

Some Challenging Mathematical Problems in Evolution of Dispersal and Population Dynamics

Yuan Lou

Department of Mathematics
The Ohio State University
Columbus, Ohio 43210, USA
lou@math.ohio-state.edu

May 15, 2007

Abstract. We discuss the effects of dispersal (either random or biased) and spatial heterogeneity on population dynamics via reaction-advection-diffusion models. We address the question of determining optimal spatial arrangement of resources and study how advection along resource gradients affects the extinction of species. The effects of dispersal and spatial heterogeneity on the total population size of single species are carefully investigated, along with some other properties of species. These properties have important applications to invasions of rare species. Some interesting connection between the evolution of unconditional dispersal and diffusion-driven extinction is revealed. We also investigate the outcome of competition for two similar species, and show how invasion and coexistence are affected by resource utilization, inter-specific competition, and dynamics of habitat edges. In particular, interesting effects of intermediate values of dispersal rates are found. The evolution of conditional dispersal is also addressed, and we illustrate that the geometry of a habitat can play an important role in the evolution of conditional dispersal and that strong directed movement of species can induce the coexistence of competing species. If both species disperse by random diffusion and advection along environmental gradients and one species has much stronger biased movement than the other one, then at least two scenarios can occur: either both species can coexist or the “smarter” species is always the loser. These results seem to suggest that selection is against large advection along resource gradient and that an intermediate biased movement rate may

evolve. Numerous open problems will be discussed.

Key words: Reaction-diffusion-advection, evolution of dispersal, population dynamics, competing species, spatial heterogeneity, invasion, coexistence.

AMS Classification: 35B40, 35J55, 35K57, 92D25, 92D40.

Contents

1	Introduction	2
2	Linear eigenvalue problems with indefinite weight	5
2.1	Rearrangement of resources	5
2.2	Biased movement of species	10
3	Logistic models for single species	12
3.1	Total population size	12
3.2	Biased movement of species	15
4	Evolution of dispersal and related topics	17
4.1	The slower diffuser wins	18
4.2	ODE dynamics vs. PDE dynamics	19
5	Similar competing species: invasion and coexistence	22
5.1	Effects of resources	23
5.2	Effects of inter-specific competition	25
5.3	Effects of boundary condition	27
6	Evolution of conditional dispersal	28
6.1	Weak advection	29
6.2	Advection mediated coexistence	30
6.3	Evolutionarily stable dispersal strategy	32

1 Introduction

The evolution of dispersal has been one of the central topics in recent theoretical studies of population dynamics. Metapopulation models have been widely used for spatially structured populations (Lehman and Tilman [78]; Hanski [52]), and one of the primary criticisms for these models is that the

dispersal functions are usually so simplified that the results can be misleading (Travis and French [120]). In fact, classical metapopulation models often are not even spatially explicit and thus it is difficult to use them to gain insight into the effects of different dispersal mechanisms. Models such as those used in [61, 94] are more accurately described as discrete diffusion models and they do incorporate mechanistic assumptions about dispersal and treat population dynamics explicitly. We refer to Sections 1.4 and 2.6.2 of [12] for more detailed discussions.

Two theories dominate current investigations on dispersal: (i) the “source-sink model” (Hastings [54]; Holt [60]; Hanski and Thomas [53]; Doebeli [36]; Travis and Dytham [119]), in which individuals disperse at fixed constant rates, regardless of the local environment; and (ii) the “balanced dispersal model” (McPeck and Holt [94]), in which the dispersal is conditional since the dispersal rate depends on a combination of local biotic and abiotic factors such as habitat quality. It is well accepted that conditional dispersal can be a crucial factor in population dynamics (Turchin [121]; Travis and French [120]; Bowler and Benton [6]; Armsworth and Roughgarden [1, 2]).

One central question is: which patterns of dispersal can confer some sort of selective or ecological advantage? When habitat quality varies spatially but remains constant in time, the source-sink model predicts that the selection is for slow dispersal (Hastings [54]; Holt [60]). However, McPeck and Holt [94] showed that when there is conditional dispersal, e.g., with dispersal depending on patch carrying capacity, dispersal can evolve in a spatially varying environment.

In reality, species are neither completely ignorant of the surrounding environment nor will their movement perfectly track resource gradients. It is more likely that their movements combine both random and directed ones: for instance, adding some amount of random movement to a purely directed movement strategy might help an individual escape a local trap to find distant but better sources (Armsworth and Roughgarden [1]). In other words, a balanced combination of both random and directed movement might help the species better utilize available resources and thus maximize its chance of survival.

Since the pioneering work of Skellam [117], there have been tremendous theoretical advances in reaction-diffusion modeling of invasions and species interactions (Okubo and Levin [106]; Murray [101]; Shigesada and Kawasaki [115]; Cantrell and Cosner [12]). The book by Cantrell and Cosner [12], which covers many major issues in spatial ecology via the reaction-diffusion approach, motivates this current survey. We will discuss some of the most recent progress on applications of reaction-advection-diffusion equations to

population dynamics and the evolution of dispersal, including both unconditional dispersal and conditional dispersal. Our main goal is to introduce the readers to the current state of the art in this area and raise some questions for further research.

This paper is organized as follows. In Sect. 2 we discuss the question of determining the optimal spatial arrangement of resources and study the effects of advection along resource gradients on extinction of species.

Sect. 3 is devoted to studying single species, with the main focus on the effects of dispersal and spatial heterogeneity on the total population size and other properties of species. These properties have important implications for invasions of rare species.

Sects. 4-6 are devoted to the study of two competing species in a heterogeneous environment. In Sect. 4 we investigate the evolution of unconditional dispersal, diffusion-driven extinction, and their intimate connections.

Sect. 5 is concerned with the outcome of competition for two similar species, and we show how invasion and coexistence are affected by resource utilization, inter-specific competition, and dynamics of habitat edges. In particular, interesting effects of *intermediate* values of dispersal rates are found.

Finally in Sect. 6 we study the evolution of conditional dispersal and show how the geometry of a habitat can play an important role in the evolution of dispersal, and that strong directed movement of species can induce the coexistence of competing species. We also consider the situation when both species disperse by random diffusion and advection along environmental gradients and one species has much stronger biased movement than the other one. The species with stronger biased movement behaves like a specialist as it mainly pursues resources at places of locally most favorable environments. The other species has a rather balanced mixed dispersal strategy and can be regarded as a generalist. It is shown that at least two scenarios can occur: If the generalist's biased movement rate is relatively smaller than its own random movement rate, then both species can coexist; If its biased movement is relatively stronger than its random movement, then the generalist is always the winner, regardless of the initial condition. These results seem to suggest that selection is against large advection and that an intermediate biased movement rate may evolve.

Throughout this survey numerous open problems will be discussed and some conjectures will be presented. We also refer to recent excellent surveys of Ni [103, 104] on competition models with density-dependent diffusion, Levin et al. [79] on the evolution of plant dispersal, Neuhauser [102] on dynamics of metapopulation models.

2 Linear eigenvalue problems with indefinite weight

In this section we discuss two linear eigenvalue problems with indefinite weight subject to no-flux boundary conditions. These linear eigenvalue problems are particularly important since they are closely connected to predictions of persistence vs. extinction of species in reaction-diffusion models.

Subsection 2.1 is concerned with the question of determining the optimal spatial arrangement of favorable and unfavorable regions for species to survive, and the conclusion for a one dimensional closed habitat is that a single favorable region at one of the two ends of the whole habitat provides the best opportunity for the species to survive.

In subsection 2.2 we study the effects of advection along environmental gradients on dynamics of logistic type reaction-diffusion models for population growth. The local population growth rate is assumed to be spatially inhomogeneous, and the advection is taken to be a multiple of the gradient of the local population growth rate. It is also assumed that the boundary acts as a reflecting barrier to the population. It turns out that the effects of such advection depends crucially on the shape of the habitat: if the habitat is convex, the movement in the direction of the gradient of the growth rate is always beneficial to the population, while such advection can be harmful for certain non-convex habitats.

These results depend crucially on boundary conditions, e.g., the results for Dirichlet are different [4, 8, 9].

2.1 Rearrangement of resources

The linear eigenvalue problem with indefinite weight

$$\begin{cases} \Delta\varphi + \lambda m(x)\varphi = 0 & \text{in } \Omega, \\ \frac{\partial\varphi}{\partial n} = 0 & \text{on } \partial\Omega \end{cases} \quad (2.1)$$

and its variants have been extensively investigated for last two decades since they play crucial roles in studying nonlinear mathematical models from population biology. Throughout this paper we shall assume that the habitat Ω is a bounded region in \mathbb{R}^N with smooth boundary $\partial\Omega$ and n is the outward unit normal vector on $\partial\Omega$. The zero-flux boundary condition in (2.1) means that no individuals cross the boundary of the habitat.

The function $m(x)$ represents local intrinsic growth rate of species at location x . It reflects the quality and quantity of resources available at the

point x , and is often referred as an indefinite weight since it may change sign in Ω . For this subsection, we assume that the function m is non-constant, bounded and measurable in Ω . Define

$$\Omega_+ = \{x \in \Omega : m(x) > 0\}, \quad \Omega_- = \{x \in \Omega : m(x) < 0\}.$$

The subdomain Ω_+ can be viewed as a *source* as the species has positive intrinsic growth rate there; likewise, the region Ω_- can be regarded as a *sink*.

We call λ a *principal eigenvalue* of (2.1) if λ has a positive eigenfunction $\varphi \in H^1(\Omega)$. By elliptic regularity and the Sobolev embedding theorem [47], the function φ satisfies $\varphi \in W^{2,q}(\Omega) \cap C^{1,\gamma}(\bar{\Omega})$ for every $q > 1$ and every $\gamma \in (0, 1)$, and $\varphi > 0$ in $\bar{\Omega}$. Clearly, $\lambda = 0$ is a principal eigenvalue of (2.1) with positive constants as its eigenfunctions. Of particular importance and interest is the existence of *positive* principal eigenvalues.

If (2.1) has a positive eigenvalue $\lambda_1(m)$ with corresponding positive eigenfunction φ_1 , integrating the equation of φ_1 we have

$$\int_{\Omega} m\varphi_1 = 0,$$

which implies that both Ω_+ and Ω_- have positive Lebesgue measure; dividing the equation of φ_1 by φ_1 and then integrating in Ω , we find

$$\lambda_1(m) \int_{\Omega} m = - \int_{\Omega} \frac{|\nabla\varphi_1|^2}{\varphi_1^2} < 0$$

since φ_1 is not equal to any positive constant (as m is not identically equal to any constant). In summary, the condition

(A1) The set Ω_+ has positive Lebesgue measure, and $\int_{\Omega} m < 0$

is necessary for the existence of a positive principal eigenvalue. This condition turns out to be also sufficient as shown by the following result [4, 7, 44, 56, 114]:

Theorem 2.1. *The eigenvalue problem (2.1) has a positive principal eigenvalue (denoted by $\lambda_1(m)$) if and only if (A1) holds. Moreover, $\lambda_1(m)$ is the only positive principal eigenvalue and it is simple; it is also the smallest positive eigenvalue of (2.1), and is given by*

$$\lambda_1(m) = \inf_{\varphi \in \mathcal{S}(m)} \frac{\int_{\Omega} |\nabla\varphi|^2}{\int_{\Omega} m(x)\varphi^2}, \quad (2.2)$$

where

$$\mathcal{S}(m) := \left\{ \varphi \in H^1(\Omega) : \int_{\Omega} m(x)\varphi^2 > 0 \right\}.$$

As an application, we consider the diffusive logistic equation

$$\begin{aligned} u_t &= \Delta u + \lambda u[m(x) - u] && \text{in } \Omega \times \mathbb{R}^+, \\ \frac{\partial u}{\partial n} &= 0 && \text{on } \partial\Omega \times \mathbb{R}^+, \\ u(x, 0) &\geq 0, \quad u(x, 0) \not\equiv 0 && \text{in } \bar{\Omega}, \end{aligned} \tag{2.3}$$

where $u(x, t)$ represents the density of a species at location x and time t . Hence, only non-negative solutions of (2.3) are of interest. Again, the function $m(x)$ represents the intrinsic growth rate of a species, which is positive in the favorable part of habitat (Ω_+) and negative in unfavorable one (Ω_-). The integral $\int_{\Omega} m$ can be viewed as a measure of the total resources in a spatially heterogeneous environment.

So far as invasion of species is concerned, λ^{-1} acts like the diffusion coefficient. To see this, we set $\mu = \lambda^{-1}$ and introduce the new time variable τ with $\tau = \lambda t$. Then the equation of u can be rewritten as

$$u_{\tau} = \mu \Delta u + u[m(x) - u].$$

Set $\mu_1(m) = \lambda_1(m)$ (we define $\mu_1(m) = +\infty$ if $\lambda_1(m) = 0$). It is well-known that

(i) if $\mu \geq \mu_1(m)$, i.e., $\lambda \leq \lambda_1(m)$, then $u(x, t) \rightarrow 0$ uniformly in $\bar{\Omega}$ as $t \rightarrow \infty$ for all non-negative and non-trivial initial data, i.e., the species goes to extinction;

(ii) if $\mu < \mu_1(m)$, i.e., $\lambda > \lambda_1(m)$, then $u(x, t) \rightarrow u^*(x)$ uniformly in $\bar{\Omega}$ as $t \rightarrow \infty$, where u^* is the unique positive steady state of (2.3) in $W^{2,q}(\Omega)$ for every $q > 1$, i.e., the invasion occurs.

We are mainly concerned with the dependence of the principal eigenvalue $\lambda_1(m)$ of (2.1) on the weight function $m(x)$. In particular, we are interested in how spatial variation in the environment of the habitat affects the maintenance of species. To be more precise, let m_0 be some constant satisfying $m_0 \in (0, 1)$, and assume

(A2) $-1 \leq m(x) \leq 1$ a.e. in Ω , and $\int_{\Omega} m \leq -m_0|\Omega|$.

We address the following mathematical question:

Question. Among all functions $m(x)$ that satisfy (A1) and (A2), which $m(x)$ will yield the smallest $\lambda_1(m)$?

This question is motivated by the following biological consideration: the species can survive if and only if $\lambda > \lambda_1(m)$, and the smaller $\lambda_1(m)$ is, the more likely that the species can exist. Biologically, it is equivalent to determining the optimal spatial arrangement of the favorable and unfavorable parts of the habitat for species to survive. This question was first addressed by Cantrell and Cosner in [8, 9], and it remains largely open.

The question is also mathematically meaningful: by (A1) and Theorem 2.1, the positive principal eigenvalue $\lambda_1(m)$ exists and is unique. Furthermore, the infimum of $\lambda_1(m)$ among all those m that satisfy both (A1) and (A2) is positive by a result of Saut and Scheurer [113]:

Theorem 2.2. *Suppose that (A1) holds. Then*

$$\lambda_1(m) \geq \frac{\nu_1 \left| \int_{\Omega} m \right|}{\int_{\Omega} m^2(x) dx + \left| \int_{\Omega} m \right| \sup_{\Omega} m},$$

where ν_1 is the smallest positive eigenvalue of the Laplace operator with homogeneous zero Neumann boundary condition.

For any $m_0 \in (0, 1)$, we define

$$\mathcal{M} = \{m \in L^{\infty}(\Omega) : m(x) \text{ satisfies (A1) and (A2)}\}, \quad (2.4)$$

and set

$$\lambda_{inf} := \inf_{m \in \mathcal{M}} \lambda_1(m).$$

As an immediate consequence of Theorem 2.2, we have

$$\lambda_{inf} \geq \frac{\nu_1 m_0}{1 + m_0} > 0.$$

The existence and profile of global minimizers of $\lambda_1(m)$ in \mathcal{M} with Dirichlet boundary condition was first addressed by Cantrell and Cosner in [8], in which Cantrell and Cosner showed that there exists some measurable set $E \subset \Omega$ with $|E| > 0$ such that $\lambda_1(\chi_E - \chi_{\Omega \setminus E}) = \lambda_{inf}$. The result of Cantrell and Cosner can be viewed as saying that there exists a “bang-bang” type optimal control for minimizing $\lambda_1(m)$ in \mathcal{M} . For Neumann boundary condition, a stronger result is established in [90]:

Theorem 2.3. *The infimum λ_{inf} is attained by some $m \in \mathcal{M}$. Moreover, if $\lambda_1(m) = \lambda_{inf}$, then m can be represented as $m(x) = \chi_E - \chi_{\Omega \setminus E}$ a.e. in Ω for some measurable set $E \subset \Omega$.*

Theorem 2.3 implies that the global minimizers of $\lambda_1(m)$ in \mathcal{M} must be of “bang-bang” type, and is indeed contained in the set

$$\mathcal{M}_\alpha = \{m : m = \chi_E - \chi_{\Omega \setminus E} \text{ for some } E \subset \Omega \text{ with } |E| = \alpha|\Omega|\},$$

where $\alpha = (1 - m_0)/2$. It is easy to check that every $m \in \mathcal{M}_\alpha$ satisfies $\int_\Omega m = -m_0|\Omega|$, i.e., $\mathcal{M}_\alpha \subset \mathcal{M}$.

By Theorem 2.3 and the above discussion, in order to determine all of the global minimizers of $\lambda_1(m)$ in \mathcal{M} , it suffices to characterize $E \subset \Omega$ such that the corresponding weight function $m(x) = \chi_E - \chi_{\Omega \setminus E}$ minimizes the principal eigenvalue $\lambda_1(m)$ in \mathcal{M}_α . Recently, the following complete characterization of all global minimizers of $\lambda_1(m)$ in \mathcal{M} when $N = 1$ are established in [90]:

Theorem 2.4. *Suppose that $N = 1$, $\Omega = (0, 1)$, and $\alpha = (1 - m_0)/2$. Then $\lambda_1(m) = \lambda_{inf}$ for some function $m \in \mathcal{M}$ if and only if $m = \chi_E - \chi_{\Omega \setminus E}$ a.e. in $(0, 1)$, where either $|E \cap (0, \alpha)| = \alpha$ or $|E \cap (1 - \alpha, 1)| = \alpha$.*

Theorem 2.4 implies that when Ω is an interval, then there are exactly two global minimizers of $\lambda_1(m)$ (up to change of a set of measure zero). This substantially improves previous work in the one-dimensional case. In [9] Cantrell and Cosner studied the case when Ω is the unit interval $(0, 1)$ under three different boundary conditions (Dirichlet, Neumann, and Robin type). For Neumann boundary condition, they showed that if $m(x) \equiv 1$ on a “single” subinterval of fixed length and $m(x) = -1$ on the remainder of the interval, then the smallest value of $\lambda_1(m)$ with $m(x)$ so restricted occurs when the subinterval where $m(x) \equiv 1$ is at one of the ends of the interval $(0, 1)$; they also considered the situation when $m(x) \equiv -1$ in a “single” subinterval of fixed length, and $m(x) \equiv 1$ on the remainder of $(0, 1)$. They proved that in the latter case, the smallest value for $\lambda_1(m)$ occurs when $m(x) \equiv -1$ at one of the ends of $(0, 1)$. Some new ideas based on a characterization of critical points and continuous dependence of $\lambda_1(m)$ with respect to m are given in [90], and the analysis in [90] can also be useful in handling Dirichlet, Robin, and periodic boundary conditions.

The characterization of the optimal set E in \mathcal{M}_α for higher-dimensional domains is a difficult problem, even for two dimensional balls or rectangles (see [73] for some recent progress on cylindrical domains). For general domains, we have the following

Conjecture. The set E is always connected and $\partial E \cap \partial\Omega$ has positive surface measure. If Ω is convex, then Ω/E is also connected.

For the connectivity of E , the geometry of Ω might be irrelevant. However, the convexity assumption on Ω appears necessary in order to ensure the connectivity of Ω/E since for dumbbell type domains, Ω/E may have multiple connected components. We also conjecture that if Ω is a ball, then E is rotationally symmetric with respect to some diameter of the ball.

Similarly, little is known for eigenvalue problem (2.1) but with Dirichlet, Robin and periodic boundary conditions in higher dimensions. We refer to [5] for recent progress in related problems, where symmetrization methods are extensively employed. The symmetrization idea for the Dirichlet case was also discussed earlier in [8]. For other related works, see [42, 76, 77] and references therein.

2.2 Biased movement of species

If the environment is spatially heterogeneous, the population may have a tendency to move along the gradient of the resources in addition to random dispersal. This leads Belgacem and Cosner [4] to add an advection term to (2.3) and consider the model

$$\begin{cases} \frac{\partial u}{\partial t} = \nabla \cdot [\nabla u - \alpha u \nabla m] + \lambda(m - u)u & \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \quad (2.5)$$

The flux of population density is given by $\mathbf{J} = -\nabla u + \alpha u \nabla m$, where α measures the tendency of the population to move up along the gradient of $m(x)$, and $m(x)$ is assumed to be twice continuously differentiable in $\bar{\Omega}$.

It is also shown in [4] that the effects of the advection term $\alpha u \nabla m$ depend critically on boundary conditions: for no-flux boundary conditions, sufficiently rapid movement in the direction of $m(x)$ is always beneficial, and the movement up the gradient of $m(x)$ may be either beneficial or harmful for zero Dirichlet boundary condition.

According to [4], for every α , there exists a unique non-negative constant $\lambda_* = \lambda_*(\alpha)$ such that the following holds:

- (i) If $\lambda > \lambda_*$, (2.5) has a unique positive steady state which is globally attracting among non-trivial non-negative solutions of (2.5);

(ii) If $\lambda_* > 0$ and $0 < \lambda \leq \lambda_*$, then all non-negative solutions of (2.5) converge to zero as $t \rightarrow \infty$.

The constant λ_* is the principal eigenvalue of an eigenvalue problem related to (2.5). By [4] (see also [3]), λ_* can be characterized by

$$\lambda_* := \inf_{\varphi \in \mathcal{S}} \frac{\int_{\Omega} e^{\alpha m} |\nabla \varphi|^2}{\int_{\Omega} e^{\alpha m} m \varphi^2}, \quad (2.6)$$

where

$$\mathcal{S} = \left\{ \varphi \in W^{1,2}(\Omega) : \int_{\Omega} e^{\alpha m} m \varphi^2 > 0 \right\}. \quad (2.7)$$

It can be shown [31] that if $\int_{\Omega} m \geq 0$, then $\lambda_* \equiv 0$ for $\alpha \geq 0$; if m changes sign and $\int_{\Omega} m < 0$, then there exists a unique $\alpha_* > 0$ such that $\lambda_* > 0$ if $\alpha < \alpha_*$, and $\lambda_* \equiv 0$ if $\alpha \geq \alpha_*$. Throughout this subsection, we shall also assume (A1).

Question. If we start with $\alpha = 0$, i.e., without directed motion up the gradient of $m(x)$, is increasing α always beneficial to the survival of population?

In terms of λ_* , for small α , this is equivalent to asking whether $\lambda'_*(0) < 0$. Since the population can survive if and only if $\lambda > \lambda_*$, intuitively we may expect that the smaller λ_* is, the more likely it is that the population will survive. In this connection, the following result is proved in [31].

Theorem 2.5. *Suppose that (A1) holds.*

- (i) *For any convex domain Ω and any $m(x)$, $\lambda'_*(0) < 0$;*
- (ii) *There exist some non-convex Ω and $m(x)$ such that $\lambda'_*(0) > 0$.*

Part (ii) seems to be counterintuitive because movement in the increasing direction of the local growth rate should always be helpful to the population. One possible explanation is that for some non-convex habitats such as dumbbell type ones, an individual moving in the direction of increasing $m(x)$ may “hit” the boundary of the habitat and cannot go further, but a randomly moving individual moves in all possible directions with equal probability, and thus might eventually be able to “turn the corner” and move into the region with more favorable resource levels.

The type of domains constructed in (ii) are so called thin domains, and there has been some active research on the equilibria and dynamics of evolution equations in thin domains: e.g., bistable scalar equation in thin tubular

domains [123], Navier-Stokes equations in thin 3D domains [112], reaction-diffusion equations in thin domains [50], the Lotka-Volterra competition-diffusion system in thin tubular domains [72], Ginzburg-Landau equation in thin domains [25], subharmonic solutions [108], etc.; See also the survey [111] about PDEs in thin domains.

Theorem 2.5 is a local result which deals only with small α . With some extra conditions on $m(x)$, the following global result is established in [31].

Theorem 2.6. *Suppose that (A1) holds, Ω is convex, and the matrix $(m_{x_i x_j})_{1 \leq i, j \leq n}$ is non-positive. Then $\lambda'_*(\alpha) < 0$ for all $0 \leq \alpha < \alpha_*$. In particular, this implies that*

$$\lambda_*(0) = \max_{\alpha \geq 0} \lambda_*(\alpha). \quad (2.8)$$

The biological meaning of (2.8) is that the movement in the increasing direction of m is always beneficial to the population. For general $m(x)$, we have the following

Conjecture. If Ω is convex, then (2.8) always holds.

3 Logistic models for single species

The dynamics of mathematical models for single species are not only of independent interest, they are also quite crucial in studying dynamics of multiple interacting species, especially issues concerning invasions of rare species. In this section we focus on logistic type population models with either random diffusion or biased movement along the gradient of resources. In Subsect. 3.1 we study the effects of dispersal rate and spatial heterogeneity on the total population size. Subsect. 3.2 is concerned with how biased movement of species affects the total population size and the density distribution of species.

3.1 Total population size

In this subsection we study the effects of dispersal and spatial heterogeneity of the environment on the total population size of a single species. Such a consideration is not just out of curiosity, but rather aims at interesting

connections with the issue of invasions of species. The connection will be become clear in later sections. More precisely, we consider

$$\begin{cases} \mu\Delta\theta + \theta[m(x) - \theta] = 0 & \text{in } \Omega, & \theta > 0 \text{ in } \Omega, \\ \frac{\partial\theta}{\partial n} = 0 & \text{on } \partial\Omega, \end{cases} \quad (3.1)$$

where the migration rate μ is assumed to be a positive constant and the function $\theta = \theta(x, \mu)$ represents the density of the species at location x .

Though most of our analysis covers the case $\int_{\Omega} m(x) dx \leq 0$, throughout this subsection, for the sake of clarity, we posit that

(A3) $m(x)$ is non-constant, bounded and measurable, and $\int_{\Omega} m(x) dx > 0$.

For solutions of (3.1), most of the following results are well known.

Theorem 3.1. *Suppose that assumption (A3) holds.*

(a) *For every $\mu > 0$, the problem (3.1) has a unique positive solution $\theta(x, \mu)$ such that $\theta \in W^{2,p}(\Omega)$ for every $p \geq 1$.*

(b) *As $\mu \rightarrow 0+$, $\theta(x, \mu) \rightarrow m_+(x)$ in $L^p(\Omega)$ for every $p \geq 1$, where $m_+(x) = \sup\{m(x), 0\}$; as $\mu \rightarrow \infty$, $\theta(x, \mu) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} m(x) dx$ in $W^{2,p}(\Omega)$ for every $p \geq 1$.*

(c) *If $m(x)$ is Hölder continuous in $\bar{\Omega}$, then $\theta \in C^2(\bar{\Omega})$. Moreover, $\theta(x, \mu) \rightarrow m_+(x)$ in $L^\infty(\Omega)$ as $\mu \rightarrow 0$, and $\theta(x, \mu) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} m(x) dx$ in $C^2(\bar{\Omega})$ as $\mu \rightarrow \infty$.*

We refer the proofs of parts (a) and (c) to [82] and the references therein.

In view of part (b) of Theorem 3.1, it is natural to introduce the function

$$F(\mu) \equiv \begin{cases} \int_{\Omega} m_+(x) dx, & \mu = 0, \\ \int_{\Omega} \theta(x, \mu) dx, & \mu > 0, \\ \int_{\Omega} m(x) dx, & \mu = \infty, \end{cases}$$

which can be interpreted as the total population size of the species. By assumption (A3) and part (b) of Theorem 3.1, F is a continuous, positive function in $[0, \infty]$.

If the spatial environment is homogeneous, i.e., $m(x)$ is equal to some positive constant \bar{m} , then $\theta(x, \mu) \equiv \bar{m}$ is the unique positive solution of

(3.1) for every $\mu > 0$. In this case, the total population size of the species is given by $F(\mu) = |\Omega|\bar{m}$, which is independent of μ . However, if the spatial environment is heterogeneous, i.e., $m(x)$ is a non-constant function, the story changes dramatically:

Theorem 3.2. ([82]) *Suppose that assumption (A3) holds.*

- (a) *The function $F(\mu)$ satisfies $F(\mu) > F(\infty)$ for every $\mu \in (0, \infty)$.*
- (b) *If $m(x) \geq 0$ in Ω , then for every $\mu \in (0, \infty)$, the function $F(\mu)$ satisfies*

$$F(0) = F(\infty) < F(\mu).$$

Part (a) of Theorem 3.2 implies that spatial heterogeneity increases the population size of species. To make this assertion precise, set $\bar{m} = \int_{\Omega} m(x) dx / |\Omega|$, and write $F = F(\mu, m)$ instead of $F(\mu)$ to indicate the dependence of F on the function m . Part (a) implies that $F(\mu, m) > F(\mu, \bar{m})$ for every $\mu > 0$. In other words, given any $\mu > 0$ and any function g with $\int_{\Omega} g(x) dx = 0$ and $g \not\equiv 0$, we have $F(\mu, \bar{m} + \lambda g) > F(\mu, \bar{m})$ for every $\lambda \neq 0$. Hence, with the dispersal rate being fixed, the population size $F(\mu, \bar{m} + \lambda g)$, as a function of λ , attains a strict absolute minimum at $\lambda = 0$.

Part (b) of Theorem 3.2 implies that when $m(x)$ is non-negative, the total population size is minimized at $\mu = 0$ and $\mu = \infty$, and maximized at some intermediate value μ^* . The value of μ^* is determined by the habitat Ω and $m(x)$.

It will be of interest to understand the precise shape of $F(\mu)$ due to its crucial role in invasion of species. One natural conjecture is that $F(\mu)$ has a unique local maximum (and thus it must be the global maximum) in $(-\infty, +\infty)$. However, this conjecture is false (V. Hutson, personal communication) even for the case when $m(x)$ is a perturbation of positive constants.

If the function $m(x)$ changes sign, $F(\mu) > F(\infty)$ still holds for every $\mu \in [0, \infty)$. Hence, F is minimized at $\mu = \infty$, but is no longer minimized at $\mu = 0$. Interestingly, when Ω is an interval, the maximum of F is still attained at some intermediate dispersal rate:

Theorem 3.3. ([82]) *Suppose that $\Omega = (0, 1)$, $m \in C^2[0, 1]$, m changes sign, and $m(x) = 0$ has only nondegenerate roots in $[0, 1]$. Then there exist positive constants μ_0 and c_0 such that $F(\mu) - F(0) \geq c_0\mu^{\frac{2}{3}}$ for every $\mu \in (0, \mu_0)$. Thus,*

$$F(\infty) < F(0) < \sup_{0 < \mu < \infty} F(\mu).$$

Theorems 3.2 and 3.3 suggest that the total population size of species is usually maximized at some intermediate migration rate, and this fact has interesting applications to multiple species in the context of ecological invasions [82].

Another interesting problem is to maximize the total population for certain classes of $m(x)$ (with μ being fixed). Recent investigations (V. Hutson, personal communication) show that the results can be different for one-dimensional and higher dimensional domains. For example, given any $m_0 > 0$, the total population size, as a function of m , is a bounded (non-linear) functional in the set $\{m \in L^\infty(\Omega) : m \geq 0 \text{ in } \Omega, \int_\Omega m = m_0|\Omega|\}$ for one-dimensional habitats, but is unbounded for high dimensional habitats. This suggests that one needs to consider the problem of maximizing $\int_\Omega \theta$ in a smaller set such as $\{m : 0 \leq m \leq 1 \text{ in } \Omega, \int_\Omega m = m_0|\Omega|\}$ with $m_0 \in (0, 1)$. The restriction that m , which is the per capita rate of increase when the species is rare, is uniformly bounded, seems biologically reasonable.

From the control point of view, if we regard $\int_\Omega \theta$ as gain and $\|m\|_{L^2(\Omega)}$ as cost, it is also interesting to maximize the “profit” such as $\int_\Omega \theta - \|m\|_{L^2(\Omega)}$ instead of the total population size alone.

3.2 Biased movement of species

Throughout this subsection, we assume that $\lambda > \lambda_*(\alpha)$ so that the elliptic problem

$$\begin{cases} \nabla \cdot [\nabla \tilde{u} - \alpha \tilde{u} \nabla m] + \lambda(m - \tilde{u})\tilde{u} = 0 & \text{in } \Omega, \\ \frac{\partial \tilde{u}}{\partial n} - \alpha \tilde{u} \frac{\partial m}{\partial n} = 0 & \text{on } \partial\Omega \end{cases} \quad (3.2)$$

has a unique positive solution, which we denote as $\tilde{u} = \tilde{u}(x, \alpha)$. We will study various properties of \tilde{u} , including the total population size, the maximum value of \tilde{u} , and the concentration of \tilde{u} at the maximum of $m(x)$.

When α is positive and small, the movement along the gradient of resources is relatively weak in comparison to random dispersal. For every fixed λ , it is shown [31] that increasing α is always beneficial to the persistence of the species for any convex habitat, but can be harmful in certain non-convex habitats. This implies that the direction of selection of conditional dispersal can depend on the geometry of the habitat.

What happens if α increases and becomes suitably large? It turns out that large α always ensure the persistence of the species, independent of the geometry of the habitat. In other words, a conditional dispersal strategy

can be advantageous over unconditional ones since it uses more information about resources. However, over pursuing this extra information can also be costly. Recently, we found that if the set of critical points of $m(x)$ has Lebesgue measure zero, then the total population size tends to zero as $\alpha \rightarrow \infty$ (see [22]), i.e.,

$$\lim_{\alpha \rightarrow \infty} \int_{\Omega} \tilde{u}(x; \alpha) dx = 0. \quad (3.3)$$

In other words, the species has to pay a price if the species is “smart” but gets too “greedy”, as small populations are more likely to go extinct. However, the population density may not approach zero everywhere:

Theorem 3.4. *Suppose that m is non-constant.*

(a) *If $\alpha \leq 1/\max_{\bar{\Omega}} m$, then*

$$\tilde{u}(x) < \max_{\bar{\Omega}} m \cdot e^{\alpha[m(x) - \max_{\bar{\Omega}} m]}$$

for every $x \in \bar{\Omega}$. In particular, $\max_{\bar{\Omega}} \tilde{u} < \max_{\bar{\Omega}} m$.

(b) *If $m(x) > 0$ in $\bar{\Omega}$ and $\alpha \geq 1/\min_{\bar{\Omega}} m$, then*

$$\tilde{u}(x) > \max_{\bar{\Omega}} m \cdot e^{\alpha[m(x) - \max_{\bar{\Omega}} m]} \quad (3.4)$$

for every $x \in \bar{\Omega}$. In particular, $\max_{\bar{\Omega}} \tilde{u} > \max_{\bar{\Omega}} m$.

Hence, for sufficiently large α , if $m(x) > 0$ in $\bar{\Omega}$, then solutions of (3.2) are concentrated at the global maxima of $m(x)$. Another interesting consequence of Theorem 3.4 is that $\max_{\bar{\Omega}} \tilde{u} - \max_{\bar{\Omega}} m$, as a function of α , changes sign as α varies from zero to ∞ . This fact will have interesting applications to the invasion of rare species in the study of the evolution of conditional dispersal. We conjecture that $\max_{\bar{\Omega}} \tilde{u} - \max_{\bar{\Omega}} m$ changes sign exactly once for all $\alpha \in (0, +\infty)$.

The case of $m(x)$ being positive everywhere corresponds to the situation when there are only sources all over the whole habitat, and it is natural to enquire what happens when environments comprise both sources and sinks:

Conjecture. For any non-constant function $m(x)$, the solution of (3.2) is always concentrated at every local maximum of $m(x)$.

This conjecture is true when Ω is an interval and $m(x)$ has no critical points. More precisely, it is shown [22] that if $m'(x) > 0$ in $[0, 1]$, then for

sufficiently large α , $\tilde{u}'(x) > 0$ in $[0, 1]$, $\tilde{u}(x) \rightarrow 0$ uniformly in $[0, c]$ for every $c \in (0, 1)$ as $\alpha \rightarrow \infty$, and

$$u(1) \geq \int_0^1 m > 0$$

for large α , provided that $\int_0^1 m > 0$. If Ω is an interval and $m(x)$ is not monotone, under suitable conditions we can show that concentration of \tilde{u} is only possible at critical points of $m(x)$. In this connection, we make the following assumption.

(A4) Suppose that $\Omega = (0, 1)$, $m_x(0) \geq 0 \geq m_x(1)$, and $m(x)$ has finitely many critical points in $[0, 1]$, denoted by $\{x_1, \dots, x_k\}$.

Theorem 3.5. ([22]) *Suppose that (A4) holds and $\Omega = (0, 1)$. Then $\tilde{u}(x) \rightarrow 0$ uniformly in every compact subset of $[0, 1] \setminus \{x_1, \dots, x_k\}$ as $\alpha \rightarrow \infty$. In particular, $\tilde{u}(x) \rightarrow 0$ pointwise for every $x \in [0, 1] \setminus \{x_1, \dots, x_k\}$ as $\alpha \rightarrow \infty$.*

4 Evolution of dispersal and related topics

It is natural to inquire which patterns of dispersal can confer some selective or ecological advantage, see, [4, 31, 35, 61, 68, 94] and references therein. Unconditional dispersal does not depend on habitat quality or population density, while conditional dispersal does depend on some or all of such factors. For instance, passive diffusion as considered by Dockery et al. [35] and Hutson et al. [68] is a type of unconditional dispersal. Diffusion combined with directed movement along resource gradients, as considered by Belgacem and Cosner [4] and Cosner and Lou [31], is an example of conditional dispersal, because the bias in the direction of dispersal depends on the spatial distribution of resources. It was shown in both patch and diffusion models (McPeck and Holt [94]; Dockery et al. [35]) that for unconditional dispersal in spatially varying but temporally constant environments slower dispersal rates is selected, and the results in Hastings [54] essentially say that decreasing dispersal rate increases some measures of fitness in logistic models. However, for unconditional dispersal in spatially and temporally varying environments faster dispersal rates may be selected in both patch models [94] and diffusion models [68]. In this section we focus on the effects of unconditional dispersal on the dynamics of two competing species in a spatially varying (but temporally constant) environment.

The semilinear parabolic system

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + u[m(x) - u - bv] && \text{in } \Omega \times (0, \infty), \\ \frac{\partial v}{\partial t} &= \nu \Delta v + v[m(x) - cu - v] && \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 && \text{on } \partial\Omega \times (0, \infty) \end{aligned} \quad (4.1)$$

models two species that are competing for the same resources, where $u(x, t)$ and $v(x, t)$ represent the population densities of competing species 1 and 2 with respective dispersal rates μ and ν , the function $m(x)$ represents their common intrinsic growth rate, and b and c are inter-specific competition coefficients. We shall assume that μ , ν , b , and c are positive constants, and $u(x, 0)$ and $v(x, 0)$ are non-negative functions that are not identically equal to zero.

If we assume that the initial data $u(x, 0)$ and $v(x, 0)$ are non-negative and not identically zero, then by maximum principle [45, 110], $u(x, t) > 0$ and $v(x, t) > 0$ for every $x \in \bar{\Omega}$ and every $t > 0$. Moreover, $u(x, t)$ and $v(x, t)$ are classical solutions of (4.1) and exist for all time $t > 0$. Of particular interest are the dynamics and coexistence states of (4.1). We say that a steady state (u_e, v_e) of (4.1) is a *coexistence state* if both components are positive, and it is a *semi-trivial state* if one component is positive and the other is zero. Under assumption (A3), (4.1) has two semi-trivial states, denoted by $(\theta(\cdot, \mu), 0)$ and $(0, \theta(\cdot, \nu))$ for every $\mu > 0$ and every $\nu > 0$, where $\theta(\cdot, \mu)$ is the unique positive solution of (3.1).

For the last two decades there has been tremendous interest, by both mathematicians and ecologists, in two-species Lotka-Volterra competition models with spatially homogeneous or heterogeneous interactions, see [9, 10, 11, 12, 18, 19, 28, 29, 33, 35, 38, 39, 40, 41, 46, 55, 59, 62, 63, 64, 65, 66, 71, 75, 80, 81, 93, 96, 107, 109] and references therein. For competition models with density-dependent diffusion, we refer to [27, 69, 83, 87, 88, 89, 93, 95, 97, 98, 116] and references therein.

4.1 The slower diffuser wins

Consider the case when $b = c = 1$. It is shown in [35] that if $\mu < \nu$, then $(\theta(\cdot, \mu), 0)$ is globally asymptotically stable among all non-negative non-trivial initial data. In other words, *the slower diffuser wins*. By symmetry, a similar conclusion holds when $\mu > \nu$. In particular, (4.1) has no coexistence states if $\mu \neq \nu$.

Why is the slower diffuser always the winner? Such a phenomenon is a little surprising at the first look: if $\mu = \nu = 0$, it is clear that neither species will die out; in fact, the two species will coexist since they are identical. However, as soon as the diffusion is turned on for both species, the slower diffuser becomes the eventual winner as time evolves. This shows that the PDE dynamics are dramatically different from the ODE dynamics.

A possible biological explanation is that as time evolves, the effective growth rate $a(x, t) := m(x) - u(x, t) - v(x, t)$ for both species will eventually change sign in the habitat Ω . The slower diffuser keeps relatively low density in the region where $a(x, t)$ is negative, which seems to help it gain some competitive advantage.

A challenging open problem is whether the slowest diffuser still wins the competition in the context of N competing species with $N \geq 3$. One major new mathematical difficulty in solving this open problem is that competition models for three or more species are not monotone systems. For recent progress on patch models, see [74] and references therein.

Similar results hold true for the case of nonlocal dispersions, and we refer to [67] for the details. However, when the intrinsic growth rate varies periodically in time, it is shown in [94] for patch models and in [68] for diffusion models that the slower diffuser may not always be the winner. That is to say, the effects of spatial and temporal variations can be quite different. Clearly, understanding the effects of temporal variation is mathematically very challenging and biologically rich.

4.2 ODE dynamics vs. PDE dynamics

To motivate our discussion, we assume for the moment that $0 < b, c < 1$. If $m(x) \equiv \bar{m}$ for some positive constant \bar{m} , then every solution (u, v) of (4.1) converges to $(\frac{1-b}{1-bc}\bar{m}, \frac{1-c}{1-bc}\bar{m})$ for all diffusion rates μ, ν , and arbitrary initial data. In other words, the PDE dynamics are no different from the corresponding ODE ones. In fact, for any autonomous reaction-diffusion system with no-flux boundary conditions, if the initial data are constants, then the corresponding PDE solutions remain spatially homogeneous. In other words, the dynamics of ODEs are “embedded” in the dynamics of corresponding PDEs (this is different from Dirichlet or Robin conditions which induces a hidden spatially inhomogeneous effect). However, for non-autonomous reaction-diffusion systems with no-flux boundary conditions, things can go quite differently. To this end, we investigate the asymptotic behavior of solutions of (4.1) when $m(x)$ is a non-constant positive function

and $0 < b, c < 1$.

If $\mu = \nu = 0$ in (4.1), we can regard (4.1) as a system of two ordinary differential equations, solutions of which converge to $(\frac{1-b}{1-bc}m(x), \frac{1-c}{1-bc}m(x))$ for every $x \in \Omega$. In other words, the kinetic system of (4.1) has a unique, globally asymptotically stable positive equilibrium (depending on x). It is shown in [65] that if μ and ν are sufficiently small, the function $m(x)$ is positive, and $0 < b, c < 1$, then (4.1) has a unique, globally asymptotic stable positive steady state (u^*, v^*) . Moreover, (u^*, v^*) converges to $(\frac{1-b}{1-bc}m(x), \frac{1-c}{1-bc}m(x))$ in $L^\infty(\Omega)$ as $\mu \rightarrow 0$ and $\nu \rightarrow 0$. That is, when both μ and ν are small, the dynamics of (4.1) behave similarly to those of (4.1) with $\mu = \nu = 0$. It would be very interesting to discover whether this type of result holds for other important classes of interacting species, for example for $N(\geq 3)$ competing species.

When both μ and ν are sufficiently large, it is not difficult to see that (4.1) again has a unique, globally asymptotically stable positive steady state (u^{**}, v^{**}) . Moreover, (u^{**}, v^{**}) converges to $(\frac{1-b}{1-bc} \frac{1}{|\Omega|} \int_\Omega m, \frac{1-c}{1-bc} \frac{1}{|\Omega|} \int_\Omega m)$ as $\mu \rightarrow \infty$ and $\nu \rightarrow \infty$. In fact, when μ and ν are sufficiently large, the dynamics of (4.1) can be approximated by that of the corresponding “spatially averaged” ODE. Consult [23, 30, 49, 51] and references therein for the connection between the dynamics of PDEs with large diffusion and that of corresponding “spatially averaged” ODEs.

Hence, it seems reasonable to expect that for other ranges of dispersal rates, the dynamics of (4.1) should still be well behaved; *e.g.*, the two competing species can coexist, as in the case when μ and ν are both small or both large, or in the case when $m(x)$ is equal to some positive constant. However, as we shall see later, given any non-constant positive function $m(x)$, there exists a set of parameters $b, c \in (0, 1)$ and $\mu, \nu > 0$ such that one of the semi-trivial steady states of (4.1) is the global attractor of (4.1). Therefore, the joint action of spatial heterogeneity and diffusion can drive one of the species to extinction. Such “diffusion-driven extinction” or “diffusion-driven blowup” phenomena have been studied in [11, 70, 86, 100, 105, 107, 122]. It was proved in [70, 105] that there exist some initial data such that without diffusion species 1 drives species 2 to extinction, whereas the opposite holds for certain dispersal rates. In [107] by numerical investigations Pacala and Roughgarden made the following counterintuitive observations: (i) without diffusion one competitor can not invade the other at any location but with diffusion invasion is possible; (ii) without diffusion one competitor can invade the other at every location but with diffusion invasion may fail. These observations were explained and rigorously verified later on by Cantrell and Cosner in [11]. In [82], the spatial heterogeneity is also incorporated in the

nonlinearity and the extinction result holds for arbitrary initial conditions.

We start by studying the joint effects of diffusion and spatial heterogeneity on the invasion of the species 2 when it is rare. The case of species 1 is similar. Mathematically, this is equivalent to studying the stability of the semi-trivial steady state $(\theta(x, \mu), 0)$ of (4.1).

For the rest of this subsection, we focus on the case $0 < c < 1$. The stability of $(\theta, 0)$ when $c \in (0, 1)$ can be described by

Theorem 4.1. *If assumption (A3) holds and $m(x)$ is non-negative, then there exists some constant $c_* = c_*(m, \Omega) \in (0, 1)$ such that the following results hold.*

- (a) *For every $c \in (0, c_*)$, the steady state $(\theta, 0)$ is unstable when $\mu > 0$ and $\nu > 0$.*
- (b) *For every $c \in (c_*, 1)$, there exists $\bar{\nu} = \bar{\nu}(c, m, \Omega) > 0$ such that (i) for every $\nu \in (0, \bar{\nu})$, the steady state $(\theta, 0)$ is unstable when $\mu > 0$; (ii) for every $\nu > \bar{\nu}$, the steady state $(\theta, 0)$ changes stability at least twice as μ increases from 0 to ν .*

A much more detailed description of the region in the $\mu\nu$ -plane where $(\theta, 0)$ is stable is given in [82], Sect. 4. For the case when $m(x)$ changes sign, the stability of $(\theta, 0)$ is somewhat different. We refer to [82] for details.

The most interesting region is where $c_* < c < 1$ and $\nu > \bar{\nu}$, where we have the following:

- (a) If $b > 1$, it is well known that without dispersal, species 2 always drives species 1 to extinction. However, with dispersal, for some ranges of dispersal rates, species 2 may fail to invade when rare.
- (b) If $b < 1$, it is well known that, without dispersal, species 1 always coexists with species 2. Surprisingly, for certain dispersal rates, species 1 is able to drive species 2 to extinction for arbitrary initial conditions.

For every $c > 0$, define

$$\Sigma_c = \{(\mu, \nu) \in (0, \infty) \times (0, \infty) : (\theta, 0) \text{ is linearly stable}\}. \quad (4.2)$$

Theorem 4.2. *If assumption (A3) holds and $m(x)$ is non-negative, then for every $c \in (c_*, 1)$, there exists $b_* = b_*(c, \Omega, m) \in (0, 1]$ such that if $b \in (0, b_*)$ and $(\mu, \nu) \in \Sigma_c$, then $(\theta, 0)$ is globally asymptotically stable.*

We conjecture that Theorem 1.9 holds with $b_* = 1$:

Conjecture. If assumption (A3) holds, $m(x)$ is non-negative, and $b = 1$, then for every $c \in (c_*, 1)$ and $(\mu, \nu) \in \Sigma_c$, $(\theta, 0)$ is globally asymptotically stable.

By Theorem 4.1, the set Σ_c is non-empty for every $c \in (c_*, 1)$. It is not difficult to see that $\Sigma_{c_1} \subset \Sigma_{c_2}$ for any $c_1 < c_2$ with $c_1, c_2 \in (c_*, 1)$. In fact, the set Σ_c converges to the set $\{(\mu, \nu) : 0 < \mu < \nu\}$ as $c \rightarrow 1-$, and this conjecture gives another perspective on why the slower diffuser wins for the case when $b = c = 1$.

5 Similar competing species: invasion and coexistence

To motivate our discussions, we start with the semilinear parabolic system

$$\begin{aligned} u_t &= \mu \Delta u + u [m(x) - u - v] && \text{in } \Omega \times (0, \infty), \\ v_t &= \mu \Delta v + v [m(x) - u - v] && \text{in } \Omega \times (0, \infty), \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 && \text{on } \partial\Omega \times (0, \infty). \end{aligned} \tag{5.1}$$

Clearly, the two species are identical in all aspects except their initial conditions. By assumption (A3), (5.1) has a family of coexistence states, given by $\{(s\theta, (1-s)\theta) : 0 < s < 1\}$, which attracts all solutions with nonnegative nontrivial initial data, where $\theta = \theta(\cdot, \mu)$ is the unique positive solution of 3.1. Moreover, for any nonnegative nontrivial initial data, the solution of (5.1) converges to $(s_0\theta, (1-s_0)\theta)$ for some $s_0 \in (0, 1)$, where s_0 depends on the initial data. It is an interesting problem to determine how this structure changes under small perturbations:

Question. What happens when the two species are slightly different, that is, when system (5.1) is perturbed?

Biologically, suppose that random mutation produces a different phenotype of species which is slightly different from the original species, e.g., different colors for butterflies, different sizes of wings for birds, etc. It is fairly reasonable to expect that these two species will have to compete for rather similar (if not exactly the same) resources. The major concern is whether the mutant can invade when rare; if so, will the invading species force the extinction of the resident species or coexist with it?

Mathematically, the question leads to the study of various perturbations of system (5.1). Several interesting and surprising phenomena will be revealed in the next few subsections using this approach. What is particularly attractive is that this perturbation method can yield lots of information on competing species for *intermediate* values of diffusion rates, which is in general hard to find.

5.1 Effects of resources

In [66] a perturbation of the intrinsic growth rate in (5.1) is considered. The system studied there has the form

$$u_t = \mu \Delta u + u[m(x) + \tau g(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \quad (5.2a)$$

$$v_t = \mu \Delta v + v[m(x) - u - v] \quad \text{in } \Omega \times (0, \infty), \quad (5.2b)$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{on } \Omega \times (0, \infty). \quad (5.2c)$$

The two species are almost identical except for their intrinsic growth rates which differ by a function of $\tau g(x)$, where τ is a positive constant and $g(x)$ is a smooth function. In this situation, some new phenomena are discovered. By (A3), if $\int_{\Omega} g > 0$, (5.2) has two semi-trivial states in the form of $(\tilde{u}, 0)$ and $(0, \theta)$ for every $\mu > 0$.

It was shown in [63] that if $\int_{\Omega} g > 0$, then for large enough μ , $(\tilde{u}, 0)$ is a global attractor. In particular, $(\tilde{u}, 0)$ is asymptotically stable and $(0, \theta(x, \mu))$ is unstable. That is, the species u always drives the species v to extinction, no matter what the initial data may be. On the other hand, [63] also demonstrates that if $m_+ - (m + \tau g)_+$ (a_+ denotes the positive part of function $a(x)$) changes sign, then for small enough μ both semi-trivial states $(\tilde{u}, 0)$ and $(0, \theta)$ of (5.2) are unstable. This in turn implies that there is at least one stable coexistence state of (5.2) for small μ .

The simplest interpretation of these results suggest that as μ decreases from a large value, a branch of coexistence states of (5.2) bifurcates from $(\tilde{u}, 0)$ at some value μ_0 and remains in the interior of the positive cone for all $\mu < \mu_0$. Surprisingly, numerical computations show that this is not always the case. For reasonable choices of $m(x)$ and $g(x)$, the branch of coexistence states bifurcating from $(\tilde{u}, 0)$ at μ_0 will connect to $(0, \theta)$ at μ_1 for some $\mu_1 < \mu_0$, and $(0, \theta)$ becomes globally attracting for some range of μ as μ decreases. Eventually, another branch of coexistence states of (5.2) bifurcates from $(0, \theta)$ at μ_2 for some $\mu_2 < \mu_1$, and remains in the positive cone for the rest of μ . This is surprising for the situation $\int_{\Omega} g > 0$ because

species u was chosen to have better average reproductive rate than species v .

The study in [66] on the stability of $(0, \theta)$ partially confirms the numerical results, i.e., the stability can change and indeed can do so more than once as the diffusion rate μ is varied:

Theorem 5.1. *Suppose that (A3) holds and $\int_{\Omega} g(x) > 0 > \int_{\Omega} g(x)m_+^2(x)$. Then there exists a unique $\tau_0 > 0$ such that:*

- (i) $\tau > \tau_0$ implies that $(0, \theta)$ is unstable for any $\mu > 0$;
- (ii) $\tau < \tau_0$ implies that $(0, \theta)$ changes stability at least once as μ varies from zero to infinity. It changes stability at least twice, provided g and m are both positive on a nonempty subset of Ω .

The stability of $(0, \theta)$ means that the first species with low density u can not invade. Theorem 5.1 qualitatively illustrates how the invasion of rare species relies on both dispersal rate and the difference between its intrinsic growth rate and that of resident species. We conjecture that for case (ii), whenever $(0, \theta)$ is locally asymptotically stable, it is globally asymptotically stable.

For small τ , it is further shown in [66] that for any fixed positive integer k , one can choose the function g from an open set of possibilities such that $(\tilde{u}, 0)$ and $(0, \theta)$ exchange their stability at least k times as the diffusion rate μ varies over $(0, \infty)$. As a consequence, there are at least k branches of coexistence states of (5.2) which connect $(\tilde{u}, 0)$ and $(0, \theta)$. Moreover, co-existent states are unique and globally asymptotically stable if they exist. This confirms the previous conjecture, at least for the case when τ is positive and small. Biologically, this implies that with small variations of the phenotype, the stability of the two species varies with diffusion rate in a very complex manner, and it is unpredictable which species will survive. It also suggests that mutation leads to multiple opportunities for coexistence and thus potentially for speciation.

For small τ , which is more biologically realistic, these switches of stabilities between the two semi-trivial steady states happen within narrow regions of μ . But as τ increases, such regions widen up. Nonetheless, it suggests that there is no surprise in finding a large range of coexisting phenotypes which differ only in one small manner, e.g., the manner in which they utilize the resources of the environment.

When $m(x)$ is a positive constant, it was recently shown in [48] that for any $\tau > 0$ and any non-trivial function g satisfying $\int_{\Omega} g(x) dx = 0$, for sufficiently large μ , $v(x, t) \rightarrow 0$ as $t \rightarrow \infty$. In other words, when both

competing species have sufficiently large dispersal rates, the species with larger spatial variation in its intrinsic growth rate has the better chance of survival. We also refer to [48] for some related work on patch models, and to [85] for a similar approach in the study of evolution of gene frequency under joint forces of migration and selection.

5.2 Effects of inter-specific competition

We consider the system

$$u_t = \mu \Delta u + u \{m(x) - u - [1 + \tau g(x)]v\} \quad \text{in } \Omega \times (0, \infty), \quad (5.3a)$$

$$v_t = \mu \Delta v + v \{m(x) - v - [1 + \tau h(x)]u\} \quad \text{in } \Omega \times (0, \infty), \quad (5.3b)$$

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \quad \text{on } \Omega \times (0, \infty), \quad (5.3c)$$

where the two species are identical except for their interspecific competition rates, which are given by $1 + \tau g(x)$ and $1 + \tau h(x)$, respectively. Here τ is a positive constant and $g(x)$, $h(x)$ are two smooth functions. In comparison to (5.2), some new structure of coexistence equilibria of (5.3) is found.

Let u , v denote the densities of the resident species and the mutant, respectively. Define

$$\Omega_+ = \{x \in \Omega : g(x) > 0 > h(x)\}, \quad \Omega_- = \{x \in \Omega : g(x) < 0 < h(x)\}.$$

In Ω_+ , the mutant has the competitive advantage. If diffusion is not present, then the mutant not only can invade, but also goes to fixation, i.e., it forces the extinction of the original phenotype. The outcome is reversed in Ω_- . Biologically, when diffusion is present, it would be interesting to determine whether the mutant can coexist with the original species, and/or whether the mutant can invade. Clearly, such phenomena can occur only when spatial heterogeneity is involved since the answer is negative if both g and h are constant functions.

Since g and h can be rather general, the dynamics of (5.3) and the structures of coexistence states can potentially be very complicated, and it seems impossible to find any simple criteria which could characterize them. However, quite amazingly, for small τ , the dynamics and coexistence states of (5.3) essentially depend on two scalar functions of $\mu \in (0, \infty)$ defined by

$$G(\mu) = \int_{\Omega} g(x) \theta^3(x, \mu) dx, \quad (5.4a)$$

$$H(\mu) = \int_{\Omega} h(x) \theta^3(x, \mu) dx, \quad (5.4b)$$

where $\theta(x, \mu)$ is the unique positive solution of (3.1). The following theorem shows how G and H determine the structure of coexistence states and their stability.

Theorem 5.2. ([84]) *Assume that functions G and H have no common roots. Let μ_1 and μ_2 be two consecutive roots of the function GH and assume that they are both simple roots.*

(i) *If $GH < 0$ in (μ_1, μ_2) , then for $\mu \in [\mu_1, \mu_2]$, system (5.3) has no coexistence states provided that τ is small and positive.*

(ii) *If $GH > 0$ in (μ_1, μ_2) , then for each sufficiently small $\tau > 0$ there exist numbers $\underline{\mu} = \underline{\mu}(\tau) \approx \mu_1$, $\bar{\mu} = \bar{\mu}(\tau) \approx \mu_2$ such that for each $\mu \in (\underline{\mu}, \bar{\mu})$, (5.3) has a unique coexistence state, and $(u(\underline{\mu}), v(\underline{\mu}))$, $(u(\bar{\mu}), v(\bar{\mu}))$ are semi-trivial states of (5.3). Moreover, the coexistence state is stable if and only if both $G(\mu)$ and $H(\mu)$ are negative in (μ_1, μ_2) .*

In statement (ii), the following two scenarios can occur:

(a) $(u(\underline{\mu}), v(\underline{\mu}))$ and $(u(\bar{\mu}), v(\bar{\mu}))$ are semi-trivial states of the same type, that is, each of them equals $(\theta, 0)$ (at the corresponding value of μ) or each of them equals $(0, \theta)$,

(b) $(u(\underline{\mu}), v(\underline{\mu}))$ and $(u(\bar{\mu}), v(\bar{\mu}))$ are of different types: one of them equals $(\theta, 0)$ and the other one equals $(0, \theta)$.

In the case (a) we call the curve $\{(u(\mu), v(\mu)) : \mu \in (\underline{\mu}, \bar{\mu})\}$ a *branch* between $\underline{\mu}$ and $\bar{\mu}$; in the case (b) we call it a *loop*. If the coexistence states on the branch or loop are stable we call it a *stable branch* or a *stable loop*, respectively. It turns out that (5.3) can have an arbitrarily high number of stable loops and branches.

Theorem 5.3. ([84]) *Suppose that (A3) holds, $m \in C^\gamma(\bar{\Omega})$ and $m_+^3 \notin C^{\gamma+1}(\bar{\Omega})$ for some $\gamma > 0$. Then, for any given positive integers l and b , there exist smooth functions g and h such that (5.3) has at least l stable loops and at least b stable branches for each sufficiently small $\tau > 0$.*

Theorem 5.3 reveals complex and intriguing effects of diffusion and spatial heterogeneity of the environment on the invasion of rare species and coexistence of interacting species. The existence of (stable) loops appears to be a new phenomenon, as it does not occur in the model studied in [66]. Also, in contrast to the results of [66], the range of coexistence in terms of μ , that is, the projection of a branch or loop of coexistence states onto the μ -axis, is of order $O(1)$ as $\tau \rightarrow 0$.

5.3 Effects of boundary condition

Recently there has been considerable interest in how habitat edges change species interactions inside the habitat. For instance, in [16] Cantrell, Cosner and Fagan demonstrated how degrading the quality of the “matrix” habitat surrounding a habitat patch could reverse the nature of competitive two-species dynamics inside the patch so that a nominally “inferior” species outcompetes a “superior” one. However, the result in Theorem 6.2 of [16] does not rule out the possibility that the competitive advantage might switch back and forth between species 1 and species 2 a number of times before ultimately belonging to species 2. This observation raises a very interesting question, both ecologically and mathematically. Namely,

Question. Can a competitive advantage in such models reverse more than once as the level of degradation in the “matrix” habitat surrounding Ω increases?

To address such a question we examine the system

$$\begin{aligned} u_t &= \Delta u + u[1 + \epsilon g(x) - u - v] && \text{in } \Omega \times (0, \infty), \\ v_t &= \Delta v + v[1 - u - v] && \text{in } \Omega \times (0, \infty), \\ (1-s)\frac{\partial u}{\partial n} + su = 0 &= (1-s)\frac{\partial v}{\partial n} + sv && \text{on } \partial\Omega \times (0, \infty), \end{aligned} \tag{5.5}$$

where s ranges over $[0, 1]$. The perturbed system (5.5) is completely determined by the choice of the function g . It is shown in [20] that there exist functions g for which (5.5) exhibits multiple reversals of competitive advantage as the hostility of the “matrix” habitat surrounding Ω (which is measured by s) increases. This is distinct from the results in [16], since here the competitive advantage that one species has over the other is necessarily independent of initial configurations of species densities. In other words, when one of the species has the advantage, it competitively excludes the other over time. Moreover, under appropriate conditions on g , the regions in (ϵ, s) space in which one species excludes the other in (5.5) are bordered by values for which (5.5) admits a unique globally attracting componentwise positive equilibrium.

For other work on understanding the effects of habitat edges on species interactions, we refer to [15, 17, 43] and references therein. We also refer to [13] for some very interesting recent work concerning the effects of nonlinear boundary condition of the type

$$[1 - s(u)]\frac{\partial u}{\partial n} + s(u)u = 0$$

on the persistence of species in logistic population models, where $s(u) \in [0, 1]$ is a smooth function. It models the mechanism of inducing an Allee effect in the Glanville fritillary butterfly. Among other things, it is shown in [13] that under certain situations a branch of positive solutions satisfying $0 < u < 1$ connects with two trivial solutions $u \equiv 0$ and $u \equiv 1$ for *intermediate* values of dispersal rates. It will be of interest to see the effects of such nonlinear boundary conditions on multiple interacting species.

6 Evolution of conditional dispersal

A common underlying assumption of dispersal models is that dispersal is unconditional, i.e., organisms move at constant rates and in a nondirectional random manner. However, it is more probable that organisms can sense and respond effectively to local environmental cues by moving in the direction of increasingly favorable habitats. One of the simplest realistic approaches is to assume that organisms display taxis and can move up along the gradient of a local population growth rate. Diffusion combined with directed movement upward along resource gradients, as considered by Belgacem and Cosner [4] and Cosner and Lou [31], is an example of conditional dispersal, because the bias in the direction of dispersal depends on the spatial distribution of resources. In context of two-patch models, McPeck and Holt [94] showed in spatially varying but temporally constant environment conditional dispersal can be advantageous. In diffusion-advection models for a single population in a spatially varying but temporally constant environment, Belgacem and Cosner [4] and Cosner and Lou [31] showed that conditional dispersal involving both diffusion and directed movement up resource gradients can sometimes (but not always) make persistence more likely. For related work on balanced dispersal we refer to [37, 99] and references therein. We also refer to [14, 74] for recent progress on the evolution of conditional dispersal in patch models.

This section is devoted to studying conditional dispersal in context of competition between two populations that are ecologically identical except in their dispersal mechanisms.

We first assume that there is a random component to the dispersal of both competitors but that when resources are distributed in a spatially heterogeneous way, one of the competitors also has a tendency to move upward along the resource gradient while the other does not. Such directed motion introduces a drift or advection term into the diffusion equation. The dispersal of the two competitors may be described in terms of the fluxes

$J_u = -\mu\nabla u + \alpha(\nabla m)u$ and $J_v = -\nu\nabla v$, where $\alpha \geq 0$. If we assume there is no flux across $\partial\Omega$, we obtain the competition model

$$\begin{aligned} u_t &= \nabla \cdot [\mu\nabla u - \alpha u\nabla m] + (m - u - v)u \\ v_t &= \nabla \cdot [\nu\nabla v] + (m - u - v)v \end{aligned} \quad (6.1)$$

in $\Omega \times (0, \infty)$, with boundary conditions

$$\mu \frac{\partial u}{\partial n} - \alpha u \frac{\partial m}{\partial n} = \frac{\partial v}{\partial n} = 0. \quad (6.2)$$

When assumption (A3) holds, (6.1)-(6.2) has two semi-trivial states, denoted by $(\tilde{u}, 0)$ and $(0, \theta(\cdot, \nu))$, for every $\mu > 0$, $\nu > 0$, and $\alpha \geq 0$ (see [31]), where \tilde{u} is the unique positive solution of (3.2). Throughout this section, we assume that m is twice continuously differentiable.

6.1 Weak advection

For fixed μ, ν with $\mu \neq \nu$, the dynamics of (6.1)-(6.2) is similar to that of (4.1) for sufficiently small α . More precisely, there exists some small positive constant $\alpha_0 = \alpha_0(\mu, \nu, \Omega, m)$ such that if $\alpha \in (0, \alpha_0)$, $(\tilde{u}, 0)$ is the global attractor of (6.1)-(6.2) among all non-negative and non-trivial initial data if $\mu < \nu$, and $(0, \theta(\cdot, \nu))$ is the global attractor if $\mu > \nu$.

The case $\mu = \nu$ is quite delicate. This is due to the fact that (4.1) with $\mu = \nu$ is a degenerate system: it has a family of coexistence states, each of which is neutrally stable, and as a whole is a global attractor. For sufficiently small positive α , (6.1)-(6.2) can be viewed as a perturbation of (4.1).

For $\mu > 0$, define

$$\alpha^*(\mu) = \frac{\int_{\Omega} \theta(x, \mu) \nabla \theta(x, \mu) \cdot \nabla m(x) dx}{\int_{\Omega} |\nabla \theta(x, \mu)|^2 dx}.$$

As will be seen later, this quantity plays a crucial role in studying dynamics of (6.1)-(6.2) for small positive α .

For any $\mu_0 > 0$, $\mu_1, \nu_1 \in \mathbb{R}^1$, and $\alpha_1 > 0$, let

$$(\mu, \nu, \alpha) = (\mu_0 + \mu_1 s + o(s), \mu_0 + \nu_1 s + o(s), \alpha_1 s + o(s)), \quad (6.3)$$

where s is positive and small.

Theorem 6.1. *Suppose that (A3) holds and Ω is convex. Then we have:*

(a) *For every $\mu > 0$, $\alpha^*(\mu) > 0$.*

(b) *Let μ, ν, α be given as in (6.3). If $\alpha_1 > (\mu_1 - \nu_1)/\alpha^*(\mu_0)$, then for positive small s , $(\tilde{u}, 0)$ is globally asymptotically stable. In particular, if $(\mu, \nu) = (\mu_0, \mu_0)$, $(\tilde{u}, 0)$ is globally asymptotically stable for small positive α .*

Theorem 6.1 is established in [21, 22], and it has some interesting consequences: e.g., for the case $\mu_1 > \nu_1$, it implies that the competitor that moves toward more favorable environments may have a competitive advantage even if it diffuses more rapidly than the other competitor. This is in strong contrast with the case in which both competitors disperse only by random diffusion, where the slower diffuser always wins. It means that the advantage gained from the directed movement upward resource gradients can compensate the disadvantage created by faster diffusion.

The convexity of Ω is needed in the proof of Theorem 6.1 to ensure that $\alpha^*(\mu) > 0$ for all $\mu > 0$, which allows us to exclude the possibility of coexistence states for small $\alpha > 0$. The proof of $\alpha^*(\mu) > 0$ is given in [21], where we applied the fact $\partial(|\nabla\theta|^2)/\partial n \leq 0$ on $\partial\Omega$, which holds true for convex domains only. We should point out that the convexity assumption on domain Ω seems to be necessary, as shown by the following result [21].

Theorem 6.2. *Given any $\mu_0 > 0$, there exist non-convex domain Ω and smooth function $m(x)$ such that:*

(a) *$\alpha^*(\mu_0) < 0$, and $\alpha^*(\mu)$ changes sign at least once in $(0, \mu_0)$;*

(b) *Let μ, ν, α be given by (6.3). If $\alpha_1 > (\mu_1 - \nu_1)/\alpha^*(\mu_0)$, then for positive small s , $(0, \theta(\cdot, \nu))$ is globally asymptotically stable. In particular, if $(\mu, \nu) = (\mu_0, \mu_0)$, $(0, \theta(\cdot, \mu_0))$ is globally asymptotically stable for small positive α .*

For the case $\mu_1 < \nu_1$, part (b) of Theorem 6.2 implies that for certain non-convex habitats, a slower diffuser which also moves toward more favorable environments may not have the competitive advantage. This is in strong contrast with both the case of a convex habitat and the case of $\alpha = 0$.

6.2 Advection mediated coexistence

In this subsection we are concerned with the much more interesting and challenging case wherein α is large, and show how strong advection can induce stable coexistence of competing species. In particular, we shall investigate

the stability of $(\tilde{u}, 0)$ and $(0, \theta(\cdot, \nu))$, and the existence and qualitative properties of coexistence states. The stability of $(\tilde{u}, 0)$ and properties of coexistence states rely crucially on qualitative properties of \tilde{u} given in Subsection 3.2.

For sufficiently large α , we have the following result.

Theorem 6.3. *Suppose that $\int_{\Omega} m > 0$ and the set of critical points of $m(x)$ has Lebesgue measure zero. Then for sufficiently large α , both $(\tilde{u}, 0)$ and $(0, \theta(\cdot, \nu))$ are unstable. Moreover, system (6.1)-(6.2) has at least one stable coexistence state.*

In fact, it can be shown that every coexistence state (u_{α}, v_{α}) of (6.1)-(6.2) satisfies $u_{\alpha} \rightarrow 0$ in $L^2(\Omega)$ and $v_{\alpha} \rightarrow \theta(\cdot, \nu)$ in $W^{2,2}(\Omega)$ as $\alpha \rightarrow \infty$. If we further assume that (A4) holds, $u_{\alpha} \rightarrow 0$ pointwise for every $x \in [0, 1] \setminus \{x_1, \dots, x_k\}$.

Since (6.1)-(6.2) is a strongly monotone system, as in other competition models, the existence and stability of coexistence states follow from the instability of the two semi-trivial states and the theory of continuous monotone systems [32, 57, 62, 92, 118]. Furthermore, (6.1)-(6.2) has at least one asymptotically stable coexistence state [58]. For the discrete-time counterparts of results for monotone systems, we refer to [34, 56] and references therein.

Theorem 6.3 was established in [22] under the extra condition that m has at least one isolated global maximum. The new improvement is given in [26].

From the biological point of view, Theorem 6.3 is surprising at the first look. If $\mu < \nu$ and α is small, the species u always wins the competition. As α increases, the species u has the tendency to move toward more favorable regions, so it has more competitive advantage than the species v and should still be the sole winner of the competition. However, the above theorem tells us that “smarter” species may not necessarily win the competition. A possible explanation for such coexistence is that as α becomes large, the “smarter” competitor moves toward and concentrates at places of locally more favorable environments, leaving enough room for the other species to survive in places with less resources.

It is shown in [22] that for any positive steady state solution (u_{α}, v_{α}) of (6.1-6.2), $\|u_{\alpha}\|_{L^2(\Omega)} \rightarrow 0$ as $\alpha \rightarrow \infty$, *i.e.*, the total population size of species u , becomes sufficiently small if α is large. It is natural to inquire whether the density function $u_{\alpha} \rightarrow 0$ in $L^{\infty}(\Omega)$ as $\alpha \rightarrow \infty$. As shown in our next result,

the answer is negative in general. We will also show that u_α is concentrated at the global maximum of $m(x)$ in some cases.

Theorem 6.4. ([26]) *Suppose that $\int_\Omega m(x) dx > 0$ and all critical points of m are non-degenerate. Let \mathcal{M} be the set of points of local maxima of m . Then for any positive steady state (u_α, v_α) of (6.1-6.2),*

$$\liminf_{\alpha \rightarrow \infty} \max_{\bar{\Omega}} u_\alpha \geq \max_{\mathcal{M}} [m - \theta] > 0.$$

Assume further that $m(x)$ satisfies $\partial_n m \leq 0$ on $\partial\Omega$, and there exists $x_0 \in \Omega$ such that $\{x \in \bar{\Omega} : \nabla m(x) = 0\} = \{x_0\}$ and $\det(D^2 m(x_0)) \neq 0$. Then as $\alpha \rightarrow \infty$, $v_\alpha \rightarrow \theta$ in $C^{1+\beta}(\bar{\Omega})$ for every $\beta \in (0, 1)$, and

$$\left\| u_\alpha \cdot e^{\alpha[\max_{\bar{\Omega}} m - m(x)]/\mu} - 2^{N/2} [m(x_0) - \theta(x_0)] \right\|_{L^\infty(\Omega)} \rightarrow 0. \quad (6.4)$$

Theorem 6.4 shows that if m has a unique local maximum in $\bar{\Omega}$ which is also non-degenerate, then the “smarter” species is concentrated near this local maximum. For general m , we have the following

Conjecture. For sufficiently large α , (6.1)-(6.2) has a unique coexistence state, denoted by (u_α, v_α) , which is globally asymptotically stable among non-negative non-trivial initial data. Moreover, as $\alpha \rightarrow \infty$, u_α concentrates at all local maxima of $m(x)$ in $\bar{\Omega}$.

6.3 Evolutionarily stable dispersal strategy

In this subsection we discuss the situation in which both competitors have a tendency to move upward along the resource gradient, and the equations that describe this competition model are

$$\begin{aligned} u_t &= \nabla \cdot [\mu \nabla u - \alpha u \nabla m] + (m - u - v)u & \text{in } \Omega \times (0, \infty), \\ v_t &= \nabla \cdot [\nu \nabla v - \beta v \nabla m] + (m - u - v)v & \text{in } \Omega \times (0, \infty), \end{aligned} \quad (6.5)$$

with no-flux boundary conditions

$$[\mu \nabla u - \alpha u \nabla m] \cdot n = [\nu \nabla v - \beta v \nabla m] \cdot n = 0,$$

where α and β are non-negative constants. The competitors represent different phenotypes of the same species which differ only in their dispersal mechanisms. We ask what type of dispersal strategy confers a competitive

advantage. Our goal is to search for the regions of $(\alpha, \beta, \mu, \nu)$ in which either competition exclusion holds or stable coexistence occurs. A particularly interesting question is whether there exists one dispersal strategy which is evolutionarily stable, i.e., a population using it cannot be invaded by a small number of individuals of other competing species that uses a different strategy.

Even though the dispersal strategies for both species have same components, i.e., random movement and biased movement along resource gradients, they can be quite different. For instance, the species with stronger biased movement behaves like a specialist as it mainly pursues resources at places of locally most favorable environments. The species with moderate biased movement has a rather balanced dispersal strategy, so it can be regarded as a generalist. It is fairly natural to ask the following

Question. For arbitrary but fixed $\beta > 0$, do the two species always coexist if α is sufficiently large?

By previous coexistence results for the case $\beta = 0$, one might expect that the specialist and generalist should still coexist stably. However, we will show that the answer depends crucially upon the ratio β/ν , and at least two scenarios can occur: if the generalist's biased movement rate is relatively smaller than its own random movement rate, then indeed both species can coexist stably. However, if the biased movement of the generalist is relatively stronger than its random movement, then the generalist is always the winner, regardless of initial conditions. More precisely, we have the following two results which complement and contrast each other.

Theorem 6.5. ([24]) *Suppose that the set of critical points of $m(x)$ has measure zero. If $\beta/\nu \leq 1/\max_{\bar{\Omega}} m$, then for sufficiently large α , both semi-trivial states are unstable, and (6.5) has at least one stable positive steady state.*

Theorem 6.5 is a generalization of the results in [22, 26] for the case $\beta = 0$. What happens if β/ν is suitably larger? It turns out that the answer is dramatically different.

Theorem 6.6. ([24]) *Suppose that $m > 0$ in $\bar{\Omega}$, $\partial_n m < 0$ on $\partial\Omega$, m has only one critical point in $\bar{\Omega}$, denote by x_0 , and x_0 satisfies $x_0 \in \Omega$ and $D^2m(x_0) < 0$. If $\beta/\nu \geq 1/\min_{\bar{\Omega}} m$, then for sufficiently large α , the semi-trivial steady state $(0, \theta)$ is globally asymptotically stable.*

These results may have potential applications to the evolution of dispersal and population dynamics. In the context of dynamics of generalist and specialist, $\beta/\nu \leq 1/\max_{\bar{\Omega}} m$ implies that the two species can coexist stably for sufficiently large α , i.e., both generalist and specialist can coexist. However, for the case $\beta/\nu \geq 1/\min_{\bar{\Omega}} m$, competitive exclusion happens: the generalist always wins. That is, strong advection along resource gradients can be disadvantageous to the specialist and can even cause the extinction of the specialist in some circumstances. This seems to suggest that selection is for intermediate biased movement rate.

Two special but biologically relevant cases are worth mentioning:

(i) $\mu = \nu$ but $\alpha \neq \beta$. For this case, the competing species are identical in all aspects except their advection coefficients. When $\alpha > 0$ is small and $\beta = 0$, it is known that if Ω is convex then u is the winner in the competition. If α is large and $\beta = 0$, then both species can persist. For the general case $\alpha, \beta > 0$, we suspect that there is an evolutionarily stable dispersal strategy. Namely, there exists some α such that for any $\beta \neq \alpha$, the species v can not invade when rare.

(ii) $\mu \neq \nu$ but $\alpha = \beta$. For this case, the slower diffuser always wins if α is small. For suitably large values of α , very little is known.

Understanding these two special cases will shed light on more general situations, and can also be useful in studying other ecological problems, e.g., moving ranges of species and the effects of dispersal strategies on stream populations [91, 109].

It will also be interesting to consider N ($N \geq 3$) competing species and address similar questions. Suppose that all species are identical except their dispersal strategies.

(a) What happens if species 1 to $N - 1$ disperse only by random diffusion, and species N disperse by both random diffusion and directed movement towards habitat resources?

(b) What happens if all species have the same advection coefficients but different random dispersal rates?

(c) What happens if all species have same random dispersal rates but different advection coefficients?

We suspect that the answers to these questions are much more complicated for three or more species and rely on a solid understanding of the two-species case. Nevertheless, these are some of the interesting and challenging open problems on the evolution of conditional dispersal.

Acknowledgment. I would like to thank Profs. Stephen Cantrell, Xinfu Chen, Chris Cosner, Vivian Hutson, Chiu-Yen Kao, Salome Martinez, Konstantin Mischaikow, Thomas Nagylaki, Wei-Ming Ni, Peter Poláčik, and Eiji Yanagida for the pleasant collaborations on the projects presented here and for sharing their amazing insights. I especially thank Steve Cantrell, Chris Cosner, and Vivian Hutson for reading this manuscript carefully and for their helpful comments. I would like to thank Prof. Avner Friedman for inviting me to write this survey, and also thank him and Prof. Peter March for their warm encouragement. This work is partially supported by National Science Foundation grant DMS-0615845.

References

- [1] P.R. Armsworth and J.E. Roughgarden, The impact of directed versus random movement on population dynamics and biodiversity patterns, *Am. Nat.* **165** (2005) 449-465.
- [2] P.R. Armsworth and J.E. Roughgarden, Disturbance induces the contrasting evolution of reinforcement and dispersiveness in directed and random movers, *Evolution* **59** (2005) 2083-2096.
- [3] F. Belgacem, Elliptic Boundary Value Problems with Indefinite Weights: Variational Formulations of the Principal Eigenvalue and Applications, Pitman Research Notes in Mathematics, Vol. **368**, Longman, Harlow, U.K., 1997.
- [4] F. Belgacem and C. Cosner, The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environment, *Canadian Appl. Math. Quarterly* **3** (1995) 379-397.
- [5] H. Berestycki, F. Hamel, and L. Roques, Analysis of the periodically fragmented environment model. I. Species persistence, *J. Math. Biol.* **51** (2005) 75-113.
- [6] D.E. Bowler and T.G. Benton, Causes and consequences of animal dispersal strategies: relating individual behavior to spatial dynamics, *Biol. Rev.* **80** (2005) 205-225.
- [7] K.J. Brown and S.S. Lin, On the existence of positive eigenvalue problem with indefinite weight function, *J. Math. Anal. Appl.* **75** (1980) 112-120.
- [8] R.S. Cantrell and C. Cosner, Diffusive logistic equations with indefinite weights: population models in a disrupted environments, *Proc. Roy. Soc. Edinburgh* **112A** (1989) 293-318.

- [9] R.S. Cantrell and C. Cosner, The effects of spatial heterogeneity in population dynamics, *J. Math. Biol.* **29** (1991) 315-338.
- [10] R.S. Cantrell and C. Cosner, Should a park be an island? *SIAM J. Appl. Math.* **53** (1993) 219-252.
- [11] R.S. Cantrell and C. Cosner, On the effects of spatial heterogeneity on the persistence of interacting species, *J. Math. Biol.* **37** (1998) 103-145.
- [12] R.S. Cantrell and C. Cosner, Spatial Ecology via Reaction-Diffusion Equations, Series in Mathematical and Computational Biology, John Wiley and Sons, Chichester, UK, 2003.
- [13] R.S. Cantrell and C. Cosner, On the effects of nonlinear boundary conditions in diffusive logistic equations on bounded domains, *J. Diff. Eqs.* **231** (2006) 768-804.
- [14] R.S. Cantrell, C. Cosner, D.L. DeAngelis, and V. Padrón, The ideal free distribution as an evolutionarily stable strategy, preprint, 2007.
- [15] R.S. Cantrell, C. Cosner, and W.F. Fagan, Brucellosis, botflies and brinworms: the impact of edge habitats on pathogen transmission and species extinction, *J. Math. Biol.* **42** (2001) 95-119.
- [16] R.S. Cantrell, C. Cosner, and W.F. Fagan, Competitive reversals inside ecological preserves: the role of external habitat degradation, *J. Math Biol.* **37** (1998) 491-533.
- [17] R.S. Cantrell, C. Cosner, and W.F. Fagan, Habitat edges and predator-prey interactions: effects on critical patch size, *Math. Biosc.* **175** (2002) 31-55.
- [18] R.S. Cantrell, C. Cosner, and V. Hutson, Permanence in ecological systems with diffusion, *Proc. Roy. Soc. Edin.* **123A** (1993) 533-559.
- [19] R.S. Cantrell, C. Cosner, and V. Hutson, Ecological models, permanence and spatial heterogeneity, *Rocky Mount. J. Math.* **26** (1996) 1-35.
- [20] R.S. Cantrell, C. Cosner, and Y. Lou, Multiple reversals of competitive dominance in ecological reserves via external habitat degradation, *J. Dyn. Diff. Eqs.* **16** (2004) 973-1010.
- [21] R.S. Cantrell, C. Cosner, and Y. Lou, Movement towards better environments and the evolution of rapid diffusion, *Math Biosciences* **204** (2006) 199-214.
- [22] R.S. Cantrell, C. Cosner, and Y. Lou, Advection mediated coexistence of competing species, *Proc. Roy. Soc. Edinb.*, in press (2007).

- [23] A.N. Carvalho and J.K. Hale, Large diffusion with dispersion, *Nonl. Anal.* **17** (1991) 1139-1151.
- [24] X.F. Chen, R. Hambrock, and Y. Lou, Advection-induced coexistence and extinction in a two-species competition model, preprint, 2007.
- [25] X.Y. Chen, S. Jimbo, and Y. Morita, Stabilization of vortices in the Ginzburg-Landau equation with a variable diffusion coefficient, *SIAM J. Math. Anal.* **29** (1998) 903-912.
- [26] X.F. Chen and Y. Lou, Principal eigenvalue and eigenfunction of elliptic operator with large convection and its application to a competition model, *Indiana Univ. Math. J.*, accepted for publication, 2007.
- [27] Y.S. Choi, R. Lui, and Y. Yamada, Existence of global solutions for the Shigesada-Kawasaki-Teramoto model with weak cross-diffusion, *Disc. Cont. Dyn. Syst. A* **9** (2003) 1193-1200.
- [28] M. Conti, S. Terracini, and G. Verzini, A variational problem for the spatial segregation of reaction-diffusion systems, *Indiana Univ. Math. J.* **54** (2005) 779-815.
- [29] M. Conti, S. Terracini, and G. Verzini, Asymptotic estimates for the spatial segregation of competitive systems, *Adv. Math.* **195** (2005) 524-560.
- [30] E. Conway, D. Hoff, and J. Smoller, Large time behavior of solutions of systems of nonlinear reaction-diffusion equations, *SIAM J. Appl. Math.* **35** (1978) 1-16.
- [31] C. Cosner and Y. Lou, Does movement toward better environments always benefit a population? *J. Math. Anal. Appl.* **277** (2003) 489-503.
- [32] E.N. Dancer, Positivity of maps and applications. Topological nonlinear analysis, 303-340, *Prog. Nonlinear Differential Equations Appl.*, **15**, edited by Matzeu and Vignoli, Birkhauser, Boston, 1995.
- [33] E.N. Dancer and Y. Du, Competing species equations with diffusion, large interactions, and jumping nonlinearities, *J. Diff. Eqs.* **114** (1994) 434-475.
- [34] E.N. Dancer, P. Hess, Stability of fixed points for order-preserving discrete-time dynamical systems, *J. Reine Angew. Math.* **419** (1991) 125-139.
- [35] J. Dockery, V. Hutson, K. Mischaikow, and M. Pernarowski, The evolution of slow dispersal rates: a reaction-diffusion model, *J. Math. Biol.* **37** (1998) 61-83.
- [36] M. Doebeli, Dispersal and dynamics. *Theor. Pop. Biol.* **47** (1995) 82-106.

- [37] C.P. Doncaster, J. Clobert, B. Doligez, L. Gustafsson, and E. Danchin, Balanced dispersal between spatially varying local populations: an alternative to the source-sink model, *Am. Nat.* **150** (1997) 425-445.
- [38] Y. Du, Effects of a degeneracy in the competition model, Part II. Perturbation and dynamical behavior, *J. Diff. Eqs.* **181** (2002) 133-164.
- [39] Y. Du, Realization of prescribed patterns in the competition model, *J. Diff. Eqs.* **193** (2003) 147-179.
- [40] Y. Du, Spatial patterns for population models in a heterogeneous environment, *Taiwanese J. Math.* **8** (2004) 155-182.
- [41] Y. Du, Bifurcation and related topics in elliptic problems. Stationary partial differential equations. Vol. II, 127-209, *Handb. Differ. Equ.*, Elsevier/North-Holland, Amsterdam, 2005.
- [42] H. Evans, P. Kröger, and K. Kurata, On the placement of an obstacle or well to optimize the fundamental eigenvalue, *SIAM J. Math. Anal.* **33** (2001) 240-259.
- [43] W.F. Fagan, R.S. Cantrell, and C. Cosner, How habitat edges change species interactions: a synthesis of data and theory, *Am. Nat.* **153** (1999) 165-182.
- [44] W.H. Fleming, A selection-migration in population genetics, *J. Math. Biol.* **2** (1975) 219-223.
- [45] A. Friedman, *Partial Differential Equations of Parabolic Type*, Prentice-Hall, 1964.
- [46] J.E. Furter and J. López-Gómez, Diffusion-mediated permanence problem for a heterogeneous Lotka-Volterra competition model, *Proc. Roy. Soc. Edin.* **127A** (1997) 281-336.
- [47] D. Gilbarg and N. Trudinger, *Elliptic Partial Differential Equation of Second Order*, 2nd Ed., Springer-Verlag, Berlin, 1983.
- [48] S. Gourley and Y. Kuang, Two-species competition with high dispersal: the winning strategy, *Math. Biosci. Eng.* **2** (2005) 345-362.
- [49] J.K. Hale, Large diffusivity and asymptotic behavior in parabolic systems, *J. Math. Anal. Appl.* **118** (1986) 455-466.
- [50] J. K. Hale and G. Raugel, Reaction-diffusion equation on thin domains, *J. Math. Pures. Appl.* **71** (1992) 33-95.
- [51] J.K. Hale and K. Sakamoto, Shadow systems and attractors in reaction-diffusion equations, *Appl. Anal.* **32** (1989) 287-303.

- [52] I. Hanski, *Metapopulation Ecology*, Oxford Univ. Press, Oxford, 1999.
- [53] I. Hanski and C.D. Thomas, Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biol. Conservation* **68** (1994) 167-180.
- [54] A. Hastings, Can spatial variation alone lead to selection for dispersal? *Theor. Pop. Biol.* **33** (1983) 311-314.
- [55] A. Hastings, Spatial heterogeneity and ecological models, *Ecology* **71** (1990) 426-428.
- [56] P. Hess, *Periodic Parabolic Boundary Value Problems and Positivity*, Longman Scientific & Technical, Harlow, UK, 1991.
- [57] M.W. Hirsch, Stability and convergence in strongly monotone dynamical systems, *J. Reine Angew. Math.* **383** (1988) 1-51.
- [58] M.W. Hirsch and H.L. Smith, Asymptotically stable equilibria for monotone semiflows, *Discrete Contin. Dyn. Syst.* **14** (2006) 385-398.
- [59] E.E. Holmes, M.A. Lewis, J.E. Banks, and R.R. Veit, Partial differential equations in ecology: spatial interactions and population dynamics, *Ecology* **75** (1994) 17-29.
- [60] R.D. Holt, Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.* **28** (1985) 181-208.
- [61] R.D. Holt and M.A. McPeck, Chaotic population dynamics favors the evolution of dispersal, *Am. Nat.* **148** (1996) 709-718.
- [62] S. Hsu, H. Smith, and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.* **348** (1996) 4083-4094.
- [63] V. Hutson, J. López-Gómez, K. Mischaikow, and G. Vickers, Limit behavior for a competing species problem with diffusion, in *Dynamical Systems and Applications*, World Sci. Ser. Appl. Anal. 4, World Scientific, River Edge, NJ, 1995, 501-533.
- [64] V. Hutson, Y. Lou, and K. Mischaikow, Spatial heterogeneity of resources versus Lotka-Volterra dynamics, *J. Diff. Eqs.* **185** (2002) 97-136.
- [65] V. Hutson, Y. Lou, and K. Mischaikow, Convergence in competition models with small diffusion coefficients, *J. Diff. Eqs.* **211** (2005) 135-161.
- [66] V. Hutson, Y. Lou, K. Mischaikow, and P. Poláčik, Competing species near the degenerate limit, *SIAM J. Math. Anal.* **35** (2003) 453-491.

- [67] V. Hutson, S. Martinez, K. Mischaikow, and G.T. Vickers, The evolution of dispersal, *J. Math. Biol.* **47** (2003) 483-517.
- [68] V. Hutson, K. Mischaikow, and P. Poláčik, The evolution of dispersal rates in a heterogeneous time-periodic environment, *J. Math. Biol.* **43** (2001) 501-533.
- [69] M. Iida, M. Mimura, and H. Ninomiya, Diffusion, cross-diffusion and competitive interaction, *J. Math. Biol.* **53** (2006) 617-641.
- [70] M. Iida, M. Tatsuya, H. Ninomiya, and E. Yanagida, Diffusion-induced extinction of a superior species in a competition system, *Japan J. Indust. Appl. Math.* **15** (1998) 223-252.
- [71] J. Jiang, X. Liang, and X. Zhao, Saddle point behavior for monotone semiflows and reaction-diffusion models, *J. Diff. Eqs.* **203** (2004) 313-330.
- [72] Y. Kan-on and E. Yanagida, Existence of non-constant stable equilibria in competition-diffusion equations, *Hiroshima Math. J.* **23** (1993) 193-221.
- [73] C.Y. Kao, Y. Lou, and E. Yanagida, Principal eigenvalue for an elliptic problem with indefinite weight on cylindrical domains, in preparation, 2007.
- [74] S. Kirkland, C.-K. Li, and S.J. Schreiber, On the evolution of dispersal in patchy environments, *SIAM J. Appl. Math.* **66** (2006) 1366-1382.
- [75] K. Kishimoto and H.F. Weinberger, The spatial homogeneity of stable equilibria of some reaction-diffusion systems on convex domains, *J. Diff. Eqs.* **58** (1985) 15-21.
- [76] K. Kurata and J. Shi, Optimal spatial harvesting strategy and symmetry-breaking, preprint, 2006.
- [77] K. Kurata, M. Shibata, and S. Sakamoto, Symmetry-breaking phenomena in an optimization problem for some nonlinear elliptic equation, *Appl. Math. Optim.* **50** (2004) 259-278.
- [78] C.L. Lehman and D. Tilman, Competition in spatial habitats. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology*. Princeton Univ. Press, Princeton, NJ, 1997, pp. 185-203.
- [79] S.A. Levin, H.C. Muller-Landau, R. Nathan, and J. Chave, The ecology and evolution of seed dispersal: a theoretical perspective, *Annu. Rev. Eco. Evol. Syst.* **34** (2003) 575-604.
- [80] J. López-Gómez, Coexistence and meta-coexistence for competing species, *Houston J. Math.* **29** (2003) 483-536.

- [81] J. López-Gómez and M. Molina-Meyer, Superlinear indefinite system beyond Lotka-Volterra models, *J. Diff. Eqs.* (2006) **221** 343-411.
- [82] Y. Lou, On the effects of migration and spatial heterogeneity on single and multiple species, *J. Diff. Eqs.* **223** (2006) 400-426.
- [83] Y. Lou, S. Martinez, and W.M. Ni, On 3×3 Lotka-Volterra competition systems with cross-diffusion, *Dis. Cont. Dyn. Sys.* **6** (2000) 175-190.
- [84] Y. Lou, S. Martinez and P. Poláčik, Loops and branches of coexistence states in a Lotka-Volterra competition model, *J. Diff. Eqs.* **230** (2006) 720-742.
- [85] Y. Lou and T. Nagylaki, Evolution of A Semilinear Parabolic System for Migration and Selection without dominance, *J. Diff. Eqs.* **225** (2006) 624-665.
- [86] Y. Lou, T. Nagylaki and W.M. Ni, On diffusion-induced blowups in a cooperative model, *Nonl. Anal.: Theory, Meth. Appl.* **45** (2001) 329-342.
- [87] Y. Lou and W.M. Ni, Diffusion, self-diffusion and cross-diffusion, *J. Diff. Eqs.* **131** (1996) 79-131.
- [88] Y. Lou and W.M. Ni, Diffusion vs. cross-diffusion: an elliptic approach, *J. Diff. Eqs.* **154** (1999) 157-190.
- [89] Y. Lou, W.M. Ni, and S. Yotsutani, On a limiting system in the Lotka-Volterra competition with cross-diffusion. *Dis. Cont. Dyn. Sys.* **10** (2004) 435-458.
- [90] Y. Lou and E. Yanagida, Minimization of the principal eigenvalue with indefinite weight and applications to population dynamics, *Japan J. Indus. Appl. Math* **23** (2006) 275-292.
- [91] F. Lutscher, E. Pachepsky, and M. Lewis, The effect of dispersal patterns on stream populations, *SIAM Rev.* **47** (2005) 749-772.
- [92] H. Matano, Existence of nontrivial unstable sets for equilibriums of strongly order-preserving systems, *J. Fac. Sci. Univ. Tokyo* **30** (1984) 645-673.
- [93] H. Matano and M. Mimura, Pattern formation in competition-diffusion systems in non-convex domains, *Publ. RIMS. Kyoto Univ.* **19** (1983) 1049-1079.
- [94] M.A. McPeck and R.D. Holt, The evolution of dispersal in spatially and temporally varying environments, *Am. Nat.* **140** (1992) 1010-1027.
- [95] M. Mimura, Stationary pattern of some density-dependent diffusion system with competitive dynamics, *Hiroshima Math. J.* **11** (1981) 621-635.

- [96] M. Mimura, S.I. Ei, and Q. Fang, Effect of domain-type on the coexistence problems in a competition-diffusion system, *J. Math. Biol.* **29** (1991) 219-237.
- [97] M. Mimura and K. Kawasaki, Spatial segregation in competitive interaction-diffusion equations, *J. Math. Biol.* **9** (1980) 49-64.
- [98] M. Mimura, Y. Nishiura, A. Tesei, and T. Tsujikawa, Coexistence problem for two competing species models with density-dependent diffusion, *Hiroshima Math. J.* **14** (1984) 425-449.
- [99] D.W. Morris, J.E. Diffendorfer, and P. Lundberg, Dispersal among habitats varying in fitness: reciprocating migration through ideal habitat selection, *Oikos* **107** (2004) 559-575.
- [100] N. Mizoguchi, N. Ninomiya, and E. Yanagida, On the blowup induced by diffusion in nonlinear systems, *J. Dyn. Diff. Eqs.* **10** (1998) 619-638.
- [101] J.D. Murray, *Mathematical Biology II. Spatial models and Biomedical Applications, Interdisciplinary Applied Mathematics, Vol. 18*, 3rd ed. Springer-Verlag, New York, 2003.
- [102] C. Neuhauser, Mathematical challenges in spatial ecology, *Notices Amer. Math. Soc.* **48** (2001) 1304-1314.
- [103] W.M. Ni, Diffusion, cross-diffusion, and their spike-layer steady states, *Notices Amer. Math. Soc.* **45** (1998) 9-18.
- [104] W.M. Ni, Qualitative properties of solutions to elliptic problems. Stationary partial differential equations. Vol. I, 157-233, *Handb. Differ. Equ.*, North-Holland, Amsterdam, 2004.
- [105] H. Ninomiya, Separatrices of competition-diffusion equations, *J. Math. Kyoto Univ.* **35** (1995) 539-567.
- [106] A. Okubo and S.A. Levin, *Diffusion and Ecological Problems: Modern Perspectives, Interdisciplinary Applied Mathematics, Vol. 14*, 2nd ed. Springer, Berlin, 2001.
- [107] S. Pacala and J. Roughgarden, Spatial heterogeneity and interspecific competition, *Theor. Pop. Biol.* **21** (1982) 92-113.
- [108] P. Poláčik and E. Yanagida, Existence of stable subharmonic solutions for reaction-diffusion equations, *J. Diff. Eqs.* **169** (2001) 255-280.
- [109] A.B. Potapov and M.A. Lewis, Climate and competition: the effect of moving range boundaries on habitat invasibility, *Bull. Math. Biol.* **66** (2004) 975-1008.

- [110] M. H. Protter and H. F. Weinberger, Maximum Principles in Differential Equations, 2nd ed., Springer-Verlag, Berlin, 1984.
- [111] G. Raugel, Dynamics of partial differential equations on thin domains, *Dynamical systems* (Montecatini terme, 1994), 208-315, Lecture Notes in Math. **1609**, Springer, Berlin, 1995.
- [112] G. Raugel and G. Sell, Navier-Stokes equations on thin 3D domains. I. Global attractors and global regularity of solutions, *J. Amer. Math. Soc.* **6** (1993) 503-568.
- [113] J. C. Saut and B. Scheurer, Remarks on a nonlinear equation arising in population genetics, *Comm. Part. Diff. Eq.*, **23** (1978) 907-931.
- [114] S. Senn and P. Hess, On positive solutions of a linear elliptic boundary value problem with Neumann boundary conditions, *Math. Ann.* **258** (1982) 459-470.
- [115] N. Shigesada and K. Kawasaki, Biological Invasions: Theory and Practice, Oxford Series in Ecology and Evolution, Oxford University Press, Oxford, New York, Tokyo, 1997.
- [116] N. Shigesada, K. Kawasaki, and E. Teramoto, Spatial segregation of interacting species, *J. Theo. Biol.* **79** (1979) 83-99.
- [117] J.G. Skellam, Random dispersal in theoretical populations, *Biometrika* **38** (1951) 196-218.
- [118] H. Smith, Monotone Dynamical Systems. Mathematical Surveys and Monographs 41. American Mathematical Society, Providence, Rhode Island, U.S.A., 1995.
- [119] J.M.J. Travis and C. Dytham, Habitat persistence, habitat availability and the evolution of dispersal, *Proc. Roy. Soc. Lond. B* **266** (1999) 723-728.
- [120] J.M.J. Travis and D.R. French, Dispersal functions and spatial models: expanding our dispersal toolbox, *Ecology Letters* **3** (2000) 163-165.
- [121] P. Turchin, Qualitative Analysis of Movement, Sinauer Press, Sunderland, MA, 1998.
- [122] H.F. Weinberger, An example of blowup produced by equal diffusions, *J. Diff. Eqs.* **154** (1999) 225-237.
- [123] E. Yanagida, Existence of stable stationary solutions of scalar reaction-diffusion equations in thin tubular domains, *Appl. Anal.* **36** (1990) 171-188.