

A Analytic approximation for invader fitness (electronic supplement)

As discussed in Section 2.3 (“Defining fitness”), we assume that fluctuations in fecundity and germination are small relative to their means and for all species j write

$$F_j(t) = \langle F_j \rangle_t (1 + f_j(t)) \quad (\text{A.1})$$

$$g_j(t) = \langle g_j \rangle_t (1 + \Omega_j(t)), \quad (\text{A.2})$$

where f_j and Ω_j are $O(\sigma)$. We also assume that fluctuations in germination and fecundity causes $O(\sigma)$ fluctuations in competition and the resident populations, so that

$$C_i(t) = \langle C_i \rangle_t (1 + c_i(t)) \quad (\text{A.3})$$

$$n_j(t) = \langle n_j \rangle_t (1 + \eta_j(t)), \quad j = 1, 2. \quad (\text{A.4})$$

Substituting the perturbative expressions for germination, fecundity, and competition into the expression for the yearly invader growth rate, $\lambda_i(t)$, we find that

$$\lambda_i(t) = \frac{g_i(t)F_i(t)}{C_i(t)} + s_i(1 - g_i(t)) = \lambda^{(0)}(1 + \zeta_i^{(1)}(t) + \zeta_i^{(2)}(t)), \quad (\text{A.5})$$

where $\lambda^{(0)}$ is the growth rate in the absence of environmental variation:

$$\lambda^{(0)} = \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} + s_i(1 - \langle g_i \rangle_t), \quad (\text{A.6})$$

$\zeta_i^{(1)}(t)$ is the first order contribution to the fluctuating growth rate:

$$\zeta_i^{(1)}(t) = \frac{1}{\lambda^{(0)}} \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} [\Omega_i(t) + f_i(t) - c_i(t)] - \frac{s_i \langle g_i \rangle_t}{\lambda^{(0)}} \Omega_i(t), \quad (\text{A.7})$$

and $\zeta_i^{(2)}(t)$ is the second order contribution to growth:

$$\zeta_i^{(2)}(t) = \frac{1}{\lambda^{(0)}} \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} [\Omega_i(t)f_i(t) - (\Omega_i(t) + f_i(t))c_i(t) + c_i^2(t)]. \quad (\text{A.8})$$

From eq. 7, we know that

$$\bar{r}_i = \ln \lambda_i^{(0)} + \langle \zeta_i^{(2)} \rangle_t - \frac{1}{2} \langle \zeta_i^{(1)2} \rangle_t. \quad (\text{A.9})$$

Using our definitions for the $\zeta_i^{(1)}$ and $\zeta_i^{(2)}$, we find

$$\langle \zeta_i^{(2)} \rangle_t = \frac{1}{\lambda^{(0)}} \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} [\text{Cov}(\Omega_i, f_i) - \text{Cov}(\Omega_i + f_i, c_i) + \text{Var}(c_i)] \quad (\text{A.10})$$

$$\begin{aligned}
\langle \zeta_i^{(1)^2} \rangle_t &= \frac{1}{\lambda^{(0)^2} \left(\frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} \right)^2} [\text{Var}(\Omega_i + f_i) + \text{Var}(c_i) - 2\text{Cov}(\Omega_i + f_i, c_i)] \\
&+ \frac{1}{\lambda^{(0)^2} (s_i \langle g_i \rangle_t)^2} \text{Var}(\Omega_i) - \frac{2}{\lambda^{(0)^2} s_i \langle g_i \rangle_t} \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} [\text{Var}(\Omega_i) + \text{Cov}(\Omega_i, f_i) - \text{Cov}(\Omega_i, c_i)].
\end{aligned} \tag{A.11}$$

Substituting these into our expression for \bar{r}_i gives us eq. 8 or, equivalently, eq. 9, with

$$A_1 = \frac{1}{\lambda^{(0)}} \frac{\langle g_i \rangle_t \langle F_i \rangle_t}{\langle C_i \rangle_t} \tag{A.12}$$

$$A_2 = \frac{1}{\lambda^{(0)}} s_i \langle g_i \rangle_t. \tag{A.13}$$

This form is useful for insight, but in order to actually calculate fitness, we need to express \bar{r}_i entirely in terms of environmental fluctuations (Ω_i and f_i). This we do by writing fluctuations in invader competition (c_i) in terms of fluctuations in the resident population densities (η_1 and η_2) and writing these population fluctuations in terms of environmental fluctuations.

Let us first relate fluctuations in competition to fluctuations in resident population densities. Substituting our expression for $n_1(t)$ and $n_2(t)$ into the definition of $C_i(t)$, we find that to $O(\sigma)$

$$\langle C_i \rangle_t = \gamma_{i1} \langle g_1 \rangle_t \langle n_1 \rangle_t + \gamma_{i2} \langle g_2 \rangle_t \langle n_2 \rangle_t \tag{A.14}$$

$$c_i(t) = D_{i1}(\Omega_1 + \eta_1) + D_{i2}(\Omega_2 + \eta_2), \tag{A.15}$$

where

$$D_{i1} = \frac{\gamma_{i1} \langle g_1 \rangle_t \langle n_1 \rangle_t}{\langle C_i \rangle_t} \tag{A.16}$$

$$D_{i2} = \frac{\gamma_{i2} \langle g_2 \rangle_t \langle n_2 \rangle_t}{\langle C_i \rangle_t}. \tag{A.17}$$

We now relate population fluctuations to environmental fluctuations by returning to the population dynamics, eqs. 1 and 2. We substitute our perturbative expressions for n_j , g_j , and F_j into the equations for dynamics and expand to $O(\sigma)$. Treating the resident population fluctuations, η_1 and η_2 , as components of a vector $\boldsymbol{\eta}$ and similarly for germination fluctuations ($\boldsymbol{\Omega}$) and fecundity fluctuations (\mathbf{f}), we find that to $O(\sigma)$,

$$\boldsymbol{\eta}(t+1) = \mathbf{A}_\eta \boldsymbol{\eta}(t) + \mathbf{A}_\Omega \boldsymbol{\Omega}(t) + \mathbf{A}_f \mathbf{f}(t), \tag{A.18}$$

where

$$\mathbf{A}_{\eta 11} = \kappa_1(1 - D_{11}) + s_1(1 - \langle g_1 \rangle_t) \quad \mathbf{A}_{\eta 12} = -\kappa_1 D_{12} \tag{A.19}$$

$$\mathbf{A}_{\eta 21} = -\kappa_2 D_{21} \quad \mathbf{A}_{\eta 22} = \kappa_2(1 - D_{22}) + s_2(1 - \langle g_2 \rangle_t), \tag{A.20}$$

$$\mathbf{A}_{\Omega 11} = \kappa_1(1 - D_{11}) - s_1 \langle g_1 \rangle_t \quad \mathbf{A}_{\Omega 12} = -\kappa_1 D_{12} \quad (\text{A.21})$$

$$\mathbf{A}_{\Omega 21} = -\kappa_2 D_{21} \quad \mathbf{A}_{\Omega 22} = \kappa_2(1 - D_{22}) - s_2 \langle g_2 \rangle_t, \quad (\text{A.22})$$

$$\mathbf{A}_{\mathbf{f} 11} = \kappa_1 \quad \mathbf{A}_{\mathbf{f} 12} = 0 \quad (\text{A.23})$$

$$\mathbf{A}_{\mathbf{f} 21} = 0 \quad \mathbf{A}_{\mathbf{f} 22} = \kappa_2, \quad (\text{A.24})$$

where

$$\kappa_1 = \frac{\langle g_1 \rangle_t \langle F_1 \rangle_t}{\gamma_{11} \langle g_1 \rangle_t \langle n_1 \rangle_t + \gamma_{12} \langle g_2 \rangle_t \langle n_2 \rangle_t} = s_1(1 - g_1) \quad (\text{A.25})$$

$$\kappa_2 = \frac{\langle g_2 \rangle_t \langle F_2 \rangle_t}{\gamma_{21} \langle g_1 \rangle_t \langle n_1 \rangle_t + \gamma_{22} \langle g_2 \rangle_t \langle n_2 \rangle_t} = s_2(1 - g_2) \quad (\text{A.26})$$

and

$$D_{jk} = \frac{\gamma_{jk} \langle g_k \rangle_t \langle F_k \rangle_t}{\gamma_{j1} \langle g_1 \rangle_t \langle n_1 \rangle_t + \gamma_{j2} \langle g_2 \rangle_t \langle n_2 \rangle_t}. \quad (\text{A.27})$$

We can thus write

$$\boldsymbol{\eta}(t) = \sum_{j=0}^{t-1} \mathbf{A}_{\boldsymbol{\eta}}^{t-1-j} [\mathbf{A}_{\Omega} \boldsymbol{\Omega}(j) + \mathbf{A}_{\mathbf{f}} \mathbf{f}(j)] \quad (\text{A.28})$$

$$= \sum_{j=0}^{\infty} [\mathbf{M}_{\Omega}(t-j) \boldsymbol{\Omega}(j) + \mathbf{M}_{\mathbf{f}}(t-j) \mathbf{f}(j)], \quad (\text{A.29})$$

where

$$\mathbf{M}_{\Omega}(s) = \begin{cases} \mathbf{A}_{\boldsymbol{\eta}}^{s-1} \mathbf{A}_{\Omega} & s > 0 \\ 0 & s \leq 0 \end{cases} \quad (\text{A.30})$$

and similarly for $\mathbf{M}_{\mathbf{f}}$ (with $\mathbf{A}_{\mathbf{f}}$ instead of \mathbf{A}_{Ω}). The vector of resident population fluctuations, $\boldsymbol{\eta}(t)$, is now expressed as a convolution of kernels (\mathbf{M}_{Ω} and $\mathbf{M}_{\mathbf{f}}$) and their respective environmental fluctuations ($\boldsymbol{\Omega}$ and \mathbf{f}). We can dispose of the convolutions by taking a temporal Fourier transform:

$$\widetilde{\mathbf{M}}_{\Omega}(\omega) = \sum_{s=0}^{\infty} \mathbf{M}_{\Omega}(s) e^{-i\omega s} = \sum_{s=1}^{\infty} \mathbf{A}_{\boldsymbol{\eta}}^{s-1} \mathbf{A}_{\Omega} e^{-i\omega s} = \sum_{s=0}^{\infty} (\mathbf{A}_{\boldsymbol{\eta}} e^{-i\omega})^s \mathbf{A}_{\Omega} e^{-i\omega}. \quad (\text{A.31})$$

The eigenvalues of \mathbf{M}_{Ω} all have modulus less than 1, so this expression converges to

$$(\mathbf{I} - \mathbf{A}_{\boldsymbol{\eta}} e^{-i\omega})^{-1} e^{-i\omega} \mathbf{A}_{\Omega} = (e^{i\omega} \mathbf{I} - \mathbf{A}_{\boldsymbol{\eta}})^{-1} \mathbf{A}_{\Omega}. \quad (\text{A.32})$$

After a similar calculation for $\widetilde{\mathbf{M}}_{\mathbf{f}}(\omega)$, we arrive at

$$\widetilde{\boldsymbol{\eta}}(\omega) = (e^{i\omega} \mathbf{I} - \mathbf{A}_{\boldsymbol{\eta}})^{-1} \mathbf{A}_{\Omega} \widetilde{\boldsymbol{\Omega}}(\omega) + (e^{i\omega} \mathbf{I} - \mathbf{A}_{\mathbf{f}})^{-1} \mathbf{A}_{\mathbf{f}} \widetilde{\mathbf{f}}(\omega). \quad (\text{A.33})$$

The transfer functions $(e^{i\omega\mathbf{I}} - \mathbf{A}_\Omega)^{-1} \mathbf{A}_\Omega$ and $(e^{i\omega\mathbf{I}} - \mathbf{A}_f)^{-1} \mathbf{A}_f \tilde{\mathbf{f}}(\omega)$ are 2×2 matrices with complex elements. It is helpful to put these in polar notation, so that, for example,

$$\tilde{\eta}_1(\omega) = \mathbf{R}_{\Omega_{11}} e^{i\phi_{\Omega_{11}}(\omega)} \tilde{\Omega}_1(\omega) + \mathbf{R}_{f_{11}} e^{i\phi_{f_{11}}(\omega)} \tilde{f}_1(\omega) + \mathbf{R}_{\Omega_{12}} e^{i\phi_{\Omega_{12}}(\omega)} \tilde{\Omega}_2(\omega) + \mathbf{R}_{f_{12}} e^{i\phi_{f_{12}}(\omega)} \tilde{f}_2(\omega), \quad (\text{A.34})$$

where, for example, $\mathbf{R}_{\Omega_{11}}$ is the modulus of $(e^{i\omega\mathbf{I}} - \mathbf{A}_\Omega)^{-1} \mathbf{A}_\Omega$ and $\phi_{\Omega_{11}}$ is its phase.

The reader may (or may not) remember that we are trying to relate the population fluctuations to the environmental fluctuations. We have done so. This plus the Wiener-Khinchin theorem allows us to calculate the variances and covariances in our expression for invader fitness (\bar{r}_i).

For example, \bar{r}_i depends on $\text{Cov}(f_i, c_i)$, the covariance between invader fecundity and competition. We use eq. A.14 to substitute for c_i and learn that $\text{Cov}(f_i, c_i)$ depends on $\text{Cov}(f_i, \eta_1)$, the covariance between invader fecundity and the population density of resident 1. Enter the Wiener-Khinchin theorem, which states that if two functions $f(t)$ and $g(t)$ have zero mean, the Fourier transform of $\text{Cov}(f, g)$ is given by

$$\mathcal{F}[\text{Cov}(f, g)] = \lim_{N \rightarrow \infty} \frac{\tilde{f}^{*(N)}(\omega) \tilde{g}^{(N)}(\omega)}{N}, \quad (\text{A.35})$$

where superscript $*$ denotes the complex conjugate and $\tilde{g}^{(N)}(\omega)$ equals the Fourier transform of $g(t)$ in the limit as N approaches infinity: $\tilde{g}^{(N)}(\omega) = \sum_{t=-N/2}^{N/2} g(t) \exp(-i\omega t)$. This tells us that

$$\text{Cov}(f_i, \eta_1) = \frac{1}{2\pi} \int_{-\infty}^{\infty} \mathcal{F}[\text{Cov}(f_i, \eta_1)](\omega) d\omega = \lim_{N \rightarrow \infty} \frac{1}{N} \frac{1}{2\pi} \int_{-\infty}^{\infty} \tilde{f}_i^{*(N)}(\omega) \tilde{\eta}_1^{*(N)}(\omega) d\omega. \quad (\text{A.36})$$

Eq. A.34 gives us an expression for $\tilde{\eta}_1(\omega)$ in terms of environmental fluctuations, so that the integrand in eq. A.36 becomes

$$\begin{aligned} \lim_{N \rightarrow \infty} \mathbf{R}_{\Omega_{11}} e^{i\phi_{\Omega_{11}}(\omega)} \frac{\tilde{f}_i^{*(N)}(\omega) \tilde{\Omega}_1^{(N)}(\omega)}{N} + \mathbf{R}_{f_{11}} e^{i\phi_{f_{11}}(\omega)} \frac{\tilde{f}_i^{*(N)}(\omega) \tilde{f}_1^{(N)}(\omega)}{N} \\ + \mathbf{R}_{\Omega_{12}} e^{i\phi_{\Omega_{12}}(\omega)} \frac{\tilde{f}_i^{*(N)}(\omega) \tilde{\Omega}_2^{*(N)}(\omega)}{N} + \mathbf{R}_{f_{12}} e^{i\phi_{f_{12}}(\omega)} \frac{\tilde{f}_i^{*(N)}(\omega) \tilde{f}_2^{(N)}(\omega)}{N}. \end{aligned} \quad (\text{A.37})$$

What is to be done with all these Fourier transforms of environmental fluctuations? Here we use the Wiener-Khinchin theorem again and recall, for example, that

$$\lim_{N \rightarrow \infty} \frac{\tilde{f}_i^{*(N)}(\omega) \tilde{\Omega}_1(\omega)}{N} = \mathcal{F}[\text{Cov}(f_i, \Omega_1)], \quad (\text{A.38})$$

where the covariance is a function of lag time. These environmental covariances characterize the ecological situation under consideration and are treated as inputs. (See second appendix.) For example, if the two species germinate in different years, then $\text{Cov}(g_1, g_2)$

will be negative. If there is predictive germination, then $\text{Cov}(g_j, f_j)$ will be positive. If germination is positively autocorrelated, then $\text{Cov}(g_1, g_1)$ will have a different form than if germination fluctuates independently from year to year.

In summary, we have expressed invader fitness \bar{r}_i in terms of variances and covariances of environmental fluctuations and fluctuations in competition. Since invader competition is a function of resident density, we can rewrite fitness in terms of variances and covariances of environmental fluctuations and resident population fluctuations. These resident population fluctuations can in turn be expressed in terms of environmental fluctuations, so that ultimately, invader fitness becomes a function of environmental variances and covariances.

B The Fourier transforms of environmental covariances (electronic supplement)

We found that allowing germination or fecundity to be positively autocorrelated had little effect on our results, so for all the figures in this paper, we assume that germination and fecundity are uncorrelated between years (white noise). Using the Wiener-Khinchin theorem, it can be shown that for a white noise process $\zeta(t)$ with variance $\text{Var}(\zeta)$, the Fourier transform of the autocovariance is constant and equal to the variance:

$$\mathcal{F}[\text{Cov}(\zeta, \zeta)](\omega) = \text{Var}(\zeta). \quad (\text{B.1})$$

Thus

$$\tilde{\zeta}(\omega) = e^{i\theta} \sqrt{\text{Var}(\zeta)}, \quad (\text{B.2})$$

where θ is a phase angle to be determined.

The correlation between two sources of environmental variation is equal to the cosine of their phase difference. We measure all phase differences relative to the germination of species 1 and determine the phase angles for g_2 , f_1 , and f_2 by considering correlation structure. Thus, we say that

$$\tilde{g}_2(\omega) = e^{i\theta(g_1, g_2)} \sqrt{\text{Var}(g_2)}, \quad (\text{B.3})$$

where the phase difference $\theta(g_1, g_2)$ is 0 if the two species germinate in the same years ($\text{Corr}(g_1, g_2) = 1$) and π if the two species germinate in different years ($\text{Corr}(g_1, g_2) = -1$). Similarly, if species 2 has no predictive germination, ($\text{Corr}(g_2, f_2) = 0$), then $\theta(g_2, f_2) = \pm\pi/2$. We can use these relations to build up others. For example, if $\theta(g_1, g_2) = \pi$ and $\theta(g_2, f_2) = \pm\pi/2$, then $\theta(g_1, f_2) = \pi \pm \pi/2$.

C When should variable germination coevolve in the absence of predictive germination? (electronic supplement)

If the two species germinate in the same years and there is no predictive germination, then there is no reason to evolve variable germination: we've assumed no predictive germination and no storage effect is possible. However, we have observed that even if the species germinate in opposite years, maximizing the contribution of variable germination to a storage effect, variable germination still does not co-evolve. We present an intuitive explanation in the Results section. Here we present a mathematical argument.

If there is no predictive germination, the only two fitness terms that depend on invader germination variance are the storage effect and the fluctuation penalty. As argued in the Results section, the only way fitness can peak at some non-zero value of invader germination for both species is if the storage effect increases with invader germination variance for both species. The part of the storage effect term that varies with invader germination variance is proportional to

$$\text{Cov}(\Omega_i, c_i) = D_{i1}\text{Cov}(\Omega_i, \Omega_1 + \eta_1) + D_{i2}\text{Cov}(\Omega_i, \Omega_2 + \eta_2), \quad (\text{C.1})$$

and the storage effect increases as $\text{Cov}(\Omega_i, c_i)$ becomes more negative. In practice, the covariance of invader germination with resident germination is much larger than the covariance of invader germination with resident densities. In addition, if we assume that species 1 and 2 germinate in opposite years, the correlation of Ω_i with Ω_j is 1 if the invader and resident j are the same species and -1 if they are different species. Thus,

$$\text{Cov}(\Omega_i, c_i) \approx D_{i1}\text{Cov}(\Omega_i, \Omega_1) + D_{i2}\text{Cov}(\Omega_i, \Omega_2) \quad (\text{C.2})$$

$$= D_{i1}\sigma_{\Omega_i}\sigma_{\Omega_1} \times \begin{pmatrix} 1 & i = 1 \\ -1 & i = 2 \end{pmatrix} + D_{i2}\sigma_{\Omega_i}\sigma_{\Omega_2} \times \begin{pmatrix} -1 & i = 1 \\ 1 & i = 2 \end{pmatrix}, \quad (\text{C.3})$$

where σ_{Ω_j} is the standard deviation of species j germination. Thus, $\text{Cov}(\Omega_i, c_i)$ will become more negative as σ_{Ω_i} increases (i.e., the storage effect will increase with invader germination variance) when $D_{i1}\sigma_{\Omega_i}\sigma_{\Omega_1} < D_{i2}\sigma_{\Omega_i}\sigma_{\Omega_2}$ for $i = 1$, and when $D_{i2}\sigma_{\Omega_i}\sigma_{\Omega_2} < D_{i1}\sigma_{\Omega_i}\sigma_{\Omega_1}$ for $i = 2$. Using eq. A.16 to substitute for D_{i1} and D_{i2} and recalling that we have set $g_1 = g_2$, we find that we require

$$\gamma_{11}\langle n_1 \rangle \sigma_{\Omega_1} < \gamma_{12}\langle n_2 \rangle \sigma_{\Omega_2} \quad i = 1 \quad (\text{C.4})$$

$$\gamma_{22}\langle n_2 \rangle \sigma_{\Omega_2} < \gamma_{21}\langle n_1 \rangle \sigma_{\Omega_1} \quad i = 2. \quad (\text{C.5})$$

Putting the two together, we find that the storage effect will increase with invader germination variance for both species when $\gamma_{22}/\gamma_{21} < \gamma_{12}/\gamma_{11}$ — that is, when

$$\gamma_{11}\gamma_{22} < \gamma_{12}\gamma_{21}. \quad (\text{C.6})$$

We therefore expect variable germination to evolve in the absence of predictive variation when the between-species competition coefficients exceed the within-species competition coefficients.