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Interactive comment on "Validation of demographic equilibrium theory against tree-size distributions and biomass density in Amazonia" *by* Jonathan R. Moore et al.

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1. I suggest evaluating the role of sample size explicitly, by plotting the following vs. sample size (with sample size on log scale axis perhaps?): the AIC difference between the models, the BIC difference between the models, and the values of each of the parameters. I also recommend considering analyses of how these quantities vary with sample size in random subsamples of the full dataset (I wonder if the distribution of points in Figure 4 simply reflects the increasing spread of smaller sample sizes while following a constraint curve set by the overall distribution). Depending on what these figures reveal, it may or may not be worth including them in the main text and/or SI.

Response: We have tried the suggested approach and found no correlation with sample size for the AIC/BIC and also the fitting parameters $\mu 1$ and φ. We did though find a strong correlation of the AIC/BIC of the MST model with sample size. Reinforcing the point already made that the MST model only appears a good model when the sample size is small. We have added a plot (S30) to the supplementary material showing this and referenced to it from the main text.

2. Regarding interpretation, the relatively good fit of the 1-parameter model is interpreted as support for the MST prediction regarding growth scaling with size. This seems to me to be a bit of a stretch, considering that data on growth are not analyzed here, and that any particular size distribution is consistent with an infinite combination of growth and mortality functions. The relevant size distribution parameter is equal to the growth exponent only if growth is a power function of size and mortality is size-independent, and reality deviates considerably from these assumptions (e.g., Muller-Landau et al. 2006, Coomes & Allen 2007).

Response: Our study shows that the DET model with power-law growth and constant mortality assumptions fits well over the large scale. While we acknowledge that other more complex models of growth and mortality may also fit the distribution, our point is that this simple model with allometry based on theoretical principles does very well over these large scales of interest in climate models/DGVMs. If repeated measurements of growth and mortality were available on a very large that would be the definitive test, but until then it is sensible to use a simple model in applications such DGVMs where parameter sparsity is very desirable.

We have acknowledged your points in the discussion: -

"The clustering of φ results close to the value predicted by MST allometry (Niklas and Spatz, 2004; West et al., 2009) suggest two possibilities. Either that the clustering represents an underlying "basin of attraction" that is modified by local conditions (Price et al., 2007) or that plots do not meet the model assumptions of growth, mortality and equilibrium somehow lead to this clustering. We cannot say for certain why the plots cluster close to the MST values but it does lead to intriguing future avenues of study. It was suggested (Coomes and Allen, 2009; Coomes et al., 2011) that light competition should modify the MST scaling of growth with size. This would mean that for trunk diameter the growth scaling power would vary with size and be greater than the predicted MST value of 1/3. For our regional fits the fitted power it was slightly larger than the MST value of 1/3 in most cases but for the individual forest plots the value was very close to MST with no clear bias. So our results cannot be taken as conclusive evidence of light competition modifying the growth scaling but neither are they completely inconsistent with it."

3. Fitting the biomass distributions is clearly novel, but I'm not convinced it is very useful considering how the empirical biomass distributions are derived. As usual, individual tree biomasses are estimates based on allometric equations combining measured diameters, regional height-diameter allometries, taxonomically assigned wood densities, and an allometric equation for biomass based on diameter, height, and wood density. And then, the fits are the same sort of tests (MST vs DET) but with allometrically transformed derivations. Basically there is the same kind of data in both datasets, but the diameters are actually measured, while the biomasses are allometric estimates (see Clark and Kellner 2012). And the artefactual peak in the biomass distributions for these diameter-truncated datasets is problematic in terms of the fits (also in terms of using the resulting distributions to predict whole-forest biomass). The biomass distributions are used here to estimate whole-forest biomass, but the whole-forest biomass could instead be calculated from the diameter distributions by combining those pdfs with height-diameter allometries and mean wood densities. So in sum, the biomass distribution analyses seem to me to be largely redundant and inherently inferior, with all the objectives better met with analyses of the diameter distributions.

Response: Knowing how well a model replicates biomass of a distribution is very important when using a model for climate applications. The main reason for modelling

forests dynamically in Earth System Models is to capture changes in land carbon storage that could affect the rate of climate change. So, an important question is whether the equilibrium model can model the biomass correctly. The effect of artefactual peak is removed by comparing the allometric derived biomass and theory predictions from the same lower bound corresponding to the peak. We are not suggesting the biomass model has an application in predicting biomass from field data but is a useful check on the accuracy of the model and more intuitive climate relevant measure than statistical measures of goodness of fit.

4. What is the motivation for calculating and reporting n_l in the tables? It is not a free parameter. Why should we care about it?

Response: We have removed these from the main text but kept those in the supplementary material with an edit to the captions in the supplementary material to explain nl is calculated not fitted.

5. How exactly is whole plot biomass predicted – with what lower bound? (results in Table 8 and figure 9) Is this done with a lower bound equal to the peak of the biomass distribution, and if so, how is that peak defined exactly? Does the lower bound for prediction vary across plots, or is it fixed?

Response: We have added a new paragraph in the Biomass results section (section 4.6) to explain this.

"The value of mP was used for the lower bound for calculating the predicted biomass in equations Eq. (6), Eq. (7) and Eq. (10). The same values of mP were used to truncate the data when finding the biomass density. So, comparisons between the theory and the mass obtained directly from a combination of observation and allometry were always using the same lower truncation point for each dataset but varied between datasets. The values of mP used are given in Table 4 and the methodology used to estimate mP is in section 4.1.1."

And we have added a new sub section to the Mass Distribution results section (section 4.1): -

“When working with mass data the peak was eliminated from fitting by creating 40 bin edges (39 bins) in log-space (base e) from the smallest to largest tree in the dataset. These edges define the range of each bin and the value of each bin was selected as the midpoint in log-space. The data was then binned following these bins. Once the data was binned, the bin with the highest frequency was identified. The value of this bin was then used as the truncation point for the dataset when fitting to the dataset distribution. The binning was purely used to identify the peak and for plotting the data and not used during the MLE fitting process.”

6. Page 1, line 30. Need to explain Demographic Equilibrium Theory more at first mention.

Response: We assume the reviewer is referring to Page 2, Line30. The intro has changed but the first mention of DET now reads:

“We follow Demographic Equilibrium Theory (DET) (Muller-Landau et al., 2006b) in assuming that forests are in a steady-state with size distributions completely determined by size-dependent functions of tree growth and mortality.”

7. Equation 6. Having a comma as part of the subscript seems needlessly confusing. I recommend removing the comma.

Response: The notation to represent mass mortality to growth ratio is now μ_m1 without the comma and has been changed throughout the paper.

8. P4 L19. Shouldn’t the correction be for the largest tree mass possible, not the largest tree mass observed? The observed maximum is highly sensitive to sample size.

Response: The objective is to correct for the maximum tree size based on the sample, so sensitivity to sample size is intended. In particular, we wanted to make sure the reverse CDF plots (in the supplementary material) matched for the largest tree size,

meaning the difference in biomass density at the lower bound (DL and mP) would represent the goodness of fit regardless of sample size effects. Maximum possible tree size is not something we know of, certainly we could not find anything published on this. So we still feel this is the best solution available to us.

9. P5, L5-6. Actually, it’s more a derivation of self-thinning, that is then declared to apply also to uneven aged stands.

Response: Added a mention of self-thinning to this line. P5 First paragraph now reads: -

“Metabolic scaling theory is a theory of scaling of organisms with size, based on theories of metabolism, physics and chemistry (West, 1997; Muller-Landau et al., 2006a). This theory uses the predictions of the scaling of individuals to predict the larger scale patterns and structure of populations and communities. For forests this is in the form of using the scaling of photosynthesis of trees and the vascular structures that transport water to predict individual scaling. This is then combined with assumptions from self-thinning about how trees fill space to describe the expected forest size-distribution (Coomes, 2003; West et al., 2009). This leads to a power law distribution for trunk diameter: -”

10. L22. What is “mixed forest”?

Response: This has been clarified by adding in brackets after the term mixed forest: - “(not monoculture)”

11. L25. Why would plots with more data for smaller trees be excluded? As long as all trees above 10 cm are sampled, the data should be fine. Any plot sampled down to 1 cm will have a large proportion of measurements below 10 cm, but that doesn’t mean the data for trees above 10 cm is problematic.

Response: The point was these plots had very few measurements above 10 cm so by applying the consistent 10 cm cutoff point have too few measurements to be useful.

Line now reads: - “Two available upper montane plots with very few measurements above 10 cm were not included in the 124 plots used, as they did not have enough measurements to allow a reliable fit.”

12. Table 1. I recommend moving this to SI, as it is simply a table of parameters repeated from another paper.

Response: Done. Table 1 is now Table S1 in the supplementary material.

13. L10, last line. Why?

Response: We assume this is referring to Page 10 last line? This paragraph modified to say: -

“A correction term is added to Eq. (7) and Eq. (10) to make sure the biomass density correctly evaluates at the upper boundary (the mass of the largest tree mmax). This is because these equations only evaluate the mass up to but not including the trees with mass equal to the largest value in the dataset. Therefore, to comply with the definition above it is necessary to add the mass of the largest trees back into the total biomass.

As the large trees are so rare this correction will be equivalent to adding just one tree of the largest mass mmax in the dataset divided by A, the total area of plots in the dataset. “

14. Figure 6. If the functions are fitted only to data above the threshold, then the fitted lines should not be extended below this threshold .

Response: Changed as requested (see attached figure 6).

15. Page 25, line 11. That’s not what I see in the supplemental figures. Figure S25 and S26 have the two S. Western curves apparently right on top of each other. (In general, please give specific figure numbers etc. when referencing supplemental materials.)

Response: We have added the figure numbers to the text and we have also added an extra line to this paragraph regarding the S.Western region: “Interestingly, two regions

(S.Western and Ecuador) had a worse fit for two parameter DET-LTWD. The S.Western region though fits the biomass within 2% regardless of the choice of upper bound or DET model, so the very slight difference in the biomass density prediction is almost certainly not significant for this region. When the reverse cumulative biomass density, defined as biomass density of all trees above a given tree mass, is plotted for Ecuador (see supplementary material Figures S27 and S28) the error comes from the shape of the tail of the distribution, which is much flatter than theory. This could be due to it being a region with a smaller number of trees (4159) or could be due to higher mortality for large trees in this region.”

16. Figure 9. Why not include the MST predictions too, for comparison? Consider putting all the panels on log-log scales.

Response: We have added a new MST subpanel to figure 9 as suggest (see attached figure 9).

17. Page 29, line 20. The DET model does not inherently assume these things, that is just how it was implemented here.

Response: The discussion was totally rewritten so this line no longer exists. The new first line of the discussion reads: - “In this paper we show that the Left-Truncated Weibull (LWTD), which is consistent with the Demographic Equilibrium Theory (DET) when the mortality is size independent and the growth is a power-law of tree size”

18. This manuscript refers to the usefulness of this approach for the “Robust Ecosystem Demography” model, but that model is not explained here, and is referenced only in a manuscript in preparation. If this model is going to be mentioned, it needs to be explained in more detail here (even if it were published, and especially given that it is not).

Response: Although the RED model is one motivation for us to carry-out this study, it is far from the only one. We also wish to understand the current size-distribution of forests, regardless of the potential use of that understanding in that development of a new DGVM. In the revised manuscript we have therefore reduced the emphasis on RED as a motivating factor.

19. Figure 10. What are the units of the x axis? Please give dbh range corresponding to a 1 kg tree, for reference.

20. The derivation of closed form DET solutions is potentially neat, but it seems strange to put this in the discussion, and I found the explanation insufficient. It's stated that the derivation is made under the assumption of the perfect plasticity approximation, but a key variable in implementing the perfect plasticity approximation is the size at which individuals reach the canopy (and below which they are in the understory) and there is nothing here about deriving this critical size. In fact, it seems that there is nothing in the understory and a large fraction of space is simply empty of vegetation, which doesn't make sense for a closed-canopy forest. Farrior et al. (2016) derive size distributions for canopy individuals, understory individuals, and the whole forest under the perfect plasticity assumption combined with a power function scaling for crown area. What is the relationship of the derivation here to that work (which is not cited here)?

21. Appendix A. Please give a complete set of assumptions here. In addition to what is stated, is mortality constant for all trees (regardless of canopy status) or is mortality 100% in the understory? Are growth rates the same power function of size for all trees, or only for canopy trees, with zero growth in the understory? I recommend adding parameters to the assumption list as well (e.g., give here the power function parameters for crown area scaling with tree mass). The only way I can understand the canopy not being 100% full, would be if mortality in the understory is 100%, and the model operated in discrete time (so that gaps created by mortality were not immediately filled), but these assumptions are not stated.

Response: These three points (19-21) all refer to the RED model, a small part of which was included in this paper. As the main RED paper (Argles 2019) has now reached

public discussion in Geoscientific Model Development we have decided to remove all sections relating to RED from this paper. We now ask the reviewers and editors to refer to this paper. We have modified the introduction and discussion to reflect these changes. This includes the closed form solutions that in retrospect, are an add-on that are not required for the rest of this study.

References

Argles, A. P. K., Moore, J. R., Huntingford, C., Wiltshire, A. J., Jones, C. D., and Cox, P. M. 2019. Robust Ecosystem Demography (RED): a parsimonious approach to modelling vegetation dynamics in Earth System Models, Geoscientific Model Development, https://doi.org/10.5194/gmd-2019-300,.

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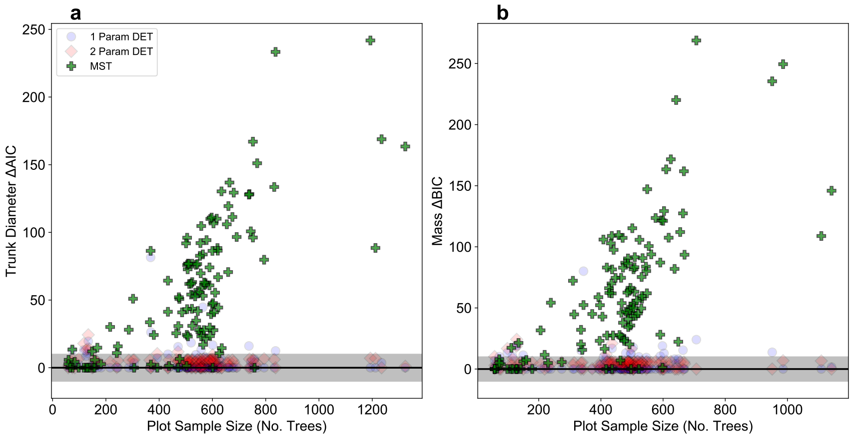

Fig. 1. Supplement Figure S30

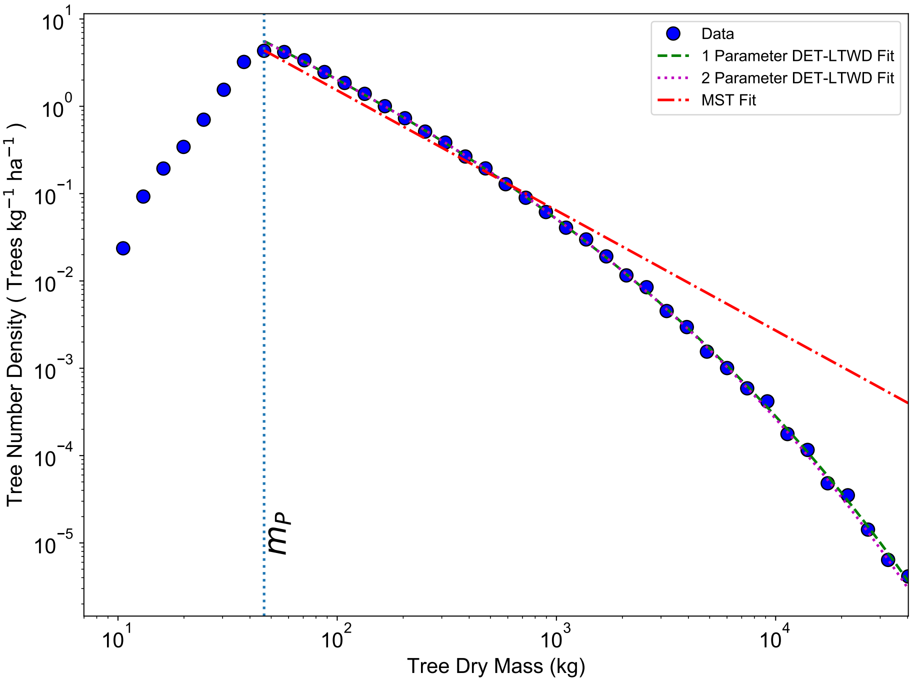

Fig. 2. Revised Figure 6

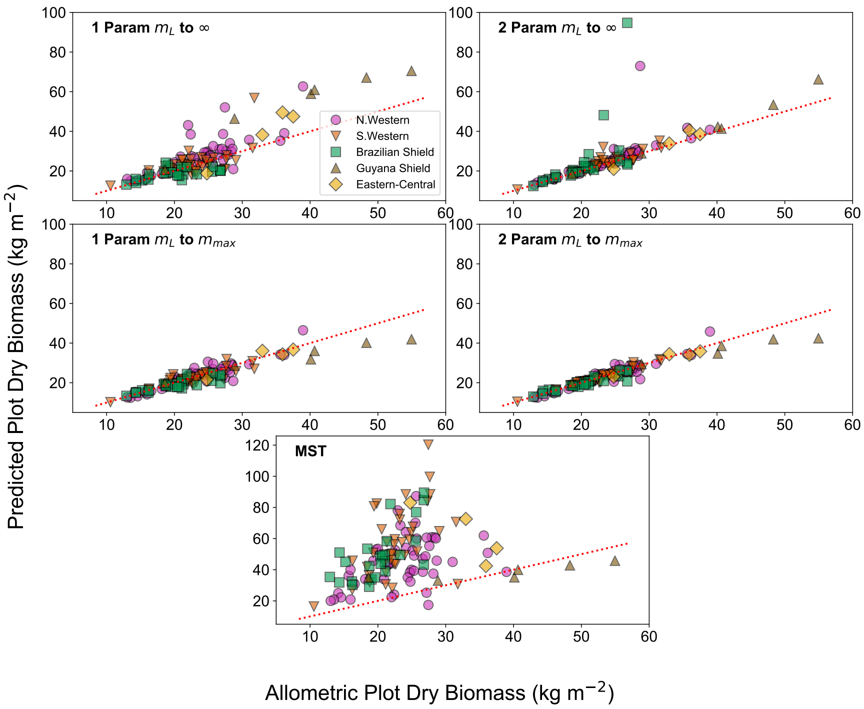

Fig. 3. Revised Figure 9