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

Jeremy W. Lichstein[1,2] and Stephen W. Pacala[1]

[1] Princeton University, Department of Ecology and Evolutionary Biology
[2] present address: University of Florida, Department of Biology, jlichstein@ufl.edu

Appendix 1: Analytical approximations for the PPA model

R_0: Lifetime reproductive success in an empty habitat
The expected number of offspring (size-D_0 individuals) produced by a single size-D_0 individual over its lifetime in an empty habitat is

$$R_0 = \int_0^\infty e^{-\mu_c t} F a_1 (D_0 + G_c t)^{a_2} dt \,.$$

The exponential term is the probability that an individual in full sunlight (i.e., the 'canopy') survives t years, given its mortality rate μ_c; F is the annual production of size-D_0 individuals per unit canopy area; and the remainder of the integrand is the canopy area ($a_1 D^{a_2}$) of an individual of age t with growth rate G_c. To solve the integral, we first change variables from time (t) to diameter (D), noting that $t = D/G_c$, and $dt = dD/G_c$:

$$R_0 = \int_{D_0}^\infty e^{-\frac{\mu_c}{G_c}(D-D_0)} F a_1 D^{a_2} dD \frac{1}{G_c} \,.$$

Rearranging and changing variables again to $x \equiv \frac{\mu_c}{G_c} D$ yields:

$$R_0 = \frac{F a_1 G_c^{a_2} e^{\frac{\mu_c}{G_c} D_0}}{\mu_c^{a_2+1}} \int_{\frac{\mu_c}{G_c} D_0}^\infty e^{-x} x^{a_2} dx = \frac{F a_1 G_c^{a_2} e^{\frac{\mu_c}{G_c} D_0}}{\mu_c^{a_2+1}} \left(\int_0^\infty e^{-x} x^{a_2} dx - \int_0^{\frac{\mu_c}{G_c} D_0} e^{-x} x^{a_2} dx \right).$$

The first integral in parentheses is a gamma function, $\Gamma(a_2 + 1)$. With realistic parameter values, the term $\frac{\mu_c}{G_c} D_0$ is approximately zero. For example, using μ_c and G_c for the late-successional species in Appendix 2 (0.005 yr^{-1} and 0.3 cm yr^{-1}, respectively), if $D_0 = 0.1$ cm, then $\frac{\mu_c}{G_c} D_0 = 0.00167$. Therefore, (i) the term $e^{\frac{\mu_c}{G_c} D_0}$ outside of the parentheses is approximately one; and (ii) the second integral inside the parentheses is approximately zero (note that the mode of $e^{-x} x^{a_2}$ is $a_2 \approx 1.5 >> \frac{\mu_c}{G_c} D_0$; see Appendix 2). Thus, a good approximation for R_0 is

(A1)
$$R_0 \approx \frac{F a_1 G_c^{a_2} \Gamma(a_2+1)}{\mu_c^{a_2+1}}$$

with equality if $D_0 = 0$.

Approximation for $\widehat{D}^*$: diameter of smallest canopy tree at equilibrium.
The equilibrium height of canopy closure ($\hat{z}^*$, the height of the shortest canopy tree) is $h_!(\widehat{D}^*)^{h_2}$, where $\widehat{D}^*$ is defined implicitly by Eqns. 4 and 8 as:

$$1 = \int_{\widehat{D}^*}^{\infty} \frac{F}{G_c} e^{-\frac{\mu_u}{G_u}(\widehat{D}^* - D_0)} e^{-\frac{\mu_c}{G_c}(D - \widehat{D}^*)} a_1 D^{a_2} dD$$

Changing variables from D to $x \equiv \frac{\mu_c}{G_c} D$ and rearranging yields

$$\frac{e^{\left(\frac{\mu_u}{G_u} - \frac{\mu_c}{G_c}\right)\widehat{D}^* - \frac{\mu_u}{G_u} D_0} \mu_c^{a_2+1}}{F a_1 G_c^{a_2}} = \int_{\frac{\mu_c}{G_c}\widehat{D}^*}^{\infty} e^{-x} x^{a_2}\, dx = \Gamma(a_2+1) - \int_0^{\frac{\mu_c}{G_c}\widehat{D}^*} e^{-x} x^{a_2} dx$$

where $\Gamma(\cdot)$ is the gamma function. Combining the late-successional values from Appendix 2 for μ_c and G_c (0.005 yr^{-1} and 0.3 cm yr^{-1}, respectively) with reasonable values for $\widehat{D}^*$ (e.g., 15 cm), the upper limit of the integral on the right is much smaller than the mode of $e^{-x}x^{a_2}$ (which equals $a_2 \approx 1.5$; see Appendix 2). Ignoring this integral and substituting Eqn. A1 leads to the approximation

$$\widehat{D}^* \approx \left(\frac{\mu_u}{G_u} - \frac{\mu_c}{G_c}\right)^{-1} \left[\frac{\mu_u}{G_u} D_0 + \ln(R_0)\right].$$

Typically, $\mu_u > \mu_c$ and $G_u < G_c$, so we expect $\frac{\mu_u}{G_u}$ to be much greater than $\frac{\mu_c}{G_c}$. For example, using the parameter values for the late-successional species in Appendix 2, $\frac{\mu_u}{G_u} = 0.5$, and $\frac{\mu_c}{G_c} = 0.0167$. Assuming $\left(\frac{\mu_u}{G_u} - \frac{\mu_c}{G_c}\right) \approx \frac{\mu_u}{G_u}$, the above approximation simplifies to

$$\widehat{D}^* \approx D_0 + \frac{G_u}{\mu_u} \ln(R_0)\,.$$