Appendix A from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

Computational Considerations

To simulate the branching processes, we used Gillespie's algorithm. Namely, given the current population state $(N_1(t), \ldots, N_n(t))$, the time to the next demographic event is exponentially distributed with rate parameter $r(t) = \sum_{i=1}^{n} (b_i + d_i)N_i(t) + \mu \sum_{i \neq j} m_{ij} N_i(t)$. When the demographic event occurs, the probabilities that this event is a birth in patch i, a death in patch i, or a dispersal event from patch i to patch j are given by $b_i N_i(t)/r(t)$, $d_i N_i(t)/r(t)$, and $\mu m_{ij} N_i(t)/r(t)$, respectively.

Extinction probabilities were computed using the generating function for the branching process (Harris [1963] 2002; Athreya and Ney [1972] 2004). The generating function is a multivariate function—$G(s) = (G_1(s), \ldots, G_n(s))$, where $s = (s_1, \ldots, s_k)$—that captures all the probabilistic information about changes in the population state. For our spatial branching process, this generating function is given by

$$G_i(s) = \frac{1}{b_i + d_i + \mu e_i} \left(d_i + b_i s_i^2 + \mu \sum_{j=1}^{n} m_{ij} s_j \right),$$

where the coefficients of 1, s_i^2, and s_j correspond to the probabilities that a demographic event of an individual in patch i corresponds to dying, giving birth, and dispersing to patch j.

The probability of extinction depends on the initial abundance and distribution of individuals on the landscape. Let q_i denote the extinction probability if there is initially one individual arriving in patch i. If $\lambda > 0$, then the extinction probabilities $q = (q_1, \ldots, q_n)$ are given by the unique solution to $G(q) = q$ satisfying $0 \leq q_i < 1$ for all i. From these extinction probabilities, it is possible to compute the probability of extinction (and the complementary probability of invasion success) for any initial distribution and abundance of individuals. Namely, if $N_i(0)$ is the initial number of individuals in patch i, then the probability that the invasion fails is given by

$$\prod_i q_i^{N_i(0)}.$$

Numerically estimating the probabilities q_i is straightforward: iterate the difference equation $s(t + 1) = G(s(t))$ with $s(0) = (0, \ldots, 0)$ until it converges to q.

Appendix B from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

Asymptotic Population Growth Rate

The solution for any linear differential equation $dN/dt = NA$ is given by $N(0)\exp(At)$ where $\exp(\cdot)$ denotes the matrix exponential. A and $\exp(A)$ share the same eigenvectors. Moreover, the eigenvalues of $\exp(A)$ are the exponentiated eigenvalues of A. If, as in our case, A has nonnegative entries on the off diagonal, then the exponentiated matrix $\exp(A)$ is a nonnegative primitive matrix. By the Perron-Frobenius theorem, there exists a positive dominant eigenvalue. Call it $\rho(A)$ and let $\lambda(A) = \ln\rho(A)$ be the corresponding dominant eigenvalue of A. For the model presented in the main text, the expected asymptotic growth rate is given by

$$f(\mu) = \lambda[\mathbf{B} - \mathbf{D} + \mu(\mathbf{M} - \mathbf{E})].$$

To show that this asymptotic growth rate decreases with the mean dispersal rate, it will be shown that $f'(\mu) < 0$. Given any $\mu = x > 0$, choose $a > 0$ such that $ax I \geq \mathbf{D} + x\mathbf{E}$, where I is the $n \times n$ identity matrix. Define

$$\mathbf{\Lambda} = \frac{1}{x}(\mathbf{B} - \mathbf{D}) + aI,$$

$$g(t) = \lambda[\mathbf{\Lambda} + t(\mathbf{M} - \mathbf{E})].$$

Our choice of a and our assumption that $\mathbf{M}$ is irreducible imply that $\mathbf{M} - \mathbf{E} + \mathbf{\Lambda}$ is a nonnegative irreducible matrix. Moreover, since the row sums of $\mathbf{M} - \mathbf{E}$ are 0, the row sums of $\mathbf{M} - \mathbf{E} + \mathbf{\Lambda}$ equal the diagonal entries of λ. The following Lemma of Kirkland et al. (2006) applied to $\mathbf{\Lambda} + t(\mathbf{M} - \mathbf{E}) = (1 - t)\mathbf{\Lambda} + t(\mathbf{M} - \mathbf{E} + \mathbf{\Lambda})$ implies that $g'(1) < 0$.

Lemma 1

Suppose that $\mathbf{A}$ is an irreducible nonnegative matrix, and let $\mathbf{D}_\mathbf{A}$ be the diagonal matrix of row sums of $\mathbf{A}$. Let $\mathbf{\Lambda}$ be a diagonal matrix such that $\mathbf{\Lambda} \geq \mathbf{D}_\mathbf{A}$. For $0 \leq t \leq 1$, let $h(t) = \lambda[(1 - t)\mathbf{\Lambda} + t\mathbf{A}]$. Then $h'(1) < 0$.

Since

$$g(t) = \frac{\lambda[x\mathbf{\Lambda} + tx(\mathbf{M} - \mathbf{E})]}{x}$$

$$= \frac{\lambda[\mathbf{B} - \mathbf{D} + ax I + tx(\mathbf{M} - \mathbf{E})]}{x}$$

$$= \frac{\lambda[\mathbf{B} - \mathbf{D} + tx(\mathbf{M} - \mathbf{E})]}{x} + a$$

$$= \frac{f(xt)}{x} + a,$$

it follows that $g'(1) = f'(x) < 0$. Since $x > 0$ was arbitrary, $f(\mu)$ is a decreasing function of $\mu > 0$ as claimed.

To identify the asymptotic growth rate at high dispersal rates ($\lim_{\mu \to \infty} f(\mu)$), define $\mathbf{C} = \mathbf{B} - \mathbf{D}$, $\mathbf{F} = \mathbf{M} - \mathbf{E}$, and

$$g(\epsilon) = \lambda(\epsilon \mathbf{C} + \mathbf{F}).$$

Let v be the right eigenvector of $\mathbf{F}$ such that $\mathbf{F}v = 0$, with $\Sigma\, v_i = 1$. For every $\epsilon \geq 0$, let $w(\epsilon)$ be the dominant left eigenvector of $\epsilon \mathbf{C} + \mathbf{F}$ such that $w(\epsilon)v = 1$ (note that w is a row vector and v is a column vector). It follows that

$$g(\epsilon) = w(\epsilon)(\epsilon \mathbf{C} + \mathbf{F})v = \epsilon w(\epsilon)\mathbf{C}v.$$

Since $w(\epsilon) = (1, \ldots, 1) + O(\epsilon)$, it follows that

$$g(\epsilon) = \epsilon(b - d) \times v + \epsilon O(\epsilon),$$

$$g'(0) = \lim_{\epsilon \to 0} \frac{g(\epsilon) - g(0)}{\epsilon}$$

$$= \lim_{\epsilon \to 0} (b - d) \times v + O(\epsilon)$$

$$= (b - d) \times v.$$

It follows that

$$\lim_{\mu \to \infty} f(\mu) = \lim_{\mu \to \infty} g\left(\frac{1}{\mu}\right)\mu$$

$$= \lim_{\epsilon \to 0} \frac{g(\epsilon)}{\epsilon}$$

$$= v \times (b - d),$$

as claimed.

Appendix C from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

(Am. Nat., vol. 174, no. 4, p. 490)

Extinction Probabilities

Define $x_i(t) = P(N(t) = 0 \mid N(0) = e_i)$ and $x(t) = (x_1(t), \ldots, x_n(t))$. The backward Kolmogorov equations (see, e.g., chap. V of Athreya and Ney [1972] 2004) for the extinction probabilities are given by

$$\frac{dx_i}{dt} = (b_i + d_i + \mu e_i)(G_i(x) - x_i)$$

$$= d_i + b_i x_i^2 + \mu \sum_{j=1}^{n} m_{ij} x_j - (b_i + d_i + \mu e_i)x_i.$$

Hence,

$$\frac{dx_i}{dt} = (1 - x_i)(d_i - b_i x_i) + \mu \left(\sum_{j=1}^{n} m_{ij} x_j - e_i x_i \right). \tag{C1}$$

Let $x^* = (x_1^*, \ldots, x_n^*) \in [0, 1]^n$ be the smallest equilibrium to the backward equations. Branching process theory (see, e.g., chap. V of Athreya and Ney [1972] 2004) implies that x^* equals the vector of extinction probabilities q. Moreover, x^* is a stable equilibrium for the backward equations whose basin of attraction includes $[0, 1)^n$.

To understand low dispersal rates, consider the limit of $\mu = 0$, in which case the dynamics of equation (C1) decouple. Separating variables and using partial fractions, the solution for x_i with $x_i(0)$ can be found to be

$$x_i(t) = \frac{1 - \exp[(b_i - d_i)t]}{1 - R_i \exp[(b_i - d_i)t]}. \tag{C2}$$

In particular, the probability of extinction is given by

$$\lim_{t \to \infty} x_i(t) = x_i^* = \min\left\{1, \frac{1}{R_i}\right\}.$$

By continuity of these extinction probabilities with respect to μ, these analytic expressions provide zeroth order approximations to extinction probabilities when $\mu > 0$.

To understand the case of high dispersal rates, let v be a row vector such that $v(\mathbf{M} - \mathbf{E}) = 0$ and $\sum_{i=1}^{n} v_i = 1$. Define $y = \sum_{i=1}^{n} v_i x_i = v \times x$ and $\epsilon = 1/\mu$. Then

$$\begin{cases} \epsilon \dfrac{dx_i}{dt} = \epsilon(1 - x_i)(d_i - b_i x_i) + \displaystyle\sum_{j=1}^{n} m_{ij} x_j - e_i x_i \\ \dfrac{dy}{dt} = \displaystyle\sum_{i=1}^{n} v_i (1 - x_i)(d_i - b_i x_i) \end{cases}, \tag{C3}$$

and the limit $\mu \to \infty$ corresponds to the limit $\epsilon \to 0$, in which case we obtain a singular perturbation problem with fast variable x and the slow variable y. In the limit with $\epsilon = 0$, we have

$$0 = \epsilon \sum_j m_{ij} x_j - e_i x_i,$$

$$\frac{dy}{dt} = \sum_i v(1 - x_i)(d_i - b_i x_i).$$

The first set of equations requires that $(\mathbf{M} - \mathbf{E})x = 0$. Since $\mathbf{M} - \mathbf{E}$ has zero row sums, $x(t) = c(t)\mathbf{1}$ for some function $c(t)$ and where $\mathbf{1}$ is a column vector of ones. Since $y(t) = \sum_{i=1}^n v_i x_i(t) = c(t) \sum_{i=1}^n v_i = c(t)$, it follows that $x(t) = y(t)\mathbf{1}$. Hence, the limiting dynamics on the slow manifold are given by

$$\frac{dy}{dt} = \sum_i v_i(1 - y)(d_i - b_i y) = (1 - y)(v \times d - v \times by). \tag{C4}$$

The solution of this differential equation is given by

$$y(t) = \frac{1 - \exp[v \times (b - d)t]}{1 - \hat{R}\exp[v \times (b - d)t]}. \tag{C5}$$

Moreover, the smallest equilibrium solution in $[0, 1]$ is given by $x_i = y = 1$ for all i if $v \times d \geq v \times b$. Otherwise, it is given by

$$y = x_i = \frac{1}{R},$$

as claimed in the main text.

Appendix D from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

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Mean Times to Extinction

Assume $\lambda < 0$. Then the branching process becomes extinct with probability 1. As in appendix C, let $x_i(t) = P(N(t) = 0 | N(0) = e_i)$ and $x(t) = (x_1(t), \ldots, x_n(t))$. Let Z_i denote the time to extinction, given that $N(0) = e_i$. In other words, $Z_i = \inf\{t \geq 0 | N(t) = 0\}$. Then $1 - x_i(t) = P(Z_i > t | N(0) = e_i)$. A standard result in probability implies that

$$\mathbf{E}(Z_i) = \int_0^\infty 1 - x_i(s)ds.$$

Let $z_i(t) = \int_0^t 1 - x_i(s)ds$. Then $\mathbf{E}(Z_i) = \lim_{t \to \infty} z_i(t)$ and

$$\frac{dz_i}{dt} = 1 - x_i. \tag{D1}$$

Hence, the extinction times can be solved for by solving the system of differential equations given by equations (C1) and (D1).

For the case of $\mu = 0$, equation (C2) implies that

$$\mathbf{E}(Z_i) = \int_0^\infty 1 - x_i(t)dt$$

$$= \int_0^\infty \frac{(1 - R_i)\exp[(b_i - d_i)t]}{1 - R_i \exp[(b_i - d_i)t]}dt$$

$$= \frac{R_i - 1}{R_i(b_i - d_i)} \int_{1-R_i}^1 \frac{du}{u}, \text{ with } u = 1 - R_i \exp[(b_i - d_i)t],$$

$$= -\frac{\ln(1 - R_i)}{b_i}.$$

Moreover, continuity of $\mathbf{E}(Z_i)$ with respect to μ implies that these mean extinction times are zeroth order approximations of $\mathbf{E}(Z_i)$ when μ is positive but sufficiently small.

To understand the case $\mu \gg 1$ (i.e., high dispersal rates relative to growth rates), the singular perturbation argument used in appendix C implies that in the limit $\mu \to \infty$, $x_i(t) = y(t)$, where $y(t)$ is given by equation (C5). Hence,

$$\mathbf{E}(Z_i) = \int_0^\infty 1 - y(t)dt = -\frac{\ln(1 - \hat{R})}{v \times b}.$$

Appendix E from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

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Single versus Multiple Releases

Assume that $k \geq 2$. This appendix shows that k propagules of size 1 have a greater likelihood of invasion success than one propagule of size k. Let q_i be the probability of invasion failure if a single invader appears in patch i. For a single release, the probability of invasion failure is given by

$$E(q_i^k) = \frac{1}{n} \sum_{i=1}^{n} q_i^k. \tag{E1}$$

To model a multiple release, let $X_1, \ldots, X_k$ be independent random variables that are uniformly distributed on $1, \ldots, n$. One can interpret X_i as the release location of the ith propagule. The probability of invasion failure of the multiple release is given by

$$E(q_{X_1} \ldots q_{X_k}). \tag{E2}$$

For patch i, let

$$N_i = \#\{j \mid X_j = i\}$$

be the number of releases in patch i. For nonnegative integers $a_1 \geq a_2 \ldots \geq a_n$ such that $\sum_{i=1}^{k} a_i = k$,

$$E[q_{X_1} \ldots q_{X_k} \mid (N_1, \ldots, N_n) = (a_{\sigma(1)}, \ldots, a_{\sigma(n)}) \text{ for a permutation } \sigma] = \frac{1}{n!} \sum_{\sigma} q_{\sigma(1)}^{a_1} \ldots q_{\sigma(n)}^{a_n}.$$

Since $a_1 + \cdots + a_i \leq k$ for $1 \leq i \leq n-1$ and $a_1 + \cdots + a_n = k$, Muirhead's inequality implies that

$$\frac{1}{n!} \sum_{\sigma} q_{\sigma(1)}^{a_1} \ldots q_{\sigma(n)}^{a_n} \leq \frac{1}{n!} \sum_{\sigma} q_{\sigma(1)}^{k}$$

$$= \frac{(n-1)!}{n!} \sum_{i=1}^{n} q_i^k$$

$$= E(q_i^k),$$

where the inequality is strict whenever $a_1 < k$ and $q_i \neq q_j$ for some $1 \leq i, j \leq n$. Summing over all the conditional expectations yields

$$E(q_i^k) \geq E(q_{X_1} \ldots q_{X_k}),$$

where the inequality is strict whenever $q_i \neq q_j$ for some $1 \leq i, j \leq n$.

Appendix F from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

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Sensitivity Analysis

To compute sensitivities of the extinction probabilities when the asymptotic growth rate is positive, recall that these probabilities are given by the smallest solution to

$$(b_i + d_i + \mu e_i)q_i = d_i + b_i q_i^2 + \mu \sum_k m_{ik} q_k. \tag{F1}$$

Implicitly differentiating equation (F1) with respect to b_i yields

$$q_i + a_i \frac{\partial q_i}{\partial b_i} = q_i^2 + 2b_i q_i \frac{\partial q_i}{\partial b_i} + \mu \sum_k m_{ik} \frac{\partial q_k}{\partial b_i},$$

where $a_i = b_i + d_i + \mu e_i$. Implicitly differentiating equation (F1) with respect to b_j with $j \neq i$ yields

$$a_i \frac{\partial q_i}{\partial b_j} = 2b_i q_i \frac{\partial q_i}{\partial b_j} + \mu \sum_k m_{ik} \frac{\partial q_k}{\partial b_j}.$$

Thus, in matrix notation, we obtain

$$\mathrm{diag}(q) + \mathrm{diag}(a)\frac{\partial q}{\partial b} = \mathrm{diag}(q \circ q) + 2\mathrm{diag}(b \circ q)\frac{\partial q}{\partial b} + \mu \mathbf{M}\frac{\partial q}{\partial b},$$

where $\partial q / \partial b$ is the derivative matrix whose ith–jth entry is $\partial q_i / \partial b_j$, $\circ$ denotes a Hadamard product, and $\mathrm{diag}(v)$ denotes a diagonal matrix whose diagonal entries are given by the entries of the vector v. Equivalently, we have

$$\mathrm{diag}[q \circ (1-q)] = [\mathrm{diag}(2b \circ q - a) + \mu \mathbf{M}]\frac{\partial q}{\partial b}.$$

Hence,

$$\frac{\partial q}{\partial b} = [\mathrm{diag}(2b \circ q - a) + \mu \mathbf{M}]^{-1}\mathrm{diag}[q \circ (1-q)].$$

Using the matrix of sensitivities, the elasticities can be computed as

$$\mathbf{E}_b = \mathrm{diag}(q)^{-1}\frac{\partial q}{\partial b}\mathrm{diag}(b),$$

where the ith–jth entry of $\mathbf{E}_b$ is $(\partial q_i / \partial b_j)(b_j / q_i)$.

On the other hand, implicitly differentiating equation (F1) with respect to d_i yields

$$q_i + a_i \frac{\partial q_i}{\partial d_i} = 1 + 2b_i q_i \frac{\partial q_i}{\partial d_i} + \mu \sum_k m_{ik} \frac{\partial q_k}{\partial d_i},$$

where $a_i = b_i + d_i + \mu e_i$. Implicitly differentiating equation (F1) with respect to d_j with $j \neq i$ yields

$$a_i \frac{\partial q_i}{\partial d_j} = 2b_i q_i \frac{\partial q_i}{\partial d_j} + \mu \sum_k m_{ik} \frac{\partial q_k}{\partial d_j}.$$

Thus, in matrix notation, we obtain

$$\text{diag}(q) + \text{diag}(a)\frac{\partial q}{\partial d} = I + 2\text{diag}(b \circ q)\frac{\partial q}{\partial d} + \mu \mathbf{M}\frac{\partial q}{\partial d},$$

where $\partial q/\partial d$ is the derivative matrix whose ith–jth entry is $\partial q_i/\partial d_j$. Equivalently, we have

$$\text{diag}(q - 1) = [\text{diag}(2b \circ q - a) + \mu \mathbf{M}]\frac{\partial q}{\partial d}.$$

Hence,

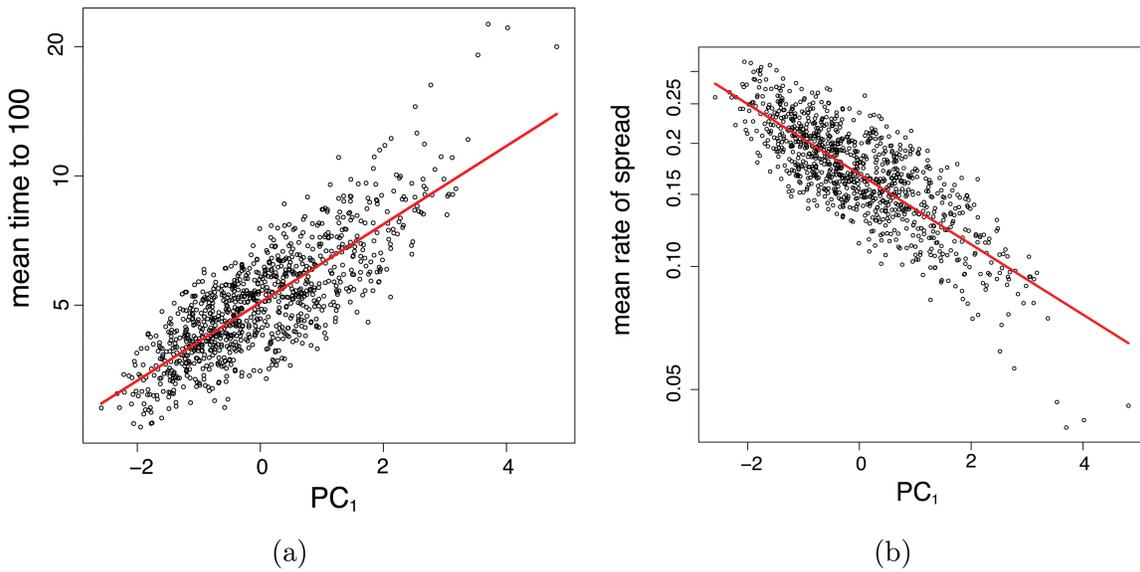$$\frac{\partial q}{\partial d} = [\text{diag}(2b \circ q - a) + \mu \mathbf{M}]^{-1}\text{diag}(q - 1).$$

Using the matrix of sensitivities, the elasticities can be computed as

$$\mathbf{E}_d = \text{diag}(q)^{-1}\frac{\partial q}{\partial d}\text{diag}(d),$$

where the ith–jth entry of $\mathbf{E}_d$ is $(\partial q_i/\partial d_j)(d_j/q_i)$.

Appendix G from S. J. Schreiber and J. O. Lloyd-Smith, "Invasion Dynamics in Spatially Heterogeneous Environments"

(Am. Nat., vol. 174, no. 4, p. 490)

Correlations between Time Lags/Spatial Spread with PC_1

(a)   (b)

Figure G1: Using the simulated data described in "Model and Methods," a linear regression was performed on the logarithm of mean time lag (i.e., time to reach 100 individuals; *a*) and the logarithm of mean rate of spatial spread (i.e., average change in fraction of landscape covered per unit time; *b*) versus the principal component PC_1 of the standardized $q - \lambda$ values. Positive values of PC_1 correspond to populations arriving in patches with high extinction risk or landscapes supporting a low metapopulation growth rate λ.