

The Effect of Travel Loss on Evolutionarily Stable Distributions of Populations in Space

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ABSTRACT: A key assumption of the ideal free distribution (IFD) is that there are no costs in moving between habitat patches. However, because many populations exhibit more or less continuous population movement between patches and traveling cost is a frequent factor, it is important to determine the effects of costs on expected population movement patterns and spatial distributions. We consider a food chain (tritrophic or bitrophic) in which one species moves between patches, with energy cost or mortality risk in movement. In the two-patch case, assuming forced movement in one direction, an evolutionarily stable strategy requires bidirectional movement, even if costs during movement are high. In the N -patch case, assuming that at least one patch is linked bidirectionally to all other patches, optimal movement rates can lead to source-sink dynamics where patches with negative growth rates are maintained by other patches with positive growth rates. As well, dispersal between patches is not balanced (even in the two-patch case), leading to a deviation from the IFD. Our results indicate that cost-associated forced movement can have important consequences for spatial metapopulation dynamics. Relevance to marine reserve design and the study of stream communities subject to drift is discussed.

Keywords: ideal free distribution, evolutionarily stable strategy, foraging strategy with movement costs, food chain, metapopulation, stream drift.

Introduction

Populations are distributed in space, often in patches of habitat scattered over a landscape or region. The distribution of animals is a consequence of the pattern of movement between these patches. There are alternative possible assumptions regarding this movement. One assumption is that animals simply move randomly between patches. Another is that the movement is driven by the imperative of maximizing fitness, so that animals move freely until they cannot do any better in terms of fitness; that is, movement to another patch would not increase or lower fitness. McPeck and Holt (1992) showed that when individuals dispersing among habitat patches differing in carrying capacity were allowed to evolve dispersal rates, the resulting genotype that could exclude all others had a rate that varied inversely with the carrying capacity of the habitat. This produced a steady state spatial distribution with equal numbers of individuals moving in each direction between patches, or “balanced dispersal.” As noted by Diffendorfer (1999), this can be viewed as an extension of the ideal free distribution (IFD) at equilibrium (animals distribute themselves in various patches proportionately to the amount of resources available in each patch; Fretwell and Lucas 1969). The IFD evens out the fitnesses of individuals of the given population across the landscape, because patches that are poorer in quality, due to lower resources or higher predator concentrations, will have lower densities of individuals. The IFD has seen success in describing habitat selection (Lin and Batzli 2001; Puseenius and Schmidt 2002) and the distributions of foraging animals in the field (e.g., Harper 1982; Oksanen et al. 1995; Jones et al. 2006) and in laboratory experiments (e.g., Milinski 1979; Regelman 1984; Korona 1990). The IFD corresponds to an evolutionarily stable strategy (ESS; a strategy that if adopted by a population prevents invasion by another population that is initially rare and uses a different strategy; e.g., Cressman et al. 2004; Cantrell et al. 2007;

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Křivan et al. 2008), for which at steady state no individual can improve fitness by moving to another patch. The prediction of these sorts of models, at least where there is no cost of movement, is that there is no net movement among patches. Inevitably, animals will move among patches for various reasons, but on each patch immigration will be balanced by emigration.

Mathematically, the dynamics of such a population on the landscape can be described by the general set of equations for N patches:

$$\begin{aligned} \frac{dP_i}{dt} = & F_i(P_i, \bar{X})P_i \\ & + \sum_{\substack{j=1 \\ j \neq i}}^N (m_{ji}P_j - m_{ij}P_i), \quad (i = 1, \dots, N), \end{aligned} \quad (1)$$

where P_i is the population size of the focal species on patch i , \bar{X} is a vector representing the set of other species populations X_i on patch i , $m_{ij}P_i$ is the total movement from patch i to patch j per unit time, and $F_i(P_i, \bar{X})$ represents the species interactions taking place on patch i . Additional equations are used to describe the dynamics of each of the other species, X_i , on each patch. These may be of similar or alternative form to equation (1), although in this article we assume species other than the focal species do not move between patches. In equation (1), the rates of movement that produce an IFD are not initially known but are determined as follows. For an IFD, the movements in and out of a patch are equal for each patch. The system of equations thereby becomes much easier to solve because

$$\sum_{\substack{j=1 \\ j \neq i}}^N (m_{ji}P_j - m_{ij}P_i) = 0, \quad (i = 1, \dots, N), \quad (2a)$$

so that at the steady state,

$$F_i(P_i, \bar{X}) = 0, \quad (i = 1, \dots, N). \quad (2b)$$

Thus, each of the N equations (2b), together with equations for all of the other species populations on each patch, can be solved for the equilibrium P_i s as well as the equilibria of the vector of other (nonmoving) species, \bar{X} , on each patch. Equations (2a) are then used to solve for the ratios of the movement coefficients, m_{ij} , that produce an IFD.

The concept of the IFD as explicated above involves the assumption that individuals move freely and without costs between patches of habitat and distribute themselves such that no individual would gain or lose fitness by exchanging its place with an individual on another patch. This assumption simplifies the analysis but is usually not warranted. While movement among patches is a ubiquitous

trait of animals, there is usually a cost or loss to the population associated with movement. Movement typically entails a loss of energy, it often increases the risk of predation or mortality due to exposure to the elements, and individuals that move may also suffer the price of not finding another suitable habitat patch (e.g., Yoder et al. 2004; Gibbs et al. 2010). A basic question is then how such loss affects the strategy of movements if the individuals are behaving according to an ESS.

The cost of movement as a factor in the IFD was introduced by Rosenzweig (1974) and Charnov (1976) and was considered subsequently by a number of mathematical ecologists (Morris 1987; Kennedy and Gray 1993, 1997; Åström 1994; Tregenza 1995; Matsumura et al. 2010). Morris (1987) presented a concise approach for including costs. Defining the fitness of populations on two patches i and j as W_i and W_j , Morris (1987) followed Fretwell and Lucas (1969) in first considering the fitness on a patch to decline linearly with increasing population density at rate b . Thus, with no cost to movement,

$$W_i = B_i - bN_i, \quad (3a)$$

$$W_j = B_j - bN_j, \quad (3b)$$

where N_i and N_j denote the population sizes on the patches and B_i and B_j are constants representing the fitness levels on each patch when densities are 0. If individuals are free to move between patches, then population size on each patch should be such that the fitness of individuals on each patch is the same as on any other patch,

$$B_i - bN_i = B_j - bN_j, \quad (4a)$$

which can be rewritten as

$$N_i = N_j + \left(\frac{1}{b}\right)(B_i - B_j). \quad (4b)$$

If, however, the cost of moving from patch i to patch j is not 0 but is $C_{ij} > 0$, then individuals should move from patch i to patch j until

$$W_i = W_j - C_{ij}. \quad (5)$$

Equation (4b) thereby becomes

$$N_i = N_j + \left(\frac{1}{b}\right)(B_i - B_j + C_{ij}). \quad (6)$$

Morris (2004) considered movement in only one direction. Extending the analysis to the case in which movement occurs in both directions and is associated with a concomitant increase in the habitat quality of the patch being left by S_{ij} number of individuals, Åström (1994) showed that

$$N_i = \frac{b_j N_j + B_i - B_j + C_{ij} - C_{ji}}{b_i} + S_{ij} - \frac{b_i S_{ji}}{b_i}. \quad (7)$$

Åström (1994) noted that equation (7) violates some assumptions of the IFD, as it implies that individuals will move even when not moving achieves a higher fitness.

A basic deduction of these analyses is that there is no further reason for individuals to move once the condition of fitness equality is achieved, with or without costs of movement. As Morris (1987, p. 380) noted, “Dispersing individuals should stop traveling and settle in a habitat whenever their fitness by doing so (minus emigration cost) is greater than what they could have attained by not dispersing in the first place.” Thus, deterministically at least, all movement should come to a stop. Stochastic movements and movements of individuals without perfect information could continue, of course. We will not consider these. However, continual movement of individuals between patches can be obligatory when the movement is determined by environment (as in stream drift) or when the long-term survival of populations has favored dispersal evolutionarily by, for example, mitigating inbreeding or enhancing postdisturbance recolonization (e.g., Gaines and McClenaghan 1980; Hanski 1999, p. 2), reducing local competition, and adapting numerous invertebrate, vertebrate, and plant species to both ephemeral environments (e.g., Roff 1974; Pusey and Wolf 1996; Ronce 2007) and other terrestrial and aquatic environments (Bullock et al. 2002). Indeed, as Morris (1991) states, dispersal is a natural consequence of natural selection. In nature, continual dispersal between patches is thus expected, even when populations have reached equilibrium size (Bohanak and Jenkins 2003).

Here, we address the question of the distribution of a population of foragers on a landscape to study the effects of movement-associated costs when dispersal is obligatory. Unlike Åström (1994), we do not assume a priori that movement between patches is reciprocal but only constrain it to occur in at least one direction. Assuming omniscient foraging individuals, we determine the movement rates in the opposite direction that give an ESS in the two-patch tritrophic case (Y. Lou and C.-H. Wu, unpublished manuscript) and that we suspect with support from numerical investigation give an ESS in the two-patch bi-trophic case and in our generalization to N patches. We compare the resulting spatial pattern with that of balanced dispersal, or IFD, when there is no travel cost.

We examine first a bitrophic chain in which the consumer is the only mobile species, and then a tritrophic food chain consisting of a focal consumer population, P , that feeds on resources, R , and is preyed on by a top predator, M , resident in a landscape of N patches (see fig. 1). Thus, the different effects of the resources and pred-

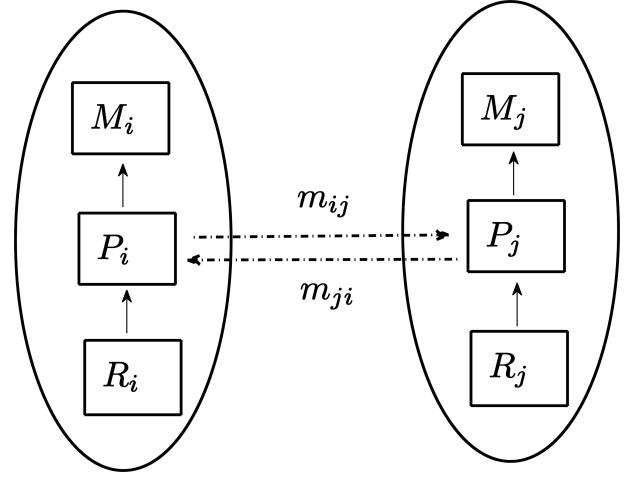


Figure 1: Schematic of the within-patch interactions for two representative patches i and j and the between-patch movement; P_i and P_j are consumers, R_i and R_j are resources, and M_i and M_j are predators. Here, we assume that only the consumers can move between patches, with rate m_{ij} from patch i to patch j and with rate m_{ji} from patch j to patch i .

ators on movement strategies can be determined. In a manner similar to previous studies (e.g., Morris 2004; Morris and Mukherjee 2006), we assume that only the consumers, P , can move between patches. Parameter values describing the nature of interspecific interactions among all species are patch specific such that each species' population size may differ between patches. One special motivating case occurs in streams when there is forced unidirectional movement (drift) of aquatic invertebrates inhabiting a section of stream in which a series of potentially different but hospitably deep pools (patches) are connected by sections of inhospitably shallow riffle habitat (Malmqvist 2002). For many stream invertebrates, downstream movement is an inevitable consequence of flow-induced drift that is associated with many of the costs mentioned above. Potentially compensatory upstream or bidirectional movement occurs via active larval crawling and adult flight (Malmqvist 2002). Drift-resistant fishes are typically the dominant predators of invertebrates in pools (Wooster 1994), where the often pool-specific production of less motile algae and detritus serves as a resource, particularly for invertebrates with burrowing life styles (Malmqvist 2002).

Model

We examine a system of an arbitrary number N of patches distributed in space. On each patch i we consider a food chain consisting of resources, denoted by R_i , a consumer,

denoted by P_i , and a predator on the consumer, denoted by M_i , in which the predator feeds only on the consumer and the resources are exploited only by the consumer. We allow the patches to be different; that is, values for the parameters on each patch that describe the resource quality and the interactions between the populations can be different. We assume that only the consumer populations P_i travel between the patches with movement rates m_{ij} denoting the rate from patch i to patch j (see fig. 1).

We are interested in the case of fractional loss, $\varepsilon_{ij} \in (0, 1)$, of individuals during movement from patch i to patch j . The parameter ε_{ij} is closely related to C_{ij} of the other authors, which is the decrease in fitness in moving from patch i to patch j . Because of that loss, as in Morris (1987), after the fitness values between the patches balance, it would be optimal for individual consumers not to travel between the patches. However, we assume that there are factors that create a need to disperse from patches. Following an approach recently used by DeAngelis et al. (2007) to study the effects of population transitions between alternative physiological states, the set of equations we use is as follows, where for $i = 1, \dots, N$,

$$\frac{dP_i}{dt} = P_i(b_i a_i R_i - d_i - f_i M_i) - \left(\sum_{j=1}^N m_{ij} \right) P_i + \left[\sum_{j=1}^N (1 - \varepsilon_{ji}) m_{ji} P_j \right], \quad (8a)$$

$$\frac{dR_i}{dt} = R_i \left[r_i \left(1 - \frac{R_i}{K_i} \right) - a_i P_i \right], \quad (8b)$$

$$\frac{dM_i}{dt} = M_i(c_i f_i P_i - d_{mi}), \quad (8c)$$

and r_i denotes the growth rate of the resource on patch i , K_i its carrying capacity, a_i the feeding rate of consumers on resources, f_i the feeding rate of predators on consumers, d_i the mortality rate of the consumer, d_{mi} the mortality rate of the predator, b_i and c_i the biomass conversion factors of the consumer and predator, respectively, and m_{ij} the rate of movement by the consumer from patch i to patch j . For simplicity, we assume logistic growth of the resource and linear (Lotka-Volterra) functional responses between the consumer and both its resource and its predator. Our analysis could be generalized to other functional forms. We will use the term “fitness” hereafter to define the per capita net growth rate; that is, the terms in the square brackets multiplying P_i in equation (8a).

We wish to address whether a small number of members of another population of consumers can invade a temporally nonvarying habitat made up of patches that can be modeled by system (8). To do this we extend model

(8) by introducing a second consumer population \hat{P}_i that also travels between the patches. We think of the original population of consumers, P_i , as a “resident” consumer genotype and \hat{P}_i as a potential “invading” mutant consumer, with all parameters on each patch identical to the resident consumer, except possibly some of its travel rates to or from patch 1. In particular, we assume that cost of travel between the patches is the same for the invader and the resident.

We therefore respecify the set of equations for all species to include the invader, \hat{P}_i , for $i = 1, \dots, N$, as

$$\frac{d\hat{P}_i}{dt} = \hat{P}_i(b_i a_i R_i - d_i - f_i M_i) - \left(\sum_{j=1}^N \hat{m}_{ij} \right) \hat{P}_i + \left[\sum_{j=1}^N (1 - \varepsilon_{ji}) \hat{m}_{ji} \hat{P}_j \right], \quad (9a)$$

$$\frac{dP_i}{dt} = P_i(b_i a_i R_i - d_i - f_i M_i) - \left(\sum_{j=1}^N m_{ij} \right) P_i + \left[\sum_{j=1}^N (1 - \varepsilon_{ji}) m_{ji} P_j \right], \quad (9b)$$

$$\frac{dR_i}{dt} = R_i \left[r_i \left(1 - \frac{R_i}{K_i} \right) - a_i P_i - a_i \hat{P}_i \right], \quad (9c)$$

$$\frac{dM_i}{dt} = M_i(c_i f_i P_i + c_i f_i \hat{P}_i - d_{mi}). \quad (9d)$$

Observations from many empirical studies of stream invertebrate dispersal (e.g., Elliot 2003) motivated us to consider two basic scenarios. In the first scenario of forced emigration from patch 1, we assume fixed positive density-independent rates of dispersal m_{1j} , $j = 2, \dots, N$, of consumers from patch 1 to all of the other patches and fixed nonnegative rates m_{ij} , $i, j = 2, \dots, N$, between all of the other patches. Then we attempt to determine the optimal rates $m_{i1, \text{opt}}$ at which the resident consumers should disperse from all the other patches back to patch 1. By the “optimal rates” or “optimal strategy” we mean the rates $m_{i1} = m_{i1, \text{opt}}$ that the resident should use so that no other genotype would be able to invade if they were identical to the resident except for these rates of return to patch 1. Therefore, in this first scenario (see fig. 2) the invading population can have different immigration rates to patch 1, denoted \hat{m}_{i1} , but must have the same emigration rates from patch 1, $\hat{m}_{1j} = m_{1j}$.

In the second scenario of forced immigration to patch 1, we assume instead that all the density-independent rates of dispersal of consumers, m_{i1} , from all the patches to patch 1 are fixed and then attempt to determine the optimal

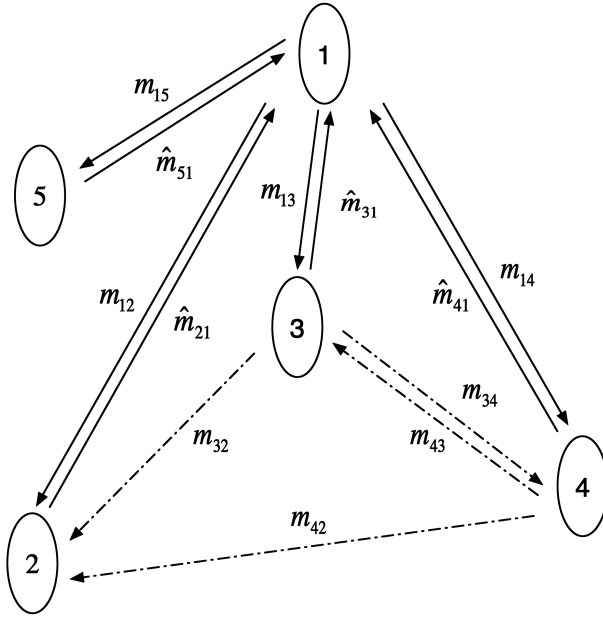


Figure 2: Schematic of a possible landscape of a habitat with five patches in scenario 1 (forced emigration from patch 1). All patches are downstream from patch 1. There are fixed positive emigration rates from patch 1. The only differences between the resident and the mutant are the immigration rates to patch 1; that is, m_{i1} need not be equal to \hat{m}_{i1} , $i = 2, 3, 4, 5$. The solid lines indicate the bidirectional movement rates between patch 1 and the other patches assumed to always be positive. The dash-dotted lines indicate positive movement rates between the other patches. Movement rates between patches other than patch 1 need not be positive. Notice, for example, that patch 5 is connected only to patch 1 and that there are only unidirectional links between patches 2 and 3 and patches 2 and 4. However, it is still possible to get from any patch to any other, although it might involve an indirect path. We try to find the optimal choices for the resident P 's rates m_{ij} , $i = 2, 3, 4, 5$, given that the mutant consumer \hat{P} 's movement rates can differ from the resident consumer's rates by only its values for \hat{m}_{i1} , $i = 2, 3, 4, 5$.

rates, $m_{1j, \text{opt}}$, at which consumers should disperse from patch 1 to all of the other patches. In this case the invading population can have different emigration rates from patch 1, denoted \hat{m}_{1j} , but must have the same immigration rates to patch 1, that is, $\hat{m}_{i1} = m_{i1}$.

Scenario 1 is likely most relevant when patch 1 is upstream from all the other patches and scenario 2 when patch 1 is downstream. These scenarios may seem similar, so one might expect that the analysis in the first scenario would be the same as that for the second scenario. However, there are asymmetries that cause these cases to be different, as demonstrated by the computations in appendix A in the online edition of the *American Naturalist*. In each of the scenarios, our objective is to determine the relationship between the immigration rates and emigration

rates between patch 1 and the other patches that gives the optimal strategy for the resident population.

More formally, we make the following assumptions:

(H_0): $m_{ii} = \hat{m}_{ii} = 0$ for all i ;

(H_1): m_{1i} , m_{i1} , \hat{m}_{1i} , and \hat{m}_{i1} are all positive for all $i \geq 2$, and $m_{ij} \geq 0$, $i \geq 2$, $j \geq 2$, $i \neq j$; and

(H_2) (scenario 1: forced emigration): $\hat{m}_{ij} = m_{ij}$, $i \geq 1$, $j \geq 2$ (see fig. 2); or

(H_2) (scenario 2: forced immigration): $\hat{m}_{ij} = m_{ij}$, $i \geq 2$, $j \geq 1$.

Note that in both cases we assume only indirect interactions between the resident and the invading consumers, as mediated by the abundance of their shared resources and their top predators.

Results

The Two-Patch Case

Before we present the general results for the relationship between m_{1k} and m_{k1} for the two scenarios for N patches, we show the results for the two-patch case. We consider both the bitrophic food chain, in which the consumer is at the top level ($M_i = 0$ for all i), and the tritrophic chain, in which the consumer is predated on as well ($M_i > 0$). For scenario 1, we give the explanation of how to obtain the optimal strategy in each case. The explanation for scenario 2 is similar and hence omitted. We focus on the coexistence equilibrium of equations (9), which we denote $E^* = (\hat{P}^*, P^*, R^*, M^*)$, where we assume that all of the components of $\hat{P}^* = (\hat{P}_1^*, \hat{P}_2^*)$, $P^* = (P_1^*, P_2^*)$, and $R^* = (R_1^*, R_2^*)$ are positive and that the components of $M^* = (M_1^*, M_2^*)$ are all 0 in the bitrophic case and positive in the tritrophic case. In each case, we can prove that there is only one equilibrium of this form, and we can find explicit expressions for the components by setting the right-hand side of (9) equal to 0 and solving.

In the bitrophic case, where all of the components of M^* are set to 0, the components of this equilibrium in scenario 1 are given by

$$R_2^* = \frac{d_2}{b_2 a_2}, \quad (10a)$$

$$R_1^* = \frac{1}{b_1 a_1} [d_1 + m_{12} - m_{12}(1 - \varepsilon_{12})(1 - \varepsilon_{21})], \quad (10b)$$

$$\hat{P}_2^* = \frac{1}{(\hat{m}_{21} - m_{21})} \left[\frac{(1 - \varepsilon_{12})m_{12}r_1}{a_1} \left(1 - \frac{R_1^*}{K_1} \right) - \frac{m_{21}r_2}{a_2} \left(1 - \frac{R_2^*}{K_2} \right) \right], \quad (10c)$$

$$P_2^* = \frac{1}{(m_{21} - \hat{m}_{21})} \left[\frac{(1 - \varepsilon_{12})m_{12}r_1}{a_1} \left(1 - \frac{R_1^*}{K_1} \right) - \frac{\hat{m}_{21}r_2}{a_2} \left(1 - \frac{R_2^*}{K_2} \right) \right], \quad (10d)$$

$$\hat{P}_1^* = \frac{\hat{m}_{21}\hat{P}_2^*}{(1 - \varepsilon_{12})m_{12}}, \quad (10e)$$

$$P_1^* = \frac{m_{21}P_2^*}{(1 - \varepsilon_{12})m_{12}}. \quad (10f)$$

We assume that the carrying capacities of the resources, K_1 and K_2 , are sufficiently large so that $K_i > R_i^*$, $i = 1, 2$.

In the tritrophic case, where all of the components of M^* are assumed to be positive, the components of this equilibrium for scenario 1 are given by

$$\hat{P}_2^* = \frac{(1 - \varepsilon_{12})m_{12}d_{m1}c_2f_2 - d_{m2}c_1f_1m_{21}}{c_1c_2f_1f_2(\hat{m}_{21} - m_{21})}, \quad (11a)$$

$$P_2^* = \frac{(1 - \varepsilon_{12})m_{12}d_{m1}c_2f_2 - d_{m2}c_1f_1\hat{m}_{21}}{c_1c_2f_1f_2(m_{21} - \hat{m}_{21})}, \quad (11b)$$

$$\hat{P}_1^* = \frac{\hat{m}_{21}\hat{P}_2^*}{(1 - \varepsilon_{12})m_{12}}, \quad (11c)$$

$$P_1^* = \frac{m_{21}P_2^*}{(1 - \varepsilon_{12})m_{12}}, \quad (11d)$$

$$R_1^* = K_1 - \frac{a_1K_1}{r_1}(\hat{P}_1^* + P_1^*) = K_1 \left(1 - \frac{a_1d_{m1}}{r_1c_1f_1} \right), \quad (11e)$$

$$R_2^* = K_2 - \frac{a_2K_2}{r_2}(\hat{P}_2^* + P_2^*) = K_2 \left(1 - \frac{a_2d_{m2}}{r_2c_2f_2} \right), \quad (11f)$$

$$M_1^* = \frac{1}{f_1P_1^*} [b_1a_1R_1^*P_1^* - d_1P_1^* - m_{12}P_1^* + (1 - \varepsilon_{21})m_{21}P_2^*], \quad (11g)$$

$$M_2^* = \frac{1}{f_2P_2^*} [b_2a_2R_2^*P_2^* - d_2P_2^* - m_{21}P_2^* + (1 - \varepsilon_{12})m_{12}P_1^*], \quad (11h)$$

Here we assume that $a_id_{mi} < r_ic_if_i$, $i = 1, 2$, so that $R_i^* > 0$, $i = 1, 2$ and that the carrying capacities K_i , $i = 1, 2$ are sufficiently large so that $M_i^* > 0$, $i = 1, 2$.

In the bitrophic case, we find the optimal strategy by determining the value of m_{21} that results in zero values for the components of the invader population at this co-

existence equilibrium. In particular, we set $\hat{P}_2^* = 0$ in equation (10c) and solve for m_{21} . Then from equation (10e), it follows that $\hat{P}_1^* = 0$ as well. The resulting optimal strategy for the resident in the bitrophic case for scenario 1 is given by

$$m_{21, \text{opt}} = (1 - \varepsilon_{12})m_{12} \frac{a_2r_1K_2(K_1 - R_1^*)}{a_1r_2K_1(K_2 - R_2^*)}. \quad (12)$$

Using a similar analysis, the resulting strategy for the resident in the bitrophic case for scenario 2 is

$$m_{12, \text{opt}} = (1 - \varepsilon_{21})m_{21} \frac{a_1r_2K_1(K_2 - R_2^*)}{a_2r_1K_2(K_1 - R_1^*)}. \quad (13)$$

In the tritrophic case, in scenario 1 the optimal movement strategy for the resident is obtained by setting $\hat{P}_2^* = 0$ in equation (11a) and solving for m_{21} to obtain

$$m_{21, \text{opt}} = (1 - \varepsilon_{12})m_{12} \frac{d_{m1}c_2f_2}{d_{m2}c_1f_1}. \quad (14)$$

A similar analysis gives the optimal strategy in scenario 2 for the tritrophic case as

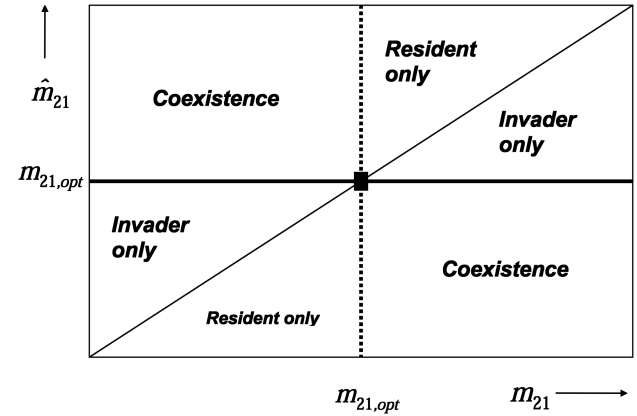


Figure 3: Diagram showing the consequences to the resident population and invader populations in scenario 1 as functions of their two respective movement strategies, m_{21} and \hat{m}_{21} , which form the X- and Y-axes of the plot. When only one population chooses the optimal or evolutionarily stable strategy, $m_{21, \text{opt}}$, then only it survives (vertical dashed line for the resident and horizontal solid line for the invader). At the intersection, where both populations choose the optimal strategy, the populations coexist. When neither population chooses the optimal strategy, then there are three basic possibilities. (1) Both strategies, m_{21} and \hat{m}_{21} , are either less than or greater than the optimal strategy, but one of the strategies is closer to the optimum than the other. Then the population with the strategy farther from the optimal strategy is excluded. (2) Both populations are either greater than or less than the optimal strategy but are identical. In this case the two populations coexist. (3) One population's strategy is greater than the optimal strategy and one population's strategy is less than the optimal strategy. Then the two populations coexist.

$$m_{12,\text{opt}} = (1 - \varepsilon_{21})m_{21} \frac{d_{m2}c_1f_1}{d_{m1}c_2f_2}. \quad (15)$$

In figure 3 we illustrate the “landscape” of results of resident and invader competition. These results were first surveyed with computer simulations of equations (9), performed using Matlab (version R2007a), in both the bi-trophic and tritrophic cases. It should be noted that these simulations are very slow to converge when the movement rate coefficients of resident and invader are close. The results illustrated in this figure were then analytically proved by Y. Lou and C.-H. Wu (unpublished manuscript) for the tritrophic case using a Lyapunov function approach. They prove that a coexistence equilibrium exists if and only if either $m_{21} < m_{21,\text{opt}} < \hat{m}_{21}$ or $\hat{m}_{21} < m_{21,\text{opt}} < m_{21}$, and whenever a coexistence equilibrium exists, it is globally asymptotically stable (i.e., it is stable and all solutions with positive initial conditions converge to this equilibrium). They also show that when no coexistence equilibrium exists; that is, if $\hat{m}_{21} < m_{21} \leq m_{21,\text{opt}}$ or $m_{21,\text{opt}} \leq m_{21} < \hat{m}_{21}$, then the boundary equilibrium with the invader absent (but the other components positive) is globally asymptotically stable. However, if $m_{21} < \hat{m}_{21} \leq m_{21,\text{opt}}$ or $m_{21,\text{opt}} \leq \hat{m}_{21} < m_{21}$, then the boundary equilibrium with the resident absent (but all other components positive) is globally asymptotically stable. In scenario 1, our model thus predicts that when the resident uses our calculated value of $m_{21,\text{opt}}$, it excludes the invader unless the invader also uses $m_{21,\text{opt}}$. Hence, $m_{21,\text{opt}}$ corresponds to an ESS. When the resident does not use $m_{21,\text{opt}}$, other outcomes can also occur depending on the relative values of m_{21} , \hat{m}_{21} , and $m_{21,\text{opt}}$.

The predictions of whether the two populations coexist or one excludes the other, based on the relative values of the movement rates, are also illustrated for scenario 1 in the tritrophic case in figure 4. When the resident uses the rate given by equation (14), the invader is always eliminated. However, if the resident does not use this rate, there is coexistence if either the resident uses a movement rate that is slower and the invader uses a rate that is faster than the optimal rate or vice versa. Since it is not likely that the resident can use the exact optimal rate if the rate the mutant uses is very close to the rate the resident uses, it is more likely that both the resident and the invader use rates that are either both faster than the rate given by equation (14) or both slower than this rate. In this case, it is the population that chooses the rate that is closer to the rate given by equation (14) that survives and excludes the other population. Thus, in the two-patch case, assuming that neither population can ever use the exact optimal rate, our model predicts that attempted invasion by a rare but very similar mutant population more likely results in total elimination of either the resident population or the

invading population, unless the mutation results in a significantly different movement rate. For example, if the resident’s actual movement rate is below the optimum (hence not at the ESS), the mutant invader’s movement rate would have to be large enough to exceed the optimal rate for coexistence to occur.

Using the parameter values in table 1, figure 4 shows how, in scenario 1, the resident and invader biomasses at equilibrium depend on \hat{m}_{21} . The residents’ biomasses (P_1 and P_2 on patches 1 and 2) are shown using thick and thin solid lines, and the invaders’ biomasses (\hat{P}_1 and \hat{P}_2) using thick and thin dashed lines, respectively. Note that either P_1 and P_2 are both 0 (and the curves overlap) or are both positive. Similarly, \hat{P}_1 and \hat{P}_2 are either both positive or both 0. All parameters for P_1 and \hat{P}_1 are identical (i.e., $m_{12} = \hat{m}_{12}$). The only possible differences between P_2 and \hat{P}_2 are the movement rates m_{21} and \hat{m}_{21} . When these movement rates are also equal (indicated by the vertical line), then on each patch both populations are identical (except for their labels), and so there is a continuum of equilibrium values and the outcome depends on the initial conditions. For the parameter values in table 1, $m_{21,\text{opt}} = 0.003740$, and so we consider three cases: A, $m_{21} = 0.0037 < m_{21,\text{opt}}$; B, $m_{21} = m_{21,\text{opt}}$; and C, $m_{21,\text{opt}} < m_{21} = 0.0038$. In A, m_{21} is fixed below $m_{21,\text{opt}}$. When $\hat{m}_{21} < m_{21}$, the invader is excluded by the resident. When $\hat{m}_{21} = m_{21}$ (the vertical line), the populations are identical. When $m_{21} < \hat{m}_{21} \leq m_{21,\text{opt}}$, the invader is successful and excludes the resident. When $\hat{m}_{21} > m_{21,\text{opt}}$, the resident and the invader coexist. In B, $m_{21} = m_{21,\text{opt}}$; that is, the resident chooses the optimal strategy, and the invader can never invade (remains at zero biomass) except if it chooses the identical strategy (the vertical line). In C, m_{21} is fixed above $m_{21,\text{opt}}$. When $\hat{m}_{21} < m_{21,\text{opt}}$, the resident and the invader coexist. When $m_{21,\text{opt}} \leq \hat{m}_{21} < m_{21}$, the invader is successful and excludes the resident. When $\hat{m}_{21} = m_{21}$, the populations are identical. When $\hat{m}_{21} > m_{21}$, the invader is excluded by the resident.

It can further be shown that the optimal strategy $m_{21,\text{opt}} = m_{21,\text{opt}}(\varepsilon_{12}, \varepsilon_{21})$ is a decreasing function of each of the costs of traveling between the patches, and varying the costs can change the outcome. We demonstrate this in scenario 1 for the tritrophic case in figure 5. We fix $\hat{m}_{21} \neq m_{21}$ and allow the cost ε to vary (where we assume that $\varepsilon = \varepsilon_{12} = \varepsilon_{21}$). Since $m_{21,\text{opt}}$, given by equation (14), decreases linearly as a function of ε , it is the size of ε that determines the relative values of m_{21} , \hat{m}_{21} , and $m_{21,\text{opt}}(\varepsilon)$ and hence, whether or not invasion is successful, and if successful, whether the invader excludes the resident or there is coexistence.

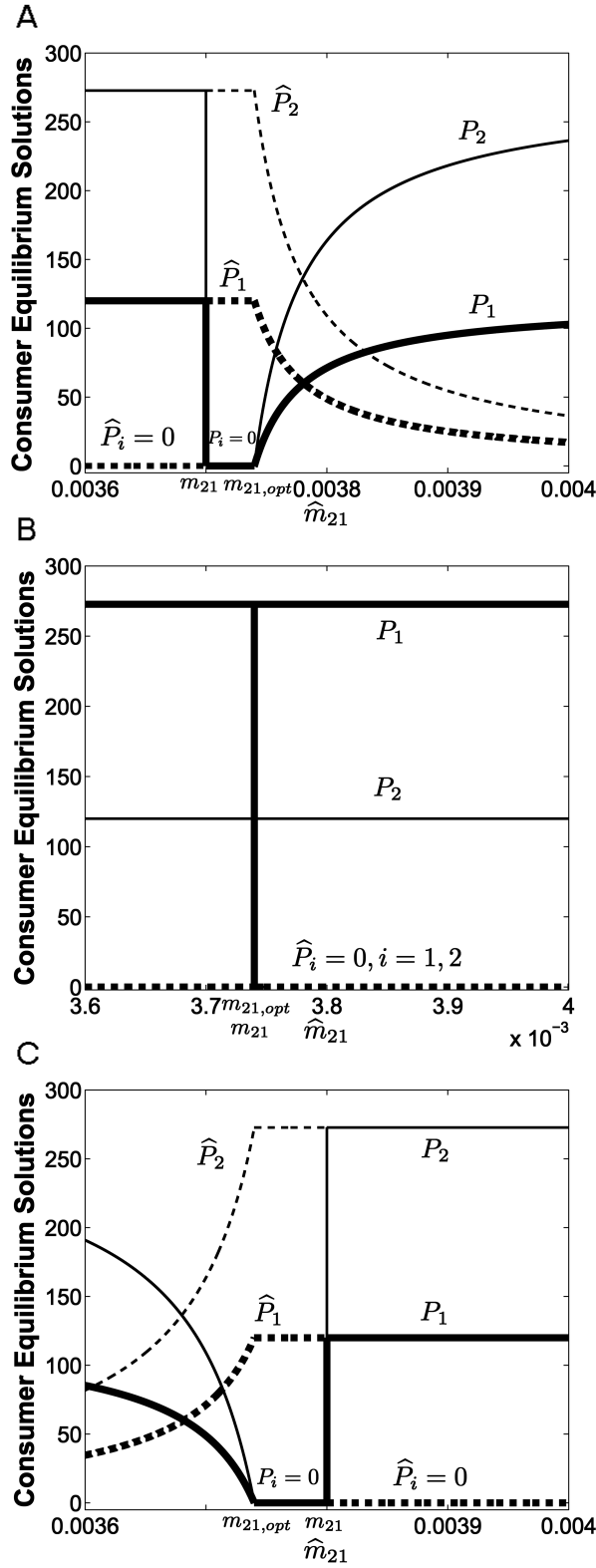


Figure 4: Dependence of equilibrium population sizes on consumer's migration rate \hat{m}_{21} for the two-patch tritrophic case of scenario 1. Resident consumer's population sizes (P_1 and P_2) shown

The N-Patch Case

Next we consider N patches, restricting attention to the tritrophic case. Because finding explicit expressions for the components of the coexistence equilibrium (the equilibrium with all components positive) for model (9) is not possible in the more general case of N patches (as it was for the two-patch case), we must use a different approach. In this case, we are instead able to find explicit expressions for the coexistence equilibrium of model (8). In order to proceed, we first introduce some notation relating this coexistence equilibrium of model (8) to a boundary equilibrium (an equilibrium with some components zero) of system (9), the equilibrium with the invader absent but all other components positive. Let $E_{(8)}^* = (P^*, R^*, M^*)$ denote a coexistence equilibrium solution of model (8), where $P^* = (P_1^*, \dots, P_N^*)$, $R^* = (R_1^*, \dots, R_N^*)$, $M^* = (M_1^*, \dots, M_N^*)$, and $P_i^* > 0$, $R_i^* > 0$, $M_i^* > 0$, $i = 1, \dots, N$. In this case (once the parameters are all fixed) there is a unique coexistence equilibrium solution with components given by

$$P_i^* = \frac{d_{mi}}{c_i f_i}, \quad (16a)$$

$$R_i^* = K_i \left(1 - \frac{a_i}{r_i} P_i^* \right), \quad (16b)$$

$$M_i^* = \frac{1}{f_i} \left(b_i a_i R_i^* - d_i - \sum_{j=1}^N m_{ji} P_j^* + \left[\sum_{j=1}^N (1 - \varepsilon_{ji}) m_{ji} \frac{P_j^*}{P_i^*} \right] \right). \quad (16c)$$

Here, we assume that $a_i d_{mi} < r_i c_i f_i$, $i = 1, \dots, N$ so that $R_i^* > 0$ and that the carrying capacities, K_i , are sufficiently large so that $M_i^* > 0$, $i = 1, \dots, N$. If we set $\bar{P}^* = (0, \dots, 0) = \bar{0}$, then if $E_{(8)}^*$ is a coexistence equilibrium of

using thick and thin solid lines for patches 1 and 2, and invader's (\hat{P}_1 and \hat{P}_2) using thick and thin dashed lines, respectively. Note that P_1 and P_2 are either both zero or both positive. Similarly, \hat{P}_1 and \hat{P}_2 are either both zero or both positive. All parameters for P_1 and \hat{P}_1 are identical (see table 1) except for m_{21} and \hat{m}_{21} . Invaders and residents are identical when $m_{21} = \hat{m}_{21}$ (indicated by the vertical line in each graph) such that a continuum of equilibrium population sizes is feasible, with outcome dependent on initial conditions. Three cases for which $m_{21,opt} = 0.00374$ are illustrated: A, $m_{21} = 0.0037 < m_{21,opt}$; B, $m_{21} = m_{21,opt}$; and C, $m_{21} < m_{21,opt}$. Notice the transition from a boundary equilibrium with one of the populations absent to the coexistence equilibrium when the invader chooses the optimal strategy, that is, when $\hat{m}_{21} = m_{21,opt}$.

Table 1: Parameter values used to illustrate the two-patch model

$\varepsilon = .15$	$a_1 = .005$	$c_1 = c_2 = .5$	$f_1 = .000050$
$m_{12} = .01$	$a_2 = .006$	$d_{m1} = .0030$	$f_2 = .000055$
$K_1 = K_2 = 100.0$	$b_1 = b_2 = .5$	$d_{m2} = .0075$	
$r_1 = r_2 = 3.0$	$d_1 = d_2 = .1$		

model (8), it follows that $E^* = (\bar{0}, P^*, R^*, M^*)$ is a boundary equilibrium of model (9).

Motivated by the approach given for the two-patch case, we aim to find movement rates $m_{ji, \text{opt}}$ under assumption (H_2 , scenario 1) or $m_{ij, \text{opt}}$ under (H_2 , scenario 2), $j = 2, \dots, N$, so that if it were possible to find the components of the coexistence equilibrium of model (9), we could set the invader components in this equilibrium equal to 0 and solve for the appropriate movement rates, to obtain the boundary equilibrium of model (9), E^* (just as we did in the two-patch case). (Fig. 4A, for example, shows that in the two-patch case, when $m_{21} = m_{21, \text{opt}}$, the coexistence equilibrium and the boundary equilibrium with the invader absent coalesce.) When the rates are chosen so that these equilibrium points meet this way, from standard bifurcation theory it follows that the “invasion matrix,” the submatrix of the “community matrix” obtained when model (9) is linearized about the boundary equilibrium E^* , must have a zero eigenvalue. In appendix A we show that the community matrix has block matrix structure, with one block corresponding to the invasion matrix telling us about whether E^* is attracting or repelling with respect to the invading population. We therefore look for the values of the movement rates for which the invasion matrix has one zero eigenvalue and all other eigenvalues have negative real parts. This approach yields the movement rates

$$m_{il, \text{opt}} = (1 - \varepsilon_{li}) m_{li} \frac{P_i^*}{P_i^*} \quad (17a)$$

$$+ \frac{1}{P_i^*} \sum_{j=2}^N \left[(1 - \varepsilon_{ji}) m_{ji} P_j^* - \frac{(1 - \varepsilon_{ij})(1 - \varepsilon_{ji})}{(1 - \varepsilon_{li})} m_{ij} P_j^* \right]$$

in scenario 1. Similarly, in scenario 2 we obtain the movement rates

$$m_{li, \text{opt}} = (1 - \varepsilon_{li}) m_{li} \frac{P_i^*}{P_i^*} \quad (17b)$$

$$+ \frac{1}{P_i^*} \sum_{j=2}^N \left[\frac{(1 - \varepsilon_{ij})}{(1 - \varepsilon_{lj})} m_{ij} P_j^* - \frac{(1 - \varepsilon_{ji})}{(1 - \varepsilon_{li})} m_{ji} P_j^* \right].$$

In the two-patch case ($N = 2$), substituting the expressions given for P_i^* , $i = 1, 2$ in equation (16a), the rate given by equation (17a) is identical to the one in equation (14), and the rate given by equation (17b) is identical to

to the one in equation (15). In the N -patch case, if $m_{ij} = 0$ whenever $i > 2$ or $j > 2$, the formulas in (17) give rates similar to the rates given in the two-patch case, since the summation term vanishes.

We caution the readers that formulas (17) are derived under the assumption that these rates, once determined, will turn out to be positive for all $i = 2, \dots, N$. In addition, we assume that, if we were considering only system (8) (the system without any invader) and the resident uses these rates, $E_{(8)}^*$ has all components positive and attracts all solutions with positive initial conditions with respect to system (8). If not, this method fails to determine whether or not there is an ESS. In particular, if any rate given by equations (17) is negative, this is clearly meaningless, and the method is inconclusive. We conjecture that when these additional assumptions hold, the movement rates in equations (17) give an ESS.

In the three-patch case, numerical simulations in Matlab and Fortran and exploration of the model using the numerical continuation and bifurcation software AUTO through the XPPAUT interface (Ermentrout 2002) support this conjecture. Our numerical investigations indicate that if the resident wishes to avoid invasion, it is advisable to

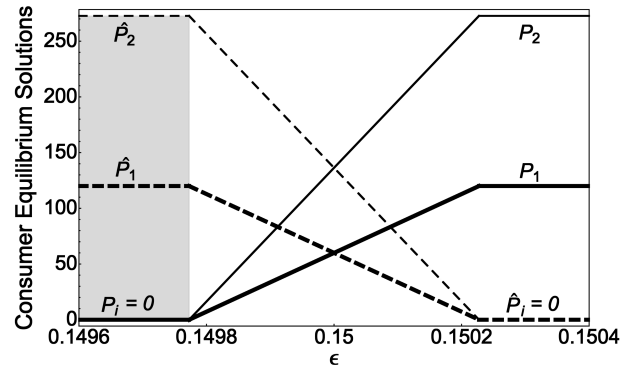


Figure 5: Since $m_{21, \text{opt}} = m_{21, \text{opt}}(\varepsilon)$ is a decreasing function of ε when $m_{21} \neq \hat{m}_{21}$ are fixed, it is the size of the cost ε that determines whether invasion is successful. This figure shows the biomasses at the stable equilibrium in the tritrophic case for scenario 1 for the parameter values in table 1 for the resident (P_1 and P_2 , thick and thin solid lines, respectively) and the invader (\hat{P}_1 and \hat{P}_2 , thick and thin dashed lines, respectively) on the two patches as functions of the cost ε when $0.003739 = m_{21} < \hat{m}_{21} = 0.003741$. The shaded region indicates exclusion of the resident by the mutant invader.

Table 2: Selected analytic and numerical models, with the number of patches and trophic levels, and predictions regarding the effects of travel costs on possible deviations from the ideal free distribution (IFD)

Model type	No. patches	No. trophic levels	Direction of movement	Effect of travel cost	Reference
Numerical (IBM)	2	2	Bidirectional	Deviation from IFD	Regelmann 1984
Numerical (IBM)	N	2	Bidirectional	Deviation from IFD for high costs	Bernstein et al. 1991
Analytical	2	2	Unidirectional (toward richer patch)	Deviation from IFD for high costs (overmatching)	Morris 1987; Kennedy and Gray 1993
Analytical	2	2	Bidirectional	No deviation from IFD	Åström 1994
Analytical	2, N	2	Bidirectional	Approaches IFD for higher costs	Matsumura et al. 2010
Analytical and numerical	2, N	2, 3	Bidirectional	Deviation from IFD	This article

Note: See the text for further discussion of some of these models. IBM = individual-based model.

use rates as close as possible to the rates given by equations (17). A typical example is described in appendix B in the online edition of the *American Naturalist*, where numerical experiments I–VI are described. In experiments I–III, the residents’ rates were both chosen very close to but not equal to the optimal rates. At least one of the invaders’ rates was chosen on the same side of the optimal rate as the residents’ rate but even farther from the optimal rate. Either exclusion of the invader by the resident or coexistence of both invader and resident populations resulted. In experiments IV and V, both the resident and the invader used the same optimal rate for one of their rates. The outcome was similar to the outcome in the two-patch case illustrated in figure 4; that is, the outcome depended on the relative values of the other rates in the same way as in the two-patch case. Finally, in experiment VI, we chose both residents’ rates as the optimal rates and at least one of the invaders’ rates as nonoptimal. In this case, when the invaders’ rates were close to the residents’ rates, convergence was too slow to determine whether the resident was excluding the invader or there was coexistence of both the invader and the resident but with the invader at an extremely low population size.

Here we define the fitness on patch i to be $b_i a_i R_i - d_i - f_i M_i$, that is, the per capita net growth rate on that patch. Our analysis also predicts the effect of the cost of movement between patches on the expected fitness of the resident on the different patches, when the resident uses the optimal movement strategy in the absence of the invader. (For the explicit formulas for the fitness on each patch, see app. A, lemma 5 in the case of scenario 1 and lemma 4 for scenario 2.) In the two-patch case, in scenario 1 the fitness of the resident is always positive on patch 1 and zero on patch 2, whereas in scenario 2 it is always zero on patch 1 and positive on patch 2. In both cases,

when it is positive, the fitness is equal to $(1 - \varepsilon_{12})(1 - \varepsilon_{21})m_{ij}$ (where $i = 1$ and $j = 2$ in scenario 1 and $i = 2$ and $j = 1$ in scenario 2) and is hence a decreasing function of the cost of travel between patches. In the N -patch case, the fitness of the resident on patch 1 is still always positive in scenario 1 and always zero in scenario 2. However, when there are more than two patches (fig. 2), the situation is more complicated. The expected fitness on any patch besides patch 1 can be positive, zero, or even negative, depending on the relative costs of travel between the patches and on which patches are connected. Therefore, both patches that are effectively net “sources” and patches that are effectively net “sinks” can emerge when the movement rates of a population among patches is optimal. This result has some relationship to the observation of Holt (1997) that one reason that sink populations may persist is because of a departure from a “free” distribution; that is, some individuals are constantly being forced from high-quality patches into low-quality patches. On the other hand, in the special case that the costs of travel between all of the patches are positive and the same (i.e., $\varepsilon_{ij} = \varepsilon \in (0, 1)$ for all i, j), then the expected fitness on all of the patches besides patch 1 is nonnegative in both scenarios 1 and 2. Examples of when it is possible to have negative fitness on a patch in the case of a three-patch habitat can be easily constructed based on lemma 5 for scenario 1 or lemma 4 in scenario 2 (see app. A). In particular, in scenario 1, the only way that patch 2 can have negative fitness is if the rate $m_{23} > 0$ and the costs of travel between patches satisfy $(1 - \varepsilon_{21}) < (1 - \varepsilon_{23})(1 - \varepsilon_{31})$. Hence, to have negative fitness on patch 2, it must be possible to travel directly from patch 2 to patch 3, and the cost of direct travel from patch 2 to patch 1 must be larger than the cost of direct travel both from patch 2 to patch 3 and from patch 3 to patch 1; that is,

both $\varepsilon_{21} > \varepsilon_{23}$ and $\varepsilon_{21} > \varepsilon_{31}$ must hold. For example, if $\varepsilon_{21} = 0.03$ and $\varepsilon_{23} = \varepsilon_{31} = 0.01$, then patch 2 would have negative fitness, as in the example discussed in appendix B. Finally, it should be noted that as $\varepsilon_{ij} \rightarrow 0$, the predicted strategies reduce to the strategies for the IFD, and the expected fitness of the resident on all of the patches approaches zero.

Discussion

Previous studies that assumed movement between patches despite travel costs used a variety of modeling approaches and assumptions and made different predictions about the effects of these costs on movement and population distribution patterns. Some individual-based simulations have predicted a decrease in patch switching (Regelmann 1984; Bernstein et al. 1991; Cezilly and Boy 1991). Kennedy and Gray (1993) and Morris (1987) analytically predicted that with greater travel costs there would be greater skewing of the distribution toward richer patches than the IFD would predict, as individuals would be attracted unidirectionally toward the richer patches. Matsumura et al. (2010) predicted that the distribution of suboptimal foragers would approach that predicted by the IFD with increasing traveling costs, as the numbers of individuals leaving rich patches would decline faster than those leaving poor patches. In table 2 we list the conclusions of a few selected models with respect to possible deviations of population distributions from the IFD.

Our approach and predictions differ from the others in a few ways. Differences in habitat quality do not play a crucial role in our analysis, since we assume that a population is self-sustaining on each patch (when there is no travel between patches), at least under the normal steady state conditions of our analysis. We start with the assumption that movement occurs either because of selective pressures such as outbreeding and recolonization or due to environmental forcing. However, it should be noted that our models take a different viewpoint from traditional metapopulation models in that they do not emphasize extinction and recolonization of patches. We consider two scenarios. In both we assume that there is one special patch, which we call patch 1. For convenience, in scenario 1 we call patch 1 the “upstream” patch, from which there is forced emigration to all other patches, and we call it the “downstream” patch in scenario 2, toward which there is forced immigration from all the other patches. We assume that these rates and the rates between any of the other patches (besides patch 1) are fixed at values out of the control of the consumer and are the same for both the resident and a potential invader. The only difference between the resident population and a potential invading population is then the return rates to patch 1 in scenario

1 and the emigration rates from patch 1 to all of the other patches in scenario 2, and we assume that these rates are the only rates under the control of the consumer population. We investigated whether there is a strategy that the resident consumer can choose so that it cannot be invaded by a small number of consumers that choose different rates, that is, whether there is an evolutionarily stable strategy (ESS). We allow movement rates between patches other than patch 1 to be positive or zero. (Note that since patch 1 is connected bidirectionally to all other patches, it is always possible to get from any patch to any other patch, although this might involve an indirect path, e.g., through patch 1.)

Our analysis produced new results that differ in key respects from earlier results on the movement patterns among habitats in which there are traveling costs. A major new result of our analysis is the prediction that, even if the cost is very high, for an ESS to exist in the two-patch case, there must be movement from downstream to upstream patches at the positive rates given by equations (14) or (15). This result applies when only the consumer population disperses, and it holds even if individuals have a nearly 100% probability of not surviving a return to the upstream patch. In the two-patch tritrophic case, the rates we derive are proved analytically (see Y. Lou and C.-H. Wu, unpublished manuscript) to give an ESS. In the two-patch bitrophic case and in the N -patch case with $N > 2$, when all of the optimal movement rates given by our formulas (17) are positive, numerical investigations (using both simulations and bifurcation continuation software) indicate that our optimal rates also give an ESS. However, under our assumptions, when there are more than two patches, the formulas that we derive for the optimal return rates might predict one or more of the rates is zero or negative, violating an assumption under which they were derived. In that case, the rates we derive are not justified and, if negative, are meaningless in any case. Hence, in the case of more than two patches, there may or may not be positive return rates that give an ESS.

It should be kept in mind that our modeling approach applies most appropriately to population dynamics on a long enough timescale for populations to reach equilibrium. Other models of movement are typically relevant to shorter timescales, as are virtually all models of habitat selection. Over shorter timescales, in particular, at the timescale of individual movement, foraging theory has attempted to calculate the quantitative features of movements between patches, given levels of resources on patches and the time, and hence energetic costs, of movement between patches (e.g., Cowie 1977; Stephens and Krebs 1986). Our results indicate that despite the fact that optimal foraging theory deals with nonequilibrium situations in which the forager is depleting local patch re-

sources, movement in both the short-term individual and long-term population cases respond to some similar factors. Our equations for $m_{ji, \text{opt}}$ in the two-patch case are proportional to $(1 - \varepsilon_{ij})$, indicating that the return movement rate from the downstream to the upstream patch decreases (or, equivalently, the mean time that an individual stays on a patch increases) with increasing loss during movement. Charnov (1976), looking at the scale of an individual forager, showed (see his eq. [2] and his fig. 3) that the time that a forager should optimally spend on a given patch increases with increasing energetic cost of movement between patches. Therefore, there is consistency between our model results for long-timescale population dynamics and the short-timescale foraging results of Charnov (1976).

Our results can also be compared to more recent theory of individual movement between patches, which shows the evolution of density dependence of the movement rate coefficients. For example, Travis et al. (1999) modeled competing dispersal strategies using an individual-based model and showed that dispersal strategies always evolved for which the probability of dispersal (equivalent to our $m_{ji, \text{opt}}$) increased as a function of local population density, at least for sufficiently high densities. Importantly, our model results according to equations (17) are quite different in this case. Rather than being dependent on only the local population size (P_i^*), the optimal movement rate coefficient, $m_{ji, \text{opt}}$ in the two-patch case is proportional to the ratio P_i^*/P_j^* , the equilibrium ratio of the receiving and the source populations.

Our model confirms the prediction of other studies, for example, that of Diffendorfer (1999), that movement without cost should result in balanced dispersal with the equilibrium population density on each patch the same as it would be without any movement. However, a second major result of our study is that our analysis predicts that the ESS for movement with cost does not produce balanced dispersal. With cost, the fluxes into and out of the upstream patch are not equal, and hence the equilibrium population density on each patch is not the same as it would be without any movement. We show that this asymmetry in the rates between two given habitat patches depends on movement costs and can occur even if the two habitat patches are entirely similar. Therefore, our model predicts deviations from balanced dispersal, though not for any reasons regarding differences in the quality of patches, a central feature of earlier work on this topic. Our results indicate that in the two-patch case, because of the imbalance in movement rates, individual fitness is higher on the upstream patch than on the downstream patch. The imbalance is necessary to motivate individuals to accommodate the cost of movement from the downstream patch. Therefore, the loss rate from travel breaks the sym-

metry of the IFD and leads to fitness differences between the two patches. This would occur even if all parameters on the two patches were identical. This may not be too surprising, because movement from the upstream patch is forced, and the individuals that move from the upstream patch lose fitness. The system thus does not represent an IFD. What is perhaps surprising, however, is that for N -patch systems, if optimal movement rates are used, fitness may be positive on some patches, thus making them effective "sources," and negative on other patches, thus making them effective "sinks." For example, in scenario 1 in the three-patch case, such sinks emerge if it is possible to get back to patch 1 indirectly via the other patch, provided that the cost of direct movement back to patch 1 is greater than the cost of travel to the other patch, as well as the cost of travel from the other patch to patch 1. This is a third major result of our study.

Our analysis extends beyond the ESS ($m_{21} = m_{21, \text{opt}}$) to the more general case in which a species' movement strategy is suboptimal, (e.g., in the two-patch case when $m_{21} < m_{21, \text{opt}}$ or $m_{21} > m_{21, \text{opt}}$). The analysis summarized in figure 3 regarding competition of two movement strategies showed the following: if the resident and invader strategies are both either greater or smaller than $m_{21, \text{opt}}$, then the one that is closest to $m_{21, \text{opt}}$ will exclude the other. If one is greater and one is smaller than $m_{21, \text{opt}}$, then the two strategies can coexist. An interesting implication of these results is that invasion by a mutant strategy is most likely to result in an extinction of either the invader or the resident rather than coexistence. This is because mutations tend to result in small changes, so that mutations great enough to result in a jump to a new strategy on the other side of $m_{21, \text{opt}}$ are likely to be rare. Although a mutation leading to coexistence is unlikely, an invading genotype from outside the local area could more likely have a movement strategy on the other side of $m_{21, \text{opt}}$. From the numerical investigations in appendix B in the three-patch case, coexistence of the resident and a similar mutant appears to be even more unlikely.

To the extent that "background" rates of dispersal in one direction are a common feature of natural systems, our results have important empirical implications. Forced unidirectional dispersal rates have been demonstrated in many invertebrate and vertebrate aquatic organisms, including in both marine and freshwater habitats (Bohonak and Jenkins 2003; Macneale et al. 2005; Shanks and Eckert 2005; Lowe et al. 2008). In some cases, drift is the main means of transport. For example, many marine, coastal species of fishes and crustaceans have been shown to drift unidirectionally during larval stages, following ocean currents (Shanks and Eckert 2005). Our results, therefore, may have particular implications for return rates in marine environments and thus for marine reserve design.

In other cases, drift may be accidental, due to organisms being caught in air or water currents. In the case of aquatic insects, the passive downstream drift caused by one-directional flow of water is a common pattern, and Müller (1954, 1982) hypothesized that insects compensate for downstream drift by a tendency for the adult forms to fly upstream to oviposit. While empirical studies have not conclusively supported the hypothesis that upstream movement of adults compensates for the loss, Anholt (1995) proposed that such upstream movement may not be necessary, as density dependence occurs in the aquatic stages of many insects, and drift of individuals from a habitat patch may be compensated for by an increase in the survival rate of those remaining on the patch. Kopp et al. (2001), nevertheless, showed through invasion analysis that even in such cases, upstream movement should be favored, because an insect genotype in which losses to drift from upstream to downstream patches are exactly compensated for by upstream movement will exclude any genotype for which this is not true. The results of Kopp et al. (2001) are precisely what are expected when there are no losses in movement between patches, so that an IFD can occur for the population on the patches. Our analyses apply to the more general situation in which mortality losses occur during movements in both directions between patches. Our results imply that a genotype having an upstream movement rate given by equation (14) or equation (15) will exclude other genotypes. Thus, in a stream system in which mortality losses occur in the downstream drift and upstream flight of adults, we expect that the reverse migration does not balance the losses caused by drift.

Our assumption that movement between patches, at least in one direction, is necessary violates the basic assumption of “free” in IFD theory. This was also noted by Åström (1994) for his model. Our results constitute a replacement of the traditional IFD for the case in which movement entails costs. These results need to be taken into account in the study of metapopulations and the evolution of dispersal given their implications for conservation and reserve design (Noon and McKelvey 1992; Hastings and Harrison 1994; Husband and Barrett 1996; Travis and Dytham 1998; Hanski 1999; Fagan and Lutscher 2006).

The forced unidirectional movements are long-term constants in our model. We realize that in real situations there are seasonal variations in movement and fluctuations in environmental conditions and populations, in response to which reciprocating migrations might occur (Morris et al. 2004). It is possible that the magnitudes of these effects may overshadow those of forced unidirectional flows on short timescales. Other studies have considered movement between patches despite travel costs and have made a num-

ber of different predictions about the effects of these costs on movement and distribution patterns.

Many of the predictions of our models appear qualitatively consistent with patterns observed in nature. Robust empirical tests will likely be challenging in all but the simplest experimental systems. In particular, strong empirical tests of our predictions regarding balanced dispersal, the possibility of negative fitness on patches, and the IFD must include forced dispersal with cost. Needed are empirical measures of the bidirectional rates of movement and movement-associated mortality at temporal scales pertinent to the dynamics of the metapopulation. Laboratory-based metapopulations (e.g., Vasseur and Fox 2009) may serve this function by providing a means to manipulate movement and mortality rates independently. Nevertheless, the development of additional and alternative mechanism-specific models, for example, individual-based models, will also be necessary to move beyond simplistic pattern-matching comparisons.

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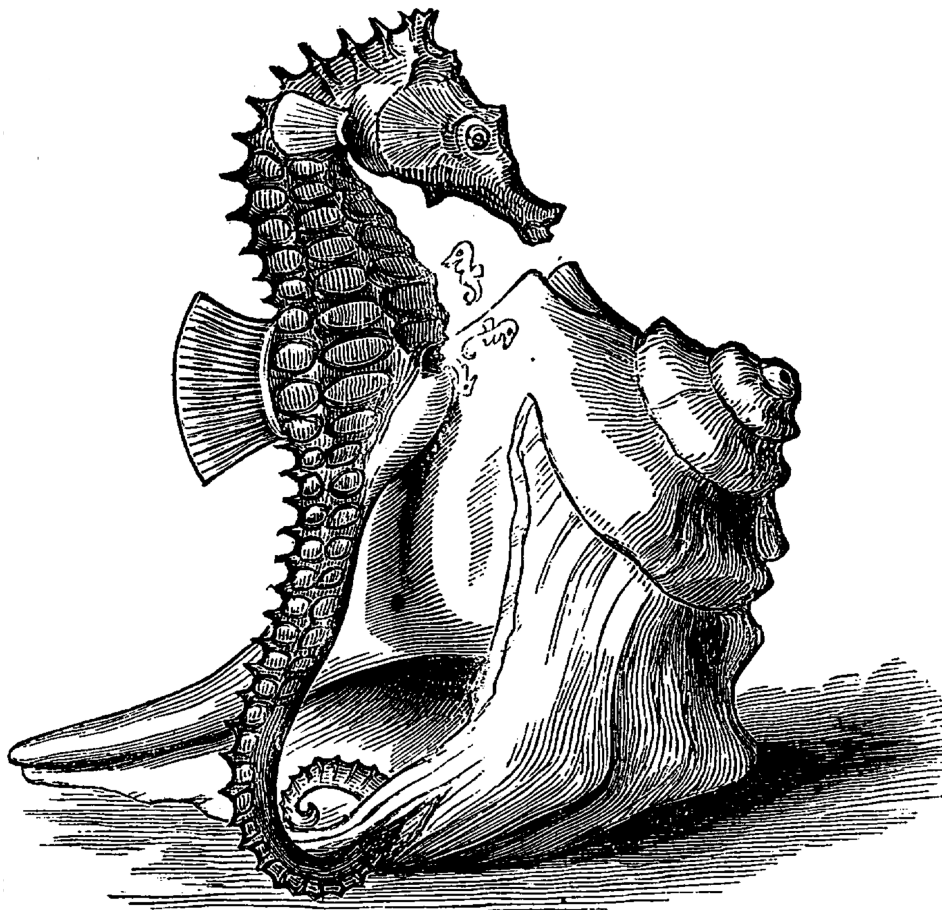
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Hippocampus hudsonius De Kay or the common Sea-horse of the Atlantic Coast. "A red-letter day! Today near noon I observed three young Sea-horses swimming about. They had just made their debut. Very minute creatures they were; but, to my great joy, nearly perfect. From that hour the *Pater-mater* kept busy setting his progeny adrift." From "The Sea-Horse and its Young," by Rev. Samuel Lockwood (*American Naturalist*, 1867, 1:225–234).

Appendix A 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)

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,

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

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,

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

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) , 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 $2 \leq i \leq N$,

$$m_{1i,\text{opt}} = (1 - \varepsilon_{i1}) \frac{P_i^*}{P_1^*} m_{11} + \frac{1}{P_1^*} \sum_{j=2}^N \left[\frac{(1 - \varepsilon_{ij})}{(1 - \varepsilon_{1j})} m_{ij} P_i^* - \frac{(1 - \varepsilon_{ji})}{(1 - \varepsilon_{1i})} m_{ji} P_j^* \right]. \quad (A3)$$

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) , 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

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

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 $2 \leq i \leq N$,

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

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

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

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

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

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' movements 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' movements 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

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