Validation of demographic equilibrium theory against tree-size distributions and biomass density in Amazonia

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Abstract. Predicting the response of forests to climate and land-use change depends on models that are able to simulate the time-varying distribution of different tree-sizes within a forest - so called *forest demography* models. A necessary condition for such models to be trustworthy is that they are able to reproduce the tree-size distributions that are observed within existing forests worldwide. In a previous study, we showed that Demographic Equilibrium Theory (DET) is able to fit tree-diameter distributions for forests across North America, using a single site-specific fitting parameter (μ) which represents the ratio of the rate of mortality to growth for a tree of a reference size. DET assumes tree-size profiles are in a steady state resulting from the balance between a size-independent rate of tree-mortality and tree growth-rates that vary as a power law of tree size (as measured by either trunk diameter or biomass). In this study, we test DET against ForestPlots data for 124 sites across Amazonia, fitting, using Maximum Likelihood Estimation, to both directly-measured trunk diameter data and also biomass estimates derived from published allometric relationships. Again we find that DET fits the observed tree-size distributions well, with best-fit values of the exponent relating growth-rate to tree mass giving a mean of $\phi = 0.71$ (0.31 for trunk diameter). This is broadly consistent exponents of $\phi = 0.75$ ($\phi = 1/3$ for trunk diameter) predicted by Metabolic Scaling Theory (MST) allometry. The fitted ϕ and μ parameters also show a clear relationship that is suggestive of life-history trade-offs. When we fix to the MST value of $\phi = 0.75$, we find that best-fit values of μ cluster around 0.25 for trunk diameter, which is similar to the best fit value we found for North America of 0.22. This suggests an as yet unexplained preferred ratio of mortality-to-growth across forests of very different types and locations.

1 Introduction

The modelling of the abundances of various tree sizes in tropical forests is important in efforts to improve understanding of land-climate feedbacks and hence anthropogenic climate change. Earth System models (ESMs) are used to model climate, but currently have a large range of uncertainty in the prediction of the land carbon sink, with as much as 500 GtC uncertainty by 2100 for 1% increase in CO_2 emissions per year (Friedlingstein et al., 2014). This uncertainty feeds-through into estimates of how much emissions need to be reduced to keep global warming within a certain level. These issues have led to the development of more advanced Dynamic Global Vegetation Models (DGVMs), used within ESMs, to more effectively represent vegetation processes (Sitch et al., 2015; Fisher et al., 2018). One of the key advances has been the inclusion of tree size-distributions, which allows better representation of land-use change and recovery from disturbance.

These more recent DGVMs broadly consist of two different approaches based on representing size either via individual-based models (Shugart et al., 2018) or using cohort-based ecosystem demography models (Moorcroft et al., 2001; Longo et al., 2019). DGVMs also need to balance additional complexity against practical considerations of usability, and computer execution time and memory usage. Key issues in the usability of complex numerical models are the understanding of the effect of many model parameters and the dependence on initial conditions (Moore et al., 2018). To solve these issues we have been exploring simplifications to the modelling of forest demography that are both parameter sparse and have steady-state solutions that can be solved for analytically (Moore et al., 2018; Argles et al., 2019).

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. Previously we showed that DET was able to fit the large-scale size-distributions of forests in North America (Moore et al., 2018), even though many of these forests are net carbon sinks (and therefore not in a precise steady-state). The current study uses the simplest reasonable form of DET that assumes growth is a power law of size and mortality is constant. This has been shown to be a useful model of underlying demographic processes, with the model parameters correlating with observations (Muller-Landau et al., 2006b; Lima et al., 2016), even though individual forest plots may deviate from the simplifying assumptions. While the growth and mortality functions of a forest are often unknown, DET can provide useful indications of the patterns of the ratio of mortality-to-growth based on observed tree-size distributions alone (Moore et al., 2018).

Amazonia is one of the largest pools of land carbon on the planet (Feldpausch et al., 2012) and may be vulnerable to climate change (Cox et al., 2000; Brienen et al., 2015). It is therefore vital that DGVMs are able to model this region well. We therefore extend the analysis of Moore et al. (2018) by fitting DET model to tree trunk-diameter data for this key region, and also to tree mass data derived from allometry, which is even more relevant for ESMs. As a baseline comparison we also fit the Metabolic Scaling Theory of forest demography (MSTF), which assumes that trees of varying sizes fill space in such a way that the size-distribution scales with trunk diameter D as D^{-2} (West et al., 2009).

In Section 2 below we summarise the theoretical basis for DET and also MSTF, deriving analytical formulae for total forest biomass in each case. Section 3 describes the Methods and data, and Section 4 describes the results. Finally discussion and conclusions are in Sections 5 and 6.

2 Theory

2.1 Demographic Equilibrium Theory (DET)

The distribution of tree sizes in a forest can be understood in terms of how the growth and mortality of the trees vary with tree size (Kohyama et al., 2003; Coomes et al., 2003; Muller-Landau et al., 2006b). The amount of trees in a given size class (i.e.