EVOLUTION OF DISPERSAL WITH STARVATION MEASURE AND COEXISTENCE

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Abstract. Many of biological species increase their dispersal rate if starvation starts. To model such a behavior we need to understand how organisms *measure* starvation and *response* to it. In this paper we compare three different ways of measuring starvation by applying them to starvation driven diffusion. The evolutional selection and coexistence of such starvation measures are studied within the context of Lotka-Volterra type competition model of two species. We will see that, if species have different starvation measures and different motility functions, both the coexistence and selection are possible.

1. Introduction

Migration is an essential component for the survival of biological organisms and various dispersal strategies have been developed by different species. The necessity of formulating a more realistic dispersal theory for biological organisms that takes into account interaction between individuals and animal response to environment has been emphasized (see Skellam [27, 28] and Okubo & Levin [24, Chapter 5]). The purpose of this paper is to develop a biodiffusion theory that takes into account the dispersal increase when food dwindles. Biological organisms mostly increase the dispersal to find food if starvation started. It is such a dispersal change, but not simply a dispersal size, that gives a better survival chance to biological species. Recently, starvation sensing mechanisms and its significance in the growth factor of a species have been extensively studied (see [10, 13]).

The starvation driven diffusion (SDD for brevity) has been recently introduced by Cho and Kim [3] to mathematically model dispersal increase in the event of starvation. One of our main interests is in the correct timing of dispersal increase in the event of starvation. To observe the effect of dispersal change we take a motility function, or a departing probability, as

$$\gamma^0(s) = \begin{cases} \ell, & 0 \le s < s^*, \\ h, & s^* \le s < \infty, \end{cases} \tag{1}$$

where h and ℓ are positive constants such that $\ell < h$. This is an extreme case that all organisms increase their departing probability (or motility) from ℓ to h if the *starvation measure* 's' increases to a critical value, $s = s^*$. This motility function magnifies the effect of dispersal increase and will provide a clear theory. Due to the singularity of γ^0 we also take a regularized motility, $\gamma = \gamma^\epsilon$, as given in (3). It is well known that the corresponding random walk model with the departing probability γ is given by a Fokker–Planck type diffusion law

$$u_t = \Delta(\gamma(s)u), \tag{2}$$

where u is the population density (see [24, §5.4]). The effect of such diffusion has been studied for the single species case in [16] when a logistic population dynamics is added. The evolution of such dispersals toward fitness has been studied in the context of Lotka-Volterra competition model recently (see [15]).

In this paper, two species (or phenotypes) competition systems are considered, where u and v denote their population densities. The main focus of our study is the effect of *starvation measure* in the evolutional selection and coexistence. Three phenotypes having three different ways of measuring starvation are tested. The first phenotype does not sense any change of environment and hence is assumed to have a constant starvation measure $s = s_0$. The second

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one takes $s=\frac{v}{m}$ in the context of competition equations (7)–(8), where v is the population of its own species and m is the amount of food supply. One can easily see that this measure increases if the population increases and the resource dwindles, which indicates that the ratio is an indicator of starvation. The third phenotype takes $s=\frac{u+v}{m}$, where $u+v$ is the total population including the competing species and is a better way to measure starvation. We will show that the evolutional selection favors the measure $s=\frac{u}{m}$ over the constant one $s=s_0$ and $s=\frac{u+v}{m}$ over $s=\frac{u}{m}$ if the critical starvation value is $s^*=1$. However, a coexistence can be obtained if $s^*\neq 1$. The results of the competition among these three phenotypes are discussed in Section 2.

There have been intensive studies on the evolution of dispersal strategies. The size effect of constant dispersal rates is particularly understood well and comprehensive discussions on discrete and continuous models can be found from [2, 4, 12, 22, 23, 24]. Numerical simulations and theoretical analysis show that a smaller dispersal rate is selected if the environment is spatially heterogeneous (see [5, 6, 11, 12, 14, 21]), and that a larger dispersal rate can be selected if there is a temporal fluctuation of the environment (see [5, 8, 11, 12, 29]). However, if an adapting behavior of organisms is included, it is not only the dispersal size that matters. In the context of Lotka-Volterra competition model with starvation driven diffusion, a dispersal strategy with better fitness property has been selected (see [15]).

In Section 2, we formulate competition problems between two species and state three main theorems about evolutional selection and coexistence. These three theorems are proved in Sections 3–5, respectively. The theorems are numerically tested in Section 6 in a two patch environment and in one space dimension. In particular, a comprehensive simulation for the global asymptotic stability is tested using a two patches environment and conjectures related to the theory are discussed and tested numerically.

2. Main results and discussions

Notice that the motility function γ^0 in (1) has a discontinuity and there is a difficulty in handling such a diffusion directly. For analysis we consider its continuous approximation,

$$\gamma^\epsilon := \gamma^0 * \eta^\epsilon, \tag{3}$$

where $\epsilon>0$ is small and the mollifier η^ϵ satisfies $\int \eta^\epsilon(x)dx=1$. For a technical simplicity, we take $\operatorname{supp}(\eta^\epsilon)\subset(0,\epsilon)$ and hence

$$\gamma^\epsilon(s)=\ell \qquad \text{for} \quad 0\le s\le s^*.$$

In the rest of this paper we denote the smooth motility function by γ without the superscript for notational simplicity unless needed. Theorems of this paper are with such a smooth approximation, $\gamma=\gamma^\epsilon$, but not γ^0.

In this paper we consider evolutional selection of three phenotypes that have different methods of measuring starvation. The first phenotype does not sense it at all and takes a constant starvation measure $s=s_0$. Then, the population model for the phenotype with a logistic reaction term is written as

$$u_t=d\Delta u+u(m(x)-u), \qquad x\in\Omega,\ t>0,$$

where u is the population density, Ω is a bounded domain with a smooth boundary, and $m(x)>0$ is a nonconstant resource distribution. The constant diffusivity is $d=\gamma(s_0)$ with the constant starvation measure s_0 and $\ell\le d\le h$. If a case with $d<\ell$ is considered, one is basically taking a different motility function. It is well-known that there exists a unique steady state of the equation with constant diffusivity, denoted by θ_d, and is globally asymptotically stable.

The starvation measure of the second phenotype is given by

$$s:=\frac{v}{m}, \tag{4}$$

where v is the population density of the second phenotype. Clearly, if the population density v increases and the resource m decreases, the starvation measure (4) increases. Therefore, the ratio in (4) actually measures starvation somewhat. However, the phenotype v does not count the presence of the other phenotype u and the consequence of this missing part is the main point to watch in this paper. For the single species case, the population model is written as

$$v_t = \Delta(\gamma(s)v) + v(m(x) - v), \qquad x \in \Omega,\ t > 0. \tag{5}$$

There is a unique steady state is denoted by $\theta_\gamma(x)$ and its global asymptotic stability has been obtained in [16] under an extra assumption on the motility:

$$\gamma(s) - (s-1)\gamma'(s) > 0 \text{ for } s > 1, \tag{6}$$

where the above motility function γ^ϵ satisfies this relation for small $\epsilon > 0$ and $s^* \cong 1$.

Remark 2.1. *In this paper we assume $m > 0$ and hence the starvation measures such as $\frac{u}{m}$ and $\frac{u+v}{m}$ are well defined. If $m \not> 0$ is considered, we may consider the reciprocal of the starvation measure $\frac{m}{u}$ or $\frac{m}{u+v}$, which may called a* satisfaction measure. *Then, the uniform parabolicity of the problem gives the positivity to the solution and hence the satisfaction measure is well defined for all $t > 0$. If the motility function γ is taken as a decreasing function of the satisfaction measure, one may obtain the same theory (see* [3, 15, 16]*).*

The first competition model of this paper is

$$\begin{aligned}
&u_t = \quad d\Delta u \quad + u[m(x) - u - v], && x \in \Omega,\quad t > 0, && (7)\\
&v_t = \Delta(\gamma(s)v) + v[m(x) - u - v], && x \in \Omega,\quad t > 0, && (8)\\
&0 = \vec{n}\cdot\nabla u = \vec{n}\cdot\nabla[\gamma(s)v], && x \in \partial\Omega,\ t > 0, && (9)\\
&0 \le u(x,0) \not\equiv 0,\ 0 \le v(x,0) \not\equiv 0, && x \in \Omega, && (10)
\end{aligned}$$

which is a Lotka-Volterra type competition model of two species. Here, the zero flux boundary condition (9) and nontrivial and nonnegative initial value (10) are imposed. The SDD in (8) is with the starvation measure in (4) and is written as

$$\Delta(\gamma(s)v) = \nabla\cdot\Big((\gamma(s) + s\gamma'(s))\nabla v - s^2\gamma'(s)\nabla m\Big),$$

which contains self-diffusion and advection, but not cross-diffusion. We assume the global existence and uniqueness of the system (7)–(10). Due to the quasilinear diffusion term and Neumann boundary condition, a separate discussion for the global well-posedness will be needed. (For linear diffusion case, see [25] and for a recent result on cross-diffusion, see [20]) Then, this problem has the monotonicity property and the global asymptotical stability of the system is given in the first theorem of this paper:

Theorem 2.1. *Let the jumping moment of the motility function in (1) be $s^* = 1$ and the resource distribution $m(x) > 0$ be nonconstant. If $d > \ell$, the semi-trivial steady state $(u, v) = (0, \theta_\gamma)$ of the system (7)–(10) is globally asymptotically stable. If $d < \ell$, the other semi-trivial steady state $(\theta_d, 0)$ is linearly stable.*

Theorem 2.1 indicates that the starvation driven dispersal is selected over the unconditional random dispersal if $d \ge \ell$. If $d = \ell$ and $\min_{x\in\Omega} m(x) > 0$, there exists a positive steady state of coexistence. For example, there exists a constant $0 < c_0 < 1$ such that $c_0\theta_d(x) \le m(x)$ in Ω and $((1-c)\theta_d, c\theta_d)$ is a positive steady state of the system (7)–(10) for any $0 < c \le c_0$. However, if $d < \ell$, we have relatively less information. It is unclear if solutions always converge to $(\theta_d, 0)$, or if a solution may converge to $(0, \theta_\gamma)$ depending on the initial value, or both species may coexist. In fact, we may numerically observe many scenarios. For example, if d is smaller than certain value, say $d < d_0$, the solution always converges to $(\theta_d, 0)$. If $d_0 < d < \ell$, then the solution may converge to either of the semi-trivial steady states or to a positive one (see Figure 1). Remember that, if $d < \ell$, the motility function of the two species should be treated as different ones since the difference in starvation measure is not enough to explain the circumstance.

The starvation measure of the third phenotype is

$$\tilde{s} := \frac{u+v}{m}, \tag{11}$$

which counts the population of both species. This is the model introduced in [3]. An analysis for the competition between the first and the third phenotypes is in [15]. Here, we use a different notation $\tilde{s}$ to distinguish it from the previous measure s in (4). The semi-trivial case is identical to the second phenotype case (5). Now we consider a competition between the second and the third phenotypes by replacing (7) with

$$u_t = \Delta(\gamma(\tilde{s})u) + u[m(x) - u - v], \quad x \in \Omega, \quad t > 0. \tag{7'}$$

The situation $\tilde{s} = 1$ is a border case that the population growth rate $m - u - v$ changes it sign. If $\tilde{s} < 1$, then the growth rate becomes positive and the population will grow. If $\tilde{s} > 1$, then the resource is not enough to support the population and the population decreases. Usually, the individuals do not know the size of the population $u + v$ nor the amount of the total resource m. However, they know if they are getting enough resource or not. Hence $\tilde{s}$ is the quantity that individuals may sense.

The diffusion of the third phenotype is written as

$$\Delta(\gamma(\tilde{s})u) = \nabla \cdot \Big(\big(\gamma(\tilde{s}) + \frac{u}{m}\gamma'(\tilde{s})\big)\nabla u + \frac{u}{m}\gamma'(\tilde{s})\nabla v - \frac{u}{m}\tilde{s}\gamma'(\tilde{s})\nabla m \Big), \tag{12}$$

which now contains self-diffusion, cross diffusion and advection. The newly added cross-diffusion term gives the species another advantage. However, we have lost the monotonicity of the problem and the analysis becomes harder. The second theorem is about the uniqueness of a stable steady state of the competition system:

Theorem 2.2. *Let $s^* = 1$ and $0 < m(x) \neq$ constant. The steady state $(\theta_\gamma, 0)$ of the system (7)′,(8)–(10) is linearly stable and the other steady state $(0, \theta_\gamma)$ is linearly neutrally stable. Moreover, there is no other steady state.*

We call that the steady state $(0, \theta_\gamma)$ is linearly neutrally stable if the first eigenvalue λ_1 of the corresponding linearized eigenvalue problem of (29) is nonnegative. The uniqueness of a stable steady state given by the theorem and the numerical simulations given in Figure 3 strongly indicate that the steady state $(\theta_\gamma, 0)$ should be globally asymptotically stable and hence the third phenotype u would be selected eventually. However, a theoretical conclusion of the global asymptotic stability is not obtained due to the lack of monotonicity of the resulting system.

Biological species may take their own way of sensing environment and may react for their survival in the event of starvation. These differences may give chances for many species to coexist by providing rooms of survival. However, it is well known that, if the environment is time independent and diffusion is with constant diffusivity, only the slowest dispersal is selected and there is no coexistence driven by diffusion (see [6]). A migration driven coexistence can be found for the competition-diffusion-advection systems when two different dispersal dynamics are involved (see [18, 19]). In the last theorem of this paper we will find a possibility of coexistence of two species in the context of starvation driven diffusion. Remember that Theorem 2.2 indicates the starvation measure $\frac{u+v}{m}$ is favored over $\frac{v}{m}$ and there seems no coexistence at least numerically. This is due to the special jumping moment $s^* = 1$. In the monotone system, it is well known that, if both semi-trivial steady states are stable (or unstable), there is a coexistence (see [9]). If s^* is small or large enough, then the motility of a semi-trivial steady state becomes constant. This implies that both semi-trivial stead states could lose their stability and so, two species may coexist. The last theorem of this paper indicates such possibility:

Theorem 2.3. *Let $0 < m(x) \neq$ constant. If $s^* \geq \frac{\max_x m(x)}{\min_x m(x)}$, both semi-trivial steady states, $(\theta_\gamma, 0)$ and $(0, \theta_\gamma)$, of the system (7)′,(8)–(10) are linearly neutrally stable. If $s^* \leq \frac{\min_x m(x)}{\max_x m(x)}$, $(\theta_\gamma, 0)$ is linearly unstable and $(0, \theta_\gamma)$ linearly neutrally stable.*

The ratio $\frac{\max_x m(x)}{\min_x m(x)}$ measures the spatial variation of the resource distribution. The theorem implies that any of the semi-trivial state of the system (7)′,(8)–(10) is not linearly stable if the jumping moment s^* is bigger than resource variation or less than its reciprocal. This indicates that there may exist a steady state that two species coexist. In fact, numerical simulations in Section 6 show various coexistence states (see Figure 4). In the context of Lotka-Volterra competition model without temporal fluctuation of environment, the timing $s^*=1$ to increase migration rate is the best one. The coexistence in the model was possible since the jumping moment is not the ideal one. One may ask further when is the best moment to increase the dispersal when the environment temporally fluctuate.

The starvation driven diffusion (or SDD) is based on the idea that certain biological organisms increase their dispersal when food dwindles. This idea let us replace the classical unconditional dispersal to a non-uniform conditional one and resolve the nonphysical situation that the dispersal is degraded by spatial heterogeneity (see [6, 15, 21]). SDD naturally takes into account animal response to environment mentioned by Skellan and Okubo. Furthermore, in the way measuring starvation, the interaction between individuals is also included. For example, the self-diffusion term $\frac{u}{m}\gamma'(\tilde{s})\nabla u$ in (12) reflects the intra-species interaction and the cross-diffusion term $\frac{u}{m}\gamma'(\tilde{s})\nabla v$ reflects the inter-species interaction. The advection term $-\frac{u}{m}\tilde{s}\gamma'(\tilde{s})\nabla m$ is the animal response to the environment. It is these terms that make SDD a realistic dispersal model for biological organisms.

3. Starvation driven diffusion versus linear diffusion

In this section we consider the case that the motility of the first phenotype is constant $d=\gamma(s_0)$ and the motility of the second phenotype is, $\gamma=\gamma(s)$ with $s=\frac{v}{m}$. Then the system (7)–(10) is written as

$$\begin{cases} u_t = \quad d\Delta u \quad + u[m-u-v], \\ v_t = \Delta(\gamma(s)v) + v[m-u-v], \\ 0 = \vec{n}\cdot\nabla u = \vec{n}\cdot\nabla[\gamma(s)v], \\ 0\le u(x,0)=u_0(x),\ 0\le v(x,0)=v_0(x), \end{cases} \tag{13}$$

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 are like this throughout the paper and will not be mentioned again.

3.1. **A linearization and an eigenvalue analysis.**

First, introduce the diffusion pressure V for the second phenotype given by

$$V := \gamma(s)v \quad \text{with} \quad s := \frac{v}{m}. \tag{14}$$

Define

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

which is identically zero under the relation (14). This functional gives a relation among unknowns. Since the resource distribution is invariant in time, $m=m(x)$, we have

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

Furthermore, since

$$\frac{\partial\mathcal{F}}{\partial v} = \gamma(s)+\gamma'(s)s > 0, \tag{15}$$

the unknown function v is decided by m and V, i.e., we may write $v=v(m,V)$ by the implicit function theorem. Hence, (13) is written as

$$\begin{cases} u_t = d\Delta u + u[m-u-v], \\ V_t = \frac{\partial\mathcal{F}}{\partial v}\{\Delta V + v[m-u-v]\}, \\ 0 = \vec{n}\cdot\nabla V = \vec{n}\cdot\nabla u, \\ 0\le u(x,0)=u_0(x),\ 0\le V(x,0)=V_0(x), \end{cases} \tag{16}$$

where

$$V_0 := \gamma\Big(\frac{v_0}{m}\Big)v_0.$$

Let (u^e, v^e) be a steady state of (13). The stability of (u^e, v^e) is identical to that of the steady state (u^e, V^e) of (16), where $V^e := \gamma(s^e)v^e$. Whenever a linearized problem is considered, the starvation measure is taken as

$$s^e = \frac{v^e}{m},$$

where (u^e, v^e) the steady state related to the linearized problem. Let $u = u^e + \phi$ and $V = V^e + \Psi$ with $|\phi|$ and $|\Psi|$ small. Then,

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

where the implicit function theorem gives

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

A steady state $(u^e(x), V^e(x))$ of (16) is called stable if the eigenvalues of the linearized eigenvalue problem,

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - 2u^e - v^e)\phi - u^e \frac{\partial v}{\partial V}\Psi, \\ \lambda\Psi = \frac{\partial \mathcal{F}}{\partial v}\left\{\Delta\Psi + (m - u^e - 2v^e)\frac{\partial v}{\partial V}\Psi - v^e\phi\right\}, \\ \ 0 \ = \vec{n}\cdot\nabla\Psi = \vec{n}\cdot\nabla\phi, \end{cases} \tag{17}$$

are strictly negative. Consider a semi-trivial steady state $(\theta_d, 0)$ of (13). Then, at the steady state, we have

$$\frac{\partial v}{\partial V} = \frac{1}{\ell}, \quad \frac{\partial \mathcal{F}}{\partial v} = \ell,$$

and the eigenvalue value problem for (16) around the steady state $(\theta_d, 0)$ is

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - 2\theta_d)\phi - \frac{\theta_d}{\ell}\Psi, \\ \lambda\Psi = \ell\Delta\Psi + (m - \theta_d)\Psi, \\ \ 0 \ = \vec{n}\cdot\nabla\Psi = \vec{n}\cdot\nabla\phi, \end{cases} \tag{18}$$

where θ_d satisfies

$$\begin{cases} 0 = d\Delta\theta_d + \theta_d[m - \theta_d], \\ 0 = \vec{n}\cdot\nabla\theta_d. \end{cases} \tag{19}$$

Similarly, let $(0, \theta_\gamma)$ be the other semi-trivial steady state and

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

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

$$\begin{cases} \lambda\phi = d\Delta\phi + (m - \theta_\gamma)\phi, \\ \lambda\Psi = (\gamma(s_\gamma) + \gamma'(s_\gamma)s_\gamma)\left\{\Delta\Psi + \frac{m - 2\theta_\gamma}{\gamma(s_\gamma) + \gamma'(s_\gamma)s_\gamma}\Psi - \theta_\gamma\phi\right\}, \\ \ 0 \ = \vec{n}\cdot\nabla\Psi = \vec{n}\cdot\nabla\phi, \end{cases} \tag{20}$$

where θ_γ satisfies

$$\begin{cases} 0 = \Delta\left(\gamma(s_\gamma)\theta_\gamma\right) + \theta_\gamma[m - \theta_\gamma], \\ 0 = \vec{n}\cdot\nabla\left(\gamma(s_\gamma)\theta_\gamma\right). \end{cases} \tag{21}$$

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

Lemma 3.1. *Let θ_d and θ_γ be the unique stable steady solution of (19) and (21), respectively.*

(i) *Let μ_1 be the first eigenvalue of*

$$\begin{cases} \mu\Psi = \ell\Delta\Psi + (m-\theta_d)\Psi, \\ 0 \ = \vec{n}\cdot\nabla\Psi. \end{cases} \tag{22}$$

If $\mu_1 > 0$, then a semi-trivial steady state solution $(\theta_d, 0)$ of (13) is linearly unstable. If $\mu_1 < 0$, then it is linearly stable.

(ii) *Let ν_1 be the first eigenvalue of*

$$\begin{cases} \nu\phi = d\Delta\phi + (m-\theta_\gamma)\phi, \\ 0 \ = \vec{n}\cdot\nabla\phi. \end{cases} \tag{23}$$

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

Proof. (i)

If $\mu_1 > 0$, then, due to (19), it is easy to see that the operator

$$\mathcal{L}_v = d\Delta + (m - 2\theta_d) - \mu_1$$

is invertible. This yields that $\mu_1 > 0$ is an eigenvalue of the linearized problem (18), and that $(\theta_d(x), 0)$ is linearly unstable.

Next, we consider the case with $\mu_1 < 0$ and show $(\theta_d, 0)$ is linearly stable. If not, the linearized problem (18) 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 (18), (19) and the assumption that $\lambda_1 \geq 0$. Hence $\Psi_1 \neq 0$. However, using the Rayleigh quotient, this yields that

$$\begin{aligned} \mu_1 &= \sup_{\Psi\in H^1(\Omega)\setminus\{0\}} \frac{\int_\Omega \left[-\ell|\nabla\Psi|^2 + (m-\theta_d)\Psi^2\right] dx}{\int_\Omega \Psi^2 dx} \\ &\geq \frac{\int_\Omega \left[-\ell|\nabla\Psi_1|^2 + (m-\theta_d)\Psi_1^2\right] dx}{\int_\Omega \Psi_1^2 dx} = \frac{\int_\Omega \lambda_1\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} \geq 0. \end{aligned}$$

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

(ii) The linearized eigenvalue problem of (21) about the steady state V_γ 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 (21), the linear operator $\Delta + (m-2\theta_\gamma)\frac{\partial v}{\partial V}$ has nonpositive eigenvalues. Thus, if $\nu_1 > 0$, 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 due to (15) and hence is invertible. Let $\{\nu_1, \phi_1\}$ be an eigen-pair of (23) and Ψ_1 satisfy

$$\mathcal{L}\Psi_1 = \theta_\gamma\phi_1.$$

Then, $\{\nu_1, (\phi_1, \Psi_1)\}$ is an eigen-pair of the linearized problem (20) and hence $(0, V_\gamma(x))$ is linearly unstable.

Since an eigenvalue of (20) is also an eigenvalue of (23), eigenvalues of (20) are all strictly negative if $\nu_1 < 0$. Therefore, $(0, V_\gamma(x))$ is linearly stable. ☐

3.2. **Proof of Theorem 2.1.**

It is widely accepted that a slower diffuser is selected over a faster one in a spatially heterogeneous environment (see Dockery *et al.* [6]). The conclusion of Theorem 2.1 partly agrees with this consensus. For example, if $d < \ell$, then $(\theta_d, 0)$ is linearly stable and hence being a slower diffusor is an advantage. However, if $d = \ell$ and $\ell < h$, then the second phenotype is selected even if it is a faster diffuser in the region of $s > 1$. In other words, being a faster diffuser in a region with less food is an advantage. The proof of the theorem is based on the stability criteria given in Lemma 3.1.

Proof of Theorem 2.1. Clearly, $(\theta_d, 0)$ is a steady state of (16). The stability of $(\theta_d, 0)$ as a steady state of (13) is determined by the signs of the first eigenvalue, denoted by μ_1, of an eigenvalue problem

$$\begin{cases} \mu\Psi = \ell\Delta\Psi + (m-\theta_d)\Psi, \\ 0 \ = \vec{n}\cdot\nabla\Psi. \end{cases}$$

Since θ_d is the unique positive solution of (19), μ_1 is positive if $d < \ell$, μ_1 is negative when $d > \ell$, and $\mu_1 = 0$ if $d = \ell$.

To show the global asymptotic stability of $(0, \theta_\gamma)$ we compute the sign of the first eigenvalue of (23) and show the monotonicity of our system. Since $m - \theta_\gamma$ is positive in a region, we obtain for a sufficiently small d that

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

Moreover, ν_1 decreases as d increases. Let $d = \ell$ and (ν_1, Ψ_1) be the first eigen-pair of (23). Then

$$\begin{aligned} \nu_1 &= \sup_{\Psi\in H^1(\Omega)\backslash\{0\}} \frac{\int_\Omega -d|\nabla\Psi|^2 + (m-\theta_\gamma)\Psi^2 dx}{\int_\Omega \Psi^2 dx} \\ &= \frac{\int_\Omega -d|\nabla\Psi_1|^2 + (m-\theta_\gamma)\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} \\ &= \frac{\int_\Omega -\ell|\nabla\Psi_1|^2 + \ell\frac{m-\theta_\gamma}{\gamma(s)}\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} + \frac{\int_\Omega (1-\frac{\ell}{\gamma(s)})(m-\theta_\gamma)\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx}. \end{aligned}$$

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

$$\int_\Omega -|\nabla\Psi_1|^2 + \frac{m-\theta_\gamma}{\gamma(s)}\Psi_1^2 dx \le 0.$$

Therefore,

$$\begin{aligned} \nu_1 &\le \frac{\int_\Omega (1-\frac{\ell}{\gamma(s)})(m-\theta_\gamma)\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx} \\ &= \frac{\left(\int_{\{m>\theta_\gamma\}} + \int_{\{m<\theta_\gamma\}}\right)(m-\theta_\gamma)(1-\frac{\ell}{\gamma(s)})\Psi_1^2 dx}{\int_\Omega \Psi_1^2 dx}. \end{aligned}$$

We get that $\gamma(s) = \ell$ when $m > \theta_\gamma$ and $\gamma(s) > \ell$ when $m < \theta_\gamma$. Since $|\{x \in \Omega \mid m < \theta_\gamma\}| > 0$, $\nu_1 < 0$. According to Lemma 3.1, there exists a positive constant $\omega_1 < \ell$ such that $(0, \theta_\gamma)$ is linearly unstable if $d < \omega_1$ and linearly stable if $d > \omega_1$.

Next, we will show that there is no positive steady state of (13) if $\ell < d$. Suppose that (u, v) is a positive steady state. Then,

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

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

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

Multiply $0=d\Delta u+u[m-u-v]$ by u and integrate, then we get that

$$d\int_\Omega |\nabla u|^2=\int_\Omega u^2(m-u-v)\geq 0.$$

Therefore, we get that

$$\begin{aligned}
0 &\geq \int_\Omega \left[-\frac{1}{d}u^2(m-u-v)+\frac{1}{\gamma(s)}u^2(m-u-v)\right]dx\\
&\geq \int_\Omega (\frac{1}{\gamma(s)}-\frac{1}{\ell})u^2(m-u-v)dx\\
&= \Big(\int_{\{s>1\}}+\int_{\{s\leq 1\}}\Big)(\frac{1}{\gamma(s)}-\frac{1}{\ell})u^2(m-u-v)dx\\
&= \int_{\{s>1\}}(\frac{1}{\gamma(s)}-\frac{1}{\ell})u^2(m-u-v)dx.
\end{aligned}$$

If $s>1$, then $m-u-v\leq m-v<0$ and $\frac{1}{\gamma(s)}-\frac{1}{\ell}<0$. Consequently, $v\leq m$ in Ω and $\gamma(s)\equiv\ell$. Therefore, (u,v) satisfies that

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

Similarly,

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

This implies that u is a constant and so v either. Since we assume that m is nonconstant this is a contradiction.

Next we show the monotonicity of the problem. Let (u_δ,v_δ) be the solution of

$$\begin{cases}(u_\delta)_t=d\Delta u_\delta+u_\delta[m+\delta-u_\delta-v_\delta],\\ (v_\delta)_t=\Delta(\gamma(\frac{v_\delta}{m})v_\delta)+v_\delta[m-\delta-u_\delta-v_\delta],\\ 0=\vec{n}\cdot\nabla u_\delta=\vec{n}\cdot\nabla(\gamma(\frac{v_\delta}{m})v_\delta),\ u_\delta(x,0)=u_{\delta,0},\ v_\delta(x,0)=v_{\delta,0},\end{cases}$$

where δ is a sufficiently small positive constant.

Claim: If $u_0(x)\leq u_{\delta,0}(x)$ and $v_0(x)\geq v_{\delta,0}(x)$, then $u(x,t)<u_\delta(x,t)$ and $v(x,t)>v_\delta(x,t)$, where (u,v) is the solution of (13).

We assume that there exist $x_0 \in \Omega$ and $t_0 > 0$ such that $v(x_0, t_0) = v_\delta(x_0, t_0)$ and $u(x_0, t_0) \leq u_\delta(x_0, t_0)$, where $v(x_0, t) > v_\delta(x_0, t)$ for any $0 < t < t_0$. Then, since $\gamma(\frac{v}{m})v$ is increasing as v is increasing,

$$\frac{\partial v - v_\delta}{\partial t}\Big|_{x=x_0,t=t_0} = [\Delta(\gamma(\frac{v}{m})v - \gamma(\frac{v_\delta}{m})v_\delta) + v(\delta + u_\delta - u)]\Big|_{x=x_0,t=t_0} > 0.$$

This is a contradiction. In the same way, we can show that $u(x,t) < u_\delta(x,t)$ for any $x \in \Omega$, $t > 0$ and $\delta > 0$.

Therefore, if $(\tilde{u}, \tilde{v})$ is the solution of (13) with the initial value $(\tilde{u}_0, \tilde{v}_0)$ such that $u_0 \leq \tilde{u}_0$ and $v_0 \geq \tilde{v}_0$, then $u(x,t) \leq \tilde{u}(x,t)$ and $v(x,t) \geq \tilde{v}(x,t)$. Moreover, from the maximum principle, if $u_0 \neq \tilde{u}_0$, then $u(x,t) < \tilde{u}(x,t)$ for any $x \in \Omega$ and $t > 0$. Therefore, if there exist $x_0 \in \Omega$ and $t_0 > 0$ such that $v(x_0, t_0) = \tilde{v}(x_0, t_0)$, where $v(x_0, t) > \tilde{v}(x_0, t)$ for any $0 < t < t_0$. Then,

$$\frac{\partial v - \tilde{v}}{\partial t}\Big|_{x=x_0,t=t_0} = [\Delta(\gamma(\frac{v}{m})v - \gamma(\frac{\tilde{v}}{m})\tilde{v}) + v(\tilde{u} - u)]\Big|_{x=x_0,t=t_0} > 0.$$

This is a contradiction. This implies that our system is monotone. Then, from the theory of monotone dynamical systems (See, e.g., Proposition 9.1 and Theorem 9.2 in [7]), $(0, \theta_\gamma)$ is globally asymptotically stable when $d \geq \ell$. □

4. COMPETITION BETWEEN TWO STARVATION MEASURES

In this section, we consider the competition model (7)–(10) with non-constant motility functions for both species,

$$\begin{cases} u_t = \Delta(\gamma(\tilde{s})u) + u[m(x) - u - v], \\ v_t = \Delta(\gamma(s)v) + v[m(x) - u - v], \\ \;0 \;= \vec{n} \cdot \nabla[d(\tilde{s})u] = \vec{n} \cdot \nabla[\gamma(s)v], \\ 0 \leq u(x,0) = u_0(x), \; 0 \leq v(x,0) = v_0(x). \end{cases} \tag{24}$$

4.1. **A linearization and an eigenvalue analysis.**

Introduce biological diffusion pressures

$$U := \gamma(\tilde{s})u, \quad V := \gamma(s)v \quad \text{with} \quad \tilde{s} := \frac{u+v}{m}, \quad s := \frac{v}{m}. \tag{25}$$

Define

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

Then, (7)–(10) can be rewritten as

$$\begin{cases} U_t = \frac{\partial \mathcal{F}}{\partial u}\{\Delta U + u[m(x) - u - v]\} + \frac{\partial \mathcal{F}}{\partial v}\{\Delta V + v[m(x) - u - v]\}, \\ V_t = \frac{\partial \mathcal{G}}{\partial v}\{\Delta V + v[m(x) - u - v]\}, \\ \;0 \;= \vec{n} \cdot \nabla U = \vec{n} \cdot \nabla V, \\ 0 \leq U(x,0) = U_0(x), \; 0 \leq V(x,0) = V_0(x), \end{cases} \tag{26}$$

where

$$U_0 := \gamma\Big(\frac{u_0 + v_0}{m}\Big)u_0 \text{ and } V_0 := \gamma\Big(\frac{v_0}{m}\Big)v_0.$$

Let $(\theta_\gamma, 0)$ and $(0, \theta_\gamma)$ be the two semi-trivial steady states of (7)–(10). The eigenvalue problem of the linearized problem of (26) about the steady state $(\theta_\gamma(x), 0)$ is

$$\begin{cases} \lambda\Phi = (\gamma(s_\gamma) + \gamma'(s_\gamma)s_\gamma)\left\{\Delta\Phi + \frac{(m-2\theta_\gamma)}{\gamma+\gamma' s_\gamma}\Phi + \frac{1}{\ell}[\frac{\gamma' s_\gamma(m-2\theta_\gamma)}{\gamma+\gamma' s_\gamma} - \theta_\gamma]\Psi\right\} \\ \qquad +\gamma'(s_\gamma)s_\gamma\left\{\Delta\Psi + \frac{m-\theta_\gamma}{\ell}\Psi\right\}, \\ \lambda\Psi = \ell\Delta\Psi + (m - \theta_\gamma)\Psi, \\ \;0 \;= \vec{n} \cdot \nabla\Phi = \vec{n} \cdot \nabla\Psi, \end{cases} \tag{27}$$

where $s_\gamma = \frac{\theta_\gamma}{m}$ and $\theta_\gamma(x)$ satisfies

$$\begin{cases} 0 = \Delta(\gamma(s_\gamma)\theta_\gamma) + \theta_\gamma[m - \theta_\gamma], \\ 0 = \vec{n} \cdot \nabla(\gamma(s_\gamma)\theta_\gamma). \end{cases} \tag{28}$$

Similarly, we may compute that the corresponding eigenvalue problem of (26) at $(0, \theta_\gamma(x))$ is

$$\begin{cases} \lambda\Phi = \gamma(s_\gamma)\left\{\Delta\Phi + \frac{m-\theta_\gamma}{\gamma(s_\gamma)}\Phi\right\}, \\ \lambda\Psi = (\gamma(s_\gamma) + \gamma'(s_\gamma)s_\gamma)\left\{\Delta\Psi + \frac{(m-2\theta_\gamma)}{\gamma(s_\gamma)+\gamma'(s_\gamma)s_\gamma}\Psi - \frac{\theta_\gamma}{\gamma(s_\gamma)}\Phi\right\}, \\ \ 0 \ = \vec{n} \cdot \nabla\Phi = \vec{n} \cdot \nabla\Psi. \end{cases} \tag{29}$$

We now show the simplified stability criteria for the semi-trivial steady states of (7)–(10) which corresponds to Lemma 3.1 in the previous section.

Lemma 4.1. *Let $\theta_\gamma(x)$ be the unique globally asymptotically stable steady state solution of (28), respectively.*

(i) *Let μ_1 denote the first eigenvalue of*

$$\begin{cases} \mu\Psi = \ell\Delta\Psi + (m - \theta_\gamma)\Psi, \\ \ 0 \ = \vec{n} \cdot \nabla\Psi. \end{cases} \tag{30}$$

The semi-trivial steady state $(\theta_\gamma(x), 0)$ is linearly unstable if $\mu_1 > 0$ and linearly stable if $\mu_1 < 0$.

(ii) *Let ν_1 denote the first eigenvalue of*

$$\begin{cases} \nu\Phi = \Delta\Phi + \frac{m-\theta_\gamma}{\gamma(s_\gamma)}\Phi, \\ \ 0 \ = \vec{n} \cdot \nabla\Phi. \end{cases} \tag{31}$$

The semi-trivial steady state $(0, \theta_\gamma(x))$ is linearly unstable if $\nu_1 > 0$ and linearly stable if $\nu_1 < 0$.

Proof. The proof is similar to the one for Lemma 3.1 and is omitted. □

4.2. **Proof of Theorem 2.2.** Now we show the second theorem.

Proof of Theorem 2.2. From Lemma 4.1 and Lemma 2 in [15], the stability of $(\theta_\gamma(x), 0)$ is determined by the sign of the first eigenvalue of the following eigenvalue problem

$$\begin{cases} \mu\Psi = \ell\Delta\Psi + (m - \theta_\gamma)\Psi, \\ \ 0 \ = \vec{n} \cdot \nabla\Psi. \end{cases}$$

Similarly, the stability of $(0, \theta_\gamma(x))$ is determined by the sign of the first eigenvalue of the following eigenvalue problem

$$\begin{cases} \nu\Phi = \Delta\Phi + \frac{m-\theta_\gamma}{\gamma(s_\gamma)}\Phi, \\ \ 0 \ = \vec{n} \cdot \nabla\Phi. \end{cases} \tag{32}$$

Then, from the proof of Theorem 2.1, $(\theta_\gamma(x), 0)$ is linearly stable. Furthermore, since $\theta_\gamma(x)$ is the positive eigenfunction of (32) with 0-eigenvalue, there exists an eigenpair $\{0, (\Phi_1, \theta_\gamma)\}$ of (27). By Lemma 4.1, $(0, \theta_\gamma(x))$ is linearly neutrally stable.

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 $\tilde U=\gamma(\frac{\tilde u+\tilde v}{m})\tilde u$ and $\tilde V=\gamma(\frac{\tilde v}{m})\tilde v$. Since $0=\Delta\tilde U+\frac{m(x)-\tilde u-\tilde v}{\gamma(\tilde s)}\tilde U$, it follows that

$$\begin{aligned} 0 &= \sup_{\Phi\in H^1(\Omega)\setminus\{0\}}\int_\Omega\left[-|\nabla\Phi|^2+\frac{m-\tilde u-\tilde v}{\gamma(\tilde s)}\Phi^2\right]dx\\ &\ge \int_\Omega\left[-|\nabla\tilde V|^2+\frac{m-\tilde u-\tilde v}{\gamma(\tilde s)}\tilde V^2\right]dx\\ &= \Big(\int_{\{m>\tilde u+\tilde v\}}+\int_{\{m<\tilde u+\tilde v\}}\Big)\Big(\frac{1}{\gamma(\tilde s)}-\frac{1}{\gamma(s)}\Big)(m-\tilde u-\tilde v)\tilde V^2dx.\end{aligned}$$

If $m>\tilde u+\tilde v$, then $1>\frac{\tilde u+\tilde v}{m}\ge\frac{\tilde v}{m}$. It follows that $\gamma(\tilde s)=\gamma(s)=\ell$. If $m<\tilde u+\tilde v$, then $m-\tilde u-\tilde v<0$. Since γ is increasing and $\tilde s\ge s$, $\frac{1}{\gamma(\tilde s)}\le\frac{1}{\gamma(s)}$. Therefore, if $\{x\in\Omega\mid m<\tilde u+\tilde v\}\cap\{x\in\Omega\mid m>\tilde v\}\neq\emptyset$, then

$$\int_{\{m<\tilde u+\tilde v\}}\Big(\frac{1}{\gamma(\tilde s)}-\frac{1}{\gamma(s)}\Big)(m-\tilde u-\tilde v)\tilde V^2dx>0.$$

This is a contradiction. This implies that $\{x\in\Omega\mid m\ge\tilde u+\tilde v\}=\Omega$ or $\{x\in\Omega\mid m<\tilde v\}=\Omega$. We assume that $\{x\in\Omega\mid m\ge\tilde u+\tilde v\}=\Omega$ and $\{x\in\Omega\mid m>\tilde u+\tilde v\}\neq\emptyset$. Divide $0=\Delta\tilde U+\tilde u[m(x)-\tilde u-\tilde v]$ by $\tilde U$ and integrate, then we get that

$$-\int_\Omega\frac{|\nabla\tilde U|^2}{\tilde U^2}dx=\int_\Omega\frac{m-\tilde u-\tilde v}{\gamma(\tilde s)}dx>0.$$

This is a contradiction. Therefore, if $\{x\in\Omega\mid m\ge\tilde u+\tilde v\}=\Omega$, then $\{x\in\Omega\mid m=\tilde u+\tilde v\}=\Omega$. This implies that $\gamma(\tilde s)\equiv\gamma(s)\equiv\ell$ and $m-\tilde u-\tilde v\equiv0$. It follows that $\Delta u\equiv\Delta v\equiv0$ and so, $\tilde u$ and $\tilde v$ are constants. Since we assume that m is nonconstant, this is a contradiction. Therefore, $\{x\in\Omega\mid m<\tilde v\}=\Omega$, and $m-\tilde u-\tilde v<0$, consequently. Multiply $0=\Delta\tilde V+\tilde v[m(x)-\tilde u-\tilde v]$ by $\tilde V$ and integrate, then we get that

$$\int_\Omega|\nabla\tilde V|^2dx=\int_\Omega\tilde V\tilde v(m-\tilde u-\tilde v)dx<0.$$

This is a contradiction.

Therefore, there is no coexisting steady state. □

5. POSSIBILITY FOR COEXISTENCE OF TWO COMPETING SPECIES

The coexistence of competing species is not obtained when the population dynamics of the species are identical and the dispersal strategies are given by a linear diffusion with different diffusivity coefficients. However, Theorem 2.3 gives two situations that any of the semi-trivial steady states is not stable and hence indicates coexistence of two competing species.

Proof of Theorem 2.3. By Lemma 1 in [16], we know that

$$\min_x m(x)\le\theta_\gamma(x)\le\max_x m(x).$$

Let $s^*\le\frac{\min_x m(x)}{\max_x m(x)}$. Then, $\gamma(\frac{\theta_\gamma}{m})\equiv h$ in Ω. Therefore, $h\Delta\theta_\gamma+\theta_\gamma(m-\theta_\gamma)=0$ in Ω. This implies that the first eigenvalue μ_1 of (30) is positive. Moreover, due to invertibility of $\Delta+\frac{m-2\theta_\gamma}{h}$, there exists an eigenpair $\{0,(\theta_\gamma,\Psi_1)\}$ of (29). Therefore, by Lemma 4.1, $(\theta_\gamma,0)$ is linearly unstable and $(0,\theta_\gamma)$ is linearly neutrally stable.

Similarly, if $s^*\ge\frac{\max_x m(x)}{\min_x m(x)}$. Then, $\gamma(\frac{\theta_\gamma}{m})\equiv\ell$ in Ω. Therefore, $\ell\Delta\theta_\gamma+\theta_\gamma(m-\theta_\gamma)=0$ in Ω. Since θ_γ is the first eigenfunction of (31) with 0-eigenvalue, there exist eigenpairs $\{0,(\Phi_1,\theta_\gamma)\}$ of (27) and $\{0,(\theta_\gamma,\Psi_1)\}$ of (29). By Lemma 4.1, $(\theta_\gamma,0)$ and $(0,\theta_\gamma)$ are linearly neutrally stable. □

In the context of the Lotka-Volterra type competition model in this paper the best moment to increase the dispersal rate is $s^*=1$ (see [15, Theorem 3]) for two reasons. Firstly, since the growth rate of the population becomes negative if $s>1$ and, secondly, since the environment or the carrying capacity is constant, there is no advantage in waiting for a better environment if $s > 1$. Therefore, the best strategy is to increase the dispersal rate immediately after $s > 1$. However, if a species increases the motility at some value $s^* \neq 1$, the best way of measuring the starvation is not necessarily selected. In fact, an overestimated or underestimated one can be selected, or both species may coexist. Theorem 2.3 shows two of such cases that the moment s^* is sufficiently away from $s^* = 1$ in compare with the environment variations. Then, it may happen $\gamma(\frac{u+v}{m}) \equiv \gamma(\frac{v}{m})$ and hence the ratio of population remains constant (see Figure 4(a)).

Notice that the analysis of the theorem is for the two extreme cases of $s^* < \frac{\min_x m(x)}{\max_x m(x)}$ and $s^* > \frac{\max_x m(x)}{\min_x m(x)}$. The other case of $\frac{\min_x m(x)}{\max_x m(x)} < s^* < \frac{\max_x m(x)}{\min_x m(x)}$ has been tested numerically in Figure 4. One can find coexistence in Figure 4(b), selection of the second phenotype in Figures 4(c), and the selection of the other phenotype in 4(d). It seems that there exist a range of steady states of coexistence depending on the choice of s^* and that the transition from a selection of one phenotype to the other is of order ϵ used to obtain regularized motility function γ^ϵ. However, these observations are only from numerical simulations and the analysis for this intermediate case is not done.

6. Numerical Simulations

In this section we present numerical simulations and compare them to the theories of this paper. Some of them are to confirm the theoretical conclusions numerically. The others are to numerically test conjectures which are not proved in the paper. In Section 6.1 we introduce two patch problem which has a low computation cost in compare with PDE models. It is this simplicity that all numerical tests including its global asymptotic behavior are possible which is given in Section 6.2. PDE model simulations are given in Section 6.3 for one dimension.

6.1. **Two patch model.** For computational simplicity, a two-patch model is numerically computed to test the theories in the earlier sections. The tested two patch model is similar to the PDE model when the resource distribution m is given by a step function. We may observe from the simulations that the theories of this paper is valid not only for the PDE model, but also for the patch model we tested.

General patch models are quite different from PDE models. However, if the connection among patches are given in a way similar to the geometry of a PDE model, the patch model is simply a discretization of a PDE model. A general patch model is written as

$$\frac{d}{dt}w_i^k = r_i w_i^k (m^k - T^k) - \sum_{l \neq k} \gamma_i^{kl} w_i^k + \sum_{l \neq k} \gamma_i^{lk} w_i^l, \tag{33}$$

where the superscript k denotes the patch number and the subscript i the species. For example, m^k and $T^k := \sum_i w_i^k$ are the carrying capacity and the total population in the k-th patch, respectively, and w_i^k is the population of the i-th species in the k-th patch. The coefficient r_i is the growth rate of the i-th species and γ_i^{kl} is the probability for the i-th species to depart the k-th patch and arrive at the l-th patch in a unit time. If $\gamma_i^{kl} = \gamma_i^{lk}$, then the dispersal strategy of the i-th species is called symmetric.

We take 2 species and 2 patches. Then, in the context of SDD, the patch model in (33) is written as

$$\frac{d}{dt}w_i^k = r_i w_i^k (m^k - w_1^k - w_2^k) - \gamma_i(s_i^k) w_i^k + \gamma_i(s_i^l) w_i^l,$$

where $k, l = 1, 2$ and $k \neq l$. Here, γ_i is the motility function of the i-th species and s_i^k is the starvation measure of the i-th species in the k-th patch. Since $s_i^1 \neq s_i^2$ in general, the dispersal of this model is not symmetric. In previous sections we have denoted the population by u and v, i.e., u corresponds to w_1 and v to w_2. The growth rates are set to be identical, i.e., $r_1 = r_2 = r$. In the simulation we fix the parameters as

$$m^1 = 2, \quad m^2 = 1, \quad h = 0.2, \quad \ell = 0.11, \quad r = 1 \quad \text{and} \quad \epsilon = 0.1. \tag{34}$$

Several values of the diffusivity coefficient d are tested of the first phenotype. Remind that the parameter ϵ is used in regularising the motility function, i.e., $\gamma := \gamma^\epsilon$.

Steady states for the patch problems with SDD can be found in [26]. The steady state for a single species case with a constant diffusivity d is denoted by $\theta_d := (\theta_d^1, \theta_d^2)$ which satisfies

$$0 = r\theta_d^k(m^k - \theta_d^k) - d\theta_d^k + d\theta_d^l, \quad k \neq l.$$

If $m^2 < m^1$, the steady state satisfies

$$m^2 < \theta_d^2 < \theta_d^1 < m^1.$$

For the single species case, the starvation measures s in (4) and $\tilde{s}$ in (11) are identical and the corresponding steady state $\theta_\gamma := (\theta_\gamma^1, \theta_\gamma^2)$ satisfies

$$0 = r\theta_\gamma^k(m^k - \theta_\gamma^k) - \gamma(s^k)\theta_\gamma^k + \gamma(s^l)\theta_\gamma^l, \quad k \neq l.$$

Then, similarly, the steady state satisfies

$$m^2 < \theta_\gamma^2 < \theta_\gamma^1 < m^1,$$

and, furthermore, if $\ell \leq d \leq h$, they satisfy a relation

$$m^2 < \theta_\gamma^2 < \theta_d^2 < \theta_d^1 < \theta_\gamma^1 < m^1.$$

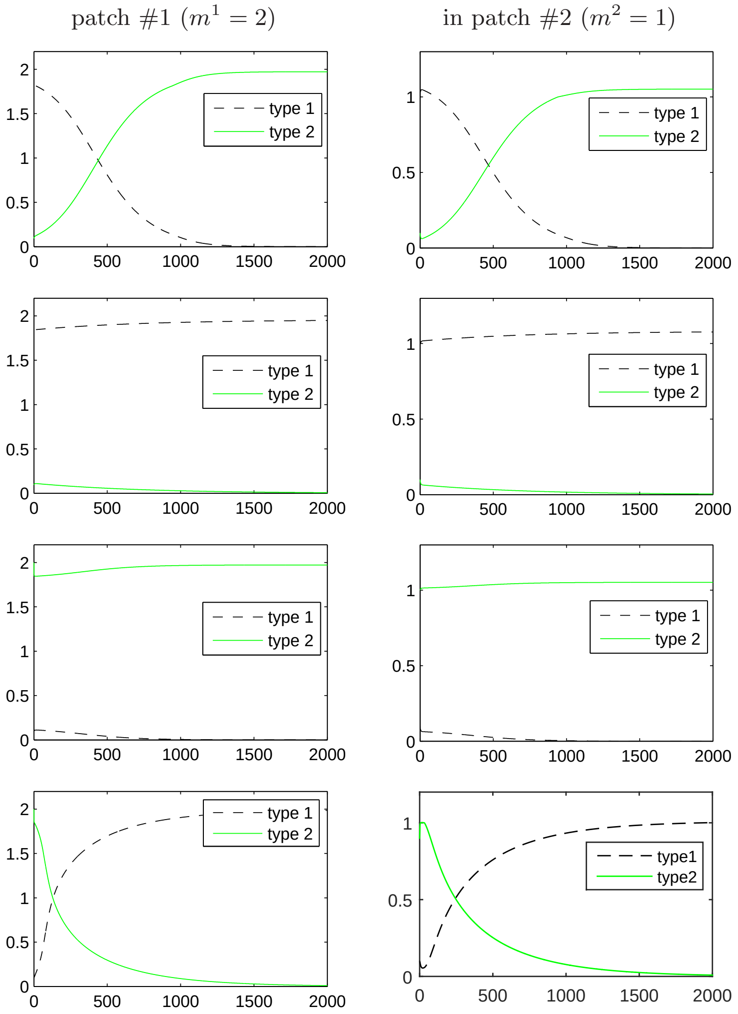
For the competition system between the first and the second phenotypes, the semi-trivial steady states are denoted by $(u, v) = (\theta_d, 0)$ or $(0, \theta_\gamma)$. If the first phenotype is replaced by the third one, then the corresponding semi-trivial steady states are $(u, v) = (\theta_\gamma, 0)$ and $(0, \theta_\gamma)$.

6.2. **Numerical simulations.** In this section we test the evolution of competition models numerically. Remember that the parameters are fixed as in (36). The other parameter d will take a few different values.

Numerical simulations in Figure 1 are to test the theories related to Theorem 2.1. The global asymptotic stability of the steady state $(u, v) = (0, \theta_\gamma)$ with $\ell \leq d$ is numerically observed in Figure 1(a). In this simulation the initial value was taken from a small neighborhood of the other semi-trivial steady state $(\theta_d, 0)$. One may observe that the solution converges to $(0, \theta_\gamma)$. The local stability of the the steady state $(\theta_d, 0)$ for a case with $d < \ell$ can be observed numerically in Figure 1(b) with $d = 0.1$. In this case the initial value has taken from a small neighborhood of $(\theta_d, 0)$ and the solution converges to this semi-trivial steady state as $t \to \infty$.

Notice that Theorem 2.1 gives relatively less information when $d < \ell$. One might ask if $(\theta_d, 0)$ is globally asymptotically stable for all $d < \ell$. The numerical simulation in Figure 1(c) shows it is not true. In the simulation, an initial value is taken from a small neighborhood of $(0, \theta_\gamma)$ and the solution converges to $(0, \theta_\gamma)$ as $t \to \infty$. This indicates that, if d is relatively close to ℓ and $d < \ell$, the asymptotic stability of $(\theta_d, 0)$ is only local and, furthermore, the other semi-trivial steady state $(0, \theta_\gamma)$ is also stable. One might also ask if there exists $d_0 < \ell$ such that $(\theta_d, 0)$ is globally asymptotically stable for all $d < d_0$. The numerical simulation in Figure 1(d) indicates that it might be the case. In the simulation an initial value has taken from a small neighborhood of $(0, \theta_\gamma)$ and the solution converges to $(\theta_d, 0)$ as $t \to \infty$ with $d = 0.01$. However, the global asymptotic stability of $(\theta_d, 0)$ for small d is not proved.

Solution trajectories of the system (7)–(10) are given in Figure 2. The diffusivity constant is taken as $d = 0.15$, which is the case of Figure 1(a). Therefore, $(u, v) = (0, \theta_\gamma)$ is globally asymptotically stable and hence all trajectories are supposed to converge toward $(0, \theta_\gamma)$. The phase plane for the first patch with carrying capacity $m^1 = 2$ is given in the figure. In the first stage all the solution trajectories are moving toward a diagonal line that connects the two semi-trivial steady states $(u, v) = (\theta_d^1, 0)$ and $(0, \theta_\gamma^1)$. This is a fast process. After the first stage, solution trajectories move along the diagonal heading to the globally asymptotically stable steady state $(u, v) = (0, \theta_\gamma^1)$ slowly. Such a two step process is sometimes called *metastability* (see [17, 1]). In particular, Figure 2 can be compared to the illustration in Beck and Wayne [1, Figure 3], where one may call the diagonal part a metastable region. Two regions along the diagonal are magnified to show the behavior of solution trajectories near the metastable region.



(a) Global asymptotic stability test for $(0, \theta_\gamma)$ with an initial value close to $(\theta_d, 0)$. Here, $d = 0.15$.

(b) Local asymptotic stability test for $(\theta_d, 0)$ with an initial value close to $(\theta_d, 0)$. Here, $d = 0.1$.

(c) Local asymptotic stability test for $(0, \theta_\gamma)$ with an initial value close to $(0, \theta_\gamma)$. Here, $d = 0.1$.

(d) Global asymptotic stability test for $(\theta_d, 0)$ with an initial value close to $(0, \theta_\gamma)$. Here, $d = 0.01$.

FIGURE 1. Numerical simulations related to Theorem 2.1. Here, $h = 0.2$ and $\ell = 0.11$. The first column is the population dynamics in patch with a carrying capacity $m^1 = 2$ and the second one is with $m^2 = 1$.

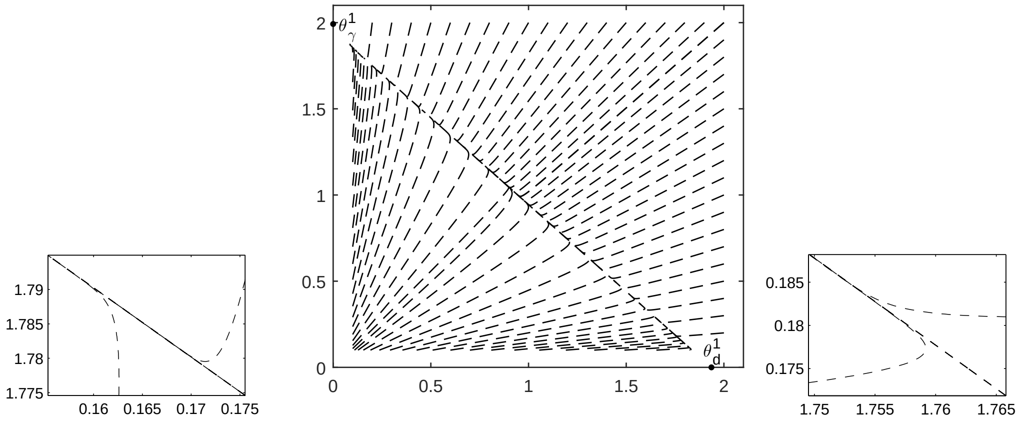


FIGURE 2. Trajectories in the phase plane. The horizontal axis is for the first phenotype u with a linear dispersal and the vertical one is for the other phenotype v with starvation driven one. Here, $d = 0.15, \ell = 0.11$ and $h = 0.2$ and $(u, v) = (0, \theta_\gamma)$ is globally asymptotically stable and hence all trajectories converges to $(0, \theta_\gamma)$. Two side figures are magnified trajectories near the diagonal region.

In the two side figures one may observe that the trajectories are curved toward the globally asymptotically stable state.

It is proved in Theorem 2.2 that the semi-trivial steady state $(u, v) = (\theta_\gamma, 0)$ is the only linearly stable steady state if u is the third phenotype that is modeled by the equation $(7)'$. Therefore, we may conjecture that the steady state is globally asymptotically stable. In Figure 3 an example of the population evolution is given, where the third phenotype u is eventually selected. In this simulation the initial value was taken from a small neighborhood of the other steady state $(0, \theta_\gamma)$ and the solution converges to $(\theta_\gamma, 0)$ as $t \to \infty$.

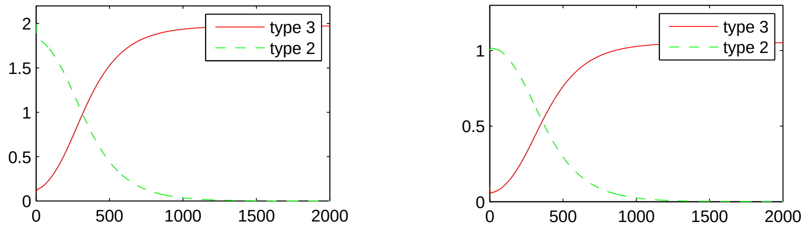


FIGURE 3. Numerical simulations related to Theorem 2.2. Here, $h = 0.2$ and $\ell = 0.11$ and the first column is the population dynamics in patch with a carrying capacity $m^1 = 2$ and the second one is with $m^2 = 1$. One may observe the global asymptotic stability of $(u, v) = (\theta_\gamma, 0)$.

Simulations given in Figure 4 are related to Theorem 2.3. In the context of Lotka-Volterra competition model the environment is fixed in time and the best moment to increase the motility is when $s = 1$. However, if $s^* \neq 1$, even the best way of measuring the starvation may not selected and the species' extinction or coexistence with other species may happen. The carrying capacities of our simulation are $m^1 = 2$ and $m^2 = 1$ and the ratio of resource variation is $\frac{\max_x m(x)}{\min_x m(x)} = 2$. Four cases are tested in Figure 4. Let w_i^k be the population of the i-th phenotype in the k-th patch in a steady state. Suppose that the dispersal size is not large in compare with the growth rate and we have

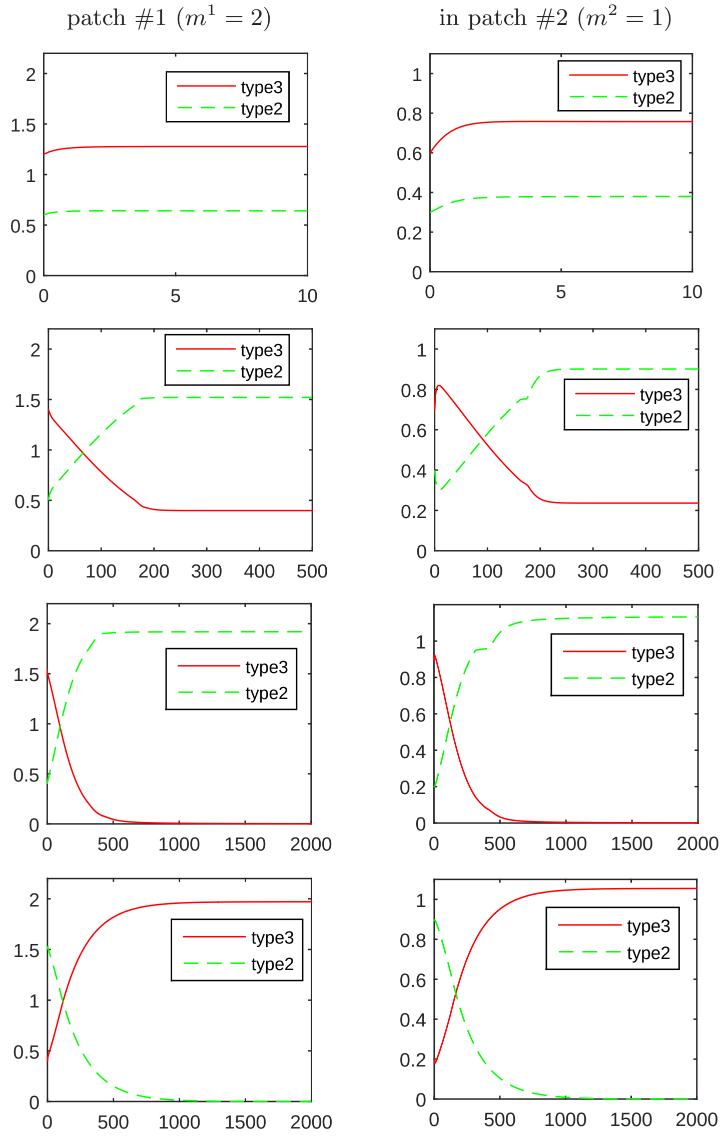
$$w_2^1 + w_3^1 \lesssim m^1 \quad \text{and} \quad w_2^2 + w_3^2 \gtrsim m^2. \tag{35}$$

If $s^* \ll 1$ and the initial values of the two species are not so small that both $\frac{u+v}{m}$ and $\frac{v}{m}$ are bigger than $s^* + \epsilon$. Then, $\gamma(\frac{u+v}{m}) \equiv \gamma(\frac{v}{m})$ all the time and the two phenotypes behave identically for all $t > 0$. Therefore, the initial population ratio of the two phenotypes is changed. Figure 4(a) is the case with $s^* < \frac{1}{2}$ which is one of the two cases in Theorem 2.3. The ratio of initial values remains constant. One may obtain a similar result for the other case with $s^* > 2$.

The other three cases in Figure 4 are for the regime with $\frac{\min_x m(x)}{\max_x m(x)} < s^* < \frac{\max_x m(x)}{\min_x m(x)}$ which was not considered in the theorem. In Figures 4(b) such a case is given with $s^* = 0.75$. We may observe that the second phenotype becomes more advantageous as s^* increases and, eventually, the third phenotype get extinct and the second one is selected when $s^* = 0.9$ as given in Figure 4(c). Another interesting phenomenon appears when we increase s^* a little bit more. Then, the third phenotype becomes alive and eventually selected when $s^* = 1.05$ as in Figure 4(d), which is in the regime $s > 1$. The transition interval from the selection of the second phenotype to the selection of the third one is related to the size of the regularization parameter ϵ. We may observe that this interval goes to zero as $\epsilon \to 0$. If the jumping moment s^* is increased more, one may observe symmetric phenomena which was obtained from the regime $s^* < 1$.

6.3. **PDE model.** In this section, we compute the PDE system $(7)'$,(8)–(10) numerically in one space dimension and compare them to the theory. This system models the competition between the second phenotype v and third one u. For the simulation we set the domain and parameters as

$$h = 0.05, \quad \ell = 0.01, \quad \epsilon = 0.01 \quad \text{and} \quad m(x) = 3 \sin x + 1, \quad 0 < x < \pi. \tag{36}$$



(a) Coexistence test with an initial value closed to $(\theta_\gamma, 0)$ when $s^* \leq \frac{\min m}{\max m}$. Here, $s^* = 0.3$.

(b) Coexistence test with an initial value close to $(0, \theta_\gamma)$. Here, $s^* = 0.75$.

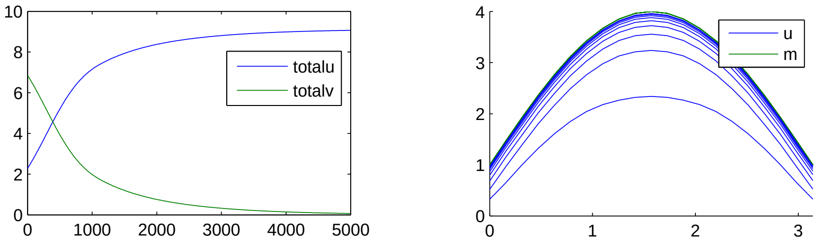
(c) Global asymptotic stability test for $(0, \theta_\gamma)$ with an initial value close to $(\theta_\gamma, 0)$. Here, $s^* = 0.95$.

(d) Global asymptotic stability test for $(\theta_\gamma, 0)$ with an initial value close to $(0, \theta_\gamma)$. Here, $s^* = 1.05$.

FIGURE 4. Numerical simulations related to Theorem 2.3. Here, $h = 0.2$ and $\ell = 0.11$.

First we test the global asymptotic stability of a semi-trivial steady state $(u, v) = (\theta_\gamma, 0)$ proved in Theorem 2.2 when $s^* = 1$. For this test we take an initial value from a small neighborhood of the other semi-trivial steady state $(0, \theta_\gamma)$. The time evolution of total population is given in the first picture of Figure 5. Observe that the total population of the second phenotype v vanishes as $t \to \infty$. This implies that the solution with the initial value around $(0, \theta_\gamma)$ converges to $(\theta_\gamma, 0)$ as $t \to \infty$, which confirms the global asymptotic stability. The second picture of Figure 5 shows the evolution of the spatial profile of the third phenotype u. with time which converges to θ_γ.

Next we test a property related to Theorem 2.3. It is shown in the theorem that, if $s^* < \frac{\min m}{\max m}$, both semi-trivial steady states are not linearly stable. Considering the fact that the existence of two unstable steady states implies the existence of another stable steady state in the monotone system, one may expect a steady of coexistence. We may observe such a steady state of coexistence numerically. In Figure 6, profiles of the two phenotypes u and v are given when the solution arrived in a steady state. The initial values are taken as $u_0(x) = \frac{1}{4}m(x)$ and $v_0(x) = \frac{3}{4}m(x)$ and the computed for $t > 0$ large enough. The simulation result shows that two species coexist and the ratio of population remains constant, i.e., $\int v(x,t)dx = 3\int u(x,t)dx$.



(a) total population asymptotics (b) convergence of $u(\cdot,t)$ to $\theta_\gamma(\cdot)$.

FIGURE 5. Numerical simulations of PDE model related to Theorem 2.2. Parameters in (36) are used with $s^* = 1$. (a) shows global asymptotic stability of $(\theta_\gamma, 0)$ and (b) show the evolution of profiles of $u(\cdot,t)$ to $\theta_\gamma(\cdot)$ as $t \to \infty$.

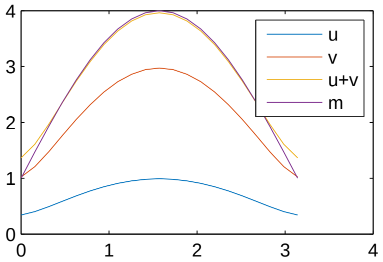


FIGURE 6. Numerical simulations related to Theorem 2.3. Parameters in (36) are used with $s^* = 0.2$. We may observe a steady state of coexistence.

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