Evolution of dispersal toward fitness[⋆]

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Abstract. It is widely believed that the slowest dispersal strategy is selected in the evolutional if the environment is temporally invariant but spatially heterogeneous. Authors claim in this paper that this belief is true only if random dispersals with constant motility are considered. However, if a dispersal strategy with fitness property is included, the size of the dispersal is not such a crucial factor anymore. Recently, a starvation driven diffusion has been introduced by Cho and Kim [7], which is a random dispersal strategy with a motility increase on starvation. The authors show that such a dispersal strategy has fitness property and that the evolutional selection favors fitness but not simply slowness. Such a conclusion is obtained from a stability analysis of a competition system between two phenotypes with different dispersal strategies of linear and starvation driven diffusions.

Key words. evolution of dispersal, fitness, local stability, starvation driven diffusion

1. Introduction

Dispersal strategy is one of the key elements in the evolution of biological species and each species has developed its own way. An existing dispersal strategy of a biological species is a result of an exceptionally long history of evolution and hence it is important to understand the

key ingredients of a dispersal strategy that provide a species a chance to survive. It is widely believed that the spatial heterogeneity of environments disfavors dispersal. However, this is a narrow perspective obtained from theories based on linear dispersal. The purpose of this paper is to show that the spatial heterogeneity of environments favors the fitness of dispersal. Therefore, there is no confliction with the well-accepted belief that the temporal fluctuation favors the size of dispersal.

The evolution of dispersal rates has been studied by many authors. Since the modern experimental techniques are limited to study such a foundation of ecology, numerical computations and theoretical analysis of mathematical models have been useful tools to understand it. Readers are referred to [4, 8, 20, 25–27] for comprehensive discussions of discrete and continuous models. It is well-accepted that spatial and temporal heterogeneities of environments occur in all scales and such heterogeneities play a key role in the evolutionary selection of dispersal rates. Numerical simulations and theoretical analysis of discrete and continuous models indicate that spatial heterogeneities reduce dispersal rates [12, 13, 19–21, 24] and temporal changes increase dispersal rates [12, 17, 19, 20, 29]. If habitats are spatially heterogeneous and temporally fluctuating, then the dispersal rate is selected by the interaction between the two [12, 19]. These studies are mostly based on uniform random dispersals, which is usually modeled by a linear diffusion with a constant diffusivity in continuous cases. However, biological organisms may increase the motility to find food if food is consumed. Such a starvation driven diffusion is an example of a non-uniform random dispersal and has been modeled by Cho and Kim [7]. Even though the biological organisms do not know the place with more food, such a motility increase produces an advection toward a better environment, i.e., a better fitness.

We will consider a Lotka-Volterra type competition model:

$$
\begin{cases}
u_t = \Delta(\gamma_1(s)u) + u[m(x) - u - v], \\
v_t = \Delta(\gamma_2(s)v) + v[m(x) - u - v], \\
0 = \mathbf{n} \cdot \nabla[\gamma_1(s)u] = \mathbf{n} \cdot \nabla[\gamma_2(s)v], \\
0 \leq u(x,0) = u_0(x), \ 0 \leq v(x,0) = v_0(x).
\end{cases}
\tag{1}
$$

In this model, the zero flux condition is given on the smooth boundary $\partial\Omega$, where $\mathbf{n}$ is the outward unit normal vector to the boundary. Unknown solutions $u(x,t)$ and $v(x,t)$ are population densities of two phenotypes of a species. The population dynamics for both phenotypes is identical in the model. Hence, one of them can be considered as a mutant of the other with a different dispersal strategies γ_i's. The variable s is the satisfaction measure on the environment, which is defined by

$$
s := \frac{m}{u + v}.
\tag{2}
$$

Then, $s = 1$ is the case that food supply m is exactly same as the food demand $u + v$. Hence, if $s < 1$, then the organisms suffer for a food shortage and, if $s > 1$, there is surplus food and everybody is satisfied.

The main feature of the model is that the motility functions γ_1 and γ_2 are decreasing functions of the satisfaction measure s. In other words, if species are satisfied with the environment, they just reduce their motility to stay at the favorable place. However, they increase their motility to find food if species are starved. Throughout this paper, we consider this *starvation driven diffusion* under two assumptions

$$m(x) \geq 0 \ \text{ is a non-constant smooth function in } \bar{\Omega}, \qquad (3)$$

$$\gamma_1(s), \gamma_2(s) > 0 \ \text{ are decreasing smooth functions for } s \geq 0. \qquad (4)$$

The spatial heterogeneity of environment is represented by a nonconstant function $m(x)$. Remember that having a nonconstant $m(x)$ is not a technical reason, but is an essential requirement of the analysis. The stability analyses in this paper are property of the spatial heterogeneity and fail if $m(x)$ is constant.

The nonlinear diffusion operator in the equations is based on a non-isothermal diffusion and readers are referred to [7] for more discussions and biological examples. For a single species case,

$$u_t = \Delta(\gamma(s)u) + u(m(x) - u), \qquad (5)$$

the global asymptotic stability of its unique positive steady state $\theta_\gamma(x)$ has been obtained in [22, Theorem 2] under an extra assumption on the motility:

$$\gamma(s) - s(s-1)\gamma'(s) > 0 \ \text{ for } \ 0 < s < 1. \qquad (6)$$

The motility function mostly considered in this paper is

$$\gamma^0(s) = \begin{cases} h & \text{if } 0 \leq s < 1, \\ \ell & \text{if } 1 \leq s < \infty, \end{cases} \qquad (7)$$

where $0 < \ell < h$ are constants. This discontinuous motility function is approximated by a smooth motility function defined by a convolution,

$$\gamma^\epsilon := \gamma^0 * \eta^\epsilon, \qquad (8)$$

where $0 < \epsilon$ is small and η^ϵ is a smooth symmetric mollifier with $\operatorname{supp} \eta^\epsilon \subset (-\epsilon, \epsilon)$ and $\int \eta^\epsilon(x)dx = 1$. Then, $\gamma^\epsilon(s) = h$ for $s < 1 - \epsilon$, $\gamma^\epsilon(s) = \ell$ for $s \geq 1 + \epsilon$, $\gamma^\epsilon \to \gamma^0$ as $\epsilon \to 0$, and γ^ϵ satisfies (6). The discontinuous motility γ^0 does not satisfy the regularity assumption (4). Hence, the case with a discontinuous motility function is always considered as the approximation sense with $\epsilon \to 0$. We may also

choose the mollifier η^ϵ on our convenience. For example, supp $\eta^\epsilon \subset (-\epsilon, 0)$ is assumed in Theorem 2 so that $\gamma^\epsilon(s) = \ell$ for $s \geq 1$.

This paper contains three theorems and the first two are proved in Section 3. These two are for the case that the first phenotype has a constant motility $\gamma_1 = d > 0$ and the second one has a non-constant motility $\gamma_2 = \gamma^\epsilon$. In the first theorem it is shown that, if the motility of a phenotype jumps when the food is not enough, then its survival against a slower diffuser is guaranteed at least.

Theorem 1 (Survival of SDD is guaranteed!). *Let $\gamma_1 = d > 0$ be constant, $\gamma_2 = \gamma^\epsilon$, and θ_d be the positive steady state of (5) with $\gamma = d$. If $m(x)$ is not a constant, $\epsilon > 0$ is sufficiently small (depending on h, ℓ, m and d), and*

$$\frac{\max_{\bar{\Omega}} m(x)}{\min_{\bar{\Omega}} m(x)} \leq \frac{h}{\ell}, \tag{9}$$

then the semi-trivial steady state $(\theta_d, 0)$ of (1) is unstable.

If the dispersal rate d goes to zero, then the fitness increases since the weight of the population reaction term increases. Hence, the steady state converges to $\theta = m$ for the single equation case. However, Theorem 1 implies that the starvation driven dispersal with γ^0 as its motility function can guarantee a survival of a phenotype no matter how small linear diffusivity the other phenotype has. This phenomenon is related to the fact that $\theta = m$ is also a steady state for (5) even without the reaction term if (9) is satisfied (see [7, Proposition 1] and [22, Section 5]).

In the second theorem we will see that a starvation driven diffuser may have an advantage over a slower linear diffuser.

Theorem 2 (Spatial heterogeneity favors SDD!). *Let $\gamma_1 = d > 0$ be constant, $\gamma_2 = \gamma^\epsilon$, and $(0, \theta_{\gamma^\epsilon})$ be a semi-trivial steady state of (1) with a mollifier such that supp $\eta^\epsilon \subset (-\epsilon, 0)$. Then,*

(i) There exists $0 < \omega_2 = \omega_2(m, h, \ell, \epsilon) < \ell$ such that, if $d < \omega_2$, then $(0, \theta_{\gamma^\epsilon})$ is linearly unstable and if $\omega_2 < d$, then $(0, \theta_{\gamma^\epsilon})$ is linearly stable.

(ii) If $\ell \leq d$, then $(0, \theta_{\gamma^\epsilon})$ is the unique stable steady state.

The linear dispersal does not provide any fitness property. However, if $\ell < h$, the starvation driven dispersal does. Theorem 2 implies that, if a phenotype increases its motility when food is not enough, this phenotype obtains a fitness property and can invade the colony of the linear diffuser.

The ω_2 in Theorem 2 is the boundary of the stability regime for the semi-trivial steady state $(0, \theta_{\gamma^\epsilon})$. One may consider a similar boundary, say ω_1, for the stability regime of $(\theta_d, 0)$. Theorem 1 implies that

$\omega_1 = 0$ if (9) holds and $\epsilon > 0$ is small enough. The positivity of such ω_1 seems true when (9) fails. However, its proof seems tricky and is open. It was conjectured from computational observations that there exist $0 \le d_1 < d_2 < \infty$ such that $(0, \theta_{\gamma^\epsilon})$ is the globally asymptotically stable if $d > d_2$, $(\theta_d, 0)$ is if $0 < d < d_1$, and two species may coexist if $d_1 < d < d_2$ (see [7, Conjecture 1 and Figure 3]). It is natural to guess that such ω_1 and ω_2 would be these two. However, we are still far from such a conclusion for the following reasons.

First, it should be shown that $(0, \theta_{\gamma^\epsilon})$ is the unique stable steady state for all $d > \omega_2$ and $(\theta_d, 0)$ is the one for $d < \omega_1$. Theorems 1 and 2 provide them partially. For a 2×2 monotone system, the uniqueness of a stable steady state gives the globally asymptotic stability (see [18]) among nonnegative and nontrivial solutions. However, since the equation for the second species involves the second derivative of the concentration of the first species, the monotonicity of the system does not come easily and is not obtained yet. Hence authors could not claim that SDD is selected because of that even though they believe so. Hence, finding a way to overcome the lack of monotonicity is the second requirement.

In the last theorem in Section 4, we consider the case that both phenotypes follow starvation driven diffusions.

Theorem 3 (Spatial heterogeneity favors fitness!). *If γ_1 and γ_2 satisfy (6), $\gamma_1(s) \le \gamma_2(s)$ for $0 \le s < 1$, $\gamma_1(s) \ge \gamma_2(s)$ for $1 < s < \infty$ and $\gamma_1 \not\equiv \gamma_2$ in a small neighborhood of $s = 1$. Then, $(0, \theta_{\gamma_2})$ is the unique stable steady state.*

The relation between the two motility functions in the theorem indicates that $\gamma_1(1) = \gamma_2(1)$ and γ_2 changes more sharply before and after $s = 1$. If the mollifier is symmetric and $\epsilon_2 < \epsilon_1$, then $\gamma_1 = \gamma^{\epsilon_1}$ and $\gamma_2 = \gamma^{\epsilon_2}$ satisfies the relation in the theorem. If the motility changes more sharply at $s = 1$, then the dispersal gives a better fitness (see Figure 2). The extreme case is γ^0 with (9), where the steady state gives the perfect fitness, i.e., $\theta = m$ is the steady state. Hence, we may conclude that a dispersal that gives a better fitness is favored by the evolution. Furthermore, the sensitivity of a species to the environments can be measured by the amount of motility change of the species. If γ_2 is bigger than γ_1 for $s \in (0, 1)$, this indicates that the second phenotype v is more eager to leave the area if the food is less than the amount to support the colony. On the other hand, if γ_2 is smaller than γ_1 for $s \in (1, \infty)$, this indicates that v is more eager to stay at the area if the food is enough. Hence the second phenotype v in Theorem 3 is more sensitive to the change of environmental conditions. One may easily guess that the sensitive phenotype will have a better fitness which has been tested in Figures 1 and 2. In the model, there is no cost for the movement and no delay effect. Theorem 3 claims that the phenotype which is more sensitive to the

environment makes a stable colony and hence the less sensitive one cannot invade them. However, the colony of less sensitive phenotypes is vulnerable since it does not make a stable colony.

The proofs of the three theorems are based on the classical eigenvalue analysis of the linearized problems. The difference is that the model of this paper contains nonlinearity not only in the zero-th order reaction term, but also in the second order diffusion term. Hence, the analysis is more complicated. However, for the stability test of a semi-trivial steady states to (1), we could obtained a simplified stability criteria in Lemma 1 and Lemma 2. These stability criteria are used repeatedly in this paper since the first step in studying global asymptotic behaviors of system (1) are to understand stability properties of semi-trivial steady states. Extension of the theories to the cases that allow stable coexisting solutions such as a strong competition situation will be more challenging.

2. Fitness by dispersal

Suppose that organisms are located in a way that each individual has the same reproduction rate with the highest rate possible. Then, the organisms may have better chance to grow. Such a state is called the ideal free distribution and the fitness is the ability to obtain it (see [9,14,15]). In nature, the population density is usually higher in a place with more food than in a place with less food. Is such a fitness of organisms a result of dispersal or population reaction? The answer would be both. However, one may see from many examples that the time scale of fitness is shorter than the one of the population growth. Hence the dispersal should be one of the main dynamics for the fitness.

The population dynamics for a single phenotype is given by

$$u_t = u(m - u).$$

For a numerical test we consider a resource (or environment) function,

$$m(x) = \begin{cases} 2, & 0 < x < 0.5, \\ 0, & 0.5 < x < 1, \end{cases} \tag{10}$$

where the domain is $\Omega = (0,1)$ and the carrying capacity of the environment is $\int m(x)dx = 1$. In this case the ideal free distribution of a fixed total population $A > 0$ is

$$R(x) = \begin{cases} 2A, & 0 < x < 0.5, \\ 0, & 0.5 < x < 1. \end{cases} \tag{11}$$

In this section we will discuss the fitness property of dispersal processes with or without the population reaction and compare them

numerically using the above example. We will see that the pheno-types that have a better fitness has more chance to survive in other sections.

2.1. Fitness by linear diffusion

In this section we will briefly review the well-known fitness property of linear diffusion. However, this discussion provides a clear view for the nonlinear diffusion case in the next section. Consider a single species case without a population dynamics:

$$u_t = du_{xx}, \quad 0 < x < 1, \ t > 0, \tag{12}$$

where the initial mass is $\int u_0(x)dx = A > 0$ and the zero flux con-dition is given on the boundary. Then, the steady state u^e satisfies $0 = (u^e)_{xx}$ which gives $u^e = A$ for all $d > 0$. Hence, the solution $u(x,t)$ converges to the constant A, i.e., $u(x,t) \to A$ as $t \to \infty$ for all $d > 0$. It is clear that this linear diffusion does not provide any fitness dynamics to the species even if $d > 0$ is small. Now consider the same problem with population dynamics, i.e.,

$$u_t = du_{xx} + u(m - u). \tag{13}$$

In this case the steady state is independent of the initial value as long as it is nontrivial and nonnegative. The steady state satisfies $0 = u_{xx} + \frac{1}{d}u(m - u)$. Hence, the nonnegative nontrivial steady state converges to m as $d \to 0$, i.e., $\theta_d \to m$ as $d \to 0$. In other words, even if the linear diffusion does not give any fitness, the equation with reaction has fitness properties which increases as $d \to 0$ (see the graphs in Figure 1 corresponding to $h = 1$). Notice that the linear diffusion with a constant diffusivity does not give any fitness behavior and hence this fitness properties comes entirely from the population reaction term. In fact, the smaller diffusivity only gives a bigger weight to the population reaction and hence increases the fitness. Hence the selection of a smaller dispersal rate with a spatial heterogeneity can be understood as a selection for fitness.

2.2. Fitness by advection

One way to add fitness to the linear dispersal is adding an advection term:

$$u_t = \text{div}(d\nabla u - cu\nabla P) + u(m(x) - u), \quad t > 0, \ x \in \Omega. \tag{14}$$

The advection term, $-cu\nabla P$, models the migration of the organisms toward food, where $c > 0$ is a scaling coefficient. In chemo-taxis

individual organisms are assumed to sense the gradient of chemo-attractants, which justifies the case with '$P = m$'. However, having such advection is guaranteed to be advantageous only if $c > 0$ is small enough. If $c > 0$ is large, the population becomes concentrated only near the maximum points of m, which gives a better chance to their competing species (see [2,3,11,16,23]). If the advection is given with '$P = m - u$' or '$P = \ln m$', then such an advection always gives a species an advantage in a competition against other species (see [1, 5,6,9,10]). In particular, the case with '$P = \ln m$' is based on the Weber-Fechner law and commonly used in the theory of chemotaxis (see [28]).

In many cases, it is not clear how species sense the gradient of m, $\ln m$ or $m - u$. Species, including human beings, often do not know where to go until they arrive at the right place even if they have a clear intension for migration. Of course, if they find food, they usually stay with the food until the food is consumed. Hence the dispersal of organisms could be understood as a random dispersal with non-constant eagerness to move. The advection produced by such a conditional random dispersal may play the key role in advection-diffusion models. In fact, the starvation driven diffusion has used in a chemotaxis modeling without a gradient-sensing mechanism (see [30]).

2.3. Fitness by starvation driven diffusion

Let a resource distribution be

$$m(x) = \begin{cases} 1.9, & 0 < x < 0.5, \\ 0.1, & 0.5 < x < 1, \end{cases} \tag{15}$$
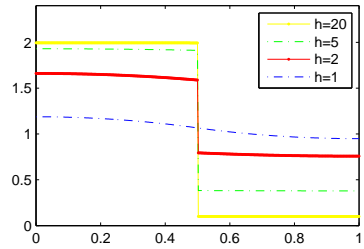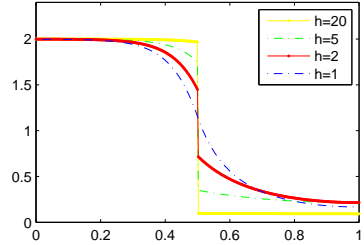
and a motility function be

$$\gamma_h^0(s) = \begin{cases} h & \text{if } 0 \leq s < 1, \\ 1 & \text{if } 1 \leq s < \infty, \end{cases} \tag{16}$$

which is the same discontinuous motility function in (7) with a fixed $\ell := 1$ for an easier comparison with the linear diffusion case. Consider a case with starvation driven diffusion without population dynamics,

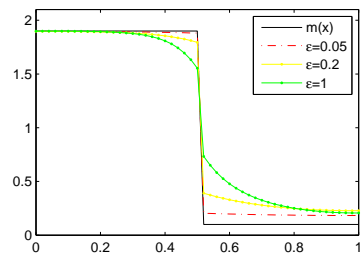$$v_t = d\left(\gamma_h^0(s)v\right)_{xx}, \quad 0 < x < 1, \ t > 0, \tag{17}$$

where the satisfaction measure is $s = \frac{m}{v}$. The steady state v^e of the problem satisfies $0 = \left(\gamma_h^0(s)v\right)_{xx}$ and hence $\gamma_h^0(s)v = $ const. Hence, the steady state with total population $A > 0$ is

$$v^e(x) = \begin{cases} 2hA/(h+1), & 0 < x < 0.5, \\ 2A/(h+1), & 0.5 < x < 1 \end{cases}$$
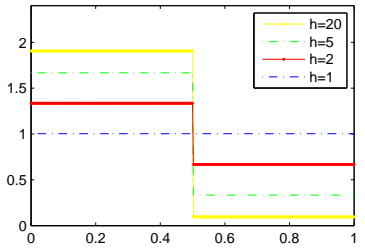
(a) steady states of (17) or $d = \infty$ (b) steady states of (18) with $d = 1$
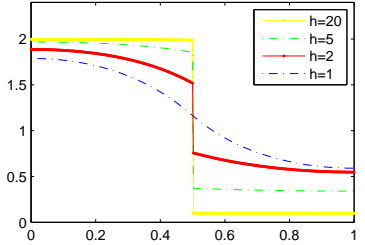
(c) steady states of (18) with $d = 0.1$ (d) steady states of (18) with $d = 0.01$

Fig. 1. Fitness by dispersal [x-axis: space, y-axis: concentration density]
(a): Steady state solutions of (17) with unit total population. (b-d): Steady state
solutions of (18) with different diffusivity $d > 0$. The steady states converge to
$m(x)$ in (10) as $h \to \infty$ with a fixed $d > 0$ or as $d \to 0$ with a fixed $h > 0$.
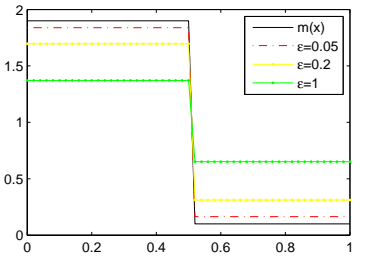
(a) steady states of (20) or $d = \infty$ (b) steady states of (20) with $d = 0.002$

Fig. 2. Fitness by dispersal [x-axis: space, y-axis: concentration density]
(a): Steady state solutions of (20) without the population reaction. (b): Steady
state solutions of (20) with $d = 0.002$'s. Here, $h = 5$ and $l = 1$. As $\epsilon \to 0$, the
motility function becomes sharper at $s = 1$ and obtains more fitness.

(see [7, Proposition 1] or [22, Thoerem 1]). In Figure 1(a) the graphs
of the steady states are plotted with several h's. The population den-
sity in the region $0 < x < 0.5$ is h times bigger than the one in
$0.5 < x < 1$. In other words, the starvation driven diffusion has such
a fitness property by itself. If $h = \ell(= 1)$, then we obtain the con-
stant steady state of the linear diffusion case which does not give any
fitness. If $h \to \infty$, the steady state converges to the ideal free distri-

bution. Notice that the steady state is independent of the coefficient $d > 0$. In other words, *the fitness obtained from the dispersal is not related to the actual size of dispersal but to the ratio of the dispersal jump.*

Now we consider the problem with the population dynamics:

$$v_t = d\big(\gamma_h^0(s)v\big)_{xx} + v(m - v), \quad 0 < x < 1, \ t > 0. \qquad (18)$$

In this case both the reaction and the diffusion have fitness property. Furthermore, as the diffusivity coefficient $d > 0$ converges to zero, the fitness effect of the population reaction increases. The steady state satisfies $0 = \big(\gamma_h^0(s)v\big)_{xx} + \frac{1}{d}v(m - v)$. The global asymptotic stability of the problem has been shown in [22, Theorem 6] for limited cases. Suppose that there exists a globally asymptotically stable steady state $\theta_{h,d}(x)$. Then it is expected that

$$\theta_{h,d}(x) \to m$$

as $h \to \infty$ with a fixed $d > 0$ or as $d \to 0$ with a fixed $h > 0$. See Figures 1(b)–(d).

Now consider a continuous motility function:

$$\gamma_h^\epsilon(s) = \begin{cases} h, & 0 \le s < 1 - \epsilon, \\ 1, & 1 + \epsilon \le s < \infty, \\ \frac{s - 1 + \epsilon}{2\epsilon} + \frac{1 + \epsilon - s}{2\epsilon}h, & \text{otherwise.} \end{cases} \qquad (19)$$

Then the corresponding reaction-diffusion equation is

$$v_t = d\big(\gamma_h^\epsilon(s)v\big)_{xx} + v(m - v), \quad 0 < x < 1, \ t > 0. \qquad (20)$$

The steady states are given in Figure 2. One can clearly observe that the fitness increases as $\epsilon \to 0$.

3. Starvation driven diffuser versus linear diffuser

The purpose of this section is to prove Theorems 1 and 2. These theorems are cases that the motility function for the first species is constant, $\gamma_1 = d$, and the second one is not, $\gamma_2 = \gamma$. Therefore, the equations in this section are

$$\begin{cases} u_t = d\Delta u + u[m - u - v], \\ v_t = \Delta(\gamma(s)v) + v[m - u - v], \\ 0 = \mathbf{n} \cdot \nabla[\gamma(s)v] = \mathbf{n} \cdot \nabla u, \\ 0 \le u(x,0) = u_0(x), \ 0 \le v(x,0) = v_0(x), \end{cases} \qquad (21)$$

where the first two equations hold for $t > 0$ and $x \in \Omega$, the Neumann boundary conditions in the third line are for $t > 0$ and $x \in \partial\Omega$, and the initial conditions in the last line are for $x \in \Omega$. The domain of variables and boundary conditions are always like this throughout the paper and will not be mentioned again.

3.1. Linearization and eigenvalue analysis

First, introduce the diffusion pressure V for the second species v:

$$V := \gamma(s)v \quad \text{with} \quad s := \frac{m}{u+v}. \tag{22}$$

If $u = v = 0$, then the satisfaction measure s is not well-defined. However, since the motility γ is bounded, we may define the diffusion pressure as $V = 0$ if $v = 0$. Define

$$\mathcal{F}(m, u, v, V) := \gamma(s)v - V,$$

which is identically zero under the relation (22). This functional gives a relation among unknowns. Since the resource distribution is assumed to be invariant in time, i.e., $m = m(x)$, we have

$$\mathcal{F}_t = \frac{\partial \mathcal{F}}{\partial u}u_t + \frac{\partial \mathcal{F}}{\partial v}v_t + \frac{\partial \mathcal{F}}{\partial V}V_t = \frac{\partial \mathcal{F}}{\partial u}u_t + \frac{\partial \mathcal{F}}{\partial v}v_t - V_t = 0.$$

Furthermore, since

$$\frac{\partial \mathcal{F}}{\partial u} = -\gamma'(s)s\frac{v}{u+v} > 0, \qquad \frac{\partial \mathcal{F}}{\partial v} = \gamma(s) - \gamma'(s)s\frac{v}{u+v} > 0, \tag{23}$$

the unknown function v can be completely decided by $m, u,$ and V by the implicit function theorem. Hence, we may write $v = v(m, u, V)$, and (21) is rewritten as

$$\begin{cases} u_t = d\Delta u + u[m - u - v], \\ V_t = \frac{\partial \mathcal{F}}{\partial u}\{d\Delta u + u[m - u - v]\} + \frac{\partial \mathcal{F}}{\partial v}\{\Delta V + v[m - u - v]\}, \\ 0 = \mathbf{n} \cdot \nabla V = \mathbf{n} \cdot \nabla u, \\ 0 \le u(x, 0) = u_0(x), \ 0 \le V(x, 0) = V_0(x), \end{cases} \tag{24}$$

where

$$V_0 := \gamma\left(\frac{m}{v_0 + u_0}\right)v_0.$$

Let (u^e, v^e) be a steady state solution of (21). The stability of (u^e, v^e) is equivalent to that of the steady state (u^e, V^e) of (24) for $V^e := \gamma(s^e)v^e$. Whenever a linearized problem is considered at a steady state, say (u^e, v^e), the satisfaction measure is always

$$s^e = \frac{m}{u^e + v^e}.$$

Let $u = u^e + \phi$ and $V = V^e + \Psi$ with $|\phi|$ and $|\Psi|$ small. Then,

$$v = v(m, u^e + \phi, V^e + \Psi) = v^e + \frac{\partial v}{\partial u}\phi + \frac{\partial v}{\partial V}\Psi + \text{higher order terms},$$

where the implicit function theorem implies

$$\frac{\partial v}{\partial V} = -\frac{\frac{\partial \mathcal{F}}{\partial V}}{\frac{\partial \mathcal{F}}{\partial v}} = \left[\gamma(s) - \gamma'(s)\frac{mv}{(u+v)^2}\right]^{-1},$$

$$\frac{\partial v}{\partial u} = -\frac{\frac{\partial \mathcal{F}}{\partial u}}{\frac{\partial \mathcal{F}}{\partial v}} = \gamma'(s)\frac{mv}{(u+v)^2}\left[\gamma(s) - \gamma'(s)\frac{mv}{(u+v)^2}\right]^{-1}.$$

Substituting these perturbed quantities to (24) gives the following linearized problem after deleting higher order terms,

$$\begin{cases} \phi_t = d\Delta\phi + (m - v^e - u^e\frac{\partial v}{\partial u} - 2u^e)\phi - u^e\frac{\partial v}{\partial V}\Psi, \\ \Psi_t = \frac{\partial \mathcal{F}}{\partial v}\left\{\Delta\Psi + (m - 2v^e - u^e)\frac{\partial v}{\partial V}\Psi + [(m - 2v^e - u^e)\frac{\partial v}{\partial u} - v^e]\phi\right\} \\ \qquad + \frac{\partial \mathcal{F}}{\partial u}\left\{d\Delta\phi + (m - v^e - u^e\frac{\partial v}{\partial u} - 2u^e)\phi - u^e\frac{\partial v}{\partial V}\Psi\right\}, \\ 0 = \mathbf{n}\cdot\nabla\Psi = \mathbf{n}\cdot\nabla\phi. \end{cases}$$

$$(25)$$

A steady state $(u^e(x), V^e(x))$ of (24) is stable if the eigenvalues of the following eigenvalue problem are strictly negative,

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - v^e - u^e\frac{\partial v}{\partial u} - 2u^e)\phi - u^e\frac{\partial v}{\partial V}\Psi, \\ \lambda\Psi = \frac{\partial \mathcal{F}}{\partial v}\left\{\Delta\Psi + (m - 2v^e - u^e)\frac{\partial v}{\partial V}\Psi + [(m - 2v^e - u^e)\frac{\partial v}{\partial u} - v^e]\phi\right\} \\ \qquad + \frac{\partial \mathcal{F}}{\partial u}\left\{d\Delta\phi + (m - v^e - u^e\frac{\partial v}{\partial u} - 2u^e)\phi - u^e\frac{\partial v}{\partial V}\Psi\right\}, \\ 0 = \mathbf{n}\cdot\nabla\Psi = \mathbf{n}\cdot\nabla\phi. \end{cases}$$

$$(26)$$

Consider the semi-trivial steady state $(\theta_d(x), 0)$ of (21). Then, at the steady state,

$$\frac{\partial v}{\partial V} = \frac{1}{\gamma(s_d)}, \quad \frac{\partial v}{\partial u} = 0, \quad \frac{\partial \mathcal{F}}{\partial v} = \gamma(s_d), \quad \frac{\partial \mathcal{F}}{\partial u} = 0, \quad s_d = \frac{m}{\theta_d},$$

and the eigenvalue value problem for (24) at $(\theta_d(x), 0)$ becomes

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - 2\theta_d)\phi - \frac{\theta_d}{\gamma(s_d)}\Psi, \\ \lambda\Psi = \gamma(s_d)\left[\Delta\Psi + \frac{m-\theta_d}{\gamma(s_d)}\Psi\right], \\ 0 = \mathbf{n}\cdot\nabla\Psi = \mathbf{n}\cdot\nabla\phi, \end{cases}$$

$$(27)$$

where θ_d satisfies

$$\begin{cases} 0 = d\Delta\theta_d + \theta_d[m - \theta_d], \\ 0 = \mathbf{n}\cdot\nabla\theta_d. \end{cases}$$

$$(28)$$

Let $(0, \theta_\gamma(x))$ be the other semi-trivial steady state and hence

$$V_\gamma := \gamma(s_\gamma)\theta_\gamma, \quad s_\gamma = \frac{m}{\theta_\gamma}.$$

Then, similarly, the eigenvalue problem corresponding to the steady state $(0, V_\gamma(x))$ becomes

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - \theta_\gamma)\phi, \\ \lambda\Psi = \frac{\partial\mathcal{F}}{\partial v}\{\Delta\Psi + (m - 2\theta_\gamma)\frac{\partial v}{\partial V}\Psi + [(m - 2\theta_\gamma)\frac{\partial v}{\partial u} - \theta_\gamma]\phi\} \\ \quad + \frac{\partial\mathcal{F}}{\partial u}\{d\Delta\phi + (m - \theta_\gamma)\phi\}, \\ 0 = \mathbf{n} \cdot \nabla\Psi = \mathbf{n} \cdot \nabla\phi, \end{cases} \quad (29)$$

where θ_γ satisfies

$$\begin{cases} 0 = \Delta(\gamma(s_\gamma)\theta_\gamma) + \theta_\gamma[m - \theta_\gamma], \\ 0 = \mathbf{n} \cdot \nabla(\gamma(s_\gamma)\theta_\gamma). \end{cases} \quad (30)$$

In the following lemma we derive stability criteria for semi-trivial steady states.

Lemma 1. *Let θ_d and θ_γ be the unique globally asymptotically stable steady solution of (28) and (30), respectively.*

(i) Let μ_1 be the largest eigenvalue of

$$\begin{cases} \mu\Psi = \Delta\Psi + \frac{m - \theta_d}{\gamma(s_d)}\Psi, \\ 0 = \mathbf{n} \cdot \nabla\Psi. \end{cases} \quad (31)$$

If $\mu_1 > 0$, then the semi-trivial steady state solution $(\theta_d, 0)$ is linearly unstable; if $\mu_1 < 0$, then $(\theta_d, 0)$ is linearly stable.
(ii) Let ν_1 be the largest eigenvalue of

$$\begin{cases} \nu\phi = d\Delta\phi + (m - \theta_\gamma)\phi, \\ 0 = \mathbf{n} \cdot \nabla\phi. \end{cases} \quad (32)$$

If $\nu_1 > 0$, then the semi-trivial steady state solution $(0, \theta_\gamma)$ of (21) is linearly unstable; if $\nu_1 < 0$, $(0, \theta_\gamma)$ is linearly stable.

Proof. (i) First, suppose $\mu_1 > 0$. Consider an eigenvalue problem

$$\begin{cases} \ell\Psi = \Delta\Psi + \frac{m - \theta_d}{\gamma(s_d)}\Psi - \frac{\lambda}{\gamma(s_d)}\Psi, \\ 0 = \nabla\Psi \cdot \mathbf{n}. \end{cases}$$

and denote the largest eigenvalue by ℓ_1^λ. When $\lambda = 0$, clearly $\ell_1^\lambda = \mu_1 > 0$. Moreover, ℓ_1^λ will be negative when λ becomes large enough. Thus, there exists $\lambda_1 > 0$ such that $\ell_1^{\lambda_1} = 0$. Due to (28), it is easy to see that the operator

$$\mathcal{L}_v = d\Delta + (m - 2\theta_d) - \lambda_1$$

is invertible. This yields that $\lambda_1 > 0$ is an eigenvalue of the linearized problem (27), which implies that $(\theta_d(x), 0)$ is linearly unstable.

Next, assume that $\mu_1 < 0$. Suppose that the linearized problem (27) has nonnegative eigenvalue $\lambda_1 \geq 0$ with the corresponding eigenfunctions (ϕ_1, Ψ_1). If $\Psi_1 \equiv 0$, then a contradiction follows due to (27), (28) and the assumption that $\lambda_1 \geq 0$. Hence $\Psi_1 \neq 0$. However, this yields that

$$\mu_1 = \sup_{\Psi \in H^1(\Omega) \setminus \{0\}} \frac{\int_\Omega \left[-|\nabla \Psi|^2 + \frac{m - \theta_d}{\gamma(s_d)} \Psi^2 \right] dx}{\int_\Omega \Psi^2 dx}$$

$$\geq \frac{\int_\Omega \left[-|\nabla \Psi_1|^2 + \frac{m - \theta_d}{\gamma(s_d)} \Psi_1^2 \right] dx}{\int_\Omega \Psi_1^2 dx} = \frac{\int_\Omega \frac{\lambda_1}{\gamma(s_d)} \Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} \geq 0.$$

This is a contradiction. Therefore, $(\theta_d(x), 0)$ is linearly stable.

(ii) Consider the linearized eigenvalue problem of (30) at V_γ, which is written as

$$\lambda \Psi = \left(\Delta + (m - 2\theta_\gamma) \frac{\partial v}{\partial V} \right) \Psi.$$

Since $\theta_\gamma(x)$ is a stable solution of (30), the linear operator $\Delta + (m - 2\theta_\gamma)\frac{\partial v}{\partial V}$ has nonpositive eigenvalues. Thus, if $\nu_1 > 0$, because of (23), the operator

$$\mathcal{L} := \Delta + (m - 2\theta_\gamma) \frac{\partial v}{\partial V} - \nu_1 \left(\frac{\partial \mathcal{F}}{\partial v} \right)^{-1}$$

has strictly negative eigenvalues and thus it is invertible. Let $\{\nu_1, \phi_1\}$ be an eigen-pair of (32) and Ψ_1 satisfy

$$\mathcal{L}\Psi_1 = -[(m - 2\theta_\gamma)\frac{\partial v}{\partial u} - \theta_\gamma]\phi_1 - \left(\frac{\partial \mathcal{F}}{\partial v} \right)^{-1} \frac{\partial \mathcal{F}}{\partial u} \{ d\Delta\phi_1 + (m - \theta_\gamma)\phi_1 \}.$$

Then, $\{\nu_1, (\phi_1, \Psi_1)\}$ is an eigen-pair of the linearized problem (29), which implies that $(0, V_\gamma(x))$ is linearly unstable.

Since an eigenvalue of (29) is also an eigenvalue of (32), eigenvalues of (29) are all strictly negative if $\nu_1 < 0$ and hence $(0, V_\gamma(x))$ is linearly stable.   □

3.2. Survival of SDD is guaranteed!

It is well-known that the slower diffuser prevails over a faster diffuser for the constant diffusivity case (see Dockery *et al.* [13]). From that point of view, Theorem 1 gives a rather striking conclusion that the starvation driven diffusion may guarantee the survival of a species no matter how slow the other competing species spreads with a linear diffusion. The proof of the theorem is based on the stability criteria in Lemma 1.

Proof (of Theorem 1). Clearly, $(\theta_d, 0)$ is a semi-trivial steady state of (24). Thanks to Lemma 1, the stability of $(\theta_d, 0)$ as a semi-trivial steady state of (21) is determined by the signs of the largest eigenvalue, denoted by μ_1, of the following eigenvalue problem

$$\begin{cases} \mu\Psi = \Delta\Psi + \frac{m-\theta_d}{\gamma^\epsilon(s)}\Psi, \\ 0 = \mathbf{n}\cdot\nabla\Psi, \end{cases}$$

where $s = m/\theta_d$.

On the one hand side,

$$\begin{aligned} \mu_1 &= \sup_{\Psi\in H^1(\Omega)\setminus\{0\}} \left(\int_\Omega \left[-|\nabla\Psi|^2 + \frac{m-\theta_d}{\gamma^\epsilon(s)}\Psi^2 \right] dx \Big/ \int_\Omega \Psi^2 dx \right) \\ &\geq \frac{1}{|\Omega|} \int_\Omega \frac{m-\theta_d}{\gamma^\epsilon(s)} dx \\ &= \frac{1}{|\Omega|} \int_{\{s>1\}} \frac{m-\theta_d}{\ell} dx + \frac{1}{|\Omega|} \int_{\{s<1\}} \frac{m-\theta_d}{h} dx + A_\epsilon, \end{aligned} \tag{33}$$

where

$$A_\epsilon := \frac{1}{|\Omega|} \int_{\{1-\epsilon<s<1\}} \left(\frac{1}{\gamma^\epsilon(s)} - \frac{1}{h} \right) (m-\theta_d) dx < 0.$$

Since $|m-\theta_d| < \epsilon\theta_d$ in the domain $\{1-\epsilon < s < 1\}$, we have $A_\epsilon \to 0$ as $\epsilon \to 0$.

Recall that θ_d satisfies

$$\begin{cases} 0 = d\Delta u + u[m-u], \\ 0 = \nabla u \cdot \mathbf{n}. \end{cases}$$

Thanks to the maximum principle and the Hopf boundary lemma, it is standard to derive that

$$\min_{\bar\Omega} m(x) \leq \theta_d(x) \leq \max_{\bar\Omega} m(x). \tag{34}$$

Moreover, obviously $\int_\Omega \theta_d[m(x) - \theta_d]dx = 0$. Thus

$$\int_{\{s>1\}} \theta_d(m-\theta_d)dx = \int_{\{s<1\}} \theta_d(\theta_d - m)dx > 0,$$

where the integrands are nonnegative. Applying (34) yields that

$$\max_{\bar\Omega} m(x) \int_{\{s>1\}} (m-\theta_d)dx > \min_{\bar\Omega} m(x) \int_{\{s<1\}} (\theta_d - m)dx.$$

Therefore, there exists $\epsilon_0 > 0$ such that

$$\frac{1}{|\Omega|} \int_{\{s>1\}} \frac{1}{\ell}(m - \theta_d)dx > \frac{1}{\ell}\frac{\min_{\bar{\Omega}} m(x)}{\max_{\bar{\Omega}} m(x)} \int_{\{s<1\}} (\theta_d - m)dx + A_\epsilon$$

for all $\epsilon < \epsilon_0$. Finally, the relation (9) gives that, for $\epsilon < \epsilon_0$,

$$\mu_1 \geq \frac{1}{|\Omega|} \int_{\{s>1\}} \frac{1}{\ell}(m - \theta_d)dx + \frac{1}{|\Omega|} \int_{\{s<1\}} \frac{1}{h}(m - \theta_d)dx + A_\epsilon$$
$$> \frac{1}{|\Omega|} \int_{\{s<1\}} (\theta_d - m)dx \left(\frac{1}{\ell}\frac{\min_{\bar{\Omega}} m(x)}{\max_{\bar{\Omega}} m(x)} - \frac{1}{h}\right) \geq 0.$$

Hence, the semi-trivial steady state $(\theta_d, 0)$ of (21) is unstable if the motility function is given by γ^ϵ with $\epsilon < \epsilon_0$. $\square$

Since the semi-trivial state $(\theta_d, 0)$ is not stable, the species dispersed with the starvation driven diffusion with motility function d can always survive no matter how small d is. The condition (9) implies that the motility variation depending on the environment is larger than the variation of the environment itself, i.e., $m(x)$. This condition indicates that the species with starvation driven diffusion reacts sensitively enough to the environment. Notice that this is the condition that gives the ideal free distribution for a single species case in [22] with the motility function d in (7). The above theorem shows that this condition guarantees survival in this competition model.

3.3. Linear diffuser cannot invade starvation driven diffuser!

Theorem 2 gives the range of the diffusion rate d where the phenotype with the starvation driven diffusion has more chance to survive than the linear diffuser, i.e., $\ell \leq d$. However, for the range $\omega_2 < d < \ell$, we have obtained the linear stability of $(0, \theta_{\gamma^\epsilon})$, but not global asymptotic stability. The proof of this theorem is also based on the stability criteria in Lemma 1.

Proof (of Theorem 2). (i) To show the instability of $(0, \theta_{\gamma^\epsilon})$ we compute the sign of the largest eigenvalue of (32). Since $m - \theta_{\gamma^\epsilon}$ is positive in a region, we obtain for a sufficiently small d that

$$\nu_1 = \sup_{\phi \in H^1(\Omega)\setminus\{0\}} \frac{\int_\Omega \left[-d|\nabla\phi|^2 + (m - \theta_{\gamma^\epsilon})\phi^2\right]dx}{\int_\Omega \phi^2 dx} > 0.$$

Moreover, ν_1 decreases as d increases. Let $d = \ell$ and (ν_1, ϕ_1) be the largest eigen-pair of (32). Then

$$
\begin{aligned}
\nu_1 &= \sup_{\phi \in H^1(\Omega) \setminus \{0\}} \frac{\int_\Omega -d|\nabla \phi|^2 + (m - \theta_{\gamma^\epsilon})\phi^2 dx}{\int_\Omega \phi^2 dx} \\
&= \frac{\int_\Omega -d|\nabla \phi_1|^2 + (m - \theta_{\gamma^\epsilon})\phi_1^2 dx}{\int_\Omega \phi_1^2 dx} \\
&= \frac{\int_\Omega -\ell|\nabla \phi_1|^2 + \frac{\ell}{\gamma^\epsilon}(m - \theta_{\gamma^\epsilon})\phi_1^2 dx}{\int_\Omega \phi_1^2 dx} + \frac{\int_\Omega (1 - \frac{\ell}{\gamma^\epsilon})(m - \theta_{\gamma^\epsilon})\phi_1^2 dx}{\int_\Omega \phi_1^2 dx},
\end{aligned}
$$

where $s = m/\theta_{\gamma^\epsilon}$.

Since the operator $\Delta + \frac{m - \theta_{\gamma^\epsilon}}{\gamma^\epsilon(s)}$ has a positive eigenfunction $\gamma^\epsilon(s)\theta_{\gamma^\epsilon}$ with 0-eigenvalue, 0 is the largest eigenvalue of $\Delta + \frac{m - \theta_{\gamma^\epsilon}}{\gamma^\epsilon(s)}$. It implies that

$$
\int_\Omega -|\nabla \phi_1|^2 + \frac{m - \theta_{\gamma^\epsilon}}{\gamma^\epsilon(s)}\phi_1^2 dx \leq 0.
$$

Therefore,

$$
\begin{aligned}
\nu_1 &\leq \frac{\int_\Omega (1 - \frac{\ell}{\gamma^\epsilon(s)})(m - \theta_{\gamma^\epsilon})\phi_1^2 dx}{\int_\Omega \phi_1^2 dx} \\
&= \frac{\left(\int_{\{m > \theta_{\gamma^\epsilon}\}} + \int_{\{m < \theta_{\gamma^\epsilon}\}} \right)(m - \theta_{\gamma^\epsilon})(1 - \frac{\ell}{\gamma^\epsilon(s)})\phi_1^2 dx}{\int_\Omega \phi_1^2 dx} < 0.
\end{aligned}
$$

Therefore, according to Lemma 1, there exists $0 < \omega_2 < \ell$, such that if $d < \omega_2$, then $(0, \theta_{\gamma^\epsilon})$ is linearly unstable and if $d > \omega_2$, then $(0, \theta_{\gamma^\epsilon})$ is linearly stable.

(ii) Now assume that $\ell \leq d$. First, according to the proof of (i), it is clear that $(0, \theta_{\gamma^\epsilon})$ is linearly stable when $\ell \leq d$.

Next, we show the instability of $(\theta_d(x), 0)$ by showing the positivity of the largest eigenvalue of (31). An analogy of (33) gives that

$$
\begin{aligned}
&\sup_{\Psi \in H^1(\Omega) \setminus \{0\}} \int_\Omega \left[-|\nabla \Psi|^2 + \frac{m - \theta_d}{\gamma^\epsilon(s)}\Psi^2 \right] dx \\
&\geq \int_\Omega \left[-|\nabla \theta_d|^2 + \frac{m - \theta_d}{\gamma^\epsilon(s)}\theta_d^2 \right] dx \\
&= \int_\Omega \left[-|\nabla \theta_d|^2 + \frac{1}{\ell}\theta_d^2(m - \theta_d) \right] dx + \int_{\{s < 1\}} (\frac{1}{\gamma^\epsilon} - \frac{1}{\ell})\theta_d^2(m - \theta_d)dx \\
&= \int_\Omega \left[-|\nabla \theta_d|^2 + \frac{d}{\ell}|\nabla \theta_d|^2 \right] dx + \int_{\{s < 1\}} (\frac{1}{\gamma^\epsilon} - \frac{1}{\ell})\theta_d^2(m - \theta_d)dx \\
&\geq \int_{\{s < 1\}} (\frac{1}{\gamma^\epsilon} - \frac{1}{\ell})\theta_d^2(m - \theta_d)dx > 0. \quad (35)
\end{aligned}
$$

Therefore, the largest eigenvalue is strictly positive and hence Lemma 1(i) implies that $(\theta_d, 0)$ is linearly unstable if $\ell \leq d$.

Now we show that there is no positive steady state of (21). Suppose (u, v), $u, v \not\equiv 0$, is a one. Then,

$$\begin{cases} 0 = d\Delta u + u[m - u - v], \\ 0 = \Delta V + v[m - u - v], \\ 0 = \mathbf{n} \cdot \nabla V = \mathbf{n} \cdot \nabla u, \end{cases}$$

where $V = \gamma^\epsilon(s)v$ and $s = \frac{m}{u+v}$. Then, it follows that,

$$
\begin{aligned}
0 &\geq \sup_{\Psi \in H^1(\Omega)\setminus\{0\}} \int_\Omega \left[-|\nabla\Psi|^2 + \frac{1}{\gamma^\epsilon(s)}\Psi^2(m - u - v) \right] dx \\
&\geq \int_\Omega \left[-|\nabla u|^2 + \frac{1}{\gamma^\epsilon(s)}u^2(m - u - v) \right] dx \\
&= \int_\Omega \left[-|\nabla u|^2 + \frac{1}{\ell}u^2(m - u - v) \right] dx \\
&\qquad + \int_{\{s<1\}} \left(\frac{1}{\gamma^\epsilon(s)} - \frac{1}{\ell} \right)u^2(m - u - v) dx \\
&\geq \int_\Omega \left[-|\nabla u|^2 + \frac{1}{\ell}u^2(m - u - v) \right] dx \\
&= \int_\Omega \left[-|\nabla u|^2 + \frac{d}{\ell}|\nabla u|^2 \right] dx \geq 0.
\end{aligned}
$$

Therefore, $\int_{\{s<1\}}(\frac{1}{\gamma^\epsilon(s)} - \frac{1}{\ell})u^2(m - u - v)dx = 0$, and it follows that $\int_{\{m<u+v\}}(m - u - v)dx = 0$. On the other hand,

$$\int_\Omega (m - u - v)dx = -\int_\Omega \frac{d|\nabla u|^2}{u^2} \leq 0.$$

Therefore, we obtain that $m \equiv u + v$ and $u \equiv c$ for some positive constant c. This implies that

$$0 = \gamma(1)\Delta v.$$

However, m is nonconstant, this is a contradiction. Therefore, if $\ell \leq d$ and $\epsilon > 0$ is small enough, $(0, \theta_{\gamma^\epsilon})$ is the only stable steady state solution. $\square$

The stability of the semi-trivial steady state $(0, \theta_{\gamma^\epsilon})$ in Theorem 2 indicates that the linear diffusers cannot invade the habitat of the starvation driven diffusers. On the other hand, the instability of the other semi-trivial steady state $(\theta_d, 0)$ indicates that the starvation driven diffuser can invade the habitat of linear diffusers. It has been observed numerically that the linear diffuser actually becomes extinct in [7].

4. Competition between two starvation driven diffusers

The purpose of this section is to prove Theorem 3 and we return to the competition model (1) with non-constant motility functions for both species.

4.1. Linearization and eigenvalue analysis

Introduce diffusion pressures

$$U := \gamma_1(s)u, \quad V := \gamma_2(s)v \quad \text{with} \quad s := \frac{m}{u+v}. \qquad (36)$$

If $u = v = 0$, then the satisfaction measure s is not defined. However, for the definition of the pressure, we may define $U = 0$ if $u = 0$ and $V = 0$ if $v = 0$. Define

$$\mathcal{F}(x,u,v,U) := \gamma_1(s)u - U \quad \text{and} \quad \mathcal{G}(x,u,v,V) := \gamma_2(s)v - V.$$

Then, (1) can be rewritten as

$$
\begin{cases}
U_t = \frac{\partial \mathcal{F}}{\partial u}\{\Delta U + u[m(x) - u - v]\} + \frac{\partial \mathcal{F}}{\partial v}\{\Delta V + v[m(x) - u - v]\}, \\
V_t = \frac{\partial \mathcal{G}}{\partial u}\{\Delta U + u[m(x) - u - v]\} + \frac{\partial \mathcal{G}}{\partial v}\{\Delta V + v[m(x) - u - v]\}, \\
0 = \mathbf{n} \cdot \nabla U = \mathbf{n} \cdot \nabla V, \\
0 \le U(x,0) = U_0(x),\ 0 \le V(x,0) = V_0(x),
\end{cases}
$$
$$(37)$$

where

$$U_0 := \gamma_1\left(\frac{m}{u_0 + v_0}\right)u_0 \quad \text{and} \quad V_0 := \gamma_1\left(\frac{m}{u_0 + v_0}\right)v_0.$$

Let (u^e, v^e) denote a steady state solution of (1). Note that the stability of (u^e, v^e) is equivalent to that of the corresponding steady state (U^e, V^e) of (37) which is determined by the signs of the largest eigenvalue of the linearized problem. Let $U = U^e + \Phi$ and $V = V^e + \Psi$ with $|\Phi|$ and $|\Psi|$ small. Then, the eigenvalue problem of the linearized problem at the steady state (U^e, V^e) is given by

$$
\begin{cases}
\lambda\Phi = \frac{\partial \mathcal{F}}{\partial u}\left\{\Delta\Phi + [G_1\frac{\partial u}{\partial U} - u^e\frac{\partial v}{\partial U}]\Phi + [G_1\frac{\partial u}{\partial V} - u^e\frac{\partial v}{\partial V}]\Psi\right\} \\
\quad + \frac{\partial \mathcal{F}}{\partial v}\left\{\Delta\Psi + [G_2\frac{\partial v}{\partial V} - v^e\frac{\partial u}{\partial V}]\Psi + [G_2\frac{\partial v}{\partial U} - v^e\frac{\partial u}{\partial U}]\Phi\right\}, \\
\lambda\Psi = \frac{\partial \mathcal{G}}{\partial u}\left\{\Delta\Phi + [G_1\frac{\partial u}{\partial U} - u^e\frac{\partial v}{\partial U}]\Phi + [G_1\frac{\partial u}{\partial V} - u^e\frac{\partial v}{\partial V}]\Psi\right\} \\
\quad + \frac{\partial \mathcal{G}}{\partial v}\left\{\Delta\Psi + [G_2\frac{\partial v}{\partial V} - v^e\frac{\partial u}{\partial V}]\Psi + [G_2\frac{\partial v}{\partial U} - v^e\frac{\partial u}{\partial U}]\Phi\right\}, \\
0 = \mathbf{n} \cdot \nabla\Phi = \mathbf{n} \cdot \nabla\Psi,
\end{cases}
$$
$$(38)$$

where $G_1 = m - 2u^e - v^e$ and $G_2 = m - u^e - 2v^e$. Denote

$$F := \begin{pmatrix} U \\ V \end{pmatrix} = \begin{pmatrix} \gamma_1(s)u \\ \gamma_2(s)v \end{pmatrix}$$

and consider it as a function of u and v. Then, the Jacobian matrix is

$$M := \begin{pmatrix} \frac{\partial U}{\partial u} & \frac{\partial U}{\partial v} \\ \frac{\partial V}{\partial u} & \frac{\partial V}{\partial v} \end{pmatrix} = \begin{pmatrix} \gamma_1 - \gamma_1' \frac{mu}{(u+v)^2} & -\gamma_1' \frac{mu}{(u+v)^2} \\ -\gamma_2' \frac{mv}{(u+v)^2} & \gamma_2 - \gamma_2' \frac{mv}{(u+v)^2} \end{pmatrix}$$

and

$$M^{-1} = \begin{pmatrix} \frac{\partial u}{\partial U} & \frac{\partial u}{\partial V} \\ \frac{\partial v}{\partial U} & \frac{\partial v}{\partial V} \end{pmatrix} = \frac{1}{|M|} \begin{pmatrix} \gamma_2 - \gamma_2' \frac{mv}{(u+v)^2} & \gamma_1' \frac{mu}{(u+v)^2} \\ \gamma_2' \frac{mv}{(u+v)^2} & \gamma_1 - \gamma_1' \frac{mu}{(u+v)^2} \end{pmatrix}.$$

Let $(\theta_{\gamma_1}, 0)$ and $(0, \theta_{\gamma_2})$ be the two semi-trivial steady states of (1). The eigenvalue problem for (37) at the semi-trivial steady state $(\theta_{\gamma_1}(x), 0)$ is

$$\begin{cases} \lambda\Phi = \frac{\partial\mathcal{F}}{\partial u}\left\{\Delta\Phi + \frac{m-2\theta_{\gamma_1}}{\gamma_1 - s\gamma_1'}\Phi + \frac{1}{\gamma_2}\left[\frac{s\gamma_1'(m-2\theta_{\gamma_1})}{(\gamma_1 - s\gamma_1')} - \theta_{\gamma_1}\right]\Psi\right\} \\ \qquad + \frac{\partial\mathcal{F}}{\partial v}\left\{\Delta\Psi + \frac{m-\theta_{\gamma_1}}{\gamma_2}\Psi\right\}, \\ \lambda\Psi = \gamma_2(s)\left\{\Delta\Psi + \frac{m-\theta_{\gamma_1}}{\gamma_2}\Psi\right\}, \\ 0 = \mathbf{n}\cdot\nabla\Phi = \mathbf{n}\cdot\nabla\Psi, \end{cases} \tag{39}$$

where $s = \frac{m}{\theta_{\gamma_1}}$, and θ_{γ_1} satisfies

$$\begin{cases} 0 = \Delta(\gamma_1(s)\theta_{\gamma_1}) + \theta_{\gamma_1}[m(x) - \theta_{\gamma_1}], \\ 0 = \mathbf{n}\cdot\nabla(\gamma_1(s)\theta_{\gamma_1}). \end{cases} \tag{40}$$

Similarly, we may compute that the corresponding eigenvalue problem for (37) at $(0, \theta_{\gamma_2}(x))$ is

$$\begin{cases} \lambda\Phi = \gamma_1(s)\left\{\Delta\Phi + \frac{m-\theta_{\gamma_2}}{\gamma_1}\Phi\right\}, \\ \lambda\Psi = \frac{\partial\mathcal{G}}{\partial u}\left\{\Delta\Phi + \frac{m-\theta_{\gamma_2}}{\gamma_1}\Phi\right\} \\ \qquad + \frac{\partial\mathcal{G}}{\partial v}\left\{\Delta\Psi + \frac{m-2\theta_{\gamma_2}}{\gamma_2 - s\gamma_2'}\Psi + \frac{1}{\gamma_1}\left[\frac{s\gamma_2'(m-2\theta_{\gamma_2})}{(\gamma_2 - s\gamma_2')} - \theta_{\gamma_2}\right]\Phi\right\}, \\ 0 = \mathbf{n}\cdot\nabla\Phi = \mathbf{n}\cdot\nabla\Psi, \end{cases} \tag{41}$$

where $s = \frac{m}{\theta_{\gamma_2}}$, and $\theta_{\gamma_2}(x)$ satisfies

$$\begin{cases} 0 = \Delta(\gamma_2(s)\theta_{\gamma_2}) + \theta_{\gamma_2}[m - \theta_{\gamma_2}], \\ 0 = \mathbf{n}\cdot\nabla(\gamma_2(s)\theta_{\gamma_2}). \end{cases} \tag{42}$$

The uniqueness and global asymptotic stability of the positive steady states $\theta_{\gamma_1}(x)$ and $\theta_{\gamma_2}(x)$ have been obtained in [22, Theorem 2 and 3].

We now show the simplified stability criteria for the semi-trivial steady states of (1) which corresponds to Lemma 1 for the previous case.

Lemma 2. *Let $\theta_{\gamma_1}(x)$ and $\theta_{\gamma_2}(x)$ be the unique globally asymptotically stable steady state solution of (40) and(42), respectively.*

(i) Let ν_1 be the largest eigenvalue of

$$\begin{cases} \nu\Psi = \Delta\Psi + \frac{m-\theta_{\gamma_1}}{\gamma_2(s)}\Psi, \\ 0 = \mathbf{n}\cdot\nabla\Psi. \end{cases} \tag{43}$$

If $\nu_1 > 0$, $(\theta_{\gamma_1}(x), 0)$ is linearly unstable; if $\nu_1 < 0$, $(\theta_{\gamma_1}(x), 0)$ is linearly stable.

(ii) Let μ_1 be the largest eigenvalue of

$$\begin{cases} \mu\Phi = \Delta\Phi + \frac{m-\theta_{\gamma_2}}{\gamma_1(s)}\Phi, \\ 0 = \mathbf{n}\cdot\nabla\Phi. \end{cases} \tag{44}$$

If $\mu_1 > 0$, $(0, \theta_{\gamma_2}(x))$ is linearly unstable; if $\mu_1 < 0$, $(0, \theta_{\gamma_2}(x))$ is linearly stable.

Proof. Parts (i) and (ii) are of the same structure and we show part (i) only. Consider an eigenvalue problem

$$\begin{cases} \ell\Psi = \Delta\Psi + \frac{m-\theta_{\gamma_1}}{\gamma_2(s)}\Psi - \frac{\lambda}{\gamma_2(s)}\Psi, \\ 0 = \nabla\Psi\cdot\mathbf{n} \end{cases}$$

and denote its largest eigenvalue by ℓ_1^λ. Clearly, $\ell_1^0 = \nu_1$. Moreover, ℓ_1^λ will be negative when λ becomes large enough. First suppose that $\nu_1 > 0$. Then, there exists $\lambda_1 > 0$ such that $\ell_1^{\lambda_1} = 0$. Then, the corresponding eigen-pair $\{\lambda_1, \Psi_1\}$ satisfies the second equation of (39).

Next, since θ_{γ_1} is a stable steady state of (40), the eigenvalue problem,

$$\begin{cases} \sigma\psi = (\gamma_1 - s\gamma_1')\Delta\psi + (m - 2\theta_{\gamma_1})\psi, \\ 0 = \nabla\psi\cdot\mathbf{n}, \end{cases} \tag{45}$$

has only nonpositive eigenvalues and hence the operator,

$$\mathcal{L} := \Delta + \frac{m - 2\theta_{\gamma_1}}{\gamma_1 - s\gamma_1'} - \frac{\lambda_1}{\gamma_1 - s\gamma_1'}$$

is strictly negative and thus invertible. Let Φ_1 be given by

$$\mathcal{L}\Phi_1 = -\frac{1}{\gamma_2}\left[\frac{s\gamma_1'(m - 2\theta_{\gamma_1})}{\gamma_1 - s\gamma_1'} - \theta_{\gamma_1}\right]\Psi_1$$
$$- \left(\frac{\partial\mathcal{F}}{\partial u}\right)^{-1}\frac{\partial\mathcal{F}}{\partial v}\left\{\Delta\Psi_1 + \frac{m - \theta_{\gamma_1}}{\gamma_2}\Psi_1\right\}.$$

Then $\{\lambda_1, (\Phi_1, \Psi_1)\}$ is an eigen-pair of the linearized problem (39) with $\lambda_1 > 0$, which implies that $(\theta_{\gamma_1}(x), 0)$ is linearly unstable.

Next, assume that $\nu_1 < 0$. Suppose that the linearized problem (39) has a nonnegative eigenvalue $\lambda_1 \geq 0$ with the corresponding eigenfunctions (Φ_1, Ψ_1).

If $\Psi_1 \equiv 0$, then one may find that $\{\lambda_1, \Phi_1\}$ is an eigen-pair of (45) due to (39). Since θ_{γ_1} is a stable steady state of (40), the largest eigenvalue of (45) is negative, which contradicts to the assumption $\lambda_1 \geq 0$.

Let $\Psi_1 \not\equiv 0$. Then,

$$
\begin{aligned}
\nu_1 &= \sup_{\Psi \in H^1(\Omega) \setminus \{0\}} \frac{\int_\Omega \left[-|\nabla \Psi|^2 + \frac{m - \theta_{\gamma_1}}{\gamma_2(s)} \Psi^2 \right] dx}{\int_\Omega \Psi^2 dx} \\
&\geq \frac{\int_\Omega \left[-|\nabla \Psi_1|^2 + \frac{m - \theta_{\gamma_1}}{\gamma_2(s)} \Psi_1^2 \right] dx}{\int_\Omega \Psi_1^2 dx} \\
&= \frac{\int_\Omega \frac{\lambda_1}{\gamma_2(s)} \Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} \geq 0,
\end{aligned}
$$

where the last equality comes from the second equation of (39). Therefore, the linearized problem (39) has strictly negative eigenvalues only and hence $(\theta_{\gamma_1}(x), 0)$ is linearly stable. □

4.2. Spatial heterogeneity favors fitness! (proof of Theorem 3)

Theorem 3 claims that a species having more sensitive to the change of environmental conditions is favored by the evolution. The proof is based on the stability criteria of Lemma 2.

Proof (of Theorem 3). The proof of the theorem consists of three steps. First we show the stability of $(0, \theta_{\gamma_2}(x))$. Let (μ_1, Φ_1) be the largest eigen-pair of (44). Then,

$$
\begin{aligned}
\mu_1 &= \sup_{\Phi \in H^1(\Omega) \setminus \{0\}} \frac{\int_\Omega -|\nabla \Phi|^2 + \frac{m - \theta_{\gamma_2}}{\gamma_1(s)} \Phi^2 dx}{\int_\Omega \Phi^2 dx} \\
&= \frac{\int_\Omega -|\nabla \Phi_1|^2 + \frac{m - \theta_{\gamma_2}}{\gamma_1(s)} \Phi_1^2 dx}{\int_\Omega \Phi_1^2 dx} \\
&= \frac{\int_\Omega -|\nabla \Phi_1|^2 + \frac{m - \theta_{\gamma_2}}{\gamma_2(s)} \Phi_1^2 dx}{\int_\Omega \Phi_1^2 dx} + \frac{\int_\Omega (m - \theta_{\gamma_2})(\frac{1}{\gamma_1(s)} - \frac{1}{\gamma_2(s)}) \Phi_1^2 dx}{\int_\Omega \Phi_1^2 dx}.
\end{aligned}
$$

Since the operator $\Delta + \frac{m - \theta_{\gamma_2}}{\gamma_2(s)}$ has a positive eigenfunction $\gamma_2(s) \theta_{\gamma_2}$ with the zero eigenvalue, $\lambda = 0$ is the largest eigenvalue of $\Delta + \frac{m - \theta_{\gamma_2}}{\gamma_2(s)}$.

It implies that

$$\int_\Omega -|\nabla \Phi_1|^2 + \frac{m - \theta_{\gamma_2}}{\gamma_2(s)} \Phi_1^2 dx \le 0.$$

Therefore,

$$\mu_1 \le \frac{\int_\Omega (m - \theta_{\gamma_2})(\frac{1}{\gamma_1(s)} - \frac{1}{\gamma_2(s)})\Phi_1^2 dx}{\int_\Omega \Phi_1^2 dx}$$

$$= \frac{\left(\int_{\{m > \theta_{\gamma_2}\}} + \int_{\{m < \theta_{\gamma_2}\}} \right)(m - \theta_{\gamma_2})(\frac{1}{\gamma_1(s)} - \frac{1}{\gamma_2(s)})\Phi_1^2 dx}{\int_\Omega \Phi_1^2 dx} < 0,$$

and hence $(0, \theta_{\gamma_2})$ is linearly stable by Lemma 2.

In the second step, we show that $(\theta_{\gamma_1}(x), 0)$ is unstable. Recall that the stability is determined by

$$\nu_1 = \sup_{\Psi \in H^1(\Omega) \setminus \{0\}} \frac{\int_\Omega \left[-|\nabla \Psi|^2 + \frac{m - \theta_{\gamma_1}}{\gamma_2(s)} \Psi^2 \right] dx}{\int_\Omega \Psi^2 dx},$$

where $s = m/\theta_{\gamma_1}$. Let $\Psi := U = \gamma_1(s)\theta_{\gamma_1}$. Since $\min_{\bar\Omega} m(x) \le \theta_{\gamma_1} \le \max_{\bar\Omega} m(x)$,

$$\nu_1 \ge \frac{\int_\Omega \left[-|\nabla U|^2 + \frac{m - \theta_{\gamma_1}}{\gamma_2(s)} U^2 \right] dx}{\int_\Omega U^2 dx}$$

$$= \frac{\int_\Omega (m - \theta_{\gamma_1})(-\frac{1}{\gamma_1(s)} + \frac{1}{\gamma_2(s)})U^2 dx}{\int_\Omega U^2 dx}$$

$$= \left(\int_{\{m > \theta_{\gamma_1}\}} + \int_{\{m < \theta_{\gamma_1}\}} \right)\left(\frac{1}{\gamma_2(s)} - \frac{1}{\gamma_1(s)} \right)(m - \theta_{\gamma_1})U^2 dx > 0.$$

Therefore, according to Lemma 2, $(\theta_{\gamma_1}, 0)$ is linearly unstable.

Finally, we show that there is no steady state of coexistence. Suppose $(\tilde u, \tilde v)$ is a steady state such that $\tilde u \not\equiv 0 \not\equiv \tilde v$. Then, we have

$$\begin{cases} 0 = \Delta \tilde U + \tilde u[m(x) - \tilde u - \tilde v], \\ 0 = \Delta \tilde V + \tilde v[m(x) - \tilde u - \tilde v], \end{cases}$$

where $\tilde U = \gamma_1(s)\tilde u$, $\tilde V = \gamma_2(s)\tilde v$, and $s = \frac{m}{\tilde u + \tilde v}$. Clearly, $(\tilde U, \tilde V)$ satisfies

$$\begin{cases} 0 = \Delta \tilde U + \frac{m(x) - \tilde u - \tilde v}{\gamma_1(s)}\tilde U, \\ 0 = \Delta \tilde V + \frac{m(x) - \tilde u - \tilde v}{\gamma_2(s)}\tilde V. \end{cases}$$

Due to the assumption that $\gamma_1 \not\equiv \gamma_2$ in a small neighborhood of $s = 1$, we have

$$\frac{m(x) - \tilde{u} - \tilde{v}}{\gamma_1(s)} \not\leqq \frac{m(x) - \tilde{u} - \tilde{v}}{\gamma_2(s)}.$$

A contradiction arises immediately. $\qquad\qquad\qquad\qquad\qquad\square$

5. Conclusions

It is widely believed that spatial heterogeneities of environments reduce dispersal rates. This belief is based on studies of linear dispersal models with constant rates. However, biological organisms change their motility depending on environmental conditions and, recently, Cho and Kim [7] modeled a dispersal strategy that increases the motility when food is not enough. In this paper such a starvation driven diffusion is taken as a dispersal strategy of phenotypes of a species and the evolution of such dispersal strategies is analyzed. The main conclusion is that spatial heterogeneities of environments increase the fitness of dispersal. Since the model is not a monotone system, authors could not claim the global asymptotic stability. However, it is proved that the semi-trivial state that consists of the phenotype with a better fitness is the only stable steady state solution (see Theorems 2 and 3). It is also proved that a phenotype with a starvation driven diffusion may survive against the slowest phenotype among all possible linear diffusers (see Theorem 1). It seems safe to claim that spatial heterogeneities of environments increase the fitness of dispersal and the temporal fluctuations increase the size of dispersal.

References

1. I. Averill, Y. Lou, and D. Munther, *On several conjectures from evolution of dispersal*, Journal of Biological Dynamics **6** (2012), 117–130.
2. Fethi Belgacem and Chris Cosner, *The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environments*, Canad. Appl. Math. Quart. **3** (1995), no. 4, 379–397. MR 1372792 (97c:92013)
3. Andriy Bezuglyy and Yuan Lou, *Reaction-diffusion models with large advection coefficients*, Appl. Anal. **89** (2010), no. 7, 983–1004. MR 2674939 (2011e:35169)
4. Robert Stephen Cantrell and Chris Cosner, *Spatial ecology via reaction-diffusion equations*, Wiley Series in Mathematical and Computational Biology, John Wiley & Sons Ltd., Chichester, 2003. MR 2191264 (2007a:92069)
5. R.S. Cantrell, C. Cosner, and Y. Lou, *Approximating the ideal free distribution via reaction-diffusion-advection equations*, J. Differential Equations **245** (2008), 3687–3703.
6. _____, *Evolution of dispersal and ideal free distribution*, Math Biosciences and Engineering **7** (2010), 17–36.

7. Eunjoo Cho and Yong-Jung Kim, *Starvation driven diffusion as a survival strategy of biological organisms*, Bull. Math. Biol. (2013).

8. Dan Cohen and Simon A. Levin, *Dispersal in patchy environments: the effects of temporal and spatial structure*, Theoret. Population Biol. **39** (1991), no. 1, 63–99. MR 1094108

9. C. Cosner, *A dynamic model for the ideal-free distribution as a partial differential equation*, Theor. Pop. Biol. **67** (2005), 101–108.

10. C. Cosner, J. Dávila, and S. Martínez, *Evolutionary stability of ideal free nonlocal dispersal*, Journal of Biological Dynamics **6** (2012), 395–405.

11. Chris Cosner and Yuan Lou, *Does movement toward better environments always benefit a population?*, J. Math. Anal. Appl. **277** (2003), no. 2, 489–503. MR 1961241 (2004d:35125)

12. U. Dieckman, B. OHara, and W. Weisser, *The evolutionary ecology of dispersal*, Trends Ecol. Evol. **14** (1999), no. 3, 88–90.

13. Jack Dockery, Vivian Hutson, Konstantin Mischaikow, and Mark Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol. **37** (1998), no. 1, 61–83. MR 1636644 (99j:92006)

14. S.D. Fretwell, *Populations in a seasonal environment*, Princeton University Press, Princeton, NJ, 1972.

15. S.D. Fretwell and H.L. Lucas Jr., *On territorial behavior and other factors influencing habitat distribution in birds. i.*, Theoretical development. Acta Biotheor (1970), no. 19, 16–36.

16. R. Hambrock and Y. Lou, *The evolution of conditional dispersal strategies in spatially heterogeneous habitats*, Bull. Math. Biol. **71** (2009), no. 8, 1793–1817. MR 2551690 (2011c:92092)

17. R. Holt and M. McPeek, *Chaotic population dynamics favors the evolution of dispersal*, The American Naturalist **148** (1996), 709–718.

18. S. B. Hsu, H. L. Smith, and Paul Waltman, *Competitive exclusion and coexistence for competitive systems on ordered Banach spaces*, Trans. Amer. Math. Soc. **348** (1996), no. 10, 4083–4094. MR 1373638 (97d:92021)

19. V. Hutson, K. Mischaikow, and P. Poláčik, *The evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol. **43** (2001), no. 6, 501–533. MR 1874400 (2002k:92014)

20. M. Johnson and M. Gaines, *Evolution of dispersal: Theoretical models and empirical tests using birds and mammals*, Ann. Rev. Ecol. Syst. **21** (1990), 449–480.

21. M. Keeling, *Spatial models of interacting populations, advanced ecological theory: Principles and applications*, J. McGlade, ed. Blackwell Science, Oxford (1999).

22. Yong-Jung Kim, Ohsang Kwon, and Fang Li, *Global asymptotic stability and the ideal free distribution in a starvation driven diffusion*, J. Math. Biol., DOI:10.1007/s00285–013–0674–6.

23. King-Yeung Lam and Wei-Ming Ni, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics*, Discrete Contin. Dyn. Syst. **28** (2010), no. 3, 1051–1067. MR 2644778 (2011c:35136)

24. M. McPeek and R. Holt, *The evolution of dispersal in spatially and temporally varying environments*, The American Naturalist **140** (1992), 1010–1027.

25. Thomas Nagylaki, *Introduction to theoretical population genetics*, Biomathematics, vol. 21, Springer-Verlag, Berlin, 1992. MR 1224677 (94i:92006)

26. Wei-Ming Ni, *The mathematics of diffusion*, CBMS-NSF Regional Conference Series in Applied Mathematics, vol. 82, Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 2011. MR 2866937

27. Akira Okubo and Simon A. Levin, *Diffusion and ecological problems: modern perspectives*, second ed., Interdisciplinary Applied Mathematics, vol. 14, Springer-Verlag, New York, 2001. MR 1895041 (2003a:92025)

28. M. J. Tindall, S. L. Porter, P. K. Maini, G. Gaglia, and J. P. Armitage, *Overview of mathematical approaches used to model bacterial chemotaxis. I. The single cell*, Bull. Math. Biol. **70** (2008), no. 6, 1525–1569. MR 2430317 (2009i:92012a)
29. J.M.J. Travis and C. Dytham, *Habitat persistence, habitat availability and the evolution of dispersal*, Proc. Roy. Soc. London B. **266** (1999), 723–728.
30. Changwook Yoon and Yong-Jung Kim, *Bacterial chemotaxis without gradient-sensing*, preprint, http://arxiv.org/abs/1307.6071 (2013).