REACTION-DIFFUSION-ADVECTION MODELS FOR THE EFFECTS AND EVOLUTION OF DISPERSAL

Chris Cosner

Department of Mathematics, University of Miami, Coral Gables, FL 33124, U.S.A.

Partially supported by NSF grants DMS-0816068 and DMS-1118623
and the Center for Partial Differential Equations, East China Normal University.

Abstract. This review describes reaction-advection-diffusion models for the ecological effects and evolution of dispersal, and mathematical methods for analyzing those models. The topics covered include models for a single species, models for ecological interactions between species, and models for the evolution of dispersal strategies. The models are all set on bounded domains. The mathematical methods include spectral theory, specifically the theory of principal eigenvalues for elliptic operators, maximum principles and comparison theorems, bifurcation theory, and persistence theory.

1. Introduction

Dispersal is an important aspect of the life histories of many, perhaps most, organisms. It allows individuals to find and interact with resources and with members of their own and other species, and allows populations to distribute themselves across space. Thus, it influences the persistence of populations and mediates interactions between populations such as predation and competition. The ecological effects of dispersal have consequences for the fitness of individuals and for the outcomes of interactions between different species, or different subspecies of a given species. As a result, the ecological effects of dispersal create selective pressures that influence the evolution of dispersal strategies. There are many approaches that have been used to model the process of dispersal and its ecological effects and evolution. One common approach is to use reaction-advection-diffusion equations and their generalizations. That approach can be technically challenging, but it has the advantage of being mechanistic in that the details of the dispersal behavior of individuals can be scaled up to derive

---

1991 *Mathematics Subject Classification.* Primary: 35B40, 35B45; Secondary: 35J55, 92D10.

Key words and phrases. reaction-diffusion, population dynamics, dispersal, ecology, evolution, bifurcation, persistence theory.

the equations describing dispersal at the level of population densities, and those equations can be used to build systems of equations describing interactions between populations. Thus, reaction-advection-diffusion models can explain how the dispersal behavior of individuals influences the ecological interactions of populations, and in turn how those ecological interactions impose forces of evolutionary selection on the behavior of individuals. This review will discuss the derivation, analysis, and interpretation of such models. It will be focused on the dynamics of populations inhabiting finite regions. It will not address the spread of populations through infinite regions, as in the case of traveling waves in biological invasions, or the formation of patterns arising from Turing instabilities or related mechanisms. The topics treated will include derivations of models from assumptions about individual movement behavior, mathematical background on methods for analyzing the models, and results about various specific ecological and evolutionary questions. The exposition assumes that readers will have a good knowledge of real analysis and some familiarity with partial differential equations, specifically the Laplace equation and the heat or diffusion equation. Many of the results and their proofs will involve eigenvalues of elliptic operators on bounded domains. Some will involve ideas from bifurcation theory or the theory of dynamical systems. Additional background material and technical details are discussed in [13]. The material is organized into sections on single species models, models addressing ecological issues for interacting species, and models addressing issues related to the evolution of dispersal. The last section gives a brief description of some alternatives to reaction-advection-diffusion models, namely discrete diffusion models and intergro-differential models.

2. Single species models

In the formulation of reaction-diffusion-advection models, three different levels of scaling are involved: the micro scale, the meso scale and the macro scale. At the micro scale, individuals engage in random (diffusive) or directed (advective) movement between adjacent patches. The details determine dispersal strategies, which are reflected in the forms of the corresponding advection and diffusion equations at the meso scale. At the meso scale, combining movement models with models for population dynamics and interactions between species leads to reaction-diffusion-advection models for population disperal, which describe population distribution and dynamics. These models describe ecological processes. At the macro scale, the outcomes of ecological processes determine the direction of evolution. In particular, evolution can act on dispersal strategies. Some dispersal strategies exclude others, some combinations can coexist and some strategies are evolutionarily stable. Questions naturally arise as follows: What forms of meso scale dispersal are feasible given specific micro scale behavior? How does the form of meso scale dispersal affect population dynamics and interactions? What forms of meso scale dispersal within a feasible class will be stable versus invasion or evolution at the macro scale? And so on. For example, the following system describes the densities u and v of two competing populations which are ecologically similar but have different dispersal strategies:

$$\begin{cases} u_t = \nabla[d_u \nabla u - \alpha u \nabla m] + (m - u - v)u & \text{in } \Omega \times (0, T), \\ v_t = d_v \nabla^2 v + (m - u - v)v & \text{in } \Omega \times (0, T), \\ [d_u \nabla u - \alpha u \nabla m] \cdot \vec{n} = \nabla v \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, T) \end{cases}$$

with nonnegative initial values, where Ω is a smooth bounded domain in $\mathbb{R}^N$ and $\vec{n}$ is the unit outer normal vector on the boundary $\partial\Omega$. The first competitor moves by a combination of random diffusion and directed movement, while the second moves only by random diffusion. Those movement patterns lead to the forms of diffusion and advection terms in the model. It is proved in [15] that if $d_u = d_v$ and $\alpha > 0$ is small, then u excludes v. However if d_u and d_v are fixed, $\alpha >> 0$, then u and v can coexist. Thus the model suggests that populations using strategies with no advection or high advection can be invaded by populations using other strategies, so strategies with no advection or high advection would be predicted to be unstable relative to evolution. These sorts of ideas will be explored in more detail in what follows, starting with descriptions of how assumptions about movement at the micro scale determine the structure of models at the meso scale.

2.1. Model formulation: dispersal and dynamics.

Now let us briefly go through the formulation of different kinds of dispersal at the micro scale in one dimension [73]. Let $u(x, t)$ and J denote the density and flux, respectively, of a population at the location x and time t. Generally, according to Fick's law,

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x} J.$$

For *simple diffusion*, at each time step Δt, individuals move randomly from $x - \Delta x$ to x or x to $x - \Delta x$ at the same rate $p_0(x)$, hence

$$\begin{aligned} J &= \frac{1}{\Delta t} p_0(x)[u(x - \Delta x, t)\Delta x - u(x, t)\Delta x] \\ &= \frac{(\Delta x)^2}{\Delta t} p_0(x) \left[\frac{u(x - \Delta x, t) - u(x, t)}{\Delta x} \right]. \end{aligned}$$

We let Δx and Δt go to zero with the standard diffusive scaling

$$\frac{(\Delta x)^2}{\Delta t} = D_0, \tag{2.1}$$

which immediately yields that

$$\lim_{\Delta x, \Delta t \to 0} J = -D(x)\frac{\partial u}{\partial x},$$

where $D(x) = D_0 p_0(x)$. Thus we have

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left(D(x)\frac{\partial u}{\partial x}\right). \tag{2.2}$$

If the dispersal probability depends on *departure* point, then

$$\begin{aligned} J &= \frac{1}{\Delta t}[p_1(x-\Delta x)u(x-\Delta x,t)\Delta x - p_1(x)u(x,t)\Delta x] \\ &= \frac{(\Delta x)^2}{\Delta t}\left[\frac{p_1(x-\Delta x)u(x-\Delta x,t) - p_1(x)u(x,t)}{\Delta x}\right]. \end{aligned}$$

Again by the diffusive scaling (2.1), it follows that

$$\lim_{\Delta x, \Delta t \to 0} J = -\frac{\partial}{\partial x}(D(x)u),$$

where $D(x) = D_0 p_1(x)$ with D_0 given by (2.1). This yields

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2}\left(D(x)u\right). \tag{2.3}$$

If the dispersal probability depends on *arrival* point, then

$$\begin{aligned} J &= \frac{1}{\Delta t}[p_2(x)u(x-\Delta x,t)\Delta x - p_2(x-\Delta x)u(x,t)\Delta x] \\ &= \frac{(\Delta x)^2}{\Delta t}p_2(x)p_2(x-\Delta x)\frac{1}{\Delta x}\left[\frac{u(x-\Delta x,t)}{p_2(x-\Delta x)} - \frac{u(x,t)}{p_2(x)}\right]. \end{aligned}$$

As in the previous cases, we derive that

$$\lim_{\Delta x, \Delta t \to 0} J = -D^2(x)\frac{\partial}{\partial x}\left(\frac{u}{D(x)}\right),$$

where $D(x) = D_0 p_2(x)$ and D_0 is given in (2.1), and thus

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[D^2(x)\frac{\partial}{\partial x}\left(\frac{u}{D(x)}\right)\right]. \tag{2.4}$$

Also, we can obtain the equation when the dispersal probability depends on both departure ($p_1(x)$) and arrival ($p_2(x)$) points using similar arguments. In this situation,

$$\begin{aligned} J &= \frac{p_1(x-\Delta x)p_2(x)u(x-\Delta x,t)\Delta x - p_1(x)p_2(x-\Delta x)u(x,t)\Delta x}{\Delta t} \\ &= \frac{(\Delta x)^2}{\Delta t}\frac{p_2(x)p_2(x-\Delta x)}{\Delta x}\left[\frac{p_1(x-\Delta x)u(x-\Delta x,t)}{p_2(x-\Delta x)} - \frac{p_1(x)u(x,t)}{p_2(x)}\right]. \end{aligned}$$

Then letting Δx, $\Delta t \to 0$, we get

$$J \to -D_2^2(x)\frac{\partial}{\partial x}\left(\frac{D_1(x)}{D_2(x)}u(x)\right),$$

where $D_1(x) = D_0^{1/2}p_1(x)$, $D_2(x) = D_0^{1/2}p_2(x)$, D_0 is given in (2.1), and thus

$$\frac{\partial u}{\partial t} = \frac{\partial}{\partial x}\left[d_2(x)\frac{\partial}{\partial x}\left(d_1(x)u\right)\right], \tag{2.5}$$

where $d_1(x) = D_1(x)/D_2(x)$ and $d_2(x) = D_2^2(x)$. Since $d_1(x)$ and $d_2(x)$ are allowed to be any positive functions, the model (2.5) generalizes all the previous models (2.2), (2.3) and (2.4).

The last model is about a different form of dispersal: advection. The flux is given by

$$J = \frac{1}{\Delta t}[q(x-\Delta x)u(x-\Delta x,t)\Delta x].$$

By letting Δx, $\Delta t \to 0$, we have $J \to e(x)u(x)$, where the advection scaling is $\Delta x/\Delta t = e_0$ and $e(x) = e_0 q(x)$. Hence the model is

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x}(e(x)u(x)). \tag{2.6}$$

Note that the advective scaling is different from the diffusive scaling.

In these models (2.2)–(2.6) mentioned above, $D(x)$, $d_i(x)$, $i = 1, 2$, or $e(x)$ could also depend on t, u or densities of other species in multi-species models. When it comes to higher dimensions, ∇ replaces $\partial/\partial x$ and $\vec{e}(x)$ becomes a vector. It is also worth pointing out that some forms of dispersal have more than one possible mechanism. For example, in the model (2.3) in higher dimensions,

$$\nabla^2(D(x)u) = \nabla\cdot[D(x)\nabla u] + \nabla\cdot[u\nabla D(x)].$$

The term on the left hand side would arise from diffusion depending on the departure point. On the right hand side, the first term is from simple diffusion while the second term represents advection down the gradient of $D(x)$. Thus there are two different mechanisms at the micro scale that could produce the same model at the meso scale.

From the biological point of view, advection can arise either from the behavior of individuals or from physical transport processes, such as winds, currents in rivers, and so on. Advection arising from behavior is likely to occur in response to gradients of environmental variables or population densities. However, physical advection does not necessarily arise in response to gradients. This distinction can be important in analyzing models, because models where advection arises from a gradient can often be converted into a symmetric (that is, variational or formally self-adjoint) form by a change of variables. In modeling, simple diffusion and diffusion based on departure point are most commonly used. For example, cross-diffusion models usually use diffusion based on departure point. Generally, there are two methods that organisms may use to follow resources: kinesis and taxis. To be more specific, kinesis refers to changes in the rate of random, undirected motion in response to a stimulus, such as a reduction of diffusion rate in favorable locations, whereas taxis is a specific, directed motion in response to a stimulus, such as advection along environmental gradients.

Next, we want to use the following single species model to talk about the dynamics at the meso scale:

$$u_t = \nabla \cdot [d_2(x)\nabla(d_1(x)u) - u\vec{e}(x)] + f(x,u)u \quad \text{in } \Omega \times (0,\infty), \tag{2.7}$$

with nonnegative initial values and usually with no flux boundary conditions, but sometimes with other boundary conditions . In some cases, f, $\vec{e}$ or d_i, $i = 1,2$ may also depend on t or u. In this model, $f(x,u)$ represents the local rate of reproduction per individual, in other words, per capita population growth rate. The evolutionary interpretation of $f(x,u)$ is the average fitness of individuals at location x with density u. The most common form of f is the logistic form: $f(x,u) = A(x) - B(x)u$, where $B(x) > 0$, $A(x)$ may change signs. In ecology, if $A(x) > 0$, the common notation is

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

where $r(x) = A(x)$ is local rate of population growth at low density and $K(x) = A(x)/B(x)$ denotes maximum density supported locally by resources available, that is, carrying capacity. However, that formulation only makes sense when $A(x) > 0$. In spatial models, the form $f(x,u) = m(x) - u$ is very common. If $B(x)$ is constant the logistic model can always be rescaled into that form. In some cases, an open question is whether models using the more general form $f(x,u) = A(x) - B(x)u$ behave like those using $f(x,u) = m(x) - u$.

Let us take a look at a simple example of a logistic model, namely

$$\begin{cases} d\nabla^2 u + (m(x) - u)u = 0 & \text{in } \Omega, \\ \nabla u \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.8}$$

Assume that $m(x) > 0$ is nonconstant. According to this assumption, plentiful resources are available. It is proved in [68] that there exists a unique positive solution $u(x)$ for all $d > 0$. Then a question is how diffusion affects the total population $\int_\Omega u(x)dx$. When $d > 0$, using (2.8), it is easy to check that the total population satisfies

$$\int_\Omega u(x)dx = d\int_\Omega \frac{|\nabla u|^2}{u^2}dx + \int_\Omega m(x)dx > \int_\Omega m(x)dx.$$

Here we use a simple fact that $u(x)$ cannot be constant since $m(x)$ is nonconstant. Therefore, *diffusion increases population.* Moreover, among other things, it is proved in [68] that

$$\lim_{d\to 0^+}\int_\Omega u(x)dx = \int_\Omega m(x)dx,$$

and

$$\lim_{d\to \infty}\int_\Omega u(x)dx = \int_\Omega m(x)dx.$$

This tells us that the total population has a global maximum for some $0 < d < \infty$. Regarding the total population, biologically it seems interesting to further investigate the following open questions. How do the number and location of the local maxima for the total population relative to d depend on Ω and $m(x)$? What happens in the more general case $\nabla^2 u + (A(x) - B(x)u)u = 0$? How about cases with variable diffusion or advection? And so on. We also want to point out that population size is not necessarily the most important thing to optimize for evolutionary advantage. We will come back to this issue later with many more details.

An alternative to logistic models are models with Allee effects [1]. A population with logistic growth has its largest per capita population growth rate at zero population density. In contrast, if the growth rate per capita increases at low density, the population is said to have an Allee effect. In other words, at low population densities, Allee effects lead to reduced reproduction or survival. If the Allee effect is strong, population growth will actually be negative when individuals become rare. A typical nonspatial model for a single species with Allee effect is

$$\frac{du}{dt} = f(u)u = r\left(1 - \frac{u}{K}\right)(u-a)u, \quad 0 < a < K.$$

It is easy to see that in this model, if the population density u is below the low density equilibrium $u = a$, the species slides into extinction. Allee effects can also arise from spatial effects and interactions between species.

2.2. **Eigenvalue methods.** A basic ecological question is how dispersal, properties of the environment (size, shape, etc.), and the distribution of resources affect population growth or decline. Let us first provide a mathematical formulation of this problem using the model (2.7) with $f(x,u) = m(x) - u$:

$$\begin{cases} u_t = \nabla\cdot[d_2(x)\nabla(d_1(x)u) - u\vec{e}(x)] + (m(x)-u)u & \text{in } \Omega\times(0,\infty),\\ [d_2(x)\nabla(d_1(x)u) - u\vec{e}(x)]\cdot\vec{n} + b(x)u = 0 & \text{on } \partial\Omega\times(0,\infty). \end{cases}$$

It is known that the linear growth or decline in populations at $u = 0$ is determined by the sign of principal eigenvalue σ_0 of the linearized problem at $u = 0$:

$$\begin{cases} \nabla\cdot[d_2(x)\nabla(d_1(x)\psi) - \psi\vec{e}(x)] + m(x)\psi = \sigma\psi & \text{in } \Omega,\\ [d_2(x)\nabla(d_1(x)\psi) - \psi\vec{e}(x)]\cdot\vec{n} + b(x)\psi = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.9}$$

If $\sigma_0 > 0$, then $u = 0$ is unstable and thus the population grows exponentially at the rate of $e^{\sigma_0 t}$. If $\sigma_0 < 0$, then $u = 0$ is stable and the population decays exponentially. Therefore, the basic ecological question can be rephrased as how σ_0 depends on $d_i(x)$, $i = 1, 2$, $m(x)$, $\vec{e}(x)$, $b(x)$ and the domain Ω.

For the convenience of readers, let us briefly summarize some known results regarding the principal eigenvalue σ_0 of (2.9). Instead of (2.9), we consider a more general eigenvalue problem

$$\mathcal{L}\psi = \sigma\psi \ \text{ in } \Omega, \ \ \mathcal{B}\psi = 0 \ \text{ on } \partial\Omega, \tag{2.10}$$

where

$$\mathcal{L}\psi = \sum_{i,j=1}^{N} a_{ij}(x)\frac{\partial^2\psi}{\partial x_i\partial x_j} + \sum_{i=1}^{N} a_i(x)\frac{\partial\psi}{\partial x_i} + a_0(x)\psi,$$

$\mathcal{L}$ is strongly elliptic, $a_{ij} = a_{ji}$, $a_{ij} \in C(\overline{\Omega})$, $a_i, a_0 \in L^\infty(\Omega)$, with either $\mathcal{B}\psi = \psi$ or $\mathcal{B}\psi = \partial\psi/\partial n + b_0(x)\psi$, $b_0 \in C(\partial\Omega)$, $b_0 \geq 0$. It is known ([7]) that the eigenvalue problem (2.10) has a unique principal eigenvalue σ_0 with $\operatorname{Re}\sigma < \sigma_0$ for any other eigenvalue σ. If $\mathcal{B}\psi = \partial\psi/\partial n + b_0(x)\psi$ then we could choose $\psi > 0$ in $\overline{\Omega}$. If $\mathcal{B}\psi = \psi$, then we may choose $\psi > 0$ in Ω with $\partial\psi/\partial n < 0$ on $\partial\Omega$. Furthermore, no other eigenvalues have positive eigenfunctions. If $a_{ij} \in C^2(\overline{\Omega})$, $a_i \in C^1(\overline{\Omega})$, then based on the Krein-Rutman theorem, σ_0 is also the principal eigenvalue for the adjoint problem

$$\mathcal{L}^*\psi^* = \sigma\psi^* \ \text{ in } \Omega, \ \ \mathcal{B}^*\psi^* = 0 \ \text{ on } \partial\Omega.$$

Moreover, it is proved ([2, Theorem 2.4]) that the following assertions are equivalent:

(i) $\sigma_0 < 0$;
(ii) $(\mathcal{L}, \mathcal{B}, \Omega)$ possesses a positive strict supersolution;
(iii) $(\mathcal{L}, \mathcal{B}, \Omega)$ satisfies the strong maximum principle.

Another observation, going back to the problem (2.9), is that if there exists $p(x)$ such that $\nabla p = \vec{e}/(d_1 d_2)$, then by setting $w = d_1 e^{-p}\psi$, the problem (2.9) can be rewritten as

$$\begin{cases} \nabla \cdot [d_2(x)e^p \nabla w] + \dfrac{m(x)}{d_1(x)} e^p w = \sigma \dfrac{1}{d_1(x)} e^p w & \text{in } \Omega, \\ \nabla w \cdot \vec{n} + \dfrac{b(x)}{d_1(x)d_2(x)} w = 0 & \text{on } \partial\Omega. \end{cases}$$

Hence the variational formula can be applied to characterize σ_0. This is sometimes useful in models with advection on environmental gradients. (See also [13], section 2.2.)

Instead of (2.10), sometimes one also needs to consider the weighted eigenvalue problem

$$\mathcal{L}\phi + \lambda m(x)\phi = 0 \ \text{ in } \Omega, \ \ \mathcal{B}\phi = 0 \ \text{ on } \partial\Omega, \tag{2.11}$$

where

$$\mathcal{L}\phi = \sum_{i,j=1}^{N} a_{ij}(x) \frac{\partial^2 \phi}{\partial x_i \partial x_j} + \sum_{i=1}^{N} a_i(x) \frac{\partial \phi}{\partial x_i}.$$

If $m(x)$ is positive and suitably smooth, results similar to those for the problem (2.10) can be obtained by the Krein-Rutman theorem. If $m(x)$ changes sign, similar results can still be proved by considerably different techniques.

Theorem 2.1 ([46]). *Under Dirichlet boundary conditions, suppose that* $m(x_0) > 0$ *for some* $x_0 \in \Omega$. *Then (2.11) admits a principal eigenvalue* λ_0 *characterized by being the unique positive eigenvalue having a positive eigenfunction. Furthermore, for any other eigenvalue* λ *with Re* $\lambda > 0$, *Re* $\lambda > \lambda_0$.

Under Neumann boundary conditions, note that 0 is a trivial eigenvalue with the eigenfunction $\phi = 1$. It can be shown by methods based on the Krein-Rutman theorem that 0 is also an eigenvalue of the adjoint operator $\mathcal{L}^*$ with an eigenfunction that can be chosen to be positive. Let ϕ^* denote the positive eigenfunction corresponding to the trivial eigenvalue of the adjoint operator $\mathcal{L}^*$. Among other things, the following result is proved in [76]:

Theorem 2.2. *Under Neumann boundary conditions, if* $\int_\Omega m(x)\phi^*(x)dx \neq 0$, *there is a unique eigenvalue* $\lambda_0 \neq 0$ *of (2.11) having a positive eigenfunction.*

The sign of λ_0 is opposite to the sign of $\int_\Omega m(x)dx$.

The two eigenvalue problems (2.10) and (2.11) with $a_0(x) = m(x)$ are closely related. When $\lambda_0 > 0$ in (2.11) it is typically the case that $\sigma_0 < 0$ in (2.10) if and only if $\lambda_0 > 1$ in (2.11). See for example [13], Corollary 2.18, and the related discussion. Some calculations for the principal eigenvalue λ_0 of (2.11) are simpler than the corresponding ones for σ_0.

For example, consider a particular case

$$\begin{cases} \nabla \cdot [d\nabla u - \alpha u \nabla m] + (m(x) - u)u = 0 & \text{in } \Omega, \\ [d\nabla u - \alpha u \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.12}$$

Assume that $d > 0$ and $\alpha \geq 0$ are constants and $m(x) \in C^3(\overline{\Omega})$, $\int_\Omega m(x)dx < 0$, $m(x_0) > 0$ for some $x_0 \in \Omega$. Because of the introduction of the advection term $\alpha u \nabla m$, the population may have a tendency to move along the gradient of $m(x)$ in addition to random dispersal and thus may concentrate near favorable environment. A natural ecological question is whether the movement in the direction of $m(x)$ is always beneficial. To study this question, consider the following two types of eigenvalue problems

$$\begin{cases} \nabla \cdot [d\nabla \psi - \alpha \psi \nabla m] + m\psi = \sigma(\alpha)\psi & \text{in } \Omega, \\ [d\nabla \psi - \alpha \psi \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega, \end{cases} \tag{2.13}$$

and

$$\begin{cases} \nabla \cdot [d\nabla \phi - \alpha \phi \nabla m] + \lambda(\alpha) m\phi = 0 & \text{in } \Omega, \\ [d\nabla \phi - \alpha \phi \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{2.14}$$

Let $\sigma_0(\alpha)$ and $\lambda_0(\alpha)$ denote the principal eigenvalues of (2.13) and (2.14) respectively. It is known that the model (2.12) predicts persistence if $\sigma_0(\alpha) > 0$ and $\sigma_0(\alpha) > 0 \Leftrightarrow \lambda_0(\alpha) < 1$ if $\lambda_0(\alpha) > 0$ exists. According to [5], $\lambda_0(\alpha) < 1$ ($\Leftrightarrow \sigma_0(\alpha) > 0$) for α large enough, which means that sufficiently rapid movement in the direction of $m(x)$ is always beneficial. In [25], among other things, it is proved that

$$\left.\frac{d\lambda_0}{d\alpha}\right|_{\alpha=0} < 0,$$

if Ω is convex. This tells us that if $\alpha > 0$ is small, movement in the direction of increasing environmental quality benefits the population in convex domains, while counterexamples exist in certain non-convex domains. The effects of the advection term $\alpha u \nabla m$ also depend critically on boundary conditions. See [5] and [25] for details.

Besides the model (2.12), there are other mechanisms that could concentrate populations near regions of favorable habitat. Examples include $\mathcal{L}u = \nabla^2(d(\gamma m(x))u)$, where $d(z) > 0$, $d'(z) < 0$, or $\mathcal{L}u = \nabla \cdot [d\nabla u - \gamma u \nabla P(m(x))]$ where $P'(z) > 0$. In the first case, the movement rate decreases in favorable regions, while in the second one, the movement is still in the direction of increasing $m(x)$, but at a rate depending on $m(x)$. The parameter γ measures how sensitive the dispersal strategy is to environmental conditions. In these cases, an open question related to the eigenvalue problems

$$\mathcal{L}\psi + m(x)\psi = \sigma\psi \text{ in } \Omega, \quad \mathcal{B}\psi = 0 \text{ on } \partial\Omega,$$

and

$$\mathcal{L}\phi + \lambda m(x)\phi = 0 \text{ in } \Omega, \quad \mathcal{B}\phi = 0 \text{ on } \partial\Omega,$$

is how the principal eigenvalues σ_0, λ_0 depend on the parameter γ.

Recall that in section 2.1, we used the model (2.8) to discuss the optimization of population size when there are abundant resources ($m(x) > 0$). Now we want to make use of eigenvalue methods to study the *optimal habitat arrangement* for population persistence when resources are limited. Let us present the question mathematically first. Consider the problem

$$d\Delta u + (m(x) - u)u = 0 \text{ in } \Omega, \quad \mathcal{B}u = 0 \text{ on } \partial\Omega, \tag{2.15}$$

where $\mathcal{B}u = u$ or $\mathcal{B}u = \partial u/\partial n + b_0(x)u$, $b_0(x) \geq 0$, suppose that

$$-m_1 \leq m(x) \leq m_2, \ \int_\Omega m(x)dx \leq m_0, \tag{2.16}$$

where the constants $m_1 > 0$, $m_2 > 0$, m_0 are given and $m_0 < 0$ in the Neumann case. Let $\lambda_0(m)$ be the principal eigenvalue of

$$\Delta\phi + \lambda m(x)\phi = 0 \text{ in } \Omega, \quad \mathcal{B}\phi = 0 \text{ on } \partial\Omega.$$

The assumptions on m imply that $\lambda_0(m) > 0$. Let $d^* = 1/\lambda_0(m)$. It is known that if $d > d^*$ then $u = 0$ is linearly stable and (2.15) has no positive solutions, while $u = 0$ is linearly unstable and (2.15) has a unique positive solution for $0 < d < d^*$. (See for example [10, 12] or [13], section 3.4.) Hence the problem of determining what choice of $m(x)$ satisfying (2.16) is optimal for population persistence is equivalent to maximizing d^*, which is equivalent to minimizing the principal eigenvalue $\lambda_0(m)$. For both Dirichlet and Neumann boundary conditions, it has been shown that the minimizer of $\lambda_0(m)$ exists and it is of bang-bang type, i.e., for some set $E \subset \Omega$,

$$m(x) = m_2\chi_E - m_1\chi_{\Omega\setminus E},$$

where $m_2|E| - m_1|\Omega \setminus E| = m_0$. The location of E depends critically on the boundary conditions. In the one dimensional case, for the Dirichlet problem, $m(x)$ is positive in the central part of Ω and negative near the boundary, while for the Neumann problem, $m(x)$ is positive on one side of the interval and negative on the other side. See [10], [11] and [69] for details. In higher dimensional cases, a partial analytic characterization of the set E for the Dirichlet problem is obtained in [10]. For the Neumann problem in higher dimensions some numerical results about the set E are obtained in [54] and [74], but the question of obtaining an analytic characterization of E for the Neumann problem in higher dimensions is open.

Finally, we want to talk about models in time varying environments and the related eigenvalue problems. Define

$$\mathcal{L}u = \partial u/\partial t - \mathcal{A}(t)u,$$

where

$$\mathcal{A}(t)u = \sum_{i,j=1}^{N} a_{ij}(x,t)\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{N} a_i(x,t)\frac{\partial u}{\partial x_i} + a_0(x,t)u.$$

Assume that $\mathcal{A}(t)$ is uniformly strongly elliptic, all coefficients are smooth and $T-$periodic in t. Under these assumptions, it is proved in [45], [62] that the problem

$$\mathcal{L}\psi = \rho\psi \text{ in } \Omega \times \mathbb{R}, \;\; \mathcal{B}\psi = 0 \text{ on } \partial\Omega \times \mathbb{R}$$

where $\mathcal{B}\psi = u$ or $\mathcal{B}\psi = \partial u/\partial n + b_0(x)u,\; b_0 \geq 0$, has a principal eigenvalue ρ_0 characterized by having a positive eigenfunction. If the coefficients of $\mathcal{A}$ do not depend on t then $\rho_0 = -\sigma_0$ where σ_0 is the principal eigenvalue of

$$\mathcal{A}\psi = \sigma\psi.$$

Moreover, for any other eigenvalue ρ, Re $\rho \geq \rho_0$. The main questions in time varying environments are analogous to those in the time-independent case: the effects of advection, variable diffusion, etc. on the principal eigenvalue ρ_0. Not much is known in this direction. One estimate is as follows: assume that the coefficients a_{ij} and a_i in the operator $\mathcal{A}(t)$ are independent of t. Define another operator

$$\widehat{\mathcal{A}}u = \sum_{i,j=1}^{N} a_{ij}(x)\frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{N} a_i(x)\frac{\partial u}{\partial x_i} + \widehat{a}_0(x)u$$

with

$$\widehat{a}_0(x) = \frac{1}{T}\int_0^T a_0(x,t)dt.$$

In [52], the authors show that $\rho_0 \leq \widehat{\rho}_0$ where ρ_0 and $\widehat{\rho}_0$ are the principal eigenvalues of

$$\partial\psi/\partial t - \mathcal{A}(t)\psi = \rho\psi \text{ in } \Omega \times \mathbb{R}, \;\; \mathcal{B}\psi = 0 \text{ on } \partial\Omega \times \mathbb{R}$$

and

$$\partial\phi/\partial t - \widehat{\mathcal{A}}\phi = \widehat{\rho}\phi \text{ in } \Omega \times \mathbb{R}, \;\; \mathcal{B}\phi = 0 \text{ on } \partial\Omega \times \mathbb{R}$$

respectively. (Since the coefficients of $\widehat{\mathcal{A}}$ do not depend on t we have $\widehat{\rho}_0 = -\widehat{\sigma}_0$ where $\widehat{\sigma}_0$ is the principal eigenvalue for $\widehat{\mathcal{A}}\psi = \sigma\psi$.) A few other estimates for principal eigenvalues of periodic-parabolic operators are given in [45, 51] but for the general problem of estimating ρ_0 or for more specific problems of determining how ρ_0 depends on parameters or coefficients such as diffusion or advection rates in particular cases there remain many open questions.

2.3. **Bifurcation theory and applications.** As mentioned before, a realistic improvement in modeling dispersal is to add density dependence. In principle, any coefficient in a reaction-advection-diffusion model or its boundary conditions could depend on population density, leading to models of the form

$$u_t = \nabla \cdot [d_2(x,u)\nabla(d_1(x,u)u) - u\vec{e}(x,u)] + f(x,u)u \quad \text{in } \Omega \times (0,\infty),$$

with the boundary condition

$$\alpha(x,u)[d_2(x,u)\nabla(d_1(x,u)u) - u\vec{e}(x,u)] \cdot \vec{n} + (1-\alpha(x,u))u = 0$$

on $\partial\Omega \times (0,\infty)$, where $\alpha(x,u) \geq 0$. It is known that for linear dispersal and boundary conditions, with $f(x,u)$ of logistic type, in many cases, either there is no positive equilibrium and $u = 0$ is globally stable among nonnegative solutions, or there is a unique positive equilibrium which is globally stable. See [13], chapter 3. However, when the dispersal is density dependent, properties of solutions may be dramatically different and bifurcation theory is a useful tool in this case. There are two major types of bifurcation results, namely local and global. Local bifurcation results give a detailed description of all of the solutions to a given problem in a neighborhood of the bifurcation point. Global bifurcation results describe the behavior of bifurcating branches of solutions both near the bifurcation point and far away from it, and sometimes can give a description of the full set of solutions for large regions of parameter space, but usually with less detail than local results. Here we will use local bifurcation theory to study a model with density-dependent diffusion. For a treatment of global bifurcation as it applies to the quasilinear elliptic systems that describe equilibria of models for interacting species with cross diffusion or other forms of density-dependent diffusion or advection, see [78] and the references in that paper.

Here is an important and fundamental result in local bifurcation theory due to Crandall and Rabinowitz :

Theorem 2.3 ([30]). *Suppose that* $\mathbb{X}$ *and* $\mathbb{Y}$ *are Banach spaces,* $(a,b) \times V \subset \mathbb{R} \times \mathbb{X}$*,* $0 \in V$ *is open, and* $\mathcal{F} : (a,b) \times V \to \mathbb{Y}$ *is twice differentiable with* $\mathcal{F}(\lambda, 0) = 0$ *for* $\lambda \in (a,b)$*. Suppose that for some* $\lambda_0 \in (a,b)$*,* $D_x\mathcal{F}(\lambda_0, 0)$ *has* 0 *as a simple eigenvalue and* $x_0 \in \mathbb{X}$ *spans* $N(D_x\mathcal{F}(\lambda_0,0))$*. Suppose further that* $D_{\lambda x}\mathcal{F}(\lambda_0,0)x_0 \notin R(D_x\mathcal{F}(\lambda_0,0))$*. Let* $W \subset \mathbb{X}$ *be any complement of span*$\{x_0\}$*. Then in a neighborhood of* $(\lambda_0, 0)$*, the solution set of* $\mathcal{F}(\lambda, x) = 0$ *consists of a trivial curve* $(\lambda, x) = (\lambda, 0)$ *and a curve* $(\lambda, x) = (\lambda(s), sx_0 + s\rho(s))$ *with* $\lambda(0) = \lambda_0$*,* $\rho(0) = 0$ *and* $\rho(s) \in W$*. If* $\mathcal{F}$ *is smooth, then so are* $\lambda(s)$ *and* $\rho(s)$*.*

In the following example, let us use bifurcation theory to investigate how nonlinear dispersal affects the behavior of solutions in a model with density-dependent diffusion. Consider

$$\begin{cases} u_t = d_1 \nabla \cdot [d_2(x,u)\nabla u] + (m(x)-u)u & \text{in } \Omega \times (0,\infty), \\ u = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{2.17}$$

Let $\lambda = 1/d_1$ and the equilibrium equation becomes

$$\nabla \cdot [d_2(x,u)\nabla u] + \lambda(m(x)-u)u = 0.$$

Denote $\mathbb{X} = \{u \in C^{2+\alpha}(\overline{\Omega}) : u = 0 \text{ on } \partial\Omega\}$, $\mathbb{Y} = C^{\alpha}(\overline{\Omega})$ and define $\mathcal{F} : \mathbb{R} \times \mathbb{X} \to \mathbb{Y}$ as $\mathcal{F}(\lambda, u) = \nabla \cdot [d_2(x,u)\nabla u] + \lambda(m(x)-u)u$. Direct calculation gives that

$$D_u\mathcal{F}(\lambda,u)\phi = \nabla \cdot \left[\frac{\partial d_2}{\partial u}(x,u)\phi\nabla u + d_2(x,u)\nabla\phi\right] + \lambda(m(x)-2u)\phi,$$

and $D_{\lambda u}\mathcal{F}(\lambda,u)\phi = m(x)\phi$. Clearly,

$$D_u\mathcal{F}(\lambda,0)\phi = \nabla \cdot [d_2(x,0)\nabla\phi] + \lambda m(x)\phi.$$

Assume that the weighted eigenvalue problem

$$\nabla \cdot [d_2(x,0)\nabla\phi] + \lambda m(x)\phi = 0 \ \text{ in } \Omega, \quad \phi = 0 \ \text{ on } \partial\Omega \tag{2.18}$$

has a positive principal eigenvalue, denoted by λ_0, with the eigenfunction ϕ_0. It is routine to check that $g \in R(D_u\mathcal{F}(\lambda_0,0))$ implies that $\int_\Omega \phi_0 g dx = 0$. But since $D_{\lambda u}\mathcal{F}(\lambda_0,0)\phi_0 = m(x)\phi_0$, we have

$$\int_\Omega D_{\lambda u}\mathcal{F}(\lambda_0,0)\phi_0^2 dx = \int_\Omega m(x)\phi_0^2 = \frac{1}{\lambda_0}\int_\Omega d_2(x,0)|\nabla\phi_0|^2 dx \neq 0$$

due to (2.18). Hence, $D_{\lambda u}\mathcal{F}(\lambda_0,0)x_0 \notin R(D_u\mathcal{F}(\lambda_0,0))$. Therefore, according to Theorem 2.3, there is a bifurcation at $\lambda = \lambda_0$ and on the bifurcating branch

$$(\lambda, u) = (\lambda(s), s\phi_0 + \xi(s)), \ \xi(s) = s\rho(s), \tag{2.19}$$

with $\lambda(0) = \lambda_0$, $\rho(0) = 0$.

We can further determine the direction of bifurcation. Substitute (2.19) into $\nabla \cdot [d_2(x,u)\nabla u] + \lambda(m(x)-u)u = 0$ and differentiate twice in s, then at $s = 0$, we obtain

$$\begin{aligned} & -\nabla \cdot [d_2(x,0)\nabla\xi''(0)] - \lambda_0 m(x)\xi''(0) \\ = \ & 2\nabla \cdot \left[\frac{\partial d_2(x,0)}{\partial u}\phi_0\nabla\phi_0\right] + 2\lambda'(0)m(x)\phi_0 - 2\lambda_0\phi_0^2. \end{aligned}$$

Multiply this equation by ϕ_0 and integrate by parts using the divergence theorem. Because ϕ_0 is the eigenfunction of the principal eigenvalue λ_0, the terms involving ξ'' drop out, and it is easy to see that

$$\lambda'(0)\int_\Omega m(x)\phi_0^2 dx = \int_\Omega \frac{\partial d_2(x,0)}{\partial u}\phi_0|\nabla\phi_0|^2 dx + \lambda_0\int_\Omega \phi_0^3 dx.$$

This relation shows that the sign of $\lambda'(0)$ depends on $\frac{\partial d_2}{\partial u}(x,0)$ since

$$\int_\Omega m(x)\phi_0^2 dx = \frac{1}{\lambda_0}\int_\Omega d_2(x,0)|\nabla\phi_0|^2 dx > 0.$$

In particular, if $\frac{\partial d_2}{\partial u}(x,0) << 0$, then

$$\lambda'(0) = \frac{\int_\Omega \frac{\partial d_2(x,0)}{\partial u}\phi_0|\nabla\phi_0|^2 dx + \lambda_0\int_\Omega \phi_0^3 dx}{\int_\Omega m(x)\phi_0^2 dx} < 0.$$

Thanks to the results in [31], the direction of bifurcation locally determines the stability of the bifurcating solution branch. In this case, $\lambda'(0) < 0$ implies that when $\lambda < \lambda_0$ and $\lambda \approx \lambda_0$, the solution branch is unstable. Then, using subsolution argument, if $\lambda < \lambda_0$ and $\lambda \approx \lambda_0$, there exists another branch of larger solutions, which are stable from below. Also, note that for $\lambda < \lambda_0$, the equilibrium solution $u = 0$ of (2.17) is linearly stable. Therefore, bistable dynamics appear in the model due to nonlinear diffusion, even though the population growth term is logistic. In other words, an Allee effect can be observed that would not be present if the population dispersed by simple diffusion. Why should the condition $\frac{\partial d_2}{\partial u}(x,0) << 0$ create an Allee effect? Let us interpret this phenomena intuitively. $\frac{\partial d_2}{\partial u}(x,0) << 0$ simply means that diffusion decreases rapidly as density increases. When there is small population density, it diffuses very fast, which leads to extinction because of the lethal boundary condition ($u = 0$ on $\partial\Omega$). However, when the population density is very large, slow diffusion at high densities can help the population concentrate near middle of the domain Ω to avoid losses from the lethal boundary. A typical feature of models with Allee effects is that for some parameter values a small change in a parameter may lead to a sudden collapse of the population, and when the population collapses it cannot recover by itself. This is referred to as a *hysteresis effect.*

Our last example is not only about the application of bifurcation theory but also about that of the eigenvalue method. We want to show that the combination of these two methods can help us study the uniqueness of positive solutions in fairly general models. Here is the main result.

Theorem 2.4. *Suppose that the positive solutions of*

$$\nabla\cdot[d(x,u)\nabla u + u\vec{e}(x,u)] + \lambda f(x,u)u = 0,$$

with suitable boundary conditions, exist only for $\lambda > \lambda_0$ *and are all linearly stable. Then the positive solution is unique for any given* λ.

The main idea of the proof is actually quite simple. First, since positive solutions are linearly stable, the continuation of all solution branches is possible by the implicit function theorem. Then notice that at $(\lambda_0, 0)$, according to bifurcation theory, the bifurcating branch is locally unique. Hence, considering the direction of bifurcation with respect to the parameter λ, one can see that nonuniqueness leads to a contradiction. (See [12] for a detailed discussion.) Consider the simple model: $\Delta u + \lambda(m(x) - u)u = 0$ with suitable boundary conditions. By eigenvalue comparison, it is easy to verify that the conditions of Theorem 2.4 are satisfied, hence the positive solution is unique. A more general model: $\nabla \cdot [d(x,u)\nabla u - u\vec{e}(x)] + \lambda(m(x) - u)u = 0$ is investigated in [12] for Dirichlet boundary conditions. When $d(x,u) \equiv d(x,0)$ or $\vec{e} \equiv 0$ and $\partial d/\partial u \geq 0$, the authors show that the hypotheses of Theorem 2.4 are satisfied. An open question is whether the hypotheses of Theorem 2.4 hold in more general cases. For example, what about $\vec{e} \neq 0$ and $\partial d/\partial u \geq 0$? (The question of uniqueness of the positive equilibrium in models with nonlinear diffusion and/or advection and spatially varying coefficients is largely open. Some additional partial results are derived for a particular model in [17], but again many questions remain open.)

3. Interacting species–ecological issues

There are three types of basic interactions between species: cooperation (mutualism), competition and predator-prey. These interaction types may vary with location or density and they may combine. Take *intraguild predation* and *apparent competition* for examples. *Intraguild predation* [50] is the killing and eating of potential competitors. This interaction represents a combination of predation and competition, because both species utilize the same prey resources and also benefit from preying upon one another. *Apparent competition* [49] occurs indirectly between two species which are both preyed upon by the same predator. An increase in one prey population causes an increase in the predator population, which however has a negative effect on the other prey.

The main ecological issues for interacting species are determining when the species can coexist and how coexistence is influenced by spatial heterogeneity and dispersal.

3.1. **Modeling.**

Let us begin our discussion with the dynamical system

$$\frac{du_i}{dt} = f_i(\vec{u})u_i,$$

where $\vec{u} = (u_1, u_2, ..., u_n),\ n \geq 2$. We first assume that f_i is of Lotka-Volterra form since that is the simplest form that is still often useful in understanding how different factors affect the outcomes of interactions between species. Lotka -Volterra models assume that the rate of interaction between species is always described by a mass action law, in the same way as in chemical reactions, so that interaction terms are always products of densities. Improvements may be needed if some unrealistic situation appears.

- *Cooperation:* $\partial f_i/\partial u_j \geq 0$, $i \neq j$. If the Lotka-Volterra form is used, i.e., $f_i = a_i - b_{ii}u_i + \sum_{j\neq i} b_{ij}u_j$, then in some cases solutions may blow up in finite time. To avoid this problem, a realistic assumption is to require that cooperative effects saturate. For example, mutualism with saturation of the mutualistic effects could be described by taking
$$f_i = a_i - b_{ii}u_i + \frac{\sum_{j\neq i} b_{ij}u_j}{1+u_j}.$$
- *Competition:* $\partial f_i/\partial u_j \leq 0$, $i \neq j$. For competion models the Lotka-Volterra form $f_i = a_i - \sum_{j=1}^{n} b_{ij}u_j$ is commonly used. The idea is that if competitors use the same resources, then competition with members of the other species should affect individuals in the same general way as competition with members of their own species, so a term similar to the logistic term in a single species model is an appropriate way to describe competition.
- *Predator-prey:* $\partial f_1/\partial u_2 \geq 0$, $\partial f_2/\partial u_1 \leq 0$ if $n = 2$ and u_1, u_2 denote population densities of predator and prey respectively. Predators may be generalists that consume prey species other than the one in the model, or specialists that depend exclusively on the prey species in the model. Generalist predators can survive even when the prey species is not present. In models for generalist predators that means the linear growth term should be positive, so a logistic term in the predator equation is required to keep the population bounded. A Lotka-Voterra model for a generalist predator and one of its prey species is given by $f_1 = a_1 - b_{11}u_1 + b_{12}u_2, f_2 = a_2 - b_{21}u_1 - b_{22}u_2$, where all coefficients are positive. For specialist predators, the predator cannot survive without the prey, so the predator population will go to zero if the prey is not present, and even without a logistic term in the predator equation the predator population will remain bounded. A Lotka-Volterra model of this situation would be given by $f_1 = -a_1 + b_{12}u_2$, $f_2 = a_2 - b_{21}u_1 - b_{22}u_2$. In Lotka-Volterra models for predation, the mass action terms $b_{12}u_1u_2$ and $b_{21}u_1u_2$ may not be completely accurate when prey densities are high, because with simple mass action the rate of consumption of prey by predators can become arbitrarily high if the prey density becomes high. In reality, it takes a predator some

time to consume a prey item, so there is a limit to how fast predators can consume prey even if there are many prey available. An improvement is the introduction of functional response, which is a more sophisticated description of the rate of prey consumption per predator. The functional response is a function of the predator and prey demnsities. Most functional responses are zero when the prey density is zero and saturate in the sense that they remain bounded as the prey density goes to infinity. Thus a typical form for the functional response is $g(u_1, u_2)u_2$. For a specialist predator with such a functional response, the usual form of the predator-prey model is: $f_1 = -a_1 + b_{12}g(u_1, u_2)u_2, f_2 = a_2 - b_{21}g(u_1, u_2)u_1 - b_{22}u_2$. Various forms of functional response $g(u_1, u_2)u_2$ are in use. For example, the Holling II type: $g(u_1, u_2)u_2 = \dfrac{u_2}{1 + hu_2}$, the Holling III type: $g(u_1, u_2)u_2 = \dfrac{u_2^2}{1 + hu_2^2}$, and the Beddington-DeAngelis type: $g(u_1, u_2)u_2 = \dfrac{u_2}{1 + hu_2 + ku_1}$ are all fairly common. The Beddington-DeAngelis response differs from the others because it depends on both predator and prey densities and decreases as the predator density increases. This describes a situation where the predators interfere with each other while hunting prey if the predator density is high.

Next, let us incorporate dispersal into the system. The simplest form is random dispersal by simple diffusion.:

$$\frac{\partial u_i}{\partial t} = d_i \Delta u_i + f_i(x, t, \vec{u})u_i, \ i = 1, 2, ...n.$$

Reaction-diffusion models of this type have been studied extensively; see[13]. In [77], a competition model with cross-diffusion and advection is formulated as follows

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = \nabla \cdot \{\nabla[(\alpha_1 + \beta_{11}u_1 + \beta_{12}u_2)u_1] + \gamma_1 u_1 \nabla U(x)\} \\ \qquad +(a_1 - b_{11}u_1 - b_{12}u_2)u_1, \\ \dfrac{\partial u_2}{\partial t} = \nabla \cdot \{\nabla[(\alpha_2 + \beta_{21}u_1 + \beta_{22}u_2)u_2] + \gamma_2 u_2 \nabla U(x)\} \\ \qquad +(a_2 - b_{21}u_1 - b_{22}u_2)u_2. \end{cases}$$

In this model, the diffusion rates of these two species depend on the departure point, their diffusion rates increase with the densities of their own population and the population of the competitor so that they avoid crowding, and individuals have a tendency to move along some environment gradient ∇U. Quite a few variations on the original cross diffusion model for competition have been studied, including predator-prey models. In deriving predator-prey models with cross diffusion or other forms of dispersal that depend on predator and prey densities it is important to be sure that the dispersal terms are realistic. Specifically, predators should not run away from prey and prey should not move toward predators. A realistic form of cross diffusion model for a predator-prey that has appeared in the literature [56] is

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = \nabla^2\{(\alpha_1 + \dfrac{\beta_{12}}{1+u_2})u_1\} + f_1 u_1, \\ \dfrac{\partial u_2}{\partial t} = \nabla^2\{(\alpha_2 + \beta_{21}u_1)u_2\} + f_2 u_2. \end{cases}$$

In this model one can see that diffusion rate of predator u_1 decreases in presence of prey u_2 but never becomes negative, and the diffusion rate of prey increases when the predator appears. Thus, predators move more slowly in the presence of prey and thus try to stay near the prey, but prey move more rapidly when predators are around to try to avoid them. The formulation and analysis of relevant and realistic models with nonlinear advection or diffusion terms raises many open questions. The model

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot \left[\dfrac{1}{R(v)} \nabla u - \dfrac{uR'(v)\nabla v}{R(v)[R(v)+g(v)]} \right] + f_1 u \\ \dfrac{\partial v}{\partial t} = d_v \nabla^2 v + f_2 v \end{cases}$$

is proposed in [57]. In this system, u and v represent densities of predator and prey respectively. $R(v) > 0$ is an increasing function which describes the turning rate of predators, while $g(v) > 0$ describes predator satiation. Note that if $g \equiv 0$, then the dispersal term for the predator u becomes $\nabla^2(u/R(v))$, which corresponds to density-dependent diffusion with the diffusion rate based on departure point. See [66] and [67] for related models.

3.2. **Monotone methods.** Arising from the study of simple systems of ordinary differential equation and single reaction-diffusion equations, the classical viewpoint for showing coexistence of interacting species is to show that there is a unique positive equilibrium that is globally attracting among all positive solutions. However for some systems, the situation is much more complicated. For example, predator-prey systems may have limit cycles and food-chain models can have chaos. In fact, even the uniqueness and local stability of equilibria are often hard to prove, especially in reaction-diffusion models. However, it may still be possible to give a reasonable characterization of coexistence in some cases by using monotone methods. It is known that single equation reaction-diffusion models typically have maximum principles. For some dynamical systems, comparison principles still apply, and in fact there is a well developed theory of monotone dynamical systems; see [79]. For example, consider

$$\frac{dv_i}{dt} = f_i(t, \vec{v}),\ 1 \leq i \leq n,$$

and suppose that $\vec{v}(t)$ and $\vec{w}(t)$ are two solutions with initial values $\vec{v}(0)$ and $\vec{w}(0)$. If $\partial f_i/\partial v_j \geq 0$, $i \neq j$, i.e., in mutualism systems, $v_i(0) \geq w_i(0)$ for $1 \leq i \leq n$ implies that $v_i(t) \geq w_i(t)$, $1 \leq i \leq n$. In a 2×2 competition system, i.e., when $n = 2$ and $\partial f_i/\partial v_j \leq 0$, $i \neq j$, if $v_1(0) \geq w_1(0)$ and $v_2(0) \leq w_2(0)$ then $v_1(t) \geq w_1(t)$ and $v_2(t) \leq w_2(t)$ for $t > 0$. However, for $n \times n$ competition systems, $n \geq 3$, and predator-prey systems, usually there are no comparison principles. Even when a dynamical system

$$\frac{dv_i}{dt} = f_i(t, \vec{v}),\ 1 \leq i \leq n,$$

has comparison principles, systems of the form

$$\frac{\partial u_i}{\partial t} = \mathcal{L}_i u_i + f_i(t, \vec{u}),\ 1 \leq i \leq n,$$

generally do not if the differential operator $\mathcal{L}_i$ in one or more of the equations depends on u_j or its derivatives for some $j \neq i$. The lack of maximum principles or comparison principles results in a series of problems. Since u_i denotes a population density, it is naturally expected that $u_i(0) \geq 0$ will imply $u_i(t) \geq 0$ for $t > 0$ and that the solution $u_i(t)$ is bounded on any finite time interval and thus exists globally. Maximum principles are valuable for obtaining such results. Without maximum principles or comparison principles, nonnegativity of solutions and a priori bounds for global existence are much more difficult to obtain. Furthermore, many versions of the method of upper and lower solutions, which are very useful in proving the coexistence or extinction of species and connecting stability to dynamics, are based on comparison principles. Therefore, we will first restrict our discussion to monotone systems, that is, systems with comparison principles.

Let us take a brief review of monotone methods. Suppose that Ω is a smooth bounded domain in $\mathbb{R}^N$, $\mathcal{L}$ is a second order linear uniformly strongly elliptic operator in Ω with smooth coefficients, with boundary conditions on $\partial\Omega$ given by $\mathcal{B}u = \alpha(x)\partial u/\partial n + (1-\alpha(x))u$ where $0 \leq \alpha(x) \leq 1$ is smooth, and $f(x,u)$ is a given smooth function in $\Omega \times \mathbb{R}$ or $\Omega \times U$ for some appropriate subset $U \subset \mathbb{R}$. For single equations, the following comparison principle is well-known.

Theorem 3.1. *Assume that*

1) $\dfrac{\partial u_1}{\partial t} - \mathcal{L}u_1 - f(x,u_1) \geq \dfrac{\partial u_2}{\partial t} - \mathcal{L}u_2 - f(x,u_2)$ *in* $\Omega \times (0,T]$*;*

2) $\mathcal{B}u_1 \geq \mathcal{B}u_2$ *on* $\partial\Omega \times (0,T]$*;*

3) $u_1(x,0) \geq u_2(x,0)$ *in* Ω*.*

Then $u_1(x,t) \geq u_2(x,t)$ *in* $\overline{\Omega} \times [0,T]$*. If in addition, any inequalities in 1), 2) or 3) become strict at some point* $x \in \Omega$*, we have* $u_1(x,t) > u_2(x,t)$ *in* $\Omega \times (0,T]$*.*

Consider the following problem

$$\frac{\partial u}{\partial t} = \mathcal{L}u + f(x,u) \ \text{ in } \Omega \times (0,T], \ \ \mathcal{B}u = 0 \ \text{ on } \partial\Omega \times (0,T]. \tag{3.1}$$

We want to describe a case in which we can use Theorem 3.1 to show the existence of steady states to the problem (3.1). First, suppose that $\underline{u}(x)$ satisfies $\mathcal{L}\underline{u} + f(x,\underline{u}) \geq 0$ in Ω, $\mathcal{B}\underline{u} \leq 0$ on $\partial\Omega$ with one of the previous two inequalities strict for some $x \in \Omega$. Let $u(x,t;\underline{u})$ denote the solution of the problem (3.1) with initial value $\underline{u}(x)$. According to Theorem 3.1, it is easy to see that $u(x,t;\underline{u}) > \underline{u}(x)$ in $\Omega \times (0,T]$. For any $\tau > 0$, set $u_1(x,t) = u(x,t+\tau;\underline{u})$ and $u_2(x,t) = u(x,t;\underline{u})$. Since $u_1(x,0) = u(x,\tau;\underline{u}) > \underline{u}(x) = u_2(x,0)$, applying Theorem 3.1 again, it follows immediately that $u(x,t+\tau;\underline{u}) = u_1(x,t) > u_2(x,t) = u(x,t;\underline{u})$, i.e., $u(x,t;\underline{u})$ is strictly increasing in t. If additionally $u(x,t;\underline{u}) \leq M$ for some $M < \infty$, then we have $\lim_{t\to\infty} u(x,t;\underline{u}) = u^*(x)$ for some $u^*(x)$ and $\mathcal{L}u^* + f(x,u^*) = 0$ in Ω by regularity. Now suppose that $u(x,t;\underline{u}) \leq M$ and suppose further that $u_0(x)$ is a linearly unstable equilibrium of the problem (3.1) and all solutions of (3.1) with positive initial values are bounded. The assumption that $u_0(x)$ is linearly unstable means that the principal eigenvalue σ_0 of the following eigenvalue problem

$$\mathcal{L}\psi + f_u(x,u_0)\psi = \sigma\psi \ \text{ in } \Omega, \ \ \mathcal{B}\psi = 0 \ \text{ on } \partial\Omega$$

is positive with the corresponding eigenfunction ψ_0. It is routine to check that $\underline{u} = u_0 + \epsilon\psi$ satisfies $\mathcal{L}\underline{u} + f(x,\underline{u}) > 0$ in Ω, $\mathcal{B}\underline{u} = 0$ on $\partial\Omega$ provided that ϵ is sufficiently small. Repeating the arguments above, it follows that there exists another equilibrium $u^*(x)$ of (3.1) and clearly $u^*(x) > u_0(x)$. Thus, if solutions are bounded and there is an unstable equilibrium then there must be solutions that start above the unstable equilibrium and increase toward another larger equilibrium. This method could be applied to show that there is a positive equilibrium for the logistic equation with diffusion if the equilibrium $u = 0$ is unstable.

For 2×2 competition systems with linear diffusion and advection, analogous results still hold. To be more specific, consider the following system

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = \mathcal{L}_1 u_1 + g_1(x, u_1, u_2) u_1 & \text{in } \Omega \times (0, \infty) \\ \dfrac{\partial u_2}{\partial t} = \mathcal{L}_2 u_2 + g_2(x, u_1, u_2) u_2 & \text{in } \Omega \times (0, \infty) \\ \mathcal{B} u_1 = \mathcal{B} u_2 = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases} \tag{3.2}$$

with $\partial g_1/\partial u_2 \leq 0$ and $\partial g_2/\partial u_1 \leq 0$. Suppose that two pairs of functions $(u_1(x,t), u_2(x,t))$ and $(v_1(x,t), v_2(x,t))$ satisfy

$$\begin{cases} \dfrac{\partial u_1}{\partial t} - \mathcal{L}_1 u_1 - g_1(x, u_1, u_2) u_1 \geq \dfrac{\partial v_1}{\partial t} - \mathcal{L}_1 v_1 - g_1(x, v_1, v_2) v_1 \\ \dfrac{\partial u_2}{\partial t} - \mathcal{L}_2 u_2 - g_2(x, u_1, u_2) u_2 \leq \dfrac{\partial v_2}{\partial t} - \mathcal{L}_2 v_2 - g_2(x, v_1, v_2) v_2 \\ \mathcal{B} u_1 \geq \mathcal{B} v_1, \mathcal{B} u_2 \leq \mathcal{B} v_2 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

Then if initially $u_1(x,0) \geq v_1(x,0)$ and $u_2(x,0) \leq v_2(x,0)$, we have $u_1(x,t) \geq v_1(x,t)$ and $u_2(x,t) \leq v_2(x,t)$. Simply speaking, the system (3.2) is called order-preserving or monotone. Suppose that the system (3.2) only admits two semi-trivial equilibria $(u_1^*(x), 0)$ and $(0, u_2^*(x))$. If they are both linearly unstable, then by monotonicity arguments similar to the one that was just described for the single equation (3.1), there exist positive steady states $(w_1^*(x), w_2^*(x))$ and $(w_1^{**}(x), w_2^{**}(x))$ satisfying $0 < w_1^* \leq w_1^{**} < u_1^*$ and $u_2^* > w_2^* \geq w_2^{**} > 0$. Furthermore the set $\{(u_1, u_2) : w_1^* \leq u_1 \leq w_1^{**} \text{ and } w_2^{**} \leq u_2 \leq w_2^*\}$ is globally attracting among positive solutions. Hence, we say these two species can coexist. It might be the case that $(w_1^*(x), w_2^*(x)) = (w_1^{**}(x), w_2^{**}(x))$, but the monotonicity argument by itself does not show that. Thus, in this case, there might or might not be a unique globally stable positive equilibrium, but there certainly will be a globally stable positive attracting set. The key idea is that if one of the semi-trivial equilibria is linearly unstable, then trajectories that start close to it will be bounded by trajectories that go in a monotone way to another equilibrium. If the other semi-trivial equilibrium is also unstable then those trajectories will be bounded away from it and thus there will be a positive attracting set and positive equilibria as described above. On the other hand, if there is no coexistence equilibrium and one of the semi-trivial equilibria is unstable, then the only other nonnegative equilibrium is the other semi-trivial equilibrium, so that solutions are forced to converge to that equilibrium, i.e., it is globally asymptotically stable, so one of the species becomes extinct.

3.3. **Persistence theory.** In the context of models for interacting species the instability of a semi-trivial equilibrium where a given species is not present means that the species can invade a system where it is not present if it is introduced at a low density. We have seen that mutual invasibility, that is, the instability of both semi-trivial equilibria, predicts coexistence in models for two competitors. A conjecture proposed by Turelli in 1978 [80] is that in models for arbitrarily many competitors *coexistence is implied by mutual invasibility.* However, this is not always true and additional conditions are required. A counter-example due to May and Leonard can be found in [70] where a three-species competition model

$$\begin{cases} \dfrac{du_1}{dt} = [1 - u_1 - \alpha u_2 - \beta u_3]u_1 \\ \dfrac{du_2}{dt} = [1 - \beta u_1 - u_2 - \alpha u_3]u_2 \\ \dfrac{du_3}{dt} = [1 - \alpha u_1 - \beta u_2 - u_3]u_3 \end{cases} \tag{3.3}$$

with $\alpha < 1 < \beta$ is studied. It is routine to check that all three semi-trivial steady states $(1,0,0)$, $(0,1,0)$ and $(0,0,1)$ are linearly unstable. However, it can be shown that the model has a globally stable positive equilibrium so that the species coexist if $\alpha+\beta < 2$ but the densities of the three species are periodically small because trajectories spiral outward toward the boundary of the positive octant if $\alpha+\beta > 2$. A key difference between the May-Leonard example and the case of two competitors is that in the models for two competitors the system is monotone but in the case of three or more it is not. This raises two interesting questions, namely, when is it true that invasibility implies coexistence, and how can we use invasibility to establish coexistence in systems that are not monotone? These questions are addressed by persistence theory.

Persistence theory was originated for Kolmogorov type ODE models

$$\frac{du_i}{dt} = f_i(\vec{u})u_i,\ i = 1, 2, ..., n,\ \vec{u} = (u_1, u_2, ..., u_n).$$

Kolmogorov type models are simply population models where the functions describing species interactions are essentially arbitrary except for the requirement that the growth rate in the equation for ith species must have the density u_i of that species as a factor, so that if the population is initially 0 it will remain 0. In such models, the sets $Y_0 = \{\vec{u} \in \mathbb{R}^N : u_i > 0,\ i = 1, 2, ..., n\}$ and $\partial Y_0 = \{\vec{u} \in \mathbb{R}^N : u_i \geq 0,\ i = 1, 2, ..., n; u_j = 0 \text{ for some } 1 \leq j \leq n\}$ are invariant. A system is *uniformly persistent* if there exists $\epsilon > 0$ such that for any trajectory $\vec{u}(t)$ with $\vec{u}(0) \in Y_0$,

$$\liminf_{t\to+\infty} d(\vec{u}(t), \partial Y_0) > \epsilon$$

where $d(\vec{u}(t), \partial Y_0)$ denotes the distance from $\vec{u}(t)$ to ∂Y_0. The key point is that the if the system is uniformly persistent then the densities of all populations are eventually bounded below by some fixed constant, so that none will become extinct. The populations might coexist at a stable equilibrium, but they might also coexist on a positive periodic orbit or even a positive strange attractor. If in addition to being uniformly persistent a system is also point dissipative, so that there is a bounded set that all trajectories eventually enter, then it is said to be permanent. It turns out that systems which are permanent must have a positive equilibrium but it is not necessarily unique or stable. Persistence theory provides criteria for determining when a system is persistent. It is formulated in terms of dynamical or semi-dynamical systems. Reaction-advection-diffusion models generate semi-dynamical systems on appropriate spaces (see for example [44, 72]) so persistence theory can be applied to them.

Two technical problems arise in applying persistence theory to PDE models that are not present in the ODE case. First, the underlying space Y is infinite dimensional and not locally compact. Second, if for example we take $Y_0 = \{\vec{u} \in [C(\overline{\Omega})]^n : u_i > 0 \text{ on } \overline{\Omega},\ i = 1, 2, ..., n\}$, then $\vec{u} \in \partial Y_0$ if for some i, $u_i(x_0) = 0$ for some $x_0 \in \Omega$ but $u_i \neq 0 \in C(\overline{\Omega})$. Therefore, additional analysis is needed in the PDE case. It turns out that the technical problems can be overcome by using regularity theory and the strong maximum principle.

Suppose that π is a semi-dynamical system on a complete metric space Y. π is *point dissipative* if there is a bounded set $U \subseteq Y$ such that for any $y \in Y$ there exists $t^* > 0$ so that $\pi(y, t)$ satisfies $\pi(y, t) \in U$ for $t > t^*$. An important background result for using persistence theory and other methods from dynamical systems theory is as follows:

Theorem 3.2 ([9]). *If π is point dissipative and there exists $t_0 > 0$ such that for any given bounded set $V \subseteq Y$, the set $\{\pi(v, t) : v \in V, t \geq t_0\}$ is compact, then π has a compact global attractor Q.*

Now consider the following system

$$\begin{cases} \dfrac{\partial u_i}{\partial t} = \mathcal{L}_i u_i + f_i(x, \vec{u}) u_i & \text{in } \Omega \times (0, \infty) \\ \dfrac{\partial u_i}{\partial n} + b_i(x) u_i = 0 & \text{on } \partial\Omega \times (0, \infty) \\ \vec{u}(x, 0) = \vec{u}_0(x), \end{cases} \tag{3.4}$$

where $1 \leq i \leq n$, Ω is bounded with $\partial\Omega$ smooth, and for each i, $\mathcal{L}_i$ is a second order elliptic operator with smooth coefficients. Let Y be a space where (3.4) generates a semidynamical system. (Depending on the details of the model and boundary conditions we may want to work in $[C(\overline{\Omega})]^n$, $[C^1(\overline{\Omega})]^n$, or some other space. See [44, 72] for detailed discussions of this topic.) Let $Y_0 = \{\vec{u} \in Y : u_i > 0 \text{ on } \overline{\Omega},\ i = 1, 2, ..., n\}$. Define $\pi(\vec{u}_0, t) = \vec{u}(x, t)$. Suppose that π is dissipative. Parabolic regularity can be used to show that for a bounded set $V \subseteq Y$ and $t_0 > 0$, the set $\{\pi(v, t) : v \in V, t \geq t_0\}$ is compact. Because of parabolic regularity and Theorem 3.2, π has a compact global attractor, denoted by Q. Let $\widetilde{X} = \pi(B(Q, \epsilon), [0, \infty))$, where $B(Q, \epsilon)$ denotes an $\epsilon-$neighborhood of Q, and $X = \pi(\widetilde{X}, t')$ for some fixed $t' > 0$. Then on X, orbits $\pi(\vec{u}_0, t)$ correspond to classical solutions of (3.4) and by the strong maximum principle, for any $\vec{u} \in S = \partial Y_0 \bigcap X$, $u_i \equiv 0$ must hold for some i, $1 \leq i \leq n$ and for $j \neq i$, either $u_j \equiv 0$ or $u_j > 0$ on $\overline{\Omega}$. Therefore, treating π as a semi-dynamical system restricted to X, the analysis is analogous to the ODE case.

For $u \in X$, define

$$\omega(u) = \bigcap_{t \geq 0} \overline{\bigcup_{s \geq t} \{\pi(u, r) : r \geq s\}}$$

and define $\alpha(u)$ to be the set of all limits of all sequences $\{y_n\} \subseteq X$ such that $\lim_{n\to\infty} \pi(y_n, t_n) = u$ for some sequence $\{t_n\}$ with $\lim_{n\to\infty} t_n = \infty$.

The *stable set* and *unstable set* of a compact invariant set M are defined to be

$$W^s(M) = \{u \in X : \omega(u) \neq \emptyset, \omega(u) \subseteq M\}$$

and

$$W^u(M) = \{u \in X : \alpha(u) \neq \emptyset, \alpha(u) \subseteq M\}$$

respectively. Assuming that M and N are isolated invariant sets, then M is *chained* to N if there exists $u \in W^u(M) \bigcap W^s(N)$, denoted by $M \to N$. A sequence of isolated invariant sets $M_1, M_2, ..., M_k$, $k \geq 1$, is called a *chain* if $M_1 \to M_2 \to ... \to M_k$. It is a *cycle* if $M_1 = M_k$.

Recall that $S = \partial Y_0 \bigcap X$. Let $\omega(S) = \bigcup_{u \in S} \omega(u)$. (Note that this is not the standard definition of the ω-limit set of a set.) The set $\omega(S)$ is *isolated* if $\omega(S) = \bigcup_{j=1}^{k} M_j$, where M_j, $1 \leq j \leq k$, are isolated invariant sets. $\omega(S)$ is called *acyclic* if it is isolated and no subcollection of $\{M_1, M_2, ..., M_k\}$ is a cycle.

The principal result on persistence can now be stated.

Theorem 3.3 ([42]). *Suppose that the assumptions of Theorem 3.2 hold and* $\omega(S)$ *is acyclic. Then* π *is uniformly persistent (permanent) if and only if for each* M_j, $1 \leq j \leq k$

$$W^s(M_j) \bigcap (X \setminus S) = \emptyset. \tag{3.5}$$

Roughly speaking, $W^s(M_j) \bigcap (X \setminus S) = \emptyset$ is an invasibility condition.

For the application of persistence theory, first take a predator-prey model

$$\tag{3.6}\begin{cases}\dfrac{\partial u_1}{\partial t} = \nabla\cdot[d_1\nabla u_1 - u_1\nabla p_1] + \left(-d + \dfrac{e(x)u_2}{1+h_1(x)u_1+h_2(x)u_2}\right)u_1 \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial u_2}{\partial t} = \nabla\cdot[d_2\nabla u_2 - u_2\nabla p_2] + (a(x)-b(x)u_2)u_2 \\ \qquad\qquad -\dfrac{c(x)u_1u_2}{1+h_1(x)u_1+h_2(x)u_2} \qquad\qquad\qquad \text{in } \Omega\times(0,\infty), \\ \alpha_i(x)[d_i\nabla u_i - u_i\nabla p_i]\cdot\vec{n} + (1-\alpha_i(x))u_i = 0,\ i=1,2 \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{on } \partial\Omega\times(0,\infty) \end{cases}$$

for example. Assume that there exists $\epsilon_0 > 0$ such that $d, b(x), d_i, h_i(x) \ge \epsilon_0$ and $\epsilon_0 \le \alpha_i(x) \le 1$, $i = 1, 2$. Note that by setting

$$v_i = e^{-p_i/d_i}u_i,$$

the boundary condition is converted to $\frac{\partial v_i}{\partial \vec{n}} + \beta_i(x)v_i = 0$. This allows use of the maximum principle for each equation individually. Moreover, since $d, b(x), h_i(x) \ge \epsilon_0$, arguments based on the maximum principle (applied to one equation at a time) and regularity theory show that the system is dissipative and bounded orbits are precompact. It then follows that the assumptions in Theorem 3.2 are satisfied. Next, let us check the other assumptions in Theorem 3.3. On the one hand, if $u_2 \equiv 0$, u_1 satisfies

$$\frac{\partial u_1}{\partial t} = \nabla\cdot[d_1\nabla u_1 - u_1\nabla p_1] - du_1,$$

thus it is easy to see that $\lim_{t\to\infty} u_1(x,t) = 0$. On the other hand, if $u_1 \equiv 0$, then u_2 satisfies

$$\tag{3.7}\frac{\partial u_2}{\partial t} = \nabla\cdot[d_2\nabla u_2 - u_2\nabla p_2] + (a(x)-b(x)u_2)u_2.$$

Assume that $u_2 \equiv 0$, as a equilibrium of (3.7), is linearly unstable. Then the stable set of $(0,0)$ is the set $\{(u_1,0) : u_1 \ge 0\}$ and (3.7) has a unique stable positive equilibrium u_2^*, and since the set of equilibria in S consists of $(0,0)$ and $(0,u_2^*)$ with $(0,0)$ unstable and $(0,u_2^*)$ stable relative to S, there are no cycles present in the semiflow restricted to S. Additionally, assume that $(0,u_2^*)$ is a linearly unstable steady state of (3.6) relative to X; then (3.5) is satisfied. Therefore, according to Theorem 3.3, the system is permanent.

Similarly, for a system with a generalist predator

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = \nabla\cdot[d_1\nabla u_1 - u_1\nabla p_1] + \left(a_1(x) - b_1(x)u_1 + \dfrac{e(x)u_2}{1+h_1(x)u_1+h_2(x)u_2}\right)u_1 \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{in } \Omega\times(0,\infty), \\ \dfrac{\partial u_2}{\partial t} = \nabla\cdot[d_2\nabla u_2 - u_2\nabla p_2] + (a(x)-b(x)u_2)u_2 - \dfrac{c(x)u_1u_2}{1+h_1(x)u_1+h_2(x)u_2} \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{in } \Omega\times(0,\infty), \\ \alpha_i(x)[d_i\nabla u_i - u_i\nabla p_i]\cdot\vec{n} + (1-\alpha_i(x))u_i = 0,\ i=1,2 \\ \qquad\qquad\qquad\qquad\qquad\qquad\qquad \text{on } \partial\Omega\times(0,\infty), \end{cases}$$

if $(u_1^*, 0)$ and $(0, u_2^*)$ are the two unique semi-trivial steady states, which are linearly unstable, then the system is permanent.

Simply speaking, *in predator-prey models (and other models that do not generate monotone semiflows), persistence theory shows that coexistence is implied by mutual invasibility and acyclicity*, just as *in 2×2 competition models, monotone methods show coexistence is implied by mutual invasibility.* An important difference between monotone and nonmonotone systems is that monotonicity also can be used to show extinction while persistence theory cannot, and in fact there are not many methods for showing extinction in nonmonotone systems. Sometimes Lyapunov functions or functionals can be used, but they are not always available and there are few general methods for constructing them. Finding ways of showing extinction in general models is an important area of research that is largely open.

Cross diffusion parabolic systems of the type

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla\cdot[(d_1+\alpha_{11}u+\alpha_{12}v)\nabla u + \beta_1 u\nabla v] + (a_1 - b_1u - c_1v)u, \\ \dfrac{\partial v}{\partial t} = \nabla\cdot[\beta_2 v\nabla u + (d_2+\alpha_{21}u+\alpha_{22}v)\nabla v] + (a_2 - b_2u - c_2v)v, \end{cases}$$

supplied with Neumann or Robin type boundary conditions, originated from the Shigesada, Kawasaki and Teramoto model [77]. Although they describe two competing species they are not monotone because of the coupling in the derivative terms. In [64] and [65], the authors investigate the dynamics of this system in $[W^{1,p}(\Omega)]^2$ with $p > N$ for $\Omega \subseteq \mathbb{R}^N$ and in particular, establish the existence of global attractors and give conditions for persistence in $[C^1(\overline{\Omega})]^2$.

Persistence is also studied in the intraguild predation model with density-dependent dispersal

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_1\Delta u + \left(r(x) - \omega_1 u - \dfrac{a_1 v}{1+h_1a_1u} - \dfrac{a_1 w}{1+h_2a_2u}\right)u, \\ \dfrac{\partial v}{\partial t} = \Delta[M(u,w)v] + g(u,v,w)v, \\ \dfrac{\partial w}{\partial t} = d_3\Delta w + \left(\dfrac{e_3a_3v}{1+h_3a_3v} + \dfrac{e_2a_2u}{1+h_2a_2u} - \mu_2 - \omega_3 w\right)w, \end{cases}$$

with Neumann boundary conditions, where u, v, w represent prey (resources), intermediate predator/intraguild prey and intraguild predator (top predator) respectively,

$$g(u,v,w) = \frac{e_1a_1u}{1+h_1a_1u} - \frac{a_3w}{1+h_3a_3v} - \mu_1 - \omega_2 v,$$

and $M(u,w) = m_\lambda(g(u,0,w))$ where m_λ is a family of functions depending on a parameter λ so that for positive constants $0 < d < d_2$ we have $m_0(g) = d_2 > 0$ for all real g, $m_\lambda(0) = d_2$ for $\lambda \geq 0$, $m_\lambda(g) \leq d_2$ but $m_\lambda(g) \geq d$ if $g > 0$, and $m_\lambda(g) \geq d_2$ with $m_\lambda(g) \to \infty$ as $\lambda \to \infty$ if $g < 0$. From the viewpoint of biology, $g(u,0,w)$, the local growth rate of v when $v \approx 0$, can be interpreted as the fitness of the intermediate predator/intraguild prey when its density is low. The diffusion coefficient $M(u,w) = m(g(u,0,w))$ in this system implies that the diffusion rate of intermediate predator depends on the departure point and is smaller when fitness is positive and larger when fitness is negative, with the strength of the effect increasing with λ. This is biologically reasonable because it reflects the idea that individuals will stay in one place longer in favorable regions but move around more in unfavorable regions to seek resources or avoid predators. It is shown in [75] that for λ sufficiently large this type of dispersal allows persistence of the intermediate predator while random dispersal does not.

In general, persistence in an $n \times n$ system requires rather complete information about each $(n-1)\times(n-1)$ subsystem with $u_i \equiv 0$ for some $1 \leq i \leq n$. This limits the application of persistence theory to $n = 2, 3$ in many cases. In quasilinear systems, it is highly nontrivial to derive a priori estimates which imply the existence of compact attractors. See [64] and [65] for example. Moreover, so far for quasilinear systems, persistence results are set in $[C^1(\overline{\Omega})]^n$. However, generally $\|u\|_{C^1(\overline{\Omega})} \geq c_0 > 0$ does not prevent $\|u\|_{L^1}$ (total population) or $\|u\|_{L^\infty}$ (maximum density) from being small, since u might oscillate rapidly with respect to space or concentrate at some locations so that the gradient if u could be large while the maximum or average of u is small. Therefore, obtaining better or easier estimates of population densities in complex models and determining when oscillation in space or concentration can happen or be ruled out are very important open questions in ecological models. Furthermore, in nonmonotone systems, the absence of a positive equilibrium does not in general imply extinction of either population. Hence another important question is how to get extinction results and other precise information on the dynamics of predator-prey models, quasilinear two-species competition models, three-species competition models, etc., where monotonicity fails.

3.4. **More examples and questions.** Systems describing two or three interacting species that disperse by simple diffusion in a spatially homogeneous environment have been widely studied using well developed methods. See [13]. However, models for situations with nonlinear diffusion, advection on gradients of resource or population density, and spatial heterogeneity are much less well understood, and current methods appear to be inadequate for their analysis. There are many interesting ecological interactions that can be described by such models, and they give rise to many interesting open problems in mathematics. However, it is important to study models that provide reasonable descriptions of situations that are ecologically interesting and which can provide new insights into the effects of dispersal on ecological interactions.

The key idea in modeling is to consider realistic situations where the type of dispersal could make a difference. Take predator-prey models as an example. Consider the model

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [\nabla(d(v)u) - \alpha u \nabla P(v)] + \left(-d + \dfrac{ecv}{1+hcv}\right) u, \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [\nabla(D(u)v) + \beta v \nabla Q(u)] + \left(m(x) - v - \dfrac{cu}{1+hcv}\right) v, \end{cases}$$

where α, $\beta > 0$, u and v represent predator and prey densities respectively. In reality, we expect that predators seek prey and prey avoid predators. Therefore, in this model, we should assume that $d'(v) \leq 0$ and $P'(v) \geq 0$, which indicates that predators diffuse more slowly when prey are present and advect up gradient of prey density. On the other hand, we should assume that $D'(u) \geq 0$ and $Q'(u) \geq 0$. This implies that prey diffuse more rapidly in the presence of predators and advect down the gradient of predator density. (Note that in the equation for u , α appears with a $-$ sign, while in the equation for v, β appears with a $+$ sign.) These assumptions about the dispersal terms imply that the predators move in ways that help them find prey but prey move in ways that help them avoid predators. A reasonable alternative model is as follows:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d\nabla u - \alpha u \nabla P(m(x))] + \left(-d + \dfrac{ecv}{1+hcv}\right) u, \\ \dfrac{\partial v}{\partial t} = D\Delta v + \left(m(x) - v - \dfrac{cu}{1+hcv}\right) v. \end{cases}$$

Assume that $P'(m) > 0$ and D is small. Under those assumptions, the prey diffuse slowly enough that their density is higher where the resources $m(x)$ are better. Predators cannot directly sense prey density but they can track the prey's resources and move up the gradients of the prey's resources. In this case the prey move at random but the predators move in a way that might help them find prey. These are also plausible assumptions about dispersal, but different from those in the previous model. A common question in these two models is how dispersal affects the persistence and dynamics of predators and prey. When further comparing these two sorts of models on the macro scale, a series of optimality or evolutionary questions arise naturally. Is it better for the predators to track the prey density, the prey's resources, or some kind of combination? To help themselves find and stay in contact with prey, is it more effective for predators to slow down their random movement when prey are present or to use directed movement up the gradient of prey density? Should either predators or prey avoid crowding by their own species? And so on.

Understanding the effects of dispersal is a very important and challenging topic. Many questions remain open even for 2×2 systems. One type of problem that is open in many cases is the question of global existence versus finite time blow-up of solutions in quasilinear models. This question is also related to the phenomenon where population densities concentrate at certain points, because concentration occurs in some forms of finite time blow-up. Taking a further look at the mechanisms that are incorporated into different types of models suggests some guesses about when concentration might occur. For purposes of comparison it is interesting to recall the case of chemotaxis models. It is known that Keller-Segel chemotaxis model (rescaled)

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [\nabla u - \chi u \nabla v], \\ \dfrac{\partial v}{\partial t} = \Delta v + (u - v), \end{cases}$$

where the constant χ is positive, can have finite time blow-up solutions in $\mathbb{R}^N$, $N \geq 2$. (For a discussion of chemotaxis models see [48].) Note that in this model, u activates v and u advects up ∇v. This feedback can lead to concentration and blow-up in higher space dimensions. However, for the Shigesada-Kawasaki-Teramoto type cross diffusion model for competition

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [(d_1 + \alpha_{11} u + \alpha_{12} v)\nabla u + \beta_1 u \nabla v] + (a_1 - b_1 u - c_1 v)u, \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [\beta_2 v \nabla u + (d_2 + \alpha_{21} u + \alpha_{22} v)\nabla v] + (a_2 - b_2 u - c_2 v)v, \end{cases}$$

u advects down ∇v and vice-versa, increasing u or v increases both diffusion rates, and also u and v inhibit each other. These effects could be expected to create negative feedbacks between the densities u and v so that concentration and blow up seem less likely. On the other hand, in predator-prey models, the prey activates the predator. If the predator also advects up the gradient of prey density, which is a biologically plausible type of movement, then the same sort of positive feedbacks are present as in the Keller-Segel model and concentration phenomena or blow-up seem more likely to occur. These kinds of analysis and guesses give us the intuition and motivation for further mathematical investigations. Some relatively recent results and some references on global existence in cross diffusion models are given in [6, 23, 63].

To conclude this section, we want to present an interesting question related to random diffusion and competition models. It is known that in some cases random dispersal is harmful for the existence of species. For example, in the problem

$$\frac{\partial u}{\partial t} = d\Delta u + (m(x) - u)u \ \text{ in } \Omega \times (0,\infty), \quad \partial u/\partial n = 0 \ \text{ on } \partial\Omega \times (0,\infty),$$

where $m(x)$ is continuous, $m(x_0) > 0$ for some $x_0 \in \Omega$ and $\int_\Omega m(x)dx < 0$, there exists $d_* > 0$ such that the problem has a globally asymptotically stable positive equilibrium if $d < d_*$ while it has no positive steady states if $d > d_*$. When it comes to the 2×2 competition dynamical system

$$\begin{cases} \dfrac{du}{dt} = (m(x) - u - c_1 v)u, \\ \dfrac{dv}{dt} = (m(x) - c_2 u - v)v, \end{cases}$$

it is known that if $c_1 > 1 > c_2$, then the competitor v always wins, i.e., for each x, $\lim_{t\to\infty} u(x,t) = 0$, $\lim_{t\to\infty} v(x,t) = v^*(x) \geq 0$. An open question is, if by incorporating random dispersal as follows

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\Delta u + (m(x) - u - c_1 v)u, \\ \dfrac{\partial v}{\partial t} = \Delta[D(u)v] + (m(x) - c_2 u - v)v, \end{cases}$$

where $D(u)$ increases with u, can the species with density u coexist with the species with density v by increasing movement of v, since that would possibly be harmful to the species with density v? (If $D(u)$ is increasing, which is plausible biologically, then if coexistence is possible at all it might require the density u to be sufficiently high, which would imply something like an Allee effect. Coexistence in models with Allee effects typically is conditional on the initial population densities, but models with Allee effects can sometimes have locally stable positive solutions.)

There are more possible cases when it comes to three-species interactions. For example, food chains, two consumers sharing a resource and possibly interfering with each other, one consumer using resources that may compete with each other, 3 competitors, and so on. All these interactions could be influenced by dispersal, especially when it is conditional on densities of other species. Consequently, there are many open topics related to effects of dispersal on persistence.

Above all, in formulating an ecological model, it is important to understand the mechanisms underlying the model and make sure that the modeling assumptions are reasonable.

4. Interacting species–evolutionary issues

Ecological and evolutionary processes are inescapably intertwined. Evolution is much slower because advantageous mutations are rare. Selection is often based on ecological factors. There are natural questions about the evolution of dispersal strategies. What strategies can evolve? Once evolved, what strategies can persist? New traits arise from mutations, hence evolutionary change within a species typically starts with a small number of individuals. A new trait can evolve if a small population that has it can invade an established population with a different trait. An existing trait can persist if a large population with it can resist invasion by any small population with any other trait. Ecological competition is the competition between populations, which is a single competitive interaction between a small number of species or subspecies that may differ in many traits. However, evolutionary competition is the competition between traits, which is a series of competitive interactions among a collection of subspecies that differ in only one or a few traits but are similar in all others. Traits that are related to behavior or life history are called *strategies*. *An evolutionarily stable strategy (ESS)* is a strategy that has the property that no established population using it can be invaded by any small population using a different strategy. *A convergent stable strategy* has the property that a population using a strategy close to it can invade a population using one which is further away.

Let us use the following simple examples to briefly explain the difference between ecological and evolutionary problems. A typical ecological question about the effects of dispersal would be to consider a system of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_u \nabla u - \alpha u \nabla \ell] + (\ell(x) - u - bv)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_v \nabla v - \beta v \nabla m] + (m(x) - cu - v)v & \text{in } \Omega \times (0,\infty), \\ \gamma[d_u \nabla u - \alpha u \nabla \ell] \cdot \vec{n} + (1-\gamma)u = 0 & \text{on } \partial\Omega \times (0,\infty), \\ \delta[d_v \nabla v - \beta v \nabla m] \cdot \vec{n} + (1-\delta)u = 0 & \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

describing two competing species with some *specific fixed types of dispersal* and ask when the parameters in the dispersal terms allow the two species coexist and when they result in one of them becoming extinct. Note that in this system, the ecological terms are different, reflecting different ecological niches for the two species. In contrast, a typical evolutionary question concerns systems of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_u \nabla u - \alpha u \nabla m] + (m(x) - u - v)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_v \nabla v - \beta v \nabla m] + (m(x) - u - v)v & \text{in } \Omega \times (0,\infty), \\ \gamma[d_u \nabla u - \alpha u \nabla m] \cdot \vec{n} + (1-\gamma)u = 0 & \text{on } \partial\Omega \times (0,\infty), \\ \gamma[d_v \nabla v - \beta v \nabla m] \cdot \vec{n} + (1-\gamma)u = 0 & \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

describing sub-populations of the same species where the ecological terms are the same but the dispersal strategies are different. A common evolutionary question in this model would be to ask whether or not there is a dispersal strategy, that is, a choice (d_u^*, α^*) for (d_u, α), such that the corresponding semi-trivial steady state $(u^*, 0)$ is stable relative to nonnegative solutions of this system for *any other possible dispersal strategy* $d_v \neq d_u^*$, $\beta \neq \alpha^*$ that the sub-population with density v might use. In general biological terms, the question is whether or not there is a dispersal strategy such that a sub-population of a species using it can resist invasion by any small sub-population of that species using any other dispersal strategy. In the specific terminology of evolutionary theory, this question is simply whether or not there exists an evolutionarily stable strategy (ESS) (d_u^*, α^*). (As in many problems about existence in mathematics, a good way to show that such strategies exist is to explicitly find them, if that is possible.)

4.1. **Selection for dispersal.** Let us begin our discussion with the models and approach introduced by Hastings [43] in 1983 . In [43], Hastings studied a model with simple diffusion and spatial variation

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_u \nabla \cdot [\mu(x)\nabla u] + f(x,u)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial u}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{4.1}$$

Suppose that $f(x,u)$ is decreasing in u, $f(x,0) > 0$ and $f(x,u) < 0$ for u large. In that case the model will have a unique positive stable equilibrium solution $u^*(x)$. Think of u^* as the density of an established resident population. Further assume that $f(x,u)$ is nonconstant when u is any given positive constant. This condition guarantees that we cannot have $f(x,u^*) \equiv 0$. Suppose otherwise. Then if $f(x,u^*) \equiv 0$, it follows that u^* has to be constant since it satisfies (4.1). Then according to that assumption, $f(x,u^*)$ is nonconstant, which is a contradiction. First, let us take a look at Hastings' approach. Think of v as an invading small population with a similar dispersal pattern but different rate and assume that v has little impact on u. Hence v satisfies

$$\begin{cases} \dfrac{\partial v}{\partial t} = d_v \nabla \cdot [\mu(x)\nabla v] + f(x,u^*+v)v & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases}$$

The linearized problem at $v = 0$ is

$$\begin{cases} d_v \nabla \cdot [\mu(x)\nabla \psi] + f(x,u^*)\psi = \sigma\psi & \text{in } \Omega, \\ \dfrac{\partial \psi}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases} \tag{4.2}$$

It is known that the invasion is possible if and only if the principle eigenvalue σ_0 of (4.2) is positive. Recall that $u^*(x)$ as the resident satisfies

$$\begin{cases} d_u \nabla \cdot [\mu(x)\nabla u^*] + f(x,u^*)u^* = 0 & \text{in } \Omega, \\ \dfrac{\partial u}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Then if $d_v < d_u$, direct computation gives

$$\begin{aligned}\sigma_0 &= \sup_{\psi \in W^{1,2}(\Omega)} \frac{-d_v \int_\Omega \mu(x)|\nabla \psi|^2 dx + \int_\Omega f(x,u^*)\psi^2 dx}{\int_\Omega \psi^2 dx} \\ &\geq \frac{-d_v \int_\Omega \mu(x)|\nabla u^*|^2 dx + \int_\Omega f(x,u^*)(u^*)^2 dx}{\int_\Omega (u^*)^2 dx} \\ &> \frac{-d_u \int_\Omega \mu(x)|\nabla u^*|^2 dx + \int_\Omega f(x,u^*)(u^*)^2 dx}{\int_\Omega (u^*)^2 dx} = 0.\end{aligned}$$

Note that the second inequality is strict since $f(x,u^*) \neq 0$ implies that $\nabla u^* \neq 0$. Therefore, following Hastings' approach, we see that u^* can be invaded by a small population using dispersal strategy $d_v \nabla \cdot [\mu(x)\nabla v]$ if and only is $d_v < d_u$. In other words, no dispersal strategy with $d_u > 0$ and $f(x,u^*) \neq 0$ can be evolutionarily stable and the strategy with $d_u = 0$ is convergent stable. What is happening that leads to this result? Consider the logistic term, i.e., $f(x,u^*) = m(x) - u^*$. In this form $m(x)$ determines the population density the environment can support at location x. It can be interpreted as describing the availability of resources for the population. For any fixed $d_u > 0$, integrating the equation satisfied by u^*, we have $\int_\Omega f(x,u^*)u^* dx = 0$. Since $f(x,u^*) = m(x) - u^*$ can not be identically zero as explained before, $f(x,u^*) = m(x) - u^*$ must change signs. This means that the equilibrium population density u^* of the resident does not match resource availability and thus it could be invaded because it leaves some resources available to an invader.

A possible objection to Hastings' approach is that it does not treat the resident and invader symmetrically. Later, in [34], that issue was addressed for a special case by using the following model:

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_u \Delta u + [m(x) - u - v]u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = d_v \Delta v + [m(x) - u - v]v & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial u}{\partial n} = \dfrac{\partial v}{\partial n} = 0 & \text{on } \partial\Omega \times (0,\infty). \end{cases} \tag{4.3}$$

In [34] it was shown that if $\int_\Omega m(x)dx > 0$, there exist two semi-trivial steady states $(u^*,0)$ and $(0,v^*)$ for all $d_u > 0$, $d_v > 0$. If $d_u > d_v$, then $(u^*,0)$ is linearly unstable and $(0,v^*)$ is linearly stable. It is also easy to verify that there are no positive steady states. These results follow from eigenvalue comparisons. Notice that this is a monotone system, hence it follows from monotone methods (Section 3.2) that $(0,v^*)$ is globally asymptotically stable. That indicates that there is selection for slower random dispersal. Why should that be the case? In the previous example (4.1), we already know that for any fixed $d_u > 0$, u^* does not match resource availability. However, it can proved that if $m(x) > 0$ in Ω, then as $d_u \to 0$, $u^* \to m(x)$ uniformly on any closed subset of Ω. Therefore the smaller the dispersal rate is, the better the population density of the species matches resource availability.

What about conditional dispersal, that is, nonrandom dispersal in response to environmental conditions? McPeek and Holt [71] found that there was selection for certain types of conditional dispersal in numerical studies of discrete time two-patch models. In the context of reaction-diffusion-advection models it seems plausible that the forms of conditional dispersal that might be favored by selection are those that allow populations to best match their resources. One idea of how to find such dispersal strategies is to introduce some kind of advection and see whether it is possible to adjust it so that it leads to a population that matches the resource $m(x)$. A natural thing to try is to incorporate advection up the gradient of resource density:

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

The effects of advection up the gradient of $m(x)$ are subtle. Roughly speaking, when $\alpha > 0$ is small, the equilibrium solution $u^*(x)$ matches the resource $m(x)$ better than simple diffusion, at least in convex domains. (In nonconvex domains there are counterexamples showing that advection up the resource gradient is not necessarily beneficial to a population; see [25].) Even in convex domains, when α is large, $u^*(x)$ will typically concentrate near peaks of $m(x)$ and thus match the resource less well. In fact, it is shown in [16] that

$$\|u^*\|_{L^2(\Omega)} \to 0 \quad \text{as } \alpha \to \infty.$$

To further understand the effects of advection on selection, consider

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_u \nabla u - \alpha u \nabla m] + (m(x) - u - v)u & \text{in } \Omega \times (0, \infty), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_v \nabla v - \beta v \nabla m] + (m(x) - u - v)v & \text{in } \Omega \times (0, \infty), \\ [d_u \nabla u - \alpha u \nabla m] \cdot \vec{n} = [d_v \nabla v - \beta v \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{4.4}$$

For simplicity, assume that Ω is convex and $\int_\Omega m(x)dx > 0$. Then semi-trivial steady states $(u^*(x), 0)$ and $(0, v^*(x))$ exist for all $d_u > 0$, $d_v > 0$, $\alpha \geq 0$ and $\beta \geq 0$. The linear stability of these two equilibrium solutions $(u^*(x), 0)$ and $(0, v^*(x))$ depends on the principal eigenvalues τ_0 and σ_0 of the eigenvalue problems

$$\begin{cases} \nabla \cdot [d_v \nabla \psi - \beta \psi \nabla m] + (m(x) - u^*)\psi = \tau \psi & \text{in } \Omega, \\ [d_v \nabla \psi - \beta \psi \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega, \end{cases} \tag{4.5}$$

and

$$\begin{cases} \nabla \cdot [d_u \nabla \phi - \alpha \phi \nabla m] + (m(x) - v^*)\phi = \sigma \phi & \text{in } \Omega, \\ [d_u \nabla \phi - \alpha \phi \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega, \end{cases} \tag{4.6}$$

respectively. Several special cases have been investigated.

Case 1. *$d_u \approx d_v$, $\alpha > 0$, $\alpha \approx 0$ and $\beta = 0$.*

In [15], the authors studied the stability of $(u^*(x), 0)$ and $(0, v^*(x))$ by perturbing the system near $d_u = d_v = d_0$, $\alpha = \beta = 0$. To be more explicit, let $\theta(x)$ be the positive solution of

$$\begin{cases} d_0 \Delta \theta + (m(x) - \theta)\theta = 0 & \text{in } \Omega, \\ \nabla \theta \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Set $d_u = d_0 + \epsilon d_{u1} + ...$, $d_v = d_0 + \epsilon d_{v1} + ...$, $\alpha = \epsilon \alpha_1 + ...$ and $\beta = 0$. Then $u^*(x) = \theta(x) + \epsilon u_1 + ...$, $v^*(x) = \theta(x) + \epsilon v_1 + ...$, and this leads to perturbed eigenvalue problems for the linear stability of $(u^*(x), 0)$ and $(0, v^*(x))$. It is verified that $\tau_0 = \epsilon \tau_1 + ...$ and $\sigma_0 = \epsilon \sigma_1 + ...$, where $\sigma_1 = -\tau_1 = (d_{v1} - d_{u1})I_1(\theta) + \alpha_1 I_2(\theta)$, $I_1(\theta) > 0$ and $I_2(\theta) > 0$. Hence clearly, if $\alpha_1 >> 1$, even with $d_{u1} > d_{v1}$, we still have $\tau_0 < 0$, $\sigma_0 > 0$ for $\epsilon \approx 0$, $\epsilon > 0$, which means that $(u^*(x), 0)$ is stable and $(0, v^*(x))$ is unstable. Therefore there could be selection for the sub-species with faster diffusion (represented by u) when it is combined with advection up the resource gradient.

If we additionally assume that the set of critical points of $m(x)$ has measure zero, there are another two cases, which are treated in [21].

Case 2. *d_u, d_v are arbitrary, α is large while β is small.* It is proved in [21] that there is a constant Λ_1 independent of β such that if

$$(\alpha, \beta) \in [\Lambda_1, \infty) \times \left[0, \frac{d_v}{\max_{\overline{\Omega}} m}\right],$$

then the equilibrium solutions $(u^*(x), 0)$ and $(0, v^*(x))$ of (4.4) are both unstable. Hence the two species can coexist.

As mentioned before, the stability of $(u^*(x), 0)$ is determined by the sign of the principal eigenvalue τ_0 of the eigenvalue problem (4.5). Setting $\rho = e^{-(\beta/d_v)m(x)}\psi$, (4.5) is converted into

$$\begin{cases} d_v\nabla\cdot[e^{(\beta/d_v)m}\nabla\rho] + e^{(\beta/d_v)m}(m(x)-u^*)\rho = \tau e^{(\beta/d_v)m}\rho & \text{in } \Omega, \\ \dfrac{\partial\rho}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

Since $\|u^*\|_{L^2(\Omega)} \to 0$ as $\alpha \to \infty$, we have

$$\int_\Omega e^{(\beta/d_v)m}(m(x)-u^*)dx \to \int_\Omega e^{(\beta/d_v)m}m(x)dx > 0.$$

Hence $\tau_0 > 0$ for α large. Similarly, the stability of $(0, v^*(x))$ is determined by the principle eigenvalue σ_0 of the converted problem

$$\begin{cases} d_u\nabla\cdot[e^{(\alpha/d_u)m}\nabla\varrho] + e^{(\alpha/d_u)m}(m(x)-v^*)\varrho = \sigma e^{(\alpha/d_u)m}\varrho & \text{in } \Omega, \\ \dfrac{\partial\varrho}{\partial n} = 0 & \text{on } \partial\Omega. \end{cases}$$

For coexistence it suffices to show that the principal eigenvalue of the above problem is positive when α is large enough and β is small. A maximum principle argument shows that $max_{\overline{\Omega}}(m(x)-v^*) > 0$ if $\beta < \nu/max_{\overline{\Omega}}(m(x))$. It follows that

$$\int_{\{x:m(x)-v^*>0\}} e^{(\alpha/d_u)(m-v^*)}(m-v^*)dx \to \infty$$

as $\alpha \to \infty$. Integral estimates then can be used to show that for α large,

$$\int_\Omega e^{(\alpha/d_u)(m)}(m-v^*)dx > 0,$$

so that $\sigma_0 > 0$ for α large, as needed.

Case 3. *d_u, d_v are arbitrary, β is large and α is larger.*
This case is also studied in [21] and the following result is proved: there is an increasing function $\Lambda_2(\beta)$ defined on $[\frac{d_v}{\min_{\overline{\Omega}} m}, \infty)$ such that if $\beta \geq \frac{d_v}{\min_{\overline{\Omega}} m}$ and $\alpha \geq \Lambda_2(\beta)$ then the semi-trivial steady state $(0, v^*)$ of (4.4) is globally asymptotically stable, that is, the species v prevails.

It is quite interesting and important to interpret these results from a biological point of view. In the first case, due to the effect of advection ($\alpha > 0, \alpha \approx 0$), u^* matches the resource $m(x)$ better than v^* hence u^* wins. However, in the second case, for u^*, the advection up resource gradient is strong, hence it overmatches $m(x)$ where $m(x)$ is large and undermatches when $m(x)$ is small. However, for v^*, the advection is weak and thus v^* overmatches $m(x)$ when $m(x)$ is small and undermatches $m(x)$ when it is large. This makes it possible for u^* and

v^* to share the resources and coexist. Finally, in the third case, due to the strong advection, both u^* and v^* overmatch the resource when $m(x)$ is large and undermatch when $m(x)$ is small. But v^* matches $m(x)$ better than u^* since the advection for u^* is too strong. Therefore v^* wins.

In a summary, mathematical analysis suggests that in logistic-type models, the competitive advantage goes to strategies that allow the species to better match the resources $m(x)$.

There are many related results on the effects of advection on $m(x)$ and there has been more precise analysis of concentration phenomenon of the problem (4.4). For further discussion and detailed derivations of the results described above see [5, 8, 15, 16, 21, 22, 25, 40, 59, 61] and the references therein. However, many important questions still remain open. First, obviously in (4.4),

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_u \nabla u - \alpha u \nabla m] + (m(x) - u - v)u & \text{in } \Omega \times (0, \infty), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_v \nabla v - \beta v \nabla m] + (m(x) - u - v)v & \text{in } \Omega \times (0, \infty), \\ [d_u \nabla u - \alpha u \nabla m] \cdot \vec{n} = [d_v \nabla v - \beta v \nabla m] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases}$$

the only way for u^* or v^* to match resources perfectly is to choose $d_u = \alpha = 0$ or $d_v = \beta = 0$. Now suppose that $d_u, d_v \geq d_0 > 0$. Then one has a series of open or partially open questions as follows:

- Assume that $d_u = d_v = d_0$, is there an evolutionarily stable strategy corresponding to some particular value of α? (Recently Lam and Lou [60] have given an affirmative answer in the case of small diffusion and some conditions on $m(x)$, but they also give examples suggesting that the general case is quite subtle.)
- What if $d_u > 0$ and $d_v > 0$ are fixed? Is there a choice of α such that u wins for any β? Or is there a choice of β such that v wins for any α?
- Suppose that $d_u, d_v \geq d_0 > 0$. Is there an evolutionarily stable choice for (d_u, α)?
- Suppose that $\alpha = \beta$ is fixed. Is there an evolutionarily stable choice of d_u?

There are many other variations of these kinds of questions.

A related model which consists of three interacting species is studied in [36]. In this model, think of the competitors as predators P_1, P_2 that compete for the same prey V, where V has a spatially varying resource $R(x)$ and the predators track a combination of prey and prey resource gradients:

$$\begin{cases} \dfrac{\partial P_i}{\partial t} = \nabla \cdot (d_i \nabla P_i - \alpha_i P_i \nabla[\tau_i \nabla R + (1-\tau_i)\nabla V]) + (-k + aV)P_i \\ \hfill \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial V}{\partial t} = d_v \Delta V + [R(x) - V - b(P_1 + P_2)]V \qquad \text{in } \Omega \times (0,\infty), \\ (d_i \nabla P_i - \alpha_i P_i \nabla[\tau_i \nabla R + (1-\tau_i)\nabla V]) \cdot \vec{n} = \nabla V \cdot \vec{n} = 0 \\ \hfill \text{on } \partial\Omega \times (0,\infty), \end{cases}$$

for $i = 1, 2$. The parameters τ_i describe the relative weights that the predators give to information on prey density versus information on the density of the prey's resource. It is routine to show that each predator P_i can persist when the other is not present if $k < k_i^*$ where k_i^* is the principal eigenvalue of

$$\begin{cases} \nabla \cdot (d_i \nabla \psi - \alpha_i \psi \nabla[\tau_i \nabla R + (1-\tau_i)\nabla\theta]) + a\theta\psi = k\psi & \text{in } \Omega, \\ (d_i \nabla \psi - \alpha_i \psi \nabla[\tau_i \nabla R + (1-\tau_i)\nabla\theta]) \cdot \vec{n} = 0 & \text{on } \partial\Omega, \end{cases}$$

and $\theta(x) > 0$ satisfies

$$\begin{cases} d_v \Delta\theta + (R(x) - \theta)\theta = 0 & \text{in } \Omega, \\ \nabla\theta \cdot \vec{n} = 0 & \text{on } \partial\Omega. \end{cases}$$

In particular, in [36], it is proved that in the one dimensional case $\Omega = (0,1)$, under certain conditions on $R(x)$, k_i^* is increasing in τ_i, $i = 1, 2$ for small positive α. This implies that tracking the resource $R(x)$ instead of tracking the prey itself is helpful for each predator on its own for small positive α. Many problems regarding this model remain open, especially for higher dimensional cases.

4.2. **Ideal free distribution.** A verbal theory developed by ecologists to describe how organisms organisms are distributed in space is based on the idea that if individuals have complete knowledge of their environment and are free to move, they will locate themselves to optimize fitness. This is called the *ideal free distribution* [37], [38]. Here fitness is interpreted in the evolutionary sense of expected reproductive success rate, which typically depends on habitat and crowding. The ideal free distribution can be characterized by two key features:

- At equilibrium, all individuals at all locations will have equal fitness, since otherwise some individuals would move from locations of lower fitness to those where fitness is higher, and
- there should be no net movement at equilibrium since all individuals have optimized their locations and thus an individual moving to a new location would reduce its fitness unless it traded places with an individual who was at the location.

First, let us summarize some of the main topics related to the ideal free distribution. Questions arise at various different spatial and temporal scales. At the micro scale of individual behavior, recall that random walks based on simple diffusion, diffusion depending on arrival or departure point, and advection can produce a range of possible model forms as continuum limits. That raises questions about which kinds of local dispersal behavior can produce a global ideal free distribution. This is biologically interesting because if a population can achieve an ideal free distribution based on local behavior, a complete knowledge of the environment is not required. This makes the theory more plausible. At the meso scale of population dynamics and dispersal, what does ideal free dispersal mean in reaction-diffusion-advection equations or other types of models? Finally, at the macro scale of evolution of species, are strategies leading to ideal free distribution evolutionarily stable? (Numerical results by McPeek and Holt [71] on two-patch models suggest that this is true in the models they studied. We will see that it is in fact true in a number of settings.)

To further interpret the ideal free distribution at the meso scale, consider the following example

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d(x,u)\nabla u - \alpha u \nabla e(x,u)] + f(x,u)u & \text{in } \ \Omega \times (0,\infty), \\ [d(x,u)\nabla u - \alpha u \nabla e(x,u)] \cdot \vec{n} = 0 & \text{on } \ \partial\Omega \times (0,\infty). \end{cases}$$

Here, fitness is regarded as local intrinsic growth rate $f(x,u)$. At the meso scale, the idea for the dynamics of ideal free distribution is to add movement up gradient of $f(x,u)$ or some related quantity. At equilibrium $u^* > 0$, ideal free dispersal implies equal fitness, that is, $f(x,u^*)$ is constant. Clearly, $\int_\Omega f(x,u^*)u^* dx = 0$ due to the no-flux boundary condition. Hence we have $f(x,u^*) \equiv 0$. Note that this directly contradicts the key assumption in Hastings' approach to showing that there is selection for slower dispersal in the case of simple diffusion (see Section 4.1), which in turn suggests that there might be selection that favors ideal free dispersal since if it is possible for a population to achieve an ideal free distribution then it will match the available resources perfectly. Furthermore, there is no net movement, so it must be the case that

$$\begin{cases} \nabla \cdot [d(x,u^*)\nabla u^* - \alpha u^* \nabla e(x,u^*)] = 0 & \text{in } \ \Omega, \\ [d(x,u^*)\nabla u^* - \alpha u^* \nabla e(x,u^*)] \cdot \vec{n} = 0 & \text{on } \ \partial\Omega. \end{cases}$$

It is possible to satisfy this requirement within some classes of dispersal strategies but not others. It is not possible with simple diffusion. We will examine some types of dispersal strategies where it is possible. It turns out that certain combinations of simple diffusion and advection and certain forms of diffusion depending on arrival or departure point can support an ideal free distribution. This is how we interpret the ideal free distribution at the meso scale.

In the following, first we want to talk about several strategies which support an ideal free distribution and then further analyze the models whenever possible.

Example 1 [24]**.** Assume that individuals can sense resource and population gradients, and advect along them. Specifically, using logistic fitness $f(x,u) = m(x) - u$, assume that the advection is up the fitness gradient. Then we have

$$\frac{\partial u}{\partial t} = -\alpha \nabla \cdot [u \nabla (m(x) - u)]. \tag{4.7}$$

The following cases are studied separately.

Case 1. *Without population dynamics.* Suppose that $\Omega = (0, \infty)$ and no-flux boundary condition at $x = 0$. W.l.o.g., set $\alpha = 1$ in (4.7). Define

$$E(t) = \frac{1}{2} \int_0^\infty u^2 \left[\frac{\partial}{\partial x}(m - u) \right]^2 dx.$$

Formal computation yields that

$$E'(t) = -\int_0^\infty u \left(\frac{\partial u}{\partial t} \right)^2 dx + \frac{1}{2} \int_0^\infty \frac{\partial^2 m}{\partial x^2} u^2 \left[\frac{\partial}{\partial x}(m - u) \right]^2 dx.$$

If $\frac{\partial^2 m}{\partial x^2} \leq 0$, then $E' \leq 0$. Hence, the model is expected to stabilize with

$$u \frac{\partial}{\partial x}(m - u) = 0.$$

Therefore, fitness $m(x) - u$ is constant where $u \neq 0$.

Case 2. *With population dynamics.* Incorporating population dynamics of logistic type, we have

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

Obviously, $u^* = m(x)$ satisfies this problem, hence this model supports ideal free distribution.

Since (4.7) is a degenerate diffusion equation, it is expected to be mathematically similar to porous medium equations and related problems. An ecological model without advection but with degenerate diffusion is studied in [33]. A variation on the model (4.7) that incorporates population growth and random diffusion is studied in [17]. The assumption that there is some random movement is plausible since individuals may need to move at random to search for food or avoid predators. Here is the reaction-diffusion-advection equation with no-flux boundary condition:

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d\nabla u - \alpha u \nabla(m(x) - u)] + (m(x) - u)u & \text{in } \Omega \times (0, \infty), \\ [d\nabla u - \alpha u \nabla(m(x) - u)] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{4.8}$$

This model does not support an ideal free distribution if m depends on x, because if $u^* = m$ is an equilibrium the equation forces m to be constant. However, if individuals move rapidly up the fitness gradient (α large) or have limited random movement (d small) then the model can have an equilibrium where $u \approx m$. Among other things, the following result is proved in [17]:

Theorem 4.1. *Suppose that $m(x) > 0$ in $\overline{\Omega}$. For large α/d, the problem (4.8) has a unique positive steady state u which is globally asymptotically stable. Moreover, for any given $\eta > 0$, if $\alpha \geq \eta$ and $\alpha/d \to \infty$, then $u \to m$ in $C^2(\overline{\Omega})$.*

This result shows that a dispersal mechanism based on local information about the environment and population density can approximate the ideal free distribution and such a dispersal mechanism may sometimes be advantageous because it allows populations to approximately track resource availability.

Example 2. Conditional dispersal requires knowledge of conditions, which in turn requires sensory information. Suppose that the sensory response to a stimulus s is $G(s)$, where s might represent the number of resource items or other individuals encountered in unit time and $G(s)$ should be an increasing function. Then assume that individuals advect on the gradient of the difference between their sensory response to resources and their response to density, so that they balance seeking resources and avoiding crowding. That leads to the model

$$\begin{cases} \dfrac{\partial u}{\partial t} = -\nabla \cdot [u(\nabla G(m) - \nabla G(u))] + (m(x) - u)u & \text{in } \Omega \times (0, \infty), \\ u(\nabla G(m) - \nabla G(u)) \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases}$$

This model supports an ideal free distribution, that is, a positive equilibrium $u^* = m(x)$, if $m(x) > 0$.

According to the Weber-Frechner Law [32], the intensity of sensory response to a stimulus is logorithmic, that is $G(s) = \gamma \ln s$, where γ is a positive constant. Therefore the previous model becomes

$$\begin{cases} \dfrac{\partial u}{\partial t} = \gamma \nabla \cdot \left[\nabla u - u\dfrac{\nabla m}{m}\right] + (m(x) - u)u & \text{in } \Omega \times (0, \infty), \\ \left[\nabla u - u\dfrac{\nabla m}{m}\right] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty). \end{cases} \tag{4.9}$$

In fact, in this model, there is no direct density dependence in dispersal, hence this strategy is not directly fitness dependent and does not require density information. Instead, it can be interpreted as saying that individuals move up the resource gradient but go slower if m is large, that is, when there are a lot of resources available.

Example 3. Recall that in the micro-scale diffusion process where the dispersal probability depends on both departure point as $p_1(x)$ and arrival point as $p_2(x)$, the diffusion equation is

$$\frac{\partial u}{\partial t} = \gamma \nabla \cdot \left[p_2^2(x) \nabla \left(\frac{p_1(x)}{p_2(x)} u \right) \right] + (m(x) - u)u.$$

Suppose that $m(x) > 0$. It is easy to see that, if $\frac{p_1(x)}{p_2(x)} = \frac{\gamma_0}{m}$, then this model supports an ideal free distribution. Particularly, if $p_1(x) = \gamma_1/\sqrt{m}$ and $p_2(x) = \gamma_2\sqrt{m}$, then this diffusion equation becomes

$$\begin{aligned} \frac{\partial u}{\partial t} &= \gamma_3 \nabla \cdot \left[m(x) \nabla \left(\frac{u}{m(x)} \right) \right] \\ &= \gamma_3 \nabla \cdot \left[\nabla u - u \frac{\nabla m}{m} \right] + (m(x) - u)u, \end{aligned}$$

where $\gamma_3 = \gamma_1\gamma_2$, which is the same as the model (4.9). Another way to obtain a model which can support an ideal free distribution is to take p_2 constant and $p_1 = 1/m(x)$. Obviously, there are many more possibilities.

Now, we are ready to discuss evolutionary stability of ideal free dispersal based on advection. Consider

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_u \nabla \cdot [\nabla u - u \nabla P] + (m(x) - u - v)u & \text{in } \Omega \times (0, \infty), \\ \dfrac{\partial v}{\partial t} = d_v \nabla \cdot [\nabla v - v \nabla Q] + (m(x) - u - v)v & \text{in } \Omega \times (0, \infty), \\ [\nabla u - u \nabla P] \cdot \vec{n} = [\nabla v - v \nabla Q] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty), \end{cases} \tag{4.10}$$

where $P(x), Q(x), m(x) \in C^2(\overline{\Omega})$ and $d_u, d_v, m(x) > 0$. See [3], [18] and [39].

Theorem 4.2 ([3]). *Suppose that $P = \ln m$ and $Q - \ln m$ is not constant, then $(u^*, 0)$ is globally asymptotically stable in (4.10), where $u^* = m(x)$ is the ideal free distribution of the model (4.9).*

This shows that within the class of strategies of the form $d_u \nabla \cdot [\nabla u - u \nabla P]$, the strategies with $P = \ln m$ are the only evolutionarily stable strategies. It is worth pointing out that, according to the definition of evolutionarily stable strategies, it suffices to verify that $(u^*, 0)$ is locally stable. But unfortunately there is a difficulty in analyzing local stability of $(u^*, 0)$. Actually, this issue appears in a more general case. Suppose that the general system

$$\begin{cases} \dfrac{\partial u}{\partial t} = \mathcal{L}u + f(x, u+v)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = \mathcal{M}v + f(x, u+v)v & \text{in } \Omega \times (0,\infty), \end{cases}$$

with no-flux boundary conditions, admits a semi-trivial steady state $(u^*, 0)$, where u^* is the ideal free distribution of

$$\frac{\partial u}{\partial t} = \mathcal{L}u + f(x, u)u \quad \text{in } \Omega \times (0,\infty),$$

again with no-flux boundary condition. Hence, as in the discussion at the beginning of this subsection, one has $f(x, u^*) = 0$. Then it is routine to check that the linearized problem at $(u^*, 0)$ is

$$\begin{cases} \mathcal{L}\psi + f_u(x, u^*)u^*(\psi + \phi) = \sigma\psi & \text{in } \Omega, \\ \mathcal{M}\phi = \sigma\phi & \text{in } Omega, \end{cases} \tag{4.11}$$

with no-flux boundary conditions. In particular, if

$$\mathcal{M}\phi = \nabla \cdot [d_v(x)\nabla\phi - \phi\nabla Q(x)] \ \text{ in } \Omega$$

with boundary condition

$$[d_v(x)\nabla\phi - \phi\nabla Q(x)] \cdot \vec{n} = 0 \ \text{ on } \partial\Omega,$$

then integrating the second equation in (4.11) shows that $\sigma = 0$ is the principal eigenvalue. Therefore, the linearized problem (4.11) only yields neutral stability and nonlinear analysis is required for further results.

Fortunately, in studying the problem (4.10), monotone methods apply. See Section 3.2. Hence to prove Theorem 4.2, it suffices to verify that $(0, v^*)$ is linearly unstable and (4.10) has no coexistence steady state. This is done in [3].

In another type of model, where the dispersal probability depends on *departure* point,

$$\begin{cases} \dfrac{\partial u}{\partial t} = \Delta(d_u(x)u) + (m(x) - u - v)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = \Delta(d_v(x)v) + (m(x) - u - v)v & \text{in } \Omega \times (0,\infty), \\ \nabla(d_u(x)u) \cdot \vec{n} = \nabla(d_v(x)v) \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0,\infty), \end{cases} \tag{4.12}$$

analysis similar to that in [3] shows that if $d_u(x) = d_0/m(x)$, then

$$\begin{cases} \dfrac{\partial u}{\partial t} = \Delta(d_u(x)u) + (m(x) - u)u & \text{in } \Omega \times (0,\infty), \\ \nabla(d_u(x)u) \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases}$$

admits an ideal free distribution $u^* = m(x)$, and if $d_v(x)m(x)$ is nonconstant, then $(u^*, 0)$ is globally asymptotically stable. Again, strategies that lead to an ideal free distribution are evolutionarily stable relative to those that do not. (In general it is possible for different strategies that lead to ideal free distributions to coexist in a state of neutral stability.)

Returning to the model (4.10), there are many possible forms for $P(x)$ and $Q(x)$ and various results about how those influence coexistence or exclusion; a number of those are presented in [39]. For example, suppose that $P = \ln m + \alpha R(x)$, $Q = \ln m + \beta R(x)$ and $R(x)$ is nonconstant. If $\alpha\beta < 0$, then the semi-trivial steady states $(u^*, 0)$ and $(0, v^*)$ are unstable, hence u and v could coexist. In the system

$$\begin{cases} \dfrac{\partial u}{\partial t} = \nabla \cdot [d_u \nabla u - \alpha u \nabla \ln m] + (m(x) - u - v)u & \text{in } \Omega \times (0, \infty), \\ \dfrac{\partial v}{\partial t} = \nabla \cdot [d_v \nabla v - \beta v \nabla \ln m] + (m(x) - u - v)v & \text{in } \Omega \times (0, \infty), \\ [d_u \nabla u - \alpha u \nabla \ln m] \cdot \vec{n} = [d_v \nabla v - \beta v \nabla \ln m] \cdot \vec{n} = 0 & \text{on } \partial\Omega \times (0, \infty) \end{cases}$$

it is proved in [39] that if $\Omega \subset \mathbb{R}$ is an interval, $m'(x) > 0$, and $d_u = d_v$, then the strategy $\alpha = d_u$ is convergent stable. However, within the restricted class of strategies shown in (4.2) where only α and β are allowed to vary, there is numerical evidence of locally evolutionarily or convergent stable strategies with $\alpha \neq d_u$ if $m(x)$ is not monotone. Many detailed questions about evolutionary stability of dispersal strategies within particular classes of strategies remain open.

4.3. **Time periodic models.**

As discussed at the end of Section 2.2, for the following linear operators

$$\mathcal{L}u = \partial u/\partial t - \mathcal{A}(t)u,$$

where

$$\mathcal{A}(t)u = \sum_{i,j=1}^{N} a_{ij}(x,t) \frac{\partial^2 u}{\partial x_i \partial x_j} + \sum_{i=1}^{N} a_i(x,t) \frac{\partial u}{\partial x_i} + a_0(x,t)u$$

is uniformly strongly elliptic, all coefficients are smooth and $T-$periodic in t, there is a well developed theory for the existence of principal eigenvalues. Therefore, the ideas of comparing dispersal strategies extend to this case. However, the results are quite different.

Theorem 4.3 ([51]). *If in the following problem*

$$\begin{cases} \dfrac{\partial u}{\partial t} = d_u \Delta u + (m(x,t) - u - v)u & \text{in } \Omega \times (0,\infty), \\ \dfrac{\partial v}{\partial t} = d_v \Delta v + (m(x,t) - u - v)v & \text{in } \Omega \times (0,\infty), \\ \partial u/\partial n = \partial v/\partial n = 0 & \text{on } \partial\Omega \times (0,\infty) \end{cases}$$

where $m(x,t)$ is $T-$periodic in t, then there may be coexistence, or the semi-trivial steady state $(u^*,0)$ may be stable even when $d_u > d_v$.

Note that when $m = m(x)$, this problem is reduced to (4.3) in Section 4.1 and there is always selection for slower random dispersal. Hence, the periodic case is qualitatively different. Numerical simulation in [71] for two-patch models shows that certain conditional dispersal strategies are evolutionarily stable in time varying environments.

Generally speaking, it is not clear how anything like an ideal free distribution can be achieved in a time-periodic model by using mechanisms based on advection and variable diffusion. It may be impossible, as in the purely spatial case with only simple diffusion and advection on ∇m. There are many open questions about which conditional dispersal strategies are evolutionarily stable or convergent stable in environments that vary in both time and space.

Overall, existence theory for evolutionarily stable strategies is a very challenging topic. Based on the discussion so far, our guess is that, in models that support an ideal free distribution, the form of evolutionarily stable strategies will be those leading to the ideal free distribution. What if an ideal free distribution is impossible within a class of strategies? Is there still an evolutionarily stable strategy? How can it be characterized? This is a very large class of open problems. If restricted to *dispersal strategies based on advection and diffusion* in spatially varying but temporally constant environments, existence theory for evolutionarily stable strategies can be rephrased more explicitly as a series of topics.

(i) Identify all the dispersal strategies based on advection and diffusion that can lead to an ideal free distribution.

(ii) In a class of strategies where an ideal free distribution is possible, determine which strategies are evolutionarily stable. As mentioned earlier, a reasonable guess is that it will be those resulting in an ideal free distribution. This guess has been verified in models (4.10) and (4.12).

(iii) In classes of strategies that do not support an ideal free distribution, determine how to characterize evolutionarily stable strategies.

For strategies in time periodic cases, the same question as (iii) arises.

4.4. **Spatially discrete models.** Spatially discrete models are widely used by ecologists to describe populations in patchy habitats. They allow more general dispersal than diffusion and may be simpler to analyze in some cases since they are finite dimensional.

Let us begin our discussion with single species models which are discrete in space and continuous in time. Suppose that there is a network of n habitat patches. Let u_i denote the population in patch i, $1 \leq i \leq n$. A model for dispersal in a spatially discrete setting would typically take the form

$$\frac{d\vec{u}}{dt} = M\vec{u},$$

where $\vec{u} = (u_1, ...u_n)$ and $M = ((d_{ij}))$ is an $n \times n$ matrix with $d_{ij} \geq 0$, $i \neq j$.The matrix M it is called *irreducible* if $M : \mathbb{R}^n \to \mathbb{R}^n$ has no invariant subspace except $\mathbb{R}^n$, while it is called *primitive* if M^p has all entries positive for some power p. It is known that if M is irreducible, then $u_i(0) > 0$ for some $1 \leq i \leq n$ implies that when $t > 0$, $u_j(t) > 0$ for all $1 \leq j \leq n$. This is sufficient to establish results analogous to the strong maximum principle for parabolic equations. If M is also primitive, then M has a unique principal eigenvalue σ_0, that is, $M\vec{\phi}_0 = \sigma\vec{\phi}_0$ with $\sigma_0 > 0$ and $\vec{\phi}_0 > 0$. The dynamics of spatially discrete problems

$$\frac{du_i}{dt} = G_i(\vec{u}),$$

where $1 \leq i \leq n$, can be classified in the same way as in Section 3.1. For example, if $\partial G_i/\partial u_j \geq 0$ for $i \neq j$, the system is called a *cooperative* system. In a cooperative system, if $\vec{u}$, $\vec{v}$ are two solutions with $\vec{u}(0) \geq \vec{v}(0)$, then $\vec{u}(t) \geq \vec{v}(t)$. Thus it is a monotone dynamical system. Models for population dynamics in discrete space and continuous time are typically formulated as

$$\frac{du_i}{dt} = \sum_{j=1}^{n} d_{ij}u_j - \sum_{j=1}^{n} d_{ji}u_i + f_i(u_i)u_i, \quad i = 1 \ldots n. \tag{4.13}$$

Since the system in (4.13) is cooperative, it can be treated by monotone methods in a manner similar to a single reaction-diffusion equation. For example, if the matrix $M = ((d_{ij}))$ is irreducible and for each i we have $f_i(0) > 0$, $f_i'(u) < 0$, and $f_i(u) < 0$ for u large, then (4.13) will have a unique positive equilibrium that is globally stable among positive solutions, exactly as in the case of a reaction-diffusion model with a logistic type of nonlinearity.

Models discrete in both time and space are also very common, since many organisms only reproduce once a year. Discrete dispersal can be formulated as

$$u_i(t+1) = \sum_{j=1, j\neq i}^{n} D_{ij} u_j(t) + \left(1 - \sum_{j=1, j\neq i}^{n} D_{ji}\right) u_i(t),$$

where $1 \leq i \leq n$ and D_{ij} represents fraction of population in patch j that goes to patch i, so that $0 \leq D_{ij} \leq 1$ for all i, j. For the dynamics, generally it is expressed as

$$u(t+1) = f(t, u(t))u(t).$$

The linear case

$$u(t+1) = au(t)$$

is a very simple example. It is easy to see that, in this case, $u(t) = a^t u(0)$. Hence as $t \to \infty$, $u(t) \to \infty$ if $a > 1$, while $u(t) \to 0$ if $0 < a < 1$. For autonomous case

$$u(t+1) = f(u(t))u(t),$$

if $f(0) > 1$ and $f(u) < 1$ for u large, then there is an equilibrium u^*, i.e., $f(u^*) = 1$. Moreover, if $f(u)$ is decreasing, then u^* is unique. If $f(u)u$ is also increasing then the equilibrium is stable, but if not the equilibrium may lose stability and there may be stable periodic solutions or even chaos.

It is natural to consider multiple species models which are discrete in space. In the case of continuous time such a model for N interacting species would have the form

$$\frac{du_i^k}{dt} = \sum_{j=1}^{n} d_{ij}^k u_j^k - \sum_{j=1}^{n} d_{ji}^k u_i^k + f_i^k(u_i^1, u_i^2, ..., u_i^N) u_i^k, \tag{4.14}$$

where superscripts indicate species, so that $((d_{ij}^k))$ represents the dispersal strategy for the population of species k, where $1 \leq k \leq N$ and $1 \leq i, j \leq n$.

Suppose that $(\vec{u}^{1*}, \vec{u}^{2*}, ..., \vec{u}^{N*})$ is an equilibrium solution of (4.14). For simplicity, assume that the attempt at invasion is only made by the first species and the invader $\vec{v}^1$ uses strategy $((\widetilde{d_{ij}^1}))$. In Hastings' modeling approach (see the beginning of Section 4.1), whether $\vec{u}^{1*}$ is invasible is determined by stability of $\vec{v}^1 = 0$ relative to nonnegative initial data in the system

$$\frac{dv_i^1}{dt} = \sum_{j=1}^{n} \widetilde{d}_{ij}^1 v_j^1 - \sum_{j=1}^{n} \widetilde{d}_{ji}^1 v_i^1 + F_i^1(\vec{u}^{1*} + \vec{v}^1, \vec{u}^{2*}, ..., \vec{u}^{N*}) v_i^1, \tag{4.15}$$

where $1 \leq i \leq n$. If $\vec{v}^1 = 0$ is stable then $\vec{u}^{1*}$ is not invasible by $\vec{v}^1$; if $\vec{v}^1 = 0$ is unstable then $\vec{u}^{1*}$ is invasible by $\vec{v}^1$. We say a dispersal strategy $((d_{ij}^1))$ is ideal free relative to $(\vec{u}^{1*}, \vec{u}^{2*}, ..., \vec{u}^{N*})$ if there is no net movement of population when $(\vec{u}^{1}, \vec{u}^{2}, ..., \vec{u}^{N}) = (\vec{u}^{1*}, \vec{u}^{2*}, ..., \vec{u}^{N*})$, that is

$$\sum_{j=1}^{n} d^1_{ij} u^{1*}_j - \sum_{j=1}^{n} d^1_{ji} u^{1*}_i = 0, \;\; 1 \leq i \leq n. \tag{4.16}$$

Here comes the main question: what strategies are evolutionarily stable? Is ideal free dispersal evolutionarily stable? It turns out that ideal free dispersal is necessary for evolutionary stability under very general conditions.

Theorem 4.4 ([14]). *If $u^{1*}_i > 0$ for some i and $((d^1_{ij}))$ is not ideal free, then $\vec{v}^1 = 0$ is unstable in (4.15) for some strategy $((\widetilde{d}^1_{ij}))$ and $((\widetilde{d}^1_{ij}))$ can be chosen to be ideal free.*

This result implies that strategies that do not lead to an ideal free distribution can not be evolutionarily stable. In other words, for a strategy to be evolutionarily stable, it is necessary that it produces an ideal free distribution of the population. When is that sufficient? Consider the model

$$\frac{du^k_i}{dt} = \sum_{j=1}^{n} d^k_{ij} u^k_j - \sum_{j=1}^{n} d_{ji} u^k_i + (m_i - \sum_{\ell=1}^{N} u^\ell_i) u^k_i, \tag{4.17}$$

for $i = 1 \ldots, n$ and $k = 1 \ldots N$. Assume that $d^k_{ij} \geq 0$ for $i \neq j$, $((d_{ij}))$ is irreducible, and $m_i > 0$ for all i.

Theorem 4.5 ([19]). *If the first population has ideal free dispersal, so that its single-population equilibrium $(\vec{u}^{\,1*}, \vec{0}, \ldots \vec{0})$ equals $(\vec{m}, \vec{0}, \ldots, \vec{0})$, and if there is no nonnegative equilibrium $(0, \vec{u}^{\,2*}, \ldots \vec{u}^{\,N*})$ so that $\sum_{k=2}^{N} c_k \vec{u}^{\,k*} = \vec{m}$ for nonnegative constants c_k, then $(\vec{u}^{\,1*}, \vec{0}, \ldots, \vec{0})$ is globally asymptotically stable in* (4.17)*.*

It is worth pointing out that the proof of Theorem 4.5 relies on a Lyapunov function, because analyzing the linear stability of $(\vec{m}, \vec{0}, \ldots, \vec{0})$ in (4.17), we can only derive neutral stability. The Lyapunov function has a form similar to those that have been used to study stability in many ecological models. If we let $\vec{u} = (\vec{u}^1, \ldots, \vec{u}^N)$ the Lyapunov function is

$$V(\vec{u}) = \sum_{k=1}^{N} \sum_{i=1}^{n} u^k_i - \sum_{i=1}^{n} m_i ln u^1_i.$$

Let $\vec{u}^* = (\vec{u}^{\,1*}, \vec{0}, \ldots \vec{0}) = (\vec{m}, \vec{0}, \ldots, \vec{0})$. We get $V(u) > V(u^*)$ for $u \neq u^*$ and $dV/dt \leq 0$ along trajectories but if $dV/dt = \dot{V}(u)$ we find $\dot{V}(u) = 0$ for some $u \neq u^*$. (No direct asymptotic stability.) However, we can use LaSalle's invariance principle (see [19, 41]) to obtain the global asymptotic stability of $\vec{u}^*$. In this setting the ideal free condition (4.16) can be stated as requiring the matrix $((a_{ij})) = ((d^1_{ij} u^{1*}_j))$ to have the property of line sum symmetry, that is,

$$\sum_{j=1}^{n} a_{ij} = \sum_{j=1}^{n} a_{ji} \quad \text{for} \quad i = 1 \ldots, n.$$

It turns out that the property of line sum symmetry is equivalent to an inequality that is crucial to the analysis of the Lyapunov function; see [19, 35].

There has been some work on the evolution of dispersal in the context of models that are discrete in both space and time. That includes the numerical studies by McPeek and Holt [71]; see also [58].

4.5. **Nonlocal models.** Our last topic is nonlocal models. In such models space and time are viewed as continuous, but the dispersal terms are given by integral operators rather than by advection or diffusion operators. For a single population with density u on a bounded domain Ω, a typical nonlocal logistic model would have the form

$$\frac{\partial u}{\partial t} = \int_\Omega k(x,y)u(y,t)\,dy - u(x,t)\int_\Omega k(y,x)\,dy + u[m(x) - u] \tag{4.18}$$

for $x \in \Omega$ and $t > 0$. The kernel $k(x,y)$ describes the rate at which individuals leave point y and move to point x. Given a population density $u(x,t)$, the first term on the right represents the overall rate at which individuals arrive at point x and second term describes the overall rate at which they leave point x. Integrating the first two terms on the right side of (4.18) over Ω gives zero, indicating that there is no net gain or loss of individuals due to movement. Assume that $m(x) \in C(\bar{\Omega})$, $m > 0$, $k \in C(\bar{\Omega} \times \bar{\Omega})$, $k \geq 0$, and there exists $\delta > 0$ such that $k(x,y) > 0$ for $|x - y| < \delta$. (This last condition plays a role similar to that played by irreducibility in the matrix case; namely, it implies that the nonlocal model satisfies an analogue of the strong maximum principle.) Models similar to (4.18) and related models for interacting species have been studied by various researchers; see [4, 20, 26, 27, 28, 29, 47, 53, 55] and the references in those papers. Models such as (4.18) have many properties similar to the corresponding reaction-advection-diffusion models. For positive initial data the model (4.18) has global solutions that converge to a unique positive equilibrium, and it admits a strong maximum principle. However, it does not have the regularity properties of parabolic partial differential equations, so bounded forward orbits are not generally precompact. This difference make the analysis of nonlocal models challenging, because standard versions of results from dynamical systems such as the existence of compact attractors, some aspects of persistence theory, and the LaSalle invariance principle require some type of compactness or precompactness of bounded forward orbits. Another issue is that although the operators in (4.18) are bounded, linearized problems associated with (4.18) may not have principal eigenvalues. They generally will have spectral bounds, but there may not always be an eigenfunction corresponding to the spectral bound. Again, standard versions of results such as the Krein-Rutman theorem require some type of compactness. In the case of reaction-advection-diffusion models, the operators in the models usually are not compact themselves but they often have compact resolvents because of elliptic regularity theory. However, that is not generally true in the nonlocal case.

Models for interacting populations with nonlocal dispersal can be constructed as in the case of local dispersal. A typical form would be

$$\begin{cases} \dfrac{\partial u}{\partial t} = \displaystyle\int_\Omega k(x,y)u(y,t)dy - \int_\Omega k(y,x)u(x,t)dy + f(x,u,v)u, \\ \dfrac{\partial v}{\partial t} = \displaystyle\int_\Omega \widetilde{k}(x,y)v(y,t)dy - \int_\Omega \widetilde{k}(y,x)v(x,t)dy + g(x,u,v)v. \end{cases} \tag{4.19}$$

Models of the form (4.19) for two competing species are studied in [47, 53]. In the case of competition, the nonlocal models still satisfy comparison principles analogous to those for reaction-advection-diffusion models. Specifically, in the case of Lotka-Volterra competition, if (u^1, v^1) and (u^2, v^2) are nonnegative solutions of (4.19) with $u^1(x,0) \geq u^2(x,0)$ and $v^1(x,0) \leq v^2(x,0)$ then $u^1(x,t) \geq u^2(x,t)$ and $v^1(x,t) \leq v^2(x,t)$ for $t > 0$. In [53] the authors studied a system of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = d\displaystyle\int_\Omega k(x-y)u(y,t)dy - u(x,t) + (m(x) - u - v)u, \\ \dfrac{\partial v}{\partial t} = D\displaystyle\int_\Omega k(x-y)v(y,t)dy - v(x,t) + (m(x) - u - v)v. \end{cases} \tag{4.20}$$

They showed that if $D > d$ then the single-species equilibrium $(u^*, 0)$ is asymptotically stable. This is similar to the result for the case of ordinary diffusion studied in [34], and it implies that the strategy of not dispersing at all is convergent stable. As in the case of ordinary diffusion, nonlocal models with dispersal kernels of the form used in (4.20) and nonzero dispersal rate cannot support an ideal free distribution. In the nonlocal setting, a dispersal kernel $k(x,y)$ supports an ideal free distribution in (4.18) if $m(x) > 0$ and

$$\int_\Omega k(x,y)m(y)dy - \int_\Omega k(y,x)m(x)dy = 0, \tag{4.21}$$

so that $u^* = m(x)$ is the positive equilibrium. This condition on the modified kernel $k(x,y)m(y)$ can be viewed as a continuum analogue of the line sum symmetry condition on the matrix $((a_{ij})) = ((d^1_{ij}u^{1*}_j))$ that characterizes the ideal free condition (4.16) in the case of discrete diffusion. It was noted in [26] that kernels of the form $k(x,y) = m(x)^\alpha m(y)^{\alpha-1}$ support an ideal free distribution in (4.18). The case where $\alpha = 0$ corresponds to a strategy of leaving the location y at a rate inversely proportional to $m(y)$. This is analogous to the strategy of using diffusion with a rate based on the departure point, where the rate is taken to be $1/m(x)$ if x is the departure point. (The resulting diffusion term in that case would have the form $\Delta(u/m(x))$.) It was also shown in [26] by means of a local invasibility analysis analogous to those used in [14, 43] that the only possible evolutionarily stable strategies in the nonlocal logistic case are those that support an ideal free distribution.

It turns out that ideal free dispersal is sufficient as well as necessary for evolutionary stability in the nonlocal case. For models of the form

$$\begin{cases} \dfrac{\partial u}{\partial t} = \displaystyle\int_\Omega k(x,y)u(y,t)dy - \int_\Omega k(y,x)u(x,t)dy + (m(x) - u - v)u, \\ \dfrac{\partial v}{\partial t} = \displaystyle\int_\Omega \widetilde{k}(x,y)v(y,t)dy - \int_\Omega \widetilde{k}(y,x)v(x,t)dy + (m(x) - u - v)v \end{cases} \tag{4.22}$$

the following result is proved in [20]:

Theorem 4.6. *Suppose that* u *and* v *satisfy* (4.22) *where both* k^* *and* k *are continuous and positive on* $\bar{\Omega} \times \bar{\Omega}$ *and* $m(x)$ *is continuous, positive on* $\bar{\Omega}$*, and nonconstant. If* k^* *is a dispersal strategy that supports an ideal free distribution and* k *does not support an ideal free dispersal then the steady state* $(u^*, 0) = (m(x), 0)$ *is globally asymptotically stable in* $C(\bar{\Omega}) \times C(\bar{\Omega})$ *for all positive and continuous initial data.*

This result is analogous to Theorem 4.5, but it only covers the case of two competitors. The reason why it is possible to obtain a result for N competitors in the discrete diffusion case but not in the nonlocal case is because the LaSalle invariance principle is not available in the nonlocal case due to the lack of compactness of bounded orbits. In the nonlocal case we still can use the Lyapunov functional

$$V(t) = \int_\Omega \left[u(x,t) - m(x) + v(x,t) - m(x) ln \frac{u(x,t)}{m(x)} \right] dx.$$

to rule out coexistence states (u^{**}, v^{**}). We then show that $(0, v^*)$ is unstable. The global stability of $(m(x), 0)$ then follows from the monotonicity properties of two species competition models.

A general class of open problems arises in the context of nonlocal models, namely finding ways to overcome the lack of compactness of bounded orbits and thus extend results from the cases of ordinary and partial differential equations to the nonlocal case. This is currently an active area of research on the effects of dispersal in ecological models.

References

[1] W.C. Allee, “Animal Aggregations: A Study in General Sociology”, University of Chicago Press, Chicago, 1931.

[2] H. Amann and J. López-Gómez, *A priori bounds and multiple solutions for superlinear indefinite elliptic problems*, J. Differential Equations **146** (1998), no. 2, 336–374.

[3] I. Averill, Y. Lou and D. Munther, *On several conjectures from evolution of dispersal* J. Biological Dynamics, **6** (2012) , no.2, 117-130.

[4] P. Bates and G. Zhao, *Existence, uniqueness, and stability of the stationary solution to a nonlocal equation arising in population dispersal*, J. Math. Anal. Appl **332** (2007), no.1, 428-440.

[5] F. Belgacem and C. Cosner, *The effects of dispersal along environmental gradients on the dynamics of populations in heterogeneous environments*, Canadian Appllied Mathematics Quarterly **3** (1995), no. 4, 379–397.

[6] M. Bendahmane *Weak and classical solutions to predator–prey system with cross-diffusion*, Nonlinear Analysis: TMA **73** (2010), no. 8, 2489–2503.

[7] H. Berestycki, L. Nirenberg and S. R. S. Varadhan, *The principal eigenvalue and maximum principle for second-order elliptic operators in general domains*, Comm. Pure Appl. Math. **47** (1994), no. 1, 47–92.

[8] A. Bezuglyy and Y. Lou, *Reaction-diffusion models with large advection coefficients*, Appl. Anal. **89** (2010), no. 7, 983–1004.

[9] J.E. Billotti and J.P. LaSalle, *Dissipative periodic processes*, Bull. Amer. Math. Soc. **77** 1971 1082–1088.

[10] R. S. Cantrell and C. Cosner, *Diffusive logistic equations with indefinite weights: population models in disrupted environments,* Proc. Roy. Soc. Edinburgh Sect. A **112** (1989), no. 3–4, 293–318.

[11] R. S. Cantrell and C. Cosner, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol. **29** (1991), no. 4, 315–338.

[12] R. S. Cantrell and C. Cosner, *Diffusive logistic equations with indefinite weights: population models in disrupted environments. II*, SIAM J. Math. Anal. **22** (1991), no. 4, 1043–1064.

[13] R. S. Cantrell and C. Cosner, “Spatial Ecology via Reaction-Diffusion Equations”, Wiley Ser. Math. Comput. Biol. 2003.

[14] R. S. Cantrell, C. Cosner, D. L. DeAngelis and V. Padrón, *The ideal free distribution as an evolutionarily stable strategy*, J. of Biological Dynamics **1** (2007), no. 3, 249–271.

[15] R. S. Cantrell, C. Cosner and Y. Lou, *Movement toward better environments and the evolution of rapid diffusion*, Math. Biosci. **204** (2006), no. 2, 199–214.

[16] R. S. Cantrell, C. Cosner and Y. Lou, *Advection-mediated coexistence of competing species*, Proc. Roy. Soc. Edinburgh Sect. A **137** (2007), no. 3, 497–518.

[17] R. S. Cantrell, C. Cosner and Y. Lou, *Approximating the ideal free distribution via reaction-diffusion-advection equations*, J. Differential Equations **245** (2008), no. 12, 3687–3703.

[18] R. S. Cantrell, C. Cosner and Y. Lou, *Evolution of dispersal and the ideal free distribution*, Math. Biosci. Eng. **7** (2010), no. 1, 17–36.

[19] R.S. Cantrell, C. Cosner, and Y. Lou *Evolutionary stability of ideal free dispersal strategies in patchy environments* J. Math. Biol. **65** (2012), no. 5, 943–965.

[20] R.S Cantrell, C. Cosner, Y. Lou, and D. Ryan, *Evolutionary stability of ideal free dispersal in spatial population models with nonlocal dispersal* Canadian Applied Math. Quarterly**20** (2012), 16–38.

[21] X. Chen, R. Hambrock and Y. Lou, *Evolution of conditional dispersal: a reaction-diffusion-advection model*, J. Math. Biol. **57** (2008), no. 3, 361–386.

[22] X. Chen and Y. Lou, *Principal eigenvalue and eigenfunctions of an elliptic operator with large advection and its application to a competition model*, Indiana Univ. Math. J. **57** (2008), no. 2, 627–658.

[23] Y.S. Choi, R. Lui and Y. Yamada, *Existence of global solutions for the Shigesada-Kawasaki- Teramoto model with strongly-coupled cross diffusion*, Discrete Contin. Dyn. Syst. **10** (2004), 719–730.

[24] C. Cosner, *A dynamic model for the ideal-free distribution as a partial differential equation*, Theoretical Population Biology **67** (2005),101–108.

[25] C. Cosner and Y. Lou, *Does movement toward better environments always benefit a population*? J. Math. Anal. Appl. **277** (2003), no. 2, 489–503.

[26] C. Cosner, J. Dávila and S. Martínez, *Evolutionary stability of ideal free nonlocal dispersal*, J. Biol. Dynamics **6** (2012), 395–405.

[27] J. Coville, *On uniqueness and monotonicity of solutions of non-local reaction diffusion equation*, Annali di Matematica **185** (2006), no.3, 461–485.

[28] J. Coville, *On a simple criterion for the existence of a principal eigenfunction of some nonlocal operators*, J. Differential Equations **249** (2010), no. 1, 2921-2953.

[29] J. Coville, J. Dávila and S. Martínez, *Existence and uniqueness of solutions to a nonlocal equation with monostable nonlinearity*, SIAM J. Math. Anal.,**39** (2008), no.5, 1693-1709.

[30] M. Crandall and P. Rabinowitz, *Bifurcation from simple eigenvalues*, J. Functional Analysis **8** 1971, 321–340.

[31] M. Crandall and P. Rabinowitz, *Bifurcation, perturbation of simple eigenvalues and linearized stability*, Arch. Rational Mech. Anal. **52** (1973), 161–180.

[32] S. Dehaene, *The neural basis of the Weber-Fechner law: a logarithmic mental number line*, Trends in Cognitive Sciences **7** (2003), 145–147.

[33] M. Delgado and A. Suárez, *On the structure of the positive solutions of the logistic equation with nonlinear diffusion*, J. Math. Anal. Appl. **268** (2002), no. 1, 200–216.

[34] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, *The evolution of slow dispersal rates: a reaction diffusion model*, J. Math. Biol. **37** (1998), no. 1, 61–83.

[35] B. Eaves, A. Hoffman, U. Rothblum and H. Schneider, *Line sum symmetric scaling of square nonnegative matrices*, Mathematical Programming Study **25** (l985),124–141.

[36] S. Flaxman and Y. Lou, *Tracking prey or tracking the prey's resource? Mechanisms of movement and optimal habitat selection by predators*, J. Theoretical Biology **256** (2009), 187–200.

[37] S. D. Fretwell and H. L. Lucas, *On territorial behaviour and other factors influencing habitat distribution in birds*, I Theoretical developments. Acta Biotheoretica **19** (1970), 16–36.

[38] S. D. Fretwell, "Populations in A Seasonal Environment", Princeton University Press, 1972.

[39] R. Gejji, Y. Lou, D. Munther and J. Peyton, *Evolutionary convergence to ideal free dispersal strategies and coexistence*, Bull. Math. Biology, **74** (2012), no.2, 257–299.

[40] R. Hambrock and Y. Lou, *The evolution of conditional dispersal strategies in spatially heterogeneous habitats*, Bull. Math. Biol. **71** (2009), no. 8, 1793–1817.

[41] J. K. Hale, *Dynamical systems and stability*, J. Math. Anal. Appl. textbf 26 (1969), no.1, 39–59.

[42] J.Hale and P. Waltman, *Persistence in infinite-dimensional systems*, SIAM Journal on Mathematical Anaysis **20** (1989), no. 2, 388–395.

[43] A. Hastings, *Can spatial variation alone lead to selection for dispersal?* Theor. Popul. Biol. **24** (1983), 244–251.

[44] D. Henry "Geometric Theory of Semilinear Parabolic Equations (Lecture Notes in Mathematics 840)", Springer, Berlin, 1993.

[45] P. Hess, "Periodic-parabolic Boundary Value Problems and Positivity", Longman Scientific and Technical, New York, 1991.

[46] P. Hess and T. Kato, *On some linear and nonlinear eigenvalue problems with an indefinite weight function*, Comm. Partial Differential Equations **5** (1980), no. 10, 999–1030.

[47] G. Hetzer, T. Nguyen and W. Shen, *Coexistence and extinction in the Volterra-Lotka competition model with nonlocal dispersal* Comm. Pure and Applied Analysis **11**(2012), no.5, 1699–1722

[48] T. Hillen and K. J. Painter, *A users guide to PDE models for chemotaxis*, J. Math. Biol. **58** (2009), 183–217.

[49] R. D. Holt, *Predation, apparent competition and the structure of prey communities*, Theoretical Population Biology **12** (1977), 197–229.

[50] R. D. Holt and G. A. Polis, *A theoretical gramework for intraguild predation*, The American Naturalist **149** (1997), no. 4, 745–769.

[51] V. Hutson, K. Mischaikow and P. Polácik *The evolution of dispersal rates in a heterogenous time-periodic environment*, J. Math. Biology **43** (2001), 501–533.

[52] V. Hutson, W. Shen and G. T. Vickers, *Estimates for the principal spectrum point for certain time-dependent parabolic operators*, Proc. Amer. Math. Soc. **129** (2001), no. 6, 1669–1679.

[53] V. Hutson, S. Martínez, K. Mischaikow and G.T. Vickers, *The evolution of dispersal*, J. Math. Biol. **47** (2003), no.6, 483–517.

[54] C.-Y. Kao, Y. Lou and E. Yanagida, *Principal eigenvalue for an elliptic problem with indefinite weight on cylindrical domains*, Math. Biosci. Eng. **5** (2008), no. 2, 315–335.

[55] C.-Y. Kao, Y. Lou and W. Shen, *Random dispersal vs. nonlocal dispersal*, Discrete and Continuous Dynamical Systems, Series A **26** (2010), 551–596.

[56] T. Kadota and K. Kuto, *Positive steady states for a prey-predator model with some nonlinear diffusion terms* J. Math. Anal. Appl. **323** (2006), 1387–1401

[57] P. Kareiva and G. Odell, *Swarms of predators exhibit 'preytaxis' if individual predators use area-restricted search*, American Naturalist, **130** (1987) no. 2, 233–270.

[58] S. Kirkland, C.-K. Li, and S.J. Schreiber, *On the evolution of dispersal in patchy environments*, SIAM Journal on Applied Mathematics **66** (2006), no.4, 1366–1382.

[59] K.-Y. Lam, *Concentration phenomena of a semilinear elliptic equation with large advection in an ecological model*, J. Differential Equations **250** (2011), no. 1, 161–181.

[60] K.-Y. Lam and Y. Lou, *Evolution of conditional dispersal: evolutionarily stable strategies in spatial models* J. Math. Biology, in press, DOI 10.1007/s00285-013-0650-1

[61] K.-Y. Lam and W.-M. Ni, *Limiting profiles of semilinear elliptic equations with large advection in population dynamics*, Discrete Contin. Dyn. Syst. **28** (2010), no. 3, 1051–1067.

[62] A. C. Lazer, *Some remarks on periodic solutions of parabolic differential equations*, Dynamical systems II, 227–246, Academic Press, New York, 1982.

[63] D. Le and T.T. Nguyen, *Global existence for a class of triangular parabolic systems on domains of arbitrary dimension* Proc. of AMS **133** (2005), 1985-1992.

[64] D. Le and T. T. Nguyen, *Persistence for a class of triangular cross diffusion parabolic systems,* Adv. Nonlinear Stud. **5** (2005), no. 4, 493–514.

[65] D. Le and T. T. Nguyen, *Global attractors and uniform persistence for cross diffusion parabolic systems*, Dynam. Systems Appl. **16** (2007), no. 2, 361–377.

[66] J. M. Lee, T. Hillen and M. A. Lewis, *Continuous traveling waves for prey-taxis*, Bull. Math. Biol. **70** (2008), no. 3, 654–676.

[67] J. M. Lee, T. Hillen and M. A. Lewis, *Pattern formation in prey-taxis systems*, J. Biol. Dyn. **3** (2009), no. 6, 551–573.

[68] Y. Lou, *On the effects of migration and spatial heterogeneity on single and multiple species*, J. Differential Equations **223** (2006), no. 2, 400–426.

[69] Y. Lou and E. Yanagida, *Minimization of the principal eigenvalue for an elliptic boundary value problem with indefinite weight, and applications to population dynamics*, Japan J. Indust. Appl. Math. **23** (2006), no. 3, 275–292.

[70] R. May and W. Leonard, *Nonlinear aspects of competition between three species*, SIAM J. Appl. Math. **29** (1975), no. 2, 243–253.

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

[72] X. Mora, *Semilinear parabolic problems define semiflows on C^k spaces*, Trans. Amer. Math. Soc. **278** (1983), 21-55.

[73] A. Okubo, "Diffusion and Ecological Problems: Mathematical Models", Biomathematics, 10. Springer-Verlag, Berlin-New York, 1980.

[74] L. Roques and F. Hamel, *Mathematical analysis of the optimal habitat configurations for species persistence*, Math. Biosci. **210** (2007), no. 1, 34–59.

[75] D. Ryan, *Fitness dependent dispersal in intraguild predation communities* Dissertation, University of MIami, 2011.

[76] S. Senn and P. Hess , *On positive solutions of a linear elliptic eigenvalue problem with Neumann boundary conditions*, Math. Ann. **258** (1981/82), no. 4, 459–470.

[77] N. Shigesada, K. Kawasaki and E. Teramoto, *Spatial segregation of interacting species,* J. Theoret. Biol. **79** (1979), no. 1, 83–99.

[78] J. Shi and X. Wang, *On global bifurcation for quasilinear elliptic systems on bounded domains,* Journal of Differential Equations, **7** (2009), 2788-2812.

[79] H. L. Smith, "Monotone Dynamical Systems", American Mathematical Society 2008.

[80] M. Turelli, *Re-Examination of stability in randomly varying versus deterministic environments with comments on stochastic theory of limiting similarity* Theoretical Population Biology **13** (1978), 244-267.

E-mail address: `c.cosner@math.miami.edu`