

5 Discussion

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, fits the observed tree-size distributions for 124 forest plots across Amazonia. Our fitting was undertaken with either two free parameters or with one free parameter and the growth scaling power ϕ constrained to that specified in Metabolic Scaling Theory (1/3 for trunk diameter and 3/4 for mass, see West et al. 2009; Niklas and Spatz 2004). We also compared the performance of DET-LTWD to that of the Metabolic Scaling Theory for forest demography (MSTF, West et al. 2009). Our analyses were carried-out for both trunk diameter measurements and for trunk diameter converted allometrically to mass (Feldpausch et al., 2012).

We found that this conversion of trunk diameter to mass introduces a peak in the mass distribution that is purely an artefact of the conversion. The peak is due to the variation in mass of trees of a given trunk diameter, due to height and wood density variation leading to some small mass trees being in effect “missing” from the mass distribution. If the diameter to mass relationship was purely one-to-one, then the artefact peak would not occur. This has implications for anyone using mass size-distributions converted from trunk diameter data. Our solution was to fit only to trees with mass greater than the mass distribution peak.

The model fitting shows that Amazon size-distributions are generally better fit by the DET-LTWD based models than MSTF. The 2 and 1-parameter DET-LTWD fits were often not significantly different enough from each other for comparison by AIC or BIC (which balance the quality of the fit against the number of unknown parameters) to choose which is the best description of the size-distributions. The few plots and regions (including all plots combined) where one model was found to have a significantly better AIC or BIC score all favoured the 2-parameter model.

The best-fit growth-scaling exponent ϕ varied between plots and regions, but the mean value of ϕ across all 124 plots fell close to the values predicted by MST. For the 1-parameter DET-LTWD best-fit values of μ_1 for trunk diameter cluster tightly around 0.25 (and around $\mu_{m1} = 0.19$ for mass). This is close to the mean value of $\mu_1 = 0.22$ that we found for North American forests (Moore et al., 2018), hinting at a preferred value of the ratio of mortality to growth across different regions and forest types.

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 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.

We find the fitted 2-parameter DET-LTWD ϕ values for both mass and trunk diameter also have a well defined relationship to the fitted mortality : growth ratio μ_1 . This relationship does not appear to be a fitting artefact, as if artificial data is generated with known μ_1 and ϕ values off the observed curve the fitting process correctly fits it to the generated values, not the curve seen in this study. This relationship suggests an interesting but as yet unknown property of the Amazon forests but may represent life-history trade-offs (Uriarte et al., 2012). Trees have different strategies such as live-fast die-young pioneer species versus grow-slow live-long canopy species. This is one possible explanation of the relationship between μ_1 and ϕ , as when both are high the early growth at small size will be slower but keep increasing, while when ϕ and μ_1 are both low the early growth will be higher but more quickly level off. Interestingly no plots had low ϕ , with high μ_1 , which would correspond to uncompetitive low growth at all sizes. As these results are at the plot level rather than per tree basis, it would suggest that each site has a dominance of one life-history strategy. As no correlation of μ_1 or ϕ with plot metrics such as height or wood density, this hypothesis remains unconfirmed.

MSTF was rarely a good fit at plot, regional or all plots level for either trunk diameter or mass distributions, and significantly overestimated total biomass density, so we reject the MSTF model as a good model of forest size-distributions. This rejection is consistent with the recent study by Zhou and Lin (2018) that showed the MSTF model failed to account for the effect of size-dependent growth rate on how fast a tree transitions through a given size class. This observation explains that the assumptions of MSTF of the size distribution scaling D^{-2} is inconsistent with the assumption of individual tree resource use scaling as D^2 . Here, we have confirmed the D^{-2} (and $m^{-11/8}$) size-distribution model should be rejected for South American tropical forests. Furthermore, for most plots we can reject a general power law distribution, as the distributions observed are rarely linear when plotted in log-log space.

There was a strong correlation between sample size and how likely MSTF was to be considered either the best or a acceptable model, with small sample sizes favouring MSTF. This suggests that sample sizes may lead to difficulty identifying the best model or even wrongly choose the best model, most likely as rarer large trees are more likely to be absent from a small sample. Meaning, where practical, larger forest plots of at least a 1000 stems are desirable when analysing size-distributions.

All three models of size distribution were used to predict total biomass density by the integration of the analytical form of their respective mass distributions. One interesting implication of the resulting equations for DET is that mortality and growth only ever appear in the form of the ratio μ_1 and never independently. The ratio of mortality to growth therefore determines the equilibrium state of a forest, while the absolute magnitudes of the individual mortality and growth terms determine the transient effects away from a steady state.

When considering how well the models predicted total biomass density from the fitted size-distribution, the biggest source of error at the plot scale is the model assumption of infinite maximum tree size. However, this can be corrected for and allows the 1-parameter DET-LTWD to estimate biomass density with relative root mean square error of 10% over the 124 forest plots and 2-parameter DET-LTWD within 6%. Conversely, the MST model consistently overestimated the biomass density, often by a considerable margin. The regional scale, which has larger sample size, showed much better prediction of the biomass density and the 2-parameter DET-LTWD with finite upper bound had the smallest error in biomass density. This suggests the

DET-LTWD model is a useful model of biomass for large-scale applications such as being used to initialise a DGVM based on the continuity equation (Argles et al., 2019) or as a climate relevant measure of goodness of fit.

One of our priorities for further work is to investigate whether the commonality found in the values of μ_1 and the relationship between μ_1 and ϕ is indicative of some form of optimality operating at the forest scale.

6 Conclusions

This study demonstrates that demographic equilibrium theory (DET) is able to fit measured tree size-distributions in Amazonian forests. The fitted growth scaling parameter ϕ was clustered for both trunk diameter (0.31 ± 0.02) and mass diameter (0.71 ± 0.01) distributions close to the values predicted by Metabolic Scaling Theory (MST). The small bias seen could be indicative of deviations from MST allometry due to light competition. The fitted mortality: growth ratio parameter μ_1 was clearly related to the fitted ϕ parameter suggesting a possible life-history trade-off in the forest plots. If the DET ϕ is constrained to the MST value then the fit is often as good as the 2-parameter fit and with one less fitting parameter is preferred by the Bayesian Information Criterion and μ_1 clusters with a value (0.25 for trunk diameter) close to that of 0.22 previously reported for US forests. We therefore find evidence that the 1-parameter DET is useful in modelling forests on the global scale, particularly for applications where parameter sparsity is important (Argles et al., 2019). Further support for such applications comes from the models ability to replicate forest biomass density over large scales, when compared to the data. The relationship between μ_1 and ϕ and a common value of μ_1 between the US and Amazon may indicate some optimality principle is in play.

Code availability. Code is available on reasonable request to the corresponding author.

Author contributions. J.R.M. and P.M.C. conceived the project. J.R.M. carried out the data analysis, wrote the paper and prepared the figures. K.Z., A.A. and C.H. gave much invaluable advice on analysis, mathematics and the general direction of the project as well as commented on the manuscript.

Competing interests. The authors declare that they have no conflict of interest

Acknowledgements. This work and its contributors (J.R.M., A.A., K.Z., C.H. and P.M.C.) were supported by the European Research Council (ERC) ECCLES project and by the Newton Fund through the Met Office Climate Science for Service Partnership Brazil (CSSP Brazil), also by a Faculty Research Grant awarded by the Committee on Research from the University of California, Santa Cruz (K.Z.) and the UK Centre of Ecology and Hydrology (CEH) National Capability Fund (C.H.).

We also wish to thank Ted Feldpausch for his many helpful comments and advice regarding Amazon forests, their allometry and analysis.

We particularly wish to thank the hard-working teams of researchers working to gather the RAINFOR data and share it through the Forest-Plots network. The principal investigators (PIs) who worked on each of the forest plots used that we wish to thank are Samuel Almeida, Esteban Álvarez Dávila, Luiz Aragão, Alejandro Araujo-Murakami, Luzmila Arroyo, Timothy Baker, Jorcely Barroso, Roel Brien, Fernando Cornejo Valverde, Maria Cristina Peñuela-Mora, William Farfan-Rios, Ted Feldpausch, Eurídice Honorio Coronado, Ben Hur Marimon Junior, Eliana Jimenez-Rojas, Jon Lloyd, Yadvinder Malhi, Alexander Parada Gutierrez, Guido Pardo, Beatriz Marimon, Casimiro Mendoza, Irina Mendoza Polo, Abel Monteagudo-Mendoza, David Neill, Nadir Pallqui Camacho, Oliver Phillips, Nigel Pitman, Hirma Ramírez-