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**Eelke Jongejans, Katriona Shea, Olav Skarpaas, Dave Kelly and Stephen P. Ellner.**

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**APPENDIX A***Mathematical Details of Spatial Integral Projection Models***1. Traveling wave speed for a spatial integral projection model**

Here we show how the asymptotic traveling wave speed can be computed for a linear spatial integral projection model for population spread in one-dimensional space. The calculations are very similar to Neubert and Caswell (2000); the main point of running through them is to identify the necessary properties of the kernel. We compute traveling wave speeds rigorously, but it remains a matter of conjecture and simulation (as in the Neubert-Caswell model) that growing populations do in fact spread asymptotically as traveling waves for well-behaved dispersal distributions.

We consider spatial IPM kernels of the form

$$K(x_2, z_2 | x_1, z_1) = \tilde{K}(x_2 - x_1, z_2, z_1) \quad (\text{A.1})$$

where  $z$  = trait,  $x$  = location,  $z_1$  = trait in previous time step,  $x_1$  = location in previous time step. The right-hand side of (A1) corresponds to the assumption of spatial homogeneity, specifically that the chance of moving from one location to another depends only on the distance between them. We also assume that movement is symmetric, i.e. that

$\tilde{K}(u, z_2, z_1) = \tilde{K}(-u, z_2, z_1)$ . As in the Neubert-Caswell model, (A.1) allows the movement distribution to depend on the trait value  $z$ , but as explained below the trait-specific movement distributions must have moment-generating functions that are all defined on some finite interval. In this paper  $z$  is individual size and the set of possible  $z$  values is a closed interval, but the calculations here apply to general individual-level state spaces (e.g., any compact metric space) as in Ellner and Rees (2006).

The population dynamics are then

$$n(x_2, z_2, t+1) = \iint \tilde{K}(x_2 - x_1, z_2, z_1) n(x_1, z_1, t) dx_1 dz_1. \quad (\text{A.2})$$

Assume a traveling wave solution of (A.2) in one spatial dimension,

$$n(x, z, t) = u(x - ct, z) \quad (\text{A.3})$$

where  $c$  is the wave speed. Setting  $t=0$  and substituting (A.3) into (A.2) gives

$$u(x_2 - c, z_2) = \iint \tilde{K}(x_2 - x_1, z_2, z_1) u(x_1, z_1) dx_1 dz_1. \quad (\text{A.4})$$

Possible speeds for a wave advancing to the right are found by positing solutions of the form

$$u(y, z) = w(z) e^{-sy} \quad (\text{A.5})$$

where  $y$  is location and  $w$  gives the trait distribution of individuals in the traveling wave (this basic approach goes back at least to papers by Fisher (1937) and Kolmogorov et al. (1937), where it was used for diffusion equations; see Mollison (1991)). Substituting (A.5) into (A.4),

$$w(z_2) e^{-s(x_2 - c)} = \iint \tilde{K}(x_2 - x_1, z_2, z_1) w(z_1) e^{-sx_1} dx_1 dz_1 \quad (\text{A.6})$$

Let  $v = x_1 - x_2$ , and using the symmetry property  $K(-v, z_2, z_1) = K(v, z_2, z_1)$ ,

$$\begin{aligned} w(z_2)e^{sc} &= \iint \tilde{K}(x_2 - x_1, z_2, z_1) w(z_1) e^{-s(x_2 - x_1)} dx_1 dz_1 \\ &= \iint \tilde{K}(v, z_2, z_1) w(z_1) e^{sv} dv dz_1 \\ &= \int H_s(z_2, z_1) w(z_1) dz_1 \end{aligned} \quad (\text{A.7})$$

where

$$H_s(z_2, z_1) = \int \tilde{K}(v, z_2, z_1) e^{sv} dv. \quad (\text{A.8})$$

For each  $s$ ,  $H_s$  is a kernel in the trait space whenever it exists. Its elements are values of the moment-generating function for the spatial distribution of type- $z_2$  individuals at time  $t+1$  produced by type- $z_1$  individuals at time  $t$ . We assume that for  $s$  in some interval containing 0,  $H_s$  is defined and satisfies the assumptions of Ellner and Rees (2006) guaranteeing the existence of a unique dominant eigenvalue and corresponding positive stable trait distribution.

If we can now find a function  $w$  and a number  $s$  that satisfy equation (A.7), this shows that there is a traveling wave with velocity  $c$ . To do this, let  $\rho_s$  denote the dominant eigenvalue of  $H_s$ , and  $w_s$  the corresponding eigenvector. The solution of (A.7) that we seek is obtained by setting  $w = w_s$  and  $e^{sc} = \rho_s$ , i.e.  $c = \frac{1}{s} \log(\rho_s)$ . So long as the kernels satisfy the assumptions stated above, any such  $c > 0$  (i.e., any value of  $s$  such that  $\rho_s > 1$ ) generates a traveling wave solution moving to the right at velocity  $c$ . Note that  $H_0$  is the kernel for total population size, so the total population size grows

asymptotically if and only if  $\rho_0 > 1$ , and in that case there will exist  $s > 0$  such that  $\rho_s > 1$ , hence there will be traveling wave solutions.

A standard monotonicity argument (as in Kot et al. (1996)) shows that any model solution with the initial population limited to a finite spatial domain cannot spread faster than the slowest such wave speed, i.e.,

$$c^* = \min_{s>0} \left[ \frac{1}{s} \log(\rho_s) \right] \quad (\text{A.9})$$

is an upper bound on the rate of spread. What actually happens is, as in the Neubert-Caswell model, still a matter of simulation and conjecture. The outcome universally observed is that a growing population converges to a wave travelling at rate  $c^*$ , so that (A.9) is the asymptotic rate of spread. However, this result has been proved rigorously only for unstructured populations under some assumptions about the shape of the dispersal distribution (see Mollison 1991 for a review of these results).

For species such as plants with sessile adults and juvenile dispersal, the kernel will typically have the form

$$\tilde{K}(v, z_2, z_1) = K_d(v)Q(z_2|z_1) + \delta_0(v)G(z_2|z_1) \quad (\text{A.10})$$

where  $K_d$  is the dispersal kernel, and  $\delta_0$  is the Dirac delta function, i.e. a probability distribution single spike of unit mass at  $v=0$ . The notation in (A.10) corresponds to the situation in our *Carduus* model. Seeds in the seed bank and established individuals cannot move and  $G$  represents their survival and growth, whereas offspring (generated by the fecundity kernel  $Q$ ) disperse away from the parent. However, (A.10) would also apply

in other situations where some move, others don't, and all movers have the same dispersal pattern. For the kernel (A.10) we get

$$H_s = M(s)Q + G \quad (\text{A.11})$$

where  $M(s)$  is the moment generating function of the dispersal kernel. A practical consequence of equation (A.11) is that  $\rho_s$  exists for any  $s$  such that the  $M(s)$  is finite so long as the nonspatial kernel  $Q+G$  satisfies the conditions for existence of a dominant eigenvalue given in Ellner and Rees (2006).

Equation A.11 thus is the core of our *Carduus nutans* SIPM, which we program in R as follows. Equation A.11 says that  $H_s$  is equal to the kernel  $Q+G$  of the demographic (nonspatial) IPM, except that all demographic transition rates corresponding to seed production and dispersal are multiplied by  $M(s)$ , the moment generating function of the dispersal kernel evaluated at  $s$  (see Neubert and Caswell 2000 for explanations of moment generating functions). Let “mat” be the iteration matrix for the demographic IPM (see Ellner and Rees (2006; appendix) for R code for generating iteration matrices for IPMs). Because it is important to separate rosette survival/growth from transitions that involve production and dispersal of new seeds, we keep those vital rates in separate columns of “mat” (see also the appendix of Jongejans et al. 2008). This means for, e.g., the SIPM100 that “mat” consists of 199 columns and rows: 1 for the seed bank, 99 for size classes of new seedlings, and 99 for the size classes of surviving rosettes. To perform the necessary multiplications by  $M(s)$  we construct the matrix “Ms” with the code

```
Ms<-matrix(1,ncol=199,nrow=199); Ms[1:100,2:199]<-m
```

where  $m$  equals  $M(s)$ . Then the code " $Hs \leftarrow Ms * mat$ " multiplies by  $M(s)$  all the transitions involving dispersal (recall that "\*" is element-by-element multiplication in R), which gives the iteration matrix for the kernel  $H_s$ . Note that the entries  $Ms[1:100, 1]$  are not multiplied by  $m$ , because these correspond to seeds in the seed bank, which either remain in the seed bank or else germinate to form a rosette, in both cases without any change in location.

## 2. Sensitivity analysis of traveling wave speed

Because  $c^*$  is defined implicitly by equation (A.9) we need to use the following general result. Suppose  $Q(\theta) = \min_x f(x, \theta)$  where  $x$  and  $\theta$  are real and  $f$  is a smooth real-valued function. Let  $x_\theta$  denote the value of  $x$  at which the minimum occurs, so that

$\frac{\partial f}{\partial x}(x_\theta, \theta) = 0$ . Then

$$\frac{\partial F}{\partial \theta} = \frac{\partial}{\partial \theta} f(x_\theta, \theta) = \left[ \frac{\partial f}{\partial x} \frac{\partial x_\theta}{\partial \theta} + \frac{\partial f}{\partial \theta} \right] (x_\theta, \theta) = \frac{\partial f}{\partial \theta} (x_\theta, \theta). \quad (A.12)$$

Applying this to  $c^*$ , with  $\theta$  any parameter or component of the kernel, we get

$$\frac{\partial c^*}{\partial \theta} = \left[ \frac{1}{s \rho_1} \frac{\partial \rho_1}{\partial \theta} \right] \Big|_{s=s^*} \quad (A.13)$$

where  $s^*$  is the value of  $s$  at which the minimum occurs in (A.9). Because  $\rho_1(s)$  is the dominant eigenvalue of the kernel  $H_s$ ,  $\frac{\partial \rho_1}{\partial \theta}$  can be computed by standard sensitivity analysis methods for integral projection models (Ellner and Rees 2006).

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