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## **Appendix B from S. P. Ellner and M. Rees, “Integral Projection Models for Species with Complex Demography”** (Am. Nat., vol. 167, no. 3, p. 000)

### **Supplementary Technical Details**

This appendix fills in mathematical details from the main text and is directed mainly at theoreticians. It requires some familiarity with linear operator theory or a willingness to look up unfamiliar terms in a reference such as that by Dunford and Schwartz (1988). However, reading it is not necessary for building and using integral models because the results and their practical implications are all explained in the main text. The first section discusses the assumptions in our model related to power positivity and what can happen when they fail to hold. “Age  $\times$  Size Models with Mixing at Birth” and “Models with Uniform Senescence and Mixing at Birth” concern mixing at birth and  $u$ -boundedness in models with age structure and models with uniform senescence, respectively. “Local Stability Analysis for Density-Dependent Models” and “Spectral Radius of  $P + aF$ ” concern density-dependent models, and “Net Reproductive Rate  $R_0$ ” concerns the definition and properties of the net reproductive rate  $R_0$ .

### **Power Positivity, Compactness, and the $u$ -Bounded Property**

Because we assume that the kernel is continuous and  $\mathbf{X}$  is compact, power positivity of the kernel implies that there exists some  $c > 0$  and some  $m > 0$  such that

$$K^{(m)}(y, x) \geq c, \tag{B1}$$

which we refer to as uniform power positivity (UPP). A power-positive (PP) kernel is necessarily UPP in our model, but this is not true in general: a continuous kernel on an unbounded domain can be positive everywhere without satisfying equation (B1). Unfortunately, “mere positiveness of the kernel is, in contrast to the matrix case, not sufficient” (Krasnosel’skij et al. 1989, p. 94) for stable population growth. The behavior of our model depends on the fact that a PP kernel is necessarily UPP under our assumptions. On an unbounded state space, a biologically meaningful kernel cannot be UPP because this would imply growth to infinite population size in finite time (see “Noncompact Domains” in app. C); on a bounded but noncompact state space, UPP would have to be verified directly, along with the other operator properties used to prove stable population growth in appendix C.

The potential “misbehavior” of a PP kernel on a noncompact state space is illustrated by integrodifference equation models for spatially distributed populations. Consider a population distributed in physical space with a Gaussian distribution of offspring dispersal distances, like that of Kot et al. (1996). The kernels for these models are PP but not UPP. Although such populations may converge to an asymptotic growth rate, the typical behavior of their spatial distribution is convergence to a constant linear rate of spread (Kot et al. 1996), in the sense that the radius of the region containing any given fraction of the population grows at an asymptotically linear rate. The result is that the fraction of the population within any fixed finite region goes to 0—there is no convergence to an asymptotic population structure. These contrast with the behavior of a PP kernel on a compact space (which is therefore UPP), where the fraction of individuals in any finite region of state space converges to a positive limiting value determined by the stable distribution  $w$ .

Indefinite spread in trait space is also prevented if a PP kernel satisfies the  $u$ -bounded property, defined as follows. If there exists a probability distribution  $u(x)$  on  $\mathbf{X}$  such that for any initial population distribution  $n(x, 0) = n_0(x)$  we have  $\alpha(n_0)u(x) \leq n(x, m) \leq \beta(n_0)u(x)$ , where  $\alpha, \beta$  are positive numbers, then the  $m$ -step kernel is said to be  $u$ -bounded (Krasnosel’skij et al. 1989). In appendix C, we show that any UPP kernel in our model has an iterate that is  $u$ -bounded, and then we use the theory of  $u$ -bounded positive operators to derive

stable population growth. So, the implications underlying stable population theory in our model are either  $PP \Rightarrow UPP \Rightarrow u$ -bounded, which holds so long as the state space is compact, or mixing at birth  $\Rightarrow u$ -bounded, which holds in many age-structured models. In the main text, we have explained how biologically reasonable assumptions lead to models with a compact state space, and at the end of appendix C, we discuss the mathematical difficulties created by noncompact state spaces.

### Age $\times$ Size Models with Mixing at Birth

Childs et al. (2003) showed that an age  $\times$  size model with finite maximum age is  $u$ -bounded and therefore has stable population growth under two assumptions: a mixing at birth condition and the primitivity of the life cycle graph. Here, we extend those conditions to the weaker mixing assumption stated in the text, as a step toward analyzing models with uniform senescence. A density-independent integral projection model (IPM) can be regarded as a linear operator  $\mathbf{T}$  on a space of population distribution functions; our assumptions in the main text (continuous kernel on compact domain) imply that  $\mathbf{T}$  maps  $L_1(X)$  into itself.  $\mathbf{T}$  was called  $\mathbf{K}$  in the main text; we change notation here for consistency with Childs et al. (2003). We decompose  $\mathbf{T} = \mathbf{P} + \mathbf{F}$ , where  $\mathbf{P}$  and  $\mathbf{F}$  are the operators defined by  $P$  and  $F$ , the survival and fecundity components of the kernel.

The mixing at birth assumption is formally defined as follows. Let  $\mathbf{F}n$  denote the offspring distribution resulting from population distribution  $n$ . If there is a probability distribution  $\varphi_0$  on  $\mathbf{X}$  such that for any population distribution  $n$  there are positive numbers  $A$  and  $B$  (depending on  $n$ ) such that

$$A\varphi_0 \leq \mathbf{F}n \leq B\varphi_0, \quad (\text{B2})$$

with  $A > 0$  whenever  $\mathbf{F}n \neq 0$ , we say that the model has mixing at birth.

We first show that equation (B2) is implied by the mixing assumption of Childs et al. (2003). Let  $\mathbf{X}^+$  denote the set of population states with positive fecundity,

$$\mathbf{X}^+ = \left\{ x \in \mathbf{X} : \int_{\mathbf{X}} F(y, x) dy > 0 \right\}.$$

Recall that the integral tacitly includes all age-specific fecundity kernels. Childs et al. (2003) assumed that  $c\varphi_0(y) \leq f_a(y, x) \leq C\varphi_0(y)$  for all  $x$  in  $\mathbf{X}^+$ , where  $c$  is some positive constant and  $f_a$  is the fecundity kernel for age  $a$  individuals. More generally, suppose that  $c(x)\varphi_0(y) \leq f_a(y, x) \leq C(x)\varphi_0(y)$  for all  $x$  in  $\mathbf{X}^+$ , where  $c$  and  $C$  are positive on  $\mathbf{X}^+$  and  $\varphi_0 \in L_1(\mathbf{X})$ . Then,

$$\mathbf{F}n(y) \equiv \int_{\mathbf{X}} F(y, x)n(x)dx = \int_{\mathbf{X}^+} F(y, x)n(x)dx \geq \varphi_0(y) \int_{\mathbf{X}^+} c(x)n(x)dx,$$

so we can take  $A = \int_{\mathbf{X}^+} c(x)n(x)dx$  and, similarly,  $B = \int_{\mathbf{X}^+} C(x)n(x)dx$ . When  $\mathbf{F}n \neq 0$ , the support of  $n$  must intersect  $\mathbf{X}^+$ , so  $A$  and  $B$  are both positive.

We now derive conditions under which some iterate of  $\mathbf{T}$  is  $u$ -bounded. Define a Leslie matrix  $\mathbf{L}_0$  by assigning size distribution  $\varphi_0$  to a cohort of offspring and computing their age-specific per capita survival and fecundity, as in appendix A, section a, of Childs et al. (2003); that is, let  $l_a$  be the fraction of the cohort that survives to age  $a$ ,  $p_a = l_{a+1}/l_a$ , and let  $f_a$  be the average per capita fecundity at age  $a$  of those that survive to age  $a$ . Assume that  $\mathbf{L}_0$  is primitive and therefore power positive. Let  $n(y, 0) = n_0(y)$  be an initial size distribution. Because postreproductives are omitted (by assumption), there exists a future time  $q$  at which some births occur; that is,  $\mathbf{F}n(\cdot, q) > 0$ . The value of  $q$  can depend on  $n_0$  but cannot be larger than the maximum age  $M$ . Because  $\mathbf{L}_0$  is primitive, there exists some time interval  $Q$  such that all entries in  $\mathbf{L}_0$  are strictly positive for all  $t \geq Q$ . Hence, at any time  $R \geq M + Q$ , the population includes individuals of all ages  $j = 0, 1, 2, \dots, M$ . These individuals were necessarily born at times  $R, R - 1, R - 2, \dots, R - M$ . Define  $\alpha(n_0) > 0$  to be the minimum value of  $A(n)$  over those times and  $\beta(n_0)$  to be the maximum value of  $B(n)$  over those times. The actual distribution of age 0 individuals in each of those years is therefore between  $\alpha(n_0)\varphi_0(y)$  and  $\beta(n_0)\varphi_0(y)$ , and the population at time  $R$  consists of the combined survivors from each of those cohorts. Thus,

$$\alpha(n_0)u_0(y) \leq n(y, R) \leq \beta(n_0)u_0(y), \quad (\text{B4})$$

where  $u_0 = (\mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \dots + \mathbf{P}^M)\varphi_0$ . Because the survival kernel is bounded and continuous, it maps  $L_1(\mathbf{X})$  into itself, so  $u_0 \in L_1(\mathbf{X})$ . This is the definition of  $\mathbf{T}^R$  being  $u_0$ -bounded, which implies that stable population theory holds for  $\mathbf{T}$  (see app. C).

## Models with Uniform Senescence and Mixing at Birth

An  $m$ -year-ahead kernel  $K^{(m)}$  can be split into two parts, one resulting from survival over the next  $m$  years and the other involving some reproduction. For any  $m$ , define  $\mathbf{G}_m = \mathbf{T}^m - \mathbf{P}^m$ , the  $m$ -step-ahead operator removing the possibility of survival from the beginning to the end of the time period, and let  $G_m(y, x)$  denote the corresponding kernel,

$$G_m(y, x) = K^{(m)}(y, x) - P^{(m)}(y, x). \quad (\text{B5})$$

If there are some  $m, c > 0$  such that

$$P^{(m)}(y, x) \leq cG_m(y, x) \quad (\text{B6})$$

for all  $x, y$  in  $\mathbf{X}$ , we say that the model has uniform senescence. The demographic meaning of equation (B6) is that in the long run, one’s own survival contributes less on average to any segment of the population than one’s expected contribution via descendants—however, note that  $c$  in equation (B6) is not assumed to be small.

Truncating the model by not allowing survival past age  $m$  gives an age-structured model with a finite maximum age. In this section, we show that if uniform senescence holds and a truncated model satisfies the assumptions of the preceding section, then some iterate of the kernel is  $u$ -bounded.

Claim:  $\mathbf{P}^k \leq c\mathbf{G}_k$  for all  $k > m$ .

Proof:  $\mathbf{P}^{j+m} = \mathbf{P}^j\mathbf{P}^m \leq \mathbf{P}^j c\mathbf{G}_m = c\mathbf{P}^j\mathbf{G}_m$ . Because  $\mathbf{P}^j\mathbf{G}_m$  corresponds to a subset of all lineage pathways of length  $j + m$  that include some reproduction, it follows that  $\mathbf{P}^j\mathbf{G}_m \leq \mathbf{G}_{j+m}$ .

We now construct a family of upper bounds  $u_{0,k}$  such that  $\mathbf{T}^k$  is  $u_{0,k}$ -bounded from above for any  $k > m$ . The claim implies that  $\mathbf{T}^k \leq (1 + c)\mathbf{G}_k$  for any  $k > m$ , so it suffices to prove the upper bound for  $\mathbf{G}_k$ . We can expand and then regroup

$$\mathbf{G}_k = (\mathbf{P} + \mathbf{F})^k - \mathbf{P}^k = \sum_{a=0}^{k-1} \mathbf{P}^a \mathbf{F} \mathbf{Q}_a, \quad (\text{B7})$$

where each term in  $\mathbf{Q}_a$  is some (possibly empty) string of composed  $\mathbf{P}$ ’s and  $\mathbf{F}$ ’s. That is, starting from the left in any term in the term-by-term expansion of  $(\mathbf{P} + \mathbf{F})^k - \mathbf{P}^k$ , there is some number  $a$  of successive  $\mathbf{P}$ ’s before the first  $\mathbf{F}$ , with  $0 \leq a < k$ , and then possibly something else after that leftmost  $\mathbf{F}$ .  $\mathbf{Q}_a$  collects all the “something else” from terms with  $a$  successive  $\mathbf{P}$ ’s at the left before the first  $\mathbf{F}$ . For any initial distribution  $n_0$ ,  $\mathbf{F}\mathbf{Q}_a n_0$  is the distribution of offspring from the population distribution  $\mathbf{Q}_a n_0$ , so under mixing at birth, this is bounded above by  $B(\mathbf{Q}_a n_0)\varphi_0$ . Therefore,

$$\mathbf{G}_k n_0 \leq \sum_{a=0}^{k-1} \mathbf{P}^a B(\mathbf{Q}_a n_0)\varphi_0 \leq B_{\max}(n_0) \sum_{a=0}^{k-1} \mathbf{P}^a \varphi_0 = B_{\max}(n_0)u_{0,k}, \quad (\text{B8})$$

where  $B_{\max}(n_0) = 1 + \max\{B(\mathbf{Q}_a n_0), a = 0, 1, \dots, k-1\} > 0$  and  $u_{0,k}$  is given by equation (B4), with  $M = k - 1$ .

We now give conditions under which some iterate  $\mathbf{T}^k$  is  $u_{0,k}$ -bounded from below for some  $k > m$ . The lower bound is required to be positive, but if we mimic the derivation of equation (B8) starting from  $\mathbf{T}^k \geq \mathbf{G}_k$ , there is no guarantee that  $\min\{A(\mathbf{Q}_a n_0)\} > 0$ . To get a positive lower bound, we use an age-structured life cycle in which no individuals can live beyond age  $k - 1$ , represented schematically by

$$\tilde{\mathbf{G}} = \begin{pmatrix} \mathbf{F} & \mathbf{F} & \cdots & \mathbf{F} & \mathbf{F} \\ \mathbf{P} & 0 & \cdots & 0 & 0 \\ \vdots & \mathbf{P} & & \vdots & \vdots \\ \vdots & & \ddots & & \\ 0 & 0 & \cdots & \mathbf{P} & 0 \end{pmatrix}, \quad (\text{B9})$$

acting on the  $k$ -fold Cartesian product of  $\mathbf{X}$  with itself, corresponding to ages 0, 1, 2, ...,  $k - 1$ . If  $n_0(x)$  is an initial state distribution for  $\mathbf{T}$ , let  $\tilde{\mathbf{n}}_0 = (n_0, 0, 0, \dots, 0)$  denote the corresponding initial distribution for  $\tilde{\mathbf{G}}$ , and let  $\pi_0$  be projection from  $\mathbf{X}^k$  into  $\mathbf{X}$  by summing up individuals of all ages,

$$\pi_0 : (n_0(x), n_1(x), \dots, n_{k-1}(x)) \mapsto \sum_{a=0}^{k-1} n_a(x).$$

Then,  $\mathbf{T}^r n_0 \geq \pi_0 \tilde{\mathbf{G}}^r \tilde{\mathbf{n}}_0$  for any  $r$  because equality would hold if a  $\mathbf{P}$  were added to the bottom right corner of  $\tilde{\mathbf{G}}$ .

$\tilde{\mathbf{G}}$  is an age  $\times$  size model with finite maximum life span. If mixing at birth holds, we can again define a Leslie matrix  $\mathbf{L}_0(k)$  for a cohort of individuals born with distribution  $\varphi_0$ . Assume that  $\mathbf{L}_0(k)$  is primitive for some  $k > m$ . This is a very weak assumption in a model without explicit age structure. For example, if there are two successive ages ( $a^*$ ,  $a^* + 1$ ) at which reproduction occurs in a cohort of individuals born with distribution  $\varphi_0(y)$ , then  $\mathbf{L}_0(k)$  will be power positive for any  $k \geq a^*$ . Then, exactly as in the previous section, for any  $R$  sufficiently large  $\tilde{\mathbf{G}}^R$  is  $\tilde{u}_0$ -bounded from below with  $\tilde{u}_0 = (\mathbf{I} + \tilde{\mathbf{P}} + \tilde{\mathbf{P}}^2 + \cdots + \tilde{\mathbf{P}}^{k-1})\tilde{\varphi}_0$ , where  $\tilde{\varphi}_0 = (\varphi_0, 0, 0, \dots, 0)$  and  $\tilde{\mathbf{P}}$  is the survival component of  $\tilde{\mathbf{G}}$ , given by equation (B9) with the  $\mathbf{F}$ 's deleted. Therefore,

$$\begin{aligned} \mathbf{T}^r n_0 &\geq \pi_0 \tilde{\mathbf{G}}^R \tilde{\mathbf{n}}_0 \geq \pi_0 \alpha(n_0) \tilde{u}_0 = \alpha(n_0) \pi_0 \tilde{u}_0 = \alpha(n_0) \\ &\times \pi_0 (\mathbf{I} + \tilde{\mathbf{P}} + \tilde{\mathbf{P}}^2 + \cdots + \tilde{\mathbf{P}}^{k-1}) \tilde{\varphi}_0 \geq \alpha(n_0) \\ &\times (\mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \cdots + \mathbf{P}^{k-1}) \varphi_0 = \alpha(n_0) u_{0,k}, \end{aligned}$$

which is the definition of  $\mathbf{T}^R$  being  $u_{0,k}$ -bounded from below. Because  $\mathbf{T}^R$  is  $u_{0,k}$ -bounded from below and  $\mathbf{T}^k$  is  $u_{0,k}$ -bounded from above, some iterate of  $\mathbf{T}$  is  $u_{0,k}$ -bounded (Krasnosel'skij et al. 1989, p. 95). Thus, the conditions required for  $u_{0,k}$ -boundedness are mixing at birth, uniform senescence, and the Leslie matrix  $\mathbf{L}_0(k)$  being primitive for some  $k > m$ .

## Local Stability Analysis for Density-Dependent Models

Let  $\bar{n}$  denote an equilibrium of the density-dependent model  $n(y, t + 1) = \int_{\mathbf{x}} K(y, x, \mathbf{N}(t)) n(x, t) dx$ , and let  $z$  denote a small perturbation. Then, starting from  $\bar{n} + z$  in year  $t$ , the population in year  $t + 1$  is

$$\begin{aligned} \bar{n} + z' &= \int_{\mathbf{x}} K(y, x, \bar{\mathbf{N}} + \langle W, z \rangle) (\bar{n}(x) + z(x)) dx \\ &= \int_{\mathbf{x}} K(y, x, \bar{\mathbf{N}}) (\bar{n}(x) + z(x)) dx + \langle W, z \rangle \int_{\mathbf{x}} \frac{\partial K}{\partial N}(y, x, \bar{\mathbf{N}}) (\bar{n}(x) + z(x)) dx + O(z^2) \\ &= \bar{n} + \int_{\mathbf{x}} K(y, x, \bar{\mathbf{N}}) z(x) dx + \langle W, z \rangle \int_{\mathbf{x}} \frac{\partial K}{\partial N}(y, x, \bar{\mathbf{N}}) \bar{n}(x) dx + O(z^2). \end{aligned} \quad (\text{B10})$$

So, to leading order, we have

$$\begin{aligned}
 z' &= \int_{\mathbf{x}} K(y, x, \bar{\mathbf{N}})z(x)dx + \langle W, z \rangle \int_{\mathbf{x}} \frac{\partial K}{\partial N}(y, x, \bar{\mathbf{N}})\bar{n}(x)dx \\
 &= \int_{\mathbf{x}} J(y, x, \bar{\mathbf{N}})z(x)dx,
 \end{aligned} \tag{B11}$$

where

$$\begin{aligned}
 J(y, x, \bar{\mathbf{N}}) &= K(y, x, \bar{\mathbf{N}}) + Q(y, \bar{\mathbf{N}})W(x), \\
 Q(y, \bar{\mathbf{N}}) &= \int_{\mathbf{x}} \frac{\partial K}{\partial N}(y, x, \bar{\mathbf{N}})\bar{n}(x)dx.
 \end{aligned}$$

The linearized stability condition is that the spectral radius of the Jacobian operator  $\mathbf{J}$  defined by equation (B11) should be  $<1$ ; because  $\mathbf{J}$  is a compact operator (so long as  $J$  is continuous), the spectral radius of  $\mathbf{J}$  is the maximum magnitude of its eigenvalues. These calculations and the stability condition are very similar to the matrix case (Caswell 2001, sec. 16.4).

We now apply the general stability criterion to a model with density dependence in fecundity, as stated in the text. Specifically, consider a kernel of the form

$$K(y, x, N) = P(y, x) + g(\mathbf{N})\varphi(y)f(x). \tag{B12}$$

Here,  $f$  is the total raw fecundity of a type  $x$  individual,  $\varphi$  is the distribution of offspring types,  $\mathbf{N}$  is total offspring production (i.e.,  $W = f$ ), and the offspring survival rate  $g$  is assumed to be smooth and undercompensatory; that is,  $dg/d\mathbf{N} < 0$ , but  $d(\mathbf{N}g(\mathbf{N}))/d\mathbf{N} \geq 0$ , and we assume that the kernel  $P(y, x) + \varphi(y)f(x)$  is power positive. In the absence of population structure, equation (B12) reduces to the difference equation  $n_{t+1} = Pn_t + f n_t g(f n_t)$ , for which it is easy to prove that there exists at most one positive equilibrium, which, if it exists, is locally stable.

Exactly the same holds for equation (B12). In “Spectral Radius of  $P + aF$ ,” we derive a result implying that the spectral radius of the operator corresponding to the kernel  $P(y, x) + a\varphi(y)f(x)$  is a strictly increasing function of  $a$  for  $a \geq 0$ . Under our assumptions, the spectral radius is also the dominant eigenvalue (see app. C). Consequently, because  $g$  is decreasing, there is at most one  $\bar{\mathbf{N}} > 0$  for which the dominant eigenvalue of equation (B12) equals 1. The corresponding eigenvector is unique up to multiplicative scalings, and only one scaling will give the proper value of  $\bar{\mathbf{N}}$ , so there is at most one equilibrium for equation (B12). Some routine calculus shows that equation (B12) has a Jacobian kernel of the form  $J(\bar{n}) = \bar{P} + a\bar{F}$ , where  $\bar{P}, \bar{F}$  are the survival and fecundity components of  $K(y, x, \bar{\mathbf{N}})$  and  $0 \leq a < 1$ . The spectral radius of  $\mathbf{J}(\bar{n})$  is therefore  $<1$ , so  $\bar{n}$  is locally stable. Existence of an equilibrium can often be related to the model’s behavior at low and high densities, using results from degree theory (Krasnosel’skii and Zabreiko 1984, sec. 44). For example, an equilibrium must exist for equation (B12) if the zero equilibrium is unstable (i.e., the spectral radius for  $K(y, x, 0) > 1$ ), the total offspring production  $\mathbf{N}g(\mathbf{N})$  has a finite upper bound, and a population without recruitment cannot persist (i.e., the spectral radius for  $P < 1$ ) but dies off at a bounded rate.

### Spectral Radius of $P + aF$

We show here that the spectral radius  $\sigma(a)$  of the integral operator  $\mathbf{T}_a$  defined by the kernel  $K_a(y, x) = P(y, x) + aF(y, x)$  is a strictly increasing function of  $a$  for  $a \geq 0$ , under our usual assumptions about  $\mathbf{X}$ , continuity, and nonnegativity of kernel components and assuming that  $K_1$  is power positive (hence UPP) and that  $F$  is nonzero.

Let  $b > a > 0$ ; we need to show that  $\sigma(b) > \sigma(a)$  (the case  $a = 0$  is treated separately below). As in the matrix case, power positivity is determined by the support of the transition kernel, so both  $K_b$  and  $K_a$  are UPP and satisfy the assumptions for stable population growth in appendix C. Let  $w$  be the dominant eigenvector of  $\mathbf{T}_a$ , with eigenvalue  $\sigma(a)$ ; because of UPP,  $w$  is strictly positive. Then,  $\mathbf{T}_b w \geq \mathbf{T}_a w$ , with strict inequality at some points (because  $(b - a)F$  is nonzero and  $w$  is strictly positive). Let  $m$  be an iterate such that  $K_a^{(m)}$  (and therefore  $K_b^{(m)}$ ) is strictly positive. We then have that  $\mathbf{T}_b^m (\mathbf{T}_b w - \mathbf{T}_a w) > 0$  everywhere on  $\mathbf{X}$ , and, consequently,  $\mathbf{T}_b^{m+1} w >$

$\mathbf{T}_b^m \mathbf{T}_a w \geq \mathbf{T}_a^{m+1} w = \sigma(a)^{m+1} w$ , with the outermost inequality being strict everywhere on  $\mathbf{X}$ . Because both members of that inequality are strictly positive, their ratio is a continuous function and therefore attains its minimum value, which must be  $>1$ . Therefore, for some  $\varepsilon > 0$ , we have  $\mathbf{T}_b^{m+1} w > (1 + \varepsilon)\sigma(a)^{m+1} w$ . This implies (via the formula  $\sigma(\mathbf{A}) = \lim_{n \rightarrow \infty} \|\mathbf{A}^n\|^{1/n}$ ; or see lemma 9.2 in Krasnosel’skij et al. 1989) that  $\sigma(b) \geq (1 + \varepsilon)^{1/(m+1)} \sigma(a)$ .

Now consider  $a = 0$ . If  $\sigma(0) = 0$ , we are done because  $\sigma(b) > 0$  (in app. C, we show that this is true for any UPP kernel in our model). If  $\sigma(0) > 0$ , let  $w$  be a corresponding eigenvector scaled so that at some point,  $w(x) > 0$ . We claim that  $w$  must be nonnegative. As explained in appendix C, any eigenvector for a continuous kernel in our model must lie in  $L_1 \cap L_2$ , and its corresponding eigenvalue is the same whether we consider the operator as acting in  $L_1$  or  $L_2$ . If  $w$  is not nonnegative, then  $\mathbf{T}_0|w| \geq |\mathbf{T}_0 w|$ , with strict inequality at some point, implying that  $\|\mathbf{T}_0|w|\|_1 > \|\mathbf{T}_0 w\|_1 = \sigma(0) \|w\|_1 = \sigma(0) \||w|\|_1$ . The outermost inequality implies that the spectral radius of  $\mathbf{T}_0$  is greater than  $\sigma(0)$ , a contradiction implying that  $w$  must be nonnegative. Now, let  $m$  be an iterate such that  $K_b^{(m)}$  is strictly positive, and hence  $\mathbf{T}_b^m w > 0$  everywhere. Then, as above,  $\mathbf{T}_b \mathbf{T}_b^m w \geq \mathbf{T}_0 \mathbf{T}_b^m w$ , with strict inequality at some points. We then have that  $\mathbf{T}_b^m (\mathbf{T}_b \mathbf{T}_b^m w - \mathbf{T}_0 \mathbf{T}_b^m w) > 0$  everywhere on  $\mathbf{X}$ , implying that  $\mathbf{T}_b^{2m+1} w > \mathbf{T}_0^{2m+1} w = \sigma(0)^{2m+1} w$  everywhere. Because both sides of the outer inequality are continuous and hence bounded, some small multiple of the right-hand side will be uniformly smaller than their difference. So, again, there exists  $\varepsilon > 0$  such that  $\mathbf{T}_b^{2m+1} w > (1 + \varepsilon)\sigma(0)^{2m+1} w$ , implying  $\sigma(b) > \sigma(0)$ .

## Net Reproductive Rate $R_0$

$R_0$  is formally defined as the dominant eigenvalue of the operator  $\mathbf{R}$  corresponding to the next-generation kernel  $R = F + FP + FP^2 + \dots$ . The biological interpretation of  $\mathbf{R}$  is that  $\mathbf{R}n$  is the total offspring production over their lifetime by a set of individuals with state distribution  $n$ . However, we need to show that the series defining  $\mathbf{R}$  is actually convergent. Let  $\mathbf{P}$  and  $\mathbf{F}$  be the operators corresponding to the survival-growth and fecundity kernels, respectively. Suppose that all states suffer some unavoidable mortality; that is,  $\int_{\mathbf{X}} P(y, x) dy \leq p^* < 1$  for all  $x$ . The  $L_1$  operator norm of  $\mathbf{P}$  is then at most  $p^*$ ; hence, the sequence  $\mathbf{F} + \mathbf{F}\mathbf{P} + \mathbf{F}\mathbf{P}^2 + \dots$  is convergent and equals  $\mathbf{F}(\mathbf{I} - \mathbf{P})^{-1}$ . The corresponding kernel sum is pointwise convergent because  $P^{(k+1)}(y, x) \leq (p^*)^k$ . Using this bound, it is easy to show that the limit kernel is continuous and therefore bounded; hence,  $\mathbf{R}$  is a compact operator.

We also need a dominant eigenvalue for  $\mathbf{R}$ . As with matrix models, this requires additional assumptions because  $\mathbf{R}$  does not necessarily satisfy the assumptions for stable population growth when  $\mathbf{T} = \mathbf{P} + \mathbf{F}$  does (Cushing and Yicang 1994). Our model for *Onoropordum* satisfies two related assumptions, each of which implies a dominant eigenvalue. The first is mixing at birth. If equation (B2) holds, then for any population state  $n$ ,  $A(z)\varphi_0 \leq \mathbf{R}n \leq B(z)\varphi_0$ , where  $z = (\mathbf{I} - \mathbf{P})^{-1}n$ . Consequently,  $\mathbf{R}$  is  $u$ -bounded and therefore satisfies the operator properties P1–P3 (see app. C), which imply the existence of a unique dominant eigenvalue equal to the spectral radius. The second has to do with the operator  $\mathbf{Q} = (\mathbf{I} - \mathbf{P})^{-1}\mathbf{F}$ .  $\mathbf{R}$  and  $\mathbf{Q}$  have the same eigenvalues (this is equivalent to the familiar result for matrices that  $\mathbf{A}$  and  $\mathbf{B}\mathbf{A}\mathbf{B}^{-1}$  have the same eigenvalues). For our model,  $\mathbf{Q}$  is positive and therefore power positive, which again implies properties P1–P3 in appendix C. We know that  $\mathbf{Q}$  is positive in our model because  $\mathbf{F}n$  is positive on the complete range of offspring types for any nonzero population distribution  $n$ ; hence,  $\mathbf{Q}n = (\mathbf{I} + \mathbf{P} + \mathbf{P}^2 + \dots)\mathbf{F}n$  is positive for any possible descendant of any possible newborn, which is the entire state space.

Usually,  $R_0$  has to be computed by iterating  $\mathbf{R}$  or  $\mathbf{Q}$ , but it can be calculated explicitly if there is exact mixing at birth, meaning that  $F(y, x) = \varphi_0(y)f(x)$ . Then, the only eigenvector of  $\mathbf{R}$  is  $\varphi_0$  because the range of  $\mathbf{F}$  is the span of  $\varphi_0$ . A direct calculation then shows that  $R_0$  is the average per capita lifetime offspring production from a cohort of newborns with state distribution  $\varphi_0$ . For iterating  $\mathbf{R}$  or  $\mathbf{Q}$ , it is important to remember that the “kernel” for the identity operator is a  $\delta$  function  $I(y, x) = \delta_y(x)$ . So, however the model is implemented,  $I$  must be represented by a matrix  $\mathbf{I}$  such that  $\mathbf{I}n = n$  for any state vector  $n$ . You can then use matrix inversion to find the matrix representing  $\mathbf{Q}$  or  $\mathbf{R}$ .

Evolutionary analysis of our model uses the fact that  $R_0 - 1$  and  $\lambda - 1$  have the same sign. We now prove this under the assumptions that  $\mathbf{T}$  is power positive and that  $\mathbf{Q}$  has a positive, simple, strictly dominant eigenvalue whose corresponding right eigenvector is nonnegative (it is sufficient for this that  $\mathbf{Q}$  be power positive, as in our model, because stable population theory then holds for  $\mathbf{Q}$ ). These assumptions are very similar to those required in the matrix case by Cushing and Yicang (1994). It seems likely that  $u$ -boundedness of some iterate of  $\mathbf{T}$  would be sufficient, but a proof eludes us.

If  $\lambda = 1$ , then  $(\mathbf{P} + \mathbf{F})w = w$ ; hence,  $\mathbf{F}w = (I - \mathbf{P})w$ , and so  $\mathbf{Q}w = w$ . Thus, 1 is an eigenvalue of  $\mathbf{Q}$ . Suppose that 1 is not the dominant eigenvalue of  $\mathbf{Q}$ . Then, there exists a real eigenvalue  $\rho > 1$ , with corresponding nonnegative eigenvector  $z$ . As  $w$  is strictly positive (because  $\mathbf{T}$  is power positive), we have  $\langle w, v \rangle > 0$  in the  $L_2$  inner product and can therefore write  $w = a_1 z + a_2 u$ , with  $a_1 > 0$  and  $\langle u, z \rangle = 0$ . We can then apply to  $\mathbf{Q}$  the proof in appendix C of convergence to stable distribution (theorem 2), with the conclusion that  $\mathbf{Q}^n w / \rho^n$  converges to a nonzero multiple of  $z$ . This implies  $w = z$ ; hence, the dominant eigenvalue of  $\mathbf{Q}$  is 1; that is,  $R_0 = 1$ . Reversing this argument shows that  $\lambda = 1$  whenever  $R_0 = 1$ .

Suppose  $\lambda > 1$ . Then,  $(\mathbf{P} + \mathbf{F})w = \lambda w$  implies that  $\mathbf{F}w = \lambda w - \mathbf{P}w = (I - \mathbf{P})w + (\lambda - 1)w$ , and, therefore,

$$\begin{aligned} \mathbf{Q}w &= w + (\lambda - 1)(I - \mathbf{P})^{-1}w = w + (\lambda - 1) \\ &\times (I + \mathbf{P} + \mathbf{P}^2 + \dots)w \geq w + (\lambda - 1)w = \lambda w. \end{aligned}$$

As in the previous section, by theorem 9.4 of Krasnosel’skij et al. (1989), this implies that some eigenvalue of  $\mathbf{Q}$ , and hence the dominant eigenvalue, is at least  $\lambda$ ; that is,  $R_0 \geq \lambda > 1$ .

Suppose that  $R_0 > 1$ . Then, consider the family of operators  $\mathbf{P} + a\mathbf{F}$ , with corresponding  $\lambda(a)$ ,  $R_0(a)$ , and so on. Because  $\mathbf{Q}(a) = a\mathbf{Q}(1)$ , we have  $R_0(a) = aR_0(1)$ ; so, for  $a^* = 1/R_0(1) < 1$ , we have  $R_0(a^*) = 1$  and, therefore,  $\lambda(a^*) = 1$ . The result of the previous section then implies that  $\lambda = \lambda(1) > \lambda(a^*) = 1$ .

We have shown that  $\lambda > 1 \Leftrightarrow R_0 > 1$  and  $\lambda = 1 \Leftrightarrow R_0 = 1$ . Therefore, we must also have  $\lambda < 1 \Leftrightarrow R_0 < 1$ .

The relationship between  $R_0$  and  $\lambda$  is useful in density-dependent models where density affects only the initial survival of offspring. Specifically, suppose that the kernel has the form  $K(y, x, \mathbf{N}; \theta) = P(y, x; \theta) + g(\mathbf{N})F_0(y, x; \theta)$ , where  $\theta$  is a vector of parameters characterizing the life history of individuals after the initial impact of density dependence. As in the previous section, if  $g$  is undercompensatory, a population generally tends to a stable equilibrium. Evolutionarily stable strategy (ESS) life histories are then identified by invasibility analysis involving a resident type  $\theta_r$  at a stable equilibrium with weighted total population  $\bar{\mathbf{N}}$  and a rare invader with different parameters  $\theta_i$ . The next-generation operator for the invader is  $\mathbf{R}_i = g(\bar{\mathbf{N}})F_0(\theta_i)(I - P(\theta_i))^{-1}$ ; hence, the invader’s  $R_0$  is  $g(\bar{\mathbf{N}})\tilde{R}_0(\theta_i)$ , where  $\tilde{R}_0(\theta)$  is the dominant eigenvalue of  $F_0(\theta)(I - P(\theta))^{-1}$ .  $\tilde{R}_0$  is the net reproductive rate when offspring are counted before the initial density-dependent mortality and is a density-independent property of the adult life history. The resident’s  $R_0$  is  $g(\bar{\mathbf{N}})\tilde{R}_0(\theta_r) = 1$  because the resident has  $\lambda = 1$ . The invader therefore has  $R_0 > 1$  and consequently  $\lambda > 1$  if and only if  $\tilde{R}_0(\theta_i) > \tilde{R}_0(\theta_r)$ . The ESS adult life history is therefore characterized by maximization of  $\tilde{R}_0(\theta)$ . In models with exact mixing at birth, the dominant (and only) eigenvector of  $F_0(\theta)(I - P(\theta))^{-1}$  is the offspring distribution  $\varphi_0$ ; hence,  $\tilde{R}_0(\theta)$  is given by the integral of  $F_0(\theta)(I - P(\theta))^{-1}\varphi_0$ , which is the average per capita pre-density dependence offspring production of a randomly chosen newborn.

## References Cited Only in Appendix B

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