

ASYMMETRIC DISPERSAL AND EVOLUTIONAL SELECTION IN TWO-PATCH SYSTEM

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ABSTRACT. Biological organisms leave their habitat when the environment becomes harsh. The essence of a biological dispersal is not in the rate, but in the capability to adjust to the environmental changes. In nature, conditional asymmetric dispersal strategies appear due to the spatial and temporal heterogeneity in the environment. Authors show that such a dispersal strategy is evolutionary selected in the context two-patch problem of Lotka-Volterra competition model. They conclude that, if a conditional asymmetric dispersal strategy is taken, the dispersal is not necessarily disadvantageous even for the case that there is no temporal fluctuation of environment at all.

1. Introduction. Migration is the key survival strategy of many biological species when the habitat turns into a harsh place. If resource dwindles, temperature drops or rises, and living condition deteriorates, then biological species, from mammals and birds to single cell organisms such as amoeba, often abandon their habitat and move to another place. The essence of biological dispersal is in such a conditional variation, but not simply in the dispersal rate. The purpose of this paper is, by considering a competition system of two phenotypes, to show how such an adaptation ability can be achieved by a biological species.

If starvation starts, biological organisms know that they have to move. However, in many cases, they do not know the direction and often start to migrate by simply choosing a direction randomly. The starvation driven dispersal models such cases. Indeed, a dispersal strategy adjusting to the environmental changes can be based on such a simple mechanism as increasing dispersal rate when starvation starts. There is huge literature for spatially-distributed population dynamics with dispersal. The

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simplest way to include spatial heterogeneity and dispersal is the two-patch system. A standard model commonly used in the literature is written as

$$\begin{aligned}\dot{u}_1 &= r_1 u_1 \left(1 - \frac{u_1}{K_1}\right) + c_{12} u_2 - c_{21} u_1, \\ \dot{u}_2 &= r_2 u_2 \left(1 - \frac{u_2}{K_2}\right) + c_{21} u_1 - c_{12} u_2,\end{aligned}\tag{1}$$

where $u_i = u_i(t)$ is the population in the i -th patch at time $t > 0$ and \dot{u}_i is its time derivative. In this model, the logistic population growth is taken with the carrying capacity K_i and intrinsic growth rate r_i in the i -th patch. Other parameters $c_{ij} > 0$ are dispersal rate per population, where $c_{ij} u_j$ is the emigration flow from patch j . The dispersal is called symmetric if $c_{ij} = c_{ji}$, and is called asymmetric otherwise. This two-patch system serves as a basic model and provides key insights on population dynamics and dispersal (see [2, 9, 10, 15]). In spite of the simplicity of the model system, there are still unresolved aspects (see [1, 26]).

We first consider the two-patch system with a starvation-dependent dispersal,

$$\begin{aligned}\dot{v}_1 &= v_1(1 - s_1) + \gamma(s_2)v_2 - \gamma(s_1)v_1, \\ \dot{v}_2 &= v_2(1 - s_2) + \gamma(s_1)v_1 - \gamma(s_2)v_2, \\ (v_1(0), v_2(0)) &= (v_1^0, v_2^0) > 0,\end{aligned}\tag{2}$$

where s_i is the starvation measure at the i -th patch defined by

$$s_i := \frac{v_i}{K_i}.\tag{3}$$

The population dynamics is still described by the logistic model. We restrict the general system to a case that the two intrinsic growth rates in (1) are identical, i.e., $r_1 = r_2 = 1$, which is the case we will obtain later from a mega-patch derivation. If the population size exceeds the carrying capacity, then starvation starts. The ratio s_i denotes such harshness at the i -th patch. Notice that the migration rates are not fixed, but dynamically given by $c_{ij} = \gamma(s_j)$, where γ can be any function as long as it is an increasing function. The monotonicity of γ implies that the dispersal is enhanced by starvation. Here, we assume that γ is smooth for simplicity and hence $\gamma'(s) \geq 0$. If $s_1 \neq s_2$, the dispersal is asymmetric. If $s_1 = s_2$, it is an ideal free distribution.

If K_i is the area of patch i , then s_i is the population density at patch i and the dispersal in the model is a positively density-dependent one (see [14, 27, 28] and references therein). The evolution of density-dependent dispersal has been well-studied. Both positive and negative density-dependent dispersal are considered and either one can be selected depending on the distribution of high quality and low quality patches. However, in the context of logistic equations, the patch size and quality are indistinguishable. The two are mixed in terms of carrying capacity and asymmetric migration rates (see Section 2). On the other hand, the starvation measure s_i is a meaningful quantity in the context which combines both effects of size and quality.

The first key result of the paper is the uniqueness of the steady state solution.

Theorem 1.1. *Let $K_1 < K_2$ and γ be an increasing smooth function. If $\frac{K_2}{K_1} \leq 3$ or $\gamma(0.5) \leq 0.5$, the nontrivial steady state of (2) exists and is unique. Furthermore, the steady state (\bar{v}_1, \bar{v}_2) satisfies*

$$K_1 < \bar{v}_1 < \bar{v}_2 < K_2, \quad \bar{v}_2 > \max\left(\frac{K_2}{2}, \frac{2K_1K_2}{K_1 + K_2}\right).\tag{4}$$

The uniqueness of the steady state plays a key role in the rest of the paper. The condition $K_2 \leq 3K_1$ implies that the spatial variation is relatively small. In the case, the monotonicity of γ guarantees the uniqueness. The other condition, $\gamma(0.5) \leq 0.5$, implies that the emigration rate is less than the half of the intrinsic growth rate when the population is less than the half of the carrying capacity. This condition is needed when $K_2 > 3K_1$. We can even construct a counter example that the uniqueness fails without such extra assumptions (see Remark 1).

The main system of the paper is the competition system,

$$\begin{aligned} \dot{u}_1 &= u_1(1 - s_1) + d(u_2 - u_1), \\ \dot{u}_2 &= u_2(1 - s_2) + d(u_1 - u_2), \\ \dot{v}_1 &= v_1(1 - s_1) + \gamma(s_2)v_2 - \gamma(s_1)v_1, \\ \dot{v}_2 &= v_2(1 - s_2) + \gamma(s_1)v_1 - \gamma(s_2)v_2, \\ (u_1(0), u_2(0), v_1(0), v_2(0)) &= (u_1^0, u_2^0, v_1^0, v_2^0) > 0, \end{aligned} \tag{5}$$

where u_i and v_i denote the population of two phenotypes and s_i is the starvation measure given by

$$s_i := \frac{u_i + v_i}{K_i}. \tag{6}$$

One may consider s_i in (3) as a special case of the same s_i in (6) when $u_i = 0$. The population dynamics of the two phenotypes are identical and the difference is in their migration strategies. The first phenotype u takes a symmetric dispersal with a constant rate $c_{ij} = d > 0$ and the second phenotype v disperses asymmetrically with $c_{ij} = \gamma(s_j)$.

As mentioned, the purpose of migration is to find a better place for survival, in particular, when the environment becomes harsh for living. However, if dispersal strategies are symmetric, only the smaller dispersal rate will survive over the long term and the faster dispersal rate will be excluded eventually under spatial heterogeneity. For example, Hastings [13] showed that a spatially varying environment selects the slowest dispersal when the environment is temporally invariant (see also [22]). This observation gives a paradoxical situation that the dispersal reduces the survival chance of a species and forces us to conclude that symmetric dispersal strategies do not capture the essence of biological dispersal.

We will see that the situation is different if asymmetric dispersal strategies are taken. Indeed, we will see in the following theorem that dispersal can be selected even if there is no temporal fluctuation at all.

Theorem 1.2. *Let $K_1 < K_2$ and γ be an increasing smooth function. We assume $\frac{K_2}{K_1} \leq 3$ or $\gamma(0.5) \leq 0.5$. Let $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ and $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ be semi-trivial steady states. Then, there exists a critical dispersal rate $0 < d_* < \gamma(\frac{\bar{v}_2}{K_2})$ such that (i) there exists a positive (or coexisting) steady state of (5) if and only if $d = d_*$, (ii) E_1 is linearly stable for $d < d_*$ and is unstable for $d > d_*$, and (iii) E_2 is linearly stable for $d > d_*$ and is unstable for $d < d_*$.*

Note that the existence of a positive state means coexistence of the two species. If $d < d_*$, $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ is the only stable steady state. Hence, the asymptotic limit should be E_1 if the solution converges.¹ This implies that the species u is selected and v goes extinct. If $d > d_*$, $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ is the only stable steady

¹We could not show the global asymptotic stability but we believe so. The typical theory for problems with monotone dynamics is not applicable for the starvation driven dispersal.

state and hence the species v is selected and u goes extinct (see Figure 5). The key claim of the theorem is in the relation $d_* < \gamma(s_2)$. Note that $s_2 < s_1$ and hence $\gamma(s_2) < \gamma(s_1)$ (see Theorem 1.1). Therefore, the theorem shows that, if an asymmetric dispersal is taken, a larger dispersal rate can be selected even if there is no temporal fluctuation of environment at all. However, if $d < d_*$, the slower dispersal is still selected.

The evolution of dispersal strategies has been studied theoretically for a long time. The experimental approach for the evolution of dispersal strategy is limited since such an evolutionary process takes very long time and is not repeatable. Instead, analytical and computational approaches of mathematical models provided useful insights on biological dispersals (see [11]). One of key conclusions is that spatial heterogeneity reduces the size of symmetric dispersal and the temporal fluctuation increases it (also see [7, 29]).

The theories for discrete patch models developed into continuum PDE models in the context of reaction-diffusion equation. For more study, readers are referred to [4, 23, 24, 25]). For example, the patch system (2) is written as

$$v_t = v\left(1 - \frac{v}{m}\right) + \Delta(\gamma(s)v), \quad x \in \Omega, \quad (7)$$

where a given function $m = m(x)$ corresponds to spatially heterogeneous carrying capacities and $s = \frac{v}{m}$. Note that Fick's law is in a form of $\nabla \cdot (\gamma(s)\nabla v)$, but we assume a Fokker-Plank type diffusion. See Appendix A for their connection.

However, the reaction-diffusion equation (7) has hardly been studied even for the constant motility case, $\gamma = \text{constant}$. A much more studied case is

$$v_t = v(m - v) + \Delta(\gamma(s)v) \left(\equiv mv\left(1 - \frac{v}{m}\right) + \Delta(\gamma(s)v) \right), \quad x \in \Omega, \quad (8)$$

where $m(x)$ is now the intrinsic growth rate at position x at the same time of being the carrying capacity. Eq (8) has been studied by many authors for the constant diffusivity case, $\gamma = \text{constant}$, and then applied to competition systems (see [12, 21]). The case with increasing motility γ has been introduced in [5] to describe a biological dispersal enhanced by starvation. The global behavior of its solution is given in [18]. The evolutionary behavior of the dispersal strategy has been studied in the context of competition and prey-predator relation (see [6, 16, 17]).

The contents of this paper are as follows.

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2. Two-patch system for single species. It is often believed that a random dispersal is symmetric. However, we will see in this section that symmetry and randomness are not related. Assume that the dispersal coefficients in the two-patch system (2) are not symmetric. If the environment condition of the two patches are different, the emigration rates can be different. Even if conditions of the two patches are identical, the rates could be different if their sizes are different. We start with a derivation of two-patch system which produces asymmetric dispersal coefficients from symmetric ones.

2.1. Derivation of mega-patches. Consider the logistic population dynamics of a single species in N identical patches,

$$\dot{U}^i = U^i(1 - U^i) - \sum_{j=1}^N C^{ji}U^j + \sum_{j=1}^N C^{ij}U^i, \quad i = 1, \dots, N,$$

where U^i is the population of the species in the i -th patch and C^{ij} is the migration rate from the j -th patch to the i -th one. We start with a patch system with identical sizes (or carrying capacities), which is set to be one. The symmetry of the migration (or Laplace) matrix C is assumed to be symmetric, i.e., $C^{ij} = C^{ji}$. For simplicity, we consider a special case that patches are connected in a homogeneous way so that $C^{ij} = d > 0$ for $i \neq j$ and $C^{ii} = 0$ (see Figure 1).

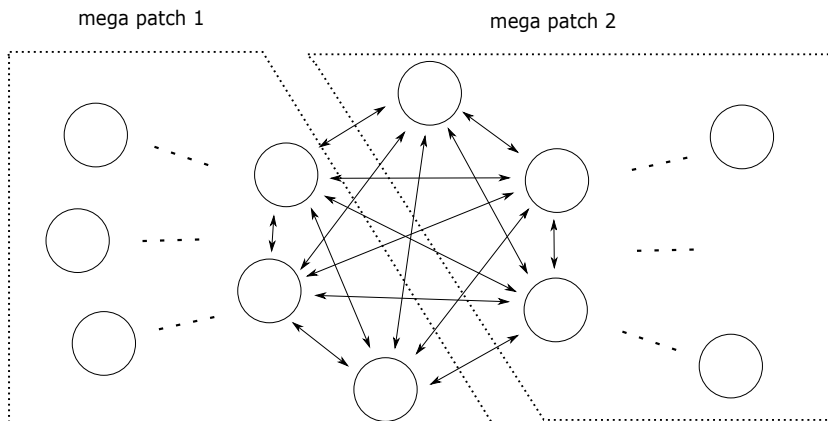


FIGURE 1. A mega patch is a collection of many smaller patches. Dispersal across mega patches are counted in a two-patch system.

We first derive a two-patch problem from these N -patches. The idea is to split the N patches into two groups and consider each group as a single mega-patch. One can easily extend this idea into general number of mega-patches. Let $K_1 + K_2 = N$ and $K_1, K_2 > 0$. The first mega-patch consists of the first K_1 regular patches and the second one of the rest. Let

$$u_1 := \sum_{i=1}^{K_1} U^i, \quad u_2 := \sum_{i=K_1+1}^N U^i.$$

Then, after adding the first K_1 equations and then the rest, we obtain

$$\begin{aligned}\dot{u}_1 &= \sum_{i=1}^{K_1} U^i(1 - U^i) - dNu_1 + dK_1(u_1 + u_2), \\ \dot{u}_2 &= \sum_{i=K_1+1}^N U^i(1 - U^i) - dNu_2 + dK_2(u_1 + u_2).\end{aligned}\tag{9}$$

Since the first K_1 patches are considered as a single environment, the population distribution in the first K_1 patches will be forgotten. Similarly, the next K_2 patches are considered as a single environment. Therefore, we cannot handle the heterogeneity inside these K_1 patches and hence we handle the problem in an averaged sense, i.e., we are forced to take

$$U^i = \frac{u_1}{K_1}, \quad i = 1, \dots, K_1, \quad \text{and} \quad U^i = \frac{u_2}{K_2}, \quad i = K_1 + 1, \dots, N.$$

After substituting these into (9), we obtain

$$\begin{aligned}\dot{u}_1 &= u_1 \left(1 - \frac{u_1}{K_1}\right) - c_{21}u_1 + c_{12}u_2, \\ \dot{u}_2 &= u_2 \left(1 - \frac{u_2}{K_2}\right) + c_{21}u_1 - c_{12}u_2,\end{aligned}\tag{10}$$

where

$$c_{12} = dK_1, \quad c_{21} = dK_2.\tag{11}$$

This derivation gives us a few insights about the two-patch model (see [20] for other cases). First, the intrinsic growth rate is independent of the patch size or carrying capacity. Hence, we set $r_1 = r_2 = 1$. Second, the sizes of obtained patches appear in the coefficients of the quadratic term. Third, the migration coefficients are not symmetric anymore. Note that the migration inside a mega-patch is not counted in the mega-patch problem and only the migration across them are counted. There are more migrations within a bigger mega-patch and, as a result, we obtain asymmetric dispersal. Fourth, the obtained dispersal rates in (11) satisfy the special ratio,

$$\frac{c_{21}}{c_{12}} = \frac{K_2}{K_1},\tag{12}$$

which is known as the balanced dispersal (see [22, 26]) or the evolutionarily stable strategy (see [3, 8]), and gives ideal free distribution. Therefore, the balanced dispersal with given dispersal rates c_{ij} is not distinguishable from symmetric dispersal in a homogeneous environment.

The relation (12) is the criterion for the balanced dispersal and, at the same time, for the homogeneity of environment. We are interested in a spatially heterogeneous case and hence consider a case $\frac{c_{21}}{c_{12}} \neq \frac{K_2}{K_1}$ by taking $K_1 \neq K_2$ and $c_{12} = c_{21}$. Instead, by replacing c_{ij} by $\gamma(s_j)$ in (2), we assume that individuals increase their migration rate if the living condition becomes harsh. The main view point of the model is in understanding how biological organisms can approach to the ultimate dispersal strategy, balanced dispersal, in a spatially heterogeneous and temporally fluctuating environment.

2.2. Steady states. The environment is not homogeneous and the migration strategy is not always optimal in general. Hence, the migration coefficients c_{ij} do not

necessarily satisfy (12). First we consider the steady state solution (θ_1, θ_2) which satisfies

$$\begin{aligned} 0 &= \theta_1 \left(1 - \frac{\theta_1}{K_1}\right) - c_{21}\theta_1 + c_{12}\theta_2, \\ 0 &= \theta_2 \left(1 - \frac{\theta_2}{K_2}\right) + c_{21}\theta_1 - c_{12}\theta_2. \end{aligned} \quad (13)$$

The property of steady states of (1) can be found in [2] for the general case when r_1 and r_2 are not identical. By focusing the case with $r_1 = r_2$, we can construct detailed structure needed in the stability analysis in following sections.

Lemma 2.1. *Let $K_i > 0$ and $c_{ij} > 0$. There exists a unique nontrivial solution of (13).*

Proof. First we show the existence of steady state. If $\frac{c_{21}}{c_{12}} = \frac{K_2}{K_1}$, then $(\theta_1, \theta_2) = (K_1, K_2)$ is a positive steady state. Suppose that $\frac{c_{21}}{c_{12}} < \frac{K_2}{K_1}$. We define

$$\begin{aligned} f(u_1) &:= \frac{1}{c_{12}} \left(\frac{u_1^2}{K_1} - u_1 + c_{21}u_1 \right), \\ F(u_1) &:= f(u_1) \left(1 - \frac{f(u_1)}{K_2}\right) + c_{21}u_1 - c_{12}f(u_1). \end{aligned}$$

Then, $F(K_1) = \frac{c_{21}}{c_{12}} \left(1 - \frac{c_{21}K_1}{c_{12}K_2}\right) K_1 > 0$ and $F(u_1) \rightarrow -\infty$ as $u_1 \rightarrow \infty$. Therefore, there exists $\theta_1 > K_1$ such that $F(\theta_1) = 0$. Let $\theta_2 = f(\theta_1)$. Then, by the definition of f , $\theta_2 = f(\theta_1)$ turns into the first equation of (13). Furthermore, $F(\theta_1) = 0$ becomes the second equation of (13). Finally, suppose that $\frac{c_{21}}{c_{12}} > \frac{K_2}{K_1}$. Then, define

$$\begin{aligned} g(u_2) &:= \frac{1}{c_{21}} \left(\frac{u_2^2}{K_2} - u_2 + c_{12}u_2 \right), \\ G(u_2) &:= g(u_2) \left(1 - \frac{g(u_2)}{K_1}\right) - c_{21}g(u_2) + c_{12}u_2. \end{aligned}$$

Then, $G(K_2) = \frac{c_{12}}{c_{21}} \left(1 - \frac{c_{12}K_2}{c_{21}K_1}\right) K_2 > 0$ and $G(u_2) \rightarrow -\infty$ as $u_2 \rightarrow \infty$. Therefore, there exists $\theta_2 > K_2$ such that $G(\theta_2) = 0$. Let $\theta_1 = g(\theta_2)$. Then, by the definition of g , $\theta_1 = g(\theta_2)$ turns into the first equation of (13). Furthermore, $G(\theta_2) = 0$ becomes the second equation of (13).

Suppose that there are two nontrivial steady states (θ_1, θ_2) and (θ'_1, θ'_2) of the system (10). From the steady state system, we can see that if $\theta_1 = \theta'_1$, then automatically $\theta_2 = \theta'_2$. Therefore, it is an appropriate assumption that $\theta_1 \neq \theta'_1$ and $\theta_2 \neq \theta'_2$ simultaneously. From the steady state system (13), we can get

$$\begin{aligned} c_{21}(\theta_1 - \theta'_1) &= (\theta_2 - \theta'_2) \left(c_{21} \frac{\theta_1}{\theta_2} + \frac{\theta'_2}{K_2} \right), \\ c_{12}(\theta_2 - \theta'_2) &= (\theta_1 - \theta'_1) \left(c_{12} \frac{\theta_2}{\theta_1} + \frac{\theta'_1}{K_1} \right). \end{aligned}$$

After multiplying the two equations, we obtain

$$c_{21}c_{12} = \left(c_{21} \frac{\theta_1}{\theta_2} + \frac{\theta'_2}{K_2} \right) \left(c_{12} \frac{\theta_2}{\theta_1} + \frac{\theta'_1}{K_1} \right),$$

which is a contradiction since the right side is bigger. Therefore, the nontrivial steady state is unique. \square

Next, we consider the steady state solution for an asymmetric case. The property depends on the ratio $\frac{c_{21}}{c_{12}}$.

Lemma 2.2. *Let $K_1 \leq K_2$ and (θ_1, θ_2) be the nontrivial steady states of (10).*

1. *If $\frac{c_{21}}{c_{12}} > \frac{K_2}{K_1}$, then $\theta_1 < K_1 \leq K_2 < \theta_2$, $\frac{K_2}{K_1} < \frac{\theta_2}{\theta_1} < \frac{c_{21}}{c_{12}}$, and $K_2 < \theta_1 + \theta_2 < K_1 + K_2$.*
2. *If $\frac{c_{21}}{c_{12}} = \frac{K_2}{K_1}$, then $\theta_1 = K_1$ and $\theta_2 = K_2$.*

3. If $\frac{c_{21}}{c_{12}} < \frac{K_2}{K_1}$, then $K_1 < \theta_1$, $\theta_2 < K_2$, $\frac{c_{21}}{c_{12}} < \frac{\theta_2}{\theta_1} < \frac{K_2}{K_1}$, and $K_1 < \theta_1 + \theta_2 < K_1 + K_2$. Furthermore, if $1 < \frac{c_{21}}{c_{12}}$, then $\theta_1 < \theta_2$.

Proof. (2) One can easily see that $\theta_1 = K_1$ and $\theta_2 = K_2$ if $\frac{c_{21}}{c_{12}} = \frac{K_2}{K_1}$.

(1) Suppose that $K_1 \leq \theta_1$. Then $\theta_2 \leq K_2$ and $c_{21}\theta_1 - c_{12}\theta_2 \leq 0$. This implies that $\frac{c_{21}}{c_{12}} \leq \frac{\theta_2}{\theta_1} \leq \frac{K_2}{K_1}$. However, this contradicts the assumption $\frac{K_2}{K_1} < \frac{c_{21}}{c_{12}}$. Therefore, $\theta_1 < K_1 \leq K_2 < \theta_2$ and hence $\frac{K_2}{K_1} < \frac{\theta_2}{\theta_1} < \frac{c_{21}}{c_{12}}$. Next, use the relations in (14) and observe

$$\begin{aligned} (K_1 + K_2) - (\theta_1 + \theta_2) &= (K_1 - \theta_1) + (K_2 - \theta_2) \\ &= \frac{K_1}{\theta_1}(c_{21}\theta_1 - c_{12}\theta_2) + \frac{K_2}{\theta_2}(-c_{21}\theta_1 + c_{12}\theta_2) \\ &= (c_{12}\theta_2 - c_{21}\theta_1)\left(\frac{K_2}{\theta_2} - \frac{K_1}{\theta_1}\right) > 0. \end{aligned}$$

(3) Suppose that $\frac{c_{21}}{c_{12}} < \frac{K_2}{K_1}$. We first show the parts related to the steady state solution (θ_1, θ_2) of (10). The steady states satisfy

$$\begin{aligned} 0 &= \theta_1\left(1 - \frac{\theta_1}{K_1}\right) - c_{21}\theta_1 + c_{12}\theta_2, \\ 0 &= \theta_2\left(1 - \frac{\theta_2}{K_2}\right) + c_{21}\theta_1 - c_{12}\theta_2. \end{aligned} \quad (14)$$

After adding the two equations, we obtain

$$\theta_1\left(1 - \frac{\theta_1}{K_1}\right) + \theta_2\left(1 - \frac{\theta_2}{K_2}\right) = 0. \quad (15)$$

Suppose that $K_2 \leq \theta_2$. Then, from the above equation, we have $\theta_1 \leq K_1$. Thus, we have $\theta_1 \leq K_1 < K_2 \leq \theta_2$ and hence $\frac{\theta_2}{\theta_1} > \frac{K_2}{K_1}$. However, from the first equation of (14), we obtain

$$0 \leq \theta_1\left(1 - \frac{\theta_1}{K_1}\right) = c_{21}\theta_1 - c_{12}\theta_2,$$

which gives $\frac{\theta_2}{\theta_1} < \frac{K_2}{K_1}$ and is a contradiction. Therefore, $K_1 < \theta_1$, $\theta_2 < K_2$, and $\frac{\theta_2}{\theta_1} < \frac{K_2}{K_1}$. Furthermore,

$$\theta_1\left(1 - \frac{\theta_1}{K_1}\right) = c_{21}\theta_1 - c_{12}\theta_2 < 0, \quad (16)$$

which gives $\frac{c_{21}}{c_{12}} < \frac{\theta_2}{\theta_1}$. Furthermore, we still have

$$(K_1 + K_2) - (\theta_1 + \theta_2) = (c_{12}\theta_2 - c_{21}\theta_1)\left(\frac{K_2}{\theta_2} - \frac{K_1}{\theta_1}\right) > 0.$$

Therefore, we have $\theta_1 + \theta_2 < K_1 + K_2$. For the comparison between θ_1 and θ_2 , we need an extra condition $1 < \frac{c_{21}}{c_{12}}$. Then, (16) gives $\theta_1 < \theta_2$. \square

The properties in Lemma 2.2 are independent of the dispersal rate. They depend only on the ratio $Q := \frac{c_{21}}{c_{12}}$. It is clear that, if $c_{12}, c_{21} \rightarrow 0$ with a fixed ratio $Q > 0$, then $\theta_i \rightarrow K_i$. Lemma 2.2(2) implies that $\theta_i \rightarrow K_i$ if $Q \rightarrow \frac{K_2}{K_1}$. Lemmas 2.2(1) and (3) show that the sum of steady states are less than the sum of carrying capacities ($\theta_1 + \theta_2 < K_1 + K_2$) for all $Q \neq \frac{K_2}{K_1}$. If we forget the condition $K_1 \leq K_2$, then Lemmas 2.2(1) and (3) are equivalent.

Lastly, we consider steady state solution for a symmetric dispersal case.

Lemma 2.3. *Let $c_{12} = c_{21} = d > 0$, $K_1 \leq K_2$, and (θ_1, θ_2) be the nontrivial steady states of (10). Then,*

1. $\theta_i \rightarrow K_i$ as $d \rightarrow 0$.
2. $\theta_i \rightarrow \frac{2K_1K_2}{K_1+K_2}$ as $d \rightarrow \infty$.
3. θ_2 decreases as $d \rightarrow \infty$.
4. If $\frac{K_2}{K_1} \leq 3$, θ_1 increases as $d \rightarrow \infty$. If $\frac{K_2}{K_1} > 3$, θ_1 increases for $d < d_0 := \frac{(1-R-\sqrt{R^2+R})^{-1}}{2}$ with $R = \frac{K_1}{K_2}$ and decrease for $d > d_0$. The maximum is $\frac{K_1+\sqrt{K_1^2+K_1K_2}}{2}$.
5. $\theta_1 + \theta_2$ decreases to $\frac{4K_1K_2}{K_1+K_2}$ as $d \rightarrow \infty$ and hence $\frac{4K_1K_2}{K_1+K_2} < \theta_1 + \theta_2$ for all $d > 0$.

Proof. It is clear that $\theta_i \rightarrow K_i$ as $d \rightarrow 0$. We consider the steady states as functions of dispersal rate d given implicitly by (14), i.e., $\theta_i = \theta_i(d)$. Then, by taking singular limits as $d \rightarrow \infty$, we have $\theta_1 - \theta_2 \rightarrow 0$. Indeed, by solving (15), we have

$$\theta_i \rightarrow \frac{2K_1K_2}{K_1 + K_2} \quad \text{as } d \rightarrow \infty.$$

By differentiating the first equation of (14) with respect to d , we obtain

$$\begin{aligned} \theta_1'(d) - \frac{2\theta_1\theta_1'(d)}{K_1} - \theta_1 - d\theta_1'(d) + \theta_2 + d\theta_2'(d) &= 0, \\ \theta_2'(d) - \frac{2\theta_2\theta_2'(d)}{K_2} - \theta_2 - d\theta_2'(d) + \theta_1 + d\theta_1'(d) &= 0. \end{aligned}$$

Since $\theta_1(0) = K_1$ and $\theta_2(0) = K_2$, we have

$$\theta_1'(0) = K_2 - K_1 \quad \text{and} \quad \theta_2'(0) = K_1 - K_2.$$

Calculations lead to

$$\theta_2'(d) = \frac{(\theta_2 - \theta_1)(1 - \frac{2\theta_1}{K_1})}{(1 - \frac{2\theta_1}{K_1} - d)(1 - \frac{2\theta_2}{K_1} - d) - d^2}.$$

Since $\theta_1 \leq \theta_2$ and $K_1 \leq \theta_1$, the numerator is zero or negative. The denominator is

$$(1 - \frac{2\theta_1}{K_1} - d)(1 - \frac{2\theta_2}{K_1} - d) - d^2 = (d\frac{\theta_2}{\theta_1} + \frac{\theta_1}{K_1})(d\frac{\theta_1}{\theta_2} + \frac{\theta_2}{K_1}) - d^2 > 0.$$

Therefore, $\theta_2'(d) \leq 0$, i.e., $\theta_2(d)$ is a decreasing function of d .

After differentiating (15) with respect to d , we obtain

$$\theta_1' = \frac{\theta_2'(1 - \frac{2\theta_2}{K_2})}{\frac{2\theta_1}{K_1} - 1}.$$

Since $K_1 \leq \theta_1$ and $\theta_2' \leq 0$, $1 - \frac{\theta_2}{K_2}$ determines the sign of θ_1' . If $\frac{K_2}{K_1} \leq 3$, then $\theta_2 \geq \frac{2K_1K_2}{K_1+K_2} \geq \frac{K_2}{2}$. Therefore, $\theta_1' \geq 0$. That is, θ_1 is monotone increasing as $d \rightarrow \infty$. On the other hand, if $\frac{K_2}{K_1} > 3$, then $\theta_2 \rightarrow \frac{2K_1K_2}{K_1+K_2} < \frac{K_2}{2}$. Since θ_2 is monotone in d , there is exactly one critical point and θ_1 changes its monotonicity once. In addition, we can see that $\theta_1' = 0$ at $\theta_2 = \frac{K_2}{2}$. After some calculations, we can see that θ_1 has its maximum $\frac{K_1+\sqrt{K_1^2+K_1K_2}}{2}$ when $2d = (1 - R - \sqrt{R^2 + R})^{-1}$ for $R = \frac{K_1}{K_2} < \frac{1}{3}$.

The derivative of $\theta_1 + \theta_2$ is given by

$$\theta_1'(d) + \theta_2'(d) = \frac{2(\frac{\theta_1}{K_1} - \frac{\theta_2}{K_2})(\theta_2 - \theta_1)(1 - \frac{2\theta_1}{K_1})}{(\frac{2\theta_1}{K_1} - 1)\{(1 - \frac{2\theta_1}{K_1} - d)(1 - \frac{2\theta_2}{K_2} - d) - d^2\}}.$$

From Lemma 2.2, one can find that the denominator is positive and the numerator is negative. This implies that $\theta_1 + \theta_2$ decreases as $d \rightarrow \infty$ and hence the limit $\frac{4K_1K_2}{K_1+K_2}$ is the infimum of $\theta_1 + \theta_2$. \square

In Figure 2, the graphs of steady states are given for dispersal rate d between 0 and 10. The carrying capacities of the two figures are chosen as examples of the two cases with $\frac{K_2}{K_1} < 3$ and $\frac{K_2}{K_1} > 3$. Find the conclusions of Lemma 2.3 from the examples. First, the steady states converge to the harmonic mean as $d \rightarrow \infty$ and to K_i 's as $d \rightarrow 0$. We can see that θ_2 is monotone decreasing in both cases. However, θ_1 is not monotone for the second case when $\frac{K_2}{K_1} > 3$. It changes its monotonicity at $d = (1 - R - \sqrt{R^2 + R})^{-1}/2 = 0.6613$.

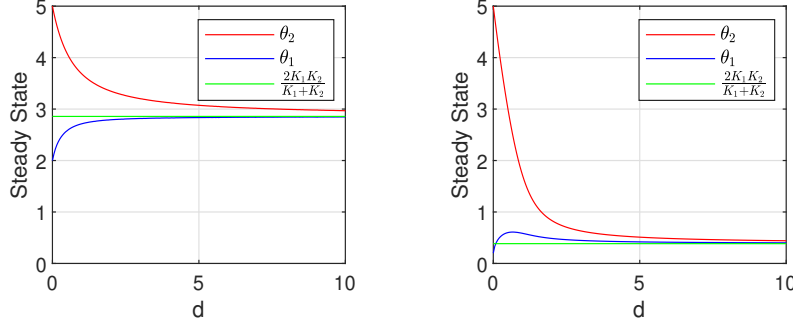


FIGURE 2. Steady state solutions of (14). In the left figure, $(K_1, K_2) = (2, 5)$ and θ_i 's are monotone. In the right one, $(K_1, K_2) = (0.2, 5)$ and θ_1 has maximum at $d = 0.6613$.

3. Uniqueness of steady states (Proof of Theorem 1.1). We first consider semi-trivial steady state solutions with a single phenotypes. If $v = 0$, the steady state for the phenotype u satisfies

$$\begin{cases} \bar{u}_1(1 - \frac{\bar{u}_1}{K_1}) + d(\bar{u}_2 - \bar{u}_1) = 0, \\ \bar{u}_2(1 - \frac{\bar{u}_2}{K_2}) + d(\bar{u}_1 - \bar{u}_2) = 0, \end{cases} \quad (17)$$

which is a special case of (13) with $c_{12} = c_{21} = d$. Hence the steady state exists uniquely by Lemma 2.1. The other semi-trivial steady state for the phenotype v satisfies

$$\begin{cases} \bar{v}_1(1 - \frac{\bar{v}_1}{K_1}) + \gamma(\frac{\bar{v}_2}{K_2})\bar{v}_2 - \gamma(\frac{\bar{v}_1}{K_1})\bar{v}_1 = 0, \\ \bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})\bar{v}_1 - \gamma(\frac{\bar{v}_2}{K_2})\bar{v}_2 = 0, \end{cases} \quad (18)$$

which contains asymmetric dispersal. However, since $\gamma(\frac{\bar{v}_1}{K_1})$ and $\gamma(\frac{\bar{v}_2}{K_2})$ are not constant, the uniqueness is not covered by Lemma 2.1. Indeed, we need an extra assumption to obtain the uniqueness. We first show the uniqueness and the existence of the steady state which are stated in Theorem 1.1.

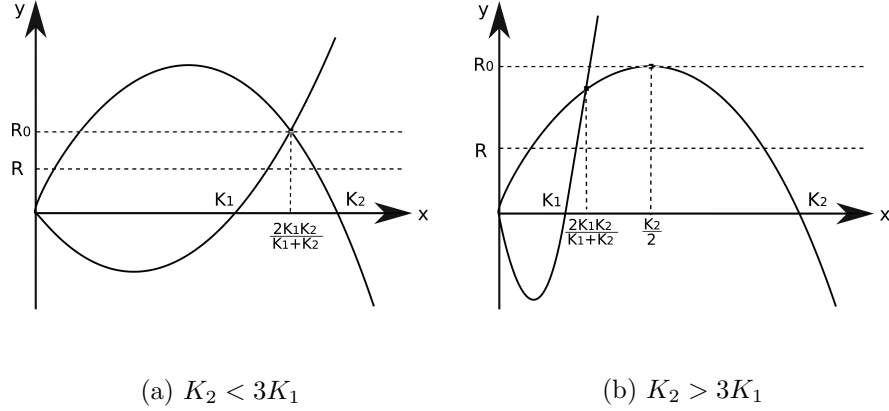


FIGURE 3. Diagrams for $y = -x(1 - \frac{x}{K_1})$ and $y = x(1 - \frac{x}{K_2})$. Steady states are intersection points with $y = R$. See (19).

Proof of Theorem 1.1. Add the two equations of (18) and obtain

$$-\bar{v}_1(1 - \frac{\bar{v}_1}{K_1}) = \bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) =: R, \quad (19)$$

where $\bar{v}_1, \bar{v}_2 > 0$. The graphs of the algebraic curves $y = -x(1 - \frac{x}{K_1})$ and $y = x(1 - \frac{x}{K_2})$ are given in Figure 3 for two cases of $K_2 < 3K_1$ and $K_2 > 3K_1$.

Suppose that $R \leq 0$. Then, we have $\bar{v}_1 \leq K_1$ and $\bar{v}_2 \geq K_2$. Since γ is an increasing function, we have

$$\bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})\bar{v}_1 - \gamma(\frac{\bar{v}_2}{K_2})\bar{v}_2 < \bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})(\bar{v}_1 - \bar{v}_2) < 0,$$

which contradicts (18). Therefore, $R > 0$ and $\bar{v}_1 > K_1$ and $\bar{v}_2 < K_2$ by (19). Find that

$$\bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})\bar{v}_1 - \gamma(\frac{\bar{v}_2}{K_2})\bar{v}_2 > \bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})(\bar{v}_1 - \bar{v}_2).$$

Therefore, if $\bar{v}_1 \geq \bar{v}_2$, it contradicts (18). Therefore, $\bar{v}_1 < \bar{v}_2$ and R should be placed $0 < R < R_0$ (see Figures 3(a) and (b)).

Now we proceed with the case with $R > 0$ and $\bar{v}_1 < \bar{v}_2$. Then, \bar{v}_2 exists on an interval $[\frac{2K_1K_2}{K_1+K_2}, K_2]$ where $\frac{2K_1K_2}{K_1+K_2}$ is the harmonic mean of K_1 and K_2 . And $\bar{v}_1 \geq K_1$ is uniquely determined by \bar{v}_2 . Hence, we may consider \bar{v}_1 as a function of \bar{v}_2 . From (18), we define a continuous function $h(\bar{v}_2)$ as follows:

$$h(\bar{v}_2) := \bar{v}_2(1 - \frac{\bar{v}_2}{K_2}) + \gamma(\frac{\bar{v}_1}{K_1})\bar{v}_1 - \gamma(\frac{\bar{v}_2}{K_2})\bar{v}_2.$$

By invoking (19), we find that $\bar{v}_1(\frac{2K_1K_2}{K_1+K_2}) = \frac{2K_1K_2}{K_1+K_2}$ and $\bar{v}_1(K_2) = K_1$. Thus, we compute

$$h(\frac{2K_1K_2}{K_1+K_2}) = \frac{2K_1K_2}{K_1+K_2} \frac{K_2 - K_1}{K_1 + K_2} + \left(\gamma(\frac{2K_2}{K_1+K_2}) - \gamma(\frac{2K_1}{K_1+K_2}) \right) \frac{2K_1K_2}{K_1+K_2} > 0,$$

$$h(K_2) = \gamma(1)K_1 - \gamma(1)K_2 < 0.$$

By the continuity of h and intermediate value theorem, there exists at least one $\bar{v}_2 \in (\frac{2K_1K_2}{K_1+K_2}, K_2)$ which satisfies $h(\bar{v}_2) = 0$ and thereby we can find a corresponding unique \bar{v}_1 .

The proof of the uniqueness requires one of two extra assumptions such that $\frac{K_2}{K_1} \leq 3$ or $\gamma(0.5) < 0.5$. First, consider the case with $\frac{K_2}{K_1} \leq 3$. Then, we observe from the relation (19) that

$$\frac{\partial \bar{v}_1}{\partial \bar{v}_2} = \frac{1 - \frac{2\bar{v}_2}{K_2}}{\frac{2\bar{v}_1}{K_1} - 1} < 0 \quad \text{for } \bar{v}_2 \in \left[\frac{2K_1K_2}{K_1 + K_2}, K_2 \right],$$

which results in

$$\frac{\partial h}{\partial \bar{v}_2} = 1 - \frac{2\bar{v}_2}{K_2} + \gamma' \left(\frac{\bar{v}_1}{K_1} \right) \frac{\bar{v}_1}{K_1} \frac{\partial \bar{v}_1}{\partial \bar{v}_2} + \gamma \left(\frac{\bar{v}_1}{K_1} \right) \frac{\partial \bar{v}_1}{\partial \bar{v}_2} - \gamma' \left(\frac{\bar{v}_2}{K_2} \right) \frac{\bar{v}_2}{K_2} - \gamma \left(\frac{\bar{v}_1}{K_1} \right) < 0,$$

where we used the monotonicity of γ . Therefore, h is strictly monotone and there exists unique zero point $\bar{v}_2 \in \left(\frac{2K_1K_2}{K_1 + K_2}, K_2 \right)$ satisfying $h(\bar{v}_2) = 0$.

If $\frac{K_2}{K_1} > 3$ and $\gamma(0.5) < 0.5$, then we find that

$$\begin{aligned} \bar{v}_1 \left(\frac{K_2}{2} \right) &= \frac{K_1 + \sqrt{K_1^2 + K_1K_2}}{2}, \\ h \left(\frac{K_2}{2} \right) &= \frac{K_2}{4} + \gamma \left(\frac{1 + \sqrt{1 + K_2/K_1}}{2} \right) \frac{K_1 + \sqrt{K_1^2 + K_1K_2}}{2} - \gamma \left(\frac{1}{2} \right) \frac{K_2}{2} > 0. \end{aligned}$$

Moreover, we have for $\bar{v}_2 \in \left[\frac{K_2}{2}, K_2 \right]$

$$\frac{\partial \bar{v}_1}{\partial \bar{v}_2} < 0, \quad \frac{\partial h}{\partial \bar{v}_2} < 0.$$

Therefore, there exists unique $\bar{v}_2 \in \left(\frac{K_2}{2}, K_2 \right)$ satisfying $h(\bar{v}_2) = 0$. (4) is a direct consequence. This completes the proof. \square

Remark 1 (Example with multiple steady states). In Theorem 1.1, the uniqueness of the steady state of (2) has been obtained under an extra assumption $K_2 \leq 3K_1$ or $\gamma(0.5) \leq 0.5$. Indeed, the monotonicity of γ alone is not enough to provide the uniqueness. We can construct a counter example. First, we take $K_1 = 2$ and $K_2 = 50$. Now we are going to find an increasing function γ that takes

$$(\theta_1, \theta_2) = (6, 20) \quad \text{and} \quad (\tilde{\theta}_1, \tilde{\theta}_2) = (6.00783, 20.4)$$

as steady states. The steady state of (2) satisfies (15) and the above steady states are chosen to satisfy it. The corresponding starvation measures are

$$(s_1, s_2) = (3, 0.4), \quad (\tilde{s}_1, \tilde{s}_2) = (3.003915, 0.408).$$

These starvation measures are ordered by

$$s_2 (= 0.4) < \tilde{s}_2 (= 0.408) < s_1 (= 3) < \tilde{s}_1 (= 3.003915).$$

If we assign γ with

$$\gamma(s_2) = 1.2, \quad \gamma(\tilde{s}_2) = 1.3098, \quad \gamma(s_1) = 2, \quad \gamma(\tilde{s}_1) = 2.4, \quad (20)$$

then both (θ_1, θ_2) and $(\tilde{\theta}_1, \tilde{\theta}_2)$ are steady states. If we construct an increasing function γ with the previous values fixed, it completes a counter example with multiple steady states.

Note a few things. First, $\frac{K_2}{K_1} = 25$ and $\gamma(0.5) \geq \gamma(0.4) = 1.2$ in the example. Hence, both conditions in the theorem fail. Second, the graph of γ is very steep at s_1 and s_2 (see Figure 4). Third, the two steady states are close to each other. These imply that, even if the monotonicity of γ alone does not give the uniqueness, one can only make the second steady state as a small perturbation of the first one by choosing γ with two steeply increasing parts.

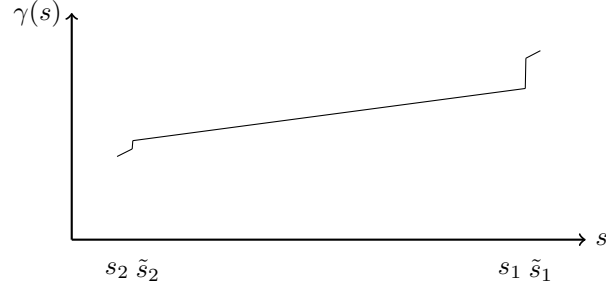


FIGURE 4. The graph of motility function $\gamma(s)$ without uniqueness. We have chosen a piecewise linear motility γ which takes the values in (20). Since s_i and \tilde{s}_i are close to each other, γ increases steeply for $s \in (s_i, \tilde{s}_i)$.

4. Linear stability analysis (Proof of Theorem 1.2). In this section we prove the main result of the paper, Theorem 1.2. The main part of the proof is the linear stability analysis of the two semi-trivial steady states $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ and $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$. We observe that the stability of E_1 is reduced by $d > 0$ and the stability of E_2 is induced by $d > 0$. We have rephrased Theorem 1.2 in the following theorem, which is equivalent to Theorem 1.2. The proof follows the logic of Theorem 4.1.

Theorem 4.1. *Let $K_1 < K_2$ and γ be an increasing smooth function. We assume $\frac{K_2}{K_1} \leq 3$ or $\gamma(0.5) \leq 0.5$. (i) There exists a $d_1 > 0$ such that $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ is linearly stable for $d < d_1$ and is unstable for $d > d_1$. (ii) There exists a d_2 such that $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ is linearly stable for $d > d_2$ and is unstable for $d < d_2$. (iii) There exists $d_3 > 0$ such that (5) has a positive steady state. (iv) Furthermore, $d_1 = d_2 = d_3 < \gamma(\frac{\bar{v}_2}{K_2})$.*

Proof. (i) The Jacobian matrix for the semitrivial steady state $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ is

$$J_1 = \begin{bmatrix} 1 - \frac{2\bar{u}_1}{K_1} - d & d & -\frac{\bar{u}_1}{K_1} & 0 \\ d & 1 - \frac{2\bar{u}_2}{K_2} - d & 0 & -\frac{\bar{u}_2}{K_2} \\ 0 & 0 & 1 - \frac{\bar{u}_1}{K_1} - \gamma_1 & \gamma_2 \\ 0 & 0 & \gamma_1 & 1 - \frac{\bar{u}_2}{K_2} - \gamma_2 \end{bmatrix} =: \begin{bmatrix} A & B \\ C & D \end{bmatrix},$$

where $\gamma_i = \gamma(\frac{\bar{u}_i}{K_i})$, $i = 1, 2$ and A, B, C, D are 2×2 matrices. Since $C = 0$, the eigenvalues of A and D determine the stability of E_1 . Since (\bar{u}_1, \bar{u}_2) satisfies (14) with $c_{12} = c_{21} = d$, we have from Lemma 2.3 that

$$K_1 < \bar{u}_1 < \bar{u}_2 < K_2, \quad \bar{u}_1 + \bar{u}_2 < K_1 + K_2.$$

Then, we see that for any $d > 0$

$$\begin{aligned} \text{tr}(A) &= 1 - \frac{2\bar{u}_1}{K_1} - d + 1 - \frac{2\bar{u}_2}{K_2} - d < 0, \\ \det(A) &= \left(1 - \frac{2\bar{u}_1}{K_1} - d\right) \left(1 - \frac{2\bar{u}_2}{K_2} - d\right) - d^2 \\ &= \left(-d \frac{\bar{u}_2}{\bar{u}_1} - \frac{\bar{u}_1}{K_1}\right) \left(-d \frac{\bar{u}_1}{\bar{u}_2} - \frac{\bar{u}_2}{K_2}\right) - d^2 > 0. \end{aligned}$$

Therefore, the eigenvalues of the symmetric matrix A are negative.

Now consider the asymmetric matrix D . Its trace is

$$\begin{aligned} \operatorname{tr}(D) &= 1 - \frac{\bar{u}_1}{K_1} - \gamma_1 + 1 - \frac{\bar{u}_2}{K_2} - \gamma_2 \\ &= \left(1 - \frac{\bar{u}_1}{K_1} - d\right) + \left(1 - \frac{\bar{u}_2}{K_2} - d\right) + 2d - \gamma_1 - \gamma_2 \\ &= -d \left(\frac{\bar{u}_2}{\bar{u}_1} + \frac{\bar{u}_1}{\bar{u}_2}\right) + 2d - \gamma_1 - \gamma_2 < -\gamma_1 - \gamma_2 < 0. \end{aligned}$$

Its determinant is

$$\begin{aligned} \det(D) &= \left(1 - \frac{\bar{u}_1}{K_1} - \gamma_1\right) \left(1 - \frac{\bar{u}_2}{K_2} - \gamma_2\right) - \gamma_1 \gamma_2 \\ &= \left(-d \frac{\bar{u}_2}{\bar{u}_1} + d - \gamma_1\right) \left(-d \frac{\bar{u}_1}{\bar{u}_2} + d - \gamma_2\right) - \gamma_1 \gamma_2 \\ &= d \left(1 - \frac{\bar{u}_1}{\bar{u}_2}\right) \left(d \left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1}\right) \\ &= d \left(1 - \frac{\bar{u}_1}{\bar{u}_2}\right) \left(1 - \frac{\bar{u}_1}{K_1} - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1}\right). \end{aligned}$$

Since $\bar{u}_1 < \bar{u}_2$, the sign of $\det(D)$ is same as the sign of

$$p(d) := 1 - \frac{\bar{u}_1}{K_1} - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1}. \quad (21)$$

If $\frac{K_2}{K_1} \leq 3$, Lemma 2.3 implies that \bar{u}_1 increases and \bar{u}_2 decreases as $d \rightarrow \infty$. Therefore, $p(d)$ decreases as $d \rightarrow \infty$. Then, by the intermediate value theorem and the asymptotic behaviors of $p(d)$ for d large and small, i.e.,

$$\lim_{d \rightarrow 0} p(d) = -\gamma(1) + \gamma(1) \frac{K_2}{K_1} > 0,$$

$$\lim_{d \rightarrow \infty} p(d) = 1 - \frac{2K_2}{K_1 + K_2} - \gamma \left(\frac{2K_2}{K_1 + K_2}\right) + \gamma \left(\frac{2K_1}{K_1 + K_2}\right) < 0,$$

there exists a unique constant $d_1 > 0$ such that $p(d) > 0$ for $d < d_1$ and $p(d) < 0$ for $d > d_1$. Therefore, E_1 is linearly stable for $d < d_1$ and unstable for $d > d_1$.

If $\frac{K_2}{K_1} > 3$ and $\gamma(0.5) < 0.5$, by Lemma 2.3, there exists $d_0 = 1/2(1 - R - \sqrt{R^2 + R}) > 0$ for $R = \frac{K_1}{K_2} < \frac{1}{3}$ such that u_1 increases for $d < d_0$ and decreases for $d > d_0$. Thus, $p(d)$ decreases for $d \in (0, d_0)$. Since $\bar{u}_2(d_0) = \frac{K_2}{2}$, we observe

$$\begin{aligned} p(d) &= d \left(1 - \frac{\bar{u}_2}{\bar{u}_1}\right) - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1} \\ &= \frac{\bar{u}_2}{\bar{u}_1} \left(d \left(\frac{\bar{u}_1}{\bar{u}_2} - 1\right) - \gamma_1 \frac{\bar{u}_1}{\bar{u}_2} + \gamma_2\right) \\ &= \frac{\bar{u}_2}{\bar{u}_1} \left(\frac{\bar{u}_2}{K_2} - 1 - \gamma_1 \frac{\bar{u}_1}{\bar{u}_2} + \gamma_2\right), \end{aligned}$$

which implies

$$p(d) \leq \frac{\bar{u}_2}{\bar{u}_1} \left(\frac{1}{2} - 1 - \gamma_1 \frac{\bar{u}_1}{\bar{u}_2} + \gamma(0.5)\right) < 0 \quad \text{for } d \in [d_0, \infty).$$

Therefore, we also conclude that there exists

$$d_1 \in (0, d_0) \quad (22)$$

such that E_1 is linearly stable for $d < d_1$ and unstable for $d > d_1$.

(ii) The Jacobian matrix for the semitrivial steady state $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ is

$$J_2 = \begin{bmatrix} 1 - \frac{\bar{v}_1}{K_1} - d & d & 0 & 0 \\ d & 1 - \frac{\bar{v}_2}{K_2} - d & 0 & 0 \\ -\tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} - \frac{\bar{v}_1}{K_1} & \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} & 1 - \frac{2\bar{v}_1}{K_1} - \tilde{\gamma}_1 - \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} & \tilde{\gamma}_2 + \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} \\ \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} & -\tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} - \frac{\bar{v}_2}{K_2} & \tilde{\gamma}_1 + \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} & 1 - \frac{2\bar{v}_2}{K_2} - \tilde{\gamma}_2 - \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} \end{bmatrix}$$

$$=: \begin{bmatrix} A & B \\ C & D \end{bmatrix},$$

where $\tilde{\gamma}_i = \gamma_i(\frac{\bar{v}_i}{K_i})$, $\tilde{\gamma}_i' = \gamma_i'(\frac{\bar{v}_i}{K_i})$, $i = 1, 2$ and A, B, C, D are 2×2 matrices. Since $B = 0$, the eigenvalues of A and D determine the stability of E_2 . From (18), the trace of D is given by

$$\begin{aligned} tr(D) &= 1 - \frac{2\bar{v}_1}{K_1} - \tilde{\gamma}_1 - \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} + 1 - \frac{2\bar{v}_2}{K_2} - \tilde{\gamma}_2 - \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} \\ &= -\tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} - \frac{\bar{v}_1}{K_1} - \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1} - \tilde{\gamma}_1 \frac{\bar{v}_1}{K_1} - \frac{\bar{v}_2}{K_2} - \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2} < 0. \end{aligned}$$

Under the assumption, $\frac{K_1}{K_2} < 3$ or $\gamma(0.5) < 0.5$, Theorem 1.1 gives

$$1 - \frac{2\bar{v}_1}{K_1} < 0 \quad \text{and} \quad 1 - \frac{2\bar{v}_2}{K_2} < 0,$$

which leads to

$$\begin{aligned} det(D) &= \left(1 - \frac{2\bar{v}_1}{K_1} - \tilde{\gamma}_1 - \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1}\right) \left(1 - \frac{2\bar{v}_2}{K_2} - \tilde{\gamma}_2 - \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2}\right) \\ &\quad - \left(\tilde{\gamma}_1 + \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1}\right) \left(\tilde{\gamma}_2 + \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2}\right) \\ &= \left(1 - \frac{2\bar{v}_1}{K_1}\right) \left(1 - \frac{2\bar{v}_2}{K_2}\right) - \left(1 - \frac{2\bar{v}_1}{K_1}\right) \left(\tilde{\gamma}_2 + \tilde{\gamma}_2' \frac{\bar{v}_2}{K_2}\right) \\ &\quad - \left(1 - \frac{2\bar{v}_2}{K_2}\right) \left(\tilde{\gamma}_1 + \tilde{\gamma}_1' \frac{\bar{v}_1}{K_1}\right) > 0. \end{aligned}$$

Therefore, the real parts of the eigenvalues of D are negative.

The trace of the symmetric matrix A is given by

$$tr(A) = 1 - \frac{\bar{v}_1}{K_1} - d + 1 - \frac{\bar{v}_2}{K_2} - d.$$

Note that

$$2 - \frac{\bar{v}_1}{K_1} - \frac{\bar{v}_2}{K_2} = \tilde{\gamma}_1 \left(1 - \frac{\bar{v}_2}{\bar{v}_1}\right) + \tilde{\gamma}_2 \left(1 - \frac{\bar{v}_1}{\bar{v}_2}\right) < \tilde{\gamma}_1 \left(2 - \frac{\bar{v}_2}{\bar{v}_1} - \frac{\bar{v}_1}{\bar{v}_2}\right) < 0.$$

Therefore, the trace of A is negative and hence A has two negative eigenvalues if and only if its determinant is negative. The determinant of A is

$$\begin{aligned} det(A) &= \left(1 - \frac{\bar{v}_1}{K_1} - d\right) \left(1 - \frac{\bar{v}_2}{K_2} - d\right) - d^2 \\ &= \left(1 - \frac{\bar{v}_1}{K_1}\right) \left(1 - \frac{\bar{v}_2}{K_2}\right) - d \left(2 - \frac{\bar{v}_1}{K_1} - \frac{\bar{v}_2}{K_2}\right), \end{aligned} \quad (23)$$

where the relation (18) is used. By Lemma 2.2(3), we have

$$\left(1 - \frac{\bar{v}_1}{K_1}\right) \left(1 - \frac{\bar{v}_2}{K_2}\right) < 0.$$

In conclusion, $\det(A)$ is a linear function of $d > 0$ with a positive slope and a negative y-intercept. Therefore, there exists a unique constant $d_2 > 0$ such that E_2 is linearly stable for $d > d_2$ and unstable for $d < d_2$.

(iii) A positive state $E_3 = (u_1^*, u_2^*, v_1^*, v_2^*)$ is a steady state solution of system (5) if and only if it satisfies

$$\begin{aligned} K_1 - (u_1^* + v_1^*) + K_1 d \left(\frac{1}{a} - 1\right) &= 0, \\ K_2 - (u_2^* + v_2^*) + K_2 d(a - 1) &= 0, \\ K_1 - (u_1^* + v_1^*) + K_1 \left(\gamma \left(\frac{u_2^* + v_2^*}{K_2}\right) \frac{1}{b} - \gamma \left(\frac{u_1^* + v_1^*}{K_1}\right)\right) &= 0, \\ K_2 - (u_2^* + v_2^*) + K_2 \left(\gamma \left(\frac{u_1^* + v_1^*}{K_1}\right) b - \gamma \left(\frac{u_2^* + v_2^*}{K_2}\right)\right) &= 0, \end{aligned} \quad (24)$$

where $a := \frac{u_1^*}{u_2^*} > 0$ and $b := \frac{v_1^*}{v_2^*} > 0$. Adding the first and third equations, and the second and fourth equations of (24), we obtain

$$\begin{aligned} d \left(\frac{1}{a} - 1\right) &= \gamma \left(\frac{u_2^* + v_2^*}{K_2}\right) \frac{1}{b} - \gamma \left(\frac{u_1^* + v_1^*}{K_1}\right), \\ d(a - 1) &= \gamma \left(\frac{u_1^* + v_1^*}{K_1}\right) b - \gamma \left(\frac{u_2^* + v_2^*}{K_2}\right). \end{aligned}$$

Add the two after a multiplication of b to the first equation and obtain

$$d(a - b) \left(1 - \frac{1}{a}\right) = 0.$$

First, suppose that $a = 1$. Then, the first two equations in (24) imply

$$u_1^* + v_1^* = K_1 \quad \text{and} \quad u_2^* + v_2^* = K_2,$$

and hence

$$\gamma \left(\frac{u_1^* + v_1^*}{K_1}\right) = \gamma \left(\frac{u_2^* + v_2^*}{K_2}\right).$$

The last two equations in (24) imply that $b = 1$ and hence

$$K_1 = u_1^* + v_1^* = u_2^* + v_2^* = K_2,$$

which contradicts the assumption $K_1 < K_2$. Therefore, $a = b \neq 1$.

Plug $u_1^* = au_2^*$ and $v_1^* = av_2^*$ into the second equation of (24), combine it with the first equation, and obtain

$$f(a) := dK_2a^3 + (1 - d)K_2a^2 + (d - 1)K_1a - dK_1 = 0. \quad (25)$$

We claim that there exists a unique zero $a_0 \in (0, 1)$ of $f(a)$ for each $d > 0$. Since $f(0) = -dK_1 < 0$ and $f(1) = K_2 - K_1 > 0$, there exists $a_0 \in (0, 1)$ such that $f(a_0) = 0$ for each $d > 0$.

Now we show the uniqueness for a given $d > 0$. Observe that

$$f'(a) = 3dK_2a^2 + 2(1 - d)K_2a + (d - 1)K_1$$

has the axis of symmetry $a = \frac{d-1}{3d}$. Thus, if $d \in (0, 1]$, then f' has two distinct zeros with different signs. Otherwise, we compute the discriminant of cubic polynomial f such that

$$D_3 = (d-1)^4 K_1^2 K_2^2 - 4d(d-1)^3 K_1^3 K_2 - 4d(d-1)^3 K_1 K_2^3 - 27d^4 K_1^2 K_2^2 + 18d^2(d-1)^2 K_1^2 K_2^2 < 0 \quad \text{for } d > 1,$$

which means that the equation (25) has one real zero and two complex conjugate zeros. Therefore, $a_0(d)$ uniquely exists for $d > 0$ and is less than 1.

Now, from (24), we introduce two functions $g(d)$ and $h(d)$ as the following:

$$g(d) := K_2 (1 + d(a_0(d) - 1)),$$

$$h(d) := K_2 \left(1 + \gamma \left(\frac{a_0(d)g(d)}{K_1} \right) a_0(d) - \gamma \left(\frac{g(d)}{K_2} \right) \right).$$

Then, the existence of $d_3 > 0$ satisfying $g(d_3) = h(d_3)$ guarantees the existence of coexistence steady states. The cubic equation (25) gives the asymptotic behavior of a_0 where d approaches 0 or ∞ such that

$$\lim_{d \rightarrow 0} a_0(d) = \frac{K_1}{K_2}, \quad \lim_{d \rightarrow \infty} a_0(d) = 1.$$

Moreover, the relation $d(a_0(d) - 1) = \frac{-K_2 a_0^2 + K_1 a_0}{K_2 a_0^2 + K_1}$ implies

$$\lim_{d \rightarrow 0} d(a_0(d) - 1) = 0, \quad \lim_{d \rightarrow \infty} d(a_0(d) - 1) = \frac{K_1 - K_2}{K_1 + K_2}.$$

Sequentially, we see that

$$\lim_{d \rightarrow 0} g(d) = K_2, \quad \lim_{d \rightarrow \infty} g(d) = \frac{2K_1 K_2}{K_1 + K_2},$$

$$\lim_{d \rightarrow 0} h(d) = K_2 \left(1 + \gamma(1) \left(\frac{K_1}{K_2} - 1 \right) \right) < K_2,$$

$$\lim_{d \rightarrow \infty} h(d) = K_2 \left(1 + \gamma \left(\frac{2K_2}{K_1 + K_2} \right) - \gamma \left(\frac{2K_1}{K_1 + K_2} \right) \right) > K_2 > \frac{2K_1 K_2}{K_1 + K_2}.$$

Therefore, there exists $d_3 \in (0, \infty)$ such that $g(d_3) = h(d_3)$.

We can construct a positive solution by taking any $u_2^*, v_2^* > 0$ such that $u_2^* + v_2^* = g(d_3)$. Then, take $u_1^* = a_0 u_2^*$ and $v_1^* = a_0 v_2^*$. Then, one can easily find that $(u_1^*, u_2^*, v_1^*, v_2^*)$ is a positive steady state. The positive steady state is not unique if it exists.

(iv) Suppose that $(u_1^*, u_2^*, v_1^*, v_2^*)$ is a coexistence steady state with $d = d_3$. Then $u_1^* + v_1^*$, $u_2^* + v_2^*$ and $a_0 = \frac{u_1^*}{u_2^*} = \frac{v_1^*}{v_2^*} \in (0, 1)$ are uniquely determined by a given d_3 . Now, we fix the ratio a_0 and let v_1^* and v_2^* go to 0, then (24) converges to

$$\begin{cases} u_1^* \left(1 - \frac{u_1^*}{K_1} \right) + d_3 (u_2^* - u_1^*) = 0, \\ u_2^* \left(1 - \frac{u_2^*}{K_2} \right) + d_3 (u_1^* - u_2^*) = 0, \\ u_1^* \left(1 - \frac{u_1^*}{K_1} \right) + \left(\gamma \left(\frac{u_2^*}{K_2} \right) u_2^* - \gamma \left(\frac{u_1^*}{K_1} \right) u_1^* \right) = 0, \\ u_2^* \left(1 - \frac{u_2^*}{K_2} \right) + \left(\gamma \left(\frac{u_1^*}{K_1} \right) u_1^* - \gamma \left(\frac{u_2^*}{K_2} \right) u_2^* \right) = 0. \end{cases} \quad (26)$$

The first and second equations of (26) coincide with (17). Furthermore, if the second and fourth equations of (26) are added, we obtain

$$d_3 \left(\frac{u_1^*}{u_2^*} - 1 \right) - \gamma \left(\frac{u_1^*}{K_1} \right) \frac{u_1^*}{u_2^*} + \gamma \left(\frac{u_2^*}{K_2} \right) = 0. \quad (27)$$

On the other hand, we rewrite (21) as

$$\begin{aligned} p(d) &= 1 - \frac{\bar{u}_1}{K_1} - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1} = d \left(1 - \frac{\bar{u}_2}{\bar{u}_1} \right) - \gamma_1 + \gamma_2 \frac{\bar{u}_2}{\bar{u}_1} \\ &= \frac{\bar{u}_2}{\bar{u}_1} \left(d \left(\frac{\bar{u}_1}{\bar{u}_2} - 1 \right) - \gamma_1 \frac{\bar{u}_1}{\bar{u}_2} + \gamma_2 \right). \end{aligned}$$

Therefore, (27) implies that $p(d_3) = 0$ and we conclude that $d_3 = d_1$.

Similarly, we may take u_1^* and u_2^* go to 0 with fixed rate a_0 . Then, (24) turns into

$$\begin{aligned} 1 - \frac{v_1^*}{K_1} &= d_3 \left(1 - \frac{v_2^*}{v_1^*} \right), \\ 1 - \frac{v_2^*}{K_2} &= d_3 \left(1 - \frac{v_1^*}{v_2^*} \right), \\ v_1^* \left(1 - \frac{v_1^*}{K_1} \right) + \left(\gamma \left(\frac{v_2^*}{K_2} \right) v_2^* - \gamma \left(\frac{v_1^*}{K_1} \right) v_1^* \right) &= 0, \\ v_2^* \left(1 - \frac{v_2^*}{K_2} \right) + \left(\gamma \left(\frac{v_1^*}{K_1} \right) v_1^* - \gamma \left(\frac{v_2^*}{K_2} \right) v_2^* \right) &= 0. \end{aligned} \quad (28)$$

The third and fourth equations of (28) are same as (18). Next, the first and the second equations of (28) yield

$$d_3 = \frac{(1 - \frac{v_1^*}{K_1})(1 - \frac{v_2^*}{K_2})}{2 - \frac{v_1^*}{K_1} - \frac{v_2^*}{K_2}}.$$

Therefore, (23) leads to

$$d_3 = d_2.$$

Collecting the above results, we finally conclude that $d_3 = d_1 = d_2$.

From (23), it suffices to show that

$$\det(E)|_{d=\gamma(\frac{\bar{v}_2}{K_2})} > 0. \quad (29)$$

A direct calculation from (18) implies that

$$\begin{aligned} 0 &= \left(1 - \frac{\bar{v}_1}{K_1} \right) \left(1 - \frac{\bar{v}_2}{K_2} \right) - \gamma \left(\frac{\bar{v}_1}{K_1} \right) \left(1 - \frac{\bar{v}_2}{K_2} \right) - \gamma \left(\frac{\bar{v}_2}{K_2} \right) \left(1 - \frac{\bar{v}_1}{K_1} \right) \\ &< \left(1 - \frac{\bar{v}_1}{K_1} \right) \left(1 - \frac{\bar{v}_2}{K_2} \right) - \gamma \left(\frac{\bar{v}_2}{K_2} \right) \left(2 - \frac{\bar{v}_1}{K_1} - \frac{\bar{v}_2}{K_2} \right), \end{aligned}$$

which is equivalent to (29). This completes the proof of (iv). \square

The three critical dispersal rates are identical and it was set d_* in Theorem 1.2 by $d_* := d_1 = d_2 = d_3$. If $d \neq d_*$, then there is only one of the two semi-trivial steady state is stable and the other is unstable. The unstable semi-trivial steady state is a saddle point. The coexistence appears only for the critical dispersal case $d = d_*$. In this case the positive steady state is not unique, but there is one parameter family.

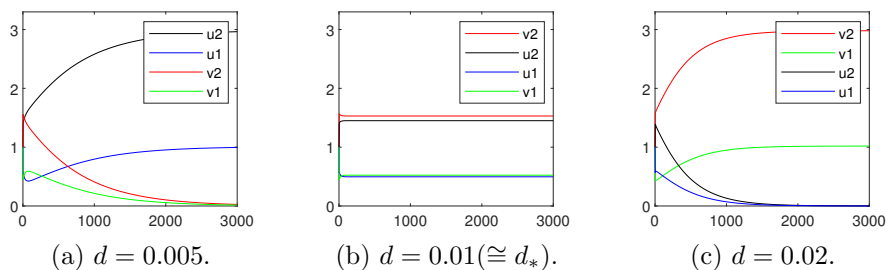


FIGURE 5. Asymptotic behavior of numerical computation of (31)-(32) with $\epsilon = 0.02$. The legends are ordered by the size of asymptotic limits.

5. Numerical simulations. In this section, we test the behavior of the solution numerically and compare the simulation to the theoretical results. The motility function $\gamma(s)$ has been chosen as an approximation of a step function,

$$\gamma^\epsilon(s) = \begin{cases} \ell & \text{for } 0 \leq s < 1 - \epsilon, \\ h & \text{for } s \geq 1 + \epsilon, \\ \frac{h - \ell}{2\epsilon}(s - (1 + \epsilon)) + h & \text{for } 1 - \epsilon \leq s < 1 + \epsilon. \end{cases} \quad (30)$$

We solve

$$\begin{aligned} \dot{u}_1 &= u_1(1 - s_1) + d(u_2 - u_1), \\ \dot{u}_2 &= u_2(1 - s_2) + d(u_1 - u_2), \\ \dot{v}_1 &= v_1(1 - s_1) + \gamma^\epsilon(s_2)v_2 - \gamma^\epsilon(s_1)v_1, \\ \dot{v}_2 &= v_2(1 - s_2) + \gamma^\epsilon(s_1)v_1 - \gamma^\epsilon(s_2)v_2, \end{aligned} \quad (31)$$

where s_i is the starvation measure at i -th patch given by

$$s_i = \frac{u_i + v_i}{K_i}, \quad i = 1, 2.$$

For numerical simulations, we fix the carrying capacities, initial values, and the parameters of the motility function by

$$u_1(0) = u_2(0) = v_1(0) = v_2(0) = 1, \quad K_1 = 1, \quad K_2 = 3, \quad h = 0.1, \quad \text{and } \ell = 0.01. \quad (32)$$

In Figure 5, numerical solutions are given with $\epsilon = 0.02$. We can observe in Figure 5(b) that, if $d = 0.01$, the two species coexist. This is the dispersal rate that corresponds to the critical one d_* in Theorem 1.2. The theorem says that, if $d < d_*$, $E_1 = (\bar{u}_1, \bar{u}_2, 0, 0)$ is stable and $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ is unstable. In the numerical simulation, we can see that the solution converges to the stable steady state in Figure 5(a). If $d > d_*$, the stability is reversed and the solution converges to $E_2 = (0, 0, \bar{v}_1, \bar{v}_2)$ in Figure 5(c).

Remember that the motility function γ is assumed to be smooth. In the stability analysis, the existence of its derivative has been used. This assumption has more than a technical reason. For example, we have tested the dependency on ϵ in Figure 6. We can see that there is a critical size of $\epsilon = \epsilon_0$ between $\epsilon = 0.1$ and $\epsilon = 0.01$ that flips the stability of semi-trivial steady states (see Figures 6(a) and 6(b)). In conclusion, if ϵ is smaller than the critical size, the species v is selected.

However, when $\epsilon = 0$, the dynamics is changed one more time and both species coexist as observed in Figure 6(c). The coexistence of this case holds for all $d > 0$.

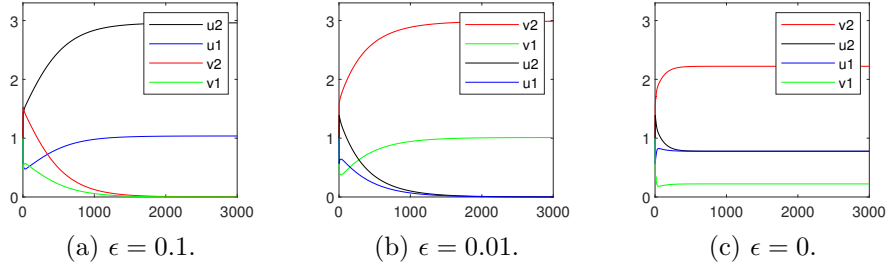


FIGURE 6. Asymptotic behavior ($h = 0.1, \ell = 0.01, d = 0.02$).
The legends are ordered by the size of asymptotic limits.

Notice that the coexistence of Theorem 1.2 is only for the specific dispersal rate $d = d_*$ (see Figure 5(b)) and the mechanisms of coexistence for the two cases are different. The theory with discontinuous motility function requires more than the analysis of this paper.

6. Discussion. Migration is the key strategy for survival of a biological species when its habitat deteriorates. The effect of symmetric dispersal, i.e., the case with $c_{ij} = c_{ji}$, has been studied well. If K_1 and K_2 are different and the dispersal is symmetric, the smallest dispersal rate is selected (see [12, 22]). In other words, symmetric dispersal reduces survival chance. However, the essence of biological dispersal is in its adaptability to environmental changes and hence asymmetric dispersal is a natural choice. We have chosen an asymmetric dispersal as in (2) which is enhanced by starvation. From the stability analysis of a linearized problem of the competition system (5), we obtained a critical dispersal rate $d_* < \gamma(\frac{v_2}{k_2})$ in Theorem 1.2 such that the asymmetric dispersal can be selected if $d_* < d$. If $d < d_*$, the smaller dispersal is still selected since the environment is not changed at all.

We did not attempt to estimate the critical diffusivity d_* . It depends on the motility function γ and the spatial heterogeneity $\frac{K_2}{K_1}$. An estimate is from (22) where d_0 is the one in Lemma (2.3)(4) with $R = \frac{K_1}{K_2}$. We can see that d_0 decreases to 0.5 as the spatial heterogeneity increases, i.e., as $R = \frac{K_1}{K_2} \rightarrow 0$. This provides an upper bound of d_* for all monotone increasing motility function γ such that $\gamma(0.5) \leq 0.5$. In the competition system (5), the two species have the same population dynamics. Since the two species are identical except their dispersal strategies, there is no parameter regime of coexistence. The two critical dispersal rates in Theorem 4.1 are identical, i.e., $d_1 = d_2$. If the two species have different population dynamics and different dispersal strategies, the two critical dispersal rates can be different and coexistence may be obtained (see [19]). In this paper, the carrying capacities, K_1 and K_2 , are fixed. However, the strength of the asymmetric dispersal enhanced by starvation will appear when the environment fluctuates temporally. In the case, the critical diffusivity d_* may decrease to zero.

Appendix A. Corresponding PDE. Consider a reaction-diffusion equation,

$$v_t = v \left(1 - \frac{v}{m} \right) + \Delta(\gamma(s)v), \quad x \in \Omega, \quad (33)$$

where v is the population density, $m = m(x)$ is the spatially heterogeneous carrying capacity, and $s = \frac{v}{m}$ is the starvation measure. In this PDE model, the effects of

domain size and habitat quality are distinguishable. If the domain Ω has boundary, the zero-flux boundary condition fits the patch problem since the population stays in the system. We can see that (33) is a PDE version of (2). For example, we may compare a finite difference scheme for (33) in one space dimension and (2). Let $x_i = i\Delta x$ be the space mesh. Then, a centered space finite difference scheme is written by

$$\dot{v}_i = v_i \left(1 - \frac{v_i}{m_i}\right) + \frac{1}{\Delta x^2} \left(\gamma(s_{i+1})v_{i+1} + \gamma(s_{i-1})v_{i-1} - 2\gamma(s_i)v_i\right),$$

where we take $m_i = m(x_i)$, $v_i(t) \cong v(x_i, t)$, and $s_i \cong \frac{v_i}{m_i}$. In other words, if grid point x_i is considered as the i -th patch, the PDE model (33) corresponds to a special patch model that individuals migrate to one of two adjacent patches and the migration matrix is given by $c_{ij} = \frac{\gamma(s_j)}{\Delta x^2}$ for $i = j \pm 1$ and $c_{ij} = 0$ otherwise.

The uniqueness of steady state solution of the PDE model (33) is not known. It is clear that the monotonicity of γ alone is not enough to obtain the uniqueness due to the counter example for the patch problem (see Remark 1). One may consider the uniqueness under similar assumptions such as $\max_{x \in \Omega} m(x) \leq 3 \min_{x \in \Omega} m(x)$ or $\gamma(0.5) \leq 0.5$.

Appendix B. Patch problem with uniqueness. Consider a two-patch problem with a modified population dynamics,

$$\begin{aligned} \dot{u}_1 &= u_1(K_1 - u_1) - \gamma\left(\frac{u_1}{K_1}\right)u_1 + \gamma\left(\frac{u_2}{K_2}\right)u_2, \\ \dot{u}_2 &= u_2(K_2 - u_2) + \gamma\left(\frac{u_1}{K_1}\right)u_1 - \gamma\left(\frac{u_2}{K_2}\right)u_2. \end{aligned} \quad (34)$$

Notice that K_i is now the growth rate and the carrying capacity at the i -th patch at the same time. For example, the population dynamics can be written by $K_i u_i (1 - \frac{u_i}{K_i})$. The model is partly similar as and different from (2). An important difference is the uniqueness of a steady state solution, which can be obtained by the monotonicity of γ only.

Theorem B.1. *Let $K_1 \leq K_2$, γ be monotone increasing, and (θ_1, θ_2) be a steady state solution of (34). (i) $K_1 \leq \theta_1 \leq \theta_2 \leq K_2$ and $K_1 + K_2 \leq \theta_1 + \theta_2$. (ii) The steady state solution of (34) is unique.*

Proof. The first part is similarly proved as Lemma 2.2 and is omitted. We prove the second part. Let (θ_1, θ_2) be a steady state. Then, it satisfies

$$\begin{aligned} 0 &= \theta_1(K_1 - \theta_1) - \gamma\left(\frac{\theta_1}{K_1}\right)\theta_1 + \gamma\left(\frac{\theta_2}{K_2}\right)\theta_2, \\ 0 &= \theta_2(K_2 - \theta_2) + \gamma\left(\frac{\theta_1}{K_1}\right)\theta_1 - \gamma\left(\frac{\theta_2}{K_2}\right)\theta_2. \end{aligned}$$

Add the two equations and obtain

$$\left(\theta_1 - \frac{K_1}{2}\right)^2 + \left(\theta_2 - \frac{K_2}{2}\right)^2 = \frac{K_1^2 + K_2^2}{4}.$$

Since θ_1 and θ_2 are related to by part (i), we may consider θ_2 as a decreasing function of θ_1 . Suppose there are two distinct steady state (θ_1, θ_2) and $(\tilde{\theta}_1, \tilde{\theta}_2)$ with $\theta_1 < \tilde{\theta}_1$. Due to the monotonicity, $\tilde{\theta}_2 < \theta_2$. Then we have

$$0 < \theta_2 - \tilde{\theta}_2 = (K_2 - \tilde{\theta}_2) - (K_2 - \theta_2) = \gamma\left(\frac{\tilde{\theta}_2}{K_2}\right) - \gamma\left(\frac{\tilde{\theta}_1}{K_1}\right)\frac{\tilde{\theta}_1}{\tilde{\theta}_2} - \gamma\left(\frac{\theta_2}{K_2}\right) + \gamma\left(\frac{\theta_1}{K_1}\right)\frac{\theta_1}{\theta_2}.$$

However, the last term is negative because of $\theta_1 < \tilde{\theta}_1$, $\tilde{\theta}_2 < \theta_2$ and monotonicity of γ . Therefore, we can conclude that the steady state of (34) is unique. \square

A PDE version of (34) can be written by

$$v_t = v(m(x) - v) + \Delta(\gamma(s)v), \quad s = \frac{v}{m}.$$

From the uniqueness of steady state of the patch problem, one might expect that the steady state solution $\theta(x)$ of the PDE model is unique under a single assumption that γ is monotone increasing. However, the uniqueness of a steady state solution has been proved in [18] under an extra assumption $\max m(x) \leq 2 \min m(x)$ or $\bar{n} \cdot \nabla m \leq 0$ on $\partial\Omega$ and $\Delta m + \frac{m^2}{2\gamma(2)} \geq 0$ in $\bar{\Omega}$. It is not clear if such extra conditions can be removed or not.

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REFERENCES

- [1] R. Arditi, L.-F. Bersier and R. P. Rohr, [The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka](#), *Ecosphere*, **7** (2016), e01599.
- [2] R. Arditi, C. Lobry and T. Sari, [Asymmetric dispersal in the multi-patch logistic equation](#), *Theoret. Popul. Biol.*, **120** (2018), 11–15.
- [3] R. S. Cantrell, C. Cosner, D. L. Deangelis and V. Padron, [The ideal free distribution as an evolutionarily stable strategy](#), *J. Biol. Dynam.*, **1** (2007), 249–271.
- [4] R. S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons, Ltd., Chichester, 2003.
- [5] E. Cho and Y.-J. Kim, [Starvation driven diffusion as a survival strategy of biological organisms](#), *Bull. Math. Biol.*, **75** (2013), 845–870.
- [6] W. Choi, S. Baek and I. Ahn, [Intraguild predation with evolutionary dispersal in a spatially heterogeneous environment](#), *J. Math. Biol.*, **78** (2019), 2141–2169.
- [7] D. Cohen and S. A. Levin, [Dispersal in patchy environments: The effects of temporal and spatial structure](#), *Theoret. Popul. Biol.*, **39** (1991), 63–99.
- [8] R. Cressman, V. Křivan and J. Garay, [Ideal free distributions, evolutionary games, and population dynamics in multiple-species environments](#), *The American Naturalist*, **164** (2004), 473–489.
- [9] D. L. DeAngelis, W.-M. Ni and B. Zhang, [Effects of diffusion on total biomass in heterogeneous continuous and discrete-patch systems](#), *Theoretical Ecology*, **9** (2016), 443–453.
- [10] D. L. DeAngelis, C. C. Travis and W. M. Post, [Persistence and stability of seeddispersed species in a patchy environment](#), *J. Theoret. Biol.*, **16** (1979), 107–125.
- [11] U. Dieckman, B. O’Hara and W. Weisser, [The evolutionary ecology of dispersal](#), *Trends Ecol. Evol.*, **14** (1999), 88–90.
- [12] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, [The evolution of slow dispersal rates: A reaction diffusion model](#), *J. Math. Biol.*, **37** (1998), 61–83.
- [13] A. Hastings, [Can spatial variation alone lead to selection for dispersal?](#), *Theoret. Popul. Biol.*, **24** (1983), 244–251.
- [14] P. H. Joachim and H. Thomas, [Evolution of density-and patch-size-dependent dispersal rates](#), *Proc. R. Soc. Lond. B*, **269** (2002).
- [15] M. L. Johnson and M. S. Gaines, [Evolution of dispersal: Theoretical models and empirical tests using birds and mammals](#), *Ann. Rev. Ecol. Syst.*, **21** (1990), 449–480.
- [16] Y.-J. Kim and O. Kwon, [Evolution of dispersal with starvation measure and coexistence](#), *Bull. Math. Biol.*, **78** (2016), 254–279.
- [17] Y.-J. Kim, O. Kwon and F. Li, [Evolution of dispersal toward fitness](#), *Bull. Math. Biol.*, **75** (2013), 2474–2498.

- [18] Y.-J. Kim, O. Kwon and F. Li, [Global asymptotic stability and the ideal free distribution in a starvation driven diffusion](#), *J. Math. Biol.*, **68** (2014), 1341–1370.
- [19] Y.-J. Kim, S. Seo and C. Yoon, [Asymmetric dispersal and ecological coexistence in two-patch system](#), preprint.
- [20] Y.-J. Kim, S. Seo and C. Yoon, [Two-patch system revisited: New perspectives](#), *Bull. Math. Biol.*, submitted.
- [21] Y. Lou, [On the effects of migration and spatial heterogeneity on single and multiple species](#), *J. Differential Equations*, **223** (2006), 400–426.
- [22] M. A. McPeck and R. D. Holt, [The evolution of dispersal in spatially and temporally varying environments](#), *The American Naturalist*, **140** (1992), 1000–1009.
- [23] T. Nagylaki, [Introduction to Theoretical Population Genetics](#), Biomathematics, 21. Springer-Verlag, Berlin, 1992.
- [24] W.-M. Ni, [The Mathematics of Diffusion](#), CBMS-NSF Regional Conference Series in Applied Mathematics, 82. Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 2011.
- [25] A. Okubo and S. A. Levin, [Diffusion and Ecological Problems: Modern Perspectives](#), 2nd edition, Interdisciplinary Applied Mathematics, 14. Springer-Verlag, New York, 2001.
- [26] R. Ramos-Jiliberto and P. M. de Espans, [The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka: Comment](#), *Ecosphere*, **8** (2017), e01895.
- [27] A. M. M. Rodrigues and R. A. Johnstone, [Evolution of positive and negative density-dependent dispersal](#), *Proc. R. Soc. B*, **281** (2014).
- [28] L. L. Sullivan, B. Li, T. E. Miller, M. G. Neubert and A. K. Shaw, [Density dependence in demography and dispersal generates fluctuating invasion speeds](#), *Proceedings of the National Academy of Sciences*, **114** (2017), 5053–5058.
- [29] J. M. J. Travis and C. Dytham, [Habitat persistence, habitat availability and the evolution of dispersal](#), *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266** (1999), 723–728.

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