two states of either sun-exposed or shaded, previous PPA studies provide the analytical solution of tree height distribution of a single-species (or single-functional-type) population. As authors suggest and show insightful examples with simulation experiments, such simplicity of PPA is advantageous in functional understanding of ecosystem properties. I congratulate authors' success in coupling PPA and biogeochemical ecosystem model.*

As is also pointed out by other reviewers, to show generality of PPA framework in global scale earth system modeling, it is better address the application to non-forest vegetation types. PPA of land-surface filling can also be applicable to short vegetation types of shrubland and grassland, as far as crown area is related to other functional dimensions of plants (either genets or ramets), such as crown-LAI, and allocation allometries. We therefore anticipate the extension of LM3-PPA with general parameterization for earth system modeling.

We agree with the reviewer on these points, and we are currently working to apply the PPA to non-tree vegetation as the reviewer suggests. We now address these points in a new section of Discussion: Section 4.6 Future challenges.

Meantime, there are a couple of limitations of PPA framework. For example, PPA does not describe spatial heterogeneity in gap dynamics as is briefly stated in Discussion. Authors suggest using patches (tiles) in varied states since disturbance (as well as invaried states of land use). Authors may rather explicitly suggest the alternative way of coupling patch-age approximation with PPA for dynamic landscape modeling.

We agree with the reviewer that the lack of horizontal heterogeneity is a limitation of the PPA model, including applications with old-growth forests undergoing gap-phase dynamics. We also agree that the ED patch-age approximation (which is already available in the LM3-PPA code, but was not implemented in the current study) could address this limitation. These points were mentioned briefly in the original MS, and we have added new text for further emphasis and clarification. In the revised MS, these points are discussed on Lines 438-444, 841-850, 940-944, and Section 5 of Appendix A.

Authors suggest k < 2 for most boreal and temperate forests, such as their example of temperate forests in north America, while maximum k can be 3 in tropical forests (Bohlman and Pacala). It is indeed an exciting question what determines k in forest ecology. Besides, at the scale of forest ecosystems, I wonder k in temperate forests usually have k < 2. In case of east Asian temperate forests, dwarf bamboo layer often entirely cover the understory (k > 2), and bamboos contribute to considerable proportion of biogeochemical processes. Another exception is non-continuous upper canopy layer in such ecosystems as tropical rain forests with emergent trees and tree savanna. These are to be improved in the next step (e.g. including shrub parameterization in PPA, and incorporating patch-age distribution into PPA).
We have modified the language to acknowledge a greater diversity of temperate forest types: Lines 323-329 now read "In many temperate and boreal forests, the potential crowns of all individuals add up to less than two (do not fill a second canopy), and so Eq 6 has no solution for k>1. However, in some forests (e.g., tropical rainforests, and temperate forests with multiple understory layers), the sum of the crown areas of all individuals combined is typically 3 to 4 times the land area…"

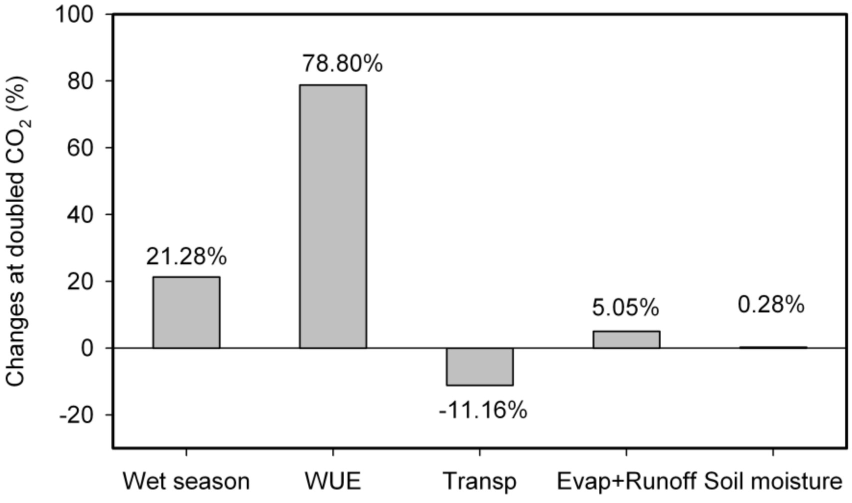
Also, we agree with the reviewer that a patch-age approximation could accommodate heterogeneity due to emergent trees, and we now mention this on Lines 845-849.

A potential importance of dynamic vegetation models (DVMs) is to predict population transition with climate change under dispersal limitation and inhibition by resident vegetation (e.g. TeeMig by Lischke et al.). As authors deal with recruitment/invasion processes in simulation experiments, it is worth comparing LM3-PPA with alternative simple height-structured tree-based ecosystem models that focus on transition prediction (e.g. TreeM-LPJ by Scherstjanoi et al. 2014).
We agree that these are important issues that could affect the time-scale of ecosystem response to global change. Our experiments were not designed to address these issues, but we now discuss them in the second paragraph of the new Discussion section (4.6 Future challenges), where we cite the suggested paper by Lischke et al. The first sentence of this paragraph is "In addition to developing parameterizations for global-scale applications, another important area for future work is to better understand the transient dynamics of vegetation response to global change." The paragraph then discusses multiple processes, including dispersal limitation, that could affect the time-scale of ecosystem response to global change.

It is an important suggestion that the optimal tree strategy under light and water competition does not bring about ecosystem-level maximum productivity, which is usually ignored in earth system simulators. I wonder there also be a miss-match between longterm genetic change towards tree optimal strategy and short-term plastic responses to rapid climate change, which can also be addressed by the present model.
We agree that this is an important question, but not one that our experiments were designed to address. We have now clarified this point on Lines 951-953, which reads: "…our competition experiments were designed only to identify the eventual outcome of competition under a given

set of conditions, and are therefore agnostic about the rate and pathway of response.” This sentence is in the second paragraph of the new Discussion section (4.6 Future challenges), where we discuss the issues raised in the last two reviewer comments: dispersal limitation, plastic vs. competitive responses, etc.

Old Figure 11



New Figure 11 (in the revised manuscript)