Interactive effects of temporal correlations, spatial heterogeneity, and dispersal on population persistence

Appendices: Mathematical Details

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A. The general approximation for the metapopulation growth rate M

Assume that \( f_i^t \) are stationary ergodic sequences with \( \mathbb{E}[\log |f^t|] < \infty \). Define \( F_t \) to be the diagonal matrix whose \( i \)-th diagonal element is given by \( f_i^t \) and \( f_t = (f_1^t, \ldots, f_n^t) \). Let \( D \) be a matrix whose columns are given by a fixed probability vector \( \mathbf{v} \), i.e., \( v_i \geq 0 \) and \( \sum_i v_i = 1 \). To consider perturbations away from \( D \), let \( Q \) be a matrix whose column sums equal 0 and such that \( D + \epsilon Q \) is a non-negative matrix for \( \epsilon \) sufficiently small. Define

\[
\begin{align*}
A_t &= B_t + \epsilon C_t \\
B_t &= DF_t \\
C_t &= QF_t
\end{align*}
\]

Let \( \gamma(\epsilon) \) be the dominant Lyapunov exponent of the random matrix products \( A_t \ldots A_1 \). As discussed in the main text, \( \gamma(0) = \mathbb{E}[\log S_1] \) where \( S_t = \sum_i v_i f_i^t \). To find \( \gamma'(0) \), we consider the random product \( 1'A_t \ldots A_1 v \) where \( 1 = (1, \ldots, 1) \). This random product equals

\[
1 \left( B_t \ldots B_1 + \epsilon \sum_{s=1}^{t} B_t \ldots B_{s+1} C_s B_{s-1} \ldots B_1 \right) v + o(\epsilon)
\]

\[
= S_t \ldots S_1 + \epsilon \sum_{s=1}^{t} S_t \ldots S_{s+2} (1F_{s+1}QF_s v) S_{s-1} \ldots S_1 + o(\epsilon)
\]

\[
= S_t \ldots S_1 + \epsilon \sum_{s=1}^{t} S_t \ldots S_{s+2} (f_{s+1}QF_s v) S_{s-1} \ldots S_1 + o(\epsilon)
\]
Taking log and using the approximation \( \log(a + \epsilon b) \approx \ln(a) + \epsilon \frac{b}{a} + o(\epsilon) \) yields

\[
\log(S_t \ldots S_1) + \epsilon \sum_{s=1}^{t} \frac{f_{s+1}QF_{s}v}{S_{s+1}S_{s}} + o(\epsilon)
\]

Dividing by \( t \), taking expectations, letting \( t \to \infty \), and using stationarity yields

\[
\gamma(\epsilon) = \mathbb{E}[\log S_1] + \epsilon \mathbb{E} \left[ \frac{f_{2}QF_{1}v}{S_2S_1} \right] + o(\epsilon) = \mathbb{E}[\log S_1] + \epsilon \mathbb{E} [R_2Q(R_1 \circ v)] + o(\epsilon)
\]

where \( R_t = (R_t^1, \ldots, R_t^n)' \) denotes the transpose, \( R_t^i = \frac{f_t^i}{S_t} \), and \( \circ \) denotes the Haddamard product.

Let \( \mathbf{E}^k(i,j) \) be a \( n \times n \) matrix whose \( k \)-th column is given by \( e_j - e_i \) and all other entries are zero. The \( \mathbf{E}^k(i,j) \) form a basis for the matrices whose column sums are zeros (i.e. the set of possible perturbations of the dispersal matrix \( D \)). If \( Q = \mathbf{E}^k(i,j) \), then the approximation is given by

\[
\gamma(\epsilon) = \mathbb{E}[\log S_1] + \epsilon v_k \mathbb{E} \left[ (R_2^i - R_2^i) R_1^k \right] + o(\epsilon)
\]

Of particular interest is the case \( k = i \) in which case the perturbation \( D + \epsilon \mathbf{E}^i(i,j) \) corresponds to a fraction \( \epsilon \) more individuals from patch \( i \) dispersing to patch \( j \). In this case,

\[
\gamma(\epsilon) = \mathbb{E}[\log S_1] + \epsilon v_i \mathbb{E} \left[ (R_2^i - R_2^i) R_1^i \right] + o(\epsilon) = \mathbb{E}[\log S_1] + \epsilon v_i \left( \mathbb{E} [R_2^i - R_1^i] \mathbb{E} [R_1^i] + \text{Cov} [R_2^i - R_2^i, R_1^i] \right) + o(\epsilon)
\]

as claimed in the main text.

**B. Approximation for the population network model**

Let \( Z_t^i \) with \( i = 0, 1 \ldots, n \) and \( t \geq 0 \) be i.i.d random variables with mean 0 and variance \( \sigma^2 \). Let \( \mathbb{E} [f] > 0 \) correspond to the expected fitness within a patch. Define

\[
f_t^i = \mathbb{E} [f] + \sqrt{\rho_{\text{space}}^i} \xi_t^0 + \sqrt{1 - \rho_{\text{space}}^i} \xi_t^i
\]

\[
\xi_{t+1}^i = \rho_{\text{time}} \xi_t^i + \sqrt{1 - \rho_{\text{time}}^2} Z_{t+1}^i
\]

\[
\xi_0^i = Z_0^i
\]
Using these definitions, we get that the spatial covariance in fitness is given by \( \operatorname{Cov} \left[ f_i^t, f_j^t \right] = \rho_{\text{space}} \sigma^2 \) for \( i \neq j \) and the temporal covariance in fitness is \( \operatorname{Cov} \left[ f_i^{t+1}, f_j^t \right] = \rho_{\text{time}} \sigma^2 \). Assume that the dispersal matrix is give by \( d_{ii} = 1 - d, d_{ij} = d/(n - 1) \) for \( i \neq j \).

Here, I consider perturbations away from the “well mixing” case corresponding to \( d = (n - 1)/n \) (i.e. \( d_{ij} = 1/n \) for all \( i, j \) and \( v_i = 1/n \) for all \( i \)). The perturbation is given by \( d = (n - 1)/n - \epsilon \) for \( \epsilon \) small. In the notation of Appendix A, this perturbation corresponds to choosing \( Q \) to be a matrix whose diagonal entries are 1 and off diagonal entries are \(-1/(n - 1) \). Applying the results from Appendix A yields

\[
M = \mathbb{E}[\log S_1] + \epsilon \mathbb{E}[R_2 Q (R_1 \circ v)] + o(\epsilon)
\]

\[
= \mathbb{E}[\log S_1] + \epsilon \sum_{i \neq j} \frac{1}{n} \frac{1}{n-1} \mathbb{E}[(R_2^i - R_2^j) R_1^i] + o(\epsilon)
\]

\[
= \mathbb{E}[\log S_1] + \epsilon \mathbb{E}[(R_2^1 - R_2^2) R_2^1] + o(\epsilon)
\]

Assume there are a large number of patches. Independence of the \( \xi_t^1, \ldots, \xi_t^n \) and the law of large numbers imply that \( \frac{1}{n} \sum_i \xi_t^i \approx 0 \). Hence, \( S_t \approx \mathbb{E}[f] + \sqrt{\rho_{\text{space}} \xi_t^0} \). The approximation \( \log(a + \epsilon) \approx \log a + \frac{\epsilon}{a} - \frac{\epsilon^2}{2a^2} + o(\epsilon^2) \) implies

\[
\mathbb{E}[\log S_1] \approx \log \mathbb{E}[f] - \frac{\sigma^2}{\mathbb{E}[f]^2} \frac{\rho_{\text{space}}}{2} + o(\rho_{\text{space}})
\]

The term \( \mathbb{E}[(R_2^1 - R_2^2) R_1^1] \) is

\[
\approx \mathbb{E} \left[ \sqrt{1 - \rho_{\text{space}}} (\xi_1^2 - \xi_2^2) \right] \mathbb{E} \left[ \frac{1}{\mathbb{E}[f]} + \sqrt{\rho_{\text{space}} \xi_1^0} \right] + \mathbb{E} \left[ \sqrt{1 - \rho_{\text{space}}} (\xi_1^2 - \xi_2^2) \right] \mathbb{E} \left[ \frac{1}{\mathbb{E}[f]} + \sqrt{\rho_{\text{space}} \xi_2^0} \right]
\]

\[
= \sqrt{1 - \rho_{\text{space}}} \mathbb{E} \left[ \xi_1^2 - \xi_2^2 \right] \mathbb{E} \left[ \frac{1}{\mathbb{E}[f]} + \sqrt{\rho_{\text{space}} \xi_1^0} \right] + (1 - \rho_{\text{space}}) \mathbb{E} \left[ \frac{\xi_1^2 \xi_1^1 - \xi_2^2 \xi_1^1}{(\mathbb{E}[f] + \sqrt{\rho_{\text{space}} \xi_1^0})(\mathbb{E}[f] + \sqrt{\rho_{\text{space}} \xi_2^0})} \right]
\]

\[
= 0 + (1 - \rho_{\text{space}}) \left( \mathbb{E}[\xi_1^2] - \mathbb{E}[\xi_2^2] \right) \mathbb{E} \left[ \frac{1}{(\mathbb{E}[f] + \sqrt{\rho_{\text{space}} \xi_1^0})(\mathbb{E}[f] + \sqrt{\rho_{\text{space}} \xi_2^0})} \right]
\]

\[
= (1 - \rho_{\text{space}}) \rho_{\text{time}} \sigma^2 \Psi
\]

To get an approximation for \( \Psi \), lets assume that \( \rho_{\text{space}} \) is sufficiently small. A first order
Taylor expansion yields
\[
\mathbb{E}[f] + \frac{1}{\sqrt{\rho_{\text{space}}}} = \mathbb{E}[f] - \frac{1}{\mathbb{E}[f]^2} \sqrt{\rho_{\text{space}}} + o(\sqrt{\rho_{\text{space}}})
\]
Therefore,
\[
\Psi = \mathbb{E}\left[\mathbb{E}\left[\mathbb{E}[f] + \sqrt{\rho_{\text{space}}} \xi_0^0\right] \mathbb{E}\left[\mathbb{E}[f] + \sqrt{\rho_{\text{space}}} \xi_0^0\right]\right]
= \mathbb{E}\left[\frac{1}{\mathbb{E}[f]} - \frac{1}{\mathbb{E}[f]^2} \sqrt{\rho_{\text{space}}} + o(\sqrt{\rho_{\text{space}}})\right]^2
= \left(\frac{1}{\mathbb{E}[f]} + o(\sqrt{\rho_{\text{space}}})\right)^2
= \frac{1}{\mathbb{E}[f]^2} + o(\sqrt{\rho_{\text{space}}})
\]
and
\[
\mathbb{E}\left[(R_1^2 - R_2^2)R_1^1\right] \approx \rho_{\text{time}} \frac{\sigma^2}{\mathbb{E}[f]^2} + o(\sqrt{\rho_{\text{space}}})
\]
Hence, for large \(n\),
\[
\gamma \approx \log \mathbb{E}[f] - \frac{\sigma^2}{\mathbb{E}[f]^2} \rho_{\text{space}} \frac{2}{\mathbb{E}[f]^2} + \epsilon \mathbb{E}\left[(R_1^2 - R_2^2)R_1^1\right] + o(\epsilon)
\]
\[
\approx \log \mathbb{E}[f] - \frac{\sigma^2}{\mathbb{E}[f]^2} \rho_{\text{space}} \frac{\sigma^2}{\mathbb{E}[f]^2} + \epsilon \rho_{\text{time}} \frac{\sigma^2}{\mathbb{E}[f]^2} + o(\sqrt{\epsilon^2 + \rho_{\text{space}}^2})
\]

C. Analysis for the two habitat model

For a two habitat model, \(d_{11} = 1 - d_1, d_{22} = 1 - d_2, d_{12} = 1 - d_2, \) and \(d_{21} = 1 - d_1\). Without loss of generality, I assume that \(\mathbb{E}[\log f^1] > \mathbb{E}[\log f^2]\). To see why there exists a dispersal strategy with \(d_2 > 0\) that maximizes \(M\), assume that \(d_2 = 0\). Then
\[
A(t) := \begin{pmatrix}
1 - d_1 & 0 \\
d_1 & 1
\end{pmatrix}
\begin{pmatrix}
\begin{pmatrix}f_t^1 & 0 \\
0 & f_t^2\end{pmatrix}
\end{pmatrix}
= \begin{pmatrix}
(1 - d_1)f_t^1 & 0 \\
d_1f_t^1 & f_t^2
\end{pmatrix}
\]
are lower triangular matrices and \(M = \max\{\mathbb{E}[\log(1-d_1) f^1], \mathbb{E}[\log f^2]\} \leq \mathbb{E}[\log f^1]\). However, \(M = \mathbb{E}[\log f^1]\) (which may not be optimal) is realized when \(d_1 = 0\) and \(d_2 > 0\). Hence, the optimal \(M\) value is achieved when \(d_2 > 0\).
To understand when does dispersal from habitat 1 to habitat 2 increases the metapopulation growth rate, I take the “well mixed” scenario to be $d_1 = 0$ and $d_2 = 1$ in which case $\mathbf{v} = (1, 0)'$. For this choice of $\mathbf{v}$, $S_t = f^1_t$. Hence, $R^1_t = 1$ and $R^2_t = f^2_t / f^1_t$. In which case,

$$M = \mathbb{E} \log S_1 + \epsilon \mathbb{E} [(R^2_2 - R^1_2) R^1_1] + o(\epsilon)$$

$$= \mathbb{E} \log f^1_1 + \epsilon \mathbb{E} [f^2_1 / f^1_1 - 1] + o(\epsilon)$$

as claimed in the main text.

When $\log f^i_t$ are normally distributed with means $\mu_i$, variances $\sigma_i^2$, and correlation coefficient $\rho_{space}$, then $\log(f^2_1 / f^1_1)$ is normally distributed with mean $\mu_2 - \mu_1$ and variance $\sigma_1^2 + \sigma_2^2 - 2\rho_{space} \sigma_1 \sigma_2$. Therefore, in this case,

$$M = \mu_1 + \epsilon \left( \exp(\mu_2 - \mu_1 + (\sigma_1^2 + \sigma_2^2 - 2\rho_{space} \sigma_1 \sigma_2)/2) - 1 \right) + o(\epsilon^2)$$

Movement into habitat 2 increases $M$ if and only if

$$\exp(\mu_2 - \mu_1 + (\sigma_1^2 + \sigma_2^2 - 2\rho_{space} \sigma_1 \sigma_2)/2) > 1$$

$$\mu_2 - \mu_1 + (\sigma_1^2 + \sigma_2^2 - 2\rho_{space} \sigma_1 \sigma_2)/2 > 0$$

$$\sigma_1^2 + \sigma_2^2 - 2\rho_{space} \sigma_1 \sigma_2 > 2(\mu_1 - \mu_2)$$

as claimed in the text.