

Chapter 8

Persistence, Competition, and Evolution

King-Yeung Lam and Yuan Lou

Abstract In this chapter we discuss some reaction–diffusion models for single and multiple populations in spatially heterogeneous environments and advective environments. Our goal is to illustrate some interesting, and perhaps surprising, effects of spatial heterogeneity and diffusion on the population dynamics. Specific topics include the logistic model, linear eigenvalue problem with indefinite weight, Lotka–Volterra competition models, reaction–diffusion models in advective environments, and the evolution of dispersal. We will introduce some basic tools for reaction–diffusion equations such as the super-sub solution method, the variational principle for principal eigenvalues, Lyapunov functionals, comparison principles for parabolic equations and systems, etc. Some recent developments will be discussed. In addition, problems with various difficulties ranging from elementary exercises to open research questions will be presented.

8.1 Introduction

Understanding the population dynamics of a single and multiple interacting species, which disperse in spatially heterogeneous environments, is an important topic in spatial ecology. Reaction–diffusion models have played a major role in the modeling

K.-Y. Lam

Department of Mathematics, The Ohio State University, Columbus, OH, USA

e-mail: lam.184@math.ohio-state.edu

Y. Lou (✉)

Institute for Mathematical Sciences, Renmin University of China, Beijing, People's Republic of China

Department of Mathematics, The Ohio State University, Columbus, OH, USA

e-mail: lou@math.ohio-state.edu

© Springer Nature Switzerland AG 2019

A. Bianchi et al. (eds.), *The Dynamics of Biological Systems*, Mathematics of Planet Earth 4, https://doi.org/10.1007/978-3-030-22583-4_8

and understanding of population dynamics in heterogeneous environments [8]. In this chapter we will restrict ourselves to a few selected topics in spatial ecology and discuss some reaction–diffusion models for the persistence of a single species, the competition of two populations, and the evolution of dispersal in spatially heterogeneous environments and advective environments.

Our first goal is to illustrate some interesting, and perhaps surprising, effects of spatial heterogeneity on the population dynamics. In Sect. 8.2 we will discuss the logistic model, including the derivation of the continuous-time logistic model from the discrete-time counterpart, a linear eigenvalue problem with indefinite weight, and the maximization of the biomass of a single species at equilibrium. In Sect. 8.3 we will discuss the classical two-species Lotka–Volterra competition models, in both homogeneous and heterogeneous environments. Section 8.4 is devoted to the evolution of random dispersal in heterogeneous environments, where it is shown that the slower dispersal rate will be selected. In Sect. 8.5 we will study the persistence of a single species and the competition of two populations in advective environments. We show that the faster dispersal rate could be selected in advective environments.

Another goal of this chapter is to introduce some basic mathematical tools for reaction–diffusion equations and systems. They include the super-solution and sub-solution method, the variational principle for principal eigenvalues, Lyapunov functionals, linear stability analysis, and the comparison principles for parabolic equations and systems. These materials will be covered in Sects. 8.2–8.5.

Beyond our two main goals, in Sect. 8.6 we will discuss some recent works and point interested readers to the related literature. In addition, some mathematical problems with various degrees of difficulties, ranging from elementary exercises to open research questions, will also be presented.

8.2 Diffusion Models for a Single Species

The dynamics of reaction–diffusion models for a single species are not only of independent interest, they are also building blocks in studying the dynamics of multiple interacting species, especially issues concerning the invasions of exotic species. In this section we focus on logistic type population models with diffusion. Many reaction–diffusion models for a single population are of the form

$$\begin{cases} u_t = d\Delta u + uf(x, u) & \text{in } \Omega \times (0, \infty), \\ \nabla u \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x) & \text{in } \Omega. \end{cases} \quad (8.1)$$

Here $u(x, t)$ is the population density, $d > 0$ is the diffusion coefficient, $f(x, u)$ represents the growth rate of the population and is differentiable in both x and u . The habitat Ω is a bounded domain in Euclidean space \mathbb{R}^N with smooth boundary $\partial\Omega$, and n is the outward unit normal vector on $\partial\Omega$. The zero Neumann boundary

condition means that there is no net movement across the boundary. The initial condition u_0 is assumed to be non-negative and not identically zero.

We present two preliminary results on the dynamics of (8.1), adapted from [8].

Proposition 8.1 *Suppose that $f(x, u) \leq g_0(x)$ for some function g which is Hölder continuous in $\bar{\Omega}$. If the principal eigenvalue, denoted as σ_1 , of*

$$\begin{cases} d\Delta\psi + g_0\psi + \sigma\psi = 0 & \text{in } \Omega, \\ \nabla\psi \cdot n = 0 & \text{on } \partial\Omega \end{cases} \quad (8.2)$$

is positive, then (8.1) has no positive steady state and all non-negative solutions of (8.1) decay exponentially to zero as $t \rightarrow \infty$.

Proof Let $\psi(x) > 0$ be an eigenfunction to σ_1 . Set $\bar{u}(x, t) = Ce^{-\sigma_1 t}\psi(x)$. Then \bar{u} satisfies

$$\bar{u}_t - d\Delta\bar{u} - \bar{u}f(x, \bar{u}) = g_0(x)\bar{u} - \bar{u}f(x, \bar{u}) \geq 0.$$

Choose $C > 0$ large such that $u(x, 0) \leq \bar{u}(x, 0)$. By the comparison principle for parabolic equations [48], $u(x, t) \leq \bar{u}(x, t) \leq C\|\psi\|_\infty e^{-\sigma_1 t}$. ■

Proposition 8.2 *Suppose that there exists some $C > 0$ such that $f(x, u) < 0$ for $u \geq C$. If the principal eigenvalue, denoted as σ_1 , of*

$$\begin{cases} d\Delta\psi + f(x, 0)\psi + \sigma\psi = 0 & \text{in } \Omega, \\ \nabla\psi \cdot n = 0 & \text{on } \partial\Omega \end{cases} \quad (8.3)$$

is negative, then (8.1) has at least one positive steady state.

Proof Consider the steady state problem of (8.1), i.e.,

$$\begin{cases} d\Delta u + uf(x, u) = 0 & \text{in } \Omega, \\ \nabla u \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.4)$$

Write $f(x, u) = f(x, 0) + f_1(x, u)$ so that $f_1(x, u) = O(u)$ for small u . Let $\psi > 0$ be an eigenfunction to σ_1 . For sufficiently small $\epsilon > 0$,

$$d\Delta(\epsilon\psi) + (\epsilon\psi)f(x, \epsilon\psi) = \epsilon\psi[-\sigma_1 + f_1(x, \epsilon\psi)] > 0,$$

i.e., $\underline{u} = \epsilon\psi$ is a sub-solution of (8.4). Since $\bar{u} = C$ is a super-solution of (8.4) and for small ϵ we have $\bar{u} \geq \underline{u}$, by the super-solution and sub-solution method [48] we see that (8.1) has a positive steady state $u(x)$ such that $\underline{u}(x) \leq u(x) \leq \bar{u}(x)$ for $x \in \Omega$. ■

A classic example of $f(x, u)$ in (8.1) is the logistic growth model:

$$f(x, u) = r(x) \left(1 - \frac{u}{K(x)} \right), \quad (8.5)$$

where $r(x), K(x) \in C(\overline{\Omega})$ are positive functions.

Exercise Consider problem (8.1). If $f(x, u) < g_0(x)$ for $x \in \overline{\Omega}$ and $u > 0$, and that the principal eigenvalue σ_1 of (8.2) is non-negative, then all non-negative solutions of (8.1) decay to zero as $t \rightarrow \infty$ (albeit not necessarily exponentially).

8.2.1 Logistic Model: From Discrete to Continuous

In this subsection we present a derivation of the logistic model from discrete-time models. The continuous-time logistic ODE model (Verhulst, 1838) is given by

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right), \quad t > 0. \quad (8.6)$$

Here r and K are two positive constants: r is the intrinsic growth rate (1/time), and K is the carrying capacity (same unit as population size).

One way to derive (8.6) is to start with discrete-time models. Let N_t denote the population size at time $t = 0, 1, 2, \dots$. The general model is usually of the form $N_{t+1} = f(N_t)$, where f is the growth function.

The geometric growth model is given by $N_{t+1} = RN_t$, where the biological meaning of parameter R can be seen from

$$R = \frac{N_{t+1}}{N_t} = \frac{\text{numbers of offsprings}}{\text{numbers of parents}}. \quad (8.7)$$

For the geometric model, $N_t/N_{t+1} = 1/R$, i.e., the parent vs offspring ratio is constant. The next level of models in terms of modeling complexity is

$$\frac{N_t}{N_{t+1}} = \text{a linear function of } N_t. \quad (8.8)$$

When $N_t \approx 0$ (N_t is rare), we expect the geometric model to be a good approximation, so that $\frac{N_t}{N_{t+1}} = \frac{1}{R}$. When $N_t \approx K$ (N_t is near the carrying capacity), we expect the population to level off, so that $\frac{N_t}{N_{t+1}} = 1$. Hence,

$$\frac{N_t}{N_{t+1}} = \text{the line passing through } \left(0, \frac{1}{R} \right) \text{ and } (K, 1) \quad (8.9)$$

$$= \frac{1}{R} + \frac{N_t}{K} \left(1 - \frac{1}{R} \right). \quad (8.10)$$

After simplification, one obtains the Beverton–Holt model

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K}N_t}, \quad t = 0, 1, 2, \dots, \quad (8.11)$$

where the constant K is the population size at which the parent vs offspring ratio is equal to one.

In the derivation above, the duration of each generation is 1. Now, if we let the duration of each generation to be some small constant $h > 0$, then over the (short) time interval h , the population multiplies by a factor of R^h , and thus we may modify (8.11) as

$$N_{t+h} = \frac{R^h N_t}{1 + \frac{R^h-1}{K}N_t}, \quad h > 0.$$

We can rewrite the above as

$$\frac{N_{t+h} - N_t}{h} = \frac{1}{h} \left(\frac{R^h N_t}{1 + \frac{R^h-1}{K}N_t} - N_t \right) \quad (8.12)$$

$$= \frac{1}{h} \cdot \frac{(R^h-1)N_t - \frac{R^h-1}{K}N_t^2}{1 + \frac{R^h-1}{K}N_t} \quad (8.13)$$

$$= \frac{R^h-1}{h} \cdot \frac{(1 - \frac{N_t}{K})N_t}{1 + \frac{R^h-1}{K}N_t}. \quad (8.14)$$

Letting $h \rightarrow 0$, we obtain the continuous-time logistic model, which relates the instantaneous rate of change of population at time t to the population at time t :

$$\frac{d}{dt}N_t = rN_t \left(1 - \frac{N_t}{K}\right), \quad t > 0, \quad (8.15)$$

where $r = \log R$.

Exercise Use the discrete-time two-species model

$$\begin{cases} N_1(t+1) = \frac{R_1 N_1(t)}{1 + \alpha_1 N_1(t) + \beta_1 N_2(t)} \\ N_2(t+1) = \frac{R_2 N_2(t)}{1 + \alpha_2 N_1(t) + \beta_2 N_2(t)} \end{cases} \quad (8.16)$$

to derive the corresponding continuous-time model

$$\begin{cases} \frac{dN_1}{dt} = r_1 N_1 (1 - C_1 N_1 - D_1 N_2) \\ \frac{dN_2}{dt} = r_2 N_2 (1 - C_2 N_1 - D_2 N_2) \end{cases}. \quad (8.17)$$

8.2.2 Logistic PDE Model

We consider a special case of the reaction–diffusion model (8.1) with logistic nonlinearity (8.5) and heterogeneous coefficients $r(x) = m(x)$ and $K(x) = m(x)$:

$$\begin{cases} u_t = d\Delta u + u(m(x) - u) & \text{in } \Omega \times (0, \infty), \\ \nabla u \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x) & \text{in } \Omega. \end{cases} \quad (8.18)$$

Another example is to add spatially heterogeneous harvesting effect to the logistic nonlinearity $ru(1 - \frac{u}{K})$ with constant coefficients r, K , so that the growth function of the population is given by

$$r(1 - \frac{u}{K}) - h(x) = r - h(x) - \frac{r}{K}u;$$

i.e., $m(x) = r - h(x)$ in this example, where $h(x)$ is the harvesting rate.

By Propositions 8.1 and 8.2, the problem of determining the existence and non-existence of positive steady state is connected with the sign of the principal eigenvalue σ_1 (i.e., the unique eigenvalue possessing a positive eigenfunction) of

$$\begin{cases} d\Delta\psi + m(x)\psi + \sigma\psi = 0 & \text{in } \Omega, \\ \nabla\psi \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.19)$$

By the variational characterization of elliptic eigenvalues, we have

$$\sigma_1 = \inf_{\psi \in H^1(\Omega), \psi \neq 0} \frac{\int_{\Omega} [d|\nabla\psi|^2 - m(x)\psi^2] dx}{\int_{\Omega} \psi^2 dx},$$

one can deduce the following result. (See, e.g., Proposition 4.4 of [47].)

Lemma 8.1 *Suppose that m is non-constant. Then σ_1 is a strictly monotone increasing function of d . Moreover,*

$$\lim_{d \rightarrow 0} \sigma_1 = -\max_{\bar{\Omega}} m, \quad (8.20)$$

$$\lim_{d \rightarrow \infty} \sigma_1 = -\frac{1}{|\Omega|} \int_{\Omega} m. \quad (8.21)$$

Furthermore, the mapping $d \mapsto \sigma_1$ is concave.

Exercise Prove Lemma 8.1.

By Lemma 8.1, we see that if $\int_{\Omega} m \geq 0$, then $\sigma_1 < 0$ for any $d > 0$. Hence, by Proposition 8.2, (8.18) has at least one positive steady state for any $d > 0$. If $\int_{\Omega} m < 0$ and $\max_{\bar{\Omega}} m > 0$, by Lemma 8.1 there exists a unique $d^* \in (0, +\infty)$ such that $\sigma_1 < 0$ for $d < d^*$; and $\sigma_1 > 0$ when $d > d^*$. Again by Propositions 8.1 and 8.2

we see that if $d > d^*$, then every non-negative solution of (8.18) converges to zero; if $d < d^*$, then (8.18) has at least one positive steady state. These discussions lead to the following result. (See, e.g., Proposition 3.3 of [8] or Theorem 4.1 of [47].)

Theorem 8.1 *Suppose that m is non-constant, positive somewhere in Ω and Hölder continuous in $\bar{\Omega}$.*

- (i) *If $\int_{\Omega} m \geq 0$, then for $d > 0$, (8.18) has a unique positive steady state and it is globally asymptotically stable among non-negative, not identically zero, continuous initial data.*
- (ii) *If $\int_{\Omega} m < 0$ and $\max_{\bar{\Omega}} m > 0$, then there exists some $d^* > 0$ such that if $d < d^*$, (8.18) has a unique positive steady state which is globally asymptotically stable; if $d > d^*$, all non-negative solutions of (8.18) converge to zero as $t \rightarrow \infty$.*

The existence and non-existence results are addressed by the discussion preceding Theorem 8.1. We now sketch the proof of the uniqueness of the positive steady state, whenever it exists. The proof of the uniqueness of positive steady state is based upon the super-solution and sub-solution method. For this purpose, we consider the steady state problem of (8.18):

$$\begin{cases} d\Delta u + u(m(x) - u) = 0 & \text{in } \Omega, \\ \nabla u \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.22)$$

We say that $\bar{u} \in C^2(\bar{\Omega})$ is a super-solution of (8.22) if it satisfies

$$\begin{cases} d\Delta \bar{u} + \bar{u}(m - \bar{u}) \leq 0 & \text{in } \Omega, \\ \nabla \bar{u} \cdot n \geq 0 & \text{on } \partial\Omega. \end{cases} \quad (8.23)$$

We can similarly define the sub-solution of (8.22) by reversing the inequalities. The following comparison principle is well known. (See, e.g., [50, 51].)

Theorem 8.2 *Suppose that (8.22) has a pair of super-solution and sub-solution such that $\underline{u} \leq \bar{u}$ in Ω . Then (8.18) has a minimal steady state u_m and a maximal steady state u_M , such that (i) $\underline{u} \leq u_m \leq u_M \leq \bar{u}$ in Ω and (ii) for each solution v of (8.22) satisfying $\underline{u} \leq v \leq \bar{u}$ in Ω , then it must hold that $u_m \leq v \leq u_M$ in Ω .*

We proceed to sketch the proof of the uniqueness result, as claimed in Theorem 8.1. Suppose, for contradiction, that there are two distinct positive steady states when $\sigma_1 < 0$, denoted by u_i , $i = 1, 2$. Since Eq. (8.22) has arbitrary large super-solutions (e.g., any constant C larger than the maximum of function m) and arbitrary small positive sub-solutions, e.g., $\epsilon\psi$, where $\epsilon > 0$ is small and $\psi > 0$ is an eigenfunction of (8.19), we can choose ϵ and C such that $\epsilon\psi \leq u_1, u_2 \leq C$. Hence, by Theorem 8.2, there exists a minimal solution and a maximal solution, denoted by u_m and u_M , respectively, satisfying $u_m \leq u_1, u_2 \leq u_M$ in Ω . Since $u_1 \not\equiv u_2$, we have $u_M \geq, \not\equiv u_m$. Multiplying the equation of u_m by u_M , the equation of u_M by u_m , subtracting and integrating the result in Ω , we see that

$$\int_{\Omega} u_m u_M (u_M - u_m) = 0,$$

which is a contradiction to the fact that $u_M \geq u_m$ and $u_M \not\equiv u_m$. Hence it is impossible for Eq. (8.22) to have two distinct positive solutions u_1, u_2 . This proves the uniqueness result.

8.2.3 An Eigenvalue Problem with Indefinite Weight

Recall that by Theorem 8.1, there exists a critical diffusion rate $d^* > 0$ so that the population as modeled by (8.18) persists if and only if $d \in (0, d^*)$. In this subsection, we will give a characterization of $1/d^*$ via the following linear eigenvalue problem with indefinite weight:

$$\begin{cases} \Delta\varphi + \lambda m(x)\varphi = 0 & \text{in } \Omega, \\ \nabla\varphi \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.24)$$

Problem (8.24) and its variants have been extensively investigated for the last two decades, since they play crucial roles in studying nonlinear models from population biology.

We call λ a *principal eigenvalue* of (8.24) if λ has a positive eigenfunction $\varphi \in H^1(\Omega)$. Clearly, $\lambda = 0$ is a principal eigenvalue of (8.24) with positive constants as its eigenfunctions. Of particular importance is the existence of *positive* principal eigenvalues.

If (8.24) has a positive eigenvalue, denoted by $\lambda_1(m)$, with corresponding positive eigenfunction φ_1 , integrating the equation of φ_1 we have

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

which implies that $m(x)$ changes sign in Ω , i.e., that both Ω_+ and Ω_- have positive Lebesgue measure, where

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

Dividing the equation of φ_1 by φ_1 and then integrating in Ω , we find

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

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 [3]:

Theorem 8.3 *The eigenvalue problem (8.24) 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 (8.24), and is given by*

$$\lambda_1(m) = \inf_{\varphi \in \mathcal{S}(m)} \frac{\int_{\Omega} |\nabla \varphi|^2}{\int_{\Omega} m(x) \varphi^2}, \quad (8.25)$$

where

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

By Theorem 8.3, one may observe that d^* in Theorem 8.1 is characterized by $d^* = 1/\lambda_1(m)$. In fact, the following well-known and useful result holds.

Proposition 8.3 *Suppose that (A1) holds. Let $d^* := 1/\lambda_1(m)$, where $\lambda_1(m)$ is the principal eigenvalue of (8.24). Then $d^* > 0$. Furthermore, let $\sigma_1(d, m)$ be the principal eigenvalue of (8.19). Then*

- (i) $\sigma_1(d, m) < 0$ when $0 < d < d^*$;
- (ii) $\sigma_1(d, m) = 0$ when $d = d^*$;
- (iii) $\sigma_1(d, m) > 0$ when $d > d^*$.

Exercise Prove Proposition 8.3 using the facts that (i) $\sigma_1(d, m)$ is concave in d ; and that (ii) $\sigma_1(d, m) = 0$ if and only if $d = d^*$.

Consider the scenario where there is limited total resource in a bounded domain Ω . What is the optimal way to distribute the resource, so as to maximize the survivorship of the population?

Given $\mu \in (0, 1)$ and $\kappa > 0$, we define

$$\mathcal{M} = \left\{ m \in L^{\infty}(\Omega) : m(x) \text{ satisfies (A1) and (A2)} \right\}, \quad (8.26)$$

where (A2) is the constraint on the resource distribution:

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

Roughly speaking, (A2) says that the habitat is unfavorable on average. Also, the resource distribution is bounded from above by κ , and below by -1 . We aim to determine the optimal arrangement of the resource so as to maximize d^* , which is equivalent to minimizing $\lambda_1(m)$. Therefore, we set

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

The existence and the profile of global minimizers of $\lambda_1(m)$ in \mathcal{M} with Dirichlet boundary condition was first addressed in [4]. For Neumann boundary conditions, we have the following result [40]:

Theorem 8.4 *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 $m(x) = \kappa \chi_E - \chi_{\Omega \setminus E}$ a.e. in Ω for some measurable set $E \subset \Omega$.*

Proof We only prove the second part of Theorem 8.4. Suppose that $m \in \mathcal{M}$ and $\lambda_1(m) = \lambda_{inf}$. Let φ be the eigenfunction of $\lambda_1(m)$ with the normalization $\sup_{\Omega} \varphi = 1$. For every $\eta \geq 0$, set $E_{\eta} := \{x \in \Omega : \varphi(x) > \eta\}$. Note that $|E_{\eta}|$, the Lebesgue measure of E_{η} , is a monotone decreasing function of η , $|E_0| = |\Omega|$ and $|E_{\eta}| = 0$ for $\eta > 1$.

Case 1. There exists some $\eta^* > 0$ such that

$$-\mu|\Omega| = \kappa|E_{\eta^*}| - |\Omega \setminus E_{\eta^*}|, \quad (8.27)$$

i.e., $|E_{\eta^*}| = (1 - \mu)|\Omega|/(1 + \kappa) > 0$. For this case, define $E^* := E_{\eta^*}$.

Case 2. There is no $\eta > 0$ such that $|E_{\eta}| = (1 - \mu)|\Omega|/(1 + \kappa)$. For this case, there exists some $\eta^* > 0$ such that $\lim_{\eta \rightarrow \eta^*+} |E_{\eta}| < (1 - \mu)|\Omega|/(1 + \kappa) \leq \lim_{\eta \rightarrow \eta^*-} |E_{\eta}|$. Therefore, there exists some measurable set E^* such that $E_{\eta^*} \subset E^* \subset \{x \in \Omega : \varphi(x) \geq \eta^*\}$ and $|E^*| = (1 - \mu)|\Omega|/(1 + \kappa)$.

Define $m^*(x) = \kappa \chi_{E^*} - \chi_{\Omega \setminus E^*}$. Equation (8.27) ensures that $\int_{\Omega} m^* = -\mu|\Omega|$. Hence, we have $m^* \in \mathcal{M}$, which implies that $\lambda_{inf} \leq \lambda_1(m^*)$.

We claim that $m(x) = m^*(x)$ a.e. in Ω . To establish our assertion, we first have

$$\begin{aligned} \int_{\Omega} (m^* - m)\varphi^2 &= \int_{E^*} (\kappa - m)\varphi^2 - \int_{\Omega \setminus E^*} (1 + m)\varphi^2 \\ &\geq (\eta^*)^2 \int_{E^*} (\kappa - m) - (\eta^*)^2 \int_{\Omega \setminus E^*} (1 + m) \\ &\geq 0, \end{aligned} \quad (8.28)$$

where the last inequality follows from (8.27) and $\int_{\Omega} m \leq -\mu|\Omega|$. Since $\int_{\Omega} m\varphi^2 > 0$, we have $\int_{\Omega} m^*\varphi^2 > 0$. Hence, $\varphi \in \mathcal{S}(m^*)$. Therefore, applying (8.25) we have

$$\lambda_1(m^*) \leq \frac{\int_{\Omega} |\nabla \varphi|^2}{\int_{\Omega} m^*\varphi^2} \leq \frac{\int_{\Omega} |\nabla \varphi|^2}{\int_{\Omega} m\varphi^2} = \lambda_1(m). \quad (8.29)$$

Since $\lambda_1(m) = \lambda_{inf} \leq \lambda_1(m^*)$, equalities must hold in (8.29). In particular, $\lambda_1(m^*) = \lambda_1(m)$ and

$$\lambda_1(m^*) = \frac{\int_{\Omega} |\nabla \varphi|^2}{\int_{\Omega} m^* \varphi^2}.$$

Therefore, from Theorem 8.3 we see that φ is also an eigenfunction of $\lambda_1(m^*)$, and it satisfies

$$\Delta \varphi + \lambda_1(m^*) m^* \varphi = 0 \quad \text{in } \Omega, \quad \nabla \varphi \cdot n = 0 \quad \text{on } \partial \Omega$$

in $W^{2,q}(\Omega)$ for every $q > 1$. Since $\varphi > 0$ in $\overline{\Omega}$, we have

$$m^* = -\frac{\Delta \varphi}{\lambda_1(m^*) \varphi} = -\frac{\Delta \varphi}{\lambda_1(m) \varphi} = m$$

a.e. in Ω . This completes the proof of Theorem 8.4. ■

Remark 8.1 Theorem 8.4 implies that the global minimizers of $\lambda_1(m)$ in \mathcal{M} are of “bang-bang” type, i.e., when the habitat is unfavorable on average, the survivorship of the population is maximized when conservational effort and resources are concentrated within a protection zone, even when the rest of the habitat is in poor condition. The original proof of Theorem 8.4 in [40] requires the additional assumption that E_{η} is continuous in η . The modified proof presented here does not make use of this assumption; see also [46]. We refer to [30] for the case when Ω is a rectangular domain in \mathbb{R}^2 .

8.2.4 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 only out of curiosity, but also useful in studying the invasion of species.

Consider the steady state problem of the diffusive logistic model:

$$\begin{cases} d\Delta \theta + \theta[m(x) - \theta] = 0 & \text{in } \Omega, \\ \theta > 0 & \text{in } \Omega, \\ \nabla \theta \cdot n = 0 & \text{on } \partial \Omega, \end{cases} \quad (8.30)$$

where the diffusion rate d is assumed to be a positive constant, $m(x)$ is the habitat quality at location x , and the function $\theta = \theta(x, d)$ represents the density of the species at location x . For the sake of clarity we posit

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

For solutions of (8.30), the following results are well known.

Theorem 8.5 *Suppose that assumption (A3) holds.*

- (i) For $d > 0$, (8.30) has a unique positive solution $\theta(x, d)$ such that $\theta \in W^{2,p}(\Omega)$ for every $p \geq 1$.
- (ii) As $d \rightarrow 0+$, $\theta(x, d) \rightarrow m_+(x)$ in $L^p(\Omega)$ for every $p \geq 1$, where $m_+(x) = \sup\{m(x), 0\}$; as $d \rightarrow \infty$, $\theta(x, d) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} m(x) dx$ in $W^{2,p}(\Omega)$ for every $p \geq 1$.
- (iii) If $m(x)$ is Hölder continuous in $\bar{\Omega}$, then $\theta \in C^2(\bar{\Omega})$. Moreover, $\theta(x, d) \rightarrow m_+(x)$ in $L^\infty(\Omega)$ as $d \rightarrow 0$, and $\theta(x, d) \rightarrow \frac{1}{|\Omega|} \int_{\Omega} m(x) dx$ in $C^2(\bar{\Omega})$ as $d \rightarrow \infty$.

Proof We only illustrate that if $m \in C(\bar{\Omega})$ and $m > 0$, then $\theta(x, d) \rightarrow m(x)$ in $L^\infty(\Omega)$ as $d \rightarrow 0$. Given any $\epsilon > 0$, choose $\bar{u} \in C^2(\bar{\Omega})$ such that $\nabla \bar{u} \cdot n = 0$ on $\partial\Omega$, and

$$m + \frac{\epsilon}{2} \leq \bar{u}(x) \leq m + \epsilon \quad \text{for } x \in \bar{\Omega}.$$

Then,

$$d\Delta\bar{u} + \bar{u}(m - \bar{u}) \leq d\Delta\bar{u} + \bar{u}(m - m - \frac{\epsilon}{2}) = d\Delta\bar{u} - \frac{\epsilon}{2}\bar{u} \leq d\Delta\bar{u} - \frac{\epsilon^2}{4} \leq 0$$

in Ω , where the last inequality holds if d is chosen sufficiently small. Hence, \bar{u} is a super-solution of (8.30). Similarly, choose $\underline{u} \in C^2(\bar{\Omega})$ such that $m - \epsilon \leq \underline{u}(x) \leq m - \frac{\epsilon}{2}$ for any $x \in \bar{\Omega}$, and $\nabla \underline{u} \cdot n = 0$ on $\partial\Omega$. One can proceed similarly to show that \underline{u} is a sub-solution for small d . Hence by the super-solution and sub-solution method [48],

$$m - \epsilon \leq \underline{u}(x) \leq \liminf_{d \rightarrow 0+} \theta(x, d) \leq \limsup_{d \rightarrow 0+} \theta(x, d) \leq \bar{u}(x) \leq m + \epsilon$$

holds in Ω . Finally, the conclusion follows from letting $\epsilon \rightarrow 0+$. ■

Exercise If $\Omega = (0, 1)$ and $m_x > 0$ in $[0, 1]$, show that $\theta_x > 0$ in $(0, 1)$.

Exercise Suppose that m is non-constant and $m \in C^1(\bar{\Omega})$. Show that $\int_{\Omega} |\nabla\theta|^2 dx$ is a strictly decreasing function of d and for any $d > 0$,

$$\int_{\Omega} |\nabla\theta|^2 dx < \int_{\Omega} |\nabla m|^2 dx. \tag{8.31}$$

Since $|\nabla\theta|$ measures the steepness of the population density distribution, we may envision $\int_{\Omega} |\nabla\theta|^2$ as the average steepness of the population distribution. Similarly, $\int_{\Omega} |\nabla m|^2$ measures the average steepness of the environmental gradient. This result suggests that the population distribution becomes flatter in average if we increase the

dispersal rate. In particular, (8.31) shows that the population distribution is always less steep than the environmental gradient, at least in some average sense.

Open Problem Is $\int_{\Omega}(\theta - \bar{\theta})^2 dx$ monotone decreasing in d , where $\bar{\theta} = |\Omega|^{-1} \int_{\Omega} \theta$? Are $\max_{\bar{\Omega}} \theta$ and $\min_{\bar{\Omega}} \theta$ also monotone in d ? Is $\|\theta\|_{L^p}$ monotone decreasing in d for large p ?

Remark 8.2 For a fixed $m \in C^\alpha(\bar{\Omega})$ where $\alpha \in (0, 1)$, is it true that there exists some positive constant C , which is independent of d , such that $\|\theta(\cdot, d)\|_{C^\alpha(\bar{\Omega})} \leq C$? Averill et al. [1] showed that if $m \in C^2(\bar{\Omega})$ and $m \geq 0$ in $\bar{\Omega}$, then $\theta_d \rightarrow m$ in $W^{1,2}(\Omega)$.

In view of part (ii) of Theorem 8.5, it is natural to introduce the function

$$F(d) := \begin{cases} \int_{\Omega} m_+(x) dx, & d = 0, \\ \int_{\Omega} \theta(x, d) dx, & d > 0, \\ \int_{\Omega} m(x) dx, & d = \infty, \end{cases} \quad (8.32)$$

which can be interpreted as the total population size of the species. By assumption (A2) and part (ii) of Theorem 8.5, 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 $\theta(x, d) \equiv \bar{m}$ is the unique positive solution of (8.30) for every $d > 0$. In this case, the total population size of the species is given by $F(d) = |\Omega|\bar{m}$, which is independent of d . However, if the spatial environment is heterogeneous, i.e., $m(x)$ is a non-constant function, the story changes dramatically:

Theorem 8.6 ([37]) *Suppose that assumption (A1) holds.*

- (i) $F(d) > F(\infty)$ for every $d \in (0, \infty)$;
- (ii) If $m(x) \geq 0$ in Ω , then for $d \in (0, \infty)$, $F(d)$ satisfies

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

Proof Divide the equation of θ_x by θ ,

$$d \frac{\Delta \theta}{\theta} + m - \theta = 0.$$

Integrating the above in Ω , we have

$$\int_{\Omega} \theta - \int_{\Omega} m = d \int_{\Omega} \frac{|\nabla \theta|^2}{\theta^2} > 0;$$

i.e., $\int_{\Omega} \theta > \int_{\Omega} m$. The rest of the proof follows from the limiting behaviors of θ as $d \rightarrow 0$ and $d \rightarrow \infty$, as stated in Theorem 8.5. ■

Remark 8.3 Part (i) of Theorem 8.6 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 $F = F(d, m)$ instead of $F(d)$ to indicate the dependence of F on the function m . Part (a) implies that $F(d, m) > F(d, \bar{m})$ for every $d > 0$. In other words, given any $d > 0$ and any function g with $\int_{\Omega} g(x) dx = 0$ and $g \not\equiv 0$, we have $F(d, \bar{m} + \lambda g) > F(d, \bar{m})$ for every $\lambda \neq 0$. Hence, with the dispersal rate being fixed, the population size $F(d, \bar{m} + \lambda g)$, as a function of $\lambda \in \mathbb{R}$, attains a strict global minimum at $\lambda = 0$. We refer to [14] and the references therein for more recent developments.

Exercise Compute $F(d, \bar{m} + \tau g)$ for small τ . What conclusion can you draw from it?

Part (ii) of Theorem 8.6 implies that when $m(x)$ is non-negative, the total population size is minimized at $d = 0$ and $d = \infty$, and maximized at some intermediate value d^* . The value of d^* is determined by the habitat Ω and $m(x)$.

It will be of interest to understand the precise shape of $F(d)$ due to its crucial role in the invasion of species. A natural conjecture is that $F(d)$ has a unique local maximum (and thus it must be the global maximum) in $(0, +\infty)$. However, this conjecture is false even for the case when $m(x)$ is a perturbation of positive constants.

Theorem 8.7 ([36]) *There exists a smooth function $g(x)$ with $\int_{\Omega} g = 0$ such that if $m = 1 + \epsilon g$, then for sufficiently small non-zero constant ϵ , the total population $F(d, m) = \int_{\Omega} \theta(x, d) dx$, as a function of d , has at least two local maxima and one local minimum in $(0, \infty)$.*

An important issue in conservation biology is to determine how resource allocation affects the population dynamics of species. As the population abundance is often a good measurement of conservation effort, it is of interest to know how resource allocation affects the total population size of species.

Assume that m is non-negative and not identically zero. Let $\theta(x)$ denote the unique positive steady state of (8.18). Given any $\delta \in (0, 1)$, define

$$U = \left\{ m \in L^{\infty}(\Omega) : 0 \leq m \leq 1, \int_{\Omega} m(x) dx = \delta |\Omega| \right\}$$

and

$$J(m) = \int_{\Omega} \theta(x) dx. \quad (8.33)$$

It is shown in [15] that there exists some $m^* \in U$ such that

$$J(m^*) = \max_{m \in U} J(m).$$

It seems that the shape of the optimal control m^* depends upon the magnitude of parameter δ . For instance, numerical simulations indicate that for rectangular domains, the optimal control m^* is concentrated at one of the corners of the rectangle when δ is small; if δ is large, the optimal control concentrates at a boundary edge of the rectangle. We refer to [15] for further discussions.

Recently Bai et al. [2] proved the following conjecture of W.-M. Ni:

Theorem 8.8 *Suppose that Ω is an interval in \mathbb{R}^1 . Then*

$$\frac{\int_{\Omega} \theta(x) dx}{\int_{\Omega} m(x) dx} < 3. \quad (8.34)$$

Furthermore, 3 is the optimal constant.

Proof Without loss of generality assume that $\Omega = (0, 1)$. For simplicity we only prove (8.34) when $m_x \geq 0$. For this case, we have $\theta_x \geq 0$ (see exercise after Theorem 8.5). Multiplying (8.30), the equation of θ , by θ_x and integrating the result in $(0, x)$ we obtain

$$\frac{d}{dx} \theta_x^2(x) = \int_0^x \theta_x \theta (\theta - m) dx \leq \int_0^x \theta_x \theta^2 = \frac{1}{3} [\theta^3(x) - \theta^3(0)] < \frac{1}{3} \theta^3(x).$$

Hence,

$$d\theta_x^2(x) < \frac{2}{3} \theta^3(x), \quad x \in [0, 1]. \quad (8.35)$$

Next, dividing the equation of θ by θ we have

$$d \frac{\theta_{xx}}{\theta} + m - \theta = 0.$$

Integrating the above equation in $(0, 1)$ we have

$$\int_0^1 \theta dx - \int_0^1 m dx = d \int_0^1 \frac{\theta_x^2}{\theta^2} dx < \frac{2}{3} \int_0^1 \theta dx,$$

where we applied (8.35) in the last inequality. Hence, (8.34) holds. \blacksquare

Open Question (W.-M. Ni) Show that there exists some positive constant $C = C(N) > 1$, which only depends on the spatial dimension $N \geq 2$, such that for any positive solution θ ,

$$\int_{\Omega} \theta(x) dx < C(N) \int_{\Omega} m(x) dx. \quad (8.36)$$

Exercise Let (u_1, u_2) be a positive solution of the two patch model

$$\begin{cases} d(u_2 - u_1) + u_1(m_1 - u_1) = 0, \\ d(u_1 - u_2) + u_2(m_2 - u_2) = 0, \end{cases} \quad (8.37)$$

where $m_1, m_2 > 0$. Show that

$$1 \leq \frac{u_1 + u_2}{m_1 + m_2} < 2.$$

8.3 Lotka–Volterra Competition Models

For the last two decades there has been tremendous interest, from both mathematicians and ecologists, in two-species Lotka–Volterra competition models in spatially heterogeneous environments; see [5–7, 9–11, 21–25, 27–29, 34, 47] and the references therein. Our main goal here is to illustrate some differences between the dynamics of Lotka–Volterra competition models in homogeneous environments and that in heterogeneous environments.

8.3.1 Homogeneous Environments

We first consider the Lotka–Volterra competition–diffusion system in homogeneous environments:

$$\begin{cases} u_t = d_1 \Delta u + u(a_1 - b_1 u - c_1 v) & \text{in } \Omega \times (0, \infty), \\ v_t = d_2 \Delta v + v(a_2 - b_2 u - c_2 v) & \text{in } \Omega \times (0, \infty), \\ \nabla u \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x) & \text{in } \Omega. \end{cases} \quad (8.38)$$

Here u, v represent the population densities of two competing species; d_1, d_2 are their diffusion rates; a_1 and a_2 are their intrinsic growth rates; b_1 and c_2 are the intra-specific competition coefficients and b_2, c_1 are the inter-specific competition coefficients. All constants are assumed to be positive, and $u_0(x), v_0(x)$ are non-negative functions that are not identically equal to zero.

Under the assumption

$$\frac{b_1}{b_2} > \frac{a_1}{a_2} > \frac{c_1}{c_2}, \quad (8.39)$$

(8.38) has a unique positive steady state, given by

$$(u^*, v^*) = \left(\frac{a_1 c_2 - a_2 c_1}{b_1 c_2 - b_2 c_1}, \frac{b_1 a_2 - b_2 a_1}{b_1 c_2 - b_2 c_1} \right). \quad (8.40)$$

It turns out that (u^*, v^*) is globally asymptotically stable:

Theorem 8.9 *Suppose that (8.39) holds. Then for any non-negative and not identically zero initial data $u(x, 0), v(x, 0) \in C(\bar{\Omega})$,*

$$\lim_{t \rightarrow \infty} (u(x, t), v(x, t)) = (u^*, v^*)$$

in $C(\bar{\Omega}) \times C(\bar{\Omega})$ norm.

Proof Consider the following system of ordinary differential equations:

$$\begin{cases} U_t = U(a_1 - b_1 U - c_1 V) & \text{in } (0, \infty), \\ V_t = V(a_2 - b_2 U - c_2 V) & \text{in } (0, \infty), \\ U(0) > 0, \quad V(0) > 0. \end{cases} \quad (8.41)$$

We claim that for any initial data $U(0) > 0, V(0) > 0$,

$$\lim_{t \rightarrow \infty} (U(t), V(t)) = (u^*, v^*). \quad (8.42)$$

To establish our assertion, define

$$E(t) = b_2 \left(U - u^* - u^* \ln \frac{U}{u^*} \right) + c_1 \left(V - v^* - v^* \ln \frac{V}{v^*} \right). \quad (8.43)$$

Then $dE/dt \leq 0$ and $dE/dt = 0$ if and only if $(U, V) = (u^*, v^*)$. Since $E(t)$ is also bounded from below, by the LaSalle's invariance principle, (8.42) holds.

By the maximum principle, we have $u(x, t), v(x, t) > 0$ for any $x \in \bar{\Omega}$ and $t > 0$. Without loss of generality we assume that $u(x, 0) > 0$ and $v(x, 0) > 0$ in $\bar{\Omega}$.

Let (\underline{U}, \bar{V}) be the solution of

$$\begin{cases} \underline{U}_t = \underline{U}(a_1 - b_1 \underline{U} - c_1 \bar{V}) & \text{in } (0, \infty), \\ \bar{V}_t = \bar{V}(a_2 - b_2 \underline{U} - c_2 \bar{V}) & \text{in } (0, \infty), \\ \underline{U}(0) = \min_{x \in \bar{\Omega}} u(x, 0) > 0, \\ \bar{V}(0) = \max_{x \in \bar{\Omega}} v(x, 0) > 0; \end{cases} \quad (8.44)$$

and let $(\overline{U}, \underline{V})$ be the solution of

$$\begin{cases} \overline{U}_t = \overline{U}(a_1 - b_1\overline{U} - c_1\underline{V}) & \text{in } (0, \infty), \\ \underline{V}_t = \underline{V}(a_2 - b_2\overline{U} - c_2\underline{V}) & \text{in } (0, \infty), \\ \overline{U}(0) = \max_{x \in \overline{\Omega}} u(x, 0) > 0, \\ \underline{V}(0) = \min_{x \in \overline{\Omega}} v(x, 0) > 0. \end{cases} \quad (8.45)$$

Note that $(\underline{U}, \overline{V})$ and $(\overline{U}, \underline{V})$ satisfy (8.38). Since

$$\underline{U}(0) \leq u(x, 0) \leq \overline{U}(0), \quad \underline{V}(0) \leq v(x, 0) \leq \overline{V}(0)$$

by the comparison principle for two-species competition model (8.38) [50],

$$\underline{U}(t) \leq u(x, t) \leq \overline{U}(t), \quad \underline{V}(t) \leq v(x, t) \leq \overline{V}(t)$$

hold for all $x \in \overline{\Omega}$ and $t \geq 0$.

By (8.41) and (8.42),

$$\lim_{t \rightarrow \infty} (\underline{U}(t), \overline{V}(t)) = \lim_{t \rightarrow \infty} (\overline{U}(t), \underline{V}(t)) = (u^*, v^*). \quad (8.46)$$

Therefore, $(u(x, t), v(x, t)) \rightarrow (u^*, v^*)$ uniformly in x as $t \rightarrow \infty$. ■

8.3.2 Competition in Heterogeneous Environment

The semilinear parabolic system

$$\begin{cases} u_t = d_1 \Delta u + u[m(x) - u - bv] & \text{in } \Omega \times (0, \infty), \\ v_t = d_2 \Delta v + v[m(x) - cu - v] & \text{in } \Omega \times (0, \infty), \\ \nabla u \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x) & \text{in } \Omega \end{cases} \quad (8.47)$$

models two species that are competing for the same resources, where $u(x, t)$ and $v(x, t)$ represent the population densities of two competing species with respective dispersal rates d_1 and d_2 , the function $m(x)$ represents their common intrinsic growth rate, and b and c are inter-specific competition coefficients. We shall assume that d_1 , d_2 , b , and c are positive constants, and $u_0(x)$, $v_0(x)$ are non-negative functions that are not identically equal to zero.

We say that a steady state of (8.47) 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 (A3), (8.47) has exactly two semi-trivial states, denoted by $(\theta_{d_1}, 0)$ and $(0, \theta_{d_2})$, where $\theta_d = \theta(\cdot, d)$ is the unique positive solution of (8.30).

We assume that $0 < b, c < 1$. If $m(x) \equiv \bar{m}$ for some positive constant \bar{m} , by Theorem 8.9, every solution (u, v) of (8.47) converges to $(\frac{1-b}{1-bc}\bar{m}, \frac{1-c}{1-bc}\bar{m})$ for all diffusion rates d_1, d_2 and any initial data. However, the dynamics of (8.47) is less transparent when m is non-constant. To this end, we start by studying the stability of the semi-trivial steady state $(\theta_{d_1}, 0)$ of (8.47). For the rest of this subsection, we focus on the case $0 < c < 1$.

Theorem 8.10 ([37]) *If (A3) holds and $m(x)$ is non-negative, then there exists some constant $c_* = c_*(m, \Omega) \in (0, 1)$ such that the followings hold:*

- (a) *For $c \in (0, c_*)$, $(\theta_{d_1}, 0)$ is unstable for any $d_1, d_2 > 0$.*
- (b) *For $c \in (c_*, 1)$, there exists $d_* = d_*(c, m, \Omega) > 0$ such that (i) for $d_2 \in (0, d_*)$, $(\theta_{d_1}, 0)$ is unstable for any $d_1 > 0$; (ii) for $d_2 > d_*$, $(\theta_{d_1}, 0)$ changes stability at least twice as d_1 increases from 0 to d_2 .*

Note that the above theorem holds regardless of the specific value $b > 0$. The most interesting case is where $c_* < c < 1$ and $d_2 > d_*$, where we have the following implications:

- (i) If $b > 1$, it is well known that without dispersal, species v always drives species u to extinction. However, with dispersal, for some ranges of dispersal rates, species v may fail to invade when rare.
- (ii) If $b < 1$, it is well known that, without dispersal, species u and v always coexist. Surprisingly, for certain dispersal rates, species u is able to drive species v to extinction for arbitrary initial conditions. (See Theorem 1.9 of [37].)

Proof We sketch the main ideas in the proof of Theorem 8.10. The stability of $(\theta_{d_1}, 0)$ is determined by the sign of the smallest eigenvalue, denoted by λ_1 , of the problem

$$\begin{cases} d_2 \Delta \varphi + (m - c\theta_{d_1})\varphi + \lambda\varphi = 0 & \text{in } \Omega, \\ \nabla \varphi \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.48)$$

Note that $\lambda_1 = \sigma_1(d_2, m - c\theta_{d_1})$. More specifically, $(\theta_{d_1}, 0)$ is stable if $\lambda_1 > 0$ and unstable if $\lambda_1 < 0$. To determine the sign of λ_1 , we observe that λ_1 is a strictly increasing function of d_2 , and that

$$\lim_{d_2 \rightarrow 0} \lambda_1 = \min_{\Omega} (c\theta_{d_1} - m) \leq \min_{\Omega} (\theta_{d_1} - m) < 0; \quad (8.49)$$

$$\lim_{d_2 \rightarrow +\infty} \lambda_1 = \frac{\int_{\Omega} \theta_{d_1}}{|\Omega|} \left(c - \frac{\int_{\Omega} m}{\int_{\Omega} \theta_{d_1}} \right). \quad (8.50)$$

Set

$$c_* = \inf_{d_1 > 0} \frac{\int_{\Omega} m}{\int_{\Omega} \theta_{d_1}}.$$

By Theorem 8.6, we see that $c_* \in (0, 1)$.

For every $c \in (0, c_*)$ and any $d_1 > 0$, $\lim_{d_2 \rightarrow +\infty} \lambda_1 \leq 0$. Since λ_1 is strictly increasing in d_2 , we see that $\lambda_1 < 0$ for any $d_1, d_2 > 0$. This proves part (a).

For every $c \in (c_*, 1)$, for simplicity assume that there exist two positive constants $\underline{d} < \bar{d}$ such that $c - \int_{\Omega} m / \int_{\Omega} \theta_{d_1} > 0$ for $d_1 \in (\underline{d}, \bar{d})$, and $c - \int_{\Omega} m / \int_{\Omega} \theta_{d_1} < 0$ for $d_1 \in (0, \underline{d}) \cup (\bar{d}, +\infty)$. Define $d^* = d^*(d_1) := 1/\lambda_1(m - c\theta_{d_1})$, i.e.,

$$d^* = \sup_{\varphi \in \mathcal{S}} \frac{\int_{\Omega} (m - c\theta_{d_1}) \varphi^2}{\int_{\Omega} |\nabla \varphi|^2},$$

where

$$\mathcal{S} = \{\varphi \in H^1(\Omega) : \int_{\Omega} (m - c\theta_{d_1}) \varphi^2 > 0\}.$$

Now, $d^* = +\infty$ if and only if $c - \int_{\Omega} m / \int_{\Omega} \theta_{d_1} \leq 0$, i.e., $d_1 \in (0, \underline{d}] \cup [\bar{d}, +\infty)$. In particular, $d^*(d_1)$ is finite when $d_1 \in (\underline{d}, \bar{d})$, and that $d^*(d_1) \rightarrow +\infty$ as $d_1 \rightarrow \underline{d}-$ or $d_1 \rightarrow \bar{d}+$. This allows us to define $d_* = \inf_{d_1 > 0} d^*(d_1)$. For $d_2 < d_*$, we have $d_2 < d^*(d_1)$ for all $d_1 > 0$. In this case, Proposition 8.3(i) says that $\lambda_1 < 0$ for all $d_1 > 0$, which implies that $(\theta_{d_1}, 0)$ is unstable for any $d_1 > 0$ and $d_2 < d_*$. For $d_2 > d_*$, we likewise have $\lambda_1 < 0$ for $d_1 \in (0, \underline{d}) \cup (\bar{d}, +\infty)$; and $\lambda_1 > 0$ in some sub-interval of (\underline{d}, \bar{d}) . Therefore λ_1 changes sign at least twice as d_1 increases from 0 to d_2 , i.e., part (b) is proved. ■

Exercise Prove that $\lambda_1 < 0$ whenever $c < 1$ and $d_1 \geq d_2$. [Hint: Observe that λ_1 is monotone increasing in c as well as in d_2 , and that $\lambda_1 = 0$ when $c = 1$ and when d_2 is increased to d_1 .]

For every $c > 0$, define

$$\Sigma_c = \{(d_1, d_2) \in \mathbb{R}^+ \times \mathbb{R}^+ : (\theta_{d_1}, 0) \text{ is linearly stable}\}. \quad (8.51)$$

Note that $\Sigma_c \subset \{(d_1, d_2) \in \mathbb{R}^+ \times \mathbb{R}^+ : d_1 < d_2\}$ since, by the comparison principle for principal eigenvalues, $\lambda_1 < 0$ for $d_1 \geq d_2$. Clearly, Σ_c is non-empty if and only if $c > c_*$.

In a series of important works [21–24], He and Ni classified the dynamics of a class of Lotka–Volterra competition–diffusion models which include system (8.47) as a special case. One of their results can be stated as follows:

Theorem 8.11 ([24]) *If assumption (A3) holds and $m(x)$ is non-negative, $c \in (c_*, 1)$ and $0 < b \leq 1$, then $(\theta_{d_1}, 0)$ is globally asymptotically stable for any $(d_1, d_2) \in \overline{\Sigma}_c$; if $d_2 \geq d_1$ or $(d_1, d_2) \notin \overline{\Sigma}_c$, then system (8.47) has a unique positive steady state which is globally asymptotically stable.*

One key ingredient in the proof of Theorem 8.11 is the following lemma:

Lemma 8.2 *If $bc \leq 1$, then any positive steady state of (8.47), if exists, is linearly stable.*

Proof Let (u, v) be any positive steady state of (8.47). The linear stability of (u, v) is determined by the sign of the principal eigenvalue, denoted by λ_1 , of the problem

$$\begin{cases} d_1 \Delta \varphi + \varphi(m - 2u - bv) - bu\psi + \lambda_1 \varphi = 0 & \text{in } \Omega, \\ d_2 \Delta \psi - cv\varphi + \psi(m - cu - 2v) + \lambda_1 \psi = 0 & \text{in } \Omega, \\ \nabla \varphi \cdot n = \nabla \psi \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.52)$$

As φ, ψ are eigenfunctions of λ_1 and thus do not change sign in Ω , we may assume without loss that $\varphi > 0$ and $\psi < 0$ in $\bar{\Omega}$. Set $\varphi = uw$ and $\psi = -vz$. Thus $w, z > 0$ in $\bar{\Omega}$ and they satisfy

$$\begin{cases} d_1 \nabla(u^2 \nabla w) - u^3 w + bu^2 vz + \lambda_1 u^2 w = 0 & \text{in } \Omega, \\ d_2 \nabla(v^2 \nabla z) + cuv^2 w - v^3 z + \lambda_1 v^2 z = 0 & \text{in } \Omega, \\ \nabla w \cdot n = \nabla z \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.53)$$

Multiplying the equation of w by w^2 and integrating the result in Ω , we have

$$-2d_1 \int_{\Omega} u^2 w |\nabla w|^2 - \int_{\Omega} (uw)^3 + b \int_{\Omega} (uw)^2 (vz) + \lambda_1 \int_{\Omega} u^2 w^3 = 0.$$

If $\lambda_1 \leq 0$, then we have

$$\int_{\Omega} (uw)^3 < b \int_{\Omega} (uw)^2 (vz).$$

By Hölder inequality,

$$\int_{\Omega} (uw)^3 < b \left[\int_{\Omega} (uw)^3 \right]^{2/3} \left[\int_{\Omega} (vz)^3 \right]^{1/3},$$

which implies that

$$\int_{\Omega} (uw)^3 < b^3 \int_{\Omega} (vz)^3. \quad (8.54)$$

Similarly, if $\lambda_1 \leq 0$, by the equation of v and similar argument we have

$$\int_{\Omega} (vz)^3 < c^3 \int_{\Omega} (uw)^3, \quad (8.55)$$

Clearly, (8.54) and (8.55) are in contradiction with $bc \leq 1$. Hence, $\lambda_1 > 0$. This completes the proof. \blacksquare

By Theorem 8.11, the parameter region where species u wins is characterized by the closure of the set Σ_c . By a previous exercise, we have seen that, $\Sigma_c \subset \{d_1 \leq d_2\}$, i.e., species u may exclude species v only if u is the slower diffuser. Furthermore, by Theorem 8.10, 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 $\{(d_1, d_2) : 0 < d_1 < d_2\}$ as $c \rightarrow 1-$, and this gives another perspective upon why the slower diffuser wins the competition for the case when $b = c = 1$. We refer to the next section for more details on the evolution of slow dispersal.

8.4 Evolution of Dispersal

It is an important question in spatial ecology to understand which patterns of dispersal can confer some selective or evolutionary advantage. Unconditional dispersal refers to movement which does not depend on habitat quality or population density. For the evolution of unconditional dispersal in the context of reaction–diffusion models, it was shown that slower dispersal rate is selected when the environment is spatially heterogeneous but temporally constant; see [16, 20]. In contrast, for unconditional dispersal in spatially and temporally varying environments faster dispersal rates may be selected in diffusion models [26]. In this section we focus on the evolution of unconditional dispersal in spatially varying but temporally constant environments.

Consider system (8.47) for the case when $b = c = 1$:

$$\begin{cases} u_t = d_1 \Delta u + u[m(x) - u - v] & \text{in } \Omega \times (0, \infty), \\ v_t = d_2 \Delta v + v[m(x) - u - v] & \text{in } \Omega \times (0, \infty), \\ \nabla u \cdot n = \nabla v \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x) & \text{in } \Omega. \end{cases} \quad (8.56)$$

The following result was established in [16]:

Theorem 8.12 *Suppose that (A3) holds. If $0 < d_1 < d_2$, then the semi-trivial steady state $(\theta_{d_1}, 0)$ of (8.56) is globally asymptotically stable among all solutions with non-negative and non-trivial initial data.*

Theorem 8.12 is surprising: when $d_1 = d_2 = 0$, two species will coexist since they are identical. However, if the diffusion rates are positive for both species, the slower diffuser always outcompetes the faster one. This also shows that the PDE dynamics cannot be predicted by the ODE dynamics in this case.

Proof We first prove the instability of $(0, \theta_{d_2})$, which is determined by the sign of the smallest eigenvalue, denoted by $\lambda_1 := \lambda_1(d_1, d_2)$, of

$$\begin{cases} d_1 \Delta \varphi + (m - \theta_{d_2})\varphi + \lambda_1 \varphi = 0 & \text{in } \Omega, \\ \nabla \varphi \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \quad (8.57)$$

Note that $\lambda_1(d_1, d_2) = \sigma_1(d_1, m - \theta_{d_2})$ and hence it is monotone increasing in d_1 . We may normalize φ such that $\varphi > 0$ and $\int_{\Omega} \varphi^2 = 1$. Denote $\varphi' = \frac{\partial \varphi}{\partial d_1}$ and $\lambda_1' = \frac{\partial \lambda_1}{\partial d_1}$. Differentiating the equation of φ with respect to d_1 , multiplying the result by φ and integrating in Ω , we have

$$\int_{\Omega} \varphi [\Delta \varphi + d_1 \Delta \varphi' + (m - \theta_{d_2}) \varphi' + \lambda_1' \varphi + \lambda_1 \varphi'] = 0,$$

from which we obtain $\lambda_1' = \int_{\Omega} |\nabla \varphi|^2 > 0$. Hence, λ_1 is strictly increasing in d_1 . Since $\lambda_1(d_2, d_2) = 0$ (where $\varphi = \theta_{d_2} / \|\theta_{d_2}\|_{L^2(\Omega)}$), we see that $\lambda_1 < 0$ if and only if $d_1 < d_2$.

Next, we claim that

$$\limsup_{t \rightarrow \infty} v(x, t) \leq \theta_{d_2}(x). \quad (8.58)$$

To establish our assertion, note that

$$v_t = d_2 \Delta v + v(m(x) - u - v) \leq d_2 \Delta v + v(m(x) - v).$$

Consider

$$\begin{cases} V_t = d_2 \Delta V + V(m - V) & \text{in } \Omega \times (0, \infty), \\ \nabla V \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty), \\ V(x, 0) = v(x, 0) & \text{in } \bar{\Omega}. \end{cases} \quad (8.59)$$

By the comparison principle of parabolic equations [48], $v(x, t) \leq V(x, t)$. Thus

$$\limsup_{t \rightarrow \infty} v(x, t) \leq \limsup_{t \rightarrow \infty} V(x, t) = \theta_{d_2}(x).$$

Therefore, for each $\varepsilon > 0$, there exists $T_1 := T_1(\varepsilon)$ such that for $t \geq T_1$ and $x \in \bar{\Omega}$,

$$v(x, t) \leq (1 + \varepsilon)\theta_{d_2}(x).$$

Consider next the solution $(U(x, t), V(x, t))$ of

$$\begin{cases} U_t = d_1 \Delta U + U(m(x) - U - V) & \text{in } \Omega \times [T_1, \infty), \\ V_t = d_2 \Delta V + V(m(x) - U - V) & \text{in } \Omega \times [T_1, \infty), \\ \nabla U \cdot n = \nabla V \cdot n = 0 & \text{on } \partial\Omega \times [T_1, \infty), \\ U(x, T_1) = \delta\varphi, V(x, T_1) = (1 + \varepsilon)\theta_{d_2} & \text{in } \bar{\Omega}. \end{cases} \quad (8.60)$$

We check that $(\delta\varphi, (1 + \varepsilon)\theta_{d_2})$ is a pair of sub-super solution of (8.60) as follows:

$$\begin{aligned} & d_2 \Delta[(1 + \varepsilon)\theta_{d_2}] + (1 + \varepsilon)\theta_{d_2}(m - \delta\varphi - (1 + \varepsilon)\theta_{d_2}) \\ &= (1 + \varepsilon)[d_2 \Delta \theta_{d_2} + \theta_{d_2}(m - \theta_{d_2}) - (\delta\varphi + \varepsilon\theta_{d_2})\theta_{d_2}] \leq 0 \end{aligned} \quad (8.61)$$

and

$$\begin{aligned}
 & d_1 \Delta(\delta\varphi) + \delta\varphi [m - \delta\varphi - (1 + \varepsilon)\theta_{d_2}] \\
 &= \delta [d_1 \Delta\varphi + \varphi(m - \theta_{d_2}) + \varphi(-\delta\varphi - \varepsilon\theta_{d_2})] \\
 &= \delta\varphi [-\lambda_1 - \delta\varphi - \varepsilon\theta_{d_2}] \geq 0,
 \end{aligned} \tag{8.62}$$

since $\lambda_1 < 0$ and δ, ε are chosen small.

By the comparison principle for two-species competitive systems, we see that $U(x, t)$ is increasing in t and $V(x, t)$ is decreasing in t . Therefore $(U(x, t), V(x, t))$ converges, as $t \rightarrow \infty$, to some limit $(U^*(x), V^*(x))$. By the elliptic regularity theory we can show that $(U^*(x), V^*(x))$ is a non-negative steady state of (8.56), with $U^* > 0$.

We claim that $V^* \equiv 0$. If not, then (U^*, V^*) is a positive steady state of (8.56), i.e., they satisfy

$$\begin{cases} d_1 \Delta U^* + U^*(m(x) - U^* - V^*) = 0 & \text{in } \Omega, \\ d_2 \Delta V^* + V^*(m(x) - U^* - V^*) = 0 & \text{in } \Omega, \\ \nabla U^* \cdot n = \nabla V^* \cdot n = 0 & \text{on } \partial\Omega. \end{cases} \tag{8.63}$$

Consider the smallest eigenvalue, denoted by $\lambda_1(d)$, of the eigenvalue problem

$$d \Delta\varphi + (m - U^* - V^*) + \lambda\varphi = 0 \quad \text{in } \Omega, \quad \nabla\varphi \cdot n = 0 \quad \text{in } \partial\Omega.$$

Since m is non-constant, one can show that $m - U^* - V^*$ is also non-constant. Hence, $\lambda_1(d)$ is strictly increasing in d . By the equation of U^* , we see that $\lambda_1(d_1) = 0$ with corresponding $\varphi = U^*$. Similarly from the equation of V^* we get $\lambda_1(d_2) = 0$, which is a contradiction, since $d_1 \neq d_2$.

Hence, $V^* = 0$ and $U^* = \theta_{d_1}$, i.e., $\lim_{t \rightarrow \infty} (U(x, t), V(x, t)) = (\theta_{d_1}, 0)$. Choose δ, ε small such that $U(x, T_1) = \delta\varphi \leq u(x, T_1)$ and $v(x, T_1) \leq (1 + \varepsilon)\theta_{d_2} = V(x, T_1)$. By the comparison principle for two-species competition systems, we have $U(x, t) \leq u(x, t)$ and $v(x, t) \leq V(x, t)$. In particular, $v(x, t) \rightarrow 0$ as $t \rightarrow \infty$ and $\liminf_{t \rightarrow \infty} u(x, t) \geq \theta_{d_1}(x)$. Since, by repeating the previous argument for (8.58), one can also show that $\limsup_{t \rightarrow \infty} u(x, t) \leq \theta_{d_1}(x)$, we have $\lim_{t \rightarrow \infty} u(x, t) = \theta_{d_1}$. This completes the proof. ■

Consider k -species competition model

$$\begin{cases} u_{i,t} = d_i \Delta u_i + u_i(m - \sum_{i=1}^k u_i) & \text{in } \Omega \times (0, \infty), \\ \nabla u_i \cdot n = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{8.64}$$

A challenging open problem is whether the slowest diffuser still wins the competition in the context of k competing species with $k \geq 3$.

Open Problem Suppose that m is positive, non-constant, and continuous in $\bar{\Omega}$. If $0 < d_1 < d_2 < \dots < d_k$ and $k \geq 3$, is $(\theta_{d_1}, 0, \dots, 0)$ globally asymptotically stable among all positive initial data?

The mathematical difficulty in solving this open problem is that competition models for three or more species are not monotone dynamical systems.

8.5 Persistence and Competition in Advective Environments

In this section we consider the persistence of a single species and the competition of two populations in advective environments. We will focus on the effects of advection and boundary conditions on the persistence and competition of populations.

8.5.1 Single Species in Advective Environment

How can populations persist in streams when they are constantly washed downstream? This question, termed as the “drift paradox” in the literatures, has received considerable attention. Speirs and Gurney [52] offered an explanation based upon the diffusive movement of organisms, and they considered the following reaction–diffusion model:

$$\begin{cases} u_t = du_{xx} - qu_x + u(r - u), & \text{for } 0 < x < L, \ t > 0, \\ du_x(0, t) - qu(0, t) = 0, & \text{for } t > 0, \\ u(L, t) = 0, & \text{for } t > 0, \\ u(x, 0) = u_0(x), & \text{for } 0 < x < L, \end{cases} \quad (8.65)$$

where $u(x, t)$ denotes the population density at location x and time t , d is the diffusion rate, L is the size of the habitat, and in the sequel, we call $x = 0$ the upstream end and $x = L$ the downstream end. The constant q is the effective speed of the current (sometimes we also call q the advection speed/rate, and we remark here that q is positive since $x = L$ is defined to be the downstream end). The constant $r > 0$ accounts for the intrinsic growth rate, which indicates the spatial homogeneity of the environment. We assume that u_0 is non-negative and not identically zero, and d , r , q , L are all positive constants. In other words, the spatial heterogeneity of the problem (8.65) is introduced solely by the drift and the boundary conditions.

Speirs and Gurney [52] studied the local stability of steady state $u = 0$ and concluded that it is unstable if and only if $q < \sqrt{4dr}$ and $L > L^*$, where

$$L^* = 2d \frac{\pi - \arctan\left(\frac{\sqrt{4dr - q^2}}{q}\right)}{\sqrt{4dr - q^2}}.$$

That is, the persistence is only possible when advection is slow relative to diffusion and the stream is long enough. It is natural to inquire whether such predictions still hold for other situations. To this end, Vasilyeva and Lutscher [53] considered the following single species problem with a different boundary condition at the downstream end $x = L$. Their model is given by

$$\begin{cases} u_t = du_{xx} - qu_x + u(r - u), & \text{for } 0 < x < L, \ t > 0, \\ du_x(0, t) - qu(0, t) = 0, & \text{for } t > 0, \\ u_x(L, t) = 0, & \text{for } t > 0, \\ u(x, 0) = u_0(x), & \text{for } 0 < x < L. \end{cases} \quad (8.66)$$

The following result, which is similar in nature to the result of Speirs and Gurney, was proved in [53]:

Theorem 8.13 *The species can persist if and only if $q < \sqrt{4dr}$ and $L > L^{**}$, where*

$$L^{**} = \begin{cases} 2d \frac{\arctan \frac{q\sqrt{4dr-q^2}}{2rd-q^2}}{\sqrt{4dr-q^2}} & \text{for } 0 < q \leq \sqrt{2dr}, \\ 2d \frac{\pi + \arctan \frac{q\sqrt{4dr-q^2}}{2rd-q^2}}{\sqrt{4dr-q^2}} & \text{for } \sqrt{2dr} < q < \sqrt{4dr}. \end{cases} \quad (8.67)$$

Proof The stability of $u = 0$ is determined by the sign of λ_1 , the smallest eigenvalue of the eigenvalue problem

$$\begin{cases} d\varphi_{xx} - q\varphi_x + r\varphi + \lambda_1\varphi = 0, & \text{for } 0 < x < L, \\ d\varphi_x(0) - q\varphi(0) = \varphi_x(L) = 0. \end{cases} \quad (8.68)$$

Set $\varphi = e^{qx/(2d)}\psi$. Then

$$\begin{cases} d\psi_{xx} + \psi(-\frac{q^2}{4d} + r + \lambda_1) = 0, & \text{for } 0 < x < L, \\ \psi_x(0) - \frac{q}{2d}\psi(0) = \psi_x(L) + \frac{q}{2d}\psi(L) = 0. \end{cases} \quad (8.69)$$

Thus

$$\psi(x) = A \cos\left(\frac{\sqrt{4d(r + \lambda_1) - q^2}}{2d}x\right) + B \sin\left(\frac{\sqrt{4d(r + \lambda_1) - q^2}}{2d}x\right).$$

As a consequence of the boundary conditions of ψ , we have

$$A = B \frac{\sqrt{4d(r + \lambda_1) - q^2}}{q}$$

and

$$\begin{aligned}
 & A \frac{-\sqrt{4d(r+\lambda_1)-q^2}}{2d} \sin\left(\frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} L\right) + B \frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} \cos\left(\frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} L\right) \\
 & + \frac{q}{2d} [A \cos\left(\frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} L\right) + B \sin\left(\frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} L\right)] = 0.
 \end{aligned} \tag{8.70}$$

Combining these two equations and using $(A, B) \neq (0, 0)$, we obtain

$$\tan\left(\frac{\sqrt{4d(r+\lambda_1)-q^2}}{2d} L\right) \left[\frac{q}{d} - \frac{2(r+\lambda_1)}{q} \right] + \frac{\sqrt{4d(r+\lambda_1)-q^2}}{d} = 0.$$

Set $\lambda_1 = 0$, then

$$\tan\left(\frac{\sqrt{4dr-q^2}}{2d} L^{**}\right) = \frac{q\sqrt{4dr-q^2}}{2rd-q^2},$$

where L^{**} is the critical length given by (8.67) so that $\lambda_1 < 0$ when $L > L^{**}$; and $\lambda_1 > 0$ when $L < L^{**}$. This finishes the proof. \blacksquare

It is natural to consider more general boundary conditions:

$$\begin{cases} u_t = du_{xx} - qu_x + u(r-u), & \text{for } 0 < x < L, t > 0, \\ du_x(0, t) - qu(0, t) = 0, & \text{for } t > 0, \\ du_x(L, t) - qu(L, t) = -bqu(L, t), & \text{for } t > 0, \\ u(x, 0) = u_0(x), & \text{for } 0 < x < L. \end{cases} \tag{8.71}$$

Here the (non-negative) parameter b measures the rate of population loss at the downstream end $x = L$ caused by the drift [38].

It is shown in [41] that the species can persist if and only if $q < q^*$ and $L > L^{***}$, where

$$q^* = \begin{cases} \sqrt{\frac{dr}{b(1-b)}} & 0 < b \leq \frac{1}{2}; \\ \sqrt{4dr} & b \geq \frac{1}{2}, \end{cases}$$

and L^{***} is an explicit function of d, r, q, b . (See Lemmas 2.1 and 2.2 of [41] for details.) It is interesting to see that the critical value q^* depends on b only for $b \leq \frac{1}{2}$, while for $b \geq \frac{1}{2}$, $q^* = \sqrt{4dr}$ is the minimal traveling wave speed for the Fisher-KPP equation in the whole real line.

Exercise

- (i) Show that L^{**} , given in (8.67), is a strictly decreasing function of d .
- (ii) Prove that there exists some $d_* > 0$ such that L^* is decreasing for $d < d_*$ and increasing for $d > d_*$. What is the biological interpretation of this result?

8.5.2 Evolution of Faster Dispersal

When the movement of organisms is subject to external forces such as river flow, how should species disperse to avoid the invasion of a mutant species with different movement strategies? In this subsection we consider a two-species competition model in an open advective environment: Individuals are exposed to unidirectional flow, with a net loss of individuals at the downstream end. We assumed that two species have the same advection rates but different dispersal rates. More specifically, we consider

$$\begin{cases} u_t = d_1 u_{xx} - qu_x + u(1 - u - v), & 0 < x < L, t > 0, \\ v_t = d_2 v_{xx} - qv_x + v(1 - u - v), & 0 < x < L, t > 0, \\ d_1 u_x(0, t) - qu(0, t) = d_2 v_x(0, t) - qv(0, t) = 0, & t > 0, \\ u_x(L, t) = v_x(L, t) = 0, & t > 0, \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), & 0 < x < L. \end{cases} \quad (8.72)$$

Theorem 8.14 ([38]) *If $d_1 > d_2$, then the semi-trivial steady state $(u^*, 0)$, whenever it exists, is globally asymptotically stable among non-negative and non-trivial solutions of (8.72), where $u^* > 0$ is the unique positive solution of*

$$\begin{cases} d_1 u_{xx}^* - qu_x^* + u^*(1 - u^*) = 0, & 0 < x < L, \\ d_1 u_x^*(0) - qu^*(0) = u_x^*(L) = 0. \end{cases} \quad (8.73)$$

Theorem 8.14 implies that in an open advective environment, unidirectional flow can put slow dispersers at a disadvantage and higher dispersal rates are being selected. In particular, in a homogeneous advective environment with the free-flow boundary condition at the downstream end, a population with higher dispersal rate will always displace one with lower dispersal rate. We refer to [12, 13, 17, 33, 42–45, 54–56] for recent developments.

In the following we illustrate that $(u^*, 0)$ is stable for $d_1 \approx d_2$, $d_1 > d_2$, and unstable for $d_1 \approx d_2$, $d_1 < d_2$. This implies that a mutant can invade when rare if and only if it has the larger dispersal rate. In terms of the adaptive dynamics theory, the joint effects of small mutation and selection will tend to increase the average diffusion rate of the species.

The stability of $(u^*, 0)$ is determined by the sign of the smallest eigenvalue, denoted by $\lambda_1 = \lambda_1(d_1, d_2)$, of the problem

$$\begin{cases} d_2 \varphi_{xx} - q\varphi_x + (1 - u^*)\varphi + \lambda_1 \varphi = 0, & 0 < x < L, \\ d_2 \varphi_x(0) - q\varphi(0) = \varphi_x(L) = 0, \\ \varphi > 0 \text{ in } (0, L). \end{cases} \quad (8.74)$$

Lemma 8.3 *Let λ_1 be the principal eigenvalue of (8.74). Then*

$$\left. \frac{\partial \lambda_1}{\partial d_2} \right|_{d_2=d_1} = \frac{\int_0^L (e^{-\frac{q}{d_1}x} u^*)_x u_x^* dx}{\int_0^L e^{-\frac{q}{d_1}x} (u^*)^2 dx} < 0.$$

In particular, for $d_1 \approx d_2$, $(u^, 0)$ is stable if $d_1 > d_2$, and unstable if $d_1 < d_2$.*

Proof We first calculate $\frac{\partial \lambda_1}{\partial d_2}$. Denote $\varphi' = \frac{\partial \varphi}{\partial d_2}$ and $\lambda'_1 = \frac{\partial \lambda_1}{\partial d_2}$, and differentiate the equation of φ with respect to d_2 , we obtain

$$\begin{cases} d_2 \varphi'_{xx} + \varphi_{xx} - q \varphi'_x + (1 - u^*) \varphi' + \lambda'_1 \varphi + \lambda_1 \varphi' = 0, & 0 < x < L, \\ d_2 \varphi'_x(0) + \varphi_x(0) - q \varphi'(0) = \varphi'_x(L) = 0. \end{cases} \quad (8.75)$$

Multiplying the first equation of (8.75) by $e^{-(q/d_2)x} \varphi$, the first equation of (8.74) by $e^{-(q/d_2)x} \varphi'$, subtracting and integrating the result in $(0, L)$, we have

$$\lambda'_1 \int_0^L e^{-(q/d_2)x} \varphi^2 - \int_0^L \left(e^{-(q/d_2)x} \varphi \right)_x \varphi_x = 0.$$

When $d_2 = d_1$, we have $\lambda_1 = 0$ and $\varphi = Cu^*$ for some positive constant C . Thus

$$\left. \frac{\partial \lambda_1}{\partial d_2} \right|_{d_2=d_1} = \frac{\int_0^L (e^{-\frac{q}{d_1}x} u^*)_x u_x^* dx}{\int_0^L e^{-\frac{q}{d_1}x} (u^*)^2 dx}. \quad (8.76)$$

We claim that $u^* < 1$ for $0 \leq x \leq L$. This follows directly from the fact that, for each constant $C \geq 1$, $\bar{u} = C$ is a strict super-solution for the equation of u^* .

Next we show that $u_x^* > 0$ for $0 \leq x < L$. Since $u_x^*(L) = 0$ and $u^* < 1$, by the equation of u^* we see that $u_{xx}^*(L) < 0$. Hence, there exists some $\delta > 0$ such that $u_x^* > 0$ in $[L - \delta, L)$. To prove $u_x^* > 0$ in $[0, L)$, we argue by the contradiction. If not, we may assume that there exists some $x_1 < L - \delta$ such that $u_x^* > 0$ in $[x_1, L)$ and $u_x^*(x_1) = 0$. Set $w = u_x^*/u^*$. Then w satisfies

$$d_1 w_{xx} + w_x(2w - q) = u^* w \quad (8.77)$$

in $(0, L)$ and $w(x_1) = w(L) = 0$, $w > 0$ in (x_1, L) . Therefore, there exists some $x_2 \in (x_1, L)$ such that $w(x_2) = \max_{x_1 \leq x \leq L} w(x)$. Hence, $w_x(x_2) = 0$ and $w_{xx}(x_2) \leq 0$, which contradicts (8.77). This proves $u_x^* > 0$ for $x \in [0, L)$.

By the assertion $u^* < 1$ we have $d_1 u_{xx}^* - qu_x^* < 0$ in $(0, L)$. Hence, $d_1 u_x^* - qu^*$ is strictly decreasing. Since $d_1 u_x^*(0) - qu^*(0) = 0$, then $d_1 u_x^* - qu^* < 0$ for $0 < x \leq L$. Therefore, $(e^{-(q/d_1)x} u^*)_x = e^{-(q/d_1)x} (u_x^* - \frac{q}{d_1} u^*) < 0$. This, together with $u_x^* > 0$ in $[0, L)$ and (8.76), shows that $\frac{\partial \lambda_1}{\partial d_2} < 0$ when $d_2 = d_1$. The proof is complete. \blacksquare

The boundary condition appears to play an important role in the outcome of evolution. In a homogeneous advective environment with the free-flow boundary conditions, larger dispersal rates evolve. In contrast, numerical simulations suggest that in a homogeneous advective environment with more hostile boundary conditions, there seems to evolve a unique, intermediate dispersal rate, which is evolutionarily stable. To be more specific, consider

$$\begin{cases} u_t = d_1 u_{xx} - qu_x + u(1 - u - v), & \text{for } 0 < x < L, t > 0, \\ v_t = d_2 v_{xx} - qv_x + v(1 - u - v), & \text{for } 0 < x < L, t > 0, \\ d_1 u_x(0, t) - qu(0, t) = d_2 v_x(0, t) - qv(0, t) = 0, & \text{for } t > 0, \\ d_1 u_x(L, t) - qu(L, t) = -bqu(L, t), & \text{for } t > 0, \\ d_2 v_x(L, t) - qv(L, t) = -bqv(L, t), & \text{for } t > 0, \\ u(x, 0) = u_0(x), v(x, 0) = v_0(x), & \text{for } 0 < x < L. \end{cases} \quad (8.78)$$

For $b \in [0, 1]$, it is shown in [38, 41] that if $d_1 > d_2$, then $(u^*, 0)$, whenever it exists, is globally asymptotically stable, i.e., the faster dispersal rate is always selected. For $b \geq 3/2$, we have the following conjecture:

Conjecture Suppose that $b \in [\frac{3}{2}, +\infty]$. Then there exists some $d_* > 0$ such that if $d_2 < d_1 \leq d_*$ or $d_* \leq d_1 < d_2$, then $(u^*, 0)$, whenever it exists, is globally asymptotically stable, where $u^* > 0$ satisfies

$$\begin{cases} d_1 u_{xx}^* - qu_x^* + u^*(1 - u^*) = 0, & \text{for } 0 < x < L, \\ d_1 u_x^*(0) - qu^*(0) = 0, \\ d_1 u_x^*(L) - qu^*(L) = -bqu^*(L). \end{cases} \quad (8.79)$$

The d_* above is a special case of an evolutionarily stable strategy (ESS) in the evolution game theory, i.e., an ESS is a strategy which, if adopted by a population in a given environment, cannot be invaded by any alternative strategy that is initially rare. When $b \in [0, 1]$, we can regard $d_* = +\infty$, i.e., $+\infty$ is an ESS.

8.6 Conclusion

In this chapter we studied some reaction–diffusion models in spatial ecology. Topics covered include the logistic model for a single species and related issues, two-species Lotka–Volterra competition models in homogeneous and heterogeneous environments, the persistence and competition in advective environments, and the evolution of dispersal in heterogeneous and advective environments. We introduced some basic tools for reaction–diffusion equations and systems, including the super-solution and sub-solution method, the variational principle for principal eigenvalues, Lyapunov functionals, the comparison principles for parabolic equations and sys-

tems. We also presented some mathematical problems, ranging from elementary exercises to open research questions. In the following we discuss several recent works and point interested readers to relevant references:

In [46] Nagahara and Yanagida proved that the optimal control m^* of the functional J (see (8.33) in subsection 2.4) is of the “bang-bang” type, i.e., there exists a measurable set $E \subset \Omega$ such that $m^* = 1$ in E and $m^* = 0$ in the complement of E . This answers a conjecture of Ding et al. [15] affirmatively.

We recall that $\theta(\cdot, d)$ is the unique positive solution of (8.30). An open problem is whether $\max_{x \in \bar{\Omega}} \theta(x, d)$ is monotone decreasing in d . Such question came from the study of predator–prey systems in heterogeneous environments [39]. If Ω is an interval and m is monotone, then $\max_{x \in \bar{\Omega}} \theta(x, d)$ is monotone decreasing in d ; see [35], which extended an earlier result in [39]. However, the question remains open for general Ω and m .

In [49] Perthame and Souganidis considered an integro-PDE model for a population structured by the spatial variables and a continuous trait variable which is the diffusion rate. Such model can be viewed as the extension of the competition model (8.56) from two-phenotypes to infinitely many phenotypes. It is shown in [49], and independently in [32], that in the limit of small mutation rate, the unique steady state solution forms a Dirac mass in the trait variable, supported at the smallest possible diffusion rate. This echoes the result of Dockery et al. in [16], i.e., the slowest diffusion rate is favored. We refer to [19, 31] for further development.

For system (8.78), the species can persist if and only if $q < q^*$ and $L > L^{***}$ (Lemmas 2.1 and 2.2 of [41]). We proved in [18] that if $0 < b \leq 3/2$, then L^{***} is strictly decreasing in d ; if $b > 3/2$, then L^{***} decreases in d first and then increases in d . This reveals a dramatic difference between $b < 3/2$ and $b > 3/2$. Our preliminary analysis of system (8.78) suggests that the conclusion of Theorem 8.14, which states that the faster diffuser can always competitively exclude the slower diffuser, may fail for some $1 < b < 3/2$, i.e., the faster dispersal rate may not be selected. This is in strong contrast to the case $0 \leq b \leq 1$ for which the faster dispersal rate is always selected [38, 41].

In conclusion, the materials presented in this chapter illustrate some interesting questions in spatial ecology and evolution. Such questions are, on the one hand, well connected with important issues in biology, and on the other hand, deeply rooted in mathematics and bringing new and exciting challenges.

Acknowledgements We sincerely thank the referee for his comments and suggestions which help improve the presentation. KYL and YL were partially supported by the NSF grant DMS-1411476 and DMS-1853561. Part of the work was done during the visit of YL to the University of Alberta to participate in the 2016 *Séminaire de Mathématiques Supérieures: Dynamics of Biological Systems Summer School*, and he thanks the organizers for the warm hospitality.

References

1. I. Averill, K.-Y. Lam, Y. Lou, The role of advection in a two-species competition model: a bifurcation approach. *Mem. Am. Math. Soc.* **245**(1161), v+117 (2017)
2. X.L. Bai, X.Q. He, F. Li, An optimization problem and its application in population dynamics. *Proc. Am. Math. Soc.* **144**, 2161–2170 (2016)
3. K.J. Brown, S.S. Lin, On the existence of positive eigenvalue problem with indefinite weight function. *J. Math. Anal. Appl.* **75**, 112–120 (1980)
4. R.S. Cantrell, C. Cosner, Diffusive logistic equations with indefinite weights: population models in a disrupted environments. *Proc. R. Soc. Edinb.* **112A**, 293–318 (1989)
5. R.S. Cantrell, C. Cosner, The effects of spatial heterogeneity in population dynamics. *J. Math. Biol.* **29**, 315–338 (1991)
6. R.S. Cantrell, C. Cosner, Should a park be an island? *SIAM J. Appl. Math.* **53**, 219–252(1993)
7. R.S. Cantrell, C. Cosner, On the effects of spatial heterogeneity on the persistence of interacting species. *J. Math. Biol.* **37**, 103–145 (1998)
8. R.S. Cantrell, C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*. Series in Mathematical and Computational Biology (Wiley, Chichester, 2003)
9. R.S. Cantrell, C. Cosner, Y. Lou, Movement towards better environments and the evolution of rapid diffusion. *Math Biosci.* **204**, 199–214 (2006)
10. R.S. Cantrell, C. Cosner, Y. Lou, Advection mediated coexistence of competing species. *Proc. R. Soc. Edinb.* **137A**, 497–518 (2007)
11. C. Cosner, Reaction-diffusion-advection models for the effects and evolution of dispersal. *Discr. Cont. Dyn. Syst.* **34**, 1701–1745 (2014)
12. R.H. Cui, Y. Lou, Spatial SIS epidemic models in advective environments. *J. Differ. Equ.* **261**, 3305–3343 (2016)
13. R.H. Cui, K.-Y. Lam, Y. Lou, Dynamics and asymptotic profiles of steady states to an epidemic model in advective environments. *J. Differ. Equ.* **263**, 2343–2373 (2017)
14. D. DeAngelis, W.-M. Ni, B. Zhang, Dispersal and spatial heterogeneity: single species. *J. Math. Biol.* **72**, 239–254 (2016)
15. W. Ding, H. Finotti, S. Lenhart, Y. Lou, Q. Ye, Optimal control of growth coefficient on a steady-state population model. *Nonlinear Anal. Real World Appl.* **11**, 688–704 (2010)
16. J. Dockery, V. Hutson, K. Mischaikow, M. Pernarowski, The evolution of slow dispersal rates: a reaction-diffusion model. *J. Math. Biol.* **37**, 61–83 (1998)
17. M. Golubitsky, W. Hao, K.-Y. Lam, Y. Lou, Dimorphism by singularity theory in a model for river ecology. *Bull. Math. Biol.* **79**, 1051–1069 (2017)
18. M. Golubitsky, W. Hao, K.-Y. Lam, Y. Lou, Evolution of dispersal for a river species in homogeneous advective environment, in preparation
19. W. Hao, K.-Y. Lam, Y. Lou, Concentration phenomena in an integro-PDE model for evolution of conditional dispersal. *Indiana Univ. Math. J.* **68**, 881–923 (2019)
20. A. Hastings, Can spatial variation alone lead to selection for dispersal? *Theor. Popul. Biol.* **24**, 244–251 (1983)
21. X. He, W.-M. Ni, The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system I: heterogeneity vs. homogeneity. *J. Differ. Equ.* **254**, 528–546 (2013)
22. X. He, W.-M. Ni, The effects of diffusion and spatial variation in Lotka-Volterra competition-diffusion system II: the general case. *J. Differ. Equ.* **254**, 4088–4108 (2013)
23. X. He, W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system: diffusion and spatial heterogeneity I. *Commun. Pure Appl. Math.* **69**, 981–1014 (2016)
24. X. He, W.-M. Ni, Global dynamics of the Lotka-Volterra competition-diffusion system with equal amount of total resources, II. *Calc. Var. Partial Differ. Equ.* **55**, Art. 25, 20 (2016)
25. S.-B. Hsu, H. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces. *Trans. Am. Math. Soc.* **348**, 4083–4094 (1996)

26. V. Hutson, K. Mischaikow, P. Poláčik, The evolution of dispersal rates in a heterogeneous time-periodic environment. *J. Math. Biol.* **43**, 501–533 (2001)
27. V. Hutson, Y. Lou, K. Mischaikow, Spatial heterogeneity of resources versus Lotka-Volterra dynamics. *J. Differ. Equ.* **185**, 97–136 (2002)
28. V. Hutson, Y. Lou, K. Mischaikow, P. Poláčik, Competing species near the degenerate limit. *SIAM J. Math. Anal.* **35**, 453–491 (2003)
29. V. Hutson, Y. Lou, K. Mischaikow, Convergence in competition models with small diffusion coefficients. *J. Differ. Equ.* **211**, 135–161 (2005)
30. C.Y. Kao, Y. Lou, E. Yanagida, Principal eigenvalue for an elliptic problem with indefinite weight on cylindrical domains. *Math. Biosci. Eng.* **5**, 315–335 (2008)
31. K.-Y. Lam, Stability of Dirac concentrations in an integro-PDE Model for evolution of dispersal. *Calc. Var. Partial Differ. Equ.* **56**, 32 pp. (2017)
32. K.-Y. Lam, Y. Lou, An integro-PDE model for evolution of random dispersal. *J. Funct. Anal.* **272**, 1755–1790 (2017)
33. K.-Y. Lam, Y. Lou, F. Lutscher, Evolution of dispersal in closed advective environments. *J. Biol. Dyn.* **9**, 188–212 (2015)
34. K.-Y. Lam, W.-M. Ni, Uniqueness and complete dynamics of the Lotka-Volterra competition diffusion system. *SIAM J. Appl. Math.* **72**, 1695–1712 (2012)
35. R. Li, Y. Lou, Some monotone properties for solutions to a reaction-diffusion model. *Discr. Contin. Dyn. Syst. B* **24**, 4445–4455 (2019)
36. S. Liang, Y. Lou, On the dependence of population size upon random dispersal rate. *Discrete Contin. Dyn. Syst. B* **17**, 2771–2788 (2012)
37. Y. Lou, On the effects of migration and spatial heterogeneity on single and multiple species. *J. Differ. Equ.* **223**, 400–426 (2006)
38. Y. Lou, F. Lutscher, Evolution of dispersal in open advective environments. *J. Math. Biol.* **69**, 1319–1342 (2014)
39. Y. Lou, B. Wang, Local dynamics of a diffusive predator-prey model in spatially heterogeneous environment. *J. Fixed Point Theory Appl.* **19**, 755–772 (2017)
40. Y. Lou, E. Yanagida, Minimization of the principal eigenvalue with indefinite weight and applications to population dynamics. *Jpn J. Indus. Appl. Math.* **23**, 275–292 (2006)
41. Y. Lou, P. Zhou, Evolution of dispersal in advective homogeneous environment: the effect of boundary conditions. *J. Differ. Equ.* **259**, 141–171 (2015)
42. Y. Lou, D.M. Xiao, P. Zhou, Qualitative analysis for a Lotka-Volterra competition system in advective homogeneous environment. *Discrete Contin. Dyn. Syst. A* **36**, 953–969 (2016)
43. Y. Lou, X.-Q. Zhao, P. Zhou, Global dynamics of a Lotka-Volterra competition-diffusion-advection system in heterogeneous environments. *J. Math. Pures Appl.* **121**, 47–82 (2019)
44. F. Lutscher, E. Pachepsky, M.A. Lewis, The effect of dispersal patterns on stream populations. *SIAM Rev.* **47**, 749–772 (2005)
45. F. Lutscher, M.A. Lewis, E. McCauley, Effects of heterogeneity on spread and persistence in rivers. *Bull. Math. Biol.* **68**, 2129–2160 (2006)
46. K. Nagahara, E. Yanagida, Maximization of the total population in a reaction-diffusion model with logistic growth. *Calc. Var. Partial Differ. Equ.* **57**, Art 80, 14pp (2018)
47. W.-M. Ni, *The Mathematics of Diffusion*. CBMS-NSF Regional Conference Series in Applied Mathematics, vol. 82 (SIAM, Philadelphia, 2011)
48. C.V. Pao, *Nonlinear Parabolic and Elliptic Equations* (Springer, Berlin, 2012)
49. B. Perthame, P.E. Souganidis, Rare mutations limit of a steady state dispersal evolution model. *Math. Model. Nat. Phenom.* **11**, 154–166 (2016)
50. M.H. Protter, H.F. Weinberger, *Maximum Principles in Differential Equations* Corrected reprint of the 1967 original (Springer, New York, 1984)
51. H.L. Smith, Monotone dynamical systems, in *An Introduction to the Theory of Competitive and Cooperative Systems*. Mathematical Surveys and Monographs, vol. 41 (American Mathematical Society, Providence, 1995)

52. D.C. Speirs, W.S. Gurney, Population persistence in rivers and estuaries. *Ecology* **82**, 1219–1237 (2001)
53. O. Vasilyeva, F. Lutscher, Population dynamics in rivers: analysis of steady states. *Can. Appl. Math. Q.* **18**, 439–469 (2011)
54. O. Vasilyeva, F. Lutscher, Competition in advective environments. *Bull. Math. Biol.* **74**, 2935–2958 (2012)
55. P. Zhou, On a Lotka-Volterra competition system: diffusion vs advection. *Calc. Var. Partial Differ. Equ.* **55**, Art. 137, 29 (2016)
56. X.-Q. Zhao, P. Zhou, On a Lotka-Volterra competition model: the effects of advection and spatial variation. *Calc. Var. Partial Differ. Equ.* **55**, Art. 73, 25 (2016)