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Scaling from trees to forests: tractable macroscopic equations for forest dynamics.
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Appendix D. Flat-top model: Equilibrium diameter distribution.

Here we derive a formula for an equilibrium diameter distribution. In the simulator with the PPA, let the light level under a single layer of canopy be L_U. This is simply the species-specific transmissivity of a crown. Again, we ignore the possibility that a second complete sub-canopy forms, which would cause the shortest saplings to be shaded by two complete layers, because this generally does not occur for reasonable parameter values. The mathematics is more cumbersome if understory plants can form a complete second canopy, but the problem is still analytically tractable.

Using equations (7) and (19) let the growth rate in the understory, G_D, be:

$$G_D = G_L \frac{C_3 L_U}{1 + C_4 L_U}, \tag{D-1}$$

and let the corresponding understory mortality be:

$$\mu_D = \mu_U + m_1 e^{m_2 G_D}. \tag{D-2}$$

Also, let D^* be the diameter corresponding to the critical canopy height z^*:

$$z^* = H_2(1 - e^{-\frac{H_1}{H_2} D^*}) \quad or \quad D^* = \frac{H_2}{H_1} \ln\left(\frac{H_2}{H_2 - z^*}\right). \tag{D-3}$$

Finally, recall that seed production in the simulator occurs at a constant rate, F, per unit of sunlit canopy area. As a result, a constant density of F seedlings are produced by a closed canopy per unit time. We may thus write the equilibrium equation for the von Foerster system (13) for the flat top model as:

$$\begin{aligned} \frac{d\widehat{N}(D)}{dD} &= -\widehat{N}(D)\frac{\mu_D}{G_D}, \quad if \;\; D < D^* \\ \frac{d\widehat{N}(D)}{dD} &= -\widehat{N}(D)\frac{\mu_L}{G_L}, \quad if \;\; D > D^* \end{aligned} \tag{D-4}$$

where, to ensure conservation of individuals as they grow across the discontinuity D^*:

$$\lim_{D \to D^* - 0} G_D \widehat{N}(D) = \lim_{D \to D^* + 0} G_L \widehat{N}(D). \tag{D-5}$$

Taking the initial diameter of seedlings, D_0 to be negligible, we have a solution of (D-4-D-5):

$$\begin{aligned} \widehat{N}(D) &= \frac{F}{G_D} e^{-\frac{\mu_D}{G_D} D}, \quad if \;\; D < \widehat{D}^* \\ \widehat{N}(D) &= \frac{F}{G_L} e^{-\frac{\mu_D}{G_D}\widehat{D}^*} e^{-\frac{\mu_L}{G_L}(D - \widehat{D}^*)}, \quad if \;\; D > \widehat{D}^*. \end{aligned} \tag{D-6}$$

Now what is the equilibrium value of $\widehat{D}^*$? To answer this question, it is again mathematically convenient to recast the problem in terms of age cohorts. Then, equation (15) that defines the threshold canopy size becomes:

$$1 = \int_0^\infty F e^{-\frac{\mu_D}{G_D}\widehat{D}^*} e^{-\mu_L \tau} \alpha (\widehat{D}^* + G_L \tau)^2 d\tau. \tag{D-7}$$

The expression on the RHS is the crown area of canopy trees at equilibrium. The variable of integration, τ, is the number of years that a cohort has been in the canopy. At equilibrium, a cohort that has spent τ years in the canopy has diameter: $\widehat{D}^* + G_L \tau$, and crown area: $\alpha(\widehat{D}^* + G_L \tau)^2$. The density in each age cohort at birth is simply F if the canopy is closed, and, because $\frac{\widehat{D}^*}{G_D}$ is the amount of time that it takes to grow in the understory to diameter $\widehat{D}^*$, $Fe^{-\frac{\mu_D}{G_D}\widehat{D}^*}$ is the equilibrium density of a cohort when it reaches the canopy, and $Fe^{-\frac{\mu_D}{G_D}\widehat{D}^*} e^{-\mu_L \tau}$ is the density of the cohort after τ years in the overstory. Thus, the RHS of (D-7) is the sum over all canopy tree cohorts of density times crown area.

Note that when $\widehat{D}^*$ is zero, the RHS of equation (D-7) is identical to the RHS of the invasion condition (22). It is straightforward to use this fact to prove that $\widehat{D}^* > 0$ whenever a species can invade an empty habitat. This is not surprising, because the model lacks density dependence until the canopy closes.

After three integrations (the first two by parts) and minor rearrangement, (D-7) becomes:

$$e^{\frac{\mu_D}{G_D}\widehat{D}^*} = F\alpha \left(\frac{(\widehat{D}^*)^2}{\mu_L} + \frac{2G_L \widehat{D}^*}{\mu_L^2} + \frac{G_L^2}{\mu_L^3} \right). \tag{D-8}$$

Then the equilibrium diameter distribution is given by (D-6-D-8) (Fig. 16a). We can also derive the equilibrium height distribution,

$$\begin{aligned} \hat{z}^* &\approx H_2 \left(1 - \left(\frac{2F\alpha G_L^2}{\mu_L^3} \right)^{-\frac{H_1}{H_2}\frac{G_D}{\mu_D}} \right) \\ \widehat{N}(z) &= \frac{F}{G_D H_1} \left(\frac{H_2}{H_2 - z} \right)^{1 - \frac{\mu_D}{G_D}\frac{H_2}{H_1}}, \; z < \hat{z}^* \\ \widehat{N}(z) &= \frac{F}{G_D H_1} e^{-\left(\frac{\mu_D}{G_D} - \frac{\mu_L}{G_L}\right)\widehat{D}^*} \left(\frac{H_2}{H_2 - z} \right)^{1 - \frac{\mu_L}{G_L}\frac{H_2}{H_1}}, \; z > \hat{z}^* \end{aligned} \tag{D-9}$$

and the equilibrium age distribution:

$$\begin{aligned} \widehat{A}^* &\approx \frac{1}{\mu_D} \ln\left(\frac{2F\alpha G_L^2}{\mu_L^3} \right) \\ \widehat{N}(A) &= Fe^{-\mu_D A}, \quad if \;\; A < \widehat{A}^* \\ \widehat{N}(A) &= Fe^{-\mu_D \widehat{A}^*} e^{-\mu_L (A - \widehat{A}^*)}, \quad if \;\; A > \widehat{A}^*. \end{aligned} \tag{D-10}$$