Appendix S1: Derivation of the optimality condition

Here I derive expressions for the resident and invader seed density distributions and use these to derive an expression for $\langle \mathrm{Cov}(\lambda_i, \nu_i)_x \rangle_t$.

First, we convert eq. 1, the equation for the dynamics of $n(x,t)$, into an equation for the relative population density $\nu(x,t) = n(x,t)/\langle n \rangle_x(t)$. I distinguish between the resident and the invader populations by using subscripts r and i, respectively, or j if the equation holds true for either population. Dividing eq. 1 by $\langle n_j \rangle_x(t+1)$ and replacing $\langle n_j \rangle_x(t+1)$ with $\widetilde{\lambda}_j(t)\langle n_j \rangle_x(t)$ on the right hand side, we obtain

$$\nu_j(x,t+1) = k_j * \left(\frac{\lambda_{1j}}{\widetilde{\lambda}_j} \nu_j \right)(x,t) + \left(\frac{\lambda_{2j}}{\widetilde{\lambda}_j} \nu_j \right)(x,t), \qquad \text{(A1)}$$

where $*$ represents convolution (i.e., $(f * g)(x) \equiv \sum_{y=-\infty}^{\infty} f(x-y)g(y)$).

Assume that fecundity, and therefore variation in population density and local growth rate, is of small amplitude so that we can write $F(x,t)$, $n_j(x,t)$, and $\lambda_j(x,t)$ in terms of their spatiotemporal averages plus perturbations of $O(\sigma)$[1]. Assume also that the deviations of spatial averages from spatiotemporal averages are $O(\sigma)$. We first write $F(x,t)$, $n_j(x,t)$, and $\lambda_{kj}(x,t)$ in terms of perturbations away from their spatial averages:

$$F(x,t) = \langle F \rangle_x(t)(1 + \epsilon(x,t)) \qquad \text{(A2)}$$

$$n_j(x,t) = \langle n_r \rangle_x(t)(1 + u_j(x,t)) \qquad \text{(A3)}$$

$$\lambda_{kj}(x,t) = \langle \lambda_{kj} \rangle_x(t)(1 + \zeta_{kj}(x,t)), \quad k = 1, 2, \qquad \text{(A4)}$$

where $\langle \cdot \rangle_x$ denotes an average over space and the perturbations ϵ, u_j, and ζ_{kj} are $O(\sigma)$ and all have spatial and temporal averages equal to zero. We then write the spatial averages in terms of perturbations away from the spatiotemporal averages:

$$\langle F \rangle_x(t) = \langle F \rangle_{x,t}(1 + \Omega(t)) \qquad \text{(A5)}$$

$$\langle n_j \rangle_x(t) = \langle n_j \rangle_{x,t}(1 + \eta_j(t)) \qquad \text{(A6)}$$

$$\langle \lambda_{kj} \rangle_x(t) = \langle \lambda_{kj} \rangle_{x,t}(1 + h_{kj}(t)), \quad k = 1, 2, \qquad \text{(A7)}$$

[1]By $g(x) = O(\sigma)$, I mean that $\left| \frac{g(x)}{\sigma} \right|$ can be made less than or equal to some positive constant K for σ small enough.

where $\langle\cdot\rangle_{x,t}$ denotes an average over time and space and Ω_j, η_j, and h_{kj} are $O(\sigma)$ and have temporal averages equal to zero. To $O(\sigma)$, then,

$$F(x,t) = \langle F\rangle_{x,t}(1 + \epsilon(x,t) + \Omega(t)) \tag{A8}$$

$$n_j(x,t) = \langle n_j\rangle_{x,t}(1 + u_j(x,t) + \eta_j(t)) \tag{A9}$$

$$\lambda_{kj}(x,t) = \langle\lambda_{kj}\rangle_{x,t}(1 + \zeta_{kj}(x,t) + h_{kj}(t)), \quad k = 1, 2. \tag{A10}$$

Note that $\lambda_j(x,t) = \lambda_{1r}(x,t) + \lambda_{2r}(x,t)$ and so $\zeta_j(x,t) = \zeta_{1r}(x,t) + \zeta_{2r}(x,t)$ and $h_j(t) = h_{1r}(t) + h_{2r}(t)$.

To $O(\sigma)$, the relative population density $\nu_j(x,t)$ equals $1 + u_j(x,t)$. Using eq. A10 to substitute for λ_{1r} and λ_{2r}, we can rewrite eq. A1 as

$$\begin{aligned} 1 + u_j(x,t+1) &= \frac{\langle\lambda_{1j}\rangle_{x,t}}{\widetilde{\lambda}_j(t)}(1 + k_j * (u_j + \zeta_{1j})(x,t) + h_{1j}(t)) \\ &\quad + \frac{\langle\lambda_{2j}\rangle_{x,t}}{\widetilde{\lambda}_j(t)}(1 + \zeta_{2j}(x,t) + u_j(x,t) + h_{2j}(t)) + O(\sigma^2). \end{aligned} \tag{A11}$$

As noted in the main body, $\widetilde{\lambda}_j(t) = \langle\lambda_j\rangle_x(t) + \mathrm{Cov}(\lambda_j, \nu_j)_x(t)$. Because ϵ, u_j, and ζ_j are $O(\sigma)$, the covariance is $O(\sigma^2)$, and so to $O(\sigma)$, we can replace $\widetilde{\lambda}_j(t)$ by $\langle\lambda_j\rangle_x(t) = \langle\lambda_j\rangle_{x,t}(1 + h_j(t))$. This gives us

$$\begin{aligned} 1 + u_j(x,t+1) &= \frac{\langle\lambda_{1j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}}(1 + k_j * (u_j + \zeta_{1j})(x,t) + h_{1j}(t) - h_j(t)) \\ &\quad + \frac{\langle\lambda_{2j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}}(1 + u_j(x,t) + \zeta_{2j}(x,t) + h_{2j}(t) - h_j(t)) + O(\sigma^2). \end{aligned} \tag{A12}$$

Noting that $\dfrac{\langle\lambda_{1j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}} + \dfrac{\langle\lambda_{2j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}} = 1$ and $\langle\lambda_{1j}\rangle_{x,t}h_{1j}(t) + \langle\lambda_{2j}\rangle_{x,t)}h_{2j}(t) = \langle\lambda_j\rangle_{x,t}h_j(t)$, all of the purely temporal dependence on the righthand side cancels out, as indeed it must, and we are left with

$$u_j(x,t+1) = \frac{\langle\lambda_{1j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}}k_j * (u_j + \zeta_{1j})(x,t) + \frac{\langle\lambda_{2j}\rangle_{x,t}}{\langle\lambda_j\rangle_{x,t}}(u_j + \zeta_{2j})(x,t) + O(\sigma^2). \tag{A13}$$

Only the dispersal kernel distinguishes the invaders from the residents, and so both populations have the same local growth rate components: $\lambda_{1j} = \lambda_1, \lambda_{2j} = \lambda_2$. Because the invader is rare, only the residents have a competitive effect and so

$$\lambda_1(x,t) = \frac{F(x,t)G}{C(x,t)} = \frac{F(x,t)G}{G(U * n_r)(x,t)}. \tag{A14}$$

Assuming that $\sum_z U(z) = 1$ and using eqs. A8 and A9,

$$\lambda_1(x,t) = \frac{\langle F\rangle_{x,t}}{\langle n_r\rangle_{x,t}}(1 + \epsilon(x,t) + \Omega(t) - (U * u_r)(x,t) - \eta(t)) + O(\sigma^2) \tag{A15}$$

so that

$$\langle\lambda_1\rangle_{x,t} = \frac{\langle F\rangle_{x,t}}{\langle n_r\rangle_{x,t}} \tag{A16}$$

$$\zeta_1(x,t) = \epsilon(x,t) - (U * u_r)(x,t). \tag{A17}$$

Similarly,

$$\lambda_2(x,t) = s(1-G) \tag{A18}$$

so that

$$\langle\lambda_2\rangle_{x,t} = s(1-G) \tag{A19}$$

$$\zeta_2(x,t) = 0. \tag{A20}$$

The average values of λ_r and λ_2 depend on the average resident population density, $\langle n_r\rangle_{x,t}$. We can use eqs. A8 and A9 to Taylor expand eq. 1, the equation for the population dynamics. Taking a spatiotemporal average, all of the $O(\sigma)$ terms vanish, so that to $O(\sigma)$,

$$\langle n_r\rangle_{x,t} = \left(\frac{\langle F\rangle_{x,t}}{\langle n_r\rangle_{x,t}} + s(1-G)\right)\langle n_r\rangle_{x,t}, \tag{A21}$$

yielding

$$\langle n_r\rangle_{x,t} = \frac{\langle F\rangle_{x,t}}{1 - s(1-G)}. \tag{A22}$$

Thus,

$$\langle\lambda_1\rangle_{x,t} = 1 - s(1-G) \tag{A23}$$

$$\langle\lambda_2\rangle_{x,t} = s(1-G) \tag{A24}$$

and

$$\langle\lambda\rangle_{x,t} \equiv \langle\lambda_1\rangle_{x,t} + \langle\lambda_2\rangle_{x,t} = 1. \tag{A25}$$

To $O(\sigma)$, therefore, the dynamics of species j are governed by

$$u_j(x,t+1) = \langle\lambda_1\rangle_{x,t} k_j * (u_j + \epsilon - U * u_r)(x,t) + \langle\lambda_2\rangle_{x,t} u_j(x,t), \tag{A26}$$

where $\langle\lambda_1\rangle_{x,t}$ and $\langle\lambda_2\rangle_{x,t}$ are given by eqs. A23 and A24.

At this point it is useful to take the discrete spatial Fourier transform, where for an infinite domain, the spatial transform is given by

$$\tilde{f}(q,t) = \lim_{N\to\infty} \sum_{x=-N/2}^{N/2} f(x,t) e^{-iqx}, \tag{A27}$$

where $q = s(2\pi/N),\ s \in \{-N/2, -N/2+1, \ldots, N/2\}$, and the inverse transform is given by

$$f(x,t) = \lim_{N\to\infty} \frac{1}{N} \sum_{s=-N/2}^{N/2} \widetilde{f}(q,t)e^{iqx} = \frac{1}{2\pi}\int_{-\pi}^{\pi} \widetilde{f}(q,t)e^{iqx}\, dq. \tag{A28}$$

Similarly, the temporal transform is given by

$$\widetilde{f}(x,\omega) = \sum_{t=-\infty}^{\infty} f(x,t)e^{-i\omega t},\ f(x,t) = \frac{1}{2\pi}\int_{-\pi}^{\pi} \widetilde{f}(x,\omega)e^{i\omega t}\, d\omega. \tag{A29}$$

The spatiotemporal transform is achieved by taking both a spatial and a temporal transform. The Fourier transform of a convolution is the product of the Fourier transforms of the convolved functions ($(\widetilde{(f * g)}(q) = \tilde{f}(q)\tilde{g}(q))$, and so, taking a spatial Fourier transform of the resident dynamics,

$$\widetilde{u}_r(q,t+1) = \left[\langle\lambda_1\rangle_{x,t}\widetilde{k}_r(q)(1-\widetilde{U}(q)) + \langle\lambda_2\rangle_{x,t}\right]\widetilde{u}_r(q,t) + \langle\lambda_1\rangle_{x,t}\widetilde{k}_r(q)\widetilde{\epsilon}(q,t). \tag{A30}$$

The population in year t, $\widetilde{u}_r(q,t)$, depends on the previous year's population which depends in turn on populations still further back in time. Assuming that $\widetilde{u}_r(q,t)$ reaches a stationary distribution independent of its initial condition, $\widetilde{u}_r(q,t=0)$, we can write

$$\widetilde{u}_r(q,t) = \sum_{j=0}^{t-1} B_u^{t-1-j}(q)B_{\epsilon_r}(q)\widetilde{\epsilon}(q,t=j), \tag{A31}$$

where

$$B_u(q) = \langle\lambda_1\rangle_{x,t}\widetilde{k}_r(q)(1-\widetilde{U}(q)) + \langle\lambda_2\rangle_{x,t} \tag{A32}$$

$$B_{\epsilon_r}(q) = \langle\lambda_1\rangle_{x,t}\widetilde{k}_r(q). \tag{A33}$$

Eq. A31 can be expressed as a discrete convolution in time:

$$\widetilde{u}_r(q,t) = \sum_{j=0}^{\infty} \widetilde{M}(q,t-j)\widetilde{\epsilon}(q,j), \tag{A34}$$

where

$$\widetilde{M}(q,n) = \begin{cases} B_u^{n-1}(q)B_{\epsilon_r}(q) & n > 0 \\ 0 & n \le 0 \end{cases}. \tag{A35}$$

Taking the temporal Fourier transform, we reach the pleasingly simple form

$$\widetilde{u}_r(q,\omega) = \widetilde{M}(q,\omega)\widetilde{\epsilon}(q,\omega), \tag{A36}$$

where

$$\widetilde{M}(q,\omega) = \sum_{s=-\infty}^{\infty} \widetilde{M}(q,s)e^{-i\omega s} = \sum_{s=1}^{\infty} B_u^{s-1}(q)B_{\epsilon_r}(q)e^{-i\omega s} = \frac{B_{\epsilon_r}(q)(e^{-i\omega} - B_u(q))}{1 + B_u^2(q) - 2B_u(q)\cos\omega}. \tag{A37}$$

Switching to polar notation, we can rewrite $\widetilde{M}(q,\omega)$ as $R(q,\omega)e^{i\phi(q,\omega)}$, where

$$R(q,\omega) = [\mathrm{Re}(\widetilde{M}(q,\omega))^2 + \mathrm{Im}(\widetilde{M}(q,\omega))^2]^{1/2} = \frac{B_{\epsilon_r}(q)}{\sqrt{1 + B_u^2(q) - 2B_u(q)\cos\omega}} \tag{A38}$$

$$\phi(q,\omega) = \tan^{-1}\left(\frac{\mathrm{Im}(\widetilde{M}(q,\omega))}{\mathrm{Re}(\widetilde{M}(q,\omega))}\right) = \tan^{-1}\left(\frac{-\sin\omega}{\cos\omega - B_u(q)}\right) \tag{A39}$$

and where we extend the range of $\tan^{-1}$ to $[-\pi,\pi)$ by declaring ϕ to be in the third quadrant ($-\pi \le \phi < -\pi/2$) if both numerator and denominator of $\tan^{-1}$'s argument are negative, the fourth quadrant ($-\pi/2 \le \phi < 0$) if the numerator is negative and the denominator positive, the first quadrant ($0 \le \phi < \pi/2$) if both the numerator and the denominator are positive, and the second quadrant ($\pi/2 \le \phi < \pi$) if the numerator is positive and the denominator negative.

We can follow the same procedure with the invader dynamics (eq. A26 with $j = i$) finding

$$\widetilde{u}_i(q,t+1) = B_{u_i}(q)\widetilde{u}_i(q,t) + B_{\epsilon_i}(q)\widetilde{\epsilon}(q,t) + B_{u_r}(q)\widetilde{u}_r(q,t), \tag{A40}$$

where

$$B_{u_i}(q) = \langle\lambda_1\rangle_{x,t}\widetilde{k}_i(q) + \langle\lambda_2\rangle_{x,t} \tag{A41}$$

$$B_{\epsilon_i}(q) = \langle\lambda_1\rangle_{x,t}\widetilde{k}_i(q) \tag{A42}$$

$$B_{u_r}(q) = -\langle\lambda_1\rangle_{x,t}\widetilde{k}_i(q)\widetilde{U}(q) \tag{A43}$$

so that

$$\widetilde{u}_i(q,t) = \sum_{j=0}^{t-1} B_{u_i}^{t-1-j}(q)\left[B_{\epsilon_i}(q)\widetilde{\epsilon}(q,t=j) + B_{u_r}(q)\widetilde{u}_r(q,t=j)\right]. \tag{A44}$$

Taking the temporal Fourier transform, we arrive at

$$\widetilde{u}_i(q,\omega) = \widetilde{M}_{\epsilon_i}(q,\omega)\widetilde{\epsilon}(q,\omega) + \widetilde{M}_{u_r}(q,\omega)R(q,\omega)e^{i\phi(q,\omega)}\widetilde{\epsilon}(q,\omega), \tag{A45}$$

where

$$\widetilde{M}_{\epsilon_i}(q,\omega) = \frac{B_{\epsilon_i}(q)\left(e^{-i\omega} - B_{u_i}(q)\right)}{1 + B_{u_i}^2(q) - 2B_{u_i}(q)\cos\omega} \tag{A46}$$

$$\widetilde{M}_{u_r}(q,\omega) = \frac{B_{u_r}(q)\,(e^{-i\omega} - B_{u_i}(q))}{1 + B_{u_i}^2(q) - 2B_{u_i}(q)\cos\omega} = \frac{B_{u_r}(q)}{B_{\epsilon_i}(q)}\widetilde{M}_{\epsilon_i}(q,\omega) \tag{A47}$$

and where I have substituted $R(q,\omega)\exp(i\phi(q,\omega))\widetilde{\epsilon}(q,\omega)$ for $\widetilde{u}_r(q,\omega)$. We can rewrite $\widetilde{M}_{\epsilon_i}(q,\omega)$ in polar notation:

$$\widetilde{M}_{\epsilon_i}(q,\omega) = G(q,\omega)e^{i\psi(q,\omega)}, \tag{A48}$$

where

$$G(q,\omega) = \frac{B_{\epsilon_i}(q)}{\sqrt{1 + B_{u_i}^2(q) - 2B_{u_i}(q)\cos\omega}} \tag{A49}$$

$$\psi(q,\omega) = \tan^{-1}\left(\frac{-\sin\omega}{\cos\omega - B_{u_i}(q)}\right) \tag{A50}$$

and the range of $\tan^{-1}$ is again extended to $[-\pi,\pi)$. Thus,

$$\widetilde{u}_i(q,\omega) = G(q,\omega)e^{i\psi(q,\omega)}\left[1 + \frac{B_{u_r}(q)}{B_{\epsilon_i}(q)}R(q,\omega)e^{i\phi(q,\omega)}\right]\widetilde{\epsilon}(q,\omega). \tag{A51}$$

Turning to the covariance,

$$\langle \mathrm{Cov}(\lambda_i,\nu_i)_x\rangle_t = \langle\lambda_i\rangle_{x,t}\langle \mathrm{Cov}(1+\zeta_i, 1+u_i)_x\rangle_t = \langle\lambda_i\rangle_{x,t}\langle\langle\zeta_i,u_i\rangle_x\rangle_t = \langle\lambda_i\rangle_{x,t}\langle\zeta_i u_i\rangle_{x,t}, \tag{A52}$$

where we have used the fact that the spatial averages of ζ_i and u_i are zero. A multi-dimensional corollary of the Wiener-Khinchin theorem [Nisbet & Gurney(1982), App. F] states that if $\langle f\rangle_{x,t} = \langle g\rangle_{x,t} = 0$, $\langle fg\rangle_{x,t}$ equals the inverse Fourier transform of $\lim_{N\to\infty}\widetilde{f}^{(N)*}(q,\omega)\widetilde{g}^{(N)}(q,\omega)/N^2$, where $\widetilde{f}^{(N)}(q,\omega)$ is the spatiotemporal Fourier transform of f taken with the sums running from the $-N/2$ to $N/2$ and superscript $*$ denotes the complex conjugate. Thus,

$$\langle \mathrm{Cov}(\lambda_i,\nu_i)_x\rangle_t = \lim_{N\to\infty}\frac{1}{N^2}\frac{\langle\lambda_i\rangle_{x,t}}{(2\pi)^2}\int_{-\pi}^{\pi}\int_{-\pi}^{\pi}\widetilde{\zeta}_i(q,\omega)\widetilde{u}_i(q,\omega)\,dq\,d\omega. \tag{A53}$$

Using eq. A17 to substitute for ζ_i and eq. A51 to substitute for u_i, noting that $B_{u_r}(q)/B_{\epsilon_i}(q) = -\widetilde{U}(q)$,

$$\begin{aligned}\langle \mathrm{Cov}(\lambda_i,\nu_i)_x\rangle_t = \lim_{N\to\infty}\frac{\langle\lambda_i\rangle_{x,t}}{(2\pi N)^2}\int_{-\pi}^{\pi}\int_{-\pi}^{\pi}&\left[\left(1 - \widetilde{U}^{(N)}(q)R(q,\omega)e^{-i\phi(q,\omega)}\right)\widetilde{\epsilon}^{(N)*}(q,\omega)\right]\\ &\cdot\left[G(q,\omega)e^{i\psi(q,\omega)}\left(1 - \widetilde{U}^{(N)}(q)R(q,\omega)e^{i\phi(q,\omega)}\right)\widetilde{\epsilon}^{(N)}(q,\omega)\right]\,dq\,d\omega,\end{aligned} \tag{A54}$$

where $R(q,\omega)$ is real by definition and $\widetilde{U}^{(N)}$ is real assuming that the competition kernel is symmetric. Only the even portion of the integrand survives, so that

$$\begin{aligned}\langle \mathrm{Cov}(\lambda_i,\nu_i)_x\rangle_t &= \lim_{N\to\infty}\frac{\langle\lambda_i\rangle_{x,t}}{(2\pi)^2}\int_{-\pi}^{\pi}\int_{-\pi}^{\pi}G(q,\omega)\cos\psi(q,\omega) \qquad \text{(A55)}\\ &\cdot\left[1 + \widetilde{U}^2(q)R^2(q,\omega) - 2\widetilde{U}(q)R(q,\omega)\cos\phi(q,\omega)\right]\frac{|\widetilde{\epsilon}|^2(q,\omega)}{N^2}\,dqd\omega\end{aligned}$$

and

$$\frac{\partial}{\partial \alpha_i}\langle \mathrm{Cov}(\lambda_i,\nu_i)_x\rangle_t = \lim_{N\to\infty}\frac{\langle\lambda_i\rangle_{x,t}}{(2\pi)^2}\int_{-\pi}^{\pi}\int_{-\pi}^{\pi}\left(\frac{G(q,\omega)}{\partial\alpha_i}\cos\psi(q,\omega) - G(q,\omega)\sin(q,\omega)\frac{\partial\psi(q,\omega)}{\partial\alpha_i}\right)$$
$$\cdot\left[1+\widetilde{U}^2(q)R^2(q,\omega) - 2\widetilde{U}(q)R(q,\omega)\cos\phi(q,\omega)\right]\frac{|\widetilde{\epsilon}|^2(q,\omega)}{N^2}\,dqd\omega. \tag{A56}$$

In the main text, I have identified the term associated with $\partial G/\partial\alpha_i$ as the smearing effect of dispersal, and the term associated with $\partial\psi/\partial\alpha_i$ I have identified as the delay reduction effect of dispersal.

We have assumed that the autocorrelation of F decays exponentially in space and time (eq. 5), so that $\mathrm{Cov}(\epsilon,\epsilon)_{x,t} = \dfrac{\mathrm{Var}(F)}{\langle F\rangle_{x,t}^2}\exp\left(\dfrac{-|x|}{\xi}\right)\exp\left(\dfrac{-|t|}{\tau}\right)$. The Wiener-Khinchin theorem then implies

$$\begin{aligned}\lim_{N\to\infty}\frac{|\widetilde{\epsilon}|^2(q,\omega)}{N^2} &= \sum_{x,t=-\infty}^{\infty}\frac{\mathrm{Var}(F)}{\langle F\rangle_{x,t}^2}\exp\left(\frac{-|x|}{\xi}\right)\exp\left(\frac{-|t|}{\tau}\right)e^{-i(qx+\omega t)} \\ &= \frac{\mathrm{Var}(F)}{\langle F\rangle_{x,t}^2}\left(\frac{1-\exp(-2/\tau)}{1-2\exp(-1/\tau)\cos(\omega)+\exp(-2/\tau)}\right) \\ &\quad\cdot\left(\frac{1-\exp(-2/\xi)}{1-2\exp(-1/\xi)\cos(q)+\exp(-2/\xi)}\right).\end{aligned} \tag{A57}$$

Reference

Nisbet, R. M. & Gurney, W. S. C. (1982). *Modelling Fluctuating Populations*. John Wiley & Sons, reprinted by The Blackburn Press, New York.