Local diversity in heterogeneous landscapes: quantitative assessment with a height-structured forest metacommunity model. *Theoretical Ecology*

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Appendix 3: Empirical estimates of individual growth variance

Species-specific estimates of mean individual growth rates and their standard deviations are reported for understory and canopy trees on each of four soil types in table S4 of Purves et al. (2008). The mean coefficient of variation (CV) from Purves et al. (2008) is 0.64. These estimates are derived from pooling thousands of inventory plots within each soil type across Michigan, Wisconsin, and Minnesota, USA using data from the U.S. Forest Service's Forest Inventory and Analysis (FIA) program (http://fia.fs.fed.us), which comprises a systematic sample of all U.S. forests. Several factors may inflate the mean CV of these data in the context of our PPA metacommunity model, including: (i) although our model, like Purves et al. (2008), recognizes only two crown classes (understory and canopy), in reality there is a continuum of canopy positions, and finer partitioning of canopy classes could reduce the CV within each class; (ii) the large geographic region analyzed by Purves et al. (2008) is not climatically uniform; and (iii) the broad FIA soil types used by Purves et al. (2008) include considerable inter-plot variation in edaphic and topographic conditions.

To address these potential biases, we estimated growth CVs at the scale of individual inventory plots using FIA data and our own unpublished data from the Chequamegon-Nicolet National Forest in Wisconsin, USA (hereafter, 'WI data'; Lichstein et al., in preparation), where we implemented a plot design similar to that of FIA (USDA 2007). Growth was defined as the annualized increment in diameter at breast height (dbh) and was estimated from repeated dbh measurements (FIA data) or from increment cores (WI data). For both analyses, we used FIA's crown class definitions (USDA 2007; Woudenberg et al. n.d.; dominant, codominant, intermediate, or overtopped), and we estimated CVs within strata defined by a unique combination of plot location, time of sampling, species, and crown class.

FIA data. The dataset we analyzed spanned the entire U.S. and included all publicly available data (http://fia.fs.fed.us) as of October 2010. We excluded plots in plantations, plots where one or more trees were harvested during the re-measurement interval (typically 5-10 years), and plots with more than one reported 'condition' (which FIA defines as a unique combination of land-owner, soil type, and disturbance history). Although the FIA dataset includes > 10^5 plots, only a small fraction of these include enough individuals in the same species and crown class to obtain a reasonable estimate of the growth CV. We performed the analysis three times using different minimum samples sizes per strata (10, 20, or 30 individuals). For example, in the analysis with a minimum sample size of 30, we calculated the sample CV for all plot×time×species×crown-class combinations with at least 30 individual growth observations. We then averaged these CVs within each crown class. Among the 12 combinations of minimum sample size (10,

20, or 30) and crown class (dominant, codominant, intermediate, or overtopped), the smallest mean CV was 0.41 and the largest was 0.63, suggesting that the mean CV of 0.64 from Purves et al. (2008) is only moderately inflated. The number of CVs contributing to the 12 mean CVs in our FIA analysis ranged from five to 7809.

WI data. Although FIA plots sample a relatively small area (0.4 ha), plots are randomly located and may therefore span multiple environmental conditions that are too subtle to be recognized by FIA field crews; i.e., FIA plots may span considerable environmental heterogeneity, despite including only a single 'condition' as defined by FIA (see previous paragraph). In contrast, our WI data were collected on plots that were intentionally located so as to minimize within-plot heterogeneity in environmental conditions. Although these data include only 19 inventory plots, they are well-suited to provide estimates of growth CV that can aid in interpreting our PPA metacommunity model (which assumes a homogeneous abiotic environment within each patch). As with FIA data, we analyzed the WI data with minimum sample sizes of 10, 20, and 30 individuals per strata. Among the 12 combinations of minimum sample size and crown class, the smallest mean CV was 0.32 and the largest was 1.20. The mean values of the mean CVs for each of the three minimum-sample-size analyses were 0.55 (96 strata with $\geq$ 10 individuals), 0.56 (62 strata with $\geq$ 20 individuals), and 0.59 (40 strata with $\geq$ 30 individuals). These results agree closely with the FIA analysis, and suggest that the random placement of FIA plots does not substantially increase variance in individual growth rates within species×crown-class categories.

Given these results, 0.5 appears to be a reasonable (and slightly conservative) estimate for the CV of growth for individuals of a given species in a given crown class in a homogeneous abiotic environment. Clark et al.'s (2003) figure 3 reveals an even higher variance in individual growth for a given light level (CV > 0.5), although some of this variance may be due to pooling data from multiple plots.

Literature cited

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