

Interactive comment on “Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes” by R. A. Fisher et al.

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This paper describes a new version the CLM model that incorporates a set of individual- based competition procedures according to the concept of the ED model, which allows the model to predict forest distributions based on competitions among individual trees. So, theoretically, it doesn't need the climatic envelopes imposed on plant functional types to define their geographical distributions. The authors tested the model's performance of predicting distributions of evergreen and deciduous forests in Eastern North America. The authors also parameterized a set of key processes by the correlations of plant traits (e.g., leaf nitrogen, V_{cmax} , respiration, and leaf life

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span) to improve the performance of the coupled model. Because of the complexity of individual based forest models and debates on the distributions of deciduous vs. evergreen trees regarding to their physiological and morphological traits, this study is a good try at coupling the processes ranging from leaf physiology to individual behavior. The paper is well written and the model is clearly described in the main text and supplemental materials. (But the tech note seems to be independent of this paper since it has a different author list.)

Reply: The tech note has a slightly different author list, since one of the authors of the tech note did not respond to correspondence on the paper. We would appreciate additional editorial guidance on the appropriate course of action in this case.

My major concerns are about the costs and benefits analysis that relate to the fundamental theories/principals about the relative advantages and competitiveness of deciduous vs. evergreen trees. I think the most valuable part of this paper is its tests and discussions about the parameter sensitivity and uncertainties of the relationships of plant traits in affecting the predictions of the distributions of evergreen and deciduous trees. The tests presented in this paper may not show how perfect the model is, but they can tell us why the model performs good or bad. This information can help in developing a better model. Here, I'm not criticizing the analyses. Presenting more details that explain the model behavior may improve the value of this paper and help the readers to understand the simulated results.

1. Costs and benefits analysis of deciduous vs. evergreen leaves The authors mentioned “carbon economy” and “costs and benefits” in introduction, but I don't find any such analysis in the methods and results. I'd like to see such analyses at different simulated biomes so that we can know why one outcompetes the other one and how the parameterization schemes affect the fitness of deciduous and evergreen trees.

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The cost-benefit analysis can explain the simulated distribution patterns. Basically, one plant can't distribute in some particular regions by two reasons: one is that it can't survive the climatic conditions of those regions. For the ensemble simulations in this study, there may be the third reason: the plant traits combinations may be carbon negative in some grids. The cost-benefit analysis can explain this. Therefore, we can check if the simulated distributions are resulted from correct reasons.

Reply: If we interpret this suggestion correctly, you are advocating a direct analysis of the costs and benefits of the alternative leaf strategies. The cost of leaves is easily calculated as the investment (in terms of LMA), divided by the lifespan (in terms of LL), giving the cost in KgC per unit area per year of leaf. The benefits (in terms of Carbon export), on the other hand, are more difficult to calculate, since they are manifested not only through leaf n_{area} and hence photosynthetic capacity, but also by the non-linear interactions of photosynthetic capacity with environmental drivers (light, CO₂, temperature etc.). Thus, the detailed physiological model is required to generate estimates of benefit in terms of assimilation, and it is not possible to do these calculations as a simple offline analysis. Further, the implementation inside the physiological model includes the impact of self-shading of leaves lower in the canopy, and thus the costs and benefits of these strategies are actually only properly assessed at the canopy scale. Put another way, differences in top leaf carbon export might be complicated by differences in shade tolerance of lower leaf layers. To address this point, we conducted additional model runs that use only one PFT at a time. Using these analyses, we can assess the differences in productivity and leaf area index of the PFT's in isolation. This removes the direct effects of light competition and allows interrogation of how the competition and productivity elements of the model combine to generate the resulting distribution. This analysis will be included in the revised version of the manuscript.

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2. Distribution patterns and successive patterns of evergreen vs. deciduous forests

This model is a carbon-only model. But ecologists have found that needle-leaved evergreen trees usually distribute in nutrient poor soils while broadleaf deciduous trees with fertile soils and theoretical explanations have been proposed to explain this pattern (e.g. Givnish 2002). Can this model predict this pattern? What reasons made this pattern happen or not happen in the model? Are they the same or different with the theories proposed by those ecologists? Because there are so many empirical relationships in a model, it always happens that one can get correct results by wrong reasons. I want the authors to check the details of why a particular PFT (evergreen or deciduous) wins or fails at some grids. Needle-leaved evergreen trees are usually pioneer species and dominant at early succession stage in temperate regions. Is this pattern observed in this model? And, how costs and benefits of leaves explain these two patterns?

Reply: The model is indeed a Carbon only model, and so does not have any specific predictions about the impacts of soil fertility on PFT distribution. We agree, however, that it is always possible to get the right result for the wrong reason. One result of the model simulations is that, given the change in leaf and root turnover cost with temperature, it is not necessary to invoke additional nutrient-based hypotheses to reconstruct the dominance of NLT at high latitudes. Further, given that the patterns appear to be generally driven by large-scale variations in climate, the direct impact of soil type on vegetation distribution is apparently not the first-order control. We do not discount, however, the possibility of a compensating bias elsewhere in the model that might undermine this conclusion, nor the idea that finer-scale variations in soils might affect local patterning of evergreen and deciduous species. This is why we deliberately do not state that we have found a definitive answer to the problem of why NET/DBT boundaries exist in their current locations. The

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successional status of NET and DBT is not consistent across these latitudes. In fact, in many systems, (e.g. those with aspen or birch as early successional plants) the opposite is the case. However, in these simulations, the difference in fitness between the chosen PFTs was generally too large to allow switching of dominance through the course of succession.

Specific questions:

1. "ENT have much lower nitrogen use efficiency than DBT". It depends on how to count it. Per unit time, ENT may have lower carbon gain per unit nitrogen. But as for "nitrogen use efficiency", it should be counted as the carbon gain during the lifetime of nitrogen in a leaf. Since evergreen leaves have much longer lifespan than deciduous leaves, the carbon gain per unit nitrogen through the whole lifetime is higher than deciduous leaves.

Reply: We re-phrased this description to indicate that the NUE values are instantaneous, and not leaf-lifetime integrated. We appreciate that this terminology is potentially confusing.

2. "we ran the models 30 years" I was wondering if the authors let the model run the whole period of forest succession? (30 years is too short for succession) So, how to determine who wins eventually at a grid? For some places, evergreen trees may occupy the stand for 30-50 year and then replaced by deciduous trees gradually.

Reply: Yes, we have run selected ensemble members through a longer successional integration (150 years). Our observations are that the models tend to drift slightly towards mono-dominance in some locations, and remain at the same proportion in others. We do not see any examples where one PFT appears to

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demonstrate 'late successional' properties. Given that the PFT's are identical except for their leaf habits, and have the same mortality, turnover, etc. the only potential way in which late successional properties would be observed would be if the species demonstrated opposing tolerances of shade inversely correlated with growth rates in the light. While this is possible solely from a leaf habit parameterization, the often large differences in productivity in the model mean that these subtle shifts in growth rates are quite unlikely to be manifested in this case where the parameter values are not calibrated in any way. Further to this, the existence of reproductive feedbacks as well as competitive interactions in the model means that the simulations often tend towards mono-dominance. These issues were discussed in Fisher et al. 2010 and here our intention was to focus on the impacts of parameter uncertainty. Therefore we do not wish to complicate the arguments in the paper by also including discussions of co-existence and succession. These will certainly be topics of forthcoming studies.

3. "the number of leaf layers over the footprint of the tree" "number of leaf layers" and "footprint of the tree" are not clear to me. According to the equation 3, they are individual tree's LAI and crown area, respectively.

Reply: We re-phrased this to "Individual tree leaf area index is the number of leaf layers within the area occupied by the tree crown"

4. "the net assimilation cost of the bottom leaf layer does not fall below zero" Theoretically, it could "fall below zero", only if they could worsen others. (I was just thinking of this when reading it. It's ok here to have "zero" as the criterion.)

Reply: To clarify, the net assimilation is calculated annually. Net assimilation may fall below zero frequently for shorter periods (night, winter). It is also

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possible that having leaves in net negative carbon balance may be sometimes advantageous from a competitive perspective, to shade out competitors. Nonetheless, this model is based on the stated hypothesis that trees construct leaves only if they are in net positive annual carbon balance. Other hypotheses are of course viable, and this is a benefit of optimality theory, that it can be stated independent of empirical relationships. Here the predictions of this hypothesis do not generate LAI predictions that appear systematically wrong, and the variability in parameters means that it is not possible to fundamentally reject this hypothesis with this analysis.

5. Here, it seems there are some foes in the base model in parameterizing LMA-leaf mass-LAI and the authors used another assumption (Eq 5) to correct it. Ideally, evergreen trees should grow faster than deciduous trees during the early succession stage because of its high LAI. After forest closed, deciduous trees will gradually replace evergreen trees because of successful regeneration. A carbon-only model should be capable of simulating this pattern. For me, it's not necessary to specifically set the initial LAI same for DBT and ENT. This would complicate the model. A delicate design of LMA and leaf lifespan can solve this problem. For the same allocation of NPP to leaves, ENT should have much higher LAI because of its long leaf lifespan, and the high LAI and long growing season of ENT leaves will make evergreen trees have a high productivity. So, the authors don't have to set a high LAI for ENT.

Reply: I don't think it is not always the case that ENT trees always grow fastest in early succession, nor that they are necessarily out-competed by DBT, so testing whether this pattern was true would need a site-specific test. The assertion that LAI for ENT should always be higher than DBT is not supported by the ground data for closed canopy forests (see Asner et al. 2003), but I am not aware of large-scale databases on this property for small-stature individuals. Further, in

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this case, we are actually increasing the LAI of small ENT's (previously it was lower than the DBT LAI), so the modification means that the DBT start out with the same and not a greater LAI than ENT, closer to the scenario suggested. It is likely that the model might be able to simulate a particular successional trajectory given a delicate design of LMA and leaf lifespan. However, since CLM(ED) is a large-scale model, the focus of the study is on how these models can be parameterized directly from trait databases (and the difficulties therein), in the absence of detailed site-specific parameter calibration. To use a carefully calibrated model for a particular site would not illustrate the point we are trying to highlight. Lastly, it is often the case that in most locations the difference in carbon economy between the ENT and DBT is very large, precluding the successional shifts in question.

Anyway, this is a new model and shouldn't have too many such kind of compromising design. It also brings me a question: In those grids that ENT wins, what makes them win?

Reply: The model is not strictly a new model, the feature in question was inherited from the Fisher et al. (2010) New Phytologist model implementation, which was the initial implementation of the PPA into the ED structure, necessitating the design of the representation of crown area. Admittedly, this could have been changed prior to the implementation of the published model. Our intention was to make the process of model development more transparent, and to illustrate the impacts of alternative representations of the carbon cycle and their impacts on biome boundary prediction.

Since the leaf lifespan is a function of temperature, there are still some kinds of "empirically derived climatic constraints" in this model. The relationship between

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temperature and leaf lifespan is a result of competition and it will change with other factors, such as CO₂.

Reply: We fully agree here. The discussion of the use of the environmentally driven traits is covered in the discussion, as follows: "Direct prediction of traits from their environmental drivers approach suffers, however, from at least three caveats. The first is that it predicts mean trait values for given environmental conditions and thus does not represent heterogeneity of plant strategies in a single location. Further, it is subject to a similar circularity of logic as the original climate envelope approach, in that the relationships of plant traits and climate may well not hold under future circumstances where both atmospheric CO₂, nitrogen deposition and other metrics of climate, are heavily modified. Lastly, under a changing climate, the shift in the mean trait values is considered as instantaneous, no genetic limits to plasticity are implied and there is no demographic inertia to the adoption of new better adapted plant types."

7. Table 1 Some of the combinations are not realistic. For example, the ENT of the Run ID 15 has a short leaf lifespan (0.6839 yrs), high LMA (483.6 gC/m²), and high Narea (4.95 g/m²). According to Osnas et al. (2013, Science) and many other studies, leaf lifespan has a good linear relationship with LMA. And it will be great if I can see a table or figure in the results showing carbon economy of these combinations. It will be helpful for readers to understand spatial distribution patterns of the traits combinations.

Reply: The trait combinations are determined from the covariance matrix derived from the GLOPNET dataset, the same data used in the Osnas et al. study. The critical point is that, while those data are typically analysed across PFT, within PFT (here defined by phenology and leaf habit) there is a much weaker correlation, as previously discussed by Reich et al. (2014). Figure 1

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shows that for ENTs, these values are within the statistical space defined by the dataset. In fact, many of the arguments here concern the difficulty of using these data to parameterize plant function, given their poor correlation values.

References

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