

Appendix A from D. L. DeAngelis et al., “The Effect of Travel Loss on Evolutionarily Stable Distributions of Populations in Space”

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Calculation of the Optimal Movement Coefficients of an Evolutionarily Stable Strategy

To understand the stability of any such equilibrium E^* , $(\bar{0}, P^*, R^*, M^*)$, a standard approach is to determine the real parts of the eigenvalues of the matrix J , the Jacobian matrix for the system (9) evaluated at this equilibrium solution. If we let $J_{(8)}$ denote the Jacobian matrix for system (8) evaluated at $E_{(8)}^*$, J has the form

$$J = \begin{bmatrix} D & \hat{0} \\ * & J_{(8)} \end{bmatrix},$$

where $\hat{0}$ denotes the $N \times 3N$ matrix with all components equal to 0, the components of the $N \times N$ matrix D are given by

$$D_{ij} = \begin{cases} (1 - \varepsilon_{ji})\hat{m}_{ji} & i \neq j \\ b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{j=1}^N \hat{m}_{ij} & i = j \end{cases}$$

for $i, j \in \{1, \dots, N\}$, where the asterisk indicates a $3N \times N$ matrix with components that are not involved in our discussion below.

Because of the special structure of the matrix, it follows that any eigenvalue λ must satisfy

$$\det(J - \lambda I_{4N}) = \det(J_{(8)} - \lambda I_{3N}) \det(D - \lambda I_N) = 0,$$

where I_m denotes the $m \times m$ identity matrix for any positive integer m .

In this appendix, we focus our discussion on the matrix D , usually referred to as the invasion matrix. Since we are assuming (H_2) (see text), it follows that the nonnegative matrix with components (\hat{m}_{ij}) is irreducible. If c is a large enough positive constant so that the diagonal entries of $\bar{D} = D + cI_N$ are positive, and if λ is any eigenvalue of \bar{D} with associated eigenvector v , then $\lambda - c$ is an eigenvalue of D with the same eigenvector. So the following is a consequence of the Perron-Frobenius theorem (Horn and Johnson 1999):

- The matrix D has a dominant eigenvalue, denoted by λ_1 , such that λ_1 is real, and the real parts of all other eigenvalues are strictly less than λ_1 .
- Both the right and the left eigenspace associated with λ_1 is one-dimensional. In particular, all of the components of the left and right eigenvectors corresponding to λ_1 can be chosen to be positive, and for all eigenvectors of other eigenvalues there exists a component that is not positive.
- λ_1 is a simple root of the characteristic polynomial of D . Using the implicit function theorem, it follows that λ_1 is a smooth function of \hat{m}_{ij} and m_{ij} , $i, j \geq 1$.

In order to justify the rates given in equations (17), we establish two preliminary results. For every $2 \leq i \leq N$, set $V_i = (D_{i2}, \dots, D_{iN})^T$, where T denotes the transpose.

LEMMA 1. Suppose that $\hat{m}_{ij} = m_{ij}$ for every i, j . If $m_{1i} > 0$ for every $2 \leq i \leq N$, V_2, \dots, V_N are linearly independent and thus form a basis of \mathbb{R}^{N-1} .

PROOF. Let $(D_{ij})_{i,j \geq 2}$ denote the $(N-1) \times (N-1)$ matrix obtained by removing the first row and first column of matrix D . We claim that if $m_{1i} > 0$ for every $2 \leq i \leq N$, then $(D_{ij})_{i,j \geq 2}$ is invertible. To see this, since the off-diagonal entries of $(D_{ij})_{i,j \geq 2}$ are all nonnegative, by the Perron-Frobenius Theorem there exists some eigenvalue of $(D_{ij})_{i,j \geq 2}$, denoted by η_1 , that is real, and the real parts of all other eigenvalues are less than or equal to η_1 .

Moreover, η_1 has a left eigenvector with all nonnegative components, denoted (v_2, \dots, v_N) ; that is,

$$(v_2, \dots, v_N)(D_{ij})_{i,j \geq 2} = \eta_1(v_2, \dots, v_N). \quad (\text{A1})$$

Recall that when $(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})$, zero is an eigenvalue of D with P^* as a right eigenvector. Hence,

$$(D_{ij})_{i,j \geq 2}(P_2^*, \dots, P_N^*)^T = -P_1^*((1 - \varepsilon_{12})m_{12}, \dots, (1 - \varepsilon_{1N})m_{1N})^T, \quad (\text{A2})$$

where $(P_2^*, \dots, P_N^*)^T$ denotes the transpose of (P_2^*, \dots, P_N^*) .

Taking the inner product of both sides of equation (A1) with the vector (P_2^*, \dots, P_N^*) , and applying the identity equation (A2), we have

$$\eta_1 \sum_{i=2}^N v_i P_i^* = -P_1^* \sum_{i=2}^N v_i (1 - \varepsilon_{1i}) m_{1i}.$$

Since $m_{1i} > 0, v_i \geq 0$ for every $i \geq 2$ and (v_2, \dots, v_N) is a nonzero vector, we see that $\eta_1 < 0$. This implies that the real parts of all eigenvalues of $(D_{ij})_{i,j \geq 2}$ are negative. Hence, $(D_{ij})_{i,j \geq 2}$ is invertible. As $V_i = (D_{i2}, \dots, D_{iN})$, $(D_{ij})_{i,j \geq 2} = (V_2, \dots, V_N)^T$. Since $(D_{ij})_{i,j \geq 2}$ is invertible, V_2, \dots, V_N are linearly independent.

We will also use the following result that is a corollary of Cramer's rule.

LEMMA 2. *Suppose that vectors V_1, \dots, V_d form a basis of \mathbb{R}^d . If some vector $V_0 \in \mathbb{R}^d$ satisfies the property that $V_1, \dots, V_{i-1}, V_0, V_{i+1}, \dots, V_d$ are linearly dependent for every $1 \leq i \leq d$, then V_0 must be the zero vector.*

We begin by justifying the rates for scenario 2 first, since the justification for scenario 1 is more difficult.

Scenario 2: Calculation of $m_{1i,\text{opt}}, 2 \leq i \leq N$

THEOREM 1. *Suppose that $R_i^* > 0$ and $M_i^* \geq 0$ for all $i = 1, \dots, N$ and that assumptions (H_0) , (H_1) , and $(H_2, \text{scenario } 2)$ hold.*

a) *If there exist $\{m_{1i,\text{opt}}\}_{i=2}^N$ with $m_{1i,\text{opt}} > 0$ for $2 \leq i \leq N$ such that $\lambda_1 \leq 0$ for $(m_{12}, \dots, m_{1N}) = (m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$ and all $(\hat{m}_{12}, \dots, \hat{m}_{1N})$ in a neighborhood of $(m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$, then for every $2 \leq i \leq N$,*

$$m_{1i,\text{opt}} = (1 - \varepsilon_{i1}) \frac{P_i^*}{P_1^*} m_{i1} + \frac{1}{P_1^*} \sum_{j=2}^N \left[\frac{(1 - \varepsilon_{ij})}{(1 - \varepsilon_{1j})} m_{ij} P_i^* - \frac{(1 - \varepsilon_{ji})}{(1 - \varepsilon_{1i})} m_{ji} P_j^* \right]. \quad (\text{A3})$$

b) *Suppose that $m_{1i,\text{opt}}$ is positive for every $i \geq 2$. If $(m_{12}, \dots, m_{1N}) = (m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$, then $\lambda_1 \equiv 0$ for any $\hat{m}_{1j} > 0, j \geq 2$.*

Under assumption $(H_2, \text{scenario } 2)$, the invasion matrix D has components

$$D_{ij} = \begin{cases} b_1 a_1 R_1^* - d_1 - f_1 M_1^* - \sum_{h=1}^N \hat{m}_{1h} & i = j = 1 \\ b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{h=1}^N m_{ih} & i = j \geq 2 \\ (1 - \varepsilon_{1i}) \hat{m}_{1i} & i \geq 2, j = 1 \\ (1 - \varepsilon_{ji}) m_{ji} & i \geq 1, j \geq 2, i \neq j \end{cases}.$$

We first note that

$$\lambda_1|_{(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})} = 0. \quad (\text{A4})$$

Biologically, this is because the invader \hat{P} is a cloned copy of the resident P . The mathematical reasoning is as follows: when $(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})$, 0 is an eigenvalue of D , with P^* as a right eigenvector. Since all components of P^* are all positive, 0 is the dominant eigenvalue of D ; that is, equation (A4) holds.

PROOF OF THEOREM 1(a). If there exist some (m_{12}, \dots, m_{1N}) with $m_{1i} > 0$ for every $2 \leq i \leq N$ such that $\lambda_1 \leq 0$

for all $(\hat{m}_{12}, \dots, \hat{m}_{1N})$ in a neighborhood of (m_{12}, \dots, m_{1N}) , then

$$\left. \frac{\partial \lambda_1}{\partial \hat{m}_{1i}} \right|_{(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})} = 0 \quad (\text{A5})$$

for every $i \geq 2$.

Under assumption $(H_2, \text{scenario } 2)$, the matrix $D - \lambda_1 I_N$, has components

$$(D - \lambda_1 I_N)_{ij} = \begin{cases} b_1 a_1 R_1^* - d_1 - f_1 M_1^* - \sum_{h=1}^N \hat{m}_{1h} - \lambda_1 & i = j = 1, \\ b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{h=1}^N m_{ih} - \lambda_1 & i = j \geq 2, \\ (1 - \varepsilon_{1i}) \hat{m}_{1i} & i \geq 2, j = 1, \\ (1 - \varepsilon_{ji}) m_{ji} & i \geq 1, j \geq 2, i \neq j \end{cases}.$$

Instead of differentiating the determinant of the matrix $D - \lambda_1 I$ with respect to \hat{m}_{1i} directly, we first do the following manipulation. Dividing the i th row of $D - \lambda_1 I$ by $(1 - \varepsilon_{1i})$ and adding it to the first row, and repeating this process for each $2 \leq i \leq n$, we see that matrix $D - \lambda_1 I$ is transformed into a new matrix, denoted by \tilde{D} , which can be expressed by

$$\tilde{D}_{ij} = \begin{cases} b_1 a_1 R_1^* - d_1 - f_1 M_1^* - \lambda_1 & i = j = 1 \\ b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{h=1}^N m_{ih} - \lambda_1 & i = j \geq 2 \\ (1 - \varepsilon_{1i}) \hat{m}_{1i} & i \geq 2, j = 1 \\ (1 - \varepsilon_{ji}) m_{ji} & i \geq 2, j \geq 2, i \neq j \\ \frac{1}{(1 - \varepsilon_{1j})} \left(b_j a_j R_j^* - d_j - f_j M_j^* - \sum_{h=1}^N m_{jh} - \lambda_1 \right) + (1 - \varepsilon_{j1}) m_{j1} - \sum_{h=2}^N \frac{(1 - \varepsilon_{jh})}{(1 - \varepsilon_{1h})} m_{jh} & i = 1, j \geq 2. \end{cases}$$

Clearly, $|D - \lambda_1 I| = 0$ is equivalent to $|\tilde{D}| = 0$. For every $2 \leq i \leq N$, differentiate the determinant of the matrix \tilde{D} with respect to \hat{m}_{1i} and evaluate the result at $(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})$. By applying both equations (A4) and (A5), we find that

$$\left. \frac{\partial |\tilde{D}|}{\partial \hat{m}_{1i}} \right|_{(\hat{m}_{12}, \dots, \hat{m}_{1N}) = (m_{12}, \dots, m_{1N})} = 0$$

if and only if the vectors $V_2, \dots, V_{i-1}, V_0, V_{i+1}, \dots, V_N$ are linearly dependent, where the vector V_0 is given by

$$V_0 = (\tilde{D}_{12}, \dots, \tilde{D}_{1N}).$$

By lemma 1, V_2, \dots, V_N are linearly independent and form a basis for \mathbb{R}^{N-1} . Therefore, by lemma 2, V_0 must be the zero vector in \mathbb{R}^{N-1} . Hence, $\tilde{D}_{1j} = 0$ for every $j \geq 2$; that is, noting that $\lambda_1 = 0$ by equation (A4),

$$\frac{1}{(1 - \varepsilon_{1j})} \left(b_j a_j R_j^* - d_j - f_j M_j^* - \sum_{h=1}^N m_{jh} \right) + (1 - \varepsilon_{j1}) m_{j1} - \sum_{h=2}^N \frac{(1 - \varepsilon_{jh})}{(1 - \varepsilon_{1h})} m_{jh} = 0. \quad (\text{A6})$$

Recall that at equilibrium we have, for every $j \geq 2$,

$$b_j a_j R_j^* - d_j - f_j M_j^* - \sum_{h=1}^N m_{jh} + \left[\sum_{h=1}^N (1 - \varepsilon_{hj}) m_{hj} \frac{P_h^*}{P_j^*} \right] = 0. \quad (\text{A7})$$

Substituting equation (A7) into equation (A6), we have

$$m_{1j} \frac{P_1^*}{P_j^*} = (1 - \varepsilon_{j1})m_{j1} + \sum_{h=2}^N \frac{(1 - \varepsilon_{jh})}{(1 - \varepsilon_{1h})} m_{jh} - \sum_{h=2}^N \frac{(1 - \varepsilon_{hi})}{(1 - \varepsilon_{1j})} m_{hj} \frac{P_h^*}{P_j^*}. \quad (\text{A8})$$

Dividing equation (A8) by P_1^*/P_j^* , we have

$$m_{1j} = (1 - \varepsilon_{j1})m_{j1} \frac{P_j^*}{P_1^*} + \sum_{h=2}^N \frac{(1 - \varepsilon_{jh})}{(1 - \varepsilon_{1h})} m_{jh} \frac{P_j^*}{P_1^*} - \sum_{h=2}^N \frac{(1 - \varepsilon_{hi})}{(1 - \varepsilon_{1j})} m_{hj} \frac{P_h^*}{P_1^*}. \quad (\text{A9})$$

This completes the proof of part (a), theorem 1. \square

LEMMA 3. *For the movement strategy given by equation (A3), the immigration and emigration flux for patch 1 is balanced; that is, if $(m_{12}, \dots, m_{1N}) = (m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$, then*

$$\sum_j (1 - \varepsilon_{j1})m_{j1}P_j^* = \left(\sum_j m_{1j,\text{opt}} \right) P_1^*; \quad (\text{A10})$$

or equivalently, the resident species at equilibrium (with invader absent) has zero fitness in patch 1:

$$b_1 a_1 R_1^* - d_1 - f_1 M_1^* = 0. \quad (\text{A11})$$

PROOF. Multiplying equation (A3) by P_1^* and summing up for $2 \leq i \leq N$, we have

$$\begin{aligned} \left(\sum_{i=2}^N m_{1i,\text{opt}} \right) P_1^* &= \sum_{i=2}^N (1 - \varepsilon_{i1})m_{i1}P_i^* + \sum_{i,h=2}^N \left[\frac{(1 - \varepsilon_{ih})}{(1 - \varepsilon_{1h})} m_{ih}P_i^* - \frac{(1 - \varepsilon_{hi})}{(1 - \varepsilon_{1i})} m_{hi}P_h^* \right] \\ &= \sum_{i=2}^N (1 - \varepsilon_{i1})m_{i1}P_i^*, \end{aligned}$$

which implies that equation (A10) holds since we assume that $m_{11} = 0$. Clearly, equation (A11) follows from equation (A10) and equation (9b) for P_1^* . \square

LEMMA 4. *If $(m_{12}, \dots, m_{1N}) = (m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$, then for every patch $i \geq 2$, the resident species at equilibrium has fitness*

$$b_i a_i R_i^* - d_i - f_i M_i^* = \begin{cases} 0 & i = 1 \\ \left[1 - (1 - \varepsilon_{1i})(1 - \varepsilon_{i1}) \right] m_{i1} + \sum_{h=2}^N m_{ih} \left[1 - (1 - \varepsilon_{ih}) \frac{(1 - \varepsilon_{1i})}{(1 - \varepsilon_{1h})} \right] & i \geq 2. \end{cases} \quad (\text{A12})$$

PROOF. This result follows by using equation (A3) in equation (9b) for P_i^* . \square

PROOF OF THEOREM 1(b). By lemmas 3 and 4, we see that if $(m_{12}, \dots, m_{1N}) = (m_{12,\text{opt}}, \dots, m_{1N,\text{opt}})$, then

$$D_{ij} = \begin{cases} - \sum_{h=1}^N \hat{m}_{1h} & i = j = 1 \\ -(1 - \varepsilon_{1i})(1 - \varepsilon_{i1})m_{i1} - \sum_{h=2}^N m_{ih}(1 - \varepsilon_{ih}) \frac{(1 - \varepsilon_{1i})}{(1 - \varepsilon_{1h})} & i = j \geq 2 \\ (1 - \varepsilon_{1i})\hat{m}_{1i} & i \geq 2, j = 1 \\ (1 - \varepsilon_{ji})m_{ji} & i \geq 1, j \geq 2, i \neq j \end{cases}.$$

Set

$$V_* = \left(1, \frac{1}{1 - \varepsilon_{12}}, \dots, \frac{1}{1 - \varepsilon_{1N}} \right).$$

Then, $V_* D = (0, \dots, 0)$. That is, the vector V_* is the left eigenvector of D corresponding to the eigenvalue 0. Since all components of V_* are positive, 0 must be the dominant eigenvalue of matrix D , and all other eigenvalues must have strictly negative real parts. \square

Scenario 1: Calculation of $m_{i1, \text{opt}}$, $2 \leq i \leq N$

THEOREM 2. Suppose that $R_i^* > 0$ and $M_i^* \geq 0$ for all $i = 1, \dots, N$ and that assumptions (H_0) , (H_1) , and (H_2) , scenario 1) hold.

a) If there exist $\{m_{i1, \text{opt}}\}_{i=2}^N$ with $m_{i1, \text{opt}} > 0$ for $2 \leq i \leq N$ such that $\lambda_1 \leq 0$ for $(m_{21}, \dots, m_{N1}) = (m_{21, \text{opt}}, \dots, m_{N1, \text{opt}})$ and all $(\hat{m}_{21}, \dots, \hat{m}_{N1})$ in a neighborhood of $(m_{21, \text{opt}}, \dots, m_{N1, \text{opt}})$, then for every $2 \leq i \leq N$,

$$m_{i1, \text{opt}} = (1 - \varepsilon_{i1})m_{i1} \frac{P_i^*}{P_i^*} + \frac{1}{P_i^*} \sum_{j=2}^N \left[(1 - \varepsilon_{ji})m_{ji}P_j^* - \frac{(1 - \varepsilon_{ij})(1 - \varepsilon_{j1})}{(1 - \varepsilon_{i1})} m_{ij}P_i^* \right]. \quad (\text{A13})$$

b) Suppose that $m_{i1, \text{opt}}$ is positive for every $i \geq 2$. If $(m_{21}, \dots, m_{N1}) = (m_{21, \text{opt}}, \dots, m_{N1, \text{opt}})$, then $\lambda_1 \equiv 0$ for any \hat{m}_{j1} , $j \geq 2$.

Under assumption (H_2) (scenario 1), the matrix D has components

$$D_{ij} = \begin{cases} b_1 a_1 R_1^* - d_1 - f_1 M_1^* - \sum_{h=1}^N m_{1h} & i = j = 1 \\ b_i a_i R_i^* - d_i - f_i M_i^* - \hat{m}_{i1} - \sum_{h \geq 2} m_{ih} & i = j \geq 2 \\ (1 - \varepsilon_{j1})\hat{m}_{j1} & i = 1, j \geq 2 \\ (1 - \varepsilon_{ji})m_{ji} & i \geq 2, j \geq 1, i \neq j \end{cases}.$$

By a similar argument as for scenario 2,

$$\lambda_1 \Big|_{(\hat{m}_{21}, \dots, \hat{m}_{N1}) = (m_{21}, \dots, m_{N1})} = 0. \quad (\text{A14})$$

PROOF OF THEOREM 2(a). If there exist some (m_{21}, \dots, m_{N1}) with $m_{i1} > 0$ for every $2 \leq i \leq N$ such that $\lambda_1 \leq 0$ for all $(\hat{m}_{21}, \dots, \hat{m}_{N1})$ in a neighborhood of (m_{21}, \dots, m_{N1}) , then

$$\frac{\partial \lambda_1}{\partial \hat{m}_{i1}} \Big|_{(\hat{m}_{21}, \dots, \hat{m}_{N1}) = (m_{21}, \dots, m_{N1})} = 0 \quad (\text{A15})$$

for every $i \geq 2$.

Under the assumption (H_2) , scenario 1), the matrix $D - \lambda_1 I_N$ has components

$$(D - \lambda_1 I_N)_{ij} = \begin{cases} b_1 a_1 R_1^* - d_1 - f_1 M_1^* - \sum_{h=1}^N m_{1h} - \lambda_1 & i = j = 1 \\ b_i a_i R_i^* - d_i - f_i M_i^* - \hat{m}_{i1} - \sum_{h \geq 2} m_{ih} - \lambda_1 & i = j \geq 2 \\ (1 - \varepsilon_{j1})\hat{m}_{j1} & i = 1, j \geq 2 \\ (1 - \varepsilon_{ji})m_{ji} & i \geq 2, j \geq 1, i \neq j \end{cases}.$$

By direct calculation, we find that for every $2 \leq k \leq N$,

$$\frac{\partial |D - \lambda_1 I_N|}{\partial \hat{m}_{k1}} \Big|_{(\hat{m}_{21}, \dots, \hat{m}_{N1}) = (m_{21}, \dots, m_{N1})} = 0$$

is equivalent to $|D_1| = 0$, where matrix D_1 is given by

$$(D_1)_{ij} = \begin{cases} b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{h=1}^N m_{ih} & i = j \geq 1, i \neq k \\ (1 - \varepsilon_{k1}) & i = 1, j = k \\ -1 & i = j = k \\ 0 & i \geq 2, i \neq k, j = k \\ (1 - \varepsilon_{ji})m_{ji} & i \geq 1, j \geq 1, i \neq j, j \neq k. \end{cases}$$

Since E^* is an equilibrium point, by equation (9b),

$$b_i a_i R_i^* - d_i - f_i M_i^* - \sum_{h \geq 1} m_{ih} = - \sum_{h \geq 1} (1 - \varepsilon_{hi}) m_{hi} \frac{P_h^*}{P_i^*}$$

for every $1 \leq i \leq N$. It follows that $|D_1| = 0$ is equivalent to $|D_2| = 0$, where matrix D_2 is given by

$$(D_2)_{ij} = \begin{cases} - \sum_{h=1}^N m_{hj} (1 - \varepsilon_{hj}) \frac{P_h^*}{P_j^*} & i = j \geq 1, i \neq k \\ (1 - \varepsilon_{k1}) & i = 1, j = k \\ -1 & i = j = k \\ 0 & i \geq 2, i \neq k, j = k \\ (1 - \varepsilon_{ji}) m_{ji} & i \geq 1, j \geq 1, i \neq j, j \neq k \end{cases} .$$

Multiplying the j th column of D_2 by P_j^* for every $j \neq k$, $|D_2| = 0$ is equivalent to $|D_3| = 0$, where matrix D_3 is given by

$$(D_3)_{ij} = \begin{cases} - \sum_{h=1}^N (1 - \varepsilon_{hj}) m_{hj} P_h^* & i = j \geq 1, i \neq k \\ (1 - \varepsilon_{k1}) & i = 1, j = k \\ -1 & i = j = k \\ 0 & i \geq 2, i \neq k, j = k \\ (1 - \varepsilon_{ji}) m_{ji} P_j^* & i \geq 1, j \geq 1, i \neq j, j \neq k \end{cases} .$$

Multiplying the i th row of D_3 by $(1 - \varepsilon_{i1})$ for each $2 \leq i \leq N$ and adding the results to the first row, $|D_3| = 0$ is equivalent to $|D_4| = 0$, where matrix D_4 is given by

$$(D_4)_{ij} = \begin{cases} A_j & i = 1, j \geq 1, j \neq k \\ - \sum_{h=1}^N (1 - \varepsilon_{hj}) m_{hj} P_h^* & i = j \geq 2, i \neq k \\ 0 & i = 1, j = k \\ -1 & i = j = k \\ 0 & i \geq 2, i \neq k, j = k \\ (1 - \varepsilon_{ji}) m_{ji} P_j^* & i \geq 1, j \geq 1, i \neq j, j \neq k \end{cases} ,$$

where A_1 is defined as

$$A_1 = \sum_{j=1}^N (1 - \varepsilon_{1j})(1 - \varepsilon_{j1}) m_{1j} P_1^* - \sum_{j=1}^N (1 - \varepsilon_{j1}) m_{j1} P_j^* ,$$

and for $i \geq 2$, A_i is defined by

$$A_i = (1 - \varepsilon_{i1}) [m_{i1} P_1^* - (1 - \varepsilon_{1i}) m_{1i} P_1^*] + \sum_{h=2}^N [(1 - \varepsilon_{ih})(1 - \varepsilon_{h1}) m_{ih} P_i^* - (1 - \varepsilon_{hi})(1 - \varepsilon_{i1}) m_{hi} P_h^*] .$$

It is easy to check that $\sum_{i=1}^N A_i = 0$ (note that $m_{11} = 0$). Since all of the entries in the k th column of D_4 are 0 except $(D_4)_{kk}$, we see that $|D_4| = 0$ is equivalent to $|D_5| = 0$, where the $(N-1) \times (N-1)$ matrix D_5 is given

by

$$(D_5)_{ij} = \begin{cases} A_j & i = 1, 1 \leq j < k \\ A_{j+1} & i = 1, k \leq j \leq N-1 \\ -\sum_{h=1}^{N-1} (1 - \varepsilon_{hj}) m_{hj} P_h^* & 2 \leq i = j < k \\ -\sum_{h=1}^{N-1} (1 - \varepsilon_{h,j+1}) m_{h,j+1} P_h^* & k \leq i = j \leq N-1 \\ (1 - \varepsilon_{j,i}) m_{j,i} P_j^* & 2 \leq i < k, 1 \leq j < k, i \neq j \\ (1 - \varepsilon_{j,i+1}) m_{j,i+1} P_j^* & k \leq i \leq N-1, 1 \leq j < k \\ (1 - \varepsilon_{j+1,i}) m_{j+1,i} P_{j+1}^* & 2 \leq i < k, k \leq j \leq N-1 \\ (1 - \varepsilon_{j+1,i+1}) m_{j+1,i+1} P_{j+1}^* & k \leq i \leq N-1, k \leq j \leq N-1, i \neq j \end{cases}.$$

Since $\sum_{i=1}^N A_i = 0$, adding the j th column to the first column for every j with $j \geq 2$, we see that $|D_5| = 0$ is equivalent to $|D_6| = 0$, where the $(N-1) \times (N-1)$ matrix D_6 is given by

$$(D_6)_{ij} = \begin{cases} -A_k & i = j = 1 \\ A_j & i = 1, 2 \leq j < k \\ A_{j+1} & i = 1, k \leq j \leq N-1 \\ -\sum_{h=1}^{N-1} (1 - \varepsilon_{hj}) m_{hj} P_h^* & 2 \leq i = j < k \\ -\sum_{h=1}^{N-1} (1 - \varepsilon_{h,j+1}) m_{h,j+1} P_h^* & k \leq i = j \leq N-1 \\ -(1 - \varepsilon_{ki}) m_{ki} P_k^* & 2 \leq i < k, j = 1 \\ -(1 - \varepsilon_{k,i+1}) m_{k,i+1} P_k^* & k \leq i \leq N-1, j = 1 \\ (1 - \varepsilon_{ji}) m_{ji} P_j^* & 2 \leq i < k, 2 \leq j < k, i \neq j \\ (1 - \varepsilon_{j,i+1}) m_{j,i+1} P_j^* & k \leq i \leq N-1, 2 \leq j < k \\ (1 - \varepsilon_{j+1,i}) m_{j+1,i} P_{j+1}^* & 2 \leq i < k, k \leq j \leq N-1 \\ (1 - \varepsilon_{j+1,i+1}) m_{j+1,i+1} P_{j+1}^* & k \leq i \leq N-1, k \leq j \leq N-1, i \neq j \end{cases}.$$

Multiply the first column of D_6 by -1 and move it to become the $(k-1)$ th column, and then move the first row to become the $(k-1)$ th row. We obtain a new matrix, denoted by D_7 . We see that $|D_6| = 0$ is equivalent to $|D_7| = 0$. To characterize D_7 , define the $(N-1) \times (N-1)$ matrix D_8 as

$$(D_8)_{ij} = \begin{cases} -\sum_{h=1}^{N-1} (1 - \varepsilon_{h,j+1}) m_{h,j+1} P_h^* & 1 \leq i = j \leq N-1 \\ (1 - \varepsilon_{j+1,i+1}) m_{j+1,i+1} P_{j+1}^* & 1 \leq i, j \leq N-1, i \neq j \end{cases}$$

and let V_i denote the $(i-1)$ th row of the matrix D_8 for every $2 \leq i \leq N$. By the definition of D_8 , we see that the $(N-1) \times (N-1)$ matrix D_7 can be obtained by replacing the $(k-1)$ th row of D_8 by the $1 \times (N-1)$ vector

$$V_0 = (A_2, \dots, A_N).$$

Since $|D_7| = 0$, $V_2, \dots, V_{k-1}, V_0, V_{k+1}, \dots, V_N$ are linearly dependent for any $2 \leq k \leq N$. By lemma 1, we see that

V_2, \dots, V_N are linearly independent and thus form a basis of \mathbb{R}^{N-1} . By lemma 2, we see that V_0 is the zero vector in \mathbb{R}^{N-1} . Hence, $A_i = 0$ for every $i \geq 2$ and $A_1 = 0$. As $A_i = 0$ directly yields equation (A13), this completes the proof of part (b), theorem 2. \square

As a direct consequence of equation (A13), we have

LEMMA 5. For the movement strategy given by equation (A13), the expected fitness of the resident species at equilibrium (with invader absent) is given by

$$b_i a_i R_i^* - d_i - f_i M_i^* = \begin{cases} \sum_{j=2}^N [1 - (1 - \varepsilon_{ij})(1 - \varepsilon_{j1})] m_{1j} & i = 1 \\ \sum_{j=2}^N \left[1 - \frac{(1 - \varepsilon_{ij})(1 - \varepsilon_{j1})}{(1 - \varepsilon_{i1})} \right] m_{ij} & i \geq 2 \end{cases}. \quad (\text{A16})$$

PROOF OF THEOREM 2(b). By lemma 5, we see that if $(m_{21}, \dots, m_{N1}) = (m_{21, \text{opt}}, \dots, m_{N1, \text{opt}})$, then

$$D_{ij} = \begin{cases} - \sum_{h=2}^N (1 - \varepsilon_{1h})(1 - \varepsilon_{h1}) m_{1h} & i = j = 1 \\ - \hat{m}_{1h} - \frac{1}{(1 - \varepsilon_{i1})} \sum_{h=2}^N (1 - \varepsilon_{ih})(1 - \varepsilon_{h1}) m_{1h} & i = j \geq 2 \\ (1 - \varepsilon_{j1}) \hat{m}_{j1} & i = 1, j \geq 2 \\ (1 - \varepsilon_{ji}) m_{ji} & i \geq 2, j \geq 1, i \neq j. \end{cases}$$

Set $V_* = (1, 1 - \varepsilon_{21}, \dots, 1 - \varepsilon_{N1})$. Then, $V_* D = (0, \dots, 0)$. That is, the vector V_* is the left eigenvector of D corresponding to the eigenvalue 0. Since all components of V_* are positive, 0 must be the dominant eigenvalue of matrix D , and all other eigenvalues must have strictly negative real parts. \square

Literature Cited Only in Appendix A

Horn, R. A., and C. R. Johnson. 1999. Matrix analysis. Cambridge University Press, Cambridge.

Appendix B from D. L. DeAngelis et al., “The Effect of Travel Loss on Evolutionarily Stable Distributions of Populations in Space”

(Am. Nat., vol. 178, no. 1, p. 15)

Interpretation of the Rates Given by Equation (17a) for the Three-Patch Tritrophic Case in Scenario 1

We describe a typical example in the three-patch case below. All parameters were fixed using the values given in table B1 except the rates m_{21} , m_{31} , \hat{m}_{21} , and \hat{m}_{31} .

The rates given by formula (17a) were calculated (to machine accuracy) using Matlab: $m_{21,\text{opt}} = 0.092409525773196$ and $m_{31,\text{opt}} = 0.335468571428571$. When the resident uses these rates, based on lemma 5, its fitness at the boundary equilibrium with the invader absent (shown here rounded to 3 decimal places, but calculated to 15 decimal places),

$$(\hat{P}^*, P^*, R^*, M^*) = (0, 0, 0, 30, 22.727, 31.818, 32.941, 43.402, 19.727, 22.476, 26.115, 49.65),$$

on patch 1 is 0.02, on patch 2 is -0.002 , and on patch 3 is 0. It is interesting to note that as predicted by lemma 5, this is an example where the fitness on patch 2 is negative.

Recall that in the two-patch case, an optimal movement rate exists given by formula (14), and when the resident chooses this rate, no other genotype using a different rate can successfully invade. This is proved analytically in Y. Lou and C.-H. Wu (unpublished manuscript) and is illustrated in figure 4. In reality, it is impossible for a resident to choose the precise optimal movement rate, so the outcome of competition (exclusion of one genotype or the other, or coexistence) will in fact always be determined by the relative values of the movement rates as illustrated in figure 4A, 4C. If the resident and the invader choose rates on opposite sides of the optimal rate, there is coexistence. Therefore, which rate is closer to the optimal rate matters only when either the resident and the invader both choose rates that are smaller or both choose rates that are larger than the optimal rate. Then, it is the population that chooses the rate closer to the optimal rates that wins, driving the other population to extinction.

This inability to select rates exactly equal to the optimal rates also occurs on a computer, due to round-off errors. This complicates numerical calculations in the immediate vicinity of the optimal rates. In particular, we do not know whether the rates we enter and think are the precise rates given by the formula are actually both slightly larger or both slightly smaller or whether one is larger and one is smaller than the precise rates. To complicate matters further, the invasion matrix has a zero eigenvalue if the precise rates are entered, making convergence very slow.

To test the predictions of our rates, we carried out a number of experiments using the AUTO interface in the software package XPPAUT (see Ermentrout 2002) to continue equilibrium solutions numerically and detect bifurcations, that is, detect changes in the stability and/or number of equilibrium solutions as the value of a parameter, called the bifurcation parameter, is varied.

Experiment I. We chose the residents’ movement rates m_{21} and m_{31} , close to the optimal rates $m_{21,\text{opt}}$ and $m_{31,\text{opt}}$, respectively, but both larger than the optimal rates; and we chose the invaders’ movement rates \hat{m}_{21} and \hat{m}_{31} , both even larger than the residents’ movement rates. As expected, the resident outcompeted the invader, driving it to extinction. Then, using one of the invaders’ movement rates, \hat{m}_{21} , as the bifurcation parameter, we allowed it to decrease. The resident continued to outcompete the invader until \hat{m}_{21} reached a critical rate, $m_1^* < m_{21,\text{opt}}$, at which there was a transcritical bifurcation resulting in the stable coexistence of both the resident and the invader for values of $\hat{m}_{21} < m_1^*$.

Experiment II. We chose the residents’ movement rates m_{21} and m_{31} , close to the optimal rates $m_{21,\text{opt}}$ and $m_{31,\text{opt}}$, respectively, but both smaller than the optimal rates; and we chose the invaders’ movement rates \hat{m}_{21} and \hat{m}_{31} , both even smaller than the residents’ movement rates. Again, as expected, the resident outcompeted the

invader, driving it to extinction. Then, using one of the invaders' movement rates, \hat{m}_{21} , as the bifurcation parameter, we allowed it to increase. The resident continued to outcompete the invader until \hat{m}_{21} reached a critical rate, $m_2^* > m_{21,opt}$, at which there was a transcritical bifurcation resulting in the stable coexistence of both the resident and the invader for values of $\hat{m}_{21} > m_2^*$.

Experiment III. We chose the residents' movements rates $\hat{m}_{21} > m_{21} > m_{21,opt}$ and $\hat{m}_{31} < m_{31} < m_{31,opt}$. Once more, as expected, the resident outcompeted the invader, driving it to extinction. Then, using the invaders' movement rates \hat{m}_{31} as the bifurcation parameter, we allowed it to increase. The resident continued to outcompete the invader until \hat{m}_{31} reached a critical rate, $m_3^* > m_{31,opt}$, at which there was transcritical bifurcation resulting in the stable coexistence of both the resident and the invader for values of $\hat{m}_{31} > m_3^*$.

Experiment IV. We chose rates $m_{31} = \hat{m}_{31} = m_{31,opt}$ and $m_{21} < m_{21,opt}$ and allowed \hat{m}_{21} to vary. As expected, the outcome was similar to that described by figure 4A in the two-patch case, with the transcritical bifurcation resulting in coexistence occurring at the optimal rate $m_{21,opt}$.

Experiment V. We chose rates $m_{31} = \hat{m}_{31} = m_{31,opt}$ and $m_{21} > m_{21,opt}$ and allowed \hat{m}_{21} to vary. As expected, the outcome was similar to that described by figure 4C in the two-patch case, with the transcritical bifurcation resulting in coexistence occurring at the optimal rate $m_{21,opt}$.

Experiment VI. We entered the rates calculated using Matlab for both of the residents' rates, and we chose two nonoptimal rates for the invaders. Convergence was too slow for us to be able to distinguish whether the invader would die out completely or coexist with the resident. Starting AUTO from the boundary equilibrium with only the resident present, AUTO did not detect a bifurcation to a coexistence equilibrium, but because of the zero eigenvalue of the invasion matrix, AUTO had difficulty determining the stability of the boundary equilibrium. It is therefore difficult to say with any certainty that no such bifurcation occurs.

Table B1. Parameter values used to illustrate the three-patch model

$a_1 = .01$	$b_1 = .5$	$c_1 = .5$	$d_1 = .01$	$r_1 = 1.7$	$K_1 = 40$	$d_{m1} = .09$
$a_2 = .009$	$b_2 = .55$	$c_2 = .55$	$d_2 = .008$	$r_2 = 1.55$	$K_2 = 50$	$d_{m2} = .1$
$a_3 = .03$	$b_3 = .48$	$c_3 = .6$	$d_3 = .011$	$r_3 = 1.8$	$K_3 = 42$	$d_{m3} = .105$
$\epsilon_{12} = .03$	$\epsilon_{21} = .03$	$\epsilon_{13} = .02$	$\epsilon_{31} = .01$	$\epsilon_{23} = .01$	$f_1 = .006$	
$m_{12} = .23$	$m_{13} = .21$	$m_{23} = .2$	$m_{32} = .0$		$f_2 = .008$	
$\hat{m}_{12} = .23$	$\hat{m}_{13} = .21$	$\hat{m}_{23} = .2$	$\hat{m}_{32} = 0$		$f_3 = .0055$	