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A Nonlocal Spatial Model on Continuous Time and Space

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A NONLOCAL SPATIAL MODEL ON CONTINUOUS TIME AND SPACE

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In this work we studied a nonlocal spatial model on continuous time and space. Based on Levins' metapopulation framework, we developed a population model with nonlocal dispersal. The dispersal is modeled by an integro-differential equation.

In the first chapter, we studied the well-posedness of a single species model. We established the existence and uniqueness of solution, and proved a version of maximum principal as well as comparison theorem. To study the stability of equilibria, we considered an eigenvalue problem and provided an estimation of the eigenvalue. Then we gave the condition of having a stable positive equilibrium, which biologically implies the persistence of species; and we also gave the condition of a stable zero equilibrium, which means the species goes extinct.

In the second chapter, we investigated the two species competition model. We did the stability analysis for the zero equilibrium and two semi-trivial equilibria. Also we have a sufficient condition for the existence of a coexistence equilibrium. Then we studied the evolutionarily stable strategy for this model. Ideal free dispersal is a kind of conditional strategy which feature dependence on environments and leads to an equilibrium distribution where there is no net movement of individuals and any location has the same environmental fitness. Suppose two competing species are identical except their dispersal strategy. We showed that a species with ideal free

dispersal can invade when rare while the other species' dispersal is not ideal free.

In chapter three we are interested in the spreading speed on a infinite domain. The case of single species has been treated in an SIS epidemiology model. For two species competition, we proved the existence of spreading speed and showed that for each wave speed greater than the spreading speed, there exists a traveling wave solution connecting the two semi-trivial equilibria for the system.

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Contents

Chapter 1

The Well-posedness of a Metapopulation Model with Nonlocal Dispersal

1.1 Background

Dispersal mechanisms are a very important factor in the persistence, interaction, and evolution of species especially in habitats that are spatially heterogeneous. There are several ways that dispersal and its effects have been modeled in spatial ecology. They reflect various assumptions about the nature of the dispersal process and its connections to population dynamics. One type of model, the patch occupancy type of metapopulation models in Levins' [44] and Hanski [31], [32], do not treat population dynamics explicitly, but instead describe the probability that a population will be present on any given patch. These can be related to population models, by thinking of each patch as the space it takes for one individual. This is essentially the idea underlying the Hamilton and May [54] type model.

There are two broad classes of models that do include population dynamics. One class typically assumes that adult individuals are mobile, that the reproduction process is independent of dispersal, and that individuals compete for resources other than space itself. The other class typically assumes that adult individuals are not mobile, but produce seeds or larvae that are mobile, so that reproduction and dispersal are combined into a single process, and that dispersers compete for space to settle. Our model is similar to the second type of population model, but in continuous time and space.

Metapopulation patch occupancy models were introduced by [44]. They treat the environment as a collection of discrete patches that may become extinct, but unoccupied patches may be colonized by individuals dispersing from other patches. Such models have been used to study many types of populations, including butterflies Hanski [30] and reef fish ([2], [39]; to name a few). Levins' model describes a system of infinitely many identical patches, then describes how colonization and extinction determine the fraction of patches occupied. Let k be the fraction of habitat potentially suitable for some species. n is the fraction of patches occupied and $k - n$ is thus the patches available. The change with time of n is determined by:

$$\frac{dn}{dt} = cn(k - n) - en$$

Levins' model [44] is spatially implicit. It assumes the habitat patches are all the same and thus the parameters are constants, that the dispersal rates between any two patches are the same, and that there are infinitely many patches so that the fraction occupied is a continuous variable. Hanski's model [30], an extension of Levins' model, can be viewed as spatially explicit. It assumes a set of habitat patches in which species occur at a dynamic colonization-extinction equilibrium. Let p_i be the probability that patch i is occupied, and let c_{ij} be the colonization rate from patch j

to i. Let e_i be the extinction rate of patch i. Hanski's model is:

$$\frac{dp_i}{dt} = (1 - p_i)\sum_j c_{ij}p_j - e_i p_i$$

Mouquet and Loreau [48] introduced a model that is considered to be similar to Hanski's for multiple species. They showed that immigration is a key factor determining persistence and extinction for any single species in a metacommunity. Mouquet and Loreau [55] and [56] studied the dynamics of the metacommunity network in which communities are linked by dispersal.

For the two types of population dynamical models, the class where all individuals are mobile includes reaction-diffusion models and their discrete diffusion analogues Cantrell and Cosner [6], integrodifferential models similar to reaction-diffusion models but with nonlocal dispersal (see Bates and Zhao [5], Hetzer, Nguyen and Shen [36], Hutson, Martinez, Mischaikow and Vickers [38]), and some types of integrodifference models in discrete time (see Kot et al. [42], etc). The second class, where adults are sessile but seeds or larvae disperse so that reproduction is combined with dispersal, include the type of models introduced by Hamilton and May [54], and Comins et al. [19], and used to study the evolution of dispersal in organisms with these life histories (see Levin and Muller-Landau [43]).

Our model is similar in concept to these latter types of models, combining the ideas coming Hanski and Mouquet-Loreau models with a general modeling viewpoint similar to [54], [19] and [43]. Our model captures competition for space and dispersal together with reproduction, but in a heterogeneous environment, explicit in space. It also tracks population dynamics, and uses continuous space, so it uses continuous kernels, representing nonlocal diffusion. Dispersal by the integral operator

$\int_\Omega k(x, y)u(y)dy$ (Holt [37]) is similar to Coville [22], Hetzer, Nguyen and Shen [36], Hutson, Mischaikow Martinez and Vickers [38].

There are various ways to model dispersal. The class of reaction-diffusion models is used to study unconditional dispersal based on derivations from random walks. The extension to conditional dispersal with spatial variation, has the form of reaction-advection-diffusion or integro-difference models (Cantrell and Cosner [6]). Reaction-diffusion models have the restrictive assumptions that the movement is derived from a random walk, which is not suitable model for the dispersal of seeds. They may be good models for animals in cases where migration and other long-distance dispersal can be ignored. However, they are not such good models for organisms that may have long distance dispersal, or for seeds or larvae that can be moved long distances by winds, or currents or animal dispersers. Lou and Ni [49], [50], [51] studied the cross-diffusion system that arises from population dynamics. There are some other modeling approaches that address long distance movement. One particular type are position saltation processes, which have been discussed for the movements involving alternating pauses and jumps across long distances (see Hadeler [29] and Othmer et al. [59]). In contrast, Hutson et al. [38] derived continuous time models in with dispersal is described by an integral operator. This class of nonlocal spatial models:

$$u_t(x, t) = \int_\Omega J(x, y)u(y, t)dy + b(x)u(x, t) + f(x, u(x, t)), \tag{1.1.1}$$

which was then studied in [5]. A Lotka-Volterra competition model was studied in [36]. Cantrell et al [10] investigated the evolutionary stability of ideal free dispersal strategies for nonlocal models. Kao et al. [40] studied the competition of one species with random dispersal and the other with nonlocal dispersal. Coville [22] studied the existence of principal eigenfunctions for the model:

$$\int_\Omega J(\frac{x-y}{g(y)})\frac{\phi(y)}{g^n(y)}dy + a(x)\phi = \rho\phi$$

The only way these model differ from reaction-diffusion models is that they allow long distance movement as well as local movement.

The above models assume that the reproduction process is separated from movement. However, for some sessile animals like sponges, corals, oysters, and some plants, adult organisms do not move but produce seeds, eggs or juveniles that can move long distance, then settle in some location, reproduction and movement cannot be separated. There are some models more related to our models in that we make this assumption, but assume discrete time. Kot and Schaffer [42] proposed the integrodifference models for population ecology.

$$N_{t+1}(x) = \int_\Omega k(x,y)f(N_t(y);y)dy$$

They described species with a growth phase and a dispersal phase which produce seeds in discrete time period on continuous habitat. Van Kirk et al. [61] studied the role of dispersal and environment heterogeneity for discrete-time models. Hardin et al. [33], [34], [35] studied survival and extinction of the population under different dispersal strategies. This integro-difference model assumes the adults do not move but produce juveniles or seeds that can disperse long distances. The nonlinear integrodifference equations with a product of dispersal kernel and growth rate model the mechanism that dispersal and reproduction occur simultaneously, because the seeds or larvae have to disperse to find places to settle and survive. The Hamilton and

May [54] model is based on a similar idea in a metapopulation framework. Those authors studied the dispersal strategies on discrete patches. The reproductive agents (offspring, seeds, etc.) disperse away from their birth location. Comins et al. [19] extended the work to transient environments and general probability distributions for the number of progeny. They allowed more than one organism to occupy each site. Hamilton and May, and Comins et al., were motivated by trying to understand the evolution of dispersal. They wanted to see what strategies were evolutionarily stable. Then Levin et al [43] studied more general situations which are still in discrete space, but where the dispersal is defined by a kernel. Muneepeerakul et al. [57] investigated the evolution of a class of dispersal kernels in metacommunities.

Our model, continuous in time and space, uses the population dynamical model proposed by Holt and Keitt [37].

$$u_t = [K(x) - u(x,t)] \int_\Omega k(x,y)u(y,t)dy - d(x)u(x,t) \tag{1.1.2}$$

This model replaced the colonization term in Levins' model with a nonlocal integral $\int_\Omega k(x,y)u(y,t)dy$. $k(x,y)$ is the "dispersal kernel". The term $(k-n)$ was replaced by $[K(x) - u(x,t)]$ where $K(x)$ represented the maximum fraction of suitable sites of the heterogeneous habitat and $u(x,t)$ depends on the location x and time t. $d(x)$ described the extinct rate at point x along the gradient. Holt and Keitt [37] studied the process of colonization and extinction in environments with spatial gradients in the availability of suitable habitat. They look a metapopulation approach, and suggested that there were two ways to model such a process: analytic continuum models and spatially explicit simulations. They used a simulation model. In this work, we will develop and use the analytic continuum model.

The quantity $k(x,y)$ is a "dispersal kernel", which can be written as $k(x,y) = D(x,y)r(y)$. $D(x,y)$ is the transition probability from y to x, and it satisfies $\int_\Omega D(x,y)dy = 1$. $r(y)$ is the reproduction rate at x along the gradient. $\int_\Omega k(x,y)u(y,t)dy$ describes the contribution to colonization at each site by colonists emanating from all other sites. The dispersal kernel $k(x,y)$ usually decreases with increasing the distance $|x-y|$. This term is similar to $\int_\Omega J(x,y)u(y,t)dy$ in (1.1.1) except $k(x,y)$ is a product of $D(x,y)$ and $r(y)$. The product of these two terms describes the reproductive agents, which are mobile and disperse from y to x. This is similar to $\int_\Omega k(x,y)f(N_t(y);y)dy$ except it is continuous in time. $K(x)$ is the potential habitat available for organisms at each site and $K(x) - u(x,t)$ is the habitat unoccupied. This integrodifferential equation with the colonization term is an extension of Levins' metapopulation framework. The model treats competition for space in a way that is mathematically similar to Hanski or Mouquet-Loreau's models, but is continuous in space; and it uses the nonlocal integral to characterize the dispersion, which is a good model for sessile animals like sponges, corals, or oysters, along with some plants, which produce larvae or seeds that can move long distances.

In this chapter, we will first establish the existence and uniqueness of solution for single species model. Then we will prove a version of maximum principle and comparison theorem. For stability analysis, we will study the linearized system around zero equilibrium. Since the nonlocal model may not have an eigenfunction associated with the spectral bound, we will consider an equivalent eigenvalue problem where the Krein-Rutman theorem (See Amann [1]) may apply. Once we have the estimation of principal eigenvalue, we can give sufficient conditions for zero equilibrium to be stable or unstable.

1.2 Existence, Uniqueness of solution and some properties.

Let $\Omega \in \mathbb{R}^n$ be a connected open domain. In applications, n =1,2 or 3.

Our model is:

$$\begin{aligned} &u_t = [K(x) - u(x,t)] \int_\Omega k(x,y)u(y,t)dy - d(x)u(x,t) \\ &u(x,0) = u_0(x) \\ &x \in \bar{\Omega} \end{aligned} \tag{1.2.1}$$

Here $u(x,t)$ represents the population density that already occupied at x and $K(x)$ is the potential suitable site. Assume we have $0 \leq u(x,0) \leq K(x)$. For the model to make sense, we further need $0 \leq u(x,t) \leq K(x)$ for $t > 0$ (this is to be proved in Maximum Principle). $k(x,y)$ represents the population dispersal rate from x to y and it is nonnegative on $\bar{\Omega} \times \bar{\Omega}$ and is continuous w.r.t x. $d(x)$ is the death rate.

Remark 1.1. *The kernel $k(x,y)$ can be written as the product: $r(y)D(x,y)$. $r(y)$ is the rate of production of seeds or juveniles, per capita, by population at location y. $D(x,y)$ denotes the rate of movement from y to x and satisfies $\int_\Omega D(x,y)dy = 1$. This assumption on $D(x,y)$ reflects the idea that there is no loss or gain of population in transit, other than what is described by the death rate $d(x)$.*

1.2.1 Existence and Uniqueness of Solution

In this section, we are going to show the existence and uniqueness of system (1.2.1).

Let $C([0,T], C(\bar{\Omega})) = X$ be the space of continuous function from $[0,T]$ to $C(\bar{\Omega})$. We have $u(x,t) \in C([0,T], C(\bar{\Omega}))$. Let $Z \subseteq C([0,T], C(\bar{\Omega}))$, and $Z = \{u(x,t)|u \in X :$

$max_{\bar{\Omega}\times[0,T]}|u(x,t)-u_0(x)| \leq M\}$. Assume $u_0(x) \in C(\bar{\Omega})$.

Theorem 1.2. *Let $K(x)$, $d(x)$ be positive and continuous on $\bar{\Omega}$. Assume $k(x,y) \geq 0$ is bounded on $\bar{\Omega}\times\bar{\Omega}$ and it is continuous with respect to x and measurable with respect to y. $u(x,0) = u_0(x)$. Assume $\int_\Omega k(x,y)$ is bounded, i.e. $\max_{x\in\bar{\Omega}} |\int_\Omega k(x,y)dy| < \infty$. There exists a unique solution for system(1.2.1) on $[0,T]$ for some $T > 0$.*

Proof. Here $u \in Z, 0 < t < T$, and $0 < T, M \leq 1$ are constants to be determined later.

Integrate (1.2.1) from 0 to t, we have

$$\mathcal{F}(u)(x) = u(x,0) + \int_0^t [\int_\Omega k(x,y)u(y,s)dy[K(x)-u(x,s)] - d(x)u(x,s)]ds \quad (1.2.2)$$

We are going to use (1.2.2) to construct a contraction mapping in order to prove the existence and uniqueness by applying Contraction Mapping Theorem.

We use norms: $\|u(x,t)\| = \max_{[0,T]\times\bar{\Omega}} |u(x,t)|$.

For $u \in Z$, $\|u\| \leq \|u_0\| + M \leq \|u_0\| + 1 = U_0$.

$$\begin{aligned}\|\mathcal{F}(u)\| \leq \|u_0\| + T \cdot [\max_{\bar{\Omega}} |\int_\Omega k(x,y)dy| \cdot \max_{\Omega} |K(x)| \cdot U_0 \\ + \max_{\bar{\Omega}} |\int_\Omega k(x,y)dy| \cdot U_0^2 + \max_{\bar{\Omega}} |d(x)| \cdot U_0]\end{aligned}$$

So the integral on the right side of (1.2.2) converges.

We require $\mathcal{F}(u) \in Z$.

$$\begin{aligned}
&\|\mathcal{F}(u) - u_0(x)\| = \| \int_0^t \{ \int_\Omega k(x,y)u(y,s)dy[K(x) - u(x,s)] - d(x)u(x,s) \ \}ds\| \\
&\leq \max_{\bar{\Omega}} | \int_\Omega k(x,y)dy| \cdot \|u\| \cdot [\max_{\bar{\Omega}} K(x) + \|u\|] \cdot t + \max_{\bar{\Omega}} d(x) \cdot \|u\| \cdot t \\
&\leq \max_{\bar{\Omega}} | \int_\Omega k(x,y)dy| \cdot U_0 \cdot [\max_{\bar{\Omega}} K(x) + U_0] \cdot t + \max_{\bar{\Omega}} d(x) \cdot U_0 \cdot t \\
&\leq t \cdot (constant \cdot U_0 + constant \cdot U_0^2)
\end{aligned}$$

Select $T_1(M)$ small enough such that for $0 < t < T_1(M)$ we have

$$\|\mathcal{F}(u) - u_0(x)\| < M$$

so $\mathcal{F}(u) \in Z$. Next we want to show that we can choose $T \leq T_1(M)$ such that

$$\|\mathcal{F}(u) - \mathcal{F}(v)\| < C\|u - v\|$$

for $u, v \in Z, C < 1$, and $u_0(x) = v_0(x)$

$$\begin{aligned}
& \|\mathcal{F}(u) - \mathcal{F}(v)\| \\
= \quad & \| \int_0^t \{ \int_\Omega k(x,y)u(y,s)dy[K(x) - u(x,s)] - d(x)u(x,s) \ \}ds \\
& - \int_0^t \{ \int_\Omega k(x,y)v(y,s)dy[K(x) - v(x,s)] - d(x)v(x,s) \ \}ds\| \\
= \quad & \| \int_0^t \{ \int_\Omega k(x,y)[u(y,s) - v(y,s)]dy \cdot K(x) - d(x) \cdot |u(x,s) - v(x,s)| - \\
& \int_\Omega k(x,y)[u(y,s)u(x,s) - v(y,s)u(x,s) + v(y,s)u(x,s) - v(y,s)v(x,s)]dy\}ds\| \\
\leq \quad & \{C_1\|u - v\| + C_2\|u - v\| + C_3\|u - v\|\} \cdot t
\end{aligned}$$

$$C_1 \leq \max_{\bar{\Omega}} | \int_\Omega k(x,y)dy| \cdot \|K(x)\|, \quad C_2 \leq \|d(x)\|,$$

$$C_3 \leq \max_{\bar{\Omega}} | \int_\Omega k(x,y)dy| \cdot (\|u\| + \|v\|) \leq 2U_0 \cdot \int_\Omega k(x,y)dy|$$

We pick $T < \min\{T_1(M), \frac{1}{C_1+C_2+C_3}\}$ and $M = 1$, then obtain a contraction on Z.

By the contraction mapping theorem, there exists a unique $u^* \in Z$ such that $\mathcal{F}(u^*) = u^*$. Then

$$u^* = u(x,0) + \int_0^t [\int_\Omega k(x,y)u^*(y,s)dy[K(x) - u^*(x,s)] - d(x)u^*(x,s)]ds. \quad (1.2.3)$$

So u^* satisfies the equation and the integrand on the right side of (1.2.3) is continuous so u^* is differentiable in t and satisfies (1.2.1) thus it is the unique solution for the system.

□

Remark 1.3. *The domain Ω is not necessarily bounded. If it is bounded and $k(x,y)$ is bounded on Ω, then the integral $\int_\Omega k(x,y)dy$ is automatically bounded. If Ω is not bounded but the kernel $k(x,y)$ satisfies some appropriate conditions, then the integral is also bounded. For example, if $k(x,y) = k(x-y)$, and $k(x-y)$ has the form of a Gaussian or exponential kernel, then $\int_\Omega k(y)dy = k_0 < \infty$ is still valid.*

We have the following hypothesis on kernel $k(x,y)$:

Hypothesis 1.4. *(1) The kernel $k(x,y) \geq 0$ is bounded for all $x, y \in \bar{\Omega}$, and $\int_\Omega k(x,y)dy < \infty$.*

(2) $k(x,y) \geq 0$ on $\bar{\Omega}$ and for any continuous function $\phi(x) \geq 0$ on Ω with $\phi(x) > 0$ for some x, we have $\int_\Omega k(x,y)\phi(y)dy > 0$.

1.2.2 Maximum Principle and Comparison Theorem

In this section we will derive a maximum principle and comparison theorems that will be important for later analysis. We will define the super-(sub-) solution which will be used in the stability analysis.

Theorem 1.5. *(Maximum Principle)*

(I) If for any fixed x, $u(x,0) \le K(x)$ and $u(x,t)$ is a solution of (1.2.1)*, then $u(x,t) < K(x)$ for $t > 0$.*

(II) If we assume further that $u(x,0) \ge 0$, $u(x,0) > 0$ on some open subset of Ω, $k(x,y) \ge 0$ and Ω is bounded, and we assume (2) in Hypothesis 1.4*, then $u(x,t) > 0$ for $t \in [0,T]$ where $u(x,t)$ exists.*

Proof. (I) Suppose $u(x,0) \le K(x)$.

If $u(x,0) = K(x)$, then $u_t(x,t)|_{t=0} = -d(x)K(x) < 0$. If $u(x,0) < K(x)$, then by continuity, there exists a small enough $t > 0$ such that $u(x,t) < K(x)$ on $(0,t)$.

So for any x there is an interval $(0, \epsilon(x))$ in which $u(x,t) < K(x)$.

Let $t_0(x) = \inf\{t > 0 : u(x,t) = K(x)\}$, we have $t_0(x) > 0$.

If $t_0(x) < T$, so $t_0(x) < +\infty$, then for any x, by (1.2.1), $u_t(x,t)|_{t=t_0(x)} < 0$.

However, since $u(x, t_0(x)) = K(x)$ by continuity, $u(x,t)$ has a maximum relative to t on $(0, t_0(x))$ at $t = t_0(x)$, and by the definition of $t_0(x)$ we have $u_t(x,t)|_{t_0(x)} \ge 0$. This is a contradiction.

So $t_0(x) = \infty$, so $t_0(x) \ge T$, i.e. $u(x,t) < K(x)$ for all $t \in [0,T]$.

(II)

Suppose $0 \le u(x,0) \le K(x)$. We already have $u(x,t) < K(x)$ for $t > 0$.

Let $\tilde{u}(x,t) = e^{at}u(x,t)$, then $u(x,t) > 0$ if and only if $\tilde{u}(x,t) > 0$ for $t > 0$. By

(1.2.1)

$$\tilde{u}_t(x,t) = a\tilde{u}(x,t) + e^{at}\cdot\int_{\Omega} k(x,y)u(y,t)dy[K(x) - u(x,t)] - d(x)\tilde{u}(x,t) \quad (1.2.4)$$

Note that if $u(x,t) \equiv 0$, then it is an equilibrium and thus a solution. If $u(x,0) \geq 0$ and $u(x,0) \not\equiv 0$, then we have $0 < k_1 \leq \int_{\Omega} k(x,y)u(y,0)dy \leq \int_{\Omega} k(x,y)K(y)dy = k_2$ for some positive number k_1, k_2, by continuity of $u(x,0)$ and hypothesis on $k(x,y)$.

Also we have $\tilde{u}(x,0) = u(x,0)$, and

$$\begin{aligned} &\tilde{u}_t(x,0) \\ &= [a - d(x)]\tilde{u}(x,0) + (\textstyle\int_{\Omega} k(x,y)u(y,0)dy)K(x) - (\int_{\Omega} k(x,y)u(y,0)dy)\tilde{u}(x,0) \end{aligned} \quad (1.2.5)$$

Thus,

$$\tilde{u}_t(x,0) \geq [a - d(x) - k_2]\tilde{u}(x,0) + k_1 K(x) \quad (1.2.6)$$

Hence by choosing $a > \max_{\bar{\Omega}} d(x) + k_2$, we can get $\tilde{u}_t(x,0) > 0$ for each x.

Let $t_0(x) = \inf\{t > 0 : \tilde{u}(x,t) = 0\}$. So $\tilde{u}(x, t_0(x)) = 0$. Then for some $t > 0$ small enough, we have $\tilde{u}(x,t) > 0$.

We want to show $\inf_{x\in\bar{\Omega}} t_0(x)$ is strictly larger than 0. Suppose $\inf_{x\in\bar{\Omega}} t_0(x) = 0$, then there must exists a sequence $(x_n, t_0(x_n))$ converging to $(x_0, t_0(x_0)) = (x_0, 0)$, $x_0 \in \bar{\Omega}$. For each x_n we have $\tilde{u}(x_n, t_0(x_n)) = 0$ and $\tilde{u}(x_0, 0) = 0$. The continuity of $k(x,y)$, $K(x)$ and $d(x)$ implies $\tilde{u}_t(x,t)$ is continuous. Since we have $\tilde{u}(x_n, t_0(x_n)) = 0$ but $\tilde{u}(x_n, t) > 0$ for $0 < t < t_0(x_n)$, we must have $\tilde{u}_t(x_n, t_0(x_n)) \leq 0$. Since $(x_n, t_0(x_n)) \to (x_0, 0)$ as $n \to \infty$, we have $u_t(x_0, 0) \leq 0$ by continuity. However, we also have $\tilde{u}(x_n, t_0(x_n)) = 0$, so again by continuity, we must have $\tilde{u}(x_0, 0) = 0$. It then follows by (1.2.6) that $\tilde{u}_t(x_0, 0) \geq k_1 K(x_0) > 0$, which is a contradiction. Thus, these is a $t^* > 0$ such that $\tilde{u}(x,t) > 0$ for all x if $0 < t < t^*$.

We want to see that $\tilde{u}(x,t) > 0$ for all $t > 0$ where the solution exists. Let $t^{**} = \sup\{t : \tilde{u}(x,s) > 0 \text{ for all } x \text{ if } 0 < s < t\}$. We know that $t^{**} \geq t^* > 0$, and by continuity we have $\tilde{u}(x, t^{**}) \geq 0$. Also, if $t^{**} < \infty$, then for any $n = 1, 2, 3, ...$ there must be some $\tilde{t}_n \in (t^{**}, t^{**} + \frac{1}{n})$ such that $\tilde{u}(\hat{x}_n, \tilde{t}_n) \leq 0$ for some $\hat{x}_n$. If $\tilde{u}(\hat{x}_n, \tilde{t}_n) = 0$, let $\hat{t}_n = \tilde{t}_n$. If $\tilde{u}(\hat{x}_n, \tilde{t}_n) < 0$, then by the intermediate value theorem there is a $\hat{t}_n \in [t^{**}, t^{**} + \frac{1}{n}]$ with $\tilde{u}(\hat{x}_n, \hat{t}_n) = 0$ (since $\tilde{u}(\hat{x}_n, t) > 0$ for $t < t^{**}$). It also follows from $\tilde{u}(\hat{x}_n, t) > 0$ for $t < t^{**}$ that $\hat{t}_n \geq t^{**}$ in this case as well. Hence, we have a sequence $(\hat{x}_n, \hat{t}_n)$ with $\hat{t}_n \geq t^{**}$, $\hat{t}_n \to t^{**}$ as $n \to \infty$, and $\tilde{u}(\hat{x}_n, \hat{t}_n) = 0$. Since $\bar{\Omega}$ is bounded, we must have a subsequence $(\hat{\hat{x}}_n)$ of $(\hat{x}_n)$ that converges to some $\hat{x}_0$, so that $\tilde{u}(\hat{x}_0, t^{**}) = 0$ by continuity (since $(\hat{\hat{x}}_n, \hat{t}_n) \to (\hat{x}_0, t^{**})$ and $\tilde{u}(\hat{\hat{x}}_n, \hat{t}_n) = 0$.)

However, for $0 < \epsilon < t^{**}$, we have

$$
\begin{aligned}
\tilde{u}(\hat{x}_0, t^{**}) = \tilde{u}(\hat{x}_0, t^{**} - \epsilon) + \int_{t^{**}-\epsilon}^{t^{**}} \tilde{u}_t(\hat{x}_0, s) ds \\
= & \tilde{u}(\hat{x}_0, t^{**} - \epsilon) + \int_{t^{**}-\epsilon}^{t^{**}} (a - d(x))\tilde{u}(\hat{x}_0, s) ds \\
& + \int_{t^{**}-\epsilon}^{t^{**}} e^{as} (\int_{\Omega} k(\hat{x}_0, y) u(y, s) dy)[K(\hat{x}_0) - u(\hat{x}_0, s)] ds
\end{aligned}
$$

We have $\tilde{u}(\tilde{x}, s) > 0$ and $u(\hat{x}_0, s) < K(\hat{x}_0)$ for $t^{**} - \epsilon \leq s < t^{**}$, so we have $\tilde{u}(\hat{x}_0, t^{**}) > 0$, contradiction.

So t^* cannot be a finite number. This shows $u(x,t) > 0$ for $t > 0$ where the solution exists, i.e. $[0, T]$. □

Corollary 1.6. *(Global Existence) From the Maximum Principle, we have* $0 \leq u(x,t) \leq K(x)$ *for all* t *where* $u(x,t)$ *exists. Similarly if* $v(x,t)$ *satisfy* (1.2.1),

$0 \leq v(x,t) \leq K(x)$ where $v(x,t)$ exists. Let $[0,T]$ be the existence interval in Theorem 1.1. Since the constants C_1 to C_3 and U_0 depend only on the coefficients of (1.2.1) *and the supremum of the initial data, and since u is uniformly bounded on $[0,T]$ by the Maximum Principle, we can repeat the argument of Maximum Principle and Comparison Theorem on $[0,T]$ to $[T,2T]$ using $u(x,T)$ as initial data and so on.*

Definition 1.7. *We say that $u(x,t)$ is a super-(sub-)solution if*

$$u_t \geq (\leq)[K(x) - u(x,t)] \int_\Omega k(x,y)u(y,t)dy - d(x)u(x,t)$$

Theorem 1.8. *(Comparison Theorem)*

Suppose $u(x,t)$ and $v(x,t)$ satisfy (1.2.1).

a) If $0 \leq v(x,0) \leq u(x,0) \leq K(x)$, then $0 \leq v(x,t) \leq u(x,t) \leq K(x)$ for all $t > 0$ where both $u(x,t), v(x,t)$ exist.

b) Moreover, if $v(x,0) < u(x,0)$ for some x, and Hypothesis 1.4 *holds, then $v(x,t) < u(x,t)$ for all $t > 0$ where both $u(x,t), v(x,t)$ exist.*

c) Suppose Ω is bounded. $u_1(x,t)$ is a sub-solution and $u_2(x,t)$ is a super-solution with $u_1(x,0) \leq u_2(x,0)$. Then $u_1(x,t) \leq u_2(x,t)$ for $t > 0$ where both $u_1(x,t), u_2(x,t)$ exist.

Proof. We are going to prove the theorem by showing that $e^{at}(u(x,t) - v(x,t)) = w(x,t)$ satisfies an equation with a solution that is uniquely determined and non-negative. We will do that by using the contraction mapping theorem on a problem related to (1.2.1).

a) Clearly if $u(x,0) \equiv v(x,0)$ then $u(x,t) \equiv v(x,t)$. If $u(x,0) \geq v(x,0)$, $u(x,0) >$

$v(x,0)$ for some x, let $\tilde{u} = e^{at}u$ and $\tilde{v} = e^{at}v$. So we have

$$\begin{aligned}\tilde{u}_t(x,t) = (a - d(x))\tilde{u}(x,t) + K(x)\int_\Omega k(x,y)\tilde{u}(y,t)dy - \int_\Omega k(x,y)u(y,t)e^{at}u(x,t)dy \\ =(a - d(x))\tilde{u}(x,t) + K(x)\int_\Omega k(x,y)\tilde{u}(y,t)dy - \int_\Omega k(x,y)\tilde{u}(y,t)dy \cdot u(x,t) \\ =(a - d(x))\tilde{u}(x,t) + K(x)\int_\Omega k(x,y)\tilde{u}(y,t)dy - \int_\Omega k(x,y)u(y,t)dy \cdot \tilde{u}(x,t)\end{aligned}$$

We have a similar expression for $\tilde{v}(x,t)$. Let $w = \tilde{u} - \tilde{v}$, so $\tilde{u} = w + \tilde{v}$ and $v(x,t) = u - w(x,t) \cdot e^{-at}$. We have $w \geq 0$ if and only if $\tilde{u} \geq \tilde{v}$ if and only if $u \geq v$. $w(x,0) = w_0(x)$. Let $[0, T_0]$ be the intersection of the existence intervals of u and v given by Theorem 1.5.

Then

$$\begin{aligned}w_t \quad & = [a - d(x)]w(x,t) + K(x)\int_\Omega k(x,y)w(y,t)dy \\ & - \int_\Omega k(x,y)u(y,t)e^{at}dy \cdot u(x,t) + \int_\Omega k(x,y)v(y,t)e^{at}dy \cdot v(x,t) \\ & = [a - d(x)]w(x,t) + K(x)\int_\Omega k(x,y)w(y,t)dy \\ & - \int_\Omega k(x,y)u(y,t)dye^{at}(u(x,t) - v(x,t)) \\ & - \int_\Omega k(x,y)u(y,t)dyv(x,t)e^{at} + \int_\Omega k(x,y)v(y,t)e^{at}v(x,t) \\ & = [a - d(x)]w(x,t) + K(x)\int_\Omega k(x,y)w(y,t)dy \\ & - \int_\Omega k(x,y)u(y,t)dyw(x,t) - \int_\Omega k(x,y)w(y,t)dyv(x,t) \\ & = [a - d(x) - \int_\Omega k(x,y)u(y,t)dy]w(x,t) \\ & + [K(x) - u(x,t) + w(x,t)e^{-at}]\int_\Omega k(x,y)w(y,t)dy\end{aligned}$$

Equation for $w(x,t)$ can be also written as

$$w_t = [a - d(x) - \int_\Omega k(x,y)u(y,t)dy]w(x,t) + [K(x) - v(x,t)]\int_\Omega k(x,y)w(y,t)dy \tag{1.2.7}$$

We now show that equation (1.2.7) with initial condition $w(x,0) = u(x,0)-v(x,0)$ has a unique solution that is nonnegative, and then since $w(x,t) = e^{at}(u(x,t)-v(x,t))$ satisfies (1.2.7), that must be the unique solution.

We can choose a large enough such that $a - d(x) - \int_\Omega k(x,y)u(y,t)dy > 0$. Since $u(x,t) \le K(x)$, the choice of a does not depend on u. In the same way that (1.2.2) is the integration of (1.2.1), integrate (1.2.7) and we have for $t \in [0, T_0]$,

$$\begin{aligned} w(x,t) =& w(x,0) + \int_0^t [a - d(x) - \int_\Omega k(x,y)u(y,s)dy]w(x,s)ds \\ &+ \int_0^t [K(x) - u(x,s) + w(x,s)e^{-as}]\int_\Omega k(x,y)w(y,s)dyds \end{aligned}$$

Suppose $0 \le w(x,0) \le \frac{M_0}{2}, 0 \le u,v \le K(x)$, $M_0 = 2max_\Omega K(x)$. Let

$$\begin{aligned} \mathcal{M}(w) = \quad & w(x,0) + \int_0^t [a - d(x) - \int_\Omega k(x,y)u(y,s)dy]w(x,s)ds \\ + \quad & \int_0^t [K(x) - u(x,s) + w(x,s)e^{-as}]\int_\Omega k(x,y)w(y,s)dyds. \end{aligned}$$

Here we use the fact that $u(x,t) \le K(x)$ such that the term $\int_0^t [K(x) - u(x,s) + w(x,s)e^{-as}]\int_\Omega k(x,y)w(y,s)dyds$ is nonnegative to get $\mathcal{M}(w) \ge 0$. Let $Z := \{w : w(x,t) \ge 0, sup_{\bar{\Omega}\times[0,T]} w(x,t) - w(x,0) \le M_0\}$, and we want to show that by selecting $T > 0$ small enough, $\mathcal{M}(w)$ maps Z into itself. $\|w(x,t)\| \le \|w_0\| + M_0 = W_0$.

$\|u\| \leq U_0$.

$$\|\mathcal{M}(w) - w(x,0)\| = \| \int_0^t [a - d(x) - \int_\Omega k(x,y)u(y,s)dy]w(x,s)ds$$
$$+ \int_0^t [K(x) - u(x,s) + w(x,s)e^{-as}] \int_\Omega k(x,y)w(y,s)dyds\|$$
$$\leq \|w\|(a + \max_{x\in\bar{\Omega}} |d(x)| + \|u\| \max_{x\in\bar{\Omega}} \int_\Omega k(x,y)dy) \cdot t$$
$$+(max_{x\in\bar{\Omega}}K(x) + \|u\| + \|w\| \max_{x\in\bar{\Omega}} \int_\Omega k(x,y)dy)\|w\| \cdot t$$

Suppose $0 \leq w \leq M_0$, since all terms above are bounded, we can choose $T_1 > 0$ small enough such that $\mathcal{M}(w) \leq M_0$ for $0 \leq t \leq T_1$ provided $t \leq T_1$.

Next we want to prove $\mathcal{M}$ is a contraction mapping. For any $0 \leq p, q \leq M_0$, with $p(x,0) = q(x,0)$,

$$\begin{aligned}
\mathcal{M}(p) - \mathcal{M}(q) = &\int_0^t [a - d(x) - \int_\Omega k(x,y)u(y,s)dy][p(x,s) - q(x,s)]ds \\
&+ \int_0^t [K(x) - u(x,s) + p(x,s)e^{-as}] \int_\Omega k(x,y)p(y,s)dyds \\
&- \int_0^t [K(x) - u(x,s) + q(x,s)e^{-as}] \int_\Omega k(x,y)q(y,s)dyds \\
= &\int_0^t [a - d(x) - \int_\Omega k(x,y)u(y,s)dy][p(x,s) - q(x,s)]ds \\
&+ \int_0^t [K(x) - u(x,s)] \int_\Omega k(x,y)(p(y,s) - q(y,s))dyds \\
&+ \int_0^t p(x,s)e^{-as} \int_\Omega k(x,y)(p(y,s) - q(y,s))dyds \\
&- \int_0^t (q(x,s) - p(x,s))e^{-as} \int_\Omega k(x,y)q(y,s)dyds
\end{aligned}$$

Since each term is bounded, we have

$$\|\mathcal{M}(p) - \mathcal{M}(q)\| \leq C_1 \cdot t\|p-q\| + C_2 \cdot t\|p-q\| + C_3 \cdot \|p-q\| + C_4 \cdot t\|p-q\|$$

Here $0 \leq C_1 \leq \max_{\bar{\Omega}}[a - d(x) - \int_\Omega k(x,y)u(y,s)dy] \leq a$,

$0 \leq C_2 \leq \max_{\bar{\Omega}} |\int_\Omega k(x,y)dy| \cdot \max_{\bar{\Omega}} |K(x)|$,

$0 \leq C_3 \leq M_0 \times \max_{\bar{\Omega}} |\int_\Omega k(x,y)dy|$,

$0 \leq C_4 \leq 2M_0 \times \max_{\bar{\Omega}} |\int_\Omega k(x,y)dy|$.

So we can select $0 < T_2 < T_1$ with T_2 small enough such that

$$\|\mathcal{M}(p) - \mathcal{M}(q)\| \leq C \cdot \|p-q\| = C \cdot \max_{\bar{\Omega}\times[0,T_2]} \|p-q\|$$

with $C < 1$.

We can conclude that for given $u(x,t)$, $v(x,t)$ the equation (1.2.7) has a unique solution $\tilde{w}$ on $(0, T_2)$ for some $T_2 > 0$. Furthermore, $\tilde{w} \geq 0$. However, w is also a solution of (1.2.7), so $\tilde{w} = w$ on $[0, T_2]$ and hence $w \geq 0$. Further, the constants C_1 to C_4 depend only on the coefficients of the model so this argument can be repeated on $[T_2, 2T_2]$, $[2T_2, 3T_2]$ and so on. So the result holds on $[0, T]$ where the solution exists. So $w \geq 0$ on $[0, T]$.

b)

We have $u(x, 0) \geq 0$ by hypothesis, so by Theorem 1.8 we have $0 \leq u(x,t) \leq K(x)$. Then for (1.2.7) $w(x,t)$ has a unique solution on $\bar{\Omega} \times [0, T_2]$ with $w(x,t) \geq 0$. We have

$$w_t = [a - d(x) - \int_\Omega k(x,y)u(y,t)dy]w(x,t) + [K(x) - v(x,t)] \int_\Omega k(x,y)w(y,t)dy$$

with $w \geq 0$ on $[0, T_2]$.

It is easy to see at the points where $w(x,0) > 0$ or $v(x,0) < K(x)$ we have $w_t(x,0) > 0$.

Because $u(x,0) \not\equiv v(x,0)$ we must have $w(x,0) > 0$ for some $x_1 \in \Omega$. We have $w(x,t) \geq 0$ by part a), so for any $x \in \bar{\Omega}$,

$$w_t \geq [K(x) - v(x,t)] \int_\Omega k(x,y)w(y,t)dy \geq 0.$$

Since $w(x,0) > 0$ for $x = x_1$, we must have $w(x_1,t) > 0$ on some interval $0 < t < \epsilon(x_1)$, so by the hypothesis on $k(x,y)$ we must have for any $x \in \bar{\Omega}$

$$\int_\Omega k(x,y)w(y,t)dy > 0 \quad on \quad 0 < t < \epsilon(x_1).$$

Also, we have $v(x,t) < K(x)$ for $t > 0$ by the maximum principle. Thus, we have $w_t(x,t) > 0$ for $0 < t < \epsilon(x_1)$ for any x, with $w(x,0) \geq 0$ and $w_t(x,0) \geq 0$. It follows that $w(x,t) > 0$ for $0 < t < \epsilon(x_1)$ for all $x \in \bar{\Omega}$. Thus $w(x,t) > 0$ on $\bar{\Omega} \times (0, \epsilon_0]$ for some ϵ_0 with $\epsilon(x_1) \geq \epsilon_0 > 0$.

Thus, at $t = \epsilon_0$ we have $0 < v(x,\epsilon_0) < u(x,\epsilon_0) < K(x)$. So the equation satisfies

$$w_t(x,\epsilon_0) > 0, w(x,\epsilon_0) > 0$$

Now let $t_0(x) = \inf\{t > \epsilon_0 : w(x,t) = 0\}$. So $t_0(x) > \epsilon_0$ for all x. If there is a finite number $t^* = \inf_{\bar{\Omega}} t_0(x)$, then by continuity $w(x,t^*) = 0$ and for any $0 < \delta <$

$\epsilon_0, w(x, t^* - \delta) > 0$.

$$w(x, t^*) = w(x, t^* - \delta) + \int_{t^*-\delta}^{t^*} w_s(x, s) ds$$

Each term in the right hand side is positive but $w(x, t^*) = 0$. So we have a contradiction.

So we have for $w(x, 0) \geq 0$ if $w(x_0, 0) > 0$ for some x_0, then $w(x, t) > 0$ for all $t > 0$ as long as it exists. And thus $\tilde{u} > \tilde{v}$ so $u > v$.

c) Suppose Ω is bounded. Let $w(x, t) = [u_2(x, t) - u_1(x, t)]e^{at}$.

$$w_t(x, t) \geq [K(x) - u_1(x, t)] \int_\Omega k(x, y) w(y, t) dy + w(x, t)[a - d(x) - \int_\Omega k(x, y) u_2(y, t) dy] \tag{1.2.8}$$

$w(x, 0) \geq 0$. Consider (1.2.8) for $0 \leq t \leq T$ for some fixed t. We will show that for any $\epsilon_0 > 0$ we have $w(x, t) \geq \epsilon_0 > 0$ on $\bar{\Omega} \times [0, T]$ so that $w(x, t) \geq 0$ on $\bar{\Omega} \times [0, T]$. Suppose $\epsilon_0 > 0$ is given. Let $z(x, t) = w(x, t) + \epsilon e^{bt}$, where b and ϵ are positive and will be chosen later. We have $z(x, 0) \geq \epsilon$. From (1.2.8) we get

$$\begin{aligned} z_t(x, t) \geq\ & [K(x) - u_1(x, t)] \int_\Omega k(x, y) dy (z(y, t) - \epsilon e^{bt}) \\ & + [a - d(x) - \int_\Omega k(x, y) u_2(y, t) dy](z(x, t) - \epsilon b^{bt}) dy + \epsilon b e^{bt} \end{aligned}$$

so,

$$\begin{aligned} z_t(x, t) \geq\ & [K(x) - u_1(x, t)] \int_\Omega k(x, y) z(y, t) dy + [a - d(x) - \int_\Omega k(x, y) u_2(y, t) dy] z(x, t) \\ & + \epsilon e^{bt}[b - [K(x) - u_1(x, t)] \int_\Omega k(x, y) dy - [a - d(x) - \int_\Omega k(x, y) u_2(y, t) dy]] \end{aligned} \tag{1.2.9}$$

Choose $b > 0$ large enough that

$$\frac{b}{2} - [K(x) - u_2(x,t)] \int_\Omega k(x,y)dy - [a - d(x) - \int_\Omega k(x,y)u(y,t)dy] > 0$$

Then $z_t(x,0) > 0$ and $z(x,t) > 0$ for small t by continuity.

Let $t_0(x) = \inf\{t : z(x,t) = 0\}$. We have $t_0(x) > 0$ for each $x \in \bar{\Omega}$. Let $t^* = \inf\{t_0(x) : x \in \bar{\Omega}\}$. We have $t^* \geq 0$. Suppose $t^* = 0$. Then there exists a sequence $\{x_n\} \in \bar{\Omega}$ with $t_0(x_n) \to 0$ as $n \to \infty$. Also, by continuity, $z(x_n, t_0(x_n)) = 0$. Choose a subsequence of $\{x_n\}$ such that $x_n \to x^*$. Again by continuity, $z(x^*, 0) = 0$. This contradicts $z(x,0) > 0$ on $\bar{\Omega}$, so we must have $t^* > 0$.

Suppose now that $t^* < T$ for some $T < \infty$. Let $t^{**} = \sup\{t \in [0,T] : z(x,t) > 0 \ \ for \ \ t < t^*\}$. We have $t^{**} \leq t^* < T$. If $t^{**} < T$ we have $z(x,t) \geq 0$ for $t \leq t^{**}$. Repeating the argument used at the end of the proof of Maximum Principle Part (II), we obtain $z(x,t) \geq 0$ on $[0, nt^{**}]$ for arbitrary $n > 0$. It is a contradiction, so we must have $t^{**} > T$ and then $t^* > T$. Thus, $z(x,t) > 0$ on $\bar{\Omega} \times [0,T]$. It follows that $w(x,t) > -\epsilon e^{bt}$ on $\bar{\Omega} \times [0,T]$. Choose $\epsilon > 0$ small enough so that $\epsilon e^{bt} < \epsilon_0$. Then we have $w(x,t) \geq -\epsilon_0$ for $0 \leq t \leq T$. Since $\epsilon_0 > 0$ was arbitrary, we have $w(x,t) \geq 0$ for $0 \leq t \leq T$ so that $u_2(x,t) \geq u_1(x,t)$ for $0 \leq t \leq T$. Since T was arbitrary, $u_2(x,t) \geq u_1(x,t)$ for $t > 0$.

□

We have a weaker condition on kernel $k(x,y)$:

Hypothesis 1.9. *(1) The kernel* $k(x,y) \geq 0$ *is bounded for all* $x, y \in \bar{\Omega}$*, and* $\int_\Omega k(x,y)dy < \infty$*.*

(2) There exist positive constants k_0 *and* δ *such that* $k(x,y) \geq c_0 > 0$ *for all*

$x, y \in \Omega$ satisfying $|x - y| < \delta$.

Corollary 1.10. *Part (II) of Theorem* 1.5 *remains valid under the weaker condition Hypothesis* 1.9 *and Ω is connected.*

Proof. We have from maximum principle (I) that if $u(x,t)$ is a solution of (1.2.1) with $u(x,0) \geq 0$ then $u(x,t) \geq 0$.

Let $w(x,t) = e^{d(x)t}u(x,t)$. Then

$$w_t = e^{d(x)t}[K(x) - u(x,t)] \int_\Omega k(x,y)u(y,t)dy$$

By maximum principle (I) we have $w_t(x,t) \geq 0$ on $\bar{\Omega}$, so if $w(x,t_0) > 0$ for some t_0 then $w(x,t) > 0$ for $t > t_0$ and hence $u(x,t) > 0$ for $t > t_0$.

Suppose $u(x,0) > 0$ for $x \in B_\gamma(x_0) \cap \bar{\Omega}$ for some $\gamma > 0$ and $x_0 \in \bar{\Omega}$ (here $B_\gamma(x_0)$ is the ball of radius γ centered at x_0). By the hypothesis on $k(x,y)$ we have $w_t(x,0) > 0$ for all $x \in B_{\delta+\gamma}(x_0) \cap \bar{\Omega}$, so for any $t > 0$ we have $w(x,t) > 0$ and thus $u(x,t) > 0$. For $x \in B_{\gamma+2\delta}(x_0) \cap \bar{\Omega}$ we then have $w_t(x,t) > 0$ for any $t > 0$, so $w(x,t) > 0$ and hence we have $u(x,t) > 0$. This argument can then be repeated to show $u(x,t) > 0$ on $B_{\gamma+N\delta}(x_0) \cap \bar{\Omega}$ for $N = 2, 3, 4, ...$ Any point in $\bar{\Omega}$ will belong to $B_{\gamma+N\delta}(x_0) \cap \bar{\Omega}$ for some N, so $u(x,t) > 0$ for $t > 0$.

□

1.3 Stability of Equilibria

1.3.1 Preliminary

In the following definitions and theorems are from Amann [1].

Definition 1.11. *1. Let V be a real vector space. An ordering in V is called linear if*

(i) $x \leqq y$ implies $x + z \leqq y + z$ for all $z \in V$.

(ii) $x \leqq y$ implies $\alpha x \leqq \alpha y$ for all $\alpha \in \mathbb{R}_+ := [0, \infty)$.

A real vector space together with a linear ordering is called an ordered vector space.

2. Let V be an ordered vector space. Let $P := \{x \in V \mid x \geqq 0\}$. And P satisfies the following properties:

(i) $P + P \subset P$;

(ii) $\mathbb{R}_+ P \subset P$;

(iii) $P \cap (-P) = \{0\}$.

Such a nonempty subset P of a real vector space V is called a cone. Every cone P defines a linear ordering in V by

$$x \leq y \quad iff \quad y - x \in P,$$

the ordering induced by P. The elements in

$$\dot{P} := P \backslash \{0\} = \{x \in V \mid x \geqq 0, x \neq 0\}$$

are called positive and P is said to be the positive cone of the ordering.

3. Let E be a Banach space ordered by a cone P. Then E is called an ordered Banach space (OBS) if the positive cone is closed.

4. Let V and W be ordered vector spaces with positive cones P and Q, respectively. A linear operator $T : V \to W$ is called positive if $T(P) \subset Q$ and strictly positive if $T(\dot{P}) \subset \dot{Q}$. If (W, Q) is an ordered Banach space and Q has nonempty interior, then

T is called strongly positive if $T(\dot{P}) \subset \mathring{Q}$.

5. Let E be a Banach space and P be the positive cone. P is total if $\overline{P - P} = E$.

We define K to be the positive cone in $C(\bar{\Omega})$ if $K = \{u \in C(\bar{\Omega}) : u(x) \geq 0, \forall x \in \bar{\Omega}\}$. For every $u(x) \in C(\bar{\Omega})$, there exists $u_1, u_2 \in K$ such that $u(x) = u_1(x) - u_2(x)$. Then the positive cone K is total in $C(\bar{\Omega})$.

Theorem 1.12. *(Krein-Rutman) Let (C, K) be an ordered Banach space with total positive cone. Let $L(C)$ denote the space of bounded linear operators from C into itself. Suppose that $T \in L(C)$ is compact and has a positive spectral radius $r(T)$. Then $r(T)$ is an eigenvalue of T and of the dual operator T^*, with eigenvectors in P and in P^*, respectively.*

The following theorem we consider strongly positive compact operators.

Theorem 1.13. *Let (C, K) be an ordered Banach space whose positive cone has nonempty interior. Let T be a strongly positive compact endomorphism of C. Then the following is true:*

1. The spectral radius $r(T)$ is positive;

2. $r(T)$ is a simple eigenvalue of T having a positive eigenvector and there is no other eigenvalue with a positive eigenvector;

3. $r(T)$ is a simple eigenvalue of T^* having a strictly positive eigenvector;

4. For every $y \in \dot{K} = K \backslash \{0\}$, the equation

$$\lambda x - Tx = y$$

has exactly one positive solution if $\lambda > r(T)$, and no positive solution for $\lambda \leq r(T)$. The equation $r(T)x - Tx = -y$ has no positive solution.

5. For every $S \in L(C)$ satisfying $S \geq T, r(S) \geq r(T)$. If $S - T$ is strongly positive, then $r(S) > r(T)$.

1.3.2 Positive Equilibrium

To study the persistence and extinction of the system, we want to analyze the stability of equilibria. Since we have the comparison theorem, the super-(sub-)solution approach shows that if the zero equilibrium is stable, then the species go extinct. If the zero is not stable, then the system will persist.

We make the following hypotheses:

Hypothesis 1.14. *(i) Ω is a bounded domain in this case, $k(x,y)$ is uniformly Lipshitz w.r.t. x, and $\max_{\bar{\Omega}\times\bar{\Omega}} |k(x,y)| < \infty$.*

(ii) $f(x) := \frac{K(x)}{d(x)}$ is uniformly Lipschitz and there exists $d_1, d_2 > 0$ such that $\forall x \in \Omega$, $0 < d_1 \leq \frac{K(x)}{d(x)} \leq d_2 < \infty$.

(iii) $k(x,y)\psi(y)dy > 0$ for all $x \in \bar{\Omega}$ if $\psi(x) \geq 0$, $\psi \in C(\bar{\Omega})$ and $\psi(x_0) > 0$ for some $x_0 \in \bar{\Omega}$.

To study the stability of zero, we linearize the equation at zero and get:

$$u_t = K(x) \int_\Omega k(x,y)u(y,t)dy - d(x)u(x,t)$$

Define $M_f[\phi](x) := \frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$. Then for eigenvalue problem $-\lambda\phi(x) = M_f[\phi](x)$, we have the following theorem:

Theorem 1.15. *Assume Hypothesis 1.4 and 1.14. Then there exists an eigenpair (λ, ϕ) satisfying*

$$-\lambda\phi(x) = \frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$$

Proof. Suppose $S \subset C(\bar{\Omega})$ is bounded so that for $u \in S$ we have $\|u\| \leq U_0$. If $v = M_f[u]$ for some $\|u\| \leq U_0$, then

$$\|v\| \leq d_2 \int_\Omega k(x,y)\|u\|dy \leq d_2(max_{\bar{\Omega}\times\bar{\Omega}}|k(x,y)|)|\Omega|U_0$$

and for $x, y \in \bar{\Omega}$,

$$\begin{aligned}
|v(x) - v(y)| \quad &= |f(x)\int_\Omega k(x,z)u(z)dz - f(y)\int_\Omega k(y,z)u(z)dz| \\
&\leq |f(x)\int_\Omega [k(x,z) - k(y,z)]u(z)dz| + |(f(x) - f(y))\int_\Omega k(x,y)u(z)dz| \\
&\leq [\sup|f(x)|\sup(\frac{|k(x,z) - k(y,z)|}{|x-y|})U_0 \\
&+ \sup(\frac{|f(x) - f(y)|}{|x-y|})\sup|k(y,z)||\Omega|U_0]|x-y| \\
&\leq C_1|x-y|
\end{aligned}$$

for some constant C_1. Thus, M_f maps bounded sets in $C(\bar{\Omega})$ into sets of functions that are uniformly bounded and equicontinuous, which have compact closure by the Arzela-Ascoli theorem. Hence M_f is compact. By the assumptions on $k(x,y)$, M_f is strongly positive, so the Krein-Rutman theorem applies. It follows that there exist $\phi(x) > 0$, $\lambda_p > 0$ so that

$$\lambda_p\phi = M_f[\phi],$$

so

$$-\lambda_p[\phi](x) = \frac{K(x)}{d(x)}\int_\Omega k(x,y)\phi(y)dy$$

□

Remark 1.16. *The hypothesis* 1.4 *can be replaced by Hypothesis* 1.9*: there exists* $\delta > 0$ *and* $c_0 > 0$ *such that for all* $x, y \in \Omega$ *satisfying* $|x-y| \leq \delta$ *we have* $k(x,y) \geq c_0 > 0$.

Proof. Let $T[w] = (\int_\Omega \tilde{k}(x,y)w(y,t)dy$ where $\tilde{k}(x,y)$ satisfies Hypothesis (1.9). The spectral radius of T is still positive. To see that, take

$$T(1) = \int_\Omega k(x,y)dy \geq \int_{\Omega_\delta} k(x,y) \cdot 1dy = c_0 \cdot |\Omega_0| = \gamma$$

where $\Omega_0 = \{y : |x-y| < \delta\} \cap \Omega$. Then

$$T^2(1) \geq \gamma T(1)$$

and so on. So we have $\|T^k\| \geq \gamma^k$. $\therefore r(T) = \lim_{k\to\infty} \|T^k\|^{\frac{1}{k}} \geq \gamma > 0$.

By the Krein Rutman Theorem we obtain a positive eigenvalue σ with a nonnegative eigenfunction $\phi(x) \geq 0$ on Ω. Suppose $\phi(x) > 0$ on a subset $\Omega_0 \subset \Omega$. Apply T on ϕ we get $T[\phi](x) = \sigma\phi(x) > 0$ on $\Omega_1 = \{x : |x-y| < \delta \ \ for \ \ y \in \Omega_0\}$. Then $T^2[\phi](x) = \sigma^2\phi(x) > 0$ on $\Omega_2 = \{x : |x-y| < \delta \ \ for \ \ y \in \Omega_1\}$, and so on. Since Ω is connected, repeat this process N times and we will eventually get Ω_N covering Ω and $\sigma^N\phi(x) > 0$ on Ω. The eigenfunction $\phi(x)$ is thus proved to be positive on Ω.

□

The next two theorems are similar from the analysis from Coville [22].

Theorem 1.17. *Define* $\Lambda = \{\lambda \in R \mid \exists\phi \in C^+(\bar{\Omega})\backslash\{0\}, s.t. M_f[\phi] + \lambda\phi(x) \leq 0\}$ *and* $\mu(M_f) = \sup\Lambda$. *Then* $\mu(M_f)$ *is well defined.*

Proof. For $0 < \psi \equiv 1$, $\psi \in C(\Omega)$ Let $c(x) = f(x) \cdot \int_\Omega k(x,y)dy \in L^\infty$ If $\lambda < -\|c\|_\infty$, then

$$M_f[\psi] + \lambda\psi \leq (c(x) - \|c\|_\infty) \leq 0$$

So Λ is nonempty.

On the other hand, $M_f[\phi] \geq 0$, $\forall \phi \in C^+(\Omega)$. Thus 0 is upper bound of Λ.

$\therefore \mu(M_f)$ is well defined. □

Theorem 1.18. *The quantity $\mu[M_f]$ equals the principal eigenvalue obtained from Theorem* 1.15*.*

Proof. For all λ_p satisfying the eigenvalue problem, we have $\lambda_p \in \Lambda$. Thus $\lambda_p \leq sup\Lambda = \mu[M_f]$.

On the other hand, if there exists $\lambda' \in \Lambda$, such that $\lambda' > \lambda_p$ then there exists $\phi \in int(C^+(\bar{\Omega}))$, such that

$$f(x)\int_\Omega k(x,y)\phi(y)dy + \lambda'\phi(x) \leq 0.$$

We also have

$$f(x)\int_\Omega k(x,y)\phi_p(y)dy + \lambda_p\phi_p(x) = 0.$$

Since $\phi(x) > 0$

$$\frac{\phi_p(x)}{\phi(x)}[f(x)\int_\Omega k(x,y)\phi(y)dy + \lambda'\phi(x)] \leq f(x)\int_\Omega k(x,y)\phi_p(y)dy + \lambda_p\phi_p(x)$$

$$f(x)\int_\Omega k(x,y)\phi_p(y)dy - f(x)\int_\Omega k(x,y)\frac{\phi(y)\phi_p(x)}{\phi(x)}dy \geq (\lambda' - \lambda_p)\phi_p(x) > 0$$

Thus,

$$f(x)\int_\Omega k(x,y)(w(y) - w(x))dy > 0, \forall x \in \bar{\Omega}$$

Let $w(x) = \frac{\phi_p(x)}{\phi(x)} \in C(\bar{\Omega})$. Suppose $w(x)$ achieves its supremum at $\bar{x} \in \bar{\Omega}$, i.e. $sup_{\bar{\Omega}}\{w(x)\} = w(\bar{x})$, $\bar{x} \in \bar{\Omega}$.

Then we obtain an inequality

$$0 < f(\bar{x}) \int_{\bar{\Omega}} k(\bar{x}, y)(w(y) - w(\bar{x}))dy \leq 0.$$

Contradiction. So we must have $\lambda' = \lambda_p$.

□

Theorem 1.19. *Assume Hypothesis* (1.4)(1), (1.9) *and* (1.14). *Let* $g(x, y) = f(x)k(x, y)$, *then there exist* $g_1, g_2, \delta > 0$, *for all* $x, y \in \Omega$, *such that* $|x - y| < \delta$, *we have* $0 < g_1 \leq g(x, y)$. *Suppose also* $g(x, y) \leq g_2$ *for all* (x, y).

So an estimation of $-\lambda$ *is* $g_1 \cdot |\Omega \cap B_{\delta/2}| \leq -\lambda \leq g_2 \cdot |\Omega|$

Proof. Consider the eigenvalue problem

$$\frac{K(x)}{d(x)} \int_{\Omega} k(x, y)\phi(y)dy = -\lambda\phi(x) \tag{1.3.1}$$

That is ,

$$\int_{\Omega} g(x, y)\phi(y)dy = -\lambda\phi(x) \tag{1.3.2}$$

By Krein-Rutman theorem we know $-\lambda > 0$ exists and we know that there exists $\phi(x) > 0$ such that for any $x \in \Omega$,

$$\int_{\Omega} g(x, y)\phi(y)dy = -\lambda\phi(x)$$

Since $g(x,y), \phi(x) > 0$, we have for any $z \in \Omega$

$$\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} g(x,y)\phi(y)dy \leq -\lambda\phi(x).$$

Thus

$$\int\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} g(x,y)\phi(y)dydx \leq -\lambda\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} \phi(x)dx.$$

If $x, y \in B_{\frac{\delta}{2}}(z)\cap\Omega$, then $|x-y| < \delta$, so $g(x,y) \geq g_1$.

$$\int\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} g_1\phi(y)dydx \leq -\lambda\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} \phi(x)dx$$

so that

$$g_1|B_{\frac{\delta}{2}}(z)\cap\Omega|\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} \phi(y)dy \leq -\lambda\int_{B_{\frac{\delta}{2}}(z)\cap\Omega} \phi(x)dx.$$

Since the integrals on the left and right sides are positive and equal, we have

$$g_1|B_{\frac{\delta}{2}}(z)\cap\Omega| \leq -\lambda$$

for any $z \in \Omega$. Hence

$$-\lambda \geq g_1|B_{\delta/2}\cap\Omega|.$$

On the other hand, $\phi(x)$ is integrable on the bounded domain Ω and $g(x,y) \leq g_2$, so

$$\begin{aligned}&-\lambda\int_\Omega \phi(x)dx = \int_\Omega\int_\Omega g(x,y)\phi(y)dydx \\ &\leq \int_\Omega\int_\Omega g_2\phi(y)dydx = g_2|\Omega|\int_\Omega \phi(y)dy.\end{aligned}$$

Again, the integrals on both sides are positive and are equal to each other so $-\lambda \leq$

$g_2|\Omega|$.

□

Thus we have

$$\frac{K(x)}{d(x)}\int_{\Omega} k(x,y)\phi(y)dy - \phi(x) = (-\lambda - 1)\phi(x) := \gamma_p \phi(x).$$

The next lemma explains the situation when the initial condition is itself a sub- or super-solution:

Lemma 1.20. *Suppose that* $k(x,y)$ *has the property* $k(x,y) \geq g_1 > 0$ *if* $|x-y| < \delta$ *for some* $g_1, \delta > 0$. *If* $u(x,t)$ *is a solution of* (1.2.1) *with* $0 \leq u(x,0) \leq K(x)$ *where* $u(x,0) = u_0(x) \in C(\bar{\Omega})$ *such that*

(1) If

$$0 < [K(x) - u_0(x)]\int_{\Omega} k(x,y)u_0(y)dy - d(x)u_0(x), \tag{1.3.3}$$

then $u(x,t)$ *is increasing in* t *and as* $t \to \infty$, $u(x,t) \to \underline{u}^*(x)$ *where* $\underline{u}^*(x)$ *is the smallest equilibrium for* (1.2.1) *satisfying* $u(x,0) \leq u(x,t) \leq K(x)$.

(2) If the inequality is replaced with

$$0 > [K(x) - u_0(x)]\int_{\Omega} k(x,y)u_0(y)dy - d(x)u_0(x), \tag{1.3.4}$$

then $u(x,t)$ *is decreasing in* t *and as* $t \to \infty$, $u(x,t) \to \overline{u}^*(x)$ *where* $\overline{u}^*(x)$ *is the largest equilibrium for* (1.2.1) *that is less than* $u(x,0)$.

Proof. By (1), $u_0(x)$ is a sub-solution to (1.2.1), and $u(x,t)$ is a solution to (1.2.1) and thus is a super-solution. We have $u(x,0) = u_0(x)$ so by Theorem 1.8 we have $u(x,t) \geq u_0(x)$. By (1) we also have $u_t(x,0) > 0$ so that for each $x \in \bar{\Omega}$, there is a $t_0(x)$

such that $u(x,t) > u_0(x)$ for $0 < t < t_0(x)$. Pick some $x_0 \in \bar{\Omega}$; then for $0 < \delta < t_0(x_0)$ we have $u(x,\delta) \geq u_0(x)$ for all x and $u(x_0,\delta) > u_0(x_0)$. (b) of Theorem 1.8 implies δ is independent of x. Let $v(x,t) = u(x,t+\delta)$. Then $v(x,t)$ is a solution. By Theorem 1.8 with $v(x,0) = u(x,\delta)$, so $v(x,0) \geq u(x,0)$ for all x and $v(x,0) > u(x,0)$ for some x, so $v(x,t) > u(x,t)$ by Theorem 1.8. Thus $u(x,t+\delta) > u(x,t)$, so that $u(x,t)$ is increasing. For each $x \in \bar{\Omega}$ we have $u(x,t) < K(x)$ for $t > 0$ by Theorem 1.5. Thus, for each x we have $u(x,t) \to u^*(x)$ as $t \to \infty$ for some $u^*(x) \leq K(x)$. By the monotone convergence theorem $u^*(x)$ is measurable and

$$\int_\Omega k(x,y)u(y,t)dy \to \int_\Omega k(x,y)u^*(y)dy.$$

Since $u(x,t) \to u^*(x)$ as $t \to \infty$, we have $u(x,t_n) \to u^*(x)$ for any sequence $t_n \to \infty$.

Then, $u^*(x)$ must be an equilibrium for (1.2.1), because if not then for some x we would have $u_t(x,t) > 0$ with $u(x,t) = u^*(x)$, contradicting $u(x,t) \to u^*(x)$ as $t \to \infty$. Finally, if u^{**} is a equilibrium of (1.2.1) with $u^{**}(x) > u(x,0) = u_0(x)$, then $u^{**}(x)$ is a solution of (1.2.1) so by Theorem 1.8 we have $u^{**}(x) \geq u^*(x)$. Hence $u^*(x)$ is the minimal equilibrium larger than $u_0(x)$.

The proof for the case (2) is identical except that in that case $u(x,t)$ decreases to the largest equilibrium less than $u_0(x)$.

□

There are two kinds of hypotheses of the kernel $k(x,y)$

(i) Hypothesis 1.4: $\int_\Omega k(x,y)\phi(y)dy > 0$ for all $x \in \bar{\Omega}$ if $\phi(x) \geq 0$, $\phi(x) > 0$ on an open set.

Or,

(ii) Hypothesis 1.9: There exist $g_1, \delta > 0$ so that if $|x - y| < \delta$ then $k(x,y) > g_1$.

Under (i) the operator M_f is strongly positive so we can use Theorem 1.13. However, we can prove something with a weaker condition (ii) because in that case there is still a principal eigenvalue $\gamma_p > 0$ and the comparison principle and maximum principle hold.

Next we assume the stronger hypothesis 1.4 and show that with (ii) $u = 0$ is locally stable if $\gamma_p < 0$ and unstable if $\gamma_p > 0$.

Theorem 1.21. *Suppose that Hypothesis* 1.4 *is satisfied and that* $\gamma_p < 0$*. Then* $u = 0$ *is locally asymptotically stable.*

Proof. Let $\phi(x) > 0$ be an eigenfunction for γ_p, normalized so that $\phi(x) < K(x)$. Then we have $\frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy - \phi(x) = \gamma_p\phi(x)$.

There will be a constant ϕ_0 such that $\phi_p(x) \geq \phi_0$ on Ω. Let $u_\epsilon = \epsilon\phi$. We have

$$\begin{aligned} &[K(x) - u_\epsilon] \int_\Omega k(x,y)u_\epsilon(y)dy - d(x)u_\epsilon(x) \\ &= d(x)\epsilon[\frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy - \phi(x)] - \epsilon^2[\phi(x) \int_\Omega k(x,y)\phi(y)dy] \\ &\leq d(x)\epsilon\gamma_p\phi(x) \end{aligned} \tag{1.3.5}$$

so for any ϵ with $0 < \epsilon \leq 1$, the solution to (1.2.1) with $u(x,0) = u_\epsilon(x)$ is decreasing by Lemma 1.20.

Claim: In this case, (1.2.1) does not have any positive equilibrium less than or equal to ϕ_0 for all x.

Now choose $\epsilon > 0$ small enough that $\max u_\epsilon(x) < \phi_0$, and let $u_2(x,t)$ be the solution to (1.2.1) with $u_2(x,0) = u_\epsilon(x)$. We have $\min u_\epsilon(x) > 0$. $u_2(x,0) = u_\epsilon(x)$. By (1.3.5) and the Lemma, $u_2(x,t)$ decreases to the largest equilibrium less than $u_2(x,0)$ which in this case is 0. Hence, any solution $v(x,t)$ of (1.2.1) with $v(x,0) < \min u_\epsilon(x)$ must have $lim_{t\to\infty} v(x,t) = 0$ by Theorem 1.8. Hence if $\gamma_p < 0$, the zero equilibrium is locally asymptotically stable.

□

Proof. (Proof of the Claim) Suppose there is such an equilibrium. Call it $v^*(x)$.

Let $\epsilon^* = \inf\{\epsilon \mid \epsilon\phi(x) > v^*(x) \text{ for all } x \in \bar{\Omega}\}$. Since $\phi(x) \geq \phi_0 \geq v^*(x) > 0$, we have $0 < \epsilon^* \leq 1$.

Let $u_1(x,t)$ be the solution to (1.2.1) with $u(x,0) = u_{\epsilon^*}(x)$. Then $u(x,0) \geq v^*(x)$ and u, v^* are both solutions of (1.2.1) so $u_1(x,t) \geq v^*(x)$ for all x and t. Also, for some $\bar{x} \in \bar{\Omega}$ we must have $u_1(\bar{x},0) = v^*(x)$. Finally, by (1.3.5), we have $u_{1t}(\bar{x},0) < 0$, so for small $t > 0$ we have

$$v^*(\bar{x}) \leq u_1(\bar{x},t) < u_1(\bar{x},0) = v^*(x),$$

which contradicts the hypothesis that $v^*(x)$ is an equilibrium. Hence, in this case, (1.2.1) cannot have any equilibrium with maximum less than ϕ_0.

□

If we assume Hypothesis 1.4 that $\int_\Omega k(x,y)\phi(y)dy > 0$ for any $\phi(x) \geq 0$ with $\phi(x)$ positive on an open set, then the operator

$$M_f[\phi](x) = f(x) \int_\Omega k(x,y)\phi(y)dy$$

is strongly positive, then Theorem 1.13 applies.

This can be used to show nonexistence of a positive equilibrium if $\gamma_p \leq 0$ (thus zero equilibrium is globally stable) and uniqueness of the positive equilibrium if $\gamma_p > 0$.

Lemma 1.22. *Suppose hypothesis* 1.4 *holds and* $\gamma_p \leq 0$. *Then there is no positive equilibrium for* (1.2.1) *with* $0 < u^*(x) \leq K(x)$.

Proof. Suppose $u^*(x) > 0$ is an equilibrium of (1.2.1). Let

$$S[\phi](x) = \frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$$

and

$$T[\phi](x) = \frac{K(x) - u^*(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$$

Since $u^*(x)$ is a solution of (1.2.1), by Theorem 1.5 we have $u^*(x) < K(x)$. So both S and T are strongly positive.

$u^*(x)$ satisfies

$$u^*(x) = \frac{K(x) - u^*(x)}{d(x)} \int_\Omega k(x,y)u^*(y)dy$$

So $r(T) = 1$.

We already have $r(S) - 1 = \gamma_p \leq 0$, so $r(S) \leq r(T)$.

However, $(S-T)\phi(x) = \frac{u^*(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$ is strongly positive, so $r(S) > r(T)$. Contradiction.

□

Theorem 1.23. *If Hypothesis* 1.4 *holds and* $\gamma_p \leq 0$, *then* $u(x,t) = 0$ *is globally asymptotically stable.*

Proof. Note that if $u_0(x) = K(x)$, then (1.3.4) is satisfied. So if $u(x,t)$ is a solution to (1.2.1) with $u(x,0) = K(x)$, then $u(x,t)$ is decreasing and as $t \to \infty$, $u(x,t) \to \bar{u}^*(x)$ where $\bar{u}^*(x)$ is the largest equilibrium for (1.2.1) and $\bar{u}^*(x) < K(x)$.

Since $\gamma_p \leq 0$, by previous lemma there is no positive equilibrium of (1.2.1), we must have $u(x,t) \to 0$.

However, Theorem 1.8 implies that if there is $v(x,t)$ satisfying (1.2.1) and $0 \le v(x,0) \le K(x)$, then $0 \le v(x,t) \le u(x,t)$, and so $v(x,t) \to 0$ as $t \to \infty$. Thus 0 is globally asymptotically stable. □

If $\gamma_p > 0$, for small $\epsilon > 0$ we have as in (1.3.5) that $u_\epsilon = \epsilon\phi$ satisfies

$$\begin{aligned}&[K(x) - u_\epsilon(x)]\int_\Omega k(x,y)u_\epsilon(y)dy - d(x)u_\epsilon(x) \\ &= d(x)\epsilon\gamma_p\phi(x) - \epsilon^2(\int_\Omega k(x,y)\phi(y)dy)\phi(x) > 0\end{aligned} \tag{1.3.6}$$

Thus, by Lemma 1.20, the solution of (1.2.1) with initial data $u(x,0) = u_\epsilon(x)$ increases toward an equilibrium $u^*(x) > 0$. Since $\epsilon > 0$ can be arbitrarily small, $u^*(x)$ will be the minimal positive equilibrium of (1.2.1).

The next lemma shows that the positive equilibrium $u^*(x)$ is unique when it exists. So if $\gamma_p > 0$, $u(x,t)$ starting from $u_\epsilon(x)$ goes to the unique positive equilibrium $u^*(x)$ as $t \to \infty$.

Lemma 1.24. *If hypothesis* 1.4 *holds and* $\gamma_p > 0$, *then equilibrium* $u^*(x)$ *in this case exists and is the minimal equilibrium of* (1.2.1)*. Moreover,* $u^*(x)$ *is the unique positive equilibrium of* (1.2.1)*.*

Proof. Suppose $u^{**} > 0$ is any other equilibrium of (1.2.1). We have $u^{**} \ge u^*(x)$ since $u^*(x)$ is minimal. Also, since $u^{**}(x)$ and $u^*(x)$ are both solutions of (1.2.1) it follows from Theorem 1.8 that if $u^{**}(x) > u^*(x)$ for some x then $u^{**}(x) > u^*(x)$ for all x.

Let

$$S[\phi](x) = \frac{K(x) - u^*(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$$
$$T[\phi](x) = \frac{K(x) - u^{**}(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$$

Then $r(S) = 1$ because $Su^* = u^* > 0$, and $r(T) = 1$ because $Tu^{**} = u^{**} > 0$.

But $(S - T)\phi = \frac{u^*(x) - u^{**}(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy$ is strongly positive since $u^{**}(x) > u^*(x)$. So $r(S) > r(T)$ which is a contradiction. Thus $u^*(x)$ is the unique positive equilibrium.

□

Theorem 1.25. *Suppose Hypothesis (ii) holds, and $\gamma_p > 0$, then $u^*(x)$ is globally asymptotically stable.*

Proof. If $u(x,0) \leq K(x)$ and $u(x,t)$ satisfies (1.2.1) then by Theorem 1.8 we have $u(x,t) \leq v(x,t)$ where $v(x,0) = K(x)$. As in the proof that 0 is globally asymptotically stable we have that $K(x)$ satisfies (1.3.4), so $v(x,t)$ decreases to the largest equilibrium that is less than $K(x)$, which is $u^*(x)$.

If $u(x,0) \geq 0$, $u(x,0) > 0$ for some x, then we have $u(x,\delta) > 0$ for some $\delta > 0$ by Theorem 1.8. We can choose $\epsilon > 0$ so that $\epsilon\phi < u(x,\delta)$ and $\epsilon\phi$ satisfies (2.5.21). Let $w(x,t)$ be the solution of (1.2.1) with $w(x,0) = \epsilon\phi(x)$, then by Lemma 1.20 we have $w(x,t)$ increasing to the minimal equilibrium of (1.2.1) that is larger than $\epsilon\phi$, which is $u^*(x)$.

Also, if z is the solution of (1.2.1) with $z(x,0) = u(x,\delta)$ then $z(x,t) \geq w(x,t)$ by Theorem 1.8; also, by uniqueness $u(x,t+\delta) = z(x,t)$. Hence, $u(x,t+\delta)$ is bounded below by $w(x,t)$, and $w(x,t) \to u^*(x)$ as $t \to \infty$. It follows that $u(x,t)$ is bounded below by $w(x, t-\delta)$ for $t \geq \delta$, so for $t > \delta$ we have $w(x, t-\delta) \leq u(x,t) \leq v(x,t)$, with $w(x, t-\delta) \to u^*(x)$ and $v(x,t) \to u^*(x)$ as $t \to \infty$. Hence $u(x,t) \to u^*(x)$ as $t \to \infty$.

□

Corollary 1.26. *From Theorem* 1.19*, Theorem* 1.23 *and* 1.25*, we have the following:*

(1) If $g_2 \cdot |\Omega| < 1$*, then zero equilibrium is asymptotically stable.*

(2) If $g_1 \cdot |\Omega \cap B_{\delta/2}| > 1$*, then as* $t \to \infty$*, the equilibrium* $u^*(x)$ *is asymptotically stable.*

1.4 Conclusions

For our nonlocal metapopulation model on continuous time and space, we obtained the existence and uniqueness for the solution for all $t > 0$ by applying contraction mapping theorem. This result holds for both Ω finite or on infinite domain. Maximum principle and comparison theorem are valid if Ω is finite and Hypothesis 1.9 is satisfied. However, to apply Krein-Rutman theorem on eigenvalue problem $-\lambda\phi(x) = \frac{K(x)}{d(x)} \int_\Omega k(x,y)\phi(y)dy - \phi(x)$, we need Hypothesis 1.4, which is stronger than Hypothesis 1.9. By the approach of super-(sub-) solution, we have the stability analysis of zero equilibrium and the unique positive equilibrium under some conditions based on the estimation of the principal eigenvalue.

Chapter 2

Two Species Competition Model

2.1 Background

In Chapter 1, we studied some basic properties for the nonlocal metapopulation model for single species. In this chapter, we will look at the coexistence and extinction for a two-species competition system. The Lotka Volterra competition model of population dynamics is based on logistic equations and describes species competition for common resources. The Lotka Volterra competition system with random dispersal usually has the following form

$$\begin{aligned} u_t &= d_1 \triangle u + u[a_1(x) - b_1(x)u - c_1(x)v], \quad x \in \Omega \\ v_t &= d_2 \triangle v + v[a_2(x) - b_2(x)u - c_2(x)v], \quad x \in \Omega \end{aligned} \tag{2.1.1}$$

This system, describing the dynamics of two competing species, has been widely investigated. The functions $a_i(x), b_i(x), c_i(x)$, $i = 1, 2$ are assumed to be smooth and nonnegative on $\bar{\Omega} \times (0, +\infty)$. d_i are the diffusion constants and they are positive. The functions $a_i(x)$ represent the growth rates, $b_1(x)$, $c_2(x)$ represents the self-regulation of each species and $c_1(x)$, $b_2(x)$ account for competition. Cosner and Lazer [21] studied the existence and stability of coexistence states for this model under two types of growth and boundary conditions.

Hetzer, Nguyen and Shen [36] considered the Lotka-Volterra competition with nonlocal dispersal:

$$\begin{aligned} u_t &= d_1[\int_\Omega k(x,y)u(y,t)dy - u(x,t)] + u[a_1(x) - b_1(x)u - c_1(x)v], \quad x \in \Omega \\ v_t &= d_2[\int_\Omega k(x,y)v(y,t)dy - v(x,t)] + v[a_2(x) - b_2(x)u - c_2(x)v], \quad x \in \Omega \end{aligned} \tag{2.1.2}$$

The system describes the population dynamics with two competing species, where dispersal is affected by long distance interaction.

In our model, we consider the competition for space between two species. The model is:

$$\begin{aligned} u_t &= [K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_1(x,y)u(y,t)dy - d_1(x)u(x,t), \quad x \in \Omega \\ v_t &= [K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_2(x,y)v(y,t)dy - d_2(x)v(x,t), \quad x \in \Omega \end{aligned} \tag{2.1.3}$$

$a(x)$ is the size of individual of species u, $b(x)$ is the size of species v. $k_i(x, y)$ are the dispersal kernel of u, v respectively. $e_i(x)$ are the death rate of each species. Chesson et al. [14] [15] and [16] have a different modeling setup but with the similar idea that species compete for spaces. It is different from the previous models where the two species compete for resources.

Another important feature is the dispersal strategy of organisms. How the species distribute in space leads to spatial distributions and biological invasions, and colonizations. The evolution of dispersal strategies is a problem of particular interest in spatial ecology, especially what dispersal strategies can be selected over the evolution process. A strategy is said to be evolutionarily stable if it cannot be invaded by a small population of mutants using any other strategy. We will investigate the evolutionary stability of a nonlocal dispersal strategy in a metapopulation framework. Cressman et al. [23] showed that the ideal free distribution is an evolutionarily stable strategy in a two-patch environment metapopulation model, from the aspect of game theory. A metapopulation is a collection of local populations distributed across a network of patches. Dispersal is viewed as the rate of colonization where individuals can recolonize a habitat once the local population has gone extinct.

Our study is based on an extension of Levins metapopulation model which assumed a infinite number of identical patches where the colonization is also driven by the dispersal of focal organisms. The modeling viewpoint is generally similar to the idea in Hamilton and May [54]. [54] assumed that the adults do not move while they produce offspring such that only one propagule (carrying capacity of each site is one) stays at home, while the others are migrants. This is a dispersal strategy which is shown to be evolutionary stable in contrast to the strategy where adults keep propagules at their own sites, even though the migrants in the dispersal strategy suffer a mortality rate during the dispersal process. The migrants and local organisms compete for space, and dispersal occurs together with reproduction, in a heterogeneous environment (sometimes temporally invariant). Comins et al. [19] extended the result to transient environments and allowed more than one organism to occupy each site. [19] showed that the migration rate can be chosen to maximize the proportion of sites occupied by considering exogenous extinction. On the other hand, Hanski's spatially explicit patch occupancy model, which is an extension of Levins' metapopulation model with a similar assumption, and Mouquet and Loreau studied the dynamics of the metacommunity model where communities are linked by dispersal. Our model (2.1.3) is continuous in time and space.

The ideal free distribution is caused by a form of conditional dispersal, known as balanced dispersal, which results in an equilibrium population that will have the same fitness at each location ([12]). This dispersal strategy is evolutionarily stable in a considerable number of situations (Fretwell et al. [28]). The ideal free distribution is a theory about how organisms would locate themselves if they were omniscient and able to move as they wanted. See Cantrell et al. [13], Cantrell, et al. [7], [8], [9], Cosner et al. [20], Cantrell et al. [10]. [9] investigated the ideal free dispersal strategy in discrete patchy environments. In contrast to Cressman et al's approach of game theory which based on comparing payoffs at equilibrium, they addressed the mechanisms and dynamics in their model. In [20] the authors extended the results developed for discrete diffusion models to the case of nonlocal dispersal models and found conditions of determining evolutionarily stable dispersal strategies. They showed that the ideal free dispersal strategy is likely to evolve and persist. For random dispersal, Dockery [25] showed that the mutant with smaller dispersal rate can not only invade the resident species but also drive it to extinction. Hutson [38] suggested that the slower dispersal is favored in nonlocal dispersal. Cantrell et al. [10] introduced a more general class of ideal free dispersal kernels that are indeed evolutionarily stable. In [24] the authors investigated the effect of cost-associated forced movement for spatial metapopulation dynamics by considering a food chain between patches.

In this chapter, we will provide proof of the existence and uniqueness of solutions to the model and prove a version of maximum principle and comparison theorem for our continuum nonlocal metapopulation model. The stability of the equilibrium $(0,0)$ in this model and the two semi-trivial equilibria will be studied. In the case that none of these three equilibria is stable, we will give a condition of the existence of coexistence state and a specific example. For evolutionarily stability analysis, we will investigate the model via competition models between two species that are identical except for their dispersal strategy. The discrete patch model for this scenario is the Mouquet-Loreau model for metacommunity network in which communities are linked by dispersal. Cantrell, Cosner, Lou, Schreiber [11] studied the dispersal strategy for Mouquet- Loreau model. In this model, dispersal occurs during the process of recruitment. The species with an ideal free dispersal strategy will invade successfully in this case.

2.2 Existence and Uniqueness

2.2.1 The model

Let

$$\begin{aligned} u_t &= [K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_1(x,y)u(y,t)dy - d_1(x)u(x,t) \\ v_t &= [K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_2(x,y)v(y,t)dy - d_2(x)v(x,t) \end{aligned} \tag{2.2.1}$$

where $u(x,t), v(x,t)$ are population density of two species respectively. $K(x)$ represents the potential suitable site for both species. $k_{1,2}(x,y)$ are dispersal kernel for two species and $d_{1,2}(x)$ are extinction rate. The variable $a(x)$ represents the individual size of species u which may depend on the location x and $b(x)$ represents the individual size for species v. For the system setup, we assume that the individuals (offspring, juveniles) of two species compete for the space, which results in the form that two equations have the same $a(x)$ and $b(x)$.

2.2.2 Existence and Uniqueness of Solution

Suppose we start with $\vec{w}(x,0) = \vec{w}_0 = (u(x,0), v(x,0)) = (u_0, v_0)$. $\vec{w} = (u,v) \in [C([0,T], C(\bar{\Omega}))]^2$.

Let $S \subseteq [C([0,T], C(\bar{\Omega}))]^2$. X is the set of continuous functions from $[0,T]$ to $C(\bar{\Omega})$. $S = \{\vec{w}(x,t) = (u(x,t), v(x,t)) \mid u(x,t), v(x,t) \in X \text{ and } \|\vec{w} - \vec{w}_0\| \leq M\}$. Here $\|\vec{w}\| = \sup_{\Omega\times[0,T]} |u(x,t)| + \sup_{\Omega\times[0,T]} |v(x,t)|$ and $0 < M, T < 1$ are constants to be determined later.

We have $\forall \vec{w} \in S$, $\|\vec{w}\| \leq \|\vec{w}_0\| + M \leq \|\vec{w}_0\| + 1 := W_0$. $\|u\| \leq \|u_0 + \frac{M}{2}\| := U_0$,$\|v\| \leq \|v_0 + \frac{M}{2}\| := V_0$.

For $\vec{w} \in S$, $0 < t < T$, define $\mathcal{F}(\vec{w}) = (\mathcal{F}_1(u), \mathcal{F}_2(v))$

$$
\begin{aligned}
&\mathcal{F}_1(u) = u(x,0) + \textstyle\int_0^t \Big([K(x) - a(x)u(x,s) - b(x)v(x,t)] \\
&\cdot \textstyle\int_\Omega k_1(x,y)u(y,t)dy - d_1(x)u(x,s)\Big)ds \\
&\mathcal{F}_2(v) = v(x,0) + \textstyle\int_0^t \Big([K(x) - a(x)u(x,s) - b(x)v(x,t)] \\
&\cdot \textstyle\int_\Omega k_2(x,y)v(y,t)dy - d_2(x)v(x,s)\Big)ds
\end{aligned}
\tag{2.2.2}
$$

First, we have

$$
\begin{aligned}
&\|\mathcal{F}_1(u)\| \\
\leq&([\|K(x)\| + \sup_\Omega |a(x)| \cdot \|u(x,s)\| + \sup_\Omega |b(x)| \|v(x,s)\|] \cdot \int_\Omega k_1(x,y)dxdy \cdot |\Omega| \\
+&\|d_1(x)\|)U_0 \cdot t + \|u_0\|
\end{aligned}
$$

Similar for $\mathcal{F}_2(v)$. So the integrals converge.

Then we want to show $\mathcal{F}(\vec{w}) \in S$.

$$
\begin{aligned}
&\|\mathcal{F}_1(u) - u_0\| \\
&\leq ([\|K(x)\| + \sup_{\Omega} |a(x)| \cdot \|u(x,s)\| + \sup_{\Omega} |b(x)| \|v(x,s)\|] \cdot \int_{\Omega} k_1(x,y) dx dy \cdot |\Omega| \\
&+ \|d_1(x)\|) U_0 \cdot t \\
&\leq constant \cdot M \cdot t
\end{aligned}
$$

We can select $T_1(M)$ small enough such that for $0 < t < T_1(M)$ we have

$$\|\mathcal{F}_1(u) - u_0(x)\| < \frac{M}{2}$$

Similarly, we can select $T_2(M)$ such that for $0 < t < T_2(M)$ we have

$$\|\mathcal{F}_2(v) - v_0(x)\| < \frac{M}{2}$$

So $\mathcal{F}(\vec{w}) \in S$.

Next we want to show that we can choose $T \leq T_3(M)$ such that

$$\|\mathcal{F}(\vec{w}_1) - \mathcal{F}(\vec{w}_2)\| < C \|\vec{w}_1 - \vec{w}_2\|$$

for $\vec{w}_1, \vec{w}_2 \in S, C < 1$, and starting from the same $\vec{w}_0 = (u_0, v_0)$.

$$\begin{aligned}
&\|\mathcal{F}_1(u_1) - \mathcal{F}_1(u_2)\| \\
&= \| \int_0^t \{ \int_\Omega k_1(x,y)u_1(y,s)dy[K(x) - a(x)u_1(x,s) - bv_1(x,s)] - d_1(x)u_1(x,s)\}ds \\
&- \int_0^t \{ \int_\Omega k_1(x,y)u_2(y,s)dy[K(x) - a(x)u_2(x,s) - bv_2(x,s)] - d_1(x)u_2(x,s)\}ds\| \\
&= \| \int_0^t \{ \int_\Omega K(x) \cdot k_1(x,y)[u_1(y,s) - u_2(y,s)]dy - d_1(x) \cdot |u_1(x,s) - u_2(x,s)| \\
&-a(x)\Big([u_1(x,s) - u_2(x,s)][\int_\Omega k_1(x,y)u_1(y,s)dy] \\
&+u_2(x,s)[\int_\Omega k_1(x,y) \cdot (u_1(y,s) - u_2(y,s))dy]\Big) \\
&-b(x)\Big([v_1(x,s) - v_2(x,s)][\int_\Omega k_1(x,y)u_1(y,s)dy] \\
&+v_2(x,s)[\int_\Omega k_1(x,y)(u_1(y,s) - u_2(y,s))dy]\Big)\| \\
&= C_1 \cdot \|u_1 - u_2\| \cdot t + C_2 \cdot \|v_1 - v_2\| \cdot t
\end{aligned}$$

Here, $C_1 = \sup_\Omega |\int_\Omega k_1(x,y)dy| \cdot \Big(\sup|K(x)| + \sup|d_1(x)| + \sup|a(x)|(\|u_1\| + \|u_2\|) + \sup|b(x)\|v_2\||\Big)$, $C_2 = \sup|b(x)| \cdot \sup_\Omega |\int_\Omega k_1(x,y)dy| \cdot \|u_1\|$

$$\begin{aligned}
&\|\mathcal{F}_2(v_1) - \mathcal{F}_2(v_2)\| \\
&= \| \int_0^t \{ \int_\Omega k_2(x,y)v_1(y,s)dy[K(x) - a(x)u_1(x,s) - bv_1(x,s)] - d_2(x)v_1(x,s) \ \}ds \\
&- \int_0^t \{ \int_\Omega k_2(x,y)v_2(y,s)dy[K(x) - a(x)u_2(x,s) - b(x)v_2(x,s)] - d_2(x)v_2(x,s) \ \}ds\| \\
&= \| \int_0^t \{ \int_\Omega K(x) \cdot k_2(x,y)[v_1(y,s) - v_2(y,s)]dy - d_2(x) \cdot |v_1(x,s) - v_2(x,s)| \\
&-a(x)\Big([u_1(x,s) - u_2(x,s)][\int_\Omega k_2(x,y)v_1(y,s)dy] \\
&+u_2(x,s)[\int_\Omega k_2(x,y) \cdot (v_1(y,s) - v_2(y,s))dy]\Big) \\
&-b(x)\Big([v_1(x,s) - v_2(x,s)][\int_\Omega k_2(x,y)v_2(y,s)dy] \\
&+v_1(x,s)[\int_\Omega k_2(x,y)(v_1(y,s) - v_2(y,s))dy]\Big)\| \\
&= C_3 \cdot \|v_1 - v_2\| \cdot t + C_4 \cdot \|u_1 - u_2\| \cdot t
\end{aligned}$$

Here $C_3 = \sup_\Omega |\int_\Omega k_2(x,y)dy| \cdot \Big(\sup|K(x)| + \sup|d_2(x)| + \sup|a(x)| \cdot \|u_2\| + \sup|b(x)| \cdot (\|v_1\| + \|v_2\|)\Big)$, $C_4 = \sup|a(x)| \cdot \sup_\Omega |\int_\Omega k_2(x,y)dy| \cdot \|v_1\|$.

Let $C = max\{C_1 + C_4, C_2 + C_3\}$. Select $t < \min\{T_1(M), T_2(M), \frac{1}{C}\}, M = 1$, we have

$$\|\mathcal{F}(\vec{w})_1 - \mathcal{F}(\vec{w}_2)\| \leq \alpha \|\vec{w}_1 - \vec{w}_2\|$$

with $\alpha < 1$. Thus $\mathcal{F}$ is a contraction on S.

Theorem 2.1. *There exists a unique solution for system* (2.2.1) *for some* $[0, T]$.

Proof. By Banach fixed point theorem, there exists a unique $\vec{w}^*$ such that $\mathcal{F}(\vec{w}^*) =$

$\vec{w}^*$. So by the previous discussion, there exists a solution to

$$\begin{aligned} u^* &= u(x,0) + \int_0^t [\int_\Omega k_1(x,y)u^*(y,s)dy[K(x,t) - a(x)u^*(x,s) - b(x)v^*(x,t)] \\ &-d_1(x)u^*(x,s)]ds \\ v^* &= v(x,0) + \int_0^t [\int_\Omega k_2(x,y)v^*(y,s)dy[K(x,t) - a(x)u^*(x,s) - b(x)v^*(x,t)] \\ &-d_2(x)v^*(x,s)]ds. \end{aligned}$$

As in the case of a single equation, the integrands are continuous, so $u^*(x)$, $v^*(x)$ are differentiable and satisfy (2.2.1).

□

Remark 2.2. *Similar to the single equation, to obtain the existence of solution, the domain Ω is not necessarily bounded. For example, if $k(x,y) = k(x-y)$ is Gaussian kernel and $\Omega = \mathbb{R}$, then we need $\int_\Omega k_i(y)dy = k_i < \infty$ and can also obtain the existence of solutions.*

In the following context, we have the following hypotheses:

(H1) $k(x,y) \geq 0$ is a C^1 function, $\int_\Omega k(x,y)dx < \infty$, $\int_\Omega k(x,y)dy < \infty$ and there is $\delta_0 > 0$ such that for any $x \in \bar{\Omega}$, we have $k(x,y) > 0$ for $y \in \bar{\Omega}$ and $\|x-y\| < \delta_0$.

(H2) $k(x,y) \geq 0$ is a C^1 function, $\int_\Omega k(x,y)dx < \infty$, $\int_\Omega k(x,y)dy < \infty$ and for all $\phi(x) \geq 0$ on Ω and $\phi(x) > 0$ for some x, we have $\int_\Omega k_(x,y)dy > 0$.

(H1) is a weak assumption on the kernel (Hypothesis 1.9). (H2) is a strong assumption (Hypothesis 1.4).

2.3 Maximum Principle

Theorem 2.3. *Suppose* $k_i(x,y) \geq 0$ *and satisfy (H1) and (H2) for* $i = 1, 2$

(I) If $0 \leq a(x)u(x,0) + b(x)v(x,0) \leq K(x)$*, and* $(u(x,t), v(x,t))$ *is a solution of the system, then* $a(x)u(x,t) + b(x)v(x,t) < K(x)$*, and either* $u \equiv 0$ *or* $u > 0$*, either* $v \equiv 0$ *or* $v > 0$ *for* $t \in [0, T]$ *where* $(u(x,t), v(x,t))$ *exists.*

(II) If we further assume $u(x,0) > 0$*,* $v(x,0) > 0$ *on some open subset of* Ω*, then* $u(x,t) > 0$ *and* $v(x,t) > 0$ *for* $t \in [0,T]$ *where* $(u(x,t), v(x,t))$ *exists.*

Proof. If $u \equiv 0$, then it becomes the single species model for v. Similarly if $v \equiv 0$.

Let $u, v \geq 0$. For $t = 0$, $u, v \geq 0$ and $u, v > 0$ for some $x \in \Omega$.

At points where $a(x)u(x,0) + b(x)v(x,0) = K(x)$, we have $u_t = -d_1(x)u(x,0)$, $v_t = -d_2(x)v(x,0)$.

If $a(x)u(x,0) + b(x)v(x,0) = K(x)$, then either $u > 0$ or $v > 0$; so since $u(x,0) \geq 0$, $v(x,0) \geq 0$, $(a(x)u(x,t) + b(x)v(x,t))_t < 0$ at $t = 0$. Otherwise $a(x)u(x,0) + b(x)v(x,0) < K(x)$. In either case there exists an interval $(0, t_0(x))$ such that $a(x)u(x,t) + b(x)v(x,t) < K(x)$ at point x.

We could have $u(x,0) \equiv 0$ (or $v(x,0) \equiv 0$). If so, then $u(x,t) \equiv 0$ (or $v(x,t) \equiv 0$), and the system reduces to the single equation model.

In any other case we would have $u(x,0) > 0$ for some x, $v(x,0) > 0$ for some x.

Since (H2), we get $u_t(x,0) > 0$, $v_t(x,0) > 0$ at any point where $u(x,0) = 0$ ($v(x,0) = 0$) and $a(x)u(x,0) + b(x)v(x,0) < K(x)$. For such values of x we have $u(x,t) > 0$ for $0 < t < t_{1u}(x)$ ($v(x,t) > 0$ for $0 < t < t_{1v}(x)$). We also get $u(x,t) > 0$ for $0 < t < t_{1u}(x)$ by continuity if $u(x,0) > 0$ (similar for v).

Consider the case $u(x,0) = 0$ and $a(x)u(x,0) + b(x)v(x,0) = K(x)$. We already know that if $a(x)u(x,0) + b(x)v(x,0) = K(x)$, then as above, (since $u(x,0), v(x,0) \geq$

0) we must have $a(x)u_t(x,0)+b(x)v_t(x,0) < 0$ so that $K(x)-a(x)u(x,t)-b(x)v(x,t) > 0$ on some interval $(0, t_0(x))$. Also, if $u = 0$ and $a(x)u(x,0) + b(x)v(x,0) = K(x)$, then $u_t(x,0) = 0$. If $u(x,0) \geq 0$ and $u(x,0) > 0$ somewhere, then by (H2),

$$\int_\Omega k_1(x,y)u(y,0)dy > 0$$

and then by continuity $\int_\Omega k_1(x,y)u(y,t)dy > 0$ on some interval $0 < t < t_2(x)$. We have

$$u_t + d_1(x)u(x,t) = [K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_1(x,y)u(y,t)dy$$

so

$$[u(x,t)e^{d_1(x)t}]_t = e^{d_1(x)t}[K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_1(x,y)u(y,t)dy$$

so

$$u(x,t) = \int_0^t e^{-d_1(x)(t-s)}[K(x) - a(x)u(x,t) - b(x)v(x,t)] \int_\Omega k_1(x,y)u(y,s)dyds.$$

The expression inside the integral will be positive for $0 < t < \min\{t_0(x), t_2(x)\}$ so again $u(x,t) > 0$ on $0 < t < t_{1u}(x)$ for some $t_{1u}(x) > 0$. Hence for each x, $u(x,t) > 0$ on $0 < t < t_{1u}(x)$. Similarly for $v(x,t)$.

Let $t_0^*(x) = \sup\{t : a(x)u(x,s) + b(x)v(x,s) < K(x) \quad for \quad 0 < s < t\}$.

Similarly, let $t_1^* = \sup\{t : u(x,s) > 0 \quad for \quad 0 < s < t\}$, $t_2^* = \sup\{t : v(x,s) > 0 \quad for \quad 0 < s < t\}$. Then $t_0^*(x)$, $t_1^*(x)$ and $t_2^*(x)$ are all positive.

Claim: $t_0^*(x) > \min\{t_1^*(x), t_2^*(x)\}$.

Proof of claim:

If $t_0^*(x) \le \min\{t_1^*(x), t_2^*(x)\}$, note that we have $a(x)u(x, t_0^*(x)) + b(x)v(x, t_0^*(x)) = K(x)$, but $a(x)u(x,t) + b(x)v(x,t) < K(x)$ for $0 < t < t_0^*(x)$, so $(a(x)u(x,t) + b(x)v(x,t))_t \ge 0$ at $t = t_0^*(x)$.

On the other hand, since $K(x) - a(x)u - b(x)v = 0$ at $(x, t_0^*(x))$, if $t_1^*(x), t_2^*(x) \ge t_0^*(x)$, then $u, v \ge 0$ at $(x, t_0^*(x))$ so $u_t = -d_1(x)u(x, t_0^*(x)) \le 0$, $v_t = -d_2(x)v(x, t_0^*(x)) \le 0$, and since $a(x)u + b(x)v = K(x)$ at $(x, t_0^*(x))$, one of those inequalities must be strict, so $(au+bv)_t < 0$ at $(x, t_0^*(x))$, which gives a contradiction.

Thus the claim holds true.

Let $g_1(x,t) = \int_\Omega k_1(x,y)u(y,t)dy$.

We have $u(z,0) \ge 0$ for all $z \in \bar{\Omega}$, $u(z,0) > 0$ for some $z \in \bar{\Omega}$. So by hypothesis (H2) on $k_1(x,y)$, we have $g_1(x,0) > 0$ for all x. Also, g_1 is continuous.

Let $t_4^*(z) = \inf\{t > 0 : g_1(z,s) > 0 \;\; for \;\; 0 < s < t\}$. Suppose $\inf_{z\in\bar{\Omega}} t_4^*(z) = 0$. We must have $g_1(z, t_4^*(z)) = 0$ by definition of $t_4^*(z)$ and continuity. Also there exist $(x_n, t_4^*(x_n))$ so that $g_1(x_n, t_4^*(x_n)) \to 0$, $t_4^*(x_n) \to 0$ as $n \to \infty$. Choosing a subsequence we get $x_n \to x^*$ so $0 = g_1(x_n, t_4^*(x_n)) \to g_1(x^*, 0) > 0$. This is a contradiction. Thus, we must have $inf_{z\in\bar{\Omega}} t_4^*(z) = t_4^{**} > 0$.

For $0 < t < t_4^{**}$, we have $g_1(x,t) = \int_\Omega k_1(x,y)u(y,t)dy$ positive for $x \in \bar{\Omega}$. (Similarly, there is a t_5^{**} so that $\int_\Omega k_2(x,y)v(y,t)dy$ is positive on $0 < t < t_5^{**}$).

Suppose $t_1^*(x) \le t_2^*(x)$ with $t_1^*(x) < t_4^{**}$. We must have $u(x, t_1^*(x)) = 0$.

Claim: This yields a contradiction. (If $t_2^*(x) \le t_1^*(x) < t_5^{**}$, we get a contradiction by a similar argument.)

Proof of claim: If $t_1^*(x) \le t_2^*(x)$ with $t_1^*(x) < t_4^{**}$, then for $0 < t < t_4^{**}$ we have $t < t_0^*(x)$ so $K(x) - a(x)u(x,t) - b(x)v(x,t) > 0$, and also $g_1(x,t) > 0$. Furthermore, we must have $u(x, t_1^*(x)) = 0$, with $u(x,t) > 0$ for $0 < t < t_1^*(x)$. We must also have $u_t(x,t) > -d_1(x)u(x,t)$ on $(0, t_1^*(x))$, with $u(x,\epsilon) > 0$ for some ϵ with $0 < \epsilon < t_1^*(x)$. However, this implies $u(x,t) \geq e^{-d_1(x)(t-\epsilon)}u(x,\epsilon) > 0$ on $(0, t_1^*(x))$, so that $u(x, t_1^*(x)) \geq e^{-d_1(x)(t_1^*(x)-\epsilon)}u(x,\epsilon) > 0$, contradiction. Hence in this case we get $t_4^{**} \leq t_1^*(x) \leq t_2^*(x)$. Thus the claim holds true.

A similar argument shows that if $t_2^*(x) < t_1^*(x)$, there is a t_5^{**} with $t_5^{**} \leq t_2^*(x) \leq t_1^*(x)$.

It follows that $\inf_{x\in\bar{\Omega}} t_1^*(x) \geq \min\{t_4^{**}, t_5^{**}\} > 0$.

Suppose $t_6^{**} = \inf_{x\in\bar{\Omega}} t_1^*(x) > 0$, for some x. Then there exists a sequence $(x_n, t_1^*(x_n))$ with $t_1^*(x_n) \to t_6^{**}$. Choose a convergent subsequence; then relabel it as x_n, so that $x_n \to x^*$. We have $u(x_n, t_1^*(x_n)) = 0$ so $u(x^*, t_6^{**}) = 0$ so $t_6^{**} \geq t_1^*(x^*)$. But by definition we have $t_6^{**} \leq t_1^*(z)$ for all z, so $t_6^{**} = t_1^*(x^*)$ and so $t_1^*(z) \geq t_1^*(x^*)$ for all z; also, $t_1^*(z) \geq \min\{t_4^{**}, t_5^{**}\} > 0$ for all z, so $t_1^*(x^*) > 0$.

We have $u(x^*, t_6^{**}) = u(x^*, t_1^*(x^*)) = 0$.

However, consider again $\tilde{u} = e^{d_1(x)t}u$, we have

$$\tilde{u}_t = [K(x) - a(x)u(x,t) - b(x)v(x,t)]e^{d_1(x)t} \int_\Omega k_1(x,y)u(y,t)dy$$

So

$$\tilde{u}(x,t) = \int_0^t [K(x) - a(x)u(x,s) - b(x)v(x,s)]e^{d_1(x)s} \int_\Omega k_1(x,y)u(y,s)dyds$$

Hence $\tilde{u}(x^*, t_1^*(x^*)) > 0$ since $K(x) - a(x)u(x,t) - b(x)v(x,t) > 0$ for $0 < t < t_0^*(x^*)$ with $t_0^*(x^*) > t_1^*(x^*)$ and by previous analysis we know $u(y,s) > 0$ on $0 < t < t_1^*(x^*)$ so $\tilde{u}(x^*, t_1^*(x^*)) > 0$. So $u(x^*, t_1^*(x^*)) > 0$, a contradiction.

It follows that $t_6^{**} = \infty$ so $t_1^*(x) = \infty$ for all x. (A similar argument shows

$t_2^*(x) = \infty$ for all x) and then $t_0^*(x) = \infty$ for all x.

This shows $u(x,t) > 0$, $v(x,t) > 0$ and $K(x) - a(x)u(x,t) - b(x)v(x,t) > 0$ for $t > 0$.

□

Corollary 2.4. *Global Existence*

Let $u(x,0) \geq 0$ *and* $v(x,0) \geq 0$, $a(x)u(x,0) + b(x)v(x,0) \leq K(x)$, *then* $(u(x,t), v(x,t))$ *exists for all* $t > 0$ *where the solution exists.*

Proof. In the case either $u(x,t) \equiv 0$ or $v(x,t) \equiv 0$, the global existence follows from the single species model. If not, from Maximum principle we have $u(x,t) > 0$, $v(x,t) > 0$ and $K(x) - a(x)u(x,t) - b(x)v(x,t) > 0$ for $t \in [0,T]$. These inequalities imply uniform bounds on u, v and the quantities determined T are in the proof of Theorem 2.1. This argument can be repeated on $[T, 2T]$, $[2T, 3T]$ and so on. So we obtain the global existence of the system. □

2.4 Comparison Principle and Global Existence

Let $X = C(\bar{\Omega}, \mathbb{R})$ be equipped with the maximum norm, and

$$X^+ = \{u \in X \mid u(x) \geq 0, x \in \bar{\Omega}\},$$

$$X^{++} := Int(X^+) := \{u \in X^+ \mid u(x) > 0, x \in \bar{\Omega}\}.$$

For given $u_1, u_2 \in X$, we define

$$u_1 \le u_2 (u_2 \ge u_1) \;\; if \;\; u_2 - u_1 \in X^+,$$
$$u_1 \ll u_2 (u_2 \gg u_1) \;\; if \;\; u_2 - u_1 \in X^{++}.$$

Define the following orderings in $X \times X$:

$$(u_1, v_1) \le_1 (\ll_1)(u_2, v_2) \;\; if \;\; u_1 \le (\ll u_2), v_1 \le (\ll) v_2,$$
$$(u_1, v_1) \le_2 (\ll_2)(u_2, v_2) \;\; if \;\; u_1 \le (\ll u_2), v_1 \ge (\gg) v_2.$$

"$\le_1$ $(\ll_1)$" is the usual order and "$\le_2$ $(\ll_2)$" is the called the competition ordering.

We assume (H1) and (H2) in following context.

Theorem 2.5. *Monotonicity*

a) If $(0,0) \le_1 (u_i, v_i)$ *for* $i = 1,2$. $(u_1(x,0), v_1(x,0)) \le_2 (u_2(x,0), v_2(x,0))$ *and* $K(x) - a(x)u_i(x,0) - b(x)v_i(x,0) \le K(x)$, *then* $(u_1(x,t), v_1(x,t)) \le_2 (u_2(x,t), v_2(x,t))$ *for* $t > 0$.

b) If $u_1(x,0) < u_2(x,0), v_1(x,0)) > v_2(x,0)$ *for some* $x \in \Omega$ *and* $a(x)u_i(x,0) + b(x)v_i(x,0) \le K(x)$, *then* $(u_1(x,t), v_1(x,t)) \ll_2 (u_2(x,t), v_2(x,t))$ *for* $t > 0$.

Proof. a) Define:

$u(x,t) = u_2(x,t) - u_1(x,t) + \epsilon e^{\alpha t}$, $\tilde{u}(x,t) = u(x,t)e^{\beta t}$.

$v(x,t) = v_1(x,t) - v_2(x,t) + \epsilon e^{\alpha t}$, $\tilde{v}(x,t) = v(x,t)e^{\beta t}$.

By previous theorem, all solutions are nonnegative with $au + bv \le K(x)$. So they are uniformly bounded and we can pick

$\alpha > max_{x\in\Omega, t\ge 0}\{-[K(x) - a(x)u_2 - b(x)v_2](\int_\Omega k_1(x,y)dy) + [a(x) - b(x)]\int_\Omega k_1(x,y)u_1(y,t)dy - d_1(x), -[K(x) - a(x)u_1 - b(x)v_1](\int_\Omega k_2(x,y)dy) + [a(x) -$

$b(x)]\int_\Omega k_2(x,y)v_2(y,t)dy - d_2(x)\}$,

$\beta > max_{x\in\Omega,t\geq 0}\{d_1(x) + a(x)\int_\Omega k_1(x,y)u_1(y,t)dy, d_2(x) + b(x)\int_\Omega k_2(x,y)v_2(y,t)dy\}$

Claim: $u > 0$, $v > 0$ for all $t > 0$ where u, v exist.

Suppose otherwise, there exists $t_0 \in [0,T]$, $t_0 = \inf\{t \in [0,T) \mid u(x,t) \leq 0$ or $v(x,t) \leq 0$ for some $x \in \bar{\Omega}\}$.

Since $u(x,0) > 0$,$v(x,0) > 0$, then by continuity, we have $t_0 > 0$.

Then for $t \in [0,t_0)$, $u(x,t) > 0$ and $v(x,t) > 0$.

For $t \in (0,t_0]$,

$$
\begin{aligned}
& \tilde{u}_t \cdot e^{-\beta\cdot t} \\
= \quad & [K(x) - a(x)u_2(x,t) - b(x)v_2(x,t)]\int_\Omega k_1(x,y)u(y,t)dy + b(x)v(x,t) \\
& \cdot \int_\Omega k_1(x,y)u_1(y,t)dy + u(x,t)(\beta - d_1(x) - a(x)\int_\Omega k_1(x,y)u_1(y,t)dy) \\
& + \epsilon e^{\alpha\cdot t}(\alpha - [K(x) - a(x)u_2 - b(x)v_2] \\
& \cdot(\int_\Omega k_1(x,y)dy) - [a(x) - b(x)]\int_\Omega k_1(x,y)u_1(y,t)dy + d_1(x)) \\
> \quad & [K(x) - a(x)u_2(x,t) - b(x)v_2(x,t)]\int_\Omega k_1(x,y)u(y,t)dy \\
& + b(x)v(x,t)\int_\Omega k_1(x,y)u_1(y,t)dy \\
& + (\beta - d_1(x) - a(x)\int_\Omega k_1(x,y)u_1(y,t)dy)u(x,t) \\
\geq \quad & 0
\end{aligned}
$$

$$
\begin{aligned}
&\tilde{v}_t \cdot e^{-\beta \cdot t} \\
&= [K(x) - a(x)u_1(x,t) - b(x)v_1(x,t)] \int_\Omega k_2(x,y)v(y,t)dy \\
&+a(x)u(x,t) \int_\Omega k_2(x,y)v_2(y,t)dy + v(x,t)(\beta - d_2(x) - b_2(x) \int_\Omega k_2(x,y)v_2(y,t)dy) \\
&+\epsilon e^{\alpha \cdot t}(\alpha - [K(x) - a(x)u_1 - b(x)v_1](\int_\Omega k_2(x,y)dy) - [a(x) - b(x)] \\
&\cdot \int_\Omega k_2(x,y)v_2(y,t)dy + d_2(x)) \\
&> [K(x) - a(x)u_1(x,t) - b(x)v_1(x,t)] \int_\Omega k_2(x,y)v(y,t)dy \\
&+a(x)u(x,t) \int_\Omega k_2(x,y)v_2(y,t)dy + (\beta - d_2(x) - b(x)) \int_\Omega k_2(x,y)v_2(y,t)dy)v(x,t) \\
&\geq 0
\end{aligned}
$$

$\therefore \tilde{u}(x,t) > 0$ for $t \in [0, t_0]$.

$\therefore u(x,t) > 0$ for $t \in [0, t_0]$. A similar argument shows $v(x,t) > 0$ on $[0, t_0]$. Contradiction!

$\because \epsilon$ can be arbitrarily small

$\therefore u_2(x,t) \geq u_1(x,t)$ for $t > 0$.

Similarly we get $v_1(x,t) \geq v_2(x,t)$.

b)

Suppose $0 \leq u_1(x,0) \leq u_2(x,0)$, $0 \leq v_2(x,0) \leq v_1(x,0)$, $a(x)u_i(x,0) + b(x)v_i(x,0) \leq K(x)$,$i = 1,2$ and $u_2(x,0 > u_1(x,0) \geq 0$ for some x.

Then by Maximum Principle and part a), we have for all $t > 0$, $0 \leq u_1(x,t) \leq u_2(x,t)$, $0 \leq v_2(x,t) \leq v_1(x,t)$, and $u_2(x,t) > 0$, $a(x)u_i(x,0) + b(x)v_i(x,0) < K(x)$, $i = 1,2$.

Also, since $u_2(x,0) \geq u_1(x,0)$ for all x, $u_2(x,0) > u_1(x,0)$ for some x, we have

$$\int_\Omega k_1(x,y)[u_2(x,0) - u_1(x,0)]dy > 0$$

(by hypothesis (H2) on $k_1(x,y)$).

Let $g(x,t) = \int_\Omega k_1(x,y)[u_2(x,t) - u_1(x,t)]dy$.

We have $g(x,0) > 0$ for all x. So if we define $t_0(x)$ as

$$t_0 = \inf\{t > 0 : g(x,t) > 0\}$$

then $t_0(x) > 0$. We have $\inf_{z\in\bar{\Omega}} t_0(z) \geq 0$.

As in the proof of maximum principle, suppose $\inf_{z\in\bar{\Omega}} t_0(z) = 0$.

Then there exists $(x_n, t_0(x_n))$ with $t_0(x_n) \to 0$ such that $g(x_n, t_0(x_n)) \to 0$. By compactness of $\bar{\Omega}$ and continuity, we can choose a subsequence and reindex such that $x_n \to x^*$ and $g(x_n, t_n)(x_n)) \to g(x^*, 0)$, but that implies $g(x^*, 0) = 0$, a contradiction.

Thus, $\inf_{z\in\bar{\Omega}} t_0(z) = t_0^* > 0$.

Now consider what happens with $u(x,t)$ near $t = 0$.

If we let $\bar{u} = e^{\beta t}(u_2 - u_1)$, $\bar{v} = e^{\beta t}(v_1 - v_2)$, we get

$$\begin{aligned}
& \bar{u}_t \cdot e^{-\beta \cdot t} \\
= \quad & [K(x) - a(x)u_2(x,t) - b(x)v_2(x,t)] \int_\Omega k_1(x,y)u(y,t)dy \\
+ \quad & b(x)v(x,t) \int_\Omega k_1(x,y)u_1(y,t)dy + u(x,t)(\beta - d_1(x) - a(x) \int_\Omega k_1(x,y)u_1(y,t)dy) \\
= \quad & [K(x) - a(x)u_2(x,t) - b(x)v_2(x,t)] \int_\Omega k_1(x,y)u(y,t)dy \\
+ \quad & b(x)v(x,t) \int_\Omega k_1(x,y)u_1(y,t)dy + (\beta - d_1(x) - a(x)) \int_\Omega k_1(x,y)u_1(y,t)dy)u(x,t).
\end{aligned}$$

Since we can choose β so that $\beta - d_1(x) - a(x) > 0$. $b(x)v(x,t) \geq 0$ and $K - a(x)u_2(x,t) - b(x)v_2(x,t) > 0$ for $t > 0$ by maximum principle, it follows that $\bar{u}_t > 0$ for $0 < t < t_0^*$, so that $\bar{u}(x,t) > 0$ for $0 < t < t_0^*$.

Let $t_1(x) = \inf\{t > 0 : \bar{u}(x,t) = 0\}$, we know $t_1(x) \geq t_0^*$ for all x, so $t_1^* = \inf_{x\in\Omega} t_1(x) \geq t_0^*$.

Suppose $t_1^* < \infty$. For $t = t_1^*$, we must have $u(x_0, t_1^*) = 0$ for some x_0. Suppose this is the case we have $\bar{u} > 0$ and thus $u > 0$ for $0 < t < t_1^*$ and for all x.

Also,

$$\begin{aligned}
& \bar{u}(x,t)e^{-\beta t} \\
= \quad & \bar{u}(x,t-\epsilon)e^{-\beta(t-\epsilon)} + \int_{t-\epsilon}^{t} ([K(x) - a(x)u(x,s) - b(x)v(x,s)] \\
& \cdot \int_\Omega k_1(x,y)u(y,s)dy) \mid_{t=s} ds \\
& + \int_{t-\epsilon}^{t} [b(x)v(x,s) \int_\Omega k_1(x,y)u_1(y,s)dy \\
& +(\beta - d_1(x) - a(x) \int_\Omega k_1(x,y)u_1(y,s)dy)u(x,s)] \mid_{t=s} ds \\
\geq \quad & \int_{t-\epsilon}^{t} [b(x)v(x,s) \int_\Omega k_1(x,y)u_1(y,s)dy \\
& +(\beta - d_1(x) - a(x) \int_\Omega k_1(x,y)u_1(y,s)dy)u(x,s)] \mid_{t=s} ds \\
> \quad & 0
\end{aligned}$$

since $u(x,t) > 0$ on $0 < t < t_1^*$, which gives a contradiction as $\bar{u}(x_0, t_1^*) > 0$.

So $t_1^* = \infty$, which implies $\bar{u}(x,t) > 0$ for all $t > 0$, thus $u_2(x,t) > u_1(x,t)$. Similar for $v_1(x,t)$ and $v_2(x,t)$.

□

Lemma 2.6. *For a solution $(u(x,t), v(x,t))$ starting from $(u(x,0), v(x,0)) =$*

$(u_0(x), v_0(x))$:

(1) If

$$0 < [K(x) - a(x)u(x,0) - b(x)v(x,0)]\int_\Omega k_1(x,y)u(y,0)dy - d_1(x)u(x,0)$$
$$0 > [K(x) - a(x)u(x,0) - b(x)v(x,0)]\int_\Omega k_2(x,y)v(y,0)dy - d_2(x)v(x,0),$$

then $u(x,t)$ is increasing in t and $u(x,t) \to \underline{u}^*(x)$ as $t \to \infty$; $v(x,t)$ is decreasing in t and $v(x,t) \to \overline{v}^*(x)$ as $t \to \infty$. $(\underline{u}^*(x), \overline{v}^*(x))$ is the smallest equilibrium larger than $(u(x,0), v(x,0))$ under the competing ordering.

(2) If

$$0 > [K(x) - a(x)u(x,0) - b(x)v(x,0)]\int_\Omega k_1(x,y)u(y,0)dy - d_1(x)u(x,0)$$
$$0 < [K(x) - a(x)u(x,0) - b(x)v(x,0)]\int_\Omega k_2(x,y)v(y,0)dy - d_2(x)v(x,0),$$

then $u(x,t)$ is decreasing of t and $u(x,t) \to \overline{u}^*(x)$ as $t \to \infty$; $v(x,t)$ is increasing of t and $v(x,t) \to \underline{v}^*(x)$ as $t \to \infty$. $(\overline{u}^*(x), \underline{v}^*(x))$ is the largest equilibrium smaller than $(u(x,0), v(x,0))$ under the competing ordering.

Proof. (1) In this case, $(u_0(x), v_0(x))$ is a sub solution, and $(u(x,t), v(x,t))$ is solution thus is a super-solution. We then by comparison principle have $(u(x,t), v(x,t)) \geq_2 (u_0(x), v_0(x))$. We also have $u_t(x,0) > 0$, $v_t(x,0) < 0$ so that for each $x \in \bar{\Omega}$ there exists a $t_0(x)$ such that $u(x,t) > u_0(x)$, $v(x,t) < v_0(x)$ for $0 < t < t_0(x)$. Pick some $x_0 \in \bar{\Omega}$; then for $0 < \delta < t_0(x)$ we have $u(x_0, \delta) > u(x_0, 0)$. Let $u_1(x,t) = u(x, t+\delta)$, $v_1(x,t) = v(x, t+\delta)$. Then $(u_1(x,t), v_1(x,t))$ is also a solution of system with $u_1(x,0) = u(x,\delta)$, $v_1(x,0) = v(x,\delta)$. So $u_1(x,0) \geq u(x,0)$, $v_1(x,0) \leq v(x,0)$ and

$u_1(x,0) > u(x,0)$, $v_1(x,0) < v(x,0)$ for some $x \in \Omega$. Thus $u(x,t)$ is increasing and $v(x,t)$ is decreasing in t. For each $x \in \Omega$, we have $a(x)u(x,t) + b(x)v(x,t) < K(x)$ for $t > 0$. Thus, for each x we have $u(x,t) \to \underline{u}^*(x)$ and $v(x,t) \to \overline{v}^*(x)$. By monotone convergence theorem

$$\int_\Omega k_1(x,y)u(y,t)dy \to \int_\Omega k_1(x,y)\overline{u}^*(y)dy$$
$$\int_\Omega k_2(x,y)v(y,t)dy \to \int_\Omega k_2(x,y)\underline{v}^*(y)dy$$

where we have $(u(x,t_n), v(x,t_n)) \to (\overline{u}^*(x), \underline{v}^*(x))$ for any sequence $t_n \to \infty$. Then $(\overline{u}^*(x), \underline{v}^*(x))$ must be an equilibrium for the system because if not then for some x we would have $u_t(x,t) > 0$, $v_t(x,t) < 0$ with $(u(x,t), v(x,t)) \to (\overline{u}^*(x), \underline{v}^*(x))$ which contradicting $(u(x,t), v(x,t)) \to (\overline{u}^*(x), \underline{v}^*(x))$ as $t \to \infty$.

Finally, if $(\overline{u}^{**}(x), \underline{v}^{**}(x))$ is an equilibrium with $\overline{u}^{**}(x) > u_0(x)$, $\underline{v}^{**}(x) < v_0(x)$, then we have $(\overline{u}^{**}(x), \underline{v}^{**}(x)) \geq_2 (\overline{u}^*(x), \underline{v}^*(x))$. Hence $(\overline{u}^*(x), \underline{v}^*(x))$ is the minimal equilibrium under the competing ordering.

(2) The proof for the case (2) is identical except reversing the inequalities.

□

Let $\gamma_1, \phi_1(x)$ be the principal eigenvalue and eigenvector of the operator

$$M_1[\phi](x) = \frac{K(x)}{d_1(x)} \int_\Omega k_1(x,y)\phi(y)dy$$

respectively. And $\gamma_2, \phi_2(x)$ be the principal eigenvalue and eigenvector of the operator

$$M_2[\phi](x) = \frac{K(x)}{d_2(x)} \int_\Omega k_2(x,y)\phi(y)dy$$

respectively.

Theorem 2.7. *Assume* $\gamma_1 \leq 1$, *then*

(i) If $\gamma_2 \leq 1$, *then* $(0,0)$ *is asymptotically stable equilibrium.*

(ii) If $\gamma_2 > 1$, *then* $(0, v^*(x))$ *is asymptotically stable equilibrium.*

Proof. Suppose $(\tilde{u}(x,t), \tilde{v}(x,t))$ starts from $(\tilde{u}(x,0), \tilde{v}(x,0)) = (\frac{K(x)}{a(x)}, 0)$. Let $(u(x,t), v(x,t))$ be any solution starting from $(u_0(x), v_0(x))$ where $u_0(x) \geq 0$, $v_0(x) \geq 0$, $K(x) - a(x)u_0(x) - b(x)v_0(x) \geq 0$. By comparison principle, we have $u(x,t) \leq \tilde{u}(x,t)$, $v(x,t) \geq \tilde{v}(x,t)$. But by analysis for single equation, 0 is globally stable and thus $\tilde{u}(x,t) \to 0$ as $t \to \infty$ by analysis for single equation. This implies $u(x,t) \to 0$ as $t \to \infty$ and there will have no equilibrium $(u^{**}(x), v^{**}(x))$ with $u^{**}(x) > 0$.

(i)

If $\gamma_2 \leq 1$, then let $(\bar{u}(x,t), \bar{v}(x,t))$ starts from $(\bar{u}(x,0), \bar{v}(x,0)) = (0, \frac{K(x)}{b(x)})$. Then for solution $(u(x,t), v(x,t))$ starting from $(u_0(x), v_0(x))$, we have $u(x,t) \geq \bar{u}(x,t)$, $v(x,t) \leq \bar{v}(x,t)$. The analysis for single equation shows that $\bar{v}(x,t) \to 0$ as $t \to \infty$ since 0 is globally stable. So then $v(x,t) \to 0$ as $t \to \infty$. So $(0,0)$ is asymptotically stable.

(ii)

If $\gamma_2 > 1$, then let $(u(x,t), v(x,t))$ start from $(u_\epsilon(x), v_\epsilon(x)) = (\epsilon\phi_1(x), \epsilon\phi_2(x))$, where $\phi_i(x)$ are eigenvector of operator M_i, $i = 1, 2$ and $\epsilon > 0$. And we have

$$\begin{aligned}
&[K(x) - a(x)\epsilon\phi_1(x) - b(x)\epsilon\phi_2(x)] \int_\Omega k_1(x,y)\epsilon\phi_1(y)dy - d_1(x)\epsilon\phi_1(x) \\
&< d_1(x)\epsilon[\frac{K(x)}{d_1(x)} \int_\Omega k_1(x,y)\phi_1(y)dy - \phi_1(x)] \\
&= d_1(x)\epsilon(\gamma_1 - 1)\phi_1(x) \leq 0,
\end{aligned}$$

and by selecting $\epsilon > 0$ sufficiently small, such that $\epsilon\phi_2(x) < v^*(x)$ and we have

$$\begin{aligned}&[K(x) - a(x)\epsilon\phi_1(x) - b(x)\epsilon\phi_2(x)] \int_\Omega k_2(x,y)\epsilon\phi_2(y)dy - d_2(x)\epsilon\phi_2(x) \\ &= d_2(x)\epsilon(\gamma_2 - 1)\phi_2(x) - \epsilon^2(a(x)\phi_1(x) + b(x)\phi_2(x)) \int_\Omega k_2(x,y)\phi_2(y)dy > 0.\end{aligned}$$

Thus $(u_\epsilon(x), v_\epsilon(x))$ is a super-solution. As $t \to \infty$, $u(x,t)$ decreases to $u^{**}(x) = 0$ and $v(x,t)$ increases to the positive equilibrium $v^*(x)$, which is the unique positive equilibrium for single equation. So then $(0, v^*(x))$ is asymptotically stable.

□

Theorem 2.8. *Assume* $\gamma_2 \le 1$, *then*

(i) If $\gamma_1 \le 1$, *then* $(0,0)$ *is asymptotically stable equilibrium.*

(ii) If $\gamma_1 > 1$, *then* $(u^*(x), 0)$ *is asymptotically stable equilibrium.*

The proof is similar to previous theorem.

Next, we give a sufficient condition of the existence of coexistence state.

Let μ_1, μ_2 be the principal eigenvalue of the problems:

$$\begin{aligned}\frac{K(x) - b(x)v^*(x)}{d_1(x)} \int_\Omega k_1(x,y)\psi_1(y)dy = \mu_1\psi_1(x), \\ \frac{K(x) - a(x)u^*(x)}{d_2(x)} \int_\Omega k_2(x,y)\psi_2(y)dy = \mu_2\psi_2(x).\end{aligned}$$

Theorem 2.9. *Suppose* $\gamma_1 > 1$, $\gamma_2 > 1$, *and moreover,* $\mu_1 > 1$, $\mu_2 > 1$, *then there exists some positive equilibrium* $(u^*(x), v^*(x))$.

Proof. If $\mu_1 > 1$, then for $\epsilon > 0$ small enough, $(\epsilon\psi_1(x), v^*(x))$ is a sub-solution since

$$\begin{aligned}
& [K(x) - b(x)v^*(x) - a(x)\epsilon\psi_1(x)] \int_\Omega k_1(x,y)\epsilon\psi_1(y)dy - d_1(x)\epsilon\psi_1(x) \\
= \quad & \epsilon d_1(x)[\frac{K(x) - v^*(x)}{d_1(x)} \int_\Omega k_1(x,y)\psi_1(y)dy - \psi_1(x)] - a(x)\epsilon^2\psi_1(x) \int_\Omega k_1(x,y)\psi_1(y)dy \\
= \quad & \epsilon[d_1(x)(\mu_1 - 1) - a(x)\epsilon \int_\Omega k_1(x,y)\psi_1(y)dy]\psi_1(x) > 0
\end{aligned}$$

Also, we have

$$\begin{aligned}
& [K(x) - b(x)v^*(x) - a(x)\epsilon\psi_1(x)] \int_\Omega k_2(x,y)v^*(y)dy - d_2(x)v^*(x) \\
& = -a(x)\epsilon\psi_1(x) \int_\Omega k_2(x,y)v^*(y)dy < 0.
\end{aligned}$$

Thus if $(\overline{u}(x,t),\ \underline{v}(x,t))$ starts from $(\overline{u}(x,0), \underline{v}(x,0)) = (\epsilon\psi_1(x), v^*(x))$, then $\overline{u}(x,t)$ increases in t and $\underline{v}(x,t)$ decreases. Similarly, if $\mu_2 > 1$, for $(\underline{u}(x,t), \overline{v}(x,t))$ starts from $(\underline{u}(x,0), \overline{v}(x,0)) = (u^*(x), \epsilon\psi_2(x))$, then $\underline{u}(x,t)$ decreases in t and $\overline{v}(x,t)$ increases.

Choose $\epsilon > 0$ such that $\epsilon\psi_2(x) < v^*(x)$, $\epsilon\psi_1(x) < u^*(x)$ for all x. Then we have $0 < \underline{u}(x,t) < \overline{u}(x,t) < K(x)$, $0 < \underline{v}(x,t) < \overline{v}(x,t) < K(x)$. So then $(\underline{u}(x,t),\ \overline{v}(x,t))$ "increases" (in the sense of compete ordering) toward a minimal positive equilibrium $(u^{**}(x), v^{**}(x))$, and $(\overline{u}(x,t),\ \underline{v}(x,t))$ "decreases" toward a maximal positive equilibrium $(u^{***}(x), v^{***}(x))$.

We will have $u^{**}(x) \leq u^{***}(x)$, and $v^{**}(x) \geq v^{***}(x)$. □

2.4.1 An Example of Coexistence in the Bounded Domain

Let $\Omega = [-L, L]$. $K = K_0 \cosh x$. $k_1(x,y) = k_2(x,y) = r$. $d_1(x) = d_0(1 + e^{-2x})$ and $d_2(x) = d_0(1 + e^{2x})$.

Consider $u(x) = ae^x$, $v(x) = ae^{-x}$.

$$\int_{-L}^{L} k_1(x,y)u(y)dy = \int_{-L}^{L} k_2(x,y)v(y)dy = (e^L - e^{-L})r = 2r\sinh L$$

$$(K(x) - u(x) - v(x))\int_{-L}^{L} k_1(x,y)u(y)dy = a(K_0 - 2a)2r\sinh L\cosh x$$

$$d_1(x)u(x) = ad_0(1 + e^{-2x})e^x = 2ad_0\cosh x$$

so $(K(x) - u(x) - v(x))\int_{-L}^{L} k_1(x,y)u(y)dy - d_1(x)u(x) = 0$ if $2ad_0 = 2ra(K_0 - 2a)\sinh L$. Similarly, $(K(x) - u(x) - v(x))\int_{-L}^{L} k_2(x,y)v(y)dy - d_2(x)v(x) = 0$ if $2ad_0 = 2ra(K_0 - 2a)\sinh L$.

So for the parameters satisfy $2ad_0 = 2ra(K_0 - 2a)\sinh L$, there is a positive equilibrium $(u(x), v(x))$.

Remark 2.10. *In this example, we can see that for a one dimensional bounded domain, one end is more favorable (same birth rate as species v but lower death rate) for species u and the other end is more favorable for species v. If, in addition, we have proper constraint on the parameters, the mechanism of nonlocal dispersal will leads to the coexistence state for the two species, i.e. species u maintain a relatively high population density in the area where it has lower death rate and species v occupied the other end.*

2.5 Evolutionarily Stable Strategy

2.5.1 Single Species

Our model:

$$u_t = [K(x) - u(x,t)] \int_{\Omega} d(x,y)r(y)u(y,t)dy - e(x)u(x,t), \quad x \in \Omega, \quad t > 0 \qquad (2.5.1)$$

$u(x,t)$ is the fraction of occupied sites at location $x \in \Omega$ and time t. $d(x,y) \in C(\bar{\Omega} \times \bar{\Omega})$ is the fraction of individuals moving from y to x satisfying $d(x,y) \geq 0$ and $\int_{\Omega} d(x,y)dx = 1$. $k(x,y) = r(y)d(x,y)$ satisfies the hypotheses (H1) and (H2). To avoid extinction, we need the principal eigenvalue $\gamma > 1$ for the operator $T[\phi] = \frac{K(x)}{e(x)} \int_{\Omega} d(x,y)r(y)\phi(y)dy = \gamma\phi(x)$. This implies there is a unique globally stable positive equilibrium $u^*(x)$. See Lemma 1.24 and Theorem 1.25.

The existence and uniqueness of solution follows from Theorem 1.2 and Corollary 1.6.

Under these conditions, the Maixmum Principle and Comparison Theorem for single species are thus obtained. We also have global existence for (2.5.1).

The equation without dispersal is:

$$u_t = [K(x) - u(x)]r(x)u(x) - e(x)u(x) \qquad (2.5.2)$$

The equilibrium distribution with no diffusion is $u^*(x) = K(x) - \frac{e(x)}{r(x)}$. The fitness at each site x characterized as growth rate is given by $[K(x) - u(x)]r(x) - e(x)$.

Definition 2.11. *$d(x, y)$ is an ideal free dispersal strategy if the growth rate is same for every location (equal fitness), i.e. $r(x)[K(x)-u^*(x)]-e(x) = r(y)[K(y)-u^*(y)]-e(y)$ for all $x, y \in \Omega$.*

Set $m(x) = r(x)K(x) - e(x) = r(x)u^*(x)$.

Lemma 2.12. *$d(x, y)$ is an ideal free distribution strategy if and only if $u^*(x) = \frac{m(x)}{r(x)}$ and*

$$\int_\Omega d(x, y)m(y)dy = m(x) \tag{2.5.3}$$

Proof. Suppose the condition of equal fitness holds.

Set $r(x)[K(x) - u^*(x)] - e(x) = r(y)[K(y) - u^*(y)] - e(y) = C$ for some constant C. Then $u^*(x) = K(x) - \frac{e(x)+C}{r(x)}$

Since $(K(x) - u^*(x)) \int_\Omega d(x, y)r(y)u^*(y)dy - e(x)u^*(x) = 0$, we have

$$\int_\Omega d(x, y)(K(y)r(y) - e(y) - C)dy = \frac{e(x)}{e(x) + C}(K(x)r(x) - e(x) - C)$$

Integrate on Ω and we get

$$\int_\Omega \int_\Omega d(x, y)(K(y)r(y) - e(y) - C)dydx = \int_\Omega \frac{e(x)}{e(x) + C}(K(x)r(x) - e(x) - C)dx$$

Therefore,

$$\int_\Omega (K(y)r(y) - e(y) - C)dy = \int_\Omega \frac{e(x)}{e(x) + C}(K(x)r(x) - e(x) - C)dx$$

So $C \cdot \int_\Omega \frac{K(x)r(x)-e(x)-C}{e(x)+C} dx = 0$ Since we know $u^*(x) < K(x)$ so $e(x) + C > 0$, also $u^*(x) > 0$, so $K(x)r(x) - e(x) - C > 0$, hence $C = 0$. So we have $u^*(x) = m(x)$ and

$\int_\Omega d(x,y)m(y)dy = m(x)$.

Once we have $C = 0$, so that $u^*(x) = K(x) - \frac{e(x)}{r(x)}$, it follows that $r(x)u^*(x) = m(x)$. Since

$$[K(x) - u^*(x)] \int_\Omega d(x,y)r(y)u^*(y)dy = e(x)u^*(x)$$

we have

$$\frac{e(x)}{r(x)} \int_\Omega d(x,y)m(y)dy = \frac{e(x)m(x)}{r(x)}$$

so $\int_\Omega d(x,y)m(y)dy = m(x)$.

If $r(x)u^*(x) = m(x)$ and $\int_\Omega d(x,y)m(y)dy = m(x)$, then

$$0 = [K(x) - u^*(x)] \int_\Omega d(x,y)m(y)dy - e(x)u^*(x)$$

$$0 = [K(x) - \frac{m(x)}{r(x)}]m(x) - \frac{e(x)m(x)}{r(x)}$$

so $m(x) = K(x)r(x) - e(x)$. In that case, $r(x)[K(x) - u^*(x)] - e(x) = 0$ for all x, so the condition of equal fitness holds.

□

Since $\int_\Omega d(y,x)dy = 1$, we have $\int_\Omega d(y,x)m(x)dy = m(x)$, so (2.5.3) implies that for $h(x,y) = d(x,y)m(y) = d(x,y)r(y)u^*(y)$, we have $\int_\Omega h(x,y)dy = \int_\Omega h(y,x)dy$. Suppose $\int_\Omega d(x,y)m(y)dy = m(x)$.

The next theorem is Theorem 2 in [10].

Theorem 2.13. *Let $h : \bar{\Omega} \times \bar{\Omega} \to [0, \infty)$ be a continuous non-negative function. Then* *the following two statements are equivalent:*

$$(i) \int_\Omega h(x,y)dy = \int_\Omega h(y,x)dy \quad for \quad all \quad x \in \Omega$$

$$(ii) \int_\Omega \int_\Omega h(x,y)\frac{f(x)}{f(y)}dxdy \geq \int_\Omega \int_\Omega h(x,y)dxdy$$

for all $f \in C(\bar{\Omega})$ *with* $f(x) > 0$ *on* $\bar{\Omega}$.

(i) is called line sum symmetry and $\int_\Omega d(x,y)r(y)u^*(y)dy$ has this property, so it satisfies property (ii) too.

2.5.2 Stability for Single Species

If we linearize a single species model at $u = 0$, we get the problem

$$K(x)\int_\Omega k(x,y)\phi(x)dy - e(x)\phi(x) = -\lambda\phi(x) \tag{2.5.4}$$

This can be written as

$$\frac{K(x)}{e(x)}\int_\Omega k(x,y)\phi(y)dy - \phi(x) = -\lambda\frac{\phi(x)}{e(x)} \tag{2.5.5}$$

or alternatively as

$$\phi(x) - T\phi(x) = \lambda\frac{\phi(x)}{e(x)} \tag{2.5.6}$$

where $T\phi(x) = \frac{K(x)}{e(x)}\int_\Omega k(x,y)\phi(y)dy$. If $\int_\Omega k(x,y)\phi(y)dy > 0$ for all x, if $\phi(x) \geq 0$ and $\phi(x) > 0$ for some x, and $k(x,y)$ is smooth, then T is strongly positive and has a principal eigenvalue $\gamma_p = r(T)$.

The strong version of Krein-Rutman Theorem applies by the hypothesis, so

$$\gamma\phi(x) - T\phi(x) = \rho(x) > 0 \tag{2.5.7}$$

has a solution $\phi(x) > 0$ if and only if $\gamma > \gamma_p$.

Lemma 2.14. *If λ is actually an eigenvalue, then*

(i) $\lambda > 0$ if and only if $\gamma_p < 1$, which implies the linear stability of equilibrium $u = 0$.

(ii) $\lambda < 0$ if and only if $\gamma_p > 1$, which implies the linear instability of equilibrium $u = 0$.

(iii) $\lambda = 0$ if and only if $\gamma_p = 1$, which gives the neutral stability.

Proof. (i)

If $\lambda > 0$, then $\lambda\frac{\phi(x)}{e(x)} = \phi(x) - T\phi(x) < 0$. So $T\phi(x) = \gamma_p\phi(x) > \phi(x)$. Thus $\gamma_p > 1$.

If $\gamma_p > 1$, then $0 < \phi(x) - \gamma_p\phi(x) = \lambda\frac{\phi(x)}{e(x)}$. Since $\frac{\phi(x)}{e(x)} > 0$ for some x, we have $\lambda < 0$.

Let $u(x,0) = \epsilon\phi(x)$, then

$$\begin{aligned}
u_t \mid_{t=0} &= [K(x) - \epsilon\phi(x)]\int_\Omega k(x,y)\epsilon\phi(y)dy - e(x)\epsilon\phi(x) \\
&= \epsilon[K(x)\int_\Omega k(x,y)\phi(y)dy - e(x)\phi(x)] - \epsilon^2\phi(x)\int_\Omega k(x,y)\phi(y)dy \\
&= -\epsilon\lambda\phi(x) - \epsilon^2\phi(x)\int_\Omega k(x,y)\phi(y)dy < 0
\end{aligned}$$

So $\epsilon\phi(x)$ is a super-solution and decreases as t increases. So $u(x,t) \to 0$ as $t \to \infty$.

(ii) Similarly, let $u(x,0) = \epsilon\phi(x)$. For $\epsilon > 0$ small enough, we have $u_t \mid_{t=0} > 0$.

Then $u(x,t)$ increases as t increases. Thus zero is not stable.

□

2.5.3 Two Species Model

For two species, a model for ecological similar competitors is:

$$\begin{aligned} u_t &= [K(x,t) - u(x,t) - v(x,t)] \cdot \int_\Omega d(x,y)r(y)u(y,t)dy - e(x,t)u(x,t) \\ v_t &= [K(x,t) - u(x,t) - v(x,t)] \cdot \int_\Omega D(x,y)r(y)v(y,t)dy - e(x,t)v(x,t) \end{aligned} \tag{2.5.8}$$

where $u(x,t), v(x,t)$ are the population at location $x \in \Omega$ and time t respectively. $d(x,y), D(x,y) \in C(\bar{\Omega} \times \bar{\Omega})$ are the fraction of individuals moving from y to x satisfying $d(x,y) \geq 0,\ \ D(x,y) \geq 0$ and $\int_\Omega d(x,y)dx = 1,\ \ \int_\Omega D(x,y)dx = 1$. The last two hypotheses reflect on assumption that the terms $d(x,y)$ and $D(x,y)$ describe movement only so that all mortality is described by $e(x)$ and there is no lose in movement. Assume $r(x)K(x) > e(x)$ for all $x \in \Omega$ to avoid extinction.

This is a special case of competitor model (2.1.3) by setting $a_i(x) = b_i(x) \equiv 1$ and the two species are identical except their dispersal strategy. Thus we obtain the existence, uniqueness and even global existence for two species model from Theorem 2.1. Moreover, kernel $D(x,y)r(y)$ and $d(x,y)r(y)$ satisfy the hypothesis on kernel.

Assume $d(x,y)$ is ideal free but $D(x,y)$ and it is not. We are going to study the stability of semi-trivial equilibria and prove the nonexistence of coexistence equilibrium.

2.5.4 Stability of $(u^*(x), 0)$

If $d(x,y)$ is an ideal free distribution, then $(u^*(x),0) = (K(x) - \frac{e(x)}{r(x)}, 0)$.

Linearization at $(u^*(x),0)$ is given by

u-equation:

$$\begin{aligned}
&\tfrac{d}{d\epsilon}\, |_{\epsilon=0} \Big([K(x) - u^*(x) - \epsilon\phi(x) - \epsilon\psi(x)] \textstyle\int_\Omega d(x,y)r(y)(u^*(y) + \epsilon\phi(y))dy \\
&-e(x)(u^*(x) + \epsilon\phi(x)) \Big) \\
&= -(\psi(x) + \phi(x)) \textstyle\int_\Omega d(x,y)u^*(y)dy + [K(x) - u^*(x)] \int_\Omega d(x,y)r(y)\phi(y)dy \\
&-e(x)\phi(x) \\
&= -\lambda\phi(x)
\end{aligned} \tag{2.5.9}$$

v-equation decouples, and gives

$$\begin{aligned}
&\tfrac{d}{d\epsilon}\, |_{\epsilon=0} \left([K(x) - u^*(x) - \epsilon\phi(x) - \epsilon\psi(x)] \textstyle\int_\Omega D(x,y)r(y)\psi(y)dy\epsilon - e(x)\epsilon\psi(x) \right) \\
&= [K(x) - u^*(x)] \textstyle\int_\Omega D(x,y)r(y)\psi(y)dy - e(x)\psi(x) \\
&= -\lambda\psi(x)
\end{aligned} \tag{2.5.10}$$

That is the same type of problem as for a single species in Lemma (1.22) with T replaced by

$$T_{u^*}\psi = \frac{K(x) - u^*(x)}{e(x)} \int_\Omega D(x,y)r(y)\psi(y)dy.$$

We get $\lambda = 0$ (for neutral stability) if $\gamma(u^*) = r(T_{u^*}) = 1$.

Equation (2.5.10) is equivalent to

$$-\lambda\psi(x) = [K(x) - u^*(x)] \int_\Omega D(x,y)r(y)\psi(y)dy - e(x)\psi(x) \tag{2.5.11}$$

which gives $\lambda = 0$ if $\gamma_p = 1$ for

$$T_{u^*}\psi = \frac{K(x) - u^*(x)}{e(x)} \int_\Omega D(x,y)r(y)\psi(y)dy.$$

We need to work with $T_{u^*}\psi = \gamma\psi$, with $T_{u^*}[\psi] = \frac{1}{r(x)} \int_\Omega D(x,y)r(y)\psi(y)dy$. From (2.5.11), eigenvalue problem (2.5.4) should be

$$-\lambda\frac{\psi(x)}{e(x)} = \frac{1}{r(x)} \int_\Omega D(x,y)r(y)\psi(y)dy - \psi(x)$$

Remark: To have no loss in transit other than the background mortality $e(x)$ we need

$$\int_\Omega [\int_\Omega D(x,y)\rho(y)dy]dx = \int_\Omega \rho(y)dy$$

which is true if $\int_\Omega D(x,y)dx = 1$ for all y_0.

We have for $\gamma = r(T_{u^*})$ that

$$\frac{1}{r(x)} \int_\Omega D(x,y)r(y)\psi(y)dy = \gamma\psi(x)$$

so

$$\int_\Omega D(x,y)r(y)\psi(y)dy = \gamma r(x)\psi(x)$$

so

$$\int_\Omega \int_\Omega D(x,y)r(y)\psi(y)dydx = \gamma \int_\Omega r(x)\psi(x)dx$$

by Fubini

$$\int_\Omega \int_\Omega D(x,y)r(y)\psi(y)dydx = \gamma \int_\Omega r(x)\psi(x)dx$$

so

$$\int_\Omega 1 \cdot r(y)\psi(y)dy = \gamma \int_\Omega r(x)\psi(x)dx$$

so $\gamma = 1$. So $(u^*(x), 0)$ is neutrally stable.

2.5.5 Stability of $(0, v^*(x))$

$v^*(x)$ satisfies

$$v_t = [K(x) - v(x,t)] \int_\Omega D(x,y)r(y,t)v(y)dy - e(x)v(x,t) \tag{2.5.12}$$

We want to study the eigenvalue problem:

$$\rho\phi(x) = [K(x) - v^*(x)] \int_\Omega d(x,y)r(y)\phi(y)dy - e(x)\phi(x) \tag{2.5.13}$$

For $\Omega \subset \mathbb{R}^N$, this eigenvalue problem is guaranteed to have a principal eigenvalue with a positive eigenfunction only if $e(x)$ achieve a global maximum at some point $x_0 \in \Omega$, and satisfy $\frac{1}{(e(x_0)-e(x))} \notin L^1(\Omega)$. That will be true if $e(x) \in C^N(\bar{\Omega})$ when $N = 1, 2$, and for $N \geq 3$ we require additional condition that all derivatives of $e(x)$ of order $N-1$ or less vanish at x_0. See Coville [22] Theorem 1.1, 1.2 and Hetzer et al. [36] Theorem 2.6. The eigenvalue problem (2.5.13) may not have a principal eigenvalue. However, we can always construct an sub-solution arbitrarily close to the equilibrium. By Theorem 2.6 in Hetzer et al., for any $\epsilon > 0$, we can find an $e_\epsilon(x)$ such that for any $\epsilon > 0$, $|e(x) - e_\epsilon(x)| \leq \epsilon$ for all x since $e_\epsilon \in C^1(\Omega)$. Then eigenvalue problem:

$$-\rho_\epsilon \phi(x) = [K(x) - v^*(x)] \int_\Omega d(x,y) r(y) \phi(y) dy - e_\epsilon(x)\phi(x) \tag{2.5.14}$$

has a principal eigenvalue ρ_ϵ. It is equivalent to

$$-\rho_\epsilon \phi(x) = [K(x) - v^*(x)] \int_\Omega d(x,y) r(y) \phi(y) dy - e(x)\phi(x) + \epsilon(x)\phi(x) \tag{2.5.15}$$

Multiply (2.5.15) by $\frac{u^*(x)}{\phi(x)[K(x)-v^*(x)]}$, then integrate both part over Ω. By line sum symmetry property of $d(x,y)r(y)u^*(y)$, we have

$$\begin{aligned}
&-\rho_\epsilon \int_\Omega \frac{u^*(x)}{K(x)-v^*(x)} dx \\
&= \int_\Omega \int_\Omega d(x,y) r(y) u^*(y) \frac{\phi(y)/u^*(y)}{\phi(x)/u^*(x)} dy dx - \int_\Omega \frac{u^*(x)e(x)}{K(x)-v^*(x)} dx + \int_\Omega \frac{u^*(x)\epsilon(x)}{K(x)-v^*(x)} dx \\
&\geq \int_\Omega r(x) u^*(x) dx - \int_\Omega \frac{e(x)u^*(x)}{K(x)-v^*(x)} dx + \int_\Omega \frac{\epsilon(x)u^*(x)}{K(x)-v^*(x)} dx
\end{aligned}$$

And since $e(x) = [K(x) - u^*(x)]r(x)$,

$$\begin{aligned}
&\int_\Omega r(x)u^*(x)dx - \int_\Omega \frac{e(x)u^*(x)}{K(x)-v^*(x)} dx + \int_\Omega \frac{\epsilon(x)u^*(x)}{K(x)-v^*(x)} dx \\
&= \int_\Omega \frac{r(x)u^*(x)[u^*(x)-v^*(x)]}{K(x)-v^*(x)} dx + \int_\Omega \frac{u^*(x)\epsilon(x)}{K(x)-v^*(x)} dx \\
&= \int_\Omega \frac{u^*(x)r(x)[u^*(x)-v^*(x)+\frac{\epsilon(x)}{r(x)}]}{K(x)-v^*(x)} dx
\end{aligned}$$

Also we have

$$[K(x)-v^*(x)]\int_\Omega D(x,y)r(y)v^*(y)dy-e(x)v^*(x)=0 \tag{2.5.16}$$

Divide (2.5.16) by $K(x)-v^*(x)$, then integrate over Ω.

$$\int_\Omega \frac{e(x)v^*(x)}{K(x)-v^*(x)}dx=\int_\Omega\int_\Omega D(x,y)r(y)v^*(x)dydx=\int_\Omega r(x)v^*(x)dx \tag{2.5.17}$$

$\therefore \int_\Omega \frac{r(x)v^*(x)[u^*(x)-v^*(x)]}{K(x)-v^*(x)}dx=0.$

$$\therefore -\rho_\epsilon\int_\Omega \frac{u^*(x)}{K(x)-v^*(x)}dx \geq \int_\Omega \frac{r(x)[u^*(x)-v^*(x)]^2}{K(x)-v^*(x)}dx+\int_\Omega \frac{u^*(x)\epsilon(x)}{K(x)-v^*(x)}dx \tag{2.5.18}$$

Since $sup_\Omega|\epsilon(x)|>0$ on $\bar{\Omega}$ can be arbitrarily small, and $\frac{u^*(x)}{K(x)-v^*(x)}$ is bounded below, $\therefore -\rho_\epsilon\int_\Omega \frac{u^*(x)}{K(x)-v^*(x)}dx \geq \int_\Omega \frac{r(x)[u^*(x)-v^*(x)]^2}{K(x)-v^*(x)}dx \geq 0$. $-\rho_\epsilon \geq \rho_0 > 0$, is independent of the choice of ϵ. The "=" holds if and only if $u^*(x)=v^*(x)$, which contradicts the fact that $D(x,y)$ is not ideal free.

Let $\bar{u}(x)=\delta\phi(x)$, $\bar{v}(x)=(1+\epsilon)v^*(x)$.

$$\begin{aligned}
& [K(x)-\bar{u}(x)-\bar{v}(x)]\int_\Omega d(x,y)r(y)\delta\phi(y)dy-e(x)\delta\phi(x)\\
= \quad & \delta[[K(x)-v^*(x)]\int_\Omega d(x,y)r(y)\phi(y)dy-e_\epsilon(x)\phi(x)+(e_\epsilon(x)-e(x))\phi(x)\\
& -\delta\phi(x)\int_\Omega d(x,y)r(y)\phi(y)dy-\epsilon v^*(x)\int_\Omega d(x,y)r(y)\phi(y)dy]\\
= \quad & \delta[-\rho_\epsilon\phi(x)+(e_\epsilon(x)-e(x))\phi(x)-(\delta\phi(x)+\epsilon v^*(x))\int_\Omega d(x,y)r(y)\phi(y)dy]>0
\end{aligned}$$

for $\rho_\epsilon > \rho_0$ and ϵ, δ small, such as

$$[K(x) - \bar{u}(x) - \bar{v}(x)] \int_\Omega d(x,y)r(y)\bar{u}(y)dy - e(x)\bar{u}(x) > 0$$

and

$$\begin{aligned} & [K(x) - \bar{u}(x) - \bar{v}(x)] \int_\Omega D(x,y)r(y)\bar{v}(y)dy - e(x)\bar{v}(x) \\ = \quad & (1+\epsilon)([(K(x) - v^*(x)) - (\delta\phi(x) + \epsilon v^*(x))] \int_\Omega D(x,y)r(y)v^*(y)dy - e(x)v^*(x)) \\ = \quad & -(1+\epsilon)(\delta\phi(x) + \epsilon v^*(x)) \int_\Omega D(x,y)r(y)v^*(y)dy < 0 \end{aligned}$$

Thus $(\bar{u}, \bar{v})$ gives a sub-solution which is independent of t. Then for $(u(x,0), v(x,0))$ with $u(x,0) \geq 0$, $u(x,0) \not\equiv 0$, $v(x,0) = v^*(x)$, we get for $t_0 > 0$ small, we will have $u(x,t_0) > 0$ $v(x,t_0) < (1 + \frac{\delta}{2})v^*(x)$, so that for ϵ, δ small, $\bar{u}(x) < u(x,t_0)$, $\bar{v}(x) > v(x,t_0)$. Then $u(x,t) > \bar{u}$ for $t \geq t_0$ and $u(x,t)$ goes to $u^{**}(x)$. $v(x,t) < \bar{v}$ for $t \geq t_0$ and $v(x,t)$ goes to $v^{**}(x)$ where $(u^{**}(x), v^{**}(x))$ is some equilibrium.

2.5.6 Nonexistence of Coexistence equilibrium

Lemma 2.15. *Suppose $d(x,y)$ is an ideal free distribution. $\int_\Omega D(x,y)m(y)dy \neq m(x)$ for some $x \in \Omega$. Then the model has no coexistence equilibrium.*

Proof. Divide the first equation of the two species by $[K(x) - u(x,t) - v(x,t)]$ and integrate, we have

$$\begin{aligned}&\int_\Omega \frac{u_t}{K(x)-u(x,t)-v(x,t)}dx\\ &=\int_\Omega\int_\Omega d(x,y)r(y)u(y,t)dydx-\int_\Omega \frac{e(x)u(x,t)}{K(x)-u(x,t)-v(x,t)}dx\\ &=\int_\Omega r(x)u(x,t)dx-\int_\Omega \frac{e(x)u(x,t)}{K(x)-u(x,t)-v(x,t)}dx\end{aligned} \tag{2.5.19}$$

Similarly,

$$\int_\Omega \frac{v_t}{K(x)-u(x,t)-v(x,t)}dx=\int_\Omega r(x)v(x,t)dx-\int_\Omega \frac{e(x)v(x,t)}{K(x)-u(x,t)-v(x,t)}dx \tag{2.5.20}$$

Adding these (2.5.19) and (2.5.20), we obtain:

$$\begin{aligned}&\int_\Omega \frac{u_t+v_t}{K(x)-u(x,t)-v(x,t)}dx\\ &=\int_\Omega r(x)(u(x,t)+v(x,t))dx-\int_\Omega \frac{e(x)(u(x,t)+v(x,t))}{K(x)-u(x,t)-v(x,t)}dx\\ &=\int_\Omega \frac{r(x)(u(x,t)+v(x,t))[u^*(x)-(u(x,t)+v(x,t))]}{K(x)-u(x,t)-v(x,t)}dx\end{aligned} \tag{2.5.21}$$

Multiply the first equation in the model by $\frac{u^*(x)}{[K(x)-u(x,t)-v(x,t)]u(x,t)}$, then integrate over Ω. By the line sum symmetry of $d(x,y)r(y)u^*(y)$ and Theorem 2.13, we have

$$\begin{aligned}&\int_\Omega\int_\Omega d(x,y)r(y)u^*(y)\frac{u(y,t)/u^*(y)}{u(x,t)u^*(x)}dxdy\\ \geq\ &\int_\Omega\int_\Omega d(x,y)r(y)u^*(y)dxdy\\ =\ &\int_\Omega r(y)u^*(y)dy=\int_\Omega r(x)u^*(x)dx\end{aligned}$$

Since $\int_\Omega d(x,y)dx=1$, we have

$$
\begin{aligned}
& \int_\Omega \frac{u^*(x)(lnu)_t}{K(x)-u(x,t)-v(x,t)}dx \\
= \quad & \int_\Omega\int_\Omega d(x,y)r(y)u^*(y)\frac{u(y,t)/u^*(y)}{u(x,t)/u^*(x)}dxdy - \int_\Omega \frac{e(x)u^*(x)}{K(x)-u(x,t)-v(x,t)}dx
\end{aligned}
$$

By line sum symmetry of $d(x,y)r(y)u^*(y)$ and the theorem, we get

$$
\begin{aligned}
& \int_\Omega \frac{u^*(x)(lnu)_t}{K(x)-u(x,t)-v(x,t)}dx \\
\geq \quad & \int_\Omega r(x)u^*(x)dx - \int_\Omega \frac{e(x)u^*(x)}{K(x)-u(x,t)-v(x,t)}dx \\
= \quad & \int_\Omega \frac{r(x)u^*(x)[K(x)-u(x,t)-v(x,t)]-e(x)u^*(x)}{K(x)-u(x,t)-v(x,t)}dx
\end{aligned}
$$

Since $[K(x)-u^*(x)]r(x) = e(x)$, we have

$$
\int_\Omega \frac{u^*(x)(lnu)_t}{K(x)-u(x,t)-v(x,t)}dx \geq \int_\Omega \frac{r(x)u^*(x)[K(x)-u(x,t)-v(x,t)]-e(x)u^*(x)}{K(x)-u(x,t)-v(x,t)}dx
$$

then,

$$
\int_\Omega \frac{u_t+v_t-u^*(x)(lnu)_t}{K(x)-u(x,t)-v(x,t)}dx \leq -\int_\Omega r(x)\frac{[u^*(x)-u(x,t)-v(x,t)]^2}{K(x)-u(x,t)-v(x,t)} \leq 0
$$

If (u,v) is an equilibrium we must have $u_t = v_t = (lnu)_t = 0$. So we have $u(x,t) + v(x,t) = u^*(x)$. In that case we have

$$
K(x)-u(x,t)-v(x,t) = K(x)-u^*(x)
$$

so that

$$\frac{K(x)-u^*(x)}{e(x)}\int_\Omega k_1(x,y)u(y)dy = u(x) \tag{2.5.22}$$

The operator $T[w] = \frac{K(x)-u^*(x)}{e(x)}\int_\Omega k_1(x,y)w(y)dy$ is strongly positive and compact, so by Krein-Rutman Theorem it has a unique simple principal eigenvalue. By (2.5.22), since $u(x) > 0$. By assumption that (u,v) is a positive equilibrium, $u(x)$ is an eigenfunction for the principal eigenvalue of T, and the eigenvalue is 1.

However,

$$\frac{K(x)-u^*(x)}{e(x)}\int_\Omega k_1(x,y)u^*(y)dy = u^*(x) > 0$$

so $u^*(x)$ is also an eigenfunction, so $u(x) = c_1u^*(x)$ for some constant c_1. Using the equation for v, if (u,v) is an equilibrium and $u+v = u^*(x)$, then $v = (1-c_1)u^*$.

$$(1-c_1)[K(x)-u^*(x)]\int_\Omega D(x,y)r(y)u^*(y)dy - e(x)u^*(x)] = 0 \tag{2.5.23}$$

If $c_1 \neq 1$, then we must have

$$[K(x)-u^*(x)]\int_\Omega D(x,y)r(y)u^*(y)dy - e(x)u^*(x) = 0 \tag{2.5.24}$$

Since $[K(x)-u^*(x)]r(x) = e(x)$ and $u^*(x) = \frac{m(x)}{r(x)}$, (2.5.24) implies

$$\frac{e(x)}{r(x)}\int_\Omega D(x,y)m(y)dy - \frac{e(x)}{r(x)}m(x) = 0$$

so that

$$\int_{\Omega} D(x,y)m(y)dy = m(x). \tag{2.5.25}$$

This contradicts the hypothesis

$$\int_{\Omega} D(x,y)m(y)dy \neq m(x),$$

so we obtain a contradiction unless $c_1 = 1$, but then $(u,v) = (u^*,0)$, so we cannot have a positive equilibrium (u,v).

□

Since $(0, v^*(x))$ is unstable and there is no coexistence equilibrium, then solutions starting near $(0, v^*(x))$ must increase in u and decrease in v as t increases until they reach another equilibrium, which must be $(u^*(x), 0)$. Then we have the following theorem:

Theorem 2.16. *Suppose that $d(x,y)$ is an ideal free dispersal strategy and $D(x,y)$ is not an ideal free dispersal strategy. Then the steady state $(u^*(x), 0)$ is globally asymptotically stable.*

Remark 2.17. *If both $d(x,y)$ and $D(x,y)$ satisfy the ideal free dispersal strategy, then the system has positive s ready states in the form of the 1-parameter family $\{(u,v) = (sm,(1-s)m) : 0 < s < 1\}$. When this occurs, the steady states are not locally asymptotically stable among positive continuous initial data.*

2.6 Conclusions and Examples

In this chapter, we extended the nonlocal metapopulation model to two species competition system. First we proved the global existence and uniqueness of solution by applying contraction mapping theorem. As in the single species model, this result can be obtained for either Ω finite or infinite domain, under the condition that $k_{1,2}(x, y)$ is integrable. For the monotonicity of the system, we need Ω to be finite and hypothesis (H1) and (H2) on kernel. We also studied the stability of two semi-trivial equilibria and provided a sufficient condition for there is a coexistence states.

Cantrell et al. [10] studied the evolutionarily stable strategy for another nonlocal model. For our model, we derived the mathematical description for ideal free distribution strategy based on Cantrell et al. [Notes on Ideal Free Distribution] where a discrete Mouquet-Loreau model was studied. For competition model, the two competing species are assumed to be identical but have different dispersal strategies. We showed that there is no coexistence equilibrium in this case. Stability analysis of two semi-trivial equilibria and the monotonicity of the system gives the conclusion that the species with ideal free dispersal strategy will not only invade by a small initial population density but also can drive the other species to extinction.

People may wonder that is there real example that organisms are "intellectual" enough to evolve the ideal free dispersal strategy. Here is an example about the how the oysters detect the surrounding environmental conditions. Zimmer-Faust and Tamburri [65] investigated the chemical identity of planktonic oyster larvae and the respond to waterborne chemical cues. They provided experimental evidence of larval settlers identifying substances and oyster settlement induced by water-soluble cues. Lillis et al. [47] studied the oyster larvae settle in response to habitat-associated underwater sounds. They showed that ”oyster larvae have the ability to respond to sounds indicative of optimal settlement sites”, which make it possible to result in equal fitness for each site in marine communities, i.e. the idea free distribution.

Chapter 3

Spreading Speed and Traveling Wave Solution for Infinite Domain

3.1 Background

In the previous two chapters we studied the single species and two species competition models on finite domain. In Chapter 3 we are interested in the model on infinite domain how the species spread and the traveling wave solutions. In this case, we need to assume the potential suitable sites and extinction rate are constants for all area. There will be further assumptions on dispersal kernel for the convenience of analysis.

Traveling wave solutions of partial differential equations in areas such as ecology, and epidemiology are getting more attention. Existence and stability as well as what initial conditions evolve to a traveling front solution, and the propagation speed of a traveling front, are questions of interest and these have been applied to studies of colonization, and spatial spread of epidemics. Our model, based on metapopulation framework with non local dispersal, becomes:

$$u_t = [K - u(x,t)] \int_{\mathbb{R}} k_1(x-y)u(y,t)dy - eu(x,t)$$

where the domain is infinite domain and the functions K and death rate e are constants. The dispersal kernel $k(x, y)$ depends only on $|x-y|$ and satisfies for all $m > 0$, $\int_{\mathbb{R}} e^{my}k(y)dy < \infty$.

We are interested in the two species competition model:

$$\begin{aligned} u_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_1(x-y)u(y,t)dy - e_1 u(x,t) \\ v_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_2(x-y)v(y,t)dy - e_2 v(x,t) \end{aligned}$$

There are three equilibria, one trivial and two semi-trivial, and we want to study if one species could drive the other species extinction. Suppose one semi-trivial equilibrium is stable and the other is unstable (say species u is the winner). Under certain conditions, if we can find a traveling wave solution connecting the two semi-trivial equilibria then we can say that v can be invaded by a small population of u and then go to extinction.

Reaction-diffusion equations can sometimes support solutions that are traveling wavefronts connecting 0 and 1. This phenomenon was studied by Fisher in [27] in models for the spatial spread of an advantageous genes.

$$u_t = \triangle u + u(1-u).$$

Fisher found traveling wave solutions for all speeds $c \geq c^*$ where c^* is the minimal wave speed and there are no such waves of slower speed. A traveling wave solution connecting 0 and 1 is $u(x-ct)$ satisfies $\lim_{t\to-\infty} u(x-ct) = 0$ and $\lim_{t\to+\infty} u(x-ct) = 1$. We call such a result a spreading result. Kolmogorov, Petrovsky and Piscounoff [41] proved it for models of the form $u_t = u_{xx} + f(u)$. Aronson and Weinberger [3], [4] extended the results to more general equations $u_t = D\nabla^2 u + f(u)$. The concept of traveling wave has been studied in the context of combustion, the spatial spread of population genetics, population biology and diseases, as well as phenomenon in other fields.

Weinberger [62] studied the discrete-time recursion system

$$u_{n+1} = Q[u_n]$$

where Q is a translation invariant time τ map. He showed the existence of traveling wave for speeds greater than or equal to the asymptotic speed of propagation, u_n. Lui [52], [53] developed the mathematical theory and extended the methods to multi species cooperative system. Lui's work can be applied to partial differential, integro-differential, or finite difference equations.

Neubert and Caswell [58] applied the results to interaction of stages of a single species. They modeled biological invasions with integro-difference equations for dispersal and demonstrated how to calculate the population's asymptotic invasion speed. Lewis et al [63] analyzed the linear determinacy for two cooperative models. In ecology, cooperative systems can obtained by changing variables of the competition models. Lewis, Li and Weinberger [63] and [45] extended Lui's results and applied them to invasion processes of models for cooperation or competition. They gave the conditions that lead to the propagation speed of the invader agreeing with the linearized problem. They studied the case that when there are only two equilibria: 0 and $\beta \gg 0$, the system admits a single spreading speed c^* with hair-trigger property in the following sense: For every positive ϵ,

(i) if u_0 vanishes outside a bounded interval and $0 \leq u_0 \ll \beta$, then

$$\lim_{n\to\infty}\left[\sup_{|x|\geq n[c^*+\epsilon]} |u_n(x)|\right] = 0;$$

(ii) for any constant vector $\omega \gg 0$, there is a positive number R_ω such that if $u_0 \geq \omega$ on an interval of length $2R_\omega$, then

$$\lim_{n\to\infty}\left[\sup_{|x|\geq n[c^*-\epsilon]} |\beta - u_n(x)|\right] = 0.$$

Liang and Zhao [46] developed this theory for monotone discrete and continuous-time semi-flows with weaker compactness assumptions. In the case Q is sub-homogeneous they proved that the choice of R_ω can be independent of the number ω. They also established the existence of minimal wave speeds under a weaker compactness assumption. Weng and Zhao [64] studied a multi-type SIS epidemic model which has a similar form as our model. The multi-type SIS model was presented by Rass and Radcliffe [60]. The single species case of our model is a special case of Weng and Zhao's model for $n = 1$ after changing variables. However, for two species competition, we cannot use their result because we have three equilibria in the system. Fang and Zhao [26] studied the traveling waves for three prototypical non-compact systems including a nonlocal dispersal competition model which allowed there is an intermediate equilibrium when there are additional equilibria between 0 and β. For two species competition in our model, we mainly used the theory in Fang and Zhao [26] to show the existence of spreading speed and traveling wave solutions.

3.2 Single Species Model

Let $u(x,t)$ be the population density at x. The model for single species is:

$$u_t = [K - u(x,t)] \int_{\mathbb{R}} k(x-y)u(y,t)dy - e_0 u(x,t) \tag{3.2.1}$$

Change variables, we obtain

$$u_t = [K - u(x,t)] \int_{\mathbb{R}} k(y)u(x-y,t)dy - e_0 u(x,t) \tag{3.2.2}$$

This case has been treated by Weng and Zhao [64]. This is a special case of their model with $n = 1$. We have the following hypothesis on the kernel:

(H1) $k(x) = k_0 d(x,y) \geq 0$, $k(x) = k(-x)$, for all $u \in \mathbb{R}$, $\int_{\mathbb{R}} k(x)dx = k_0$, $\int_{\mathbb{R}} d(x)dx = 1$ and for any $\alpha > 0$, $\int_{\mathbb{R}} e^{\alpha x} f(x)dx < \infty$.

The case with no dispersal is:

$$u_t = [K - u(t)]k_0 u(t) - e_0 u(t) \tag{3.2.3}$$

Lemma 3.1. *If $Kk_0 \leq e_0$, then the zero equilibrium is globally asymptotically stable.*

If $Kk_0 > e_0$, then positive equilibrium $u^* = K - \frac{e_0}{k_0}$ is globally asymptotically stable.

Let $W = [0, K]$. $u(x,t) \in C(\mathbb{R} \times \mathbb{R}_+, \mathbb{W})$. This is a special case of [64] with $n = 1$. Then we have the following conclusions.

3.2.1 Existence and Uniqueness

The following theorem is Theorem 2.1 in [64].

Theorem 3.2. *For any $\phi \in C(\mathbb{R}, W)$, system* (3.2.2) *has a unique solution $u(x,t;\phi)$ satisfying $u(x,0;\phi) = \phi$ and $u(\cdot;\phi) \in C(\mathbb{R} \times \mathbb{R}_+, W)$.*

3.2.2 Comparison Principle and Super-(Sub-) solutions

Definition 3.3. *A function $\bar{u} \in C^1(\mathbb{R}\times\mathbb{R}_+, W)$ is called a super-solution if it satisfies*

$$\bar{u}_t \geq [K - \bar{u}(x,t)] \int_{\mathbb{R}} k(x-y)\bar{u}(y,t)dy - e_0\bar{u}(x,t).$$

A function $\underline{u} \in C^1(\mathbb{R} \times \mathbb{R}_+, W)$ is called a sub-solution if it satisfies

$$\underline{u}_t \geq [K - \underline{u}(x,t)] \int_{\mathbb{R}} k(x-y)\underline{u}(y,t)dy - e_0\underline{u}(x,t).$$

The following theorem is Theorem 2.2 in Weng and Zhao [2006].

Theorem 3.4. *Let $\bar{u}$ and $\underline{u}$ be super and sub solutions respectively. If $\bar{u}(\cdot,0) \geq \underline{u}(\cdot,0)$, then $\bar{u}(\cdot,t) \geq \underline{u}(\cdot,t)$ for all $t \geq 0$. Furthermore, for any $\phi \in C(\mathbb{R}, W)$ with $\phi \not\equiv 0$, we have $u(x,t;\phi) \gg 0$ for all $(x,t) \in \mathbb{R} \times (0,+\infty)$.*

Theorem 3.4 implies that the model (3.2.2) generates a strongly monotone semi flow, so that the results of Liang and Zhao [46] can be used.

Weng and Zhao [64] showed in their Lemma 3.2 that if $e_0 > 0$ and $Kk_0 - e_0 > 0$ the solution map Q_t for (3.2.2) has only the fixed points 0 and u^* in the interval $[0, u^*]$.

We have the following hypothesis

(H2) Either $e_0 = 0$ or $e_0 > 0$ and $Kk_0 - e_0 > 0$.

3.2.3 Asymptotic Spreading Speed

Let $Q_t[\phi](x)$ be the solution $u(x,t)$ of system (3.2.2). When $\tau = 1$ we have time one map Q_1.

Then from Theorem 2.17 in Liang and Zhao [46] and Theorem 3.1 and 3.2 in Weng and Zhao [64], we have

Theorem 3.5. *Assume (H1)-(H2). Let c^* be the spreading speed of time one map Q_1. Then we have the following:*

(1) For any $c > c^*$, if $\phi \in \mathcal{C}_{u^*}$ with $0 \ll \phi \ll u^*$ and $\phi(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty,|x|\geq tc} u(x,t;\phi) = 0$.

(2) For any $c < c^*$, if $\phi \in \mathcal{C}_{u^*}$ with $\phi \not\equiv 0$, then $\lim_{t\to\infty,|x|\leq tc} u(x,t;\phi) = u^*$.

c^* is the asymptotic speed of spread of Q_1.

Theorem 3.6. *Assume (H1)-(H2). Let c^* be the asymptotic speed of spread of Q_1. Then $c^* = inf_{\alpha>0}\frac{1}{\alpha}(\int_{\mathbb{R}} e^{\alpha y}k(y)dy - e_0)$.*

3.2.4 Traveling Waves

The following theorem comes from Theorem 4.1 and 4.2 in [64].

Definition 3.7. *A traveling wave solution of system* (3.2.2) *is a solution with the form*

$$\phi(s) := \phi(x + ct) = u(x,t)$$

where $c > 0$ is the wave speed, $s = x + ct$. ϕ is called the wave profile.

The next theorem comes from Theorem 3.3 in [64].

Theorem 3.8. *Assume (H1)-(H2) and let c^* be the asymptotic speed of spread of Q_1. Then*

(1) For any $c \geq c^*$, the system has a traveling wave $\phi(x+ct)$ connecting 0 to u^* such that $\phi(s)$ is continuous and nondecreasing in $s \in \mathbb{R}$.

(2) For any $c \in (0, c^*)$, system has no traveling wave $\phi(x+ct)$ connecting 0 to u^*.

Remark 3.9. *This is equivalent that*

(1) For any $c \geq c^*$, the system has a traveling wave $\phi(x-ct)$ connecting u^* to 0.

(2) For any $c \in (0, c^*)$, system has no traveling wave $\phi(x-ct)$ connecting u^* to 0.

3.3 Two Species Competition

Then we consider the two species competition model:

$$\begin{aligned} u_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_1(x-y)u(y,t)dy - e_1 u(x,t) \\ v_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_2(x-y)v(y,t)dy - e_2 v(x,t) \end{aligned} \tag{3.3.1}$$

Change variables, the system becomes:

$$\begin{aligned} u_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy - e_1 u(x,t) \\ v_t &= [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_2(y)v(x-y,t)dy - e_2 v(x,t) \end{aligned} \tag{3.3.2}$$

Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$. We use

$\geq (\gg, >)$ and $\leq (<, \ll)$ as the standard ordering in space $\mathcal{C}$. Define $\mathcal{C}_r := \{u \in \mathcal{C} : r \geq u \geq 0\}$. $k_i = \int_{\mathbb{R}} k_i(s)ds = \int_{\mathbb{R}} k_i d_i(s) = k_i \cdot 1 = k_i$, $i = 1, 2$.

Similar as the single species model, we have the following hypotheses:

Hypothesis 3.10. *(1)* $k_i(x) \geq 0$, $k_i(x) = k_i(-x)$, $\forall x \in \mathbb{R}$, $i = 1, 2$ *and there exists some constant* $c > 0$ *such that for any* $\mu > c$, $\int_{\mathbb{R}} e^{\mu x} k_i(x)dx < \infty$.

(2) There exists $k_0, \delta > 0$ *such that* $k_i(y) \geq k_0 > 0$ *for* $|y| \leq \delta$.

3.3.1 Existence, Uniqueness and Comparison Principle

The existence and uniqueness of solution can be obtained from the proof of two species competition (See Remark 2.2). Thus we have

Theorem 3.11. *There exists a unique solution for system* (3.3.2)

Proof. By Banach fixed point theorem, there exists a unique $\vec{w}^*$ such that $\mathcal{F}(\vec{w}^*) = \vec{w}^*$. So

$$\begin{aligned} u^* &= u(x,0) + \int_0^t \left([K - u(x,s) - av(x,t)] \cdot \int_{\mathbb{R}} k_1(y)u(x-y,t)dy - e_1 u(x,s) \right) ds \\ v^* &= v(x,0) + \int_0^t \left([K - u(x,s) - av(x,t)] \cdot \int_{\mathbb{R}} k_2(y)v(x-y,t)dy - e_2 v(x,s) \right) ds \end{aligned} \tag{3.3.3}$$

□

3.3.2 Comparison Principal

Definition 3.12. *A function* $\overline{\mathbf{u}} = (\overline{u}(x,t), \overline{v}(x,t)) \in C^1(\mathbb{R} \times \mathbb{R}_+, W)$ *is called an upper solution if it satisfies*

$$\begin{aligned} \overline{u}_t &\geq [K - \overline{u}(x,t) - a\overline{v}(x,t)] \int_{\mathbb{R}} k_1(y)\overline{u}(x-y,t)dy - e_1\overline{u}(x,t) \\ \overline{v}_t &\leq [K - \overline{u}(x,t) - a\overline{v}(x,t)] \int_{\mathbb{R}} k_2(y)\overline{v}(x-y,t)dy - e_2\overline{v}(x,t) \end{aligned} \tag{3.3.4}$$

A function $\underline{\mathbf{u}} \in C^1(\mathbb{R} \times \mathbb{R}_+, W)$ *is called an lower solution if it satisfies*

$$\begin{aligned} \underline{u}_t &\leq [K - \underline{u}(x,t) - a\underline{v}(x,t)] \int_{\mathbb{R}} k_1(y)\underline{u}(x-y,t)dy - e_1\underline{u}(x,t) \\ \underline{v}_t &\geq [K - \underline{u}(x,t) - a\underline{v}(x,t)] \int_{\mathbb{R}} k_2(y)\underline{v}(x-y,t)dy - e_2\underline{v}(x,t) \end{aligned} \tag{3.3.5}$$

3.3.3 Monotonicity

Definition 3.13. *A function* $\overline{\mathbf{u}} = (\overline{u}(x,t), \overline{v}(x,t)) \in C^1(\mathbb{R} \times \mathbb{R}_+, W)$ *is called an upper solution if it satisfies*

$$\begin{aligned} \overline{u}_t &\geq [K - \overline{u}(x,t) - a\overline{v}(x,t)] \int_{\mathbb{R}} k_1(y)\overline{u}(x-y,t)dy - e_1\overline{u}(x,t) \\ \overline{v}_t &\leq [K - \overline{u}(x,t) - a\overline{v}(x,t)] \int_{\mathbb{R}} k_2(y)\overline{v}(x-y,t)dy - e_2\overline{v}(x,t) \end{aligned} \tag{3.3.6}$$

A function $\underline{\mathbf{u}} \in C^1(\mathbb{R} \times \mathbb{R}_+, W)$ *is called an lower solution if it satisfies*

$$\begin{aligned} \underline{u}_t &\leq [K - \underline{u}(x,t) - a\underline{v}(x,t)] \int_{\mathbb{R}} k_1(y)\underline{u}(x-y,t)dy - e_1\underline{u}(x,t) \\ \underline{v}_t &\geq [K - \underline{u}(x,t) - a\underline{v}(x,t)] \int_{\mathbb{R}} k_2(y)\underline{v}(x-y,t)dy - e_2\underline{v}(x,t) \end{aligned} \tag{3.3.7}$$

Theorem 3.14. *(Maximum Principle)*

(i) If $(0,0) \leq_1 (u(x,0), v(x,0))$ *and* $u(x,0) + av(x,0) \leq K$*, then* $(0,0) \leq_1 (u(x,t), v(x,t))$ *and* $u(x,t) + av(x,t) \leq K$ *for all* $t > 0$ *where* (u,v) *exists.*

(ii) If further we assume $u(x,0) > 0$*,* $v(x,0) > 0$ *on some* x*, then* $u(x,t) > 0$ *and* $v(x,t) > 0$ *for* $t > 0$ *where* (u,v) *exists.*

Proof. (i) Let $w(x,t) = K - u(x,t) - av(x,t)$, we have

$$\begin{aligned}
&u_t = w(x,t) \textstyle\int_{\mathbb{R}} k_1(x-y)u(y,t)dy - e_1 u(x,t) \\
&v_t = w(x,t) \textstyle\int_{\mathbb{R}} k_2(x-y)v(y,t)dy - e_2 v(x,t) \\
&w_t = -w(x,t) \left(\textstyle\int_{\mathbb{R}} k_1(x-y)u(y,t)dy + a \int_{\mathbb{R}} k_2(x-y)v(y,t)dy \right) \\
&+e_1 u(x,t) + a e_2 v(x,t)
\end{aligned} \tag{3.3.8}$$

Then $w_t = -(u_t + av_t)$.

We know the original competition system has a unique solutions on some $[0,T]$. If we can show that solution to (3.3.8) with initial data (u_0, v_0, w_0) are uniquely determined and nonnegative, then we will have $u(x,t) \geq 0$, $v(x,t) \geq 0$ and $u(x,t) + av(x,t) \leq K$ for $t \in [0,T]$ where solutions exist.

Rewrite (3.3.8) with initial data u_0, v_0, w_0 as:

$$\begin{aligned}
u_t + e_1 u(x,t) &= w(x,t) \int_{\mathbb{R}} k_1(y)u(x-y,t)dy \\
v_t + e_2 v(x,t) &= w(x,t) \int_{\mathbb{R}} k_2(y)v(x-y,t)dy
\end{aligned}$$

So we have

$$u(x,t) = u_0(x)e^{-e_1 t} + \int_0^t e^{-e_1(t-s)}[K - u(x,s) - av(x,s)] \int_{\mathbb{R}} k_1(y)u(x-y,s)dyds$$

$$v(x,t) = v_0(x)e^{-e_2 t} + \int_0^t e^{-e_2(t-s)}[K - u(x,s) - av(x,s)] \int_{\mathbb{R}} k_2(y)v(x-y,s)dyds \tag{3.3.9}$$

$$w(x,t) = w_0(x)e^{-I[(u,v)](t)} + \int_0^t e^{-I[(u,v)](t-s)}(e_1 u(x,s) + ae_2 v(x,s))ds.$$

where $I[(u,v)](t) = \int_0^t \int_{\mathbb{R}}[k_1(y)u(x-y,s) + ak_2(y)v(x-y,s)]dyds$, then

$$(e^{I[(u,v)](t)})_t = e^I[(u,v)](t)(e_1 u(x,t) + ae_2 v(x,t))$$

Let

$$\begin{aligned}
&\mathcal{F}_1[u,v,w](x,t) = u_0(x)e^{-e_1 t} + \int_0^t e^{-e_1(t-s)}[K - u(x,s) - av(x,s)] \\
&\cdot \int_{\mathbb{R}} k_1(y)u(x-y,s)dyds \\
&\mathcal{F}_2[u,v,w](x,t) = v_0(x)e^{-e_2 t} + \int_0^t e^{-e_2(t-s)}[K - u(x,s) - av(x,s)] \\
&\cdot \int_{\mathbb{R}} k_2(y)v(x-y,s)dyds \\
&\mathcal{F}_3[u,v,w](x,t) = w_0(x)e^{-I[(u,v)](t)} + \int_0^t e^{-I[(u,v)](t-s)}(e_1 u(x,s) + ae_2 v(x,s))ds.
\end{aligned} \tag{3.3.10}$$

Clearly, we have u, v, w are nonnegative and continuous, and so are $\mathcal{F}_1, \mathcal{F}_2, \mathcal{F}_3$ for u_0, v_0, w_0 nonnegative. Start with space $X = C(\mathbb{R} \times [0,T])^3$ and u_0, v_0, w_0. Let $\mathcal{F} = (\mathcal{F}_1(u,v,w), \mathcal{F}_2(u,v,w), \mathcal{F}_3(u,v,w))$. Let Z be a subspace of X, and $Z = \{(u,v,w) \in X \mid \sup_{\mathbb{R}\times[0,T]} \|u - e^{-e_1 t}u_0\| + \|v - e^{-e_2 t}v_0\| + \|w - e^{-I[(u_0,v_0)](t)}w_0\| \leq M\}$ where $M, T > 0$ are constant to be determined later. Let $k_i = \int_{\mathbb{R}} k_i(y)dy$, $i = 1, 2$.

So $u \geq 0$, $v \geq 0$ and $K - u - av \geq 0$ for $[0,t]$ where solution exists. $\|u\| + \|v\| +$

$\|w\| \leq M + \|u_0\| + \|v_0\| + \|w_0\|$ is bounded. $\|u\|$, $\|v\|$, $\|w\|$ are bounded.

$$\begin{aligned} \|\mathcal{F}_1(u) - e^{-e_1 t}u_0\| = & \quad \| \int_0^t e^{-e_1(t-s)} \left(w(x,s) \int_{\mathbb{R}} k_1(y)u(x-y,s)dy \right) ds\| \\ \leq & \quad \|w\|k_1\|u\|t \end{aligned}$$

$$\begin{aligned} \|\mathcal{F}_2(v) - v_0 e^{-e_1 t}\| = & \quad \| \int_0^t e^{-e_2(t-s)} \left(w(x,s) \int_{\mathbb{R}} k_2(y)v(x-y,s)dy \right) ds\| \\ \leq & \quad \|w\|k_2\|v\|t \end{aligned}$$

By selecting $T_1 < \min\{\frac{M}{3\|w\|k_1\|u\|}, \frac{M}{3\|w\|k_2\|v\|}\}$, we can get $|u(x,t) - e^{-e_1 t}u_0(x)| < M/3$, $|v(x,t) - e^{-e_2 t}v_0(x)| < M/3$. Then for $t \in [0, T_1]$, we have

$$\begin{aligned} & \|\mathcal{F}_3(w) - e^{-I[(u_0,v_0)](t)}w_0\| \\ = \quad & w_0(e^{-I[(u,v)](t)} - e^{-I[(u_0,v_0)](t)}) + \int_0^t e^{-I[(u,v)](t-s)}(e_1 u(x,s) + a e_2 v(x,s)) \end{aligned}$$

$I[(u,v)](t) = \int_0^t \int_{\mathbb{R}} [k_1(y)u(x-y,s) + ak_2(y)u(x-y,s)]dyds$. The terms inside the integral is bounded by constant depend on M and e^z is Lipschitz, so we have

$$\begin{aligned} & e^{-I[(u,v)](t)} - e^{-I[(u_0,v_0)](t)} \leq C(M)(I[(u,v)](t) - I[(u_0,v_0)](t)) \\ & = C(M) \int_0^t [k_1(y)(u(x-y,s) - u_0(y)) + ak_2(y)(v(x-y,s) - v_0(y))]dyds \\ & \leq C(M)t(k_1\|u-u_0\| + ak_2\|v-v_0\|)\frac{M}{3} := C(M)Ct \end{aligned}$$

and

$$
\begin{aligned}
& \|\mathcal{F}_3(w) - e^{-I[(u_0,v_0)](t)} w_0\| \\
\leq \quad & \|w_0\| C(M) C t + t(e_1\|u\| + a e_2 \|v\|)
\end{aligned}
$$

By selecting $T < \min\{T_1, \frac{M}{3(\|w_0\|C(M)C + e_1\|u\| + ae_2\|v\|)}\}$, we have $|w(x,t) - e^{-I[(u_0,v_0)](t)}| < M/3$. Then $\mathcal{F} : Z \to Z$.

Next we need to show $\mathcal{F}$ is a contraction.

$$
\begin{aligned}
& \|\mathcal{F}_1(u_1, v_1, w_1) - \mathcal{F}_1(u_2, v_2, w_2)\| \\
= \quad & \| \int_0^t e^{-e_1(t-s)} [(w_1(x,s) - w_2(x,s)) \int_{\mathbb{R}} k_1(y) u_1(x-y,s) dy \\
+ \quad & w_2(x,s) \int_{\mathbb{R}} k_1(y)(u_1(x-y,s) - u_2(x-y,s)) dy] ds \| \\
\leq \quad & (\|w_1 - w_2\| \|u_1\| + \|w_2\| \|u_1 - u_2\|) \cdot t k_1
\end{aligned}
$$

$$
\begin{aligned}
& \|\mathcal{F}_2(u_1, v_1, w_1) - \mathcal{F}_2(u_2, v_2, w_2)\| \\
= \quad & \| \int_0^t e^{-e_1(t-s)} [(w_1(x,s) - w_2(x,s)) \int_{\mathbb{R}} k_2(y) v_1(x-y,s) dy \\
+ \quad & w_2(x,s) \int_{\mathbb{R}} k_2(y)(v_1(x-y,s) - v_2(x-y,s)) dy] ds \| \\
\leq \quad & (\|w_1 - w_2\| \|v_1\| + \|w_2\| \|v_1 - v_2\|) \cdot t k_2
\end{aligned}
$$

$$
\begin{aligned}
& \mathcal{F}_3(u_1, v_1, w_1) - \mathcal{F}_3(u_2, v_2, w_2) \\
= \quad & w_0(e^{-I[(u_1,v_1)](t)} - e^{-I[(u_2,v_2)](t)}) + \int_0^t e^{-I[(u_1,v_1)](t-s)}(e_1 u_1(x,s) + a e_2 v_1(x,s)) \\
- \quad & \int_0^t e^{-I[(u_2,v_2)](t-s)}(e_1 u_2(x,s) + a e_2 v_2(x,s)).
\end{aligned}
$$

Here,

$$
\begin{aligned}
& |e^{-I[(u_1,v_1)](t)} - e^{-I[(u_2,v_2)](t)}| \\
\leq \quad & C(M)|\int_0^t k_1(y)[u_1(x-y,s) - u_2(x-y,s)]dyds \\
& +a\int_0^t k_2(y)[v_1(x-y,s) - v_2(x-y,s)]dyds| \\
\leq \quad & C(M)[k_1(\|u_1 - u_2\| + ak_2\|v_1 - v_2\|)]t
\end{aligned}
$$

and

$$
\begin{aligned}
& |\int_0^t e^{-I[(u_1,v_1)](t-s)}(e_1u_1(x,s)+ae_2v_1(x,s))dyds \\
& -\int_0^t e^{-I[(u_2,v_2)](t-s)}(e_1u_2(x,s)+ae_2v_2(x,s))dyds| \\
= \quad & |\int_0^t e^{-I[(u_1,v_1)](t-s)}(e_1u_1(x,s)+ae_2v_1(x,s))dyds \\
& -\int_0^t e^{-I[(u_2,v_2)](t-s)}(e_1u_1(x,s)+ae_2v_1(x,s))dyds| \\
& +|\int_0^t e^{-I[(u_2,v_2)](t-s)}(e_1u_1(x,s)+ae_2v_1(x,s))dyds \\
& -\int_0^t e^{-I[(u_2,v_2)](t-s)}(e_1u_2(x,s)+ae_2v_2(x,s))dyds| \\
= \quad & |\int_0^t [e^{-I[(u_1,v_1)](t-s)} - e^{-I[(u_2,v_2)](t-s)}](e_1u_1(x,s)+ae_2v_1(x,s))dyds| \\
& +|\int_0^t e^{-I[(u_2,v_2)](t-s)}[e_1(u_1(x,s)-u_2(x,s))+ae_2(v_1(x,s)-v_2(x,s))]dyds| \\
& \leq |(e_1\|u_1\|+ae_2\|v_1\|)[k_1(\|u_1-u_2\|+ak_2\|v_1-v_2\|)]C(M)\frac{t^2}{2}| \\
& +t|e_1(\|u_1-u_2)+ae_2(\|v_1-v_2\|)| \\
\leq \quad & (C_1(M)t^2+e_1t)\|u_1-u_2\|+(D_1(M)t^2+e_2t)\|v_1-v_2\|
\end{aligned}
$$

Denote

$$
\begin{aligned}
& \|\mathcal{F}_3(u_1,v_1,w_1)-\mathcal{F}_3(u_2,v_2,w_2)\| \\
& \leq [C_1(M)t+C_2(M)]t\|u_1-u_2\|+[D_1(M)t+D_2(M)]t\|v_1-v_2\|
\end{aligned}
$$

So

$$
\begin{aligned}
&|\mathcal{F}(u_1, v_1, w_1) - \mathcal{F}(u_2, v_2, w_2)| \\
&\leq (\|w_1 - w_2\|\|u_1\| + \|w_2\|\|u_1 - u_2\|) \cdot tk_1 + (\|w_1 - w_2\|\|v_1\| + \|w_2\|\|v_1 - v_2\|) \cdot tk_2 \\
&+[C_1(M)t + C_2(M)]t\|u_1 - u_2\| + [D_1(M)t + D_2(M)]t\|v_1 - v_2\|
\end{aligned}
$$

By selecting $t > 0$ small enough, we have $\|\mathcal{F}(u_1, v_1, w_1) - \mathcal{F}(u_2, v_2, w_2)\| \leq \|(u_1, v_1, w_1) - (u_2, v_2, w_2)\|$. Thus we have $\mathcal{F}$ is a contraction map.

By Contraction Mapping Theorem, $\mathcal{F}$ has a unique fixed point, i.e. (u^*, v^*, w^*), satisfying $\mathcal{F}(u^*, v^*, w^*) = (u^*, v^*, w^*)$ is uniquely determined. And (u^*, v^*, w^*) is nonnegative. This implies (i) of the Maximum Principle.

(ii)

Once we have $K - u(x, 0) - av(x, 0) > 0$ for some x, then by continuity, for some $t_0(x)$, $K - u(x, t) - av(x, t) > 0$ for $0 \leq t < t_0(x)$.

If $K - u(x, 0) - av(x, 0) = 0$, then

$$
\begin{aligned}
u_t(x, 0) &= -e_1 u(x, 0) \\
v_t(x, 0) &= -e_2 v(x, 0)
\end{aligned}
$$

with either $u_t < 0$ or $v_t < 0$ since $u(x, 0) \geq 0$, $v(x, 0) \geq 0$ and $K - u(x, 0) - av(x, 0) = K$. Thus $(K - u(x, 0) - av(x, 0))_t < 0$ so again $K - u(x, t) - av(x, t) < 0$ for $0 < t < t_0(x)$ for some $t_0(x)$.

Given any fixed x, suppose that

$$
t_1(x) = \sup\{t : K - u(x, s) - av(x, s) > 0 \ \ for \ \ 0 < s < t\} < \infty.
$$

Then $K - u(x,t) - av(x,t) \geq 0$ on $(0, t_1(x))$, so $K - u(x,t_1(x)) - av(x,t_1(x)) = 0$, so $(K - u(x,t) - av(x,t))_t \leq 0$ at $(x, t_1(x))$.

Also, $(K - u(x,t) - av(x,t))_t = -u_t - av_t$, $u_t = -e_1 u$ and $v_t = -e_2 v$ at $(x, t_1(x))$ with $u, v \geq 0$ and $u + av = K > 0$, so $u_t \leq 0$, $v_t \leq 0$ and either $u_t < 0$ or $v_t < 0$. So $(K - u - av)_t(x, t_1(x)) > 0$, contradiction. Thus $t_1(x) = \infty$. Hence, $K - u(x,t) - av(x,t) > 0$ for $t > 0$.

Now we use the condition on kernel that there exists $\delta, k_0 > 0$ such that $k_i(y) \geq k_0 > 0$ for $|y| \leq \delta$.

$$u(x,t) = u(x,0)e^{-e_1 t} + \int_0^t e^{-e_1(t-s)}[K - u(x,s) - av(x,s)] \int_{\mathbb{R}} k_1(y)u(x-y,s)dyds$$

Suppose $u(x,0) > 0$, $v(x,0) > 0$ for $x \in B_\gamma(x_0)$, then by continuity there is a $t_0 > 0$ such that $u(x,t) > 0$, $v(x,t) > 0$ for $t \in (0, t_0]$. By the hypothesis on kernel $k_i(y)$ we have for all $x \in B_{\gamma+\delta}(x_0)$,

$$u(x,t) = u(x,0)e^{-e_1 t} + \int_0^t e^{-e_1(t-s)}[K - u(x,s) - av(x,s)] \int_{\delta}^{-\delta} k_1(y)u(x-y,s)dyds > 0$$

for $(x,t) \in B_{\gamma+\delta}(x_0) \times (0, t_0]$. For $x \in B_{\gamma+2\delta}(x_0)$, we also have $u(x,t) > 0$ for $(x,t) \in B_{\gamma+2\delta}(x_0) \times (0, t_0]$. Repeat this argument on $B_{\gamma+N\delta}$ for $N \to \infty$. Then we have $u(x,t) > 0$ for $(x,t) \in \mathbb{R} \times (0, t_0]$.

We also have

$$u(x,2t_0) = u(x,t_0)e^{-e_1 t} + \int_{t_0}^{2t_0} e^{-e_1(t-s)}[K - u(x,s) - av(x,s)] \int_{\mathbb{R}} k_1(y)u(x-y,s)dyds$$

We can repeat this argument on $t \in [nt_0, (n+1)t_0]$ as long as $(u(x,t), v(x,t))$ exists.

Thus we have $u(x,t) > 0$, $v(x,t) > 0$ for $t > 0$ where (u,v) exists.

□

Theorem 3.15. *(i)Let* $(u_1(x,t), v_1(x,t))$ *be sub-solution and* $(u_2(x,t), v_2(x,t))$ *be super-solution of the system. If* $(u_2(x,0), v_2(x,0)) \geq_2 (u_1(x,0), v_1(x,0))$*, then* $(u_2(x,t), v_2(x,t)) \geq_2 (u_1(x,t), v_1(x,t))$ *for* $t > 0$ *where the solution exists.*

(ii) If $(u_1(x,t), v_1(x,t))$ *and* $(u_2(x,t), v_2(x,t))$ *are solutions starting from* $(u_1(x,0), v_1(x,0))$ *and* $(u_2(x,0), v_2(x,0))$ *respectively, and* $(u_2(x,0), v_2(x,0)) \geq_2 (u_1(x,0), v_1(x,0))$*, then* $(u_2(x,t), v_2(x,t)) \geq_2 (u_1(x,t), v_1(x,t))$ *for* $t > 0$ *where the solution exists.*

(iii)Moreover, if $u_2(x,0) > u_1(x,0)$ *and* $v_1(x,0) > v_2(x,0)$ *on some open subset of* $\mathbb{R}$*, then* $(u_2(x,t), v_2(x,t)) \gg_2 (u_1(x,t), v_1(x,t))$*.*

Proof. Define:

$u(x,t) = u_2(x,t) - u_1(x,t) + \epsilon e^{\alpha t}$, $\tilde{u}(x,t) = u(x,t)e^{\beta t}$.

$v(x,t) = v_1(x,t) - v_2(x,t) + \epsilon e^{\alpha t}$, $\tilde{v}(x,t) = v(x,t)e^{\beta t}$.

By previous theorem, all solutions are nonnegative with $au + bv \leq K(x)$. So they are uniformly bounded.

Claim: $\tilde{u} > 0$, $\tilde{v} > 0$ for all $t \in (0,T)$ where solution exists.

By selecting $\beta > 0$ sufficiently large, we have

$$\tilde{u}_t \cdot e^{-\beta \cdot t}$$
$$\geq [K - u_2(x,t) - av_2(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy + av(x,t) \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy$$
$$+ u(x,t)(\beta - e_1 - \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy)$$
$$+ \epsilon e^{\alpha \cdot t}(\alpha - (K - u_2 - av_2)k_1 - (1-a) \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy + e_1)$$
$$> [K - u_2(x,t) - av_2(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy + av(x,t) \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy$$
$$+ (\beta - e_1 - \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy)u(x,t)$$
$$\geq 0$$

$$\tilde{v}_t \cdot e^{-\beta \cdot t}$$
$$\geq [K - u_1(x,t) - av_1(x,t)] \int_{\mathbb{R}} k_2(y)v(x-y,t)dy + u(x,t) \int_{\mathbb{R}} k_2(y)v_2(x-y,t)dy$$
$$+ v(x,t)(\beta - e_2 - a \int_{\mathbb{R}} k_2(y)v_2(x-y,t)dy)$$
$$+ \epsilon e^{\alpha \cdot t}(\alpha - (K - u_1 - av_1)k_2 - (1-a) \int_{\mathbb{R}} k_2(y)v_2(x-y,t)dy + e_2)$$
$$> [K - u_1(x,t) - av_1(x,t)] \int_{\mathbb{R}} k_2(y)v(x-y,t)dy + u(x,t) \int_{\mathbb{R}} k_2(y)v_2(x-y,t)dy$$
$$+ (\beta - e_2 - a \int_{\mathbb{R}} k_2(y)v_2(x-y,t)dy)v(x,t)$$
$$\geq 0$$

So we must have $\tilde{u} > 0$.

$\because \epsilon$ can be arbitrarily small

$\therefore u_2(x,t) \geq (u_1(x,t))$ for $t > 0$ where solution exists.

Similarly we get $v_1(x,t) \geq v_2(x,t)$.

(ii) It is a special case of (i).

(iii) Let $p(x,t) = e^{\beta t}(u_2(x,t) - u_1(x,t))$, $q(x,t) = (v_1(x,t) - v_2(x,t))e^{\beta t}$. Suppose $u_1(x,0) < u_2(x,0)$ on some $B_\gamma(x_1)$ at some $B_\gamma(x_1)$. Then at $t = 0$

$$\begin{aligned}
e^{-\beta t}p_t \quad &= [K - u_2(x,t) - av_2(x,t)] \int_{\mathbb{R}} k_1(y)(u_2(x-y,t) - u_1(x-y,t))dy \\
&+[\beta - \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy - e_1](u_2(x,t) - u_1(x,t)) \\
&+a(v_1 - v_2) \int_{\mathbb{R}} k_1(y)u_2(x-y,t)dy
\end{aligned}$$

let $\beta > \int_{\mathbb{R}} k_1(y)u_1(x-y,t)dy + e_1$ be sufficiently large, we have $p_t > 0$ for $t = 0$. But this implies that $p(x,t) > 0$ on $[0,t_0]$ for some t_0.

Then for $x \in B_{\gamma+\delta}(x_1)$, we also have $p_t > 0$. Repeat this process on $B_{\gamma+2\delta}$, $B_{\gamma+3\delta}$ and so on until we have for $x \in \mathbb{R}$, we have $p_t > 0$ on $[0,t_0]$. Then $p(x,t) > 0$ for where $p(x,t)$ exists, i.e. $u_2(x,t) > u_1(x,t)$ for $t \in [0,t_0]$ where t_0 only depends on the coefficients of system. Repeat this argument on $[t_0, 2t_0]$, $[2t_0, 3t_0]$, etc. Then we obtain $u_2(x,t) > u_1(x,t)$, $v_1(x,t) > v_2(x,t)$ for where the solution exists.

Similar argument applies for $v_1(x,t) > v_2(x,t)$ for where solution exists.

□

Corollary 3.16. *(Global Existence) For $\phi = (u_0, v_0) \in S$, then $(u(\cdot,t;\phi), v(\cdot,t;\phi))$ exists for all $t > 0$.*

Proof. We have the global existence for single species and thus $(u(\cdot,t;(u_0,0)), v(\cdot,t;(u_0,0)))$ and $(u(\cdot,t;(0,v_0)), v(\cdot,t;(0,v_0)))$ exists for all $t > 0$. Also we have $(u(\cdot,t;(u_0,0)), v(\cdot,t;(u_0,0))) \leq_2 (u(\cdot,t;(u_0,v_0)), v(\cdot,t;(u_0,v_0))) \leq_2$

$(u(\cdot,t;(0,v_0)),v(\cdot,t;(0,v_0)))$. Then we obtain the global existence for the two competitive species model.

□

Theorem 3.17. *Let $k_i(x) = k_i \cdot d_i(x)$, where k_i is the birth rate and $\int_{\mathbb{R}} d_i(x)dx = 1$, for $i = 1, 2$. If $\frac{k_1}{e_1} \neq \frac{k_2}{e_2}$, without loss of generality, assume $\frac{k_1}{e_1} > \frac{k_2}{e_2}$ then there exists no coexistent equilibrium if $\frac{k_1}{e_1}d_1(x) > \frac{k_2}{e_2}d_2(x)$ for all $x \in \mathbb{R}$.*

Proof. If there is a positive equilibrium $(u^*(x), v^*(x))$, then it must satisfy

$$K - u^*(x) - av^*(x) = \frac{e_1 u^*(x)}{\int_{\mathbb{R}} k_1(x-y)u^*(y)dy},$$
$$K - u^*(x) - av^*(x) = \frac{e_2 v^*(x)}{\int_{\mathbb{R}} k_2(x-y)v^*(y)dy}.$$

Then, $\frac{k_2}{e_2}u^*(x)\int_{\mathbb{R}} d_2(x,y)v^*(y)dy = \frac{k_1}{e_1}v^*(x)\int_{\mathbb{R}} d_1(x,y)u^*(y)dy$. Integrate on $\mathbb{R}$, then since $d_i(y)$ is symmetric,

$$\frac{k_2}{e_2}\int_{\mathbb{R}}\int_{\mathbb{R}} d_2(x-y)u^*(x)v^*(y)dydx = \frac{k_1}{e_1}\int_{\mathbb{R}}\int_{\mathbb{R}} d_1(x-y)u^*(x)v^*(y)dydx$$

If $\frac{k_1}{e_1}d_1(x) > \frac{k_2}{e_2}d_2(x)$ for all $x \in \mathbb{R}$, this cannot be true.

Thus there exists no coexistent equilibrium. □

Theorem 3.18. *If $\frac{e_1}{k_1} < \frac{e_2}{k_2}$, then the semi-trivial equilibrium $(K - \frac{e_1}{k_2}, 0)$ is asymptotically stable and $(0, \frac{1}{a}(K - \frac{e_2}{k_2}))$ is unstable.*

Proof. Let $u^* = K - \frac{e_1}{k_1}$, $v^* = \frac{1}{a}(K - \frac{e_2}{k_2})$. We have $\int_{\mathbb{R}} k_i(x-y)dy = k_i\int_{\mathbb{R}} d_i(x-y)dy = k_i \cdot 1 = k_i$, for all $x \in \mathbb{R}$ and $i = 1, 2$.

Let $(u(x,t), v(x,t))$ start from $(u^* - \epsilon, \epsilon)$.

$$v_t = [K - u^*] \int_{\mathbb{R}} k_2(x-y)\epsilon dy - e_2\epsilon + \epsilon^2[1-a] \int_{\mathbb{R}} k_2(x-y)dy$$
$$= \epsilon[\frac{e_1}{k_1}k_2 \int_{\mathbb{R}} d_2(x-y)dy - e_2] + \epsilon^2[1-a] \int_{\mathbb{R}} k_2(x-y)dy$$

Since $\frac{e_1}{k_1} < \frac{e_2}{k_2}$, we can select ϵ small enough such that

$$v_t < \epsilon[\frac{e_2}{k_2}k_2 - e_2] = 0.$$

Then $(u^* - \epsilon, \epsilon)$ goes to $(u^*, 0)$ as t increase. Thus $(u^*, 0)$ is asymptotically stable.

If $(u(x,t), v(x,t))$ start from $(\epsilon, v^* - \epsilon)$,

$$u_t = [K - av^*] \int_{\mathbb{R}} k_1(x-y)\epsilon dy - e_1\epsilon - \epsilon^2[1-a] \int_{\mathbb{R}} k_1(x-y)\phi_1(y)dy$$
$$= \epsilon[\frac{e_2}{k_2}k_1 \int_{\mathbb{R}} d_1(x-y)dy - e_1] - \epsilon^2[1-a] \int_{\mathbb{R}} k_1(x-y)dy$$

Since $\frac{e_1}{k_1} < \frac{e_2}{k_2}$, we can select ϵ small enough such that

$$u_t > \epsilon[\frac{e_1}{k_1}k_1 - e_1] = 0.$$

Then $u(x,t)$ increases near $t = 0$ as t increases. So $(\epsilon, v^* - \epsilon)$ is asymptotically unstable.

□

3.4 Spreading Speed and Traveling Waves

In the following text, we assume $\frac{e_1}{k_1} < \frac{e_2}{k_2}$, thus the semi trivial equilibrium $(0, \frac{1}{a}(K - \frac{e_2}{k_2}))$ is asymptotically unstable and $(K - \frac{e_1}{k_2}, 0)$ is stable. Also assume $\frac{k_1}{e_1}d_1(x) > \frac{k_2}{e_2}d_2(x)$ for all $x \in \mathbb{R}$ then there is no coexistence equilibrium. $(0,0)$ is the equilibrium between them $(0, \frac{1}{a}(K - \frac{e_2}{k_2})) \leq_2 (0,0) \leq_2 (K - \frac{e_1}{k_2}, 0)$ under competing ordering.

3.4.1 Preliminary

The following statements and theorems are from Fang and Zhao [26].

Let (X, X^+) be a Banach Lattice with the norm $|\cdot|$ and the positive cone X^+. For any u and v in a Banach lattice, $\max\{u,v\}$ is defined to be the least upper bound of u and v and $\min\{u,v\}$ to be the greatest lower bound of u and v.

Let $\mathcal{M}$ be all non increasing and bounded functions from $\mathbb{R}$ to X. We equip $\mathcal{M}$ with the compact open topology. We say a subset $\mathcal{S}$ of $\mathcal{M}$ is bounded if $\{|\phi(x)| : \phi \in \mathcal{S}, x \in \mathbb{R}\}$ is bounded. For any $u, v \in X$, $u \geq (>, \gg) v$ if $u - v \in X^+(X^+ \backslash \{0\}, IntX^+)$. For any $u, v \in \mathcal{M}$, $u \geq v$ if $u(x) \geq v(x)$ for all $x \in \mathbb{R}$. For any given subset $\mathcal{A} \subset \mathcal{M}$ and number $s \in \mathbb{R}$, define $A(s) := \{u(s) : u \in A\}$. For two subsets B_1, B_2 of X, we define $\max\{B_1, B_2\} := \{\max\{u_1, u_2\} : u_1 \in B_1, u_2 \in B_2\}$. We use the Kuratowski measure of non compactness in X. For any bounded set B, define: $\alpha(B) := \inf\{r : B\ has\ a\ finite\ cover\ of\ diameter < r\}$. It is easy to see that B is pre compact if and only if $\alpha(B) = 0$. We also have $\alpha(\max\{B_1, B_2\}) \leq \alpha(B_1) + \alpha(B_2)$.

For any $y \in \mathbb{R}$, we introduce translation operator t_y on $\mathcal{M}$ by $T_y[u](x) = u(x-y)$ for all $x \in \mathbb{R}$. Let the map $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ where $\mathcal{M}_\beta := \{u \in \mathcal{M} : 0 \leq u \leq \beta\}$ and $\beta \in IntX^+$. We have the following assumptions:

(A1) (Translation invariance) $T_y \circ Q = Q \circ T_y$ for all $y \in \mathbb{R}$.

(A2) (Continuity) If $u_k \to u$ in $\mathcal{M}$, then $Q[u_k](x) \to Q[u](x)$ in X almost everywhere.

(A3) (Point-α-contraction) There exists $k \in [0,1)$ such that for any $\mathcal{U} \subset \mathcal{M}_\beta$, $\alpha(Q[\mathcal{U}](0)) \leq k\alpha(\mathcal{U}(0))$.

(A4) (Monotonicity) $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ is monotone (order-preserving) in the sense that $Q[u] \geq Q[v]$ whenever $u \geq v$ in $\mathcal{M}_\beta$.

(A5) (Monostability) Q admits two fixed points 0 and β in X^+, and $lim_{n\to\infty} Q^n[\omega] = \beta$ for any $\omega \in X^+$ with $0 \ll \omega \leq \beta$.

With (A1), we have (A3) equivalent to

$$\alpha(Q[\mathcal{U}](x)) \leq k\alpha(\mathcal{U}(x)) \quad \forall \mathcal{U} \subset \mathcal{M}_\beta, \quad x \in \mathbb{R}.$$

Let $\omega \in X$ with $0 \ll \omega \ll \beta$. Choose ϕ to be a continuous function from $\mathbb{R}$ to X with the following properties:

(B1) ϕ is a non increasing function.;

(B2) $\phi(x) = 0$, for all $x \geq 0$.

(B3) $\phi(-\infty) = \omega$.

Let c and κ be given real numbers with $\kappa \in (0,1]$. Following [42], we define an operator $R_{c,\kappa}$ by $R_{c,\kappa}[a](s) := \max\{\kappa\phi(s), T_{-c}Q[a](s)\}$ and a sequence of functions $a_n(c,\kappa;s)$ by the recursion:

$$a_0(c,\kappa;s) = \kappa\phi(s), \quad a_{n+1}(c,\kappa;s) = R_{c,\kappa}[a_n(c,\kappa;\cdot)](s).$$

Denote $R_c = R_{c,1}$, $a_n(c;s) = a_n(c,1;s)$. The following lemmas are Lemma 3.2-3.6

from [26].

Lemma 3.19. *The following statements are valid:*

(1) $R_c : \mathcal{M}_\beta \to \mathcal{M}_\beta$ is order-preserving.

(2) $a_n(c; s)$ is nondecreasing in n and non increasing in both s and c.

(3) For each n, $a_n(c; -\infty) \geq Q^n[\omega]$ and $a_n(c; +\infty) = 0$.

(4) For each $s \in \mathbb{R}$, $a_n(c; s)$ converges to $a(c; s)$ in X and $a(c; s)$ is non increasing in both s and c.

(5) $a(c; -\infty) = \beta$ and $a(c; +\infty)$ exists in X.

Lemma 3.20. *The following statements are valid:*

(1) $a(c; \cdot) \in \mathcal{M}$ and $R_c[a(c; \cdot)](s) = a(c; s)$ for almost all $s \in \mathbb{R}$.

(2) $a(c, +\infty) \in X$ is a fixed point of Q.

Lemma 3.21. *$a(c; +\infty) = \beta$ if and only if $a_n(c; 0) \gg \omega$ for some n.*

Now we define the number

$$c_+^* = \sup\{c : a(c; +\infty) = \beta\},$$

then we have

Lemma 3.22. *$c_+^* > -\infty$.*

Now we define

$$\bar{c}_+ = \sup\{c : a(c; +\infty) > 0\}.$$

Clearly, $c_+^* \leq \bar{c}_+$ because $a(c; \cdot)$ is non increasing in c. Since $a(c; \infty)$ is a fixed point of Q, we have $c_+^* = \bar{c}_+$ provided that Q has no fixed point in X_β other than 0 and β. Moreover, $a(c; +\infty) = \beta$ if and only if $c < c_+^*$ and $a(c; +\infty) > 0$ if and only if $c < \bar{c}_+$.

c_+^* and $\bar{c}_+$ are the lower and upper bounds of rightward spreading speeds for the discrete-time system respectively. In the case where $\bar{c}_+ = c_+^*$, the system admits a single rightward spreading speed.

The following theorem is Theorem 4.2 from [26].

Theorem 3.23. *Let $\{Q_t\}_{t\geq 0}$ be a continuous-time semi flow on $\mathcal{M}_\beta$. Assume that for any $t > 0$, Q_t satisfies (A1), (A3)-(A5) with fixed points replaced by equlibria of $\{Q_t\}_{t\geq 0}$ in (A5). Let c_+^* and $\bar{c}_+$ be defind as before with $Q = Q_1$ and $c_+^* \leq \bar{c}_+$. Then the following statements are valid:*

(1) For any $c \geq c_+^*$, there is a left-continuous traveling wave $W(x-ct)$ connecting β to some equilibrium $\beta_1 \in X_\beta \backslash \{\beta\}$.

(2) If, in addition, 0 is an isolated equilibrium of $\{Q_t\}_{t\geq 0}$ in X_β, then for any $c \geq \bar{c}_+$ either of the following holds true:

(i) There exists a left-continuous traveling wave $W(x-ct)$ connecting β to 0.

(ii) $\{Q_t\}_{t\geq 0}$ has two ordered equilibria α_1, α_2 in $X_\beta \backslash \{0, \beta\}$ such that there exist a left-continuous traveling wave $W_1(x-ct)$ connedting α_1 to 0 and a left continuous $w_2(x-ct)$ connecting β to α_2.

(3) For any $c < c_+^*$, there is no traveling wave connecting β to 0, and for any $c < \bar{c}_+$, there is no traveling wave connecting β to 0.

Further, if each Q_t maps left-continuous functions to left-continuous functions, then the above obtained traveling waves satisfy $Q_t[Q](x) = W(x-ct)$, for all $x \in \mathbb{R}$ and $t \geq 0$.

3.4.2 Two species competition model

Recall our model (3.3.2):

$$u_t = [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy - e_1 u(x,t)$$
$$v_t = [K - u(x,t) - av(x,t)] \int_{\mathbb{R}} k_2(y)v(x-y,t)dy - e_2 v(x,t)$$

Assume that: $\frac{e_1}{k_1} < K < \frac{e_2}{k_2}$. The equilibria:

$$E_0 := (0,0), \quad E_1 := (0, \frac{1}{a}(K - \frac{e_2}{k_2})), \quad E_2 := (K - \frac{e_1}{k_1}, 0).$$

Change the variable: $w(x,t) = \frac{1}{a}(K - \frac{e_2}{k_2}) - v(x,t)$, we obtain the system:

$$\begin{aligned} u_t &= [\tfrac{e_2}{k_2} - u(x,t) + aw(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy - e_1 u(x,t) \\ w_t &= [\tfrac{e_2}{k_2} - u(x,t) + aw(x,t)] \int_{\mathbb{R}} k_2(y)w(x-y,t)dy - k_2 K w(x,t) + \tfrac{k_2 K - e_2}{a} u(x,t) \end{aligned} \tag{3.4.1}$$

Then the three equilibria become:

$$\bar{E}_0 := (0, \frac{1}{a}(K - \frac{e_2}{k_2})), \quad \bar{E}_1 := (0,0), \quad \bar{E}_2 := (K - \frac{e_1}{k_1}, \frac{1}{a}(K - \frac{e_2}{k_2})).$$

Let Q be the time-one map of the system:

$$\begin{aligned} Q[u](x) &= [\tfrac{e_2}{k_2} - u(x) + aw(x)] \int_{\mathbb{R}} k_1(y)u(x-y)dy - e_1 u(x) \\ Q[w](x) &= [\tfrac{e_2}{k_2} - u(x) + aw(x)] \int_{\mathbb{R}} k_2(y)w(x-y)dy - k_2 K w(x) + \tfrac{k_2 K - e_2}{a} u(x) \end{aligned} \tag{3.4.2}$$

The next Lemma is Lemma 3.3 from [64]. It will be used later in proof of Theorem 3.25.

Lemma 3.24. *Let* $\Phi_1(\lambda) = K\int_{\mathbb{R}} k_1(y)e^{\lambda y}dy - e_1$*,* $\Phi_2(\lambda) = K\int_{\mathbb{R}} k_2(y)e^{\lambda y}dy - k_2K$*, then* Φ_i *satisfy the following properties:*

(i) $\Phi(\lambda) \to \infty$ *as* λ *decreases to* 0*.*

(ii) $\Phi(\lambda)$ *is decreasing near* 0*.*

(iii) $\Phi'(\lambda)$ *changes sign at most once on* $(0, \infty)$*.*

(iv) $\lim_{\lambda\to\infty} \Phi(\lambda)$ *exists, where the limit may be infinite.*

Theorem 3.25. *Let* $\bar{c}_+ \geq c_+^*$ *be defined as before with* Q *be* Q_1 *time-one map of system* (3.3.2)*. Then the following statements are valid:*

(i) $\bar{c}_+$ *is the minimal wave speed of* (3.3.2) *in the sense that for any* $c \geq \bar{c}_+$*, there is a traveling wave* $(U(x-ct), V(x-ct))$ *connecting* E_2 *to* E_1*, with wave profile component* U *non increasing and* V *non decreasing, and for any* $c < \bar{c}_+$*, there is no such traveling wave.*

(ii) $\bar{c}_+ = c_+^*$*, and hence, system* (3.3.2) *admits a single rightward spreading speed.*

Proof. (i) Let $X = \mathcal{R}^2$, $\beta = \bar{E}_2$. $\mathcal{U}$ is a subset of $\mathcal{M}_\beta$ as in $(A3)$. Since system (3.3.2) has a comparison principle, so does (3.4.2). It then follows that the solution map Q_t for (3.4.2) maps $\mathcal{M}_\beta$ into itself. It is easy to check translation invariance property since $T_z \circ Q = Q \circ T_z$ for all $z \in \mathbb{R}$. Since all bounded sets in $\mathbb{R}^2$ are pre compact, we have $\alpha(\mathcal{U}(0)) = 0$ and $\alpha(Q_t[\mathcal{U}(0)]) = 0$ as in the proof of Theorem 5.1 in Fang, Zhao [2014]. Therefore the conditions in Theorem 3.23 are satisfied. We obtain $\bar{c}_+$ as the minimal wave speed, in the sense that for any $c \geq \bar{c}_+$ there exists a left-continuous traveling wave $W(x-ct)$ connecting β to 0 and for any $c < \bar{c}_+$, there is no traveling wave connecting β to 0. Moreover, since the terms of right hand side of

$$\begin{aligned} & u(x,t) = u(x,0) + \int_0^t \Big([K - u(x,s) - av(x,s)] \cdot \int_{\mathbb{R}} k_1(y)u(x-y,s)dy \\ & -e_1 u(x,s) \Big) ds \\ & v(x,t) = v(x,0) + \int_0^t \Big([K - u(x,s) - av(x,s)] \cdot \int_{\mathbb{R}} k_2(y)v(x-y,s)dy \\ & -e_2 v(x,s) \Big) ds \end{aligned} \tag{3.4.3}$$

are differentiable with respect to t, the obtained traveling waves are also classical solutions of (3.3.2).

To prove the theorem by using Theorem 3.23, we need to exclude the second positivity in (2). Assume that (2)(ii) holds true for some $c \geq \bar{c}_+$. Then since $\bar{E}_0$ is the only equilibrium between 0 and β, $\alpha_1 = \alpha_2 = \bar{E}_0$. Restrict the system on the order interval $[\bar{E}_1, \bar{E}_0]$ and we obtain

$$w_t = [\frac{e_1}{k_1} - aw(x,t)] \int_{\mathbb{R}} k_2(y)w(x-y,t)dy - k_2 K w(x,t). \tag{3.4.4}$$

Then by Theorem 3.8, there is a non increasing traveling wave $W(x-ct)$ connecting $\frac{1}{a}(K - \frac{e_2}{k_2})$ and 0.

The system restricted on the order interval $[\bar{E}_1, \bar{E}_0]$ is:

$$u_t = [K - u(x,t)] \int_{\mathbb{R}} k_1(y)u(x-y,t)dy - e_1 u(x,t). \tag{3.4.5}$$

Also there is a non increasing traveling wave $U(x-ct)$ connecting $\frac{e_1}{k_1}$ to 0. Let $\tilde{W}(x-ct) = \frac{1}{a}(K - \frac{e_2}{k_2}) - W(x-ct)$, it is a non decreasing traveling wave connecting

0 and $\frac{1}{a}(K - \frac{e_2}{k_2})$ of the system:

$$\tilde{w}_t = [K - a\tilde{w}(x,t)] \int_{\mathbb{R}} k_2(y)\tilde{w}(x-y,t)dy - e_2\tilde{w}(x,t). \tag{3.4.6}$$

(3.4.5) admits a positive spreading speed $c_1^* > 0$, and (3.4.6) admits a positive spreading speed $c_2^* > 0$. Thus we have $c \geq c_1^* > 0$. But also $-c \geq c_2^* > 0$. Contradiction.

(ii)

Assume $\bar{c}_+ > c_+^*$. By (1) and (3), 3.4.2 has a non increasing traveling wave $(U_1(x - c_+^*t), W_1(x - c_+^*t))$ connecting $\bar{E}_2$ to $\bar{E}_0$. $\therefore$ $W_1 \equiv \frac{1}{a}(K - \frac{e_2}{k_2})$. And $U_1(x - c_+^*t)$ is a traveling wave of (3.4.5) connecting $K - \frac{e_1}{k_1}$ and 0. So we have $c_+^* \geq c_1^* > 0$. Let

$$F_1(\lambda, c) := \lambda c - K \int_{\mathbb{R}} k_1(y)e^{\lambda y}dy + e_1.$$

By Lemma 3.24, we have that c_1^* is the only solution satisfies the following equations:

$$\begin{aligned} &\lambda > 0, \\ &F_1(\lambda, c) = 0, \\ &\partial_\lambda F_1(\lambda, c) = 0. \end{aligned} \tag{3.4.7}$$

Let λ_1^* and c_1^* satisfy (3.4.7). Choose a number $c_1 \in (c_+^*, \bar{c}_+)$, then $c_1 > c_+^* > c_1^*$. So there exists $\lambda_1 > 0$ such that $F_1(\lambda_1, c_1) > 0$.

Let

$$F_2(\lambda, c) := \lambda c - \frac{e_2}{k_2} \int_{\mathbb{R}} k_2(y)e^{\lambda y}dy + k_2K.$$

Then c_2^* is the only solution of

$$\begin{aligned} &\lambda > 0, \\ &F_2(\lambda, c) = 0, \\ &\partial_\lambda F_2(\lambda, c) = 0. \end{aligned} \tag{3.4.8}$$

Let λ_2^* and c_2^* satisfy (3.4.8). Since $c_1 \geq c_2^* > 0$, there exists λ_2 such that $f_2(\lambda_2, c_1) > 0$.

Define

$$\bar{u}(x,t) = \min\{e^{-\lambda_1(x-c_1t)}, K\}, \quad \bar{w}(x,t) = \min\{e^{-\lambda_2(x-c_1t)}, \frac{e_2}{k_2 a}\}.$$

Next we show that $(\bar{u}(x,t), \bar{w}(x,t))$ is an upper solution to (3.4.2).

For all $x - c_1 t > -\frac{1}{\lambda_1} lnK$, $\bar{u}(x,t) = e^{-\lambda_1(x-c_1t)}$ and hence,

$$\begin{aligned} & e^{\lambda_1(x-c_1t)}\left(\bar{u}_t - [K - \bar{u}(x,t)]\int_{\mathbb{R}} k_1(y)\bar{u}(x-y,t)dy + e_1\bar{u}(x,t)\right) \\ = \quad & e^{\lambda_1(x-c_1t)}\left(\lambda_1 c_1 e^{-\lambda_1(x-c_1t)} - K\int_{\mathbb{R}} k_1(y)e^{\lambda_1 y}dy e^{-\lambda_1(x-c_1t)} + e_1 e^{-\lambda_1(x-c_1t)}\right) \\ = \quad & \lambda_1 c_1 - K\int_{\mathbb{R}} k_1(y)e^{\lambda_1 y}dy + e_1 > 0 \end{aligned}$$

For all $x - c_1 t < -\frac{1}{\lambda_1} lnK$, $\bar{u}(x,t) = K$ and hence,

$$\begin{aligned} & e^{\lambda_1(x-c_1t)}\left(\bar{u}_t - [K - K]\int_{\mathbb{R}} k_1(y)\bar{u}(y,t)dy + e_1\bar{u}(x,t)\right) \\ = \quad & e^{\lambda_1(x-c_1t)} e_1 K > 0 \end{aligned}$$

For all $x - c_1t < -\frac{1}{\lambda_2} ln \frac{k_2 a}{e_2}$, $\bar{w}(x,t) = e^{-\lambda_2(x-c_1t)}$ and hence,

$$\begin{aligned} & e^{\lambda_2(x-c_1t)}\left(\bar{w}_t - [\frac{e_2}{k_2} - a\bar{w}(x,t)]\int_{\mathbb{R}} k_2(y)\bar{w}(x-y,t)dy + k_2K\bar{w}(x,t)\right) \\ = \quad & e^{\lambda_2(x-c_1t)}\left(\lambda_2 c_1 e^{-\lambda_2(x-c_1t)} - \frac{e_2}{k_2}\int_{\mathbb{R}} k_2(y)e^{\lambda_2 y}dy e^{-\lambda_2(x-c_1t)} + k_2Ke^{-\lambda_2(x-c_1t)}\right) \\ = \quad & \lambda_2 c_1 - \frac{e_2}{k_2}\int_{\mathbb{R}} k_2(y)e^{\lambda_2 y}dy + k_2K > 0 \end{aligned}$$

For all $x - c_1t > -\frac{1}{\lambda_2} ln \frac{k_2 a}{e_2}$, $\bar{w}(x,t) = \frac{e_2}{k_2 a}$ and hence,

$$\begin{aligned} & e^{\lambda_2(x-c_1t)}\left(\bar{w}_t - [\frac{e_2}{k_2} - a\bar{w}(x,t)]\int_{\mathbb{R}} k_2(y)\bar{w}(x-y,t)dy + k_2K\bar{w}(x,t)\right) \\ = \quad & e^{\lambda_2(x-c_1t)}\left(0 - 0 + k_2Ke^{-\lambda_2(x-c_1t)}\right) \\ = \quad & k_2K > 0 \end{aligned}$$

$\therefore$ $(\bar{u}, \bar{w})$ is an upper traveling wave solution of (3.4.2).

Let $\phi(x)$ be defined as in (B1)-(B3). Choose $L > 0$ sufficiently large such that $(\bar{u}(x-L,0), \bar{w}(x-L,0)) \geq \phi(x)$. Denote $(\bar{u}(x-L,0), \bar{w}(x-L,0)) = \psi(x)$. We have,

$$Q_t[\phi](x) \leq Q_t[\psi](x) \leq ((\bar{u}(x-L,t), \bar{w}(x-L,t))), \quad \forall t \geq 0, \quad x \in \mathbb{R},$$

where Q_t is the solution operator of system (3.4.2), the first inequality follows from comparison principle and the second follows from the fact that $(\bar{u}, \bar{w})$ is an upper solution.

Let a_n be defined as in the recursion and $Q = Q_1$ be the time-one map. Let $a = \lim_{n\to\infty} a_n$, $a_0 = \phi$. Then,

$$a_1(c_1, x) = \max\{\phi(x), T_{-c_1}Q[a_0](x)\} \leq \max\{\psi(x), Q[\psi](x + c_1)\}.$$

Since

$$
\begin{aligned}
Q[\psi](x+c_1) \le &\quad ((\bar{u}(x+c_1-L,1), \bar{w}(x+c_1-L,1))) \\
= &\quad (\min\{e^{-\lambda_1(x-L)}, K\}, \min\{e^{-\lambda_2(x-L)}, \frac{e_2}{k_2 a}\}) \\
\le &\quad (e^{-\lambda_1(x-L)}, e^{-\lambda_2(x-L)}) \\
= &\quad (\bar{u}(x-L,0), \bar{w}(x-L,0)) = \psi(x).
\end{aligned}
$$

So then $a_1(c_1, x) \le \psi(x)$.

Assume $a_n(c_1, x) \le \psi(x)$, then

$$
a_{n+1}(c_1, x) = \max\{\phi(x), T_{-c_1}Q[a_n](x)\} \le \max\{\psi(x), Q[\psi](x+c_1)\} \le \psi(x).
$$

So we have $a_n(c_1, x) \le \psi(x)$ for all $n \ge 0$. Then we have

$$
\lim_{x\to+\infty} \lim_{n\to+\infty} a_n(c_1, x) \le \lim_{x\to+\infty} \lim_{n\to+\infty} \psi(x) = (0,0).
$$

However, $\lim_{x\to+\infty} lim_{n\to+\infty} a_n(c_1, x) = a(c_1; +\infty)$. By the property of c_+^* and $\bar{c}_+$, we have $a(c; +\infty) \ne \bar{E}_2$ since $c_1 > c_+^*$ and $a(c; +\infty) > 0$ since $c_1 < \bar{c}_+$. So we must have $a(c_1; +\infty) = \bar{E}_1 \ne (0,0)$. Contradiction!

Thus we proved $\bar{c}_+ = c_+^*$.

3.5 Conclusions

The single species model for an infinite domain has already been treated in [64] and the conclusions of spreading speed and existence of traveling wave profiles can be drawn directly from the special case when $n = 1$.

For two species competition model, the theory of spreading speeds and monotone traveling waves for cooperative and competitive systems of reaction diffusion equations in Weinberger et al. [63] and [45] cannot be applied because nonlocal system is not compact. Liang and Zhao [46] extended the theory to systems with weaker compactness. Their theory can be applied to the multi-type SIS model in [64], in which the single species model for our nonlocal metapopulation model has been treated as a special case. However, we cannot apply this theory to the two species competition system because it can only deal with the case where there are only two equilibria. If there is a coexistence steady state, the system can be restricted to the region where there are only zero and the positive equilibria, and the two semi-trivial equilibria will not be in the region. In our system, under certain conditions there will be three equilibria: zero and two semi-trivial equilibria. We have to deal with the case where there is an intermediate equilibrium (zero) between the two semi-trivial equilibria. Fang and Zhao [26] developed the theory and similar proof of their Theorem 5.3 can be applied to our model. We do not have linear determinacy for this model but without the additional conditions, we can still obtain the spreading speed which is also the minimal wave speed, as well as existence of traveling wave solutions when the wave speed is no less than the minimal wave speed.

$\square$

Chapter 4

Summary and Future Study

In this project we studied a spatial model based on metapopulation framework on continuous time and space, with nonlocal dispersal. Dispersal, which evolves in response to any kind of alternation in the environment, has been recognized to be an imoportant life-history trait. It plays a prominent role in metapopulation dynamics, species invasion and hence in population dynamics ([17]). Movement has consequences for individuals as well as for populations and communities, and its effects on inclusive fitness are ultimately the selecting forces for dispersal, migration and other types of movement that affect the distribution of individuals ([18]). There are a number of observations, such as "Random dispersal in the theoretical populations", that have profoundly affected the study of spatial ecology. [6] provided general study of ecological spatial modeling discussion of reaction-diffusion models. There are many challenges in spatial ecology: the impact of space on community structure, incorporating the scale and structure of landscapes into mathematical models, and developing the connections between spatial ecology and the three other disciplines of evolutionary theory, epidemiology, and economics ([12]). [12] has provided many sections on those topics.

In Chapter 1 we established the existence of solution of the single species model and monotonicity of the system. We also studied an eigenvalue problem for the stability analysis and gave the estimation of principal eigenvalue. Then by the monotonicity of system, we concluded that under certain conditions zero equilibrium is asymptotically stable and under other conditions the unique positive equilibrium is stable, which results in the extinction of persistence of a species. In Chapter 2 we considered the two species competition, including competing for space and the evolution of dispersal strategies. The system is monotone under the compete ordering. In the analysis of semi-trivial equilibria, we used the eigenvalue problem and conclusions from Chapter 1 to obtain the stability analysis. A sufficient condition for a coexistence equilibrium was given and we also showed that in the case of two competing species with different dispersal strategy, there is no coexistence equilibrium and the ideal free dispersal strategy is evolutionarily stable. In Chapter 3 we are interested in the spreading speed and traveling waves on infinite domain for both single species and two species competition model. The study of traveling waves and spreading speed is based on semi-flows theory of monostable type with weak compactness. In two species competition, the assumption that they compete for space leads to the competition-exclusion. This problem needs to be treated by the theory in [26] where extra equilibria are allowed between zero and positive equilibrium for the monostable system.

There are several versions of existence, uniqueness of the solutions and maximum principles, comparison theorems. However, these conclusions require different hypotheses. The existence and uniqueness of solutions are valid on both finite and infinite domain if the dispersal kernel is integrable. However, in the case that the variable of potential suitable site $K(x)$ and the death rate $e(x)$ are not constant, to establish maximum principle and comparison theorem we need to restrict to finite domain Ω and have more hypotheses on the kernel $k(x, y)$. When the domain is infinite and parameters are constant, we can prove the monotonicity of the system but using different approaches and have different hypothesis on $k(x, y)$. For the two species competition model, unlike the general Lotka-Volterra competition model, we require the competing parameter to be the same for both species since they are competing for space and the parameters represent the size of each individual. Biologically this assumption is reasonable for the model setup but it results in the case that there is one more equilibrium between zero and positive equilibrium in the study of spreading speed and traveling waves. Many theories cannot apply for our model and we need the approach with a weaker compactness condition for a more general case to fix it.

There are several types of dispersal models such as reaction-diffusion equations and the nonlocal integro-differential equation where the dispersal and reproduction are separated. These models share some features with our model, e.g. existence and uniqueness of solutions, monotonicity, ideal free dispersal is evolutionarily stable strategy, etc. However, the conditions and the approaches are different. For example, our system does not have the compactness thus the classical results do not apply. We need to consider an equivalent eigenvalue problem in order to analyze the stability of equilibria. In the evolutionarily stable strategy study, the lack of compactness is also a problem and we fixed it by perturbation theory to construct an arbitrarily small positive sub-solution. There are many problems that are not anticipated until we worked the project out. Besides, many open topics based on this model are also interesting. A natural question will be that can we extend the system to $n \geq 3$ species. In that case, if the n species are not cooperative with each other, then the system will lost the monotonicity. The same problem arises when considering a predator-prey system based on our nonlocal metapopulation model. Another topic may be interesting is that we consider the Allee effect, i.e. the growth rate is small when the population density is small and individuals can benefit from the presence of conspecifics. In this case the system will not possess the mono-stability and there will be more than one stable steady state.

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