

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

## **Anonymous Referee #2**

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This manuscript analyzes previously published data from forest censuses at 120 plots in the Amazon and evaluates their tree size distributions are fit by alternative models. Tree diameter distributions and tree biomass distributions are fitted with (1) left-truncated Weibull distributions with two free parameters, consistent with demographic equilibrium theory (DET) under the assumption of size-independent mortality and power-function growth; (2) left-truncated Weibull distributions with one free parameter, consistent with DET, size-independent-mortality, and growth that is a pre-specified power consistent with metabolic scaling theory for tree growth ( $1/3$  power for diameter,  $3/4$  for mass); and (3) metabolic scaling theory for size distributions (MST) meaning  $-2$  power scaling for diameter distributions and  $-11/8$  power scaling for biomass distribu-

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tions. The distributions are fit for all plots combined, for geographic subsets of plots, and for individual plots. Biomass distributions are obtained by combining measured diameters with region-specific allometric equations for height, taxonomically assigned wood densities, and pantropical biomass equations based on diameter, height, and wood density. The models are fitted with maximum likelihood, and the alternative models are compared using AIC and BIC for the size distributions, as well as in terms of their ability to predict total AGB over all trees combined. The analysis is motivated in terms of the need to develop relatively simple models of size structure for global vegetation models.

The results show that size distributions are better fit by the DET-based models than by MST, and that the 2-fitted-parameter model is preferred to the 1-parameter model for the dataset as a whole whereas the 1-parameter model is preferred for most individual plots and regions. In the 2-parameter fits, the fitted parameter that is derived from the growth exponent is distributed around the values expected under MST growth theory. The two parameters of the 2-parameter fits are shown to be correlated across plots. The tree biomass distributions for these datasets are hump-shaped, reflecting the lower truncation of diameter at 10 cm combined with the variation in wood density among trees. Total plot biomass is reasonably well-predicted by the DET-based models, but not by the MST-based models, as the latter greatly overestimate biomass. The manuscript also contains an appendix that derives equations for the plot-level tree size distributions, total mass, and total mass growth from a certain set of assumptions, and that is referenced in the discussion.

The finding that MST is a poor fit and that Weibull functions are better fits for these tropical forest datasets is consistent with previous findings for other tropical forests, e.g., Muller-Landau et al. 2006, as cited. In some ways the finding that MST is a poor fit to size distributions seems like beating a dead horse at this point – the initial motivation for the MST size distribution argument always was a bit of a sleight of hand from even-aged stand self-thinning arguments used as a justification for uneven-aged stand

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size distributions, as noted by multiple previous authors, and essentially every good analysis has found that MST is not a good fit to size distributions. At the same time, I'm a firm believer that we need more replication in ecology, and that solid analyses of new datasets should always be publishable, even if the findings are not qualitatively novel. The main novel elements are (1) different datasets, (2) exactly which models are compared, (3) analysis of biomass distributions in addition to diameter distributions, and (4) the derivation of whole plot biomass and productivity functions under DET in appendix. I think the application to new datasets in itself makes the analysis publishable, and the specific models compared here are a reasonable and interesting choice. I'm not convinced that it makes sense to analyze biomass distributions. I am intrigued by the derivation, but found the presentation lacking in material needed to understand it.

One of the novel elements is comparing the relative fit of truncated Weibull distributions with 2 free parameters vs. 1 free parameter. I have some suggestions regarding the implementation and interpretation of these results. Regarding implementation, the relative fit of the 1- vs. 2-parameter models (and even MST) appears to relate strongly to sample size. The largest datasets tend to provide support for the 2-parameter models, whereas the smaller datasets support the 1-parameter models. Similarly, the larger datasets appear to have more similar values of some of the parameters, with greater spread in the small parameter datasets. The results mention these patterns in the context of explaining some outliers and suggesting that some regional differences might be due to sample sizes in different plots. 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. Regarding interpretation, the relatively good

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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).

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.

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

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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)?

Other specific comments

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?

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?

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).

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

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

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.

P5, L5-6. Actually, it's more a derivation of self-thinning, that is then declared to apply also to unevenaged stands.

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L22. What is “mixed forest”?

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.

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

L10, last line. Why?

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

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.)

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

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

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

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

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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.

## References

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