

**Paul Caplat, Ran Nathan, and Yvonne M. Buckley. 2012. Seed terminal velocity, wind turbulence, and demography drive the spread of an invasive tree in an analytical model. *Ecology* 93:368–377.**

Appendix C. Calculations for the perturbation analysis.

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### Demographic and dispersal matrices

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & F_1 e_s & F_2 e_s \\ s_j & s_j r_j & 0 & 0 \\ 0 & s_j (1 - r_j) & 0 & 0 \\ 0 & 0 & s_a & s_a \end{bmatrix}$$

$$M_i(s) = \begin{bmatrix} 1 & 1 & mgf_1(s) & mgf_2(s) \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 \end{bmatrix}$$

where  $mgf_i(s)$  is the moment-generating function of the WALD kernel, the subscript indicating the difference in parameter  $h_r$  used for the two adult-classes (noted thereafter  $h_{r_i}$ ), with  $i$  in  $\{1,2\}$ . The moment-generating function only exists for some finite interval around  $s = 0$ . It is assumed that there exists some value  $s_{max}$  such that all elements of  $M_i(s)$  exist for all  $0 \leq s < s_{max}$  with  $s_{max}$  defined as:

$$s_{max} = \frac{V_t^2}{4h_c \kappa \bar{U} \sigma_w}$$

For  $i = \{1,2\}$  we have:

$$mgf_i(s) = \exp\left[\frac{\gamma_i}{\mu_i} \left(1 - \sqrt{1 - \frac{2\mu_i^2 s}{\gamma_i}}\right)\right]$$

### Perturbation analysis

The sensitivity of spread rate  $c^*$  to a parameter  $x$  can be expressed in function of the sensitivity of  $c^*$  to a matrix transition (from stage  $l$  to stage  $k$ )  $a_{k,l}$  :

$$\frac{\partial c^*}{\partial x} = \sum_{k,l} \frac{\partial c^*}{\partial a_{k,l}} \frac{\partial a_{k,l}}{\partial x}$$

where  $\frac{\partial c^*}{\partial a_{k,l}}$  is the conventional sensitivity of  $c^*$  to a transition value (equations 26 of

Neubert and Caswell 2000):

$$\frac{\partial c^*}{\partial a_{k,l}} = \frac{m_{k,l}}{s^* \rho_1} \frac{\partial \rho_1}{\partial h_{k,l}}$$

where  $s^*$  is the value of  $s$  that minimizes  $c(s)$ ;  $m_{k,l}$  is the  $(k,l)$  element of  $M(s^*)$ ,  $\rho_1$  is the dominant eigenvalue of  $H(s) = A \circ M(s)$ ,  $h_{k,l}$  is the  $(k,l)$  element of  $H(s^*)$ . See Neubert and Caswell 2000 for the calculation of  $\frac{\partial \rho_1}{\partial h_{k,l}}$ .

(Similarly the elasticity of  $c^*$  to underlying parameters is given by:

$$\frac{x \partial c^*}{c^* \partial x} = \frac{x}{c^*} \sum_{k,l} \frac{\partial c^*}{\partial a_{k,l}} \frac{\partial a_{k,l}}{\partial x}$$

For the sake of clarity, we thereafter present the calculation of sensitivities only, as for any parameter  $x$ :

$$elasticity(x) = \frac{x}{c^*} . sensitivity(x)$$

In the case of dispersal parameters the sensitivity of  $c^*$  to a given parameter  $y$  can then be expressed as:

$$\frac{\partial c^*}{\partial y} = \frac{a_{1,4}}{s^* \rho_1} \frac{\partial m_{1,4}}{\partial y} \frac{\partial \rho_1}{\partial h_{1,4}} + \frac{a_{1,5}}{s^* \rho_1} \frac{\partial m_{1,5}}{\partial y} \frac{\partial \rho_1}{\partial h_{1,5}}$$

as in our case, elements of  $M(s)$  describing dispersal have for coordinates  $(1,4)$  and  $(1,5)$ , for values  $h_{r1}$  and  $h_{r2}$  respectively. Note that in the case of  $h_{r1}$  and  $h_{r2}$  the sensitivity is only half of the equation:

$$\frac{\partial c^*}{\partial h_{r1}} = \frac{a_{1,4}}{s^* \rho_1} \frac{\partial m_{1,4}}{\partial h_{r1}} \frac{\partial \rho_1}{\partial h_{1,4}}$$

$$\frac{\partial c^*}{\partial h_{r2}} = \frac{a_{1,5}}{s^* \rho_1} \frac{\partial m_{1,5}}{\partial h_{r1}} \frac{\partial \rho_1}{\partial h_{1,5}}$$

The calculation of sensitivities (and elasticities) requires finding the partial derivatives of the moment-generating function  $mgf_i(s)$  on the different parameters:

$$\frac{\partial m_{k,l}}{\partial y} = \frac{\partial mgf_i(s)}{\partial y} = \frac{\partial}{\partial y} \left( \exp \left[ \frac{\gamma_i}{\mu_i} \left( 1 - \sqrt{1 - \frac{2\mu_i^2 s}{\gamma_i}} \right) \right] \right)$$

where  $\mu$  and  $\gamma$  are respectively the scale and shape parameters of the kernel, defined as:

$$\mu = \frac{\bar{U}h_{ri}}{v_t}$$

and

$$\gamma = \frac{\bar{U}h_{ri}^2}{2\kappa h_c \sigma_w}$$

By substituting the parameters  $\mu$  and  $\gamma$  with the full set of parameters the formula can be calculated for each dispersal parameter:

### Horizontal wind speed

$$\frac{\partial m_{k,l}}{\partial \bar{U}} = \frac{\partial mgf_i(s)}{\partial \bar{U}}$$

$$\begin{aligned} \frac{\partial m_{k,l}}{\partial \bar{U}} &= \frac{\partial}{\partial \bar{U}} \left( \exp \left[ \frac{h_{ri}v_t}{2\kappa h_c \sigma_w} \left( 1 - \sqrt{1 - \frac{4\bar{U}h_c \kappa \sigma_w s}{v_t^2}} \right) \right] \right) \\ &= \exp \left[ \frac{h_{ri}v_t}{2\kappa h_c \sigma_w} \left( 1 - \sqrt{1 - \frac{4\bar{U}h_c \kappa \sigma_w s}{v_t^2}} \right) \right] \frac{\partial}{\partial \bar{U}} \left( \frac{h_{ri}v_t}{2\kappa h_c \sigma_w} \left( 1 - \sqrt{1 - \frac{4\bar{U}h_c \kappa \sigma_w s}{v_t^2}} \right) \right) \\ &= mgf_i(s) \frac{\partial}{\partial \bar{U}} \left( \frac{h_{ri}v_t}{2\kappa h_c \sigma_w} \left( 1 - \sqrt{1 - \frac{4\bar{U}h_c \kappa \sigma_w s}{v_t^2}} \right) \right) \\ &= mgf_i(s) \frac{\partial}{\partial \bar{U}} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} \left( v_t - \sqrt{v_t^2 - 4\bar{U}h_c \kappa \sigma_w s} \right) \right) \\ &= \frac{\partial}{\partial \bar{U}} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} (4\bar{U}h_c \kappa \sigma_w s - v_t^2) \right) \cdot \frac{mgf_i(s)}{2\sqrt{v_t^2 - 4\bar{U}h_c \kappa \sigma_w s}} \\ \frac{\partial m_{k,l}}{\partial \bar{U}} &= sh_{ri} \frac{mgf_i(s)}{R(s)} \end{aligned}$$

with

$$R(s) = \sqrt{v_t^2 - 4\bar{U}h_c \kappa \sigma_w s}$$

### Standard-deviation of vertical wind

$$\begin{aligned}
\frac{\partial m_{k,l}}{\partial \sigma_w} &= mgf_i(s) \frac{\partial}{\partial \sigma_w} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} (v_t - R(s)) \right) \\
&= mgf_i(s) \left[ (v_t - R(s)) \frac{\partial}{\partial \sigma_w} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} \right) + \frac{h_{ri}}{2\kappa h_c \sigma_w} \frac{\partial}{\partial \sigma_w} (v_t - R(s)) \right] \\
&= \frac{-h_{ri}}{2\kappa h_c \sigma_w^2} mgf_i(s) \left[ v_t - R(s) - \sigma_w \left( \frac{-4\bar{U} h_c \kappa s}{2R(s)} \right) \right] \\
&= \frac{-h_{ri}}{2\kappa h_c \sigma_w^2} mgf_i(s) \left[ v_t - \frac{R(s)^2 + 2\bar{U} h_c \kappa \sigma_w s}{R(s)} \right] \\
&= -\frac{h_{ri} mgf_i(s)}{2\kappa h_c \sigma_w^2} \left[ \frac{2\kappa h_c \bar{U} \sigma_w s - v_t^2}{R(s)} + v_t \right]
\end{aligned}$$

**Canopy height and wind velocity variable (similar derivation to standard deviation of vertical wind)**

$$\begin{aligned}
\frac{\partial m_{k,l}}{\partial h_c} &= -\frac{h_{ri} mgf_i(s)}{2\kappa \sigma_w h_c^2} \left[ \frac{2\kappa h_c \bar{U} \sigma_w s - v_t^2}{R(s)} + v_t \right] \\
\frac{\partial m_{k,l}}{\partial \kappa} &= -\frac{h_{ri} mgf_i(s)}{2\sigma_w h_c \kappa^2} \left[ \frac{2h_c \kappa \bar{U} \sigma_w s - v_t^2}{R(s)} + v_t \right]
\end{aligned}$$

**Height of release**

$$\begin{aligned}
\frac{\partial m_{k,l}}{\partial h_{ri}} &= mgf_i(s) \frac{\partial}{\partial h_{ri}} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} (v_t - R(s)) \right) \\
&= \frac{mgf_i(s)}{2\kappa h_c \sigma_w} (v_t - R(s))
\end{aligned}$$

**Seed terminal velocity**

$$\begin{aligned}
\frac{\partial m_{k,l}}{\partial v_t} &= mgf_i(s) \frac{\partial}{\partial v_t} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} (v_t - \sqrt{v_t^2 - 4\bar{U} h_c \sigma_w s}) \right) \\
&= mgf_i(s) \frac{h_{ri}}{2\kappa h_c \sigma_w} - \frac{\partial}{\partial v_t} \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} \sqrt{v_t^2 - 4\bar{U} h_c \sigma_w s} \right)
\end{aligned}$$

$$\begin{aligned}
&= mgf_i(s) \frac{h_{ri}}{2\kappa h_c \sigma_w} - \left( \frac{h_{ri}}{2\kappa h_c \sigma_w} \frac{2v_t}{2\sqrt{v_t^2 - 4\bar{U}h_c \sigma_w s}} \right) \\
&= mgf_i(s) \frac{h_{ri}}{2\kappa h_c \sigma_w} \left( 1 - \frac{v_t}{R(s)} \right)
\end{aligned}$$

### Literature Cited

Neubert, M. G. and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* **81**:1613-1628.