

# Random Dispersal vs Non-Local Dispersal

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**Abstract.** Random dispersal is essentially a local behavior which describes the movement of organisms between adjacent spatial locations. However, the movements and interactions of some organisms can occur between non-adjacent spatial locations. To address the question about which dispersal strategy can convey some competitive advantage, we consider a mathematical model consisting of one reaction-diffusion equation and one integro-differential equation, in which two competing species have the same population dynamics but different dispersal strategies: the movement of one species is purely by random walk while the other species adopts a non-local dispersal strategy. For either hostile surroundings or spatially periodic and heterogeneous environments we show that the species with random dispersal can not invade when rare, while the species with non-local dispersal and small non-local interaction distance can invade when rare. These results suggest that for hostile surroundings or spatially periodic heterogeneous environments, non-local dispersal can be preferred over random dispersal. Nevertheless, for spatially heterogeneous environments if random dispersal strategy with zero Neumann boundary condition is compared with non-local dispersal strategy with hostile surroundings, each of the two species can invade when rare and both species can coexist. The biological meaning behind is that the zero-flux boundary condition can somehow help counterbalance the disadvantage caused by local dispersal. Numerical results will be presented to shed light on the global dynamics of the system for general values of non-local interaction distance and also to point to future research directions.

**Key words:** Non-local dispersal, Random dispersal, Competition, Reaction-diffusion, Integral kernel.

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# 1 Introduction

Dispersal, the mechanism by which a species expands the distribution of its population, is a central topic in biology and ecology. The evolution of dispersal has attracted a lot of attentions for more than two decades, both theoretically and empirically; see [3, 9, 17, 20] and references therein.

The simplest type of dispersal is probably random diffusion, i.e., motion governed by random walk. As such, the dynamics of random dispersing species can be described by reaction-diffusion models. Concerning the evolution of random dispersal in a spatially inhomogeneous and temporally constant environment, Hastings [10] considered a reaction-diffusion model for two competing species in the following form:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + u f(u + v, x) && \text{in } (0, \infty) \times D, \\ \frac{\partial v}{\partial t} &= \nu \Delta v + v f(u + v, x) && \text{in } (0, \infty) \times D, \\ \frac{\partial u}{\partial n} &= \frac{\partial v}{\partial n} = 0 && \text{on } (0, \infty) \times \partial D, \end{aligned} \tag{1.1}$$

where functions  $u(t, x), v(t, x)$  are the densities of two species,  $\mu, \nu$  are their random dispersal rates,  $\Delta$  is the Laplace operator that accounts for random motion of species,  $f(\cdot, x)$  is the local reproduction rate of species,  $D$  is an open bounded domain in  $\mathbb{R}^N$  with smooth boundary  $\partial D$ ,  $n$  is the outward unit normal vector on  $\partial D$ , and the zero Neumann boundary condition  $\partial u / \partial n := \nabla u \cdot n = 0$  is prescribed on  $\partial D$  for both species. Hastings' idea is to assume that some mutation occurs and the mutant is identical to the resident species except for their random dispersal rates. He showed that the mutant can invade when rare if and only if it is the slower diffuser. Hence, the selection is against faster random dispersal in a spatially varying and temporally constant environment; see also [6]. On the other hand, for spatially heterogeneous and temporally varying environments, faster random dispersal rates can be selected [14].

Random dispersal is clearly oversimplified for describing the movement of many organisms. Random dispersal is essentially a local behavior, i.e., it describes the movements of organisms between adjacent spatial locations. However, the movements and interactions of some organisms can occur between non-adjacent spatial locations [12, 16, 18]. Nonlocal processes, in continuous space and continuous time settings, can be modeled by integro-differential equations. Concerning the evolution of nonlocal dispersal, Hutson et al. [13] proposed the following integro-differential model for two competing species:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \left[ \frac{1}{(L_u)^N} \int_D k \left( \frac{x-y}{L_u} \right) u(t, y) dy - u(t, x) \right] + u f(u + v, x) && \text{in } (0, \infty) \times \bar{D}, \\ \frac{\partial v}{\partial t} &= \nu \left[ \frac{1}{(L_v)^N} \int_D k \left( \frac{x-y}{L_v} \right) v(t, y) dy - v(t, x) \right] + v f(u + v, x) && \text{in } (0, \infty) \times \bar{D}, \end{aligned} \tag{1.2}$$

where function  $k(\cdot)$  represents the dispersal kernel, and the positive constants  $L_u, L_v$  characterize the dispersal distance (referred as *spreads* in [13]).

For the case when the two spreads are equal, i.e.,  $L_u = L_v$ , it is conjectured that the slow dispersal is always selected; i.e., if  $\mu < \nu$ , then the semi-trivial equilibrium  $(\tilde{u}, 0)$  is the global attractor for any non-trivial, non-negative initial conditions. See [13] for some

results in this direction. For the case when  $\mu = \nu$ , it is also conjectured in [13] that for sufficiently small spreads  $L_u$  and  $L_v$ , the smaller spread is preferred. More precisely, the semi-trivial equilibrium in the presence of the species with the smaller spread is globally asymptotically stable. However, if both spreads  $L_u$  and  $L_v$  are sufficiently large, then the selection of the larger spread is possible.

Given the choices of these local and nonlocal dispersal mechanisms, we wonder whether non-local dispersal mechanisms are preferred over local dispersal strategies. More precisely, in this paper we consider the following mathematical model:

$$\begin{aligned} \frac{\partial u}{\partial t} &= \mu \Delta u + uf(u + v, x) && \text{in } (0, \infty) \times D, \\ \frac{\partial v}{\partial t} &= \nu \left[ \frac{1}{\delta^N} \int_D k \left( \frac{x - y}{\delta} \right) v(t, y) dy - v(t, x) \right] + vf(u + v, x) && \text{in } (0, \infty) \times \bar{D}, \end{aligned} \quad (1.3)$$

where the equation of  $u$  will be complemented with suitable boundary conditions later. For system (1.3), two competing species have the exact same population dynamics but different dispersal strategies: the movement of species with density  $u$  is purely by random walk while the species with density  $v$  adopts a non-local dispersal strategy. The main question is: *what is the dynamics of system (1.3)?*

Under suitable conditions system (1.3) has two semi-trivial equilibria, denoted by  $(u^*, 0)$  and  $(0, v^*)$ , where  $u^*$  and  $v^*$  are some positive functions in  $D$ . Similarly as in Hastings [10] and Hutson et al. [13], in this paper we will focus on the stabilities of both  $(u^*, 0)$  and  $(0, v^*)$ , i.e., whether one species can invade or not when rare. The global dynamics of (1.3) seems to be a very challenging problem and it is currently out of our reach analytically. In order to shed light on the global picture of the dynamics of system (1.3), we shall complement our mathematical analysis with some numerical simulations. The parameter  $\delta$ , which measures the non-local interaction distance, plays an instrumental role in the dynamics of system (1.3). In this paper we will concentrate on the small  $\delta$  case analytically, and some numerical simulations will also be performed so that we can have a better picture of the dynamics of (1.3) for general values of  $\delta$ .

This paper is organized as follows: In Section 2 we first introduce linear nonlocal dispersal equations on a bounded domain with hostile surroundings and on  $\mathbb{R}^N$  with periodic environments. Roughly speaking, hostile surroundings assumes that the species  $v$  has zero density outside the habitat, and hence shares some similarity to Dirichlet boundary condition. The rest of Section 2 is devoted to studying monotonicity and spectrum of linear nonlocal dispersal operators. In Section 3, we investigate the asymptotic dynamics and qualitative properties of equilibria of nonlinear equations with nonlocal dispersal on bounded domain with hostile surroundings and on  $\mathbb{R}^N$  with periodic environments. The materials in these two sections are not only important for applications in later sections but also of independent theoretical interest. For the convenience of readers, in Section 4 we recall some principal eigenvalue theory for the Laplace operator and also results on the dynamics of logistic type scalar parabolic equations in bounded domains with Dirichlet, Neumann and periodic boundary conditions.

Section 5 is devoted to studying two species competition model (1.3), where the species with density  $u$  uses random dispersal strategy and the species with density  $v$  applies non-local dispersal strategy. Note that without loss of generality, we may assume that  $\nu = 1$  in (1.3), for otherwise, we can make a time variable change  $t \mapsto \nu t$ . We consider three

types of boundary conditions for random dispersal (zero Neumann, zero Dirichlet, and periodic boundary conditions) and two types of nonlocal dispersal (hostile surroundings and periodic environment). We will focus on three scenarios:

- (a) Random dispersal with zero Dirichlet boundary condition versus non-local dispersal with hostile surroundings. Non-local dispersal with hostile surroundings assumes that the species has zero density outside the habitat, hence its boundary behavior shares some similarity to Dirichlet boundary condition. For such comparison, We show that  $(u^*, 0)$  is locally unstable and  $(0, v^*)$  is locally stable for small  $\delta$ . Hence, the species with random dispersal can not invade when rare but the species with non-local dispersal can invade when rare. We conjecture that  $(0, v^*)$  is globally stable for small  $\delta$ , i.e., for hostile surroundings, non-local dispersal with small non-local interaction distance can be preferred over random dispersal.
- (b) Random dispersal with zero Neumann boundary condition versus non-local dispersal with hostile surroundings. For this case, we show that for small  $\delta$  and spatially heterogeneous environments both semi-trivial steady states are locally unstable and system (1.3) has at least one positive equilibrium. Hence both species can invade when rare and neither local nor non-local dispersal strategy seem to have advantage. The biological intuition is that the no-flux boundary condition can somehow counterbalance the disadvantage caused by local dispersal. We conjecture that for small  $\delta$  and spatially heterogeneous environments there is a unique positive equilibrium which is globally asymptotically stable among non-trivial non-negative initial conditions.
- (c) Random dispersal with periodic boundary condition versus non-local dispersal with spatially periodic and heterogeneous environments. For this case, we show that  $(u^*, 0)$  is locally unstable and  $(0, v^*)$  is locally stable for small  $\delta$ . Hence for spatially periodic heterogeneous environments, the species with random dispersal can not invade when rare but the species with non-local dispersal can invade when rare. We conjecture that  $(0, v^*)$  is globally stable for any  $\delta > 0$ , i.e., for periodic heterogeneous environments non-local dispersal is always preferred over random dispersal.

In Section 6 we present some numerical results on the global dynamics of system (1.3) for general  $\delta$ . These numerical results not only support our conjectures but also point to some new research directions, e.g., the dynamics of system (1.3) with  $a(x)$  sign changing can be quite different from the case when  $a(x)$  is strictly positive in  $\bar{D}$ . Finally in Section 7 we discuss our analytical and numerical results and raise some open problems.

## 2 Linear Nonlocal Dispersal Equations: Monotonicity and Spectrum

In this section, we first introduce two types of linear nonlocal dispersal operators and corresponding function spaces. We then study the monotonicity of solutions to linear nonlocal dispersal equations. The rest of this section is devoted to studying the spectrum in particular, principal eigenvalue, of linear nonlocal dispersal equations.

## 2.1 Linear nonlocal dispersal equations

In this subsection, we introduce linear nonlocal dispersal evolution equations on a bounded domain  $D \subset \mathbb{R}^N$  and on  $\mathbb{R}^N$ .

### 2.1.1 Linear nonlocal dispersal equations in bounded domains

Let  $k(\cdot) \in C^\infty(\mathbb{R}^N)$  be defined by

$$k(x) = \begin{cases} C \exp\left(\frac{1}{|x|^2-1}\right) & \text{for } |x| < 1, \\ 0 & \text{for } |x| \geq 1, \end{cases} \quad (2.1)$$

where  $C > 0$  is such that  $\int_{\mathbb{R}^N} k(x) dx = 1$ . For given  $\delta > 0$ , let

$$k_\delta(x) = \frac{1}{\delta^N} k(x/\delta). \quad (2.2)$$

Let  $D \subset \mathbb{R}^N$  be a bounded domain. Consider

$$\frac{\partial v(t, x)}{\partial t} = \nu \left[ \int_D k_\delta(x-y)v(t, y) dy - v(t, x) \right] + l(x)v(t, x), \quad x \in \bar{D}, \quad (2.3)$$

where  $l(\cdot) \in C(\bar{D})$ ,  $\nu$  is the dispersal rate, and  $\delta$  is the local interaction distance. One key assumption in (2.3) is that the density of the species is set to zero outside  $D$ , i.e., the habitat outside  $D$  is so hostile that all individuals which land there immediately die [13], and (2.3) is referred as linear nonlocal evolution equation with *hostile surroundings*. Without loss of generality, we may assume that  $\nu = 1$  in (2.3) and we assume so from now on unless specified otherwise.

Let

$$Y_{NP} = C(\bar{D}) \quad (2.4)$$

with norm  $\|v\| = \max_{x \in \bar{D}} |v(x)|$ . Denote  $\mathcal{L}(Y_{NP}, Y_{NP})$  as the space of the bounded linear operators from  $Y_{NP}$  to  $Y_{NP}$ . Given  $v_1, v_2 \in Y_{NP}$ , define  $v_1 \geq v_2$  if  $v_1(x) \geq v_2(x)$  for each  $x \in \bar{D}$ ;  $v_1 > v_2$  if  $v_1 \geq v_2$  and  $v_1 \neq v_2$ ;  $v_1 \gg v_2$  if  $v_1(x) > v_2(x)$ ,  $x \in \bar{D}$ . Put  $Y_{NP}^+ = \{v \in C(\bar{D}) | v \geq 0\}$ . Note that the interior of  $Y_{NP}^+$ , denoted by  $Y_{NP}^{++}$ , is not empty and  $Y_{NP}^{++} = \{v \in Y_{NP}^+ | v \gg 0\}$ .

Define  $I_{NP}, K_{\delta, NP}, L_{NP} : Y_{NP} \rightarrow Y_{NP}$  by

$$\begin{aligned} (I_{NP}v)(x) &= v(x), \quad x \in \bar{D}, \\ (K_{\delta, NP}v)(x) &= \int_D k_\delta(x-y)v(y) dy, \quad x \in \bar{D}, \\ (L_{NP}v)(x) &= l(x)v(x), \quad x \in \bar{D}. \end{aligned} \quad (2.5)$$

Then  $I_{NP}, K_{\delta, NP}, L_{NP} \in \mathcal{L}(Y_{NP}, Y_{NP})$ . Hence  $K_{\delta, NP}, -I_{NP} + L_{NP}$ , and  $K_{\delta, NP} - I_{NP} + L_{NP}$  generate uniformly continuous semigroups  $e^{K_{\delta, NP}t}$ ,  $e^{(-I_{NP} + L_{NP})t}$ , and  $e^{(K_{\delta, NP} - I_{NP} + L_{NP})t}$  of bounded linear operators on  $Y_{NP}$ , respectively (see [21] for reference).

Observe that for any  $v_0 \in Y_{NP}$ ,

$$(e^{(-I_{NP} + L_{NP})t}v_0)(x) = e^{(-1+l(x))t}v_0(x).$$

Hence if  $-1 + l(x) \leq 0$  for  $x \in \bar{D}$ , then  $e^{(-I_{NP} + L_{NP})t}$  is a uniformly continuous semigroup of contractions on  $Y_{NP}$ .

Observe also that (2.3) (with  $\nu = 1$ ) can be written as an ordinary differential equation on the Banach space  $Y_{NP}$ ,

$$\frac{dv}{dt} = K_{\delta, NP}v - v + L_{NP}v. \quad (2.6)$$

For any  $v_0 \in Y_{NP}$ ,  $v(t; v_0) := e^{(K_{\delta, NP} - I_{NP} + L_{NP})t}v_0$  is the unique solution of (2.6) with  $v(0; v_0) = v_0$ . Moreover we have

$$v(t; v_0) = e^{K_{\delta, NP}t}v_0 + \int_0^t e^{K_{\delta, NP}(t-s)}(-I_{NP} + L_{NP})v(s; v_0)ds \quad (2.7)$$

and

$$v(t; v_0) = e^{(-I_{NP} + L_{NP})t}v_0 + \int_0^t e^{(-I_{NP} + L_{NP})(t-s)}K_{\delta, NP}v(s; v_0)ds. \quad (2.8)$$

### 2.1.2 Linear nonlocal dispersal equations in $\mathbb{R}^N$

Let  $p_1, p_2, \dots, p_N$  be given positive constants. Consider

$$\frac{\partial v(t, x)}{\partial t} = \nu \left[ \int_{\mathbb{R}^N} k_{\delta}(x - y)v(t, y)dy - v(t, x) \right] + l_p(x)v(t, x), \quad x \in \mathbb{R}^N, \quad (2.9)$$

where  $l_p(\cdot) \in C(\mathbb{R}^N)$  and  $l_p(x_1, \dots, x_{n-1}, x_n + p_n, x_{n+1}, \dots, x_N) = l_p(x_1, \dots, x_{n-1}, x_n, x_{n+1}, \dots, x_N)$  ( $n = 1, 2, \dots, N$ ). (2.9) is referred as linear nonlocal evolution equation with *periodic environment* as the environmentally dependent local growth rate  $l_p(x)$  and the density  $v(x, t)$  are assumed to be periodic in space. The hostile surroundings clearly affect the behavior of the species density near the boundary, and one of the simplest ways to exclude such effects is to adopt some environment periodicity; See subsection 2.3.2 of [13] for more discussions. Without loss of generality, we may also assume that  $\nu = 1$  in (2.9) and we assume so from now on unless specified otherwise.

Let

$$\begin{aligned} Y_P &= \{v \in C(\mathbb{R}^N) \mid v(x_1, \dots, x_{n-1}, x_n + p_n, x_{n+1}, \dots, x_N) \\ &= v(x_1, \dots, x_{n-1}, x_n, x_{n+1}, \dots, x_N), n = 1, 2, \dots, N\} \end{aligned} \quad (2.10)$$

with norm  $\|v\| = \sup_{x \in \mathbb{R}^N} |v(x)|$ . Similarly, given  $v_1, v_2 \in Y_P$ , we define  $v_1 \geq v_2$  if  $v_1(x) \geq v_2(x)$  for each  $x \in \mathbb{R}^N$ ;  $v_1 > v_2$  if  $v_1 \geq v_2$  and  $v_1 \neq v_2$ ;  $v_1 \gg v_2$  if  $v_1(x) > v_2(x)$ ,  $x \in \mathbb{R}^N$ . Put  $Y_P^+ = \{v \in C(\mathbb{R}^N) \mid v \geq 0\}$ . Note that the interior of  $Y_P^+$ , denoted by  $Y_P^{++}$ , is not empty and  $Y_P^{++} = \{v \in Y_P^+ \mid v \gg 0\}$ .

Define  $I_P, K_{\delta, P}, L_P : Y_P \rightarrow Y_P$  by

$$\begin{aligned} (I_P v)(x) &= v(x), \quad x \in \mathbb{R}^N, \\ (K_{\delta, P} v)(x) &= \int_{\mathbb{R}^N} k_{\delta}(x - y)v(y)dy, \quad x \in \mathbb{R}^N, \\ (L_P v)(x) &= l_p(x)v(x), \quad x \in \mathbb{R}^N. \end{aligned} \quad (2.11)$$

Then  $I_P, K_{\delta,P}, L_P \in \mathcal{L}(Y_P, Y_P)$ . Hence  $K_{\delta,P}, -I_P + L_P$ , and  $K_{\delta,P} - I_P + L_P$  generate uniformly continuous semigroups  $e^{K_{\delta,P}t}, e^{(-I_P+L_P)t}$ , and  $e^{(K_{\delta,P}-I_P+L_P)t}$  of bounded linear operators on  $Y_P$ , respectively (see [21] for reference).

Similarly, for any  $v_0 \in Y_P$ ,

$$(e^{(-I_P+L_P)t}v_0)(x) = e^{(-1+l_P(x))t}v_0(x).$$

Hence if  $-1 + l_P(x) \leq 0$  for  $x \in \mathbb{R}^N$ , then  $e^{(-I_P+L_P)t}$  is a uniformly continuous semigroup of contractions on  $Y_P$ . Also (2.9) (with  $\nu = 1$ ) can be written as an ordinary differential equation on the Banach space  $Y_P$ ,

$$\frac{dv}{dt} = K_{\delta,P}v - v + L_Pv. \quad (2.12)$$

For any  $v_0 \in Y_P$ ,  $v(t; v_0) := e^{(K_{\delta,P}-I_P+L_P)t}v_0$  is the unique solution of (2.12) with  $v(0; v_0) = v_0$ . Moreover we have

$$v(t; v_0) = e^{K_{\delta,P}t}v_0 + \int_0^t e^{K_{\delta,P}(t-s)}(-I_P + L_P)v(s; v_0)ds \quad (2.13)$$

and

$$v(t; v_0) = e^{(-I_P+L_P)t}v_0 + \int_0^t e^{(-I_P+L_P)(t-s)}K_{\delta,P}v(s; v_0)ds. \quad (2.14)$$

## 2.2 Monotonicity for solutions with continuous initial data

We now study the monotonicity of the solutions of (2.3) and (2.9) (with  $\nu = 1$ ).

A continuous function  $v(t, x)$  on  $[0, \infty) \times \bar{D}$  is called a *super-solution* (*sub-solution*) of (2.3) if  $\frac{\partial v}{\partial t}(t, x)$  exists for  $t \geq 0$  and  $x \in \bar{D}$  and

$$\frac{\partial v}{\partial t}(t, x) \geq (\leq) \int_D k_\delta(x - y)v(t, y)dy - v(t, x) + l(x)v(t, x)$$

for  $t \geq 0$  and  $x \in \bar{D}$ . Super-solution and sub-solution of (2.9) can be similarly defined by replacing  $\bar{D}$  by  $\mathbb{R}^N$ .

In the following,  $Y, I, K_\delta$ , and  $L$  denote  $Y_{NP}, I_{NP}, K_{\delta,NP}$ , and  $L_{NP}$ , or  $Y_P, I_P, K_{\delta,P}$ , and  $L_P$ , respectively, depending on whether (2.3) or (2.9) is under consideration.

For given  $v_0 \in Y$ , let

$$\Psi(t)v_0 = e^{(K_\delta-I+L)t}v_0.$$

**Theorem 2.1** (Monotonicity). (1) *Assume that  $v(t, x; v_1)$  and  $v(t, x; v_2)$  are sub-solution and super-solution of (2.3) ((2.9)) on  $[0, \infty)$  with  $v(0, x; v_1) = v_1(x)$  and  $v(0, x; v_2) = v_2(x)$ , respectively ( $v_1, v_2 \in Y$ ). If  $v_1 \leq v_2$ , then  $v(t, \cdot; v_1) \leq v(t, \cdot; v_2)$  for  $t > 0$ .*

(2) *For any  $v_0 \in Y$  with  $v_0 \geq 0$ ,  $\Psi(t)v_0 \geq 0$  for  $t > 0$ .*

(3) *For any  $v_0 \in Y$  with  $v_0 > 0$ ,  $\Psi(t)v_0 \gg 0$  for all  $t > 0$ .*



*Proof.* (1) follows from the arguments of [15, Proposition 2.4]; (2) follows from (1) with  $v(t, x; v_1) \equiv 0$  and  $v(t, x; v_2) = \Psi(t)v_0$ .

(3) We prove the case that  $Y = Y_{NP}$ . The case  $Y = Y_P$  can be proved similarly.

Assume  $v_0 > 0$ . We first claim that  $e^{K_{\delta, NP}t}v_0 \gg 0$  for  $t > 0$ . In fact, note that

$$e^{K_{\delta, NP}t}v_0 = v_0 + tK_{\delta, NP}v_0 + \frac{t^2(K_{\delta, NP})^2v_0}{2!} + \cdots + \frac{t^n(K_{\delta, NP})^nv_0}{n!} + \cdots.$$

Let  $x_0 \in \bar{D}$  be such that  $v_0(x_0) > 0$ . Then by  $v_0 \in C(\bar{D})$ , there is  $r > 0$  such that  $v_0(x) > 0$  for  $x \in B(x_0, r) \cap \bar{D}$  ( $B(x_0, r) = \{x \in \mathbb{R}^N \mid \|x - x_0\| < r\}$ ). This implies that

$$(K_{\delta, NP}v_0)(x) = \int_D k_{\delta}(x-y)v_0(y)dy > 0 \quad \text{for } x \in B(x_0, r+\delta) \cap \bar{D}.$$

Then

$$((K_{\delta, NP})^n v_0)(x) > 0 \quad \text{for } x \in B(x_0, r+n\delta) \cap \bar{D}.$$

It then follows that  $e^{K_{\delta, NP}t}v_0 \gg 0$  for  $t > 0$ . Now let  $m > 1 - \min_{x \in \bar{D}} l(x)$ . Note that

$$v(t; v_0) = e^{(K_{\delta, NP} - I + L + mI - mI)t}v_0 = e^{-mIt}e^{(K_{\delta, NP} - I + L + mI)t}v_0$$

and  $(e^{-mIt}v)(x) = e^{-mt}v(x)$  for any  $v \in Y_{NP}$ . Note also that

$$e^{(K_{\delta, NP} - I + L + mI)t}v_0 = e^{K_{\delta, NP}t}v_0 + \int_0^t e^{K_{\delta, NP}(t-s)}(-I + L + mI)v(s; v_0)ds$$

for  $t > 0$ . Hence  $v(t; v_0) \gg 0$  for  $t > 0$ .  $\square$

### 2.3 Monotonicity for solutions with bounded measurable initial data

In this subsection, we show that (2.3) and (2.9) (with  $\nu = 1$ ) also generate uniformly continuous monotone semigroups of bounded operators on  $\tilde{Y}_{NP}$  and  $\tilde{Y}_P$ , where

$$\tilde{Y}_{NP} = \{v : \bar{D} \rightarrow \mathbb{R} \mid v \text{ is bounded Lebesgue measurable in } D\} \quad (2.15)$$

with norm  $\|v\| = \sup_{x \in \bar{D}} |v(x)|$  and

$$\begin{aligned} \tilde{Y}_P &= \{v : \mathbb{R}^N \rightarrow \mathbb{R} \mid v \text{ is bounded Lebesgue measurable in } \mathbb{R}^N, \\ &v(x_1, \dots, x_{n-1}, x_n + p_n, x_{n+1}, \dots, x_N) = v(x_1, \dots, x_n, \dots, x_N), n = 1, 2, \dots, N\} \end{aligned} \quad (2.16)$$

with norm  $\|v\| = \sup_{x \in \mathbb{R}^N} |v(x)|$ .

Denote  $\mathcal{L}(\tilde{Y}_{NP}, \tilde{Y}_{NP})$  ( $\mathcal{L}(\tilde{Y}_P, \tilde{Y}_P)$ ) as the space of the bounded linear operators from  $\tilde{Y}_{NP}$  to  $\tilde{Y}_{NP}$  ( $\tilde{Y}_P$  to  $\tilde{Y}_P$ ). For given  $v_1, v_2 \in \tilde{Y}_{NP}$  ( $\tilde{Y}_P$ ), define  $v_1 \geq v_2$  if  $v_1(x) \geq v_2(x)$  for  $x \in \bar{D}$  ( $x \in \mathbb{R}^N$ ),  $v_1 \gg v_2$  if there exists  $\epsilon > 0$  such that  $v_1(x) \geq v_2(x) + \epsilon$ ,  $\forall x \in \bar{D}$  ( $x \in \mathbb{R}^N$ ). Let  $\tilde{Y}_{NP}^+ = \{v \in \tilde{Y}_{NP} \mid v \geq 0\}$  and  $\tilde{Y}_P^+ = \{v \in \tilde{Y}_P \mid v \geq 0\}$ . Then the interior of  $\tilde{Y}_{NP}^+$  ( $\tilde{Y}_P^+$ ), denoted by  $\tilde{Y}_{NP}^{++}$  ( $\tilde{Y}_P^{++}$ ), is not empty, and  $\tilde{Y}_{NP}^{++} = \{v \in \tilde{Y}_{NP}^+ \mid v \gg 0\}$  ( $\tilde{Y}_P^{++} = \{v \in \tilde{Y}_P^+ \mid v \gg 0\}$ ).

Define  $\tilde{I}_{NP}, \tilde{K}_{\delta,NP}, \tilde{L}_{NP} : \tilde{Y}_{NP} \rightarrow \tilde{Y}_{NP}$  by

$$\begin{aligned} (\tilde{I}_{NP}v)(x) &= v(x), \quad x \in \bar{D}, \\ (\tilde{K}_{\delta,NP}v)(x) &= \int_D k_\delta(x-y)v(y)dy, \quad x \in \bar{D}, \\ (\tilde{L}_{NP}v)(x) &= l(x)v(x), \quad x \in \bar{D} \end{aligned} \quad (2.17)$$

for  $v \in \tilde{Y}_{NP}$ .

Define  $\tilde{I}_P, \tilde{K}_{\delta,P}, \tilde{L}_P : \tilde{Y}_P \rightarrow \tilde{Y}_P$  by

$$\begin{aligned} (\tilde{I}_Pv)(x) &= v(x), \quad x \in \mathbb{R}^N, \\ (\tilde{K}_{\delta,P}v)(x) &= \int_{\mathbb{R}^N} k_\delta(x-y)v(y)dy, \quad x \in \mathbb{R}^N, \\ (\tilde{L}_Pv)(x) &= l(x)v(x), \quad x \in \mathbb{R}^N \end{aligned} \quad (2.18)$$

for  $v \in \tilde{Y}_P$ .

Let  $\tilde{Y}, \tilde{I}, \tilde{K}_\delta,$  and  $\tilde{L}$  denote  $\tilde{Y}_{NP}, \tilde{I}_{NP}, \tilde{K}_{\delta,NP},$  and  $\tilde{L}_{NP},$  or  $\tilde{Y}_P, \tilde{I}_P, \tilde{K}_{\delta,P},$  and  $\tilde{L}_P,$  respectively, depending on whether (2.3) or (2.9) is under consideration. Clearly,  $\tilde{K}_\delta, \tilde{I}, \tilde{L} \in \mathcal{L}(\tilde{Y}, \tilde{Y})$ . Hence  $e^{\tilde{K}_\delta t}, e^{(-\tilde{I}+\tilde{L})t},$  and  $e^{(\tilde{K}_\delta-\tilde{I}+\tilde{L})t}$  are uniformly continuous semigroup of bounded linear operators on  $\tilde{Y}$ . Let  $\tilde{\Psi}(t)v_0 = e^{(\tilde{K}_\delta-\tilde{I}+\tilde{L})t}v_0$  for  $v_0 \in \tilde{Y}$ . Similar to Theorem 2.1, we have

**Theorem 2.2** (Monotonicity). (1) For any  $v_0 \in \tilde{Y}$  with  $v_0 \geq 0,$   $\tilde{\Psi}(t)v_0 \geq 0$  for  $t > 0.$

(2) For any  $v_0 \in \tilde{Y}$  with  $v_0 \gg 0,$   $\tilde{\Psi}(t)v_0 \gg 0$  for all  $t > 0.$

*Proof.* We prove the case of (2.3). The case of (2.9) can be proved similarly.

(1) We only need to prove  $\tilde{\Psi}(t)v_0 \geq 0$  for  $0 < t \ll 1.$  Observe that for given  $0 < \tau \ll 1,$   $v(t; v_0) = \tilde{\Psi}(t)v_0$  as a function from  $[0, \tau]$  to  $\tilde{Y}_{NP}$  is a fixed point of the equation:

$$v(t; v_0) = e^{(-\tilde{I}_{NP}+\tilde{L}_{NP})t}v_0 + \int_0^t e^{(-\tilde{I}_{NP}+\tilde{L}_{NP})(t-s)}\tilde{K}_{\delta,NP}v(s; v_0)ds.$$

To be more precise, for given  $v_0 \in \tilde{Y}_{NP}$  with  $v_0 \geq 0$  and  $\rho > 0,$  let

$$\mathcal{Y} = \{v(\cdot) \in C([0, \tau], \tilde{Y}_{NP}) | v(0) = v_0, \|v(t)\|_{\tilde{Y}_{NP}} \leq \rho \text{ for } t \in [0, \tau]\}$$

equipped with uniform convergence norm, i.e.,  $\|v(\cdot)\|_{\mathcal{Y}} = \sup_{t \in [0, \tau]} \|v(t)\|_{\tilde{Y}}$ . For given  $v(\cdot) \in \mathcal{Y},$  let

$$F(v)(t) = e^{(-\tilde{I}_{NP}+\tilde{L}_{NP})t}v_0 + \int_0^t e^{(-\tilde{I}_{NP}+\tilde{L}_{NP})(t-s)}\tilde{K}_{\delta,NP}v(s)ds.$$

Then  $F(v)(0) = v_0.$  The map  $0 \leq t \mapsto F(v)(t) \in \tilde{Y}_{NP}$  is continuous. When  $0 < \tau \ll 1$  and  $\rho \gg 1,$   $F(v) \in \mathcal{Y}.$  Moreover, there is  $0 < \kappa < 1$  such that for any  $v_1(\cdot), v_2(\cdot) \in \mathcal{Y},$

$$\|F(v_1)(t) - F(v_2)(t)\|_{\tilde{Y}_{NP}} = \left\| \int_0^t e^{(-\tilde{I}_{NP}+\tilde{L}_{NP})(t-s)}\tilde{K}_{\delta,NP}(v_1(s) - v_2(s))ds \right\| \leq \kappa \|v_1(\cdot) - v_2(\cdot)\|_{\mathcal{Y}}.$$

Therefore, there is a unique point  $\tilde{v}(\cdot; v_0) \in \mathcal{Y}$  such that  $\tilde{v}(t; v_0) = F(\tilde{v}(\cdot, v_0))(t)$  for  $t \in [0, \tau]$ . It then follows that  $\tilde{\Psi}(t)v_0 = \tilde{v}(t; v_0)$  for  $t \in [0, \tau]$ .

Note that  $(e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})t}v_0)(x) = e^{(-1+l(x))t}v_0(x) \geq 0$  for any  $x \in \bar{D}$ . Hence  $e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})t}v_0 \geq 0$ .

For given  $v(t) \in \tilde{Y}_{NP}^+$  for  $t \in [0, \tau]$ ,  $\tilde{K}_{\delta, NP}v(s) \geq 0$  and hence

$$\int_0^t e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})(t-s)} \tilde{K}_{\delta, NP}v(s) ds \geq 0.$$

It then follows that  $v(t; v_0) \geq 0$  for  $0 < t \ll 1$  and hence  $v(t; v_0) \geq 0$  for all  $t > 0$ .

(2) Observe that

$$(e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})t}v)(x) = e^{(-1+l(x))t}v(x).$$

It then follows that

$$\tilde{\Psi}(t)v = e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})t}v + \int_0^t K_{\delta, NP}e^{(-\tilde{I}_{NP} + \tilde{L}_{NP})(t-s)} \tilde{\Psi}(s)v ds \gg 0.$$

□

## 2.4 Spectrum

We investigate the spectrum of  $K_\delta - I + L$ . Denote  $\sigma(K_\delta - I + L)$  as the spectrum of  $K_\delta - I + L$ .  $\lambda \in \sigma(K_\delta - I + L)$  is called the *principal eigenvalue* of  $K_\delta - I + L$  if it is a real isolated eigenvalue with a nonnegative eigenfunction and for any  $\mu \in \sigma(K_\delta - I + L)$ ,  $\text{Re}(\mu) < \lambda$ . If the principal eigenvalue of  $K_\delta - I + L$  exists, we denote it by  $\lambda(\delta, l)$ .

Let  $l_{\max} = \max_{x \in \bar{D}} l(x)$  in the case of (2.3) and  $l_{\max} = \max_{x \in \mathbb{R}^N} l_p(x)$  in the case of (2.9). Note that for  $\alpha > -1 + l_{\max}$ ,  $I - L + \alpha I$  is invertible. For given  $\alpha > -1 + l_{\max}$ , define

$$U_\alpha = K_\delta(I - L + \alpha I)^{-1}.$$

Then  $U_\alpha$  is a compact operator on  $Y$ . Denote  $r(\alpha)$  as the spectrum radius of  $U_\alpha$ . We have

**Theorem 2.3.** (1)  $\alpha > -1 + l_{\max}$  is an eigenvalue of  $K_\delta - I + L$  iff 1 is an eigenvalue of  $U_\alpha$ .

(2) Each  $\lambda \in \sigma(K_\delta - I + L)$  with  $\text{Re}(\lambda) > -1 + l_{\max}$  is an isolated eigenvalue with finite multiplicity.

(3) If there is  $\alpha > -1 + l_{\max}$  such that  $r(U_\alpha) > 1$ , then there is  $\alpha_0 > -1 + l_{\max}$  such that  $r(U_{\alpha_0}) = 1$  and  $\lambda = \alpha_0$  is an isolated principal eigenvalue of  $K_\delta - I + L$  of finite algebraic multiplicity. Moreover, for any  $\mu \in \sigma(K_\delta - I + L)$ ,  $\text{Re}(\mu) < \alpha_0$ .

*Proof.* (1), (2) follow from [1, Proposition 2.1]. (3) follows from [1, Theorem 2.2]. □

**Theorem 2.4.** (1) If  $\lambda_1$  and  $\lambda_2$  are two real eigenvalues of  $K_\delta - I + L$  with positive eigenfunctions, then  $\lambda_1 = \lambda_2$ .

(2) If  $\lambda$  is an isolated real eigenvalue of  $K_\delta - I + L$  with a positive eigenfunction  $\psi(\cdot)$ , then  $\lambda$  is simple and  $\psi \in Y^{++}$ . Moreover,  $\lambda \leq l_{\max}$  and  $\lambda < l_{\max}$  if  $\psi(\cdot) \not\equiv \text{const}$ .

- (3) If  $\lambda$  is a real eigenvalue of  $K_\delta - I + L$  with a positive eigenfunction  $\psi(\cdot)$ , then  $\lambda > -1 + l_{\max}$ .

*Proof.* We prove the case of (2.3). The case of (2.9) can be proved similarly.

(1) Without loss of generality, assume that  $\lambda_1 \leq \lambda_2$ . Let  $\psi_1$  and  $\psi_2$  be positive eigenfunctions associated to  $\lambda_1$  and  $\lambda_2$ , respectively. Note that  $\Psi(t)\psi_i = e^{\lambda_i t}\psi_i$  for  $i = 1, 2$ . Then by Theorem 2.1,  $\psi_i \gg 0$  for  $i = 1, 2$ . Therefore,  $c\psi_1 \gg \psi_2$  for sufficiently large  $c$  and there is  $c_0 > 0$  such that  $c_0\psi_1 \geq \psi_2$  and there is  $x_0 \in \bar{D}$  such that  $c_0\psi_1(x_0) = \psi_2(x_0)$ . Let  $v = c_0\psi_1 - \psi_2$ . Then  $v$  satisfies

$$\begin{aligned} K_{\delta, NP}v - v + Lv &= \lambda_1 c_0 \psi_1 - \lambda_2 \psi_2 \\ &= \lambda_1 v + \lambda_1 \psi_2 - \lambda_2 \psi_2 \\ &\leq \lambda_1 v. \end{aligned}$$

By Theorem 2.1 again, either  $v \geq e^{(K_{\delta, NP} - I + L - \lambda_1 I)t}v \gg 0$  or  $v = 0$ . Since  $v(x_0) = 0$ , we must have  $v = 0$ , i.e.  $v_2 = c_0 v_1$ . This implies that  $\lambda_1 = \lambda_2$ .

(2) First note that  $\Psi(t)\psi = e^{\lambda t}\psi$ . By the strong monotonicity of  $\Psi(t)$ , we must have  $\psi \in L^{++}$ . Now assume that  $\psi_1$  and  $\psi_2$  are two eigenfunctions associated to  $\lambda$  and  $\psi_2 \in Y_{NP}^{++}$ . Then for  $0 < \epsilon \ll 1$ ,  $\psi_2 - \epsilon\psi_1 \in Y^{++}$ . Let  $\epsilon_0 > 0$  be such that  $\psi_2 - \epsilon\psi_1 \in Y_{NP}^{++}$  for  $0 < \epsilon < \epsilon_0$  and  $\psi_2 - \epsilon_0\psi_1 \notin Y_{NP}^{++}$ . Then  $\psi_2 - \epsilon_0\psi_1 \in Y_{NP}^+$ . If  $\psi_2 - \epsilon_0\psi_1 \neq 0$ , by the above arguments, we must have  $\psi_2 - \epsilon_0\psi_1 \in Y_{NP}^{++}$ , a contradiction. Hence  $\psi_2 = \epsilon_0\psi_1$ . Therefore,  $\lambda$  is simple.

Let  $x_0 \in \bar{D}$  be such that  $\psi(x_0) = \max_{x \in \bar{D}} \psi(x)$ . Note that

$$\int_D k_\delta(x_0 - y)\psi(y)dy - \psi(x_0) + l(x_0)\psi(x_0) = \lambda\psi(x_0)$$

and

$$\int_D k_\delta(x_0 - y)\psi(y)dy \leq \int_D k_\delta(x_0 - y)\psi(x_0)dy = \psi(x_0).$$

It then follows that  $\lambda \leq l(x_0) \leq l_{\max}$ .

If  $\psi(\cdot) \not\equiv \text{const}$ , then there is  $x_0 \in \bar{D}$  and  $r > 0$  such that  $\psi(x) \not\equiv \psi(x_0) = \max_{x \in \bar{D}} \psi(x)$  for  $x \in B(x_0, r) \cap \bar{D}$ . This implies that

$$\int_D k_\delta(x_0 - y)\psi(y)dy < \int_D k_\delta(x_0 - y)\psi(x_0)dy \leq \psi(x_0).$$

Hence  $\lambda < l(x_0) \leq l_{\max}$ .

- (3) Note that  $\psi(x) > 0$  for any  $x \in \bar{D}$ . Let  $x_0 \in \bar{D}$  be such that  $l(x_0) = l_{\max}$ . Then

$$\int_D k_\delta(x_0 - y)\psi(y)dy - \psi(x_0) + l(x_0)\psi(x_0) = \lambda\psi(x_0).$$

Since  $\int_D k_\delta(x_0 - y)\psi(y)dy > 0$ , we have

$$\lambda\psi(x_0) > -\psi(x_0) + l(x_0)\psi(x_0).$$

Hence  $\lambda > -1 + l_{\max}$ . □

**Theorem 2.5.** (1) *If  $\lambda$  is a real eigenvalue of  $K_\delta - I + L$  with a positive real eigenfunction, then  $\lambda$  is a simple isolated eigenvalue and for any  $\mu \in \sigma(K_\delta - I + L)$ ,  $\operatorname{Re}(\mu) < \lambda$ .*

(2) *If  $K_\delta - I + L$  has a principal eigenvalue  $\lambda(\delta, l)$ , then*

$$\lambda(\delta, l) = \lim_{t \rightarrow \infty} \frac{\ln \|\Psi(t)v_0\|}{t}$$

for  $v_0(x) \equiv 1$ .

(3) *If  $l_1(x) \leq l_2(x)$  and  $\lambda_1$  and  $\lambda_2$  are real eigenvalues of  $K_\delta - I + L_1$  and  $K_\delta - I + L_2$  with positive eigenfunctions  $\psi_1, \psi_2$ , respectively, where  $L_i = L$  with  $l(x)$  being replaced by  $l_i(x)$  ( $i = 1, 2$ ), then  $\lambda_1 \leq \lambda_2$ .*

*Proof.* (1) First by Theorem 2.4 (3),  $\lambda > -1 + l_{\max}$ . Then by Theorem 2.3 (2) and Theorem 2.4 (2),  $\lambda$  is an isolated simple eigenvalue. By Theorem 2.3 (1), (3), and Theorem 2.4 (1), for any  $\mu \in \sigma(K_\delta - I + l)$ ,  $\operatorname{Re}(\mu) < \lambda$ . (1) is thus proved.

(2) Let  $\phi \in Y^{++}$  be an eigenfunction of  $K_\delta - I + l$  associated to  $\lambda(\delta, l)$  and  $Y_1 = \operatorname{span}\{\phi\}$ . Then there is a subspace  $Y_2 \subset Y$  such that  $Y = Y_1 \oplus Y_2$ . Note that for any  $\mu \in \sigma((K_\delta - I + L)|_{Y_2})$ ,  $\operatorname{Re}(\mu) < \lambda$ . Hence for any  $\tilde{v}_0 \in Y^{++}$  with  $\tilde{v}_0 = v_{01} + v_{02}$ ,  $0 \neq v_{01} \in Y_1$  and  $v_{02} \in Y_2$ , there holds

$$\lim_{t \rightarrow \infty} \frac{\ln \|\Psi(t)\tilde{v}_0\|}{t} = \lim_{t \rightarrow \infty} \frac{\ln \|\Psi(t)(v_{01} + v_{02})\|}{t} = \lim_{t \rightarrow \infty} \frac{\ln \|\Psi(t)v_{01}\|}{t} = \lambda(\delta, l).$$

For any  $\tilde{v}_0 \in Y^{++}$ , there is  $\kappa > 0$  such that  $\tilde{v}_0 \leq \kappa v_0$ , where  $v_0 \equiv 1$ . It then follows that

$$\lim_{t \rightarrow \infty} \frac{\ln \|\Psi(t)v_0\|}{t} = \lambda(\delta, l).$$

(3) Let  $\Psi_i(t) = e^{(K_\delta - I + L_i)t}$  for  $i = 1, 2$ . Let  $v_0 \equiv 1$ . Then  $0 < \Psi_1(t)v_0 \leq \Psi_2(t)v_0$  for  $t \geq 0$ . Hence

$$\|\Psi_1(t)v_0\| \leq \|\Psi_2(t)v_0\| \quad \text{for } t > 0.$$

By (2), we obtain that

$$\lambda_1 = \lim_{t \rightarrow \infty} \frac{1}{t} \ln \|\Psi_1(t)v_0\| \leq \lim_{t \rightarrow \infty} \frac{1}{t} \ln \|\Psi_2(t)v_0\| = \lambda_2.$$

□

**Theorem 2.6.** (1) *There is  $\delta_0 > 0$  such that for any  $0 < \delta < \delta_0$ ,  $K_\delta - I + L$  has a simple principal eigenvalue  $-1 + l_{\max} < \lambda(\delta, l) \leq l_{\max}$ .*

(2)  *$\lambda(\delta, l) \rightarrow l_{\max}$  as  $\delta \rightarrow 0$ . In particular, if  $l_{\max} > 0$ , then  $\lambda(\delta, l) > 0$  for  $0 < \delta \ll 1$ .*

*Proof.* (1) We prove the non-periodic case. The periodic case can be proved similarly. First we prove the existence of principal eigenvalue  $\lambda(\delta, l)$  for  $0 < \delta \ll 1$ . Observe that

$$U_\alpha v = K_{\delta, NP}(I - L + \alpha I)^{-1}v = \int_D \frac{k_\delta(x-y)v(y)}{1-l(y)+\alpha} dy.$$

Assume that  $x_0 \in \bar{D}$  is such that  $l(x_0) = l_{\max}$ . Then for any  $0 < \epsilon < 1$ , there are  $\sigma_0^* > 0$  and  $x_0^* \in \text{Int}D$  such that  $B(\sigma_0^*, x_0^*) \subset \bar{D}$  and

$$l(x_0) - l(x) < \epsilon/2 \quad \text{for } x \in B(\sigma_0^*, x_0^*).$$

Let  $0 < \sigma_0 < \sigma_0^*$ . For any  $0 < \delta < \sigma_0^* - \sigma_0$  and  $x \in B(\sigma_0^*, x_0^*) \setminus B(\sigma_0, x_0^*)$ , let

$$E(\delta, x) = B(\delta, x) \cap B(\|x - x_0^*\|, x_0^*).$$

Then it is not difficult to see that there is  $\gamma_0^*$  such that

$$\inf_{0 < \delta < \delta_0, x \in B(\sigma_0^*, x_0^*) \setminus B(\sigma_0, x_0^*)} \int_{E(\delta, x)} k_\delta(y - x) dy \geq \gamma_0^*.$$

Let

$$\psi(r) = \begin{cases} \cos(\frac{\pi r}{2\sigma_0^*}) & \text{for } |r| \leq \sigma_0^*, \\ 0 & \text{for } r \geq \sigma_0^*. \end{cases}$$

and

$$v_0(x) = \psi(\|x - x_0^*\|) \quad \text{for } x \in D.$$

Then  $\text{supp}(v_0) \subset B(\sigma_0^*, x_0^*)$  and for any  $\epsilon < \eta < 1$

$$\begin{aligned} (U_{l_{\max} - \eta} v_0)(x) &= \int_{B(\sigma_0^*, x_0^*)} \frac{k_\delta(x - y) v_0(y)}{1 - \eta + l_{\max} - l(y)} dy \\ &\geq \frac{1}{1 - \eta + \epsilon/2} \int_{B(\sigma_0^*, x_0^*)} k_\delta(x - y) v_0(y) dy. \end{aligned}$$

Clearly, for any  $\gamma > 1$  and  $\epsilon < \eta < 1$ ,

$$(U_{l_{\max} - \eta} v_0)(x) \geq \gamma v_0(x) \quad \text{for } x \in \bar{D} \setminus B(\sigma_0^*, x_0^*). \quad (2.19)$$

Since  $\int_{B(\sigma_0^*, x_0^*)} k_\delta(x - y) v_0(y) dy \rightarrow v_0(x)$  as  $\delta \rightarrow 0$  uniformly for  $x \in \bar{D}$  and  $\min_{x \in B(\sigma_0, x_0^*)} v_0(x) > 0$ , there are  $\gamma_0 > 1$  and  $0 < \delta_0 < \sigma_0^* - \sigma_0$  such that for any  $0 < \delta < \delta_0$ ,  $\epsilon < \eta < 1$ ,

$$(U_{l_{\max} - \eta} v_0)(x) \geq \gamma_0 v_0(x) \quad \text{for } x \in B(\sigma_0, x_0^*) = \{x \in D \mid \|x - x_0^*\| \leq \sigma_0\}. \quad (2.20)$$

Observe that for any  $0 < \delta < \delta_0$  and  $x \in B(\sigma_0^*, x_0^*) \setminus B(\sigma_0, x_0^*)$ ,

$$v_0(y) \geq v_0(x) \quad \text{for } y \in E(\delta, x).$$

Hence for  $0 < \delta < \delta_0$  and  $x \in B(\sigma_0^*, x_0^*) \setminus B(\sigma_0, x_0^*)$ ,

$$\begin{aligned} (U_{l_{\max} - \eta} v_0)(x) &\geq \frac{1}{1 - \eta + \epsilon/2} \int_{B(\sigma_0^*, x_0^*)} k_\delta(x - y) v_0(y) dy \\ &\geq \frac{1}{1 - \eta + \epsilon/2} \left( \int_{E(\delta, x)} k_\delta(y - x) dy \right) v_0(x) \\ &\geq \frac{\gamma_0^*}{1 - \eta + \epsilon/2} v_0(x). \end{aligned} \quad (2.21)$$

Choose  $\epsilon < \eta < 1$  such that  $\frac{\gamma_0^*}{1-\eta+\epsilon/2} \geq \gamma_0$ . Then by (2.19)-(2.21),

$$(U_{l_{\max}-\eta}v_0)(x) \geq \gamma_0 v_0(x) \quad \text{for any } x \in \bar{D}.$$

This implies that

$$r(l_{\max} - \eta) \geq \gamma_0 > 1$$

for  $0 < \delta \leq \delta_0$ . Therefore, by Theorem 2.3 (3), for any  $0 < \delta < \delta_0$ ,  $K_{\delta,NP} - I + L$  has a simple principal eigenvalue  $\lambda(\delta, l)$  and  $-1 + l_{\max} < \lambda(\delta, l) \leq l_{\max}$ .

(2) First, we consider the non-periodic case. Observe that the principal eigenvalue of  $K_\delta - I + L$  in  $C(\bar{D})$  is also the principal eigenvalue of  $K_\delta - I + L$  in  $L^2(D)$ . Observe also that for any  $u, v \in L^2(D)$ ,

$$\begin{aligned} \int_D \left[ \int_D k_\delta(y-x)u(y)dy \right] v(x)dx &= \int_D \left[ \int_D k_\delta(y-x)v(x)dx \right] u(y)dy \\ &= \int_D \left[ \int_D k_\delta(y-x)v(y)dy \right] u(x)dx. \end{aligned}$$

Hence  $K_\delta - I + L$  is a self-adjoint operator on  $L^2(D)$ . Then by [7],

$$\lambda(\delta, l) = \sup_{u \in L^2(D), \|u\|=1} \int_D (K_\delta u - u + lu)u dx$$

where  $\|u\|^2 = \int_D |u(x)|^2 dx$ . Now for any  $\epsilon > 0$ , let  $x_0^*$  and  $\sigma_0^*$  be as in (1). Let  $u_0$  be a smooth function with  $\text{supp}(u_0) \cap D \subset D_0 = B(\sigma_0^*, x_0^*)$  and  $\|u_0\| = 1$ . Then

$$\begin{aligned} \lambda(\delta, l) &\geq \int_D \left( \int_D k_\delta(y-x)u_0(y)dy - u_0(x) + l(x)u_0(x) \right) u_0(x)dx \\ &\geq (l_{\max} - \epsilon) + \int_D \left( \int_D k_\delta(y-x)u_0(y)dy - u_0(x) \right) u_0(x)dx. \end{aligned}$$

Note that

$$\int_D k_\delta(y-x)u_0(y)dy \rightarrow u_0(x) \quad \text{as } \delta \rightarrow 0 \quad \text{for each } x \in \text{Int}(D)$$

and

$$\left| \int_D k_\delta(y-x)u_0(y)dy \right| \leq \max_{y \in \bar{D}} |u_0(y)| \quad \text{for } x \in D.$$

Hence,

$$\int_D \left( \int_D k_\delta(y-x)u_0(y)dy - u_0(x) \right) u_0(x)dx \rightarrow 0 \quad \text{as } \delta \rightarrow 0.$$

It then follows that

$$l_{\max} \geq \lambda(\delta, l) \geq l_{\max} - 2\epsilon \quad \text{for } \delta \ll 1.$$

This implies that  $\lambda(\delta, l) \rightarrow l_{\max}$  as  $\delta \rightarrow 0$ .

Next, we consider the periodic case. Let  $p_1, p_2, \dots, p_N$  be the periods of  $l(x)$  and  $D = [0, p_1] \times [0, p_2] \times [0, p_N]$ . Similar to the above, the principal eigenvalue of  $K_\delta - I + L$  in  $C_{\text{per}}(\mathbb{R}^N) = \{u \in C(\mathbb{R}^N) | u \text{ is periodic}\}$  is also the principal eigenvalue of  $K_\delta - I + L$  in

$L^2_{\text{per}}(\mathbb{R}^N)$ . We claim that  $K_\delta - I + L$  is also self-adjoint. To this end, it suffices to prove that for any  $u, v \in L^2_{\text{per}}(\mathbb{R}^N)$ ,

$$\int_D \left[ \int_{\mathbb{R}^N} k_\delta(y-x)u(y)dy \right] v(x)dx = \int_D \left[ \int_{\mathbb{R}^N} k_\delta(y-x)v(y)dx \right] u(x)dx.$$

First, we prove this for the case  $N = 1$  and  $D = [0, 1]$ . In such case, we have

$$\begin{aligned} \int_0^1 \int_{\mathbb{R}} k_\delta(y-x)u(y)dyv(x)dx &= \int_0^1 \left[ \int_{x-\delta}^{x+\delta} k_\delta(y-x)u(y)dy \right] v(x)dx \\ &= \int_{-\delta}^\delta \left[ \int_0^{y+\delta} k_\delta(y-x)v(x)dx \right] u(y)dy \\ &\quad + \int_\delta^{1-\delta} \left[ \int_{y-\delta}^{y+\delta} k_\delta(y-x)v(x)dx \right] u(y) \\ &\quad + \int_{1-\delta}^{1+\delta} \left[ \int_{y-\delta}^1 k_\delta(y-x)v(x)dx \right] u(y)dy. \end{aligned}$$

Note that

$$\begin{aligned} &\int_{-\delta}^0 \left[ \int_0^{y+\delta} k_\delta(y-x)v(x)dx \right] u(y)dy \\ &= \int_{1-\delta}^1 \left[ \int_0^{\tilde{y}-1+\delta} k_\delta(\tilde{y}-1-x)v(x)dx \right] u(\tilde{y})d\tilde{y} \quad (\text{by } y = \tilde{y} - 1, \quad u(\tilde{y} - 1) = u(\tilde{y})) \\ &= \int_{1-\delta}^1 \left[ \int_1^{\tilde{y}+\delta} k_\delta(\tilde{y}-\tilde{x})v(\tilde{x})u(\tilde{y})d\tilde{x} \right] d\tilde{y} \quad (\text{by } x = \tilde{x} - 1, \quad v(\tilde{x} - 1) = v(\tilde{x})) \\ &= \int_{1-\delta}^1 \left[ \int_1^{y+\delta} k_\delta(y-x)v(x)u(y)dx \right] dy. \end{aligned}$$

Similarly, we can prove that

$$\int_1^{1+\delta} \left[ \int_{y-\delta}^1 k_\delta(y-x)v(x)u(y)dx \right] dy = \int_0^\delta \left[ \int_{y-\delta}^0 k_\delta(y-x)v(x)u(y)dx \right] dy.$$

Therefore,

$$\begin{aligned} \int_0^1 \int_{\mathbb{R}} k_\delta(y-x)u(y)v(x)dydx &= \int_0^1 \left[ \int_{x-\delta}^{x+\delta} k_\delta(y-x)u(y)v(x)dy \right] dx \\ &= \int_0^1 \left[ \int_{y-\delta}^{y+\delta} k_\delta(y-x)v(x)u(y)dx \right] dy \\ &= \int_0^1 \left[ \int_{\mathbb{R}} k_\delta(y-x)v(y)u(x)dy \right] dx. \end{aligned}$$

This implies that  $K_\delta - I + L$  is self-adjoint for the case  $D = [0, 1]$ . Next, we illustrate the proof of the case  $D = [0, p_1] \times [0, p_2]$ , and the general case can be done in the same way iteratively. First,

$$\int_D \int_{\mathbb{R}^2} k_\delta(y-x)u(y)dyv(x)dx = \int_0^{p_1} \left[ \int_{|y_1-x_1|<\delta} \Gamma(x_1, y_1)dy_1 \right] dx_1,$$



where

$$\Gamma(x_1, y_1) = \int_0^{p_2} \left[ \int_{|y_2 - x_2| < \sqrt{\delta^2 - (x_1 - y_1)^2}} k_\delta(y - x) u(y) dy_2 \right] v(x) dx_2.$$

Almost identical to the proof of the case  $D = [0, 1]$ , it can be shown that

$$\Gamma(x_1, y_1) = \int_0^{p_2} \left[ \int_{|y_2 - x_2| < \sqrt{\delta^2 - (x_1 - y_1)^2}} k_\delta(y - x) u(y_1, x_2) dx_2 \right] v(x_1, y_2) dy_2 := \tilde{\Gamma}(x_1, y_1),$$

and also that

$$\int_0^{p_1} \left[ \int_{|x_1 - y_1| < \delta} \tilde{\Gamma}(x_1, y_1) dy_1 \right] dx_1 = \int_0^{p_1} \left[ \int_{|x_1 - y_1| < \delta} \tilde{\Gamma}(y_1, x_1) dx_1 \right] dy_1.$$

Combining the above we have

$$\begin{aligned} \int_D \left[ \int_{\mathbb{R}^2} k_\delta(y - x) u(y) dy \right] v(x) dx &= \int_D \left[ \int_{|y - x| < \delta} k_\delta(y - x) v(y) dy \right] u(x) dx \\ &= \int_D \left[ \int_{\mathbb{R}^2} k_\delta(y - x) v(y) dy \right] u(x) dx, \end{aligned}$$

i.e.,  $K_\delta - I + L$  is self-adjoint. Then by the similar arguments as in the non-periodic case,

$$\lambda(\delta, l) \rightarrow l_{\max} \quad \text{as } \delta \rightarrow 0.$$

□

**Remark 2.7.** In the proof of part (2), we used space  $L^2(D)$  and claimed that  $\lambda(\delta, l)$  is also the principal eigenvalue of  $K_\delta - I + L$  on  $L^2(D)$ . The reason is as follows: Let  $\sigma(K_\delta - I + L)$  and  $\tilde{\sigma}(K_\delta - I + L)$  be the spectrum of  $K_\delta - I + L$  on  $C(\bar{D})$  and  $L^2(D)$ , respectively. First, we note that Theorem 2.3 holds for both  $C(\bar{D})$  and  $L^2(D)$ ; Theorem 2.4 (1) holds for  $L^2(D)$  if  $\lambda_1, \lambda_2 > -1 + l_{\max}$  (for such  $\lambda$ 's, the corresponding eigenfunctions are necessary in  $C(\bar{D})$ ) and Theorem 2.4 (2) holds for  $L^2(D)$  if  $\lambda > -1 + l_{\max}$ ; Theorem 2.5 (1) holds for  $L^2(D)$  if  $\lambda > -1 + l_{\max}$  and Theorem 2.5 (2) holds for  $L^2(D)$ . Next, applying the exact same arguments in Theorem 2.6 (1) to  $K_\delta - I + L$  on  $L^2(D)$ , there is  $\alpha > -1 + l_{\max}$  such that the spectral radius of  $K_\delta(I - L + \alpha I)^{-1}$  is greater than 1. Then by Theorem 2.3 (3), there is  $\alpha_0 > -1 + l_{\max}$  such that the spectral radius of  $K_\delta(I - L + \alpha_0 I)^{-1}$  is 1 and  $\tilde{\lambda}(\delta, l) := \alpha_0$  is an isolated eigenvalue of  $K_\delta - I + L$  of finite multiplicity. Moreover, for any  $\mu \in \tilde{\sigma}(K_\delta - I + L)$ ,  $\text{Re}(\mu) < \tilde{\lambda}(\delta, l)$ . By Theorem 2.4 (2),  $\lambda(\delta, l)$  is simple. Hence  $\tilde{\lambda}(\delta, l)$  is the principal eigenvalue of  $K_\delta - I + L$  on  $L^2(D)$  and it is simple. Now it is clear that  $\lambda(\delta, l) \in \tilde{\sigma}(K_\delta - I + L)$  and  $\tilde{\lambda}(\delta, l) \in \sigma(K_\delta - I + L)$  (since the principal eigenfunction associated with  $\tilde{\lambda}(\delta, l)$  is actually in  $C(\bar{D})$ ). Hence we must have  $\lambda(\delta, l) \leq \tilde{\lambda}(\delta, l)$  and  $\tilde{\lambda}(\delta, l) \leq \lambda(\delta, l)$ . Therefore,  $\lambda(\delta, l) = \tilde{\lambda}(\delta, l)$ .

### 3 Nonlinear Nonlocal Dispersal Equations

In this section, we first investigate the asymptotic dynamics of nonlinear nonlocal dispersal equations on bounded domain  $D \subset \mathbb{R}^N$  with hostile surroundings and on  $\mathbb{R}^N$  with periodic

environment. The second part of this section is devoted to studying qualitative properties of corresponding steady state solutions, which will play important roles in Section 5. We remark that in [4], the asymptotic dynamics of some nonlocal differential equations on  $\mathbb{R}$  with periodic conditions is studied.

### 3.1 Asymptotic dynamics

Consider

$$\frac{\partial v}{\partial t} = K_{\delta, NP}v - v + vg(x, v), \quad x \in \bar{D}, \quad (3.1)$$

where  $g$  is a smooth function. We assume that

**(NL-NP)**  $g(x, 0) > 0$  and  $g_v(x, v) := \frac{\partial g(x, v)}{\partial v} < 0$  for  $x \in \bar{D}$  and  $v \geq 0$ , and  $g(x, v) < 0$  for  $x \in \bar{D}$  and  $v \gg 1$ .

Let  $Y_{NP}$  be as in (2.4), i.e.  $Y_{NP} = C(\bar{D})$ . Then for any  $v_0 \in Y_{NP}$ , (3.1) has a unique (local) solution  $v(t; v_0)$  with  $v(0; v_0) = v_0$ . We denote  $v(t; v_0)$  by  $V_{NP}(t; v_0)$ .

Let  $p_1, p_2, \dots, p_N$  be given positive constants. Consider

$$\frac{\partial v}{\partial t} = K_{\delta, P}v - v + vg(x, v), \quad x \in \mathbb{R}^N, \quad (3.2)$$

where  $g$  is a smooth function. We assume that

**(NL-P)**  $g(x_1, \dots, x_{n-1}, x_n + p_n, x_{n+1}, \dots, x_N, v) = g(x_1, \dots, x_{n-1}, x_n, x_{n+1}, \dots, x_N, v)$  ( $n = 1, 2, \dots, N$ ),  $g(x, 0) > 0$  and  $g_v(x, v) := \frac{\partial g(x, v)}{\partial v} < 0$  for  $x \in \mathbb{R}^N$  and  $v \geq 0$ , and  $g(x, v) < 0$  for  $x \in \mathbb{R}^N$  and  $v \gg 1$ .

Let  $Y_P$  be as in (2.10). Similarly, for any  $v_0 \in Y_P$ , (3.2) has a unique (local) solution  $v(t; v_0)$  with  $v(0; v_0) = v_0$ . We denote  $v(t; v_0)$  by  $V_P(t)v_0$ .

In the following,  $Y$  and  $V(t)$  denote  $Y_{NP}$  and  $V_{NP}(t)$  or  $Y_P$  and  $V_P(t)$ , respectively, depending on whether (3.1) or (3.2) is under consideration.

We first study the monotonicity property of  $v(t; v_0)$  with respect to  $v_0$ .

For given  $v(t, x)$  which is continuous on  $[0, T] \times \bar{D}$  ( $[0, T] \times \mathbb{R}^N$ ),  $v(t, x)$  is called a super-solution (sub-solution) of (3.1) ((3.2)) on  $[0, T]$  if  $\frac{\partial v}{\partial t}$  exists for  $(t, x) \in [0, T] \times \bar{D}$  ( $[0, T] \times \mathbb{R}^N$ ) and

$$\frac{\partial v}{\partial t}(t, x) \geq (\leq) K_{\delta}v(t, x) - v(t, x) + v(t, x)g(x, v(t, x))$$

for  $(t, x) \in [0, T] \times \bar{D}$  ( $[0, T] \times \mathbb{R}^N$ ), where  $K_{\delta} = K_{\delta, NP}$  ( $K_{\delta, P}$ ).

**Theorem 3.1** (Monotonicity). (1) Assume that  $v(t, x; v_1)$  and  $v(t, x; v_2)$  are sub-solution and super-solution of (3.1) ((3.2)) on  $[0, T]$  with  $v(0, x; v_1) = v_1(x)$  and  $v(0, x; v_2) = v_2(x)$ , respectively. If  $v_1 \leq v_2$ , then  $v(t, \cdot; v_1) \leq v(t, \cdot; v_2)$  for  $0 \leq t < T$ .

(2) If  $v_0 \in Y^+$ , then  $V(t)v_0$  exists for all  $t > 0$  and  $V(t)v_0 \in Y^+$  for  $t > 0$ ; moreover  $V(t)v_0 \in Y^{++}$  provided that  $v_0 \neq 0$ .

(3) If  $0 \leq v_1 \leq v_2$ , then  $V(t)v_1 \leq V(t)v_2$  for  $t > 0$ ; moreover  $V(t)v_1 \ll V(t)v_2$  if  $v_1 \neq v_2$ .

*Proof.* (1) Let  $v(t, x) = v(t, x; v_2) - v(t, x; v_1)$ . Then  $v(t, x)$  satisfies

$$\begin{aligned} \frac{\partial v}{\partial t}(t, x) &\geq K_\delta v(t, x) - v(t, x) + g(x, v(t, x; v_2))v \\ &\quad + v(t, x; v_1) \cdot \int_0^1 g_v(x, sv(t, x; v_1) + (1-s)v(t, x; v_2))ds \cdot v. \end{aligned}$$

Then by Theorem 2.1,  $v(t, \cdot) \geq 0$  and hence  $v(t, \cdot; v_2) \geq v(t, \cdot; v_1)$  for  $t \in [0, T)$ .

(2) Let  $v^+ \gg 1$  be such that  $v_0 \leq v^+$  and  $v^+g(x, v^+) < 0$  for all  $x \in \bar{D}$  in the case of (3.1) and for all  $x \in \mathbb{R}^N$  in the case of (3.2). Then  $v(t, x) \equiv v^+$  is a super-solution of (3.1) or (3.2) on  $[0, \infty)$ . Note that  $v(t, x; 0) = 0$  for all  $t \geq 0$ . By (1), we have  $0 \leq V(t)v_0 \leq v^+$  for any  $t \geq 0$  at which  $V(t)v_0$  exists. This implies that  $V(t)v_0$  exists for all  $t > 0$  and  $V(t)v_0 \geq 0$  for  $t > 0$ . Moreover, by Theorem 2.1,  $V(t)v_0 \gg 0$  provided  $v_0 \neq 0$ .

(3) It follows from (2) and Theorem 2.1.  $\square$

**Theorem 3.2.** (1) *There is  $\delta_0 > 0$  such that for any  $0 < \delta < \delta_0$ , there is a unique positive equilibrium solution  $v^* \in Y^{++}$  of (3.1) which is globally stable in the sense that for any  $v_0 \in Y^{++}$ ,  $V(t)v_0 \rightarrow v^*$  as  $t \rightarrow \infty$ .*

(2) *For any  $\delta > 0$ , there is a unique positive equilibrium solution  $v^* \in Y^{++}$  of (3.2) which is globally stable in the sense that for any  $v_0 \in Y^{++}$ ,  $V(t)v_0 \rightarrow v^*$  as  $t \rightarrow \infty$ .*

(3) *Consider (3.1). Let  $l(x) = g(x, v^*(x))$ . Then  $l_{\max} > 0$ .*

To prove this theorem, we first introduce the so called part metric in  $Y^{++}$ . For  $v_1, v_2 \in Y^{++}$ , there is  $\alpha > 1$  such that  $v_1/\alpha \leq v_2 \leq \alpha v_1$ . Define

$$\rho(v_1, v_2) = \inf\{\ln \alpha \mid \alpha \geq 1, v_1/\alpha \leq v_2 \leq \alpha v_1\}$$

for any  $v_1, v_2 \in Y^{++}$ . Then  $\rho(v_1, v_2) = \rho(v_2, v_1)$  and  $\rho(v, v) = 0$ . Note that if  $\alpha_n > 1$ ,  $v_1/\alpha_n \leq v_2 \leq \alpha_n v_1$  and  $\alpha_n \rightarrow \alpha$ , then  $v_1/\alpha \leq v_2 \leq \alpha v_1$ . Hence

$$\rho(v_1, v_2) = \min\{\ln \alpha \mid \alpha \geq 1, v_1/\alpha \leq v_2 \leq \alpha v_1\}. \quad (3.3)$$

**Lemma 3.3.** *For any  $v_1, v_2 \in Y^{++}$ ,  $v_1 \neq v_2$ ,  $\rho(V(t)v_1, V(t)v_2)$  strictly decreases as  $t$  increases.*

*Proof.* We prove the case of (3.1). The case of (3.2) can be proved similarly.

Given  $v_1, v_2 \in Y^{++}$  with  $v_1 \neq v_2$ , let  $\alpha > 1$  be such that  $v_1/\alpha \leq v_2 \leq \alpha v_1$ . Then  $V(t)v_2 \leq V(t)(\alpha v_1)$  for  $t > 0$ . Let  $v(t) = \alpha V(t)v_1$ . Then  $v(t)$  satisfies

$$\begin{aligned} \frac{\partial v}{\partial t} &= \int_D k_\delta(x-y)v(t)(y)dy - v(t)(x) + v(t)(x)g(x, V(t)v_1) \\ &= \int_D k_\delta(x-y)v(t)(y)dy - v(t) + v(t)g(x, v(t)) + v(t)g(x, V(t)v_1) - v(t)g(x, v(t)) \\ &> \int_D k_\delta(x-y)v(t)(y)dy - v(t) + v(t)g(x, v(t)). \end{aligned}$$

Therefore  $V(t)(\alpha v_1) \ll \alpha V(t)v_1$ . Similarly,  $(1/\alpha)V(t)v_1 \ll V(t)(v_1/\alpha)$ . Hence  $v(t; v_1)/\alpha \ll v(t; v_2) \ll \alpha v(t; v_1)$ . This implies that  $\rho(v(t; v_1), v(t; v_2)) < \rho(v_1, v_2)$  for  $t > 0$ . The lemma then follows.  $\square$

Observe that for any  $v_0 \in \tilde{Y}$ , (3.1) ((3.2)) has also a unique solution  $\tilde{v}(t; v_0)$  with initial condition  $\tilde{v}(0; v_0) = v_0$ . Put  $\tilde{V}(t)v_0 = \tilde{v}(t; v_0)$ . Similarly, we can define part metric  $\tilde{\rho}(v_1, v_2)$  for any  $v_1, v_2 \in \tilde{Y}^{++}$ . Moreover, we also have

**Lemma 3.4.** *For any  $v_1, v_2 \in \tilde{Y}^{++}$ ,  $v_1 \neq v_2$ ,  $\tilde{\rho}(\tilde{V}(t)v_1, \tilde{V}(t)v_2)$  strictly decreases as  $t$  increases.*

*Proof of Theorem 3.2.* (1) We first prove the existence of a positive equilibrium by super- and sub-solutions method. First of all, let  $v^+ \gg 1$ . Then

$$K_{\delta, NP}v^+ - v^+ + v^+g(x, v^+) < 0.$$

This implies that  $v(t; v^+) < v^+$  for  $0 < t \ll 1$  and hence  $v(t_1; v^+) \geq v(t_2; v^+)$  for any  $t_2 > t_1 > 0$ . Therefore there is  $v^* \in \tilde{Y}_{NP}^+$  such that  $\lim_{t \rightarrow \infty} v(t; v^+)(x) = v^*(x)$  for  $x \in \bar{D}$ . Moreover, for any  $c \in \bar{D}$  and  $t > 0$ ,  $\limsup_{x \rightarrow c} v^*(x) \leq \limsup_{x \rightarrow c} v(t; v^+)(x)$ . Note that  $\limsup_{x \rightarrow c} v(t; v^+)(x) = v(t; v^+)(c)$  and  $\lim_{t \rightarrow \infty} v(t; v^+)(c) = v^*(c)$ . Hence  $\limsup_{x \rightarrow c} v^*(x) \leq v^*(c)$  and then  $v^*(x)$  is upper semicontinuous. Observe that for any  $s, t > 0$ ,

$$v(t+s; v^+) - v(t; v^+) = \int_0^s \left( K_{\delta, NP}v(t+\tau; v^+) - v(t+\tau; v^+) + v(t+\tau; v^+)g(x, v(t+\tau; v^+)) \right) d\tau.$$

By Lebesgue Dominant Convergence Theorem, we have

$$v^* - v^* = \int_0^s \left( K_{\delta, NP}v^* - v^* + v^*g(x, v^*) \right) d\tau.$$

Hence

$$K_{\delta, NP}v^* - v^* + v^*g(x, v^*) = 0$$

and then  $\tilde{V}(t)v^* \equiv v^*$ .

Next, by **(NL-NP)**, there is  $\delta_0 > 0$  such that for  $0 < \delta < \delta_0$ ,  $v \equiv 0$  is unstable. Hence for any  $0 < \delta < \delta_0$ , there is  $0 < v_- \ll 1$  and  $T > 0$  such that  $v(T; v_-) \geq v_-$ . We then have  $v(kT; v_-) \geq v((k-1)T; v_-)$  for  $n = 1, 2, \dots$ . Hence there is  $v_* \in \tilde{Y}_{NP}^{++}$  such that  $\lim_{k \rightarrow \infty} v(kT; v_-) = v_*$ ,  $v_*$  is lower semicontinuous, i.e.,  $\liminf_{x \rightarrow c} v_*(x) \geq v_*(c)$ , and  $\tilde{V}(kT)v_* \equiv v_*$ .

Clearly,  $v_* \leq v^*$  (hence  $v_*, v^* \in Y_{NP}^{++}$ ) and  $\tilde{\rho}(\tilde{V}(kT)v_*, \tilde{V}(kT)v^*) = \tilde{\rho}(v_*, v^*)$ . If  $v_* \neq v^*$ , we must have  $\tilde{\rho}(\tilde{V}(kT)v_*, \tilde{V}(kT)v^*) < \tilde{\rho}(v_*, v^*)$ , a contradiction. Therefore  $v_* = v^*$ . Since  $v_*$  is lower semicontinuous and  $v^*$  is upper semicontinuous, we must have  $v^*$  is continuous and then  $v^* \in C(\bar{D})$  and  $V(t)v^* \equiv v^*$ . The existence of a positive equilibrium is thus proved.

Next, we prove that  $v^*$  is globally stable. For any  $v_0 \in Y^{++}$ , there are  $0 < v_- \ll 1$  and  $v^+ \gg 1$  such that  $v_- \leq v_0 \leq v^+$  and  $v^+ \geq v^*$ . Hence  $v(t; v_-) \leq v(t; v_0) \leq v(t; v^+)$  and  $v(t; v^+) \geq v^*$ . Note that  $v = v(t; v^+) - v(t; v_-)$  satisfies

$$\begin{aligned} \frac{\partial v}{\partial t} &= K_{\delta, NP}v - v + g(x, v(t; v^+))v + [g(x, v(t; v^+)) - g(x, v(t; v_-))]v(t; v_-) \\ &= K_{\delta, NP}v - v + g(x, v(t; v^+))v + (g_v(x, \tilde{v})v(t; v_-))v \\ &\leq K_{\delta, NP}v - v + l(x)v + (g_v(x, \tilde{v})v(t; v_-))v \end{aligned}$$

where  $l(x) = g(x, v^*(x))$  and  $\tilde{v}$  lies between  $v(t; v^+)$  and  $v(t; v_-)$ . By  $g_u(x, \tilde{v}) < 0$  and  $\lambda(\delta, l) = 0$ , we must have  $v(t; v^+) - v(t; v_-) \rightarrow 0$  as  $t \rightarrow \infty$ . Therefore,  $v^*$  is globally stable and hence is also a unique positive equilibrium of (3.1).

(2) Observe that for any  $\delta > 0$ ,  $v(t; v^+)$  decreases as  $t$  increases for  $v^+ \gg 1$  and  $v(t; v_-)$  increases as  $t$  increases for  $0 < v_- \ll 1$ . Then by the arguments in (1), (3.2) has a unique positive equilibrium  $v^*$  which is globally stable.

(3) Note that  $\lambda(\delta, l) = 0$ . If  $v^*(\cdot) \not\equiv \text{const}$ , then  $\lambda(\delta, l) < l_{\max}$  and hence  $l_{\max} > 0$ . If  $v^* \equiv \text{const}$ , then

$$0 = (K_{\delta, NP} v^*)(x) - v^* + l(x)v^* = \left( \int_D k_\delta(x-y)dy - 1 + l(x) \right) v^* < l(x)v^*$$

for any  $x \in \partial D$ . Hence  $l_{\max} > 0$ .  $\square$

### 3.2 Qualitative properties of equilibria

Let  $v_{\delta, NP}^*$  denote the unique positive equilibrium of (3.1) for  $0 < \delta \ll 1$ , and let  $v_{\delta, P}^*$  denote the unique positive equilibrium of (3.2) for  $\delta > 0$ . We remark that when  $\delta > 0$  is not small, (3.1) may not have positive equilibria.

We assume that the  $g$ 's in (3.1) and (3.2) are the same and satisfy **(NL-P)**. Our first theorem provides fairly precise estimate for  $v_{\delta, P}^*$ , which also yields an upper bound for  $v_{\delta, NP}^*$ .

**Theorem 3.5.** (1) For  $0 < \delta \ll 1$ ,  $v_{\delta, NP}^*(x) \leq v_{\delta, P}^*(x)$  for  $x \in D$ .

(2) Suppose that  $g(x, v) = a(x) - v$ ,  $a \in C^3(\mathbb{R}^N)$  and  $a > 0$  in  $\mathbb{R}^N$ . Then there exist some positive constants  $M_1$  and  $\delta_1$ , both independent of  $\delta$ , such that if  $\delta < \delta_1$ , then

$$\|v_{\delta, P}^* - a - \delta^2 \kappa(\Delta a/a)\| \leq M_1 \delta^3 \quad (3.4)$$

where

$$\kappa := \frac{1}{2} \int_{\mathbb{R}^N} k(z) z_1^2 dz > 0.$$

*Proof.* (1) Observe that

$$\int_D k_\delta(y-x) v_{\delta, P}^*(y) dy \leq \int_{\mathbb{R}^N} k_\delta(y-x) v_{\delta, P}^*(y) dy.$$

This implies that  $v = v_{\delta, P}^*$  is a super-solution of (3.1). Then by the arguments of Theorem 3.2,  $v_{\delta, NP}^* \leq v_{\delta, P}^*$  for  $x \in D$ .

(2) Set

$$\bar{v} = a + \delta^2 \kappa(\Delta a/a) + M_1 \delta^3,$$

where  $M_1$  is some positive constant to be determined later. One can check that

$$K_\delta \bar{v} - \bar{v} = \delta^2 \kappa(\Delta a) + \delta^3 \psi(x; \delta),$$

where  $\|\psi\|_{C(\mathbb{R}^N)} \leq M_2$  for some  $M_2 > 0$ , independent of small  $\delta$  and  $M_1$ , provided that  $a \in C^3(\mathbb{R}^N)$  (this smoothness of  $a$  is needed by Taylor expansion).

Also, one has

$$\bar{v}[a - \bar{v}] = -\delta^2 \kappa(\Delta a) - aM_1\delta^3 + O(\delta^4).$$

Hence,

$$K_\delta \bar{v} - \bar{v} + \bar{v}[a - \bar{v}] = -aM_1\delta^3 + \delta^3 \psi(x; \delta) + O(\delta^4).$$

Since  $a > 0$  in  $\mathbb{R}^N$  and  $a$  is periodic in  $x_n$  with period  $p_n$  for  $n = 1, 2, \dots, N$ , choosing  $M_1 \geq 3M_2/\min_{\mathbb{R}^N} a$  we have

$$K_\delta \bar{v} - \bar{v} + \bar{v}[a - \bar{v}] \leq -M_2\delta^3 < 0$$

for small positive  $\delta$ . That is,  $\bar{v}$  is a super-solution. Similarly, one can show that  $\underline{v} = a + \delta^2 \kappa(\Delta a/a) - M_1\delta^3$  is a sub-solution if we choose  $M_1$  larger if necessary. By the super-solution method and the uniqueness of  $v_{\delta, NP}^*$ , we see that (3.4) holds.  $\square$

**Theorem 3.6.** *Suppose that  $D = (0, 1)$ ,  $g(x, v) = a(x) - v$ ,  $a > 0$  and  $a \in C^3(\bar{D})$ . Then  $v_{\delta, NP}^* \rightarrow a$  pointwisely in  $D$  as  $\delta \rightarrow 0$ .*

Recall  $v_{\delta, NP}^*$  satisfies

$$v_{\delta, NP}^*(x) = \int_D k_\delta(y - x) v_{\delta, NP}^*(y) dy + v_{\delta, NP}^*(x)[a(x) - v_{\delta, NP}^*(x)]. \quad (3.5)$$

We first establish some uniform positive lower bound of  $v_{\delta, NP}^*$  for  $\delta \ll 1$  in the case that  $D = (0, 1)$ .

**Lemma 3.7.** *Suppose that  $D = (0, 1)$  and  $a > 0$  in  $[0, 1]$ . For any  $\eta \in (0, 1/2)$ , there exists some constant  $\delta_0 := \delta_0(\eta) \in (0, \frac{\eta}{2})$  such that for  $\delta < \delta_0$ ,*

$$v_{\delta, NP}^*(x) \geq \gamma_0 := \frac{1}{2} \min_D a \quad (3.6)$$

for every  $x \in [\eta, 1 - \eta]$ .

*Proof.* Set

$$\underline{v}(x) = \begin{cases} \frac{\gamma_0}{\eta} x, & 0 \leq x \leq \eta; \\ \gamma_0, & \eta \leq x \leq 1 - \eta; \\ \gamma_0 - \frac{\gamma_0}{\eta}(x - 1 + \eta), & 1 - \eta \leq x \leq 1. \end{cases} \quad (3.7)$$

We claim that for  $\delta$  small,  $\underline{v}$  is a sub-solution of (3.5), i.e, for every  $0 \leq x \leq 1$ ,

$$\underline{v}(x) \leq \int_D k_\delta(y - x) \underline{v}(y) dy + \underline{v}(x)[a(x) - \underline{v}(x)]. \quad (3.8)$$

Clearly, (3.6) follows from this assertion. We divide the proof of our assertion into several cases:

Case 1.  $0 \leq x \leq \delta$ . For this case, (3.8) is equivalent to (after substitution and dividing both sides by  $\gamma_0/\eta$ )

$$x \leq \int_D k_\delta(y - x) \cdot y dy + x[a(x) - (\gamma_0/\eta)x], \quad (3.9)$$

which is equivalent to (using  $0 \leq x \leq \delta$  and  $y = x + \delta z$ )

$$x \leq \int_{-x/\delta}^1 k(z)(x + \delta z) dz + x[a(x) - (\gamma_0/\eta)x], \quad (3.10)$$

which is equivalent to (using  $1 - \int_{-x/\delta}^1 k(z) dz = \int_{-1}^{-x/\delta} k(z) dz$ )

$$x \cdot \int_{-1}^{-x/\delta} k(z) dz \leq \delta \int_{-x/\delta}^1 k(z)z dz + x[a(x) - (\gamma_0/\eta)x]. \quad (3.11)$$

Since  $x \leq \delta$ , we have  $a(x) - (\gamma_0/\eta)x \geq a(x) - \gamma_0 > 0$ . Hence, it suffices to check that

$$x \cdot \int_{-1}^{-x/\delta} k(z) dz \leq \delta \int_{-x/\delta}^1 k(z)z dz \quad (3.12)$$

for every  $0 \leq x \leq \delta$ . To establish (3.12), for  $0 \leq y \leq 1$ , set

$$f(y) = \int_{-y}^1 k(z)z dz - y \int_{-1}^{-y} k(z) dz.$$

It is easy to check that

$$f'(y) = - \int_{-1}^{-y} k(z) dz < 0$$

for every  $0 \leq y < 1$ . Since  $f(1) = 0$ , we have  $f(y) > 0$  for  $0 \leq y < 1$ , from which (3.12) follows by setting  $y = x/\delta$ . Hence,  $\underline{v}(x)$  satisfies (3.8) for  $0 \leq x \leq \delta$ .

Case 2.  $\delta \leq x \leq \eta/2$ . For this case,

$$\int_D k_\delta(y-x)\underline{v}(y) dy = \int_{-1}^1 k(z)\frac{\gamma_0}{\eta}(x + \delta z) dz = \frac{\gamma_0}{\eta}x = \underline{v}(x)$$

for every  $\delta \leq x \leq \eta/2$ . Also

$$a(x) - \underline{v}(x) \geq \min_D a - (\gamma_0/\eta) \cdot \frac{\eta}{2} = \min_D a - \frac{\gamma_0}{2} > 0.$$

Hence,  $\underline{v}(x)$  satisfies (3.8) for  $\delta \leq x \leq \eta/2$ .

Case 3.  $\eta/2 \leq x \leq 1/2$ . For this case,  $\underline{v} \geq \gamma_0/2$  and  $a(x) - \underline{v}(x) \geq a(x) - \gamma_0 \geq \gamma_0$ . Hence,

$$\underline{v}(x)[a(x) - \underline{v}(x)] \geq \gamma_0^2/2.$$

On the other hand, since  $|\underline{v}(x) - \underline{v}(y)| \leq (\gamma_0/\eta)|x - y|$ , we have

$$\left| \int_D k_\delta(y-x)\underline{v}(y) dy - \underline{v}(x) \right| = \left| \int_D k(z)[\underline{v}(x + \delta z) - \underline{v}(x)] dz \right| \leq \delta \frac{\gamma_0}{\eta} \int_{-1}^1 k(z)|z| dz \rightarrow 0$$

as  $\delta \rightarrow 0$ . Hence, if  $\delta$  is small,  $\underline{v}(x)$  satisfies (3.8) for  $\eta/2 \leq x \leq 1/2$ .

The rest of cases can be handled similarly so we omit the rest of the proof.  $\square$

*Proof of Theorem 3.6.* We argue by contradiction. If not, passing to a sequence of  $\delta$  if necessary, we may assume that there exists  $x_1 \in D$ , constant  $\gamma > 0$  such that

$$|v_{\delta, NP}^*(x_1) - a(x_1)| \geq \gamma$$

for small  $\delta$ .

Choose  $\eta = (1/2)\text{dist}(x_1, \partial D)$  in previous lemma we see that for small  $\delta$ ,  $v_{\delta, NP}^*(x) \geq 2\theta$  for every  $x$  satisfying  $\text{dist}(x, \partial D) \geq \eta$ , where  $\theta = \gamma_0/2$ .

Due to the upper bound  $v_{\delta, NP}^*(x) \leq a(x) + M\delta^2$  in  $\bar{D}$  for small  $\delta$ , we have

$$a(x_1) - v_{\delta, NP}^*(x_1) \geq \gamma.$$

Hence,

$$v_{\delta, NP}^*(x_1) \geq \int_D k_\delta(y - x_1)v_{\delta, NP}^*(y)dy + \gamma v_{\delta, NP}^*(x_1).$$

Therefore,

$$\begin{aligned} (1 - \gamma)v_{\delta, NP}^*(x_1) &\geq \int_D k_\delta(y - x_1)v_{\delta, NP}^*(y)dy \\ &= \int_{|y-x_1| \leq \delta} k_\delta(y - x_1)v_{\delta, NP}^*(y)dy \\ &\geq \min_{|y-x_1| \leq \delta} v_{\delta, NP}^*(y) \\ &= v_{\delta, NP}^*(x_2) \end{aligned} \quad (3.13)$$

for some  $x_2$  satisfying  $|x_2 - x_1| \leq \delta$ . Note that  $x_1$  is independent of  $\delta$  but  $x_2$  may depend on  $\delta$ . Also note that for every  $x$  satisfying  $\delta \leq \text{dist}(x, \partial D)$ , then  $\int_{|y-x| \leq \delta} k_\delta(y - x)dy = 1$ .

Now we estimate  $a(x_2) - v_{\delta, NP}^*(x_2)$ :

$$\begin{aligned} a(x_2) - v_{\delta, NP}^*(x_2) &\geq a(x_2) - (1 - \gamma)v_{\delta, NP}^*(x_1) \\ &\geq a(x_1) - \|a\|_{C^1(D)}|x_2 - x_1| - (1 - \gamma)v_{\delta, NP}^*(x_1) \\ &\geq [a(x_1) - v_{\delta, NP}^*(x_1)] + \gamma v_{\delta, NP}^*(x_1) - \|a\|_{C^1(D)}\delta \\ &\geq \gamma + 2\gamma\theta - \|a\|_{C^1(D)}\delta \\ &\geq (1 + \theta)\gamma, \end{aligned} \quad (3.14)$$

provided that  $\delta \leq (\gamma\theta)/\|a\|_{C^1(D)}$ .

Repeating the above process,

$$\begin{aligned} (1 - (1 + \theta)\gamma)v_{\delta, NP}^*(x_2) &\geq \int_D k_\delta(y - x_2)v_{\delta, NP}^*(y)dy \\ &= \int_{|y-x_2| \leq \delta} k_\delta(y - x_2)v_{\delta, NP}^*(y)dy \\ &\geq \min_{|y-x_2| \leq \delta} v_{\delta, NP}^*(y) \\ &= v_{\delta, NP}^*(x_3) \end{aligned} \quad (3.15)$$

for some  $x_3$  satisfying  $|x_3 - x_2| \leq \delta$ . Note that this process works provided that  $2\delta < \text{dist}(x_1, \partial D)$  (so that  $\int_{|y-x_2| \leq \delta} k_\delta(y - x_2)dy = 1$ ).

Now we estimate  $a(x_3) - v_{\delta, NP}^*(x_3)$ . Since  $|x_2 - x_1| \leq \delta$ , we have  $\text{dist}(x_2, \partial D) \geq \eta$  as long as  $\delta \leq \eta$ . Hence, by previous lemma we have  $v_{\delta, NP}^*(x_2) \geq 2\theta$ . Then

$$\begin{aligned} a(x_3) - v_{\delta, NP}^*(x_3) &\geq a(x_3) - (1 - (1 + \theta)\gamma)v_{\delta, NP}^*(x_2) \\ &\geq a(x_2) - \|a\|_{C^1(D)}|x_3 - x_2| - (1 - (1 + \theta)\gamma)v_{\delta, NP}^*(x_2) \\ &\geq [a(x_2) - v_{\delta, NP}^*(x_2)] + (1 + \theta)\gamma v_{\delta, NP}^*(x_2) - \|a\|_{C^1(D)}\delta \\ &\geq (1 + \theta)\gamma + 2\gamma(1 + \theta)\theta - \|a\|_{C^1(D)}\delta \\ &\geq (1 + \theta)^2\gamma, \end{aligned} \quad (3.16)$$



provided that  $\delta \leq (\gamma\theta)/\|a\|_{C^1(D)}$ . Since  $|x_3 - x_1| \leq |x_3 - x_2| + |x_2 - x_1| \leq 2\delta$  and  $\text{dist}(x_3, \partial D) \geq \text{dist}(x_1, \partial D) - |x_3 - x_1| \geq \text{dist}(x_1, \partial D) - 2\delta$ , it suffices to have  $2\delta \leq \eta = (1/2)\text{dist}(x_1, \partial D)$  to ensure that  $\text{dist}(x_3, \partial D) \geq \eta$ .

Therefore, we can find a sequence of  $x_n$ , as long as  $(n-1)\delta \leq \eta := (1/2)\text{dist}(x_1, \partial D)$  (to ensure that  $\text{dist}(x_n, \partial D) \geq \eta$ ), such that

$$a(x_n) - v_{\delta, NP}^*(x_n) \geq (1 + \theta)^{n-1}\gamma.$$

This implies that  $\max_{x \in \bar{D}} a \geq a(x_n) \geq (1 + \theta)^{n-1}\gamma$ , which is impossible for large  $n$  (i.e., small  $\delta$ ).  $\square$

## 4 Random Dispersal

For the convenience of readers, in this section we recall some principal eigenvalue theory for the Laplace operator and also results on the dynamics of logistic type scalar parabolic equations in bounded domains with Dirichlet, Neumann and periodic boundary conditions.

First, let  $D \subset \mathbb{R}^N$  be a smooth domain. Consider

$$\frac{\partial u}{\partial t} = \mu \Delta u + h(x)u, \quad x \in D, \quad u = 0, \quad x \in \partial D, \quad (4.1)$$

where  $h(\cdot) \in C(\bar{D})$  and  $\mu > 0$  is a constant.

Let

$$X_D = C_0(\bar{D}) := \{u \in C(\bar{D}) | u(x) = 0 \text{ for } x \in \partial D\}. \quad (4.2)$$

Then (4.1) generates a continuous semigroup  $\{\Phi_D(t)\}_{t \geq 0}$  of bounded operators on  $X_D$ . Note that  $u(t; u_0) = \Phi_D(t)u_0$  is the solution of (4.1) with initial condition  $u(0; u_0) = u_0 \in X_D$ . Note also that  $X_D^+$  is defined as usual, i.e.  $X_D^+ = \{u \in X_D | u(x) \geq 0 \text{ for } x \in D\}$ .

Next we consider

$$\frac{\partial u}{\partial t} = \mu \Delta u + h(x)u, \quad x \in D, \quad \frac{\partial u}{\partial n} = 0, \quad x \in \partial D, \quad (4.3)$$

where  $h(\cdot) \in C(\bar{D})$  and  $\mu > 0$  is a constant. Let  $X_N = C(\bar{D})$ . Then (4.3) generates a continuous semigroup  $\{\Phi_N(t)\}_{t \geq 0}$  of bounded operators on  $X_N$ . Note that  $u(t; u_0) = \Phi_N(t)u_0$  is the solution of (4.3) with initial condition  $u(0; u_0) = u_0 \in X_N$ . Note also that  $X_N^+ = \{u \in X_N | u(x) \geq 0 \text{ for } x \in \bar{D}\}$ , and  $X_N^+$  has non-empty interior  $X_N^{++} = \{u \in X_N | u(x) > 0 \text{ for } x \in \bar{D}\}$ .

Let  $p_1, p_2, \dots, p_N$  be given positive constants. Consider

$$\frac{\partial u}{\partial t} = \mu \Delta u + h_p(x)u, \quad u(t, x) \in X_P, \quad x \in \mathbb{R}^N, \quad (4.4)$$

where  $h_p(\cdot) \in X_P$  and

$$\begin{aligned} X_P &= \{u \in C(\mathbb{R}^N) | u(x_1, \dots, x_{n-1}x_n + p_n, x_{n+1}, \dots, x_N) \\ &= u(x_1, \dots, x_n, \dots, x_N), n = 1, 2, \dots, N\}. \end{aligned} \quad (4.5)$$

Then (4.4) generates a continuous semigroup  $\{\Phi_P(t)\}_{t \geq 0}$  of bounded operators on  $X_P$ . Note that  $u(t; u_0) = \Phi_P(t)u_0$  is the solution of (4.4) with initial condition  $u(0; u_0) = u_0 \in X_P$ .

$X_P$ . Similarly,  $X_P^+ = \{u \in X_P | u(x) \geq 0 \text{ for } x \in \mathbb{R}^N\}$  and  $X_P^+$  has non-empty interior  $X_P^{++} = \{u \in X_P | u(x) > 0 \text{ for } x \in \mathbb{R}^N\}$ .

Let  $\lambda_D(\mu, h)$ ,  $\lambda_N(\mu, h)$ , and  $\lambda_P(\mu, h_p)$  be the principal eigenvalues of the eigenvalue problems associated to (4.1), (4.3), and (4.4), respectively. In the following,  $X$ ,  $\Phi(t)$ , and  $\lambda(\mu, h)$  denote  $X_D$ ,  $\Phi_D(t)$ , and  $\lambda_D(\mu, h)$ , or  $X_N$ ,  $\Phi_N(t)$ , and  $\lambda_N(\mu, h)$ , or  $X_P$ ,  $\Phi_P(t)$ , and  $\lambda_P(\mu, h_p)$ , depending on whether (4.1) or (4.3) or (4.4) is under consideration, unless specified otherwise.

**Theorem 4.1.** (1) *If  $h_1(x) \leq h_2(x)$  for  $x \in D$  ( $x \in \mathbb{R}^N$  in the case of periodic boundary condition), then  $\lambda(\mu, h_1) \leq \lambda(\mu, h_2)$  and  $\lambda(\mu, h_1) < \lambda(\mu, h_2)$  if in addition there is  $x_0 \in D$  ( $x_0 \in \mathbb{R}^N$  in the case of periodic boundary condition) such that  $h_1(x_0) < h_2(x_0)$ .*

(2)  $\lambda(\mu, h)$  decreases as  $\mu$  increases.

(3)  $\lim_{\mu \rightarrow 0} \lambda(\mu, h) = h_{\max}$ .

(4) *Consider (4.3). If  $h(x) \equiv h_0 = \text{constant}$ , then  $\lambda_N(\nu, h) = h_0$ . If  $h(x) \neq \text{constant}$ , then  $\bar{h} < \lambda_N(\mu, h) < h_{\max}$ , where  $\bar{h} = \frac{1}{|D|} \int_D h(x) dx$ .*

(5) *Consider (4.4). If  $h(x) \equiv h_0 = \text{constant}$ , then  $\lambda_P(\mu, h) = h_0$ . If  $h(x) \neq \text{constant}$ , then  $\bar{h} < \lambda_P(\mu, h) < h_{\max}$ , where  $\bar{h} = \frac{1}{|D|} \int_D h(x) dx$  and  $D = [0, p_1] \times [0, p_2] \times \cdots \times [0, p_N]$ .*

Theorem 4.1 for Dirichlet and Neumann boundary conditions are well known; see [2]. The periodic case can be proved by similar arguments as those for the Neumann case.

We now turn to consider the following parabolic equation with Dirichlet boundary condition:

$$\frac{\partial u}{\partial t} = \mu \Delta u + u f(x, u), \quad x \in D, \quad u = 0, \quad x \in \partial D, \quad (4.6)$$

where  $f$  is a smooth function. We assume that

**(R-D)**  $f(x, 0) > 0$  and  $f_u(x, u) := \frac{\partial f(x, u)}{\partial u} < 0$  for  $x \in \bar{D}$  and  $u \geq 0$ , and  $f(x, u) < 0$  for  $x \in \bar{D}$  and  $u \gg 1$ . Moreover,  $\lambda_D(\mu, f(\cdot, 0)) > 0$ .

Let  $X_D$  be as in (4.2). Then for any  $u_0 \in X_D$ , (4.6) has a unique (local) solution  $u(t; u_0)$  with  $u(0; u_0) = u_0$ . Moreover, if  $u_0 \geq 0$ , then  $u(t; u_0)$  exists for all  $t > 0$ . Put  $U_D(t)u_0 = u(t; u_0)$  for  $u_0 \in X_D$ .

For the following parabolic equation with Neumann boundary condition

$$\frac{\partial u}{\partial t} = \mu \Delta u + u f(x, u), \quad x \in D, \quad \frac{\partial u}{\partial n} = 0, \quad x \in \partial D, \quad (4.7)$$

we assume that  $f$  is a smooth function on  $\bar{D} \times \mathbb{R}$  and

**(R-N)**  $f(x, 0) > 0$  and  $\frac{\partial f}{\partial u}(x, u) < 0$  for  $x \in \bar{D}$  and  $u \geq 0$ ; and  $f(x, u) < 0$  for  $x \in \bar{D}$  and  $u \gg 1$ ; there is no constant  $c$  such that  $f(x, c) = 0$ .

Let  $X_N$  be as in (4.3). Then for any  $u_0 \in X_N$ , (4.7) has a unique (local) solution  $u(t, \cdot; u_0)$  with  $u(0, \cdot; u_0) = u_0(\cdot)$ . Moreover if  $u_0 \geq 0$ , then  $u(t; u_0)$  exists for all  $t > 0$ . Put  $U_N(t)u_0 = u(t, \cdot; u_0)$ .

Given positive constants  $p_1, p_2, \dots, p_N$ , consider

$$\frac{\partial u}{\partial t} = \mu \Delta u + u f(x, u), \quad x \in \mathbb{R}^N, \quad u(t, \cdot) \in X_P, \quad (4.8)$$

where  $f$  is a smooth function and  $X_P$  is as in (4.4). We assume that

**(R-P)**  $f(x_1, \dots, x_{n-1}, x_n + p_n, x_{n+1}, \dots, x_N) = f(x_1, \dots, x_n, \dots, x_N)$  for  $x = (x_1, \dots, x_N) \in \mathbb{R}^N$  and  $n = 1, 2, \dots, N$ ;  $f(x, 0) > 0$  and  $\frac{\partial f}{\partial u}(x, u) < 0$  for  $x \in \mathbb{R}^N$  and  $u \geq 0$ ; and  $f(x, u) < 0$  for  $x \in \mathbb{R}^N$  and  $u \gg 1$ ; there is no constant  $c$  such that  $f(x, c) = 0$ .

Observe that for any  $u_0 \in X_P$ , (4.8) has a unique (local) solution  $u(t, \cdot; u_0)$  with  $u(0, \cdot; u_0) = u_0(\cdot)$ . Moreover if  $u_0 \geq 0$ , then  $u(t; u_0)$  exists for all  $t > 0$ . Put  $U_P(t)u_0 = u(t, \cdot; u_0)$ .

In the following,  $X$  and  $U(t)$  denote  $X_D$  and  $U_D(t)$ , or  $X_N$  and  $U_N(t)$ , or  $X_P$  and  $U_P(t)$ , respectively, depending on whether (4.6) or (4.7) or (4.8) is under consideration.

**Theorem 4.2.** (1) *There is a unique  $u^* \in X^+ \setminus \{0\}$  such that  $U(t)u^* \equiv u^*$ . Moreover,  $u^*$  is globally stable in the sense that for any  $u_0 \in X$  with  $u_0 > 0$ ,  $\|U(t)u_0 - u^*\|_X \rightarrow 0$  as  $t \rightarrow \infty$ .*

(2)  $h_{\max} > 0$ , where  $h(x) = f(x, u^*(x))$  and  $h_{\max} = \max_{x \in \bar{D}} h(x)$  in the case of Dirichlet and Neumann boundary conditions and  $h_{\max} = \max_{x \in \mathbb{R}^N} h(x)$  in the case of periodic boundary condition.

## 5 Two Competing Species with Different Dispersal Strategies

This section is devoted to the study of two species competition model (1.3), with

$$f(u + v, x) = a(x) - u - v,$$

where  $a(x)$  represents the intrinsic growth rate of species and is assumed to be a smooth, strictly positive function. Without loss of generality, we assume that  $\nu = 1$  in (1.3). We consider three types of boundary conditions for the species with random dispersal (zero Dirichlet, zero Neumann, and periodic boundary conditions) and two types of nonlocal dispersal (hostile surroundings and periodic environment). In this section we will focus on three scenarios: (1) Random dispersal with Dirichlet boundary condition versus non-local dispersal with hostile surroundings; (2) Random dispersal with Neumann boundary condition versus non-local dispersal with hostile surroundings; (3) Random dispersal with periodic boundary condition versus non-local dispersal with periodic environments.

We denote  $\lambda_{NL,NP}(\delta, l)$  and  $\lambda_{NL,P}(\delta, l)$  as the principal eigenvalues of (2.3) and (2.9) (with  $\nu = 1$ ) (if they exist), respectively, and denote  $\lambda_{R,D}(\mu, h)$ ,  $\lambda_{R,N}(\mu, h)$ , and  $\lambda_{R,P}(\mu, h)$  as the principal eigenvalues of (4.1), (4.3), and (4.4), respectively.

## 5.1 Hostile surroundings: random vs non-local dispersal

Consider

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u - v), & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP} v - v + v(a(x) - u - v), & x \in \bar{D}, \\ u = 0, & x \in \partial D, \end{cases} \quad (5.1)$$

where the species with density  $u$  satisfies the zero Dirichlet boundary condition. Let  $Z = X_D \times Y_{NP}$ . Then the mapping  $[Z \ni (u, v) \mapsto (u(a(\cdot) - u - v), v(a(\cdot) - u - v))]$  is smooth. Hence for any  $(u_0, v_0) \in Z$ , (5.1) has a unique (local) solution  $(u(t; u_0, v_0), v(t; u_0, v_0))$  with  $(u(0; u_0, v_0), v(0; u_0, v_0)) = (u_0, v_0)$ .

Define the following orderings in  $Z$ :

$$(u_1, v_1) \leq_1 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \leq v_2, \quad (5.2)$$

$$(u_1, v_1) \leq_2 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \geq v_2. \quad (5.3)$$

We have

**Lemma 5.1.** (1) *If  $(0, 0) \leq_1 (u_0, v_0)$ , then  $(0, 0) \leq_1 (u(t; u_0, v_0), v(t; u_0, v_0))$  for  $t > 0$  at which  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists.*

(2) *If  $(0, 0) \leq_1 (u_i, v_i)$  for  $i = 1, 2$  and  $(u_1, v_1) \leq_2 (u_2, v_2)$ , then  $(u(t; u_1, v_1), v(t; u_1, v_1)) \leq_2 (u(t; u_2, v_2), v(t; u_2, v_2))$  for  $t > 0$  at which both  $(u(t; u_1, v_1), v(t; u_1, v_1))$  and  $(u(t; u_2, v_2), v(t; u_2, v_2))$  exist.*

**Corollary 5.2.** *For any  $(u_0, v_0) \in Z^+ = X_D^+ \times Y_{NP}^+$ ,  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists for all  $t > 0$ .*

In the rest of this subsection, we assume that  $\lambda_D(\mu, a) > 0$ . Then for any  $\delta > 0$ , (5.1) has a semi-trivial equilibrium  $(u^*, 0)$ , where  $u^* \in X_D$  is the unique positive equilibrium of

$$\frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u), \quad x \in D, \quad u = 0, \quad x \in \partial D. \quad (5.4)$$

For  $\delta \ll 1$ , (5.1) has a semi-trivial equilibrium  $(0, v_{\delta, NP}^*)$ , where  $v_{\delta, NP}^* \in Y_{NP}$  is the unique positive equilibrium of

$$\frac{\partial v}{\partial t} = K_{\delta, NP} v - v + v(a(x) - v), \quad x \in \bar{D}. \quad (5.5)$$

Our main result, which concerns the stability of two semi-trivial solutions  $(u^*, 0)$ ,  $(0, v_{\delta, NP}^*)$  of (5.1) can be stated as follows:

**Theorem 5.3.** *Suppose that  $D = (0, 1)$ ,  $a > 0$  and  $a \in C^3(\bar{D})$ . Then for  $0 < \delta \ll 1$ ,  $(u^*, 0)$  is unstable and  $(0, v_{\delta, NP}^*)$  is stable.*

First, we study the stability of  $(u^*, 0)$ . The linearized equation of (5.1) at  $(u^*, 0)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_1^*(x)u - u^*(x)v, & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP}v - v + l_1^*(x)v, & x \in \bar{D}, \\ u = 0, & x \in \partial D, \end{cases} \quad (5.6)$$

where  $h_1^*(x) = a(x) - 2u^*(x)$  and  $l_1^*(x) = a(x) - u^*(x)$ .

**Lemma 5.4.** *When  $0 < \delta \ll 1$ ,  $\lambda_{NL, NP}(\delta, l_1^*) > 0$  and  $(u^*, 0)$  is unstable.*

*Proof.* Note that  $u^*$  satisfies

$$\mu \Delta u^* + l_1^*(x)u^* = 0, \quad x \in D, \quad u = 0, \quad x \in \partial D.$$

Hence we must have  $\max_{x \in \bar{D}} l_1^*(x) > 0$ .

It then follows from Theorem 2.6 that  $\lambda_{NL, NP}(\delta, l_1^*)$  exists and  $\lambda_{NL, NP}(\delta, l_1^*) > 0$  for  $0 < \delta \ll 1$ . This implies that  $\lambda_{NL, NP}(\delta, l_1^*)$  is a simple isolated eigenvalue of the following eigenvalue problem associated to (5.6),

$$\begin{cases} \mu \Delta u + h_1^*(x)u - u^*(x)v = \lambda u, & x \in D, \\ K_{\delta, NP}v - v + l_1^*(x)v = \lambda v, & x \in \bar{D}, \\ u = 0, & x \in \partial D, \end{cases} \quad (5.7)$$

i.e.,  $(u^*, 0)$  is unstable.  $\square$

Next, we consider the stability of  $(0, v_{\delta, NP}^*)$ . The linearized equation of (5.1) at  $(0, v_{\delta, NP}^*)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_2^*(x)u, & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP}v - v - v_{\delta, NP}^*(x)u + l_2^*(x)v, & x \in \bar{D}, \\ u = 0, & x \in \partial D, \end{cases} \quad (5.8)$$

where  $h_2^*(x) = a(x) - v_{\delta, NP}^*(x)$  and  $l_2^*(x) = a(x) - 2v_{\delta, NP}^*(x)$ .

**Lemma 5.5.** *Suppose that  $D = (0, 1)$ ,  $a > 0$  and  $a \in C^3(\bar{D})$ . For  $0 < \delta \ll 1$ ,  $\lambda_{R, D}(\mu, h_2^*) < 0$  and hence  $(0, v_{\delta, NP}^*)$  is stable.*

*Proof.* First note that  $a$  can be extended to a  $C^3$  periodic function on  $\mathbb{R}$ . Then by Theorem 3.6 and the uniform boundedness of  $v_{\delta, NP}^*$  for all small  $\delta$ , we have  $v_{\delta, NP}^* \rightarrow a$  in  $L_{Loc}^2(D)$  as  $\delta \rightarrow 0$ . Hence, we have  $h_2^* \rightarrow 0$  in  $L_{Loc}^2(D)$  as  $\delta \rightarrow 0$ . It then follows from [5] that  $\lambda_{R, D}(\mu, h_2^*) \rightarrow \lambda_{R, D}(\mu, 0) < 0$  as  $\delta \rightarrow 0$ . Therefore, for  $0 < \delta \ll 1$ ,  $\lambda_{R, D}(\mu, h_2^*) < 0$  and  $(0, v_{\delta, NP}^*)$  is stable.  $\square$

*Proof of Theorem 5.3.* It follows from Lemmas 5.4 and 5.5.  $\square$

## 5.2 Neumann B.C. vs non-local dispersal with hostile surroundings

Consider

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u - v), & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP} v - v + v(a(x) - u - v), & x \in \bar{D}, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial D, \end{cases} \quad (5.9)$$

where the species with density  $u$  satisfies the zero Neumann boundary condition. Let  $Z = X_N \times Y_{NP}$ . Then the mapping  $[Z \ni (u, v) \mapsto (u(a(\cdot) - u - v), v(a(\cdot) - u - v))]$  is smooth. Hence for any  $(u_0, v_0) \in Z$ , (5.9) has a unique (local) solution  $(u(t; u_0, v_0), v(t; u_0, v_0))$  with  $(u(0; u_0, v_0), v(0; u_0, v_0)) = (u_0, v_0)$ .

As before, define the following orderings in  $Z$ :

$$(u_1, v_1) \leq_1 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \leq v_2, \quad (5.10)$$

$$(u_1, v_1) \leq_2 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \geq v_2. \quad (5.11)$$

The following lemma follows from standard arguments.

**Lemma 5.6.** (1) *If  $(0, 0) \leq_1 (u_0, v_0)$ , then  $(0, 0) \leq_1 (u(t; u_0, v_0), v(t; u_0, v_0))$  for  $t > 0$  at which  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists.*

(2) *If  $(0, 0) \leq_1 (u_i, v_i)$  for  $i = 1, 2$  and  $(u_1, v_1) \leq_2 (u_2, v_2)$ , then  $(u(t; u_1, v_1), v(t; u_1, v_1)) \leq_2 (u(t; u_2, v_2), v(t; u_2, v_2))$  for  $t > 0$  at which both  $(u(t; u_1, v_1), v(t; u_1, v_1))$  and  $(u(t; u_2, v_2), v(t; u_2, v_2))$  exist.*

**Corollary 5.7.** *For any  $(u_0, v_0) \in Z^+ = X_N^+ \times Y_{NP}^+$ ,  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists for all  $t > 0$ .*

For any  $\delta > 0$ , (5.9) has a semi-trivial equilibrium  $(u^*, 0)$ , where  $u^* \in X_N$  is the unique positive equilibrium of

$$\frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u), \quad x \in D, \quad \frac{\partial u}{\partial n} = 0, \quad x \in \partial D. \quad (5.12)$$

Also for any  $0 < \delta \ll 1$ , (5.9) has a semi-trivial equilibrium  $(0, v_{\delta, NP}^*)$ , where  $v_{\delta, NP}^* \in Y_{NP}$  is the unique positive equilibrium of

$$\frac{\partial v}{\partial t} = K_{\delta, NP} v - v + v(a(x) - v), \quad x \in \bar{D}. \quad (5.13)$$

In the following we study the stability of two semi-trivial equilibria  $(u^*, 0)$ ,  $(0, v_{\delta, NP}^*)$  of (5.9) and the existence of positive equilibria of (5.9). The main result of this subsection can be stated as

**Theorem 5.8.** *Suppose that  $a$  is a non-constant positive function and  $a \in C^3(\bar{D})$ . Then for  $0 < \delta \ll 1$ , both semi-trivial equilibria are unstable and system (5.9) has at least one positive equilibrium solution  $(u^{**}, v^{**}) \in X_N^{++} \times Y_{NP}^{++}$ .*

First, we study the stability of  $(u^*, 0)$ . The linearized equation of (5.9) at  $(u^*, 0)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_1^*(x)u - u^*(x)v, & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP}v - v + l_1^*(x)v, & x \in \bar{D}, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial D, \end{cases} \quad (5.14)$$

where  $h_1^*(x) = a(x) - 2u^*(x)$  and  $l_1^*(x) = a(x) - u^*(x)$ .

**Lemma 5.9.** *Assume that  $a$  is nonconstant. When  $0 < \delta \ll 1$ ,  $\lambda_{NL, NP}(\delta, l_1^*) > 0$  and  $(u^*, 0)$  is unstable.*

*Proof.* Note that  $u^*$  satisfies

$$\mu \Delta u^* + l_1^*(x)u^* = 0, \quad x \in D, \quad \frac{\partial u^*}{\partial n} = 0, \quad x \in \partial D.$$

Hence we must have  $\max_{x \in \bar{D}} l_1^*(x) > 0$  provided that  $a$  is nonconstant. The lemma then follows from the similar arguments as those in Lemma 5.4.  $\square$

Next, we consider the stability of  $(0, v_{\delta, NP}^*)$ . The linearized equation of (5.9) at  $(0, v_{\delta, NP}^*)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_2^*(x)u, & x \in D, \\ \frac{\partial v}{\partial t} = K_{\delta, NP}v - v - v_{\delta, NP}^*(x)u + l_2^*(x)v, & x \in \bar{D}, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial D, \end{cases} \quad (5.15)$$

where  $h_2^*(x) = a(x) - v_{\delta, NP}^*(x)$  and  $l_2^*(x) = a(x) - 2v_{\delta, NP}^*(x)$ .

**Lemma 5.10.** *Suppose that  $a$  is a positive nonconstant function and  $a \in C^3(\bar{D})$ . When  $0 < \delta \ll 1$ ,  $\lambda_{R, N}(\mu, h_2^*) > 0$  and  $(0, v_{\delta, NP}^*)$  is unstable.*

*Proof.* First,  $a$  can be extended to a  $C^3$  periodic function on  $\mathbb{R}^N$ . Then by Theorem 3.5, we have

$$v_{\delta, NP}^*(x) \leq v_{\delta, P}^*(x) \leq a(x) + \delta^2 \kappa \Delta a(x) / a(x) + M_1 \delta^3 \quad (5.16)$$

for  $x \in \bar{D}$  and  $0 < \delta \ll 1$ . Hence there are  $\delta_2 > 0$  and  $M > 0$  such that

$$v_{\delta, NP}^*(x) \leq a(x) + \delta^2 M \quad (5.17)$$

for  $x \in \bar{D}$  and  $0 < \delta \leq \delta_2$ . By the uniform continuity of  $a$ , we may also assume that

$$|a(x) - a(x_0)| \leq M|x - x_0| \quad \text{for } |x - x_0| \leq \delta_2. \quad (5.18)$$

We claim that for  $0 < \delta \ll 1$ ,

$$v_{\delta, NP}^*(x) < a(x) - \sqrt{\delta} \quad \text{for } x \in \bar{D} \quad \text{with } \text{dist}(x, \partial D) \leq \delta/2. \quad (5.19)$$

In fact, assume that the claim is not true. Then for every  $0 < \delta \ll 1$ , there is  $x_\delta \in \bar{D}$ ,  $\text{dist}(x_\delta, \partial D) \leq \delta/2$  such that  $v_{\delta, NP}^*(x_\delta) \geq a(x_\delta) - \sqrt{\delta}$ . Note that

$$v_{\delta, NP}^*(x_\delta) = \int_D k_\delta(y - x_\delta) v_{\delta, NP}^*(y) dy + v_{\delta, NP}^*(x_\delta) [a(x_\delta) - v_{\delta, NP}^*(x_\delta)].$$

Hence

$$v_{\delta, NP}^*(x_\delta) \leq \int_D k_\delta(y - x_\delta) v_{\delta, NP}^*(y) dy + v_{\delta, NP}^*(x_\delta) \cdot \sqrt{\delta}.$$

This implies that

$$(1 - \sqrt{\delta}) v_{\delta, NP}^*(x_\delta) \leq \int_D k_\delta(y - x_\delta) v_{\delta, NP}^*(y) dy$$

and then

$$(a(x_\delta) - \sqrt{\delta})(1 - \sqrt{\delta}) \leq \int_D k_\delta(y - x_\delta) v_{\delta, NP}^*(y) dy = \int_{B(x_\delta, \delta) \cap D} k_\delta(y - x_\delta) v_{\delta, NP}^*(y) dy.$$

Hence by (5.17) and (5.18), for  $0 < \delta \ll 1$ ,

$$\begin{aligned} (a(x_\delta) - \sqrt{\delta})(1 - \sqrt{\delta}) &\leq \int_{B(x_\delta, \delta) \cap D} k_\delta(y - x_\delta) [a(y) + M\delta^2] dy \\ &\leq \int_{B(x_\delta, \delta) \cap D} k_\delta(y - x_\delta) dy \cdot [a(x_\delta) + M\delta + M\delta^2] \end{aligned}$$

By setting  $y = x_\delta + \delta z$  we have

$$\int_{B(x_\delta, \delta) \cap D} k_\delta(y - x_\delta) dy = \int_{\{z: |z| \leq 1, \delta z + x_\delta \in D\}} k(z) dz \leq \kappa^*, \quad (5.20)$$

where

$$\kappa^* := \int_{\{z: |z| < 1, z_N \geq -1/2\}} k(z) dz.$$

By the definition of  $k(z)$ , we see that  $0 < \kappa^* < 1$ .

To deduce the last inequality in (5.20), after rotation and translation of domain  $D$  we may assume that  $x_\delta = (0, \dots, 0, x_{N, \delta})$  with  $x_{N, \delta} = \text{dist}(x_\delta, \partial D)$ . Since  $\text{dist}(x_\delta, \partial D) \leq \delta/2$ , for small delta we have

$$\{z : |z| < 1, \delta z + x_\delta \in D\} \subset \{z : |z| < 1, z_N \geq -1/2\},$$

which implies the last inequality in (5.20). Hence,

$$[a(x_\delta) - \sqrt{\delta}](1 - \sqrt{\delta}) \leq \kappa^* [a(x_\delta) + M\delta + M\delta^2]. \quad (5.21)$$

Passing to a subsequence if necessary we may assume that  $x_\delta \rightarrow x^* \in \partial D$  as  $\delta \rightarrow 0+$ . By letting  $\delta \rightarrow 0$  in (5.21) we have  $a(x^*) \leq \kappa^* \cdot a(x^*)$ , which is a contradiction since  $a(x^*) > 0$  and  $\kappa^* \in (0, 1)$ . Therefore, the claim (5.19) holds.



Now by (5.17) and (5.19), we have

$$\begin{aligned}
& \int_D [a(x) - v_{\delta, NP}^*(x)] dx \\
&= \int_{\{x \in D, \text{dist}(x, \partial D) \leq \delta/2\}} [a(x) - v_{\delta, NP}^*(x)] dx + \int_{\{x \in D, \text{dist}(x, \partial D) > \delta/2\}} [a(x) - v_{\delta, NP}^*(x)] dx \\
&\geq \int_{\{x \in D, \text{dist}(x, \partial D) \leq \delta/2\}} \sqrt{\delta} dx - \int_{\{x \in D, \text{dist}(x, \partial D) > \delta/2\}} M \delta^2 dx \\
&> 0
\end{aligned}$$

for  $0 < \delta \ll 1$ . This together with Theorem 4.1 implies that  $\lambda_{R, N}(\mu, h_2^*) > 0$ . Observe that  $\lambda_{R, N}(\mu, h_2^*)$  is an eigenvalue of the following eigenvalue problem associated to (5.15),

$$\begin{cases} \mu \Delta u + h_2^*(x)u = \lambda u, & x \in D \\ K_{\delta, NP}v - v - v_{\delta, NP}^*(x)u + l_2^*(x)v = \lambda v, & x \in \bar{D} \\ \frac{\partial u}{\partial n} = 0, & x \in \partial D. \end{cases} \quad (5.22)$$

Therefore  $(0, v_{\delta, NP}^*)$  is unstable for  $0 < \delta \ll 1$ .  $\square$

*Proof of Theorem 5.8.* For  $0 < \delta \ll 1$ , it follows from the instability of two semi-trivial equilibria (Lemmas 5.9 and 5.10) and the monotonicity of the flow generated by system (Lemma 5.6) that (5.9) has at least one positive equilibrium solution  $(u^{**}, v^{**}) \in X_N^{++} \times Y_{NP}^{++}$ .  $\square$

### 5.3 Periodic environment: random vs non-local dispersal

Let  $p_1, p_2, \dots, p_N$  be given positive constants. Consider

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u - v), & x \in \mathbb{R}^N, \\ \frac{\partial v}{\partial t} = K_{\delta, P}v - v + v(a(x) - u - v), & x \in \mathbb{R}^N, \\ u(t, \cdot) \in X_P, v(t, \cdot) \in Y_P, \end{cases} \quad (5.23)$$

where  $a(x)$  is a smooth positive function on  $\mathbb{R}^N$  and  $a(x)$  is periodic in  $x_n$  with period  $p_n$  for  $n = 1, 2, \dots, N$ . Let  $Z = X_P \times Y_P$ . Then the mapping  $[Z \ni (u, v) \mapsto (u(a(\cdot) - u - v), v(a(\cdot) - u - v))]$  is smooth. Hence for any  $(u_0, v_0) \in Z$ , (5.23) has a unique (local) solution  $(u(t; u_0, v_0), v(t; u_0, v_0))$  with  $(u(0; u_0, v_0), v(0; u_0, v_0)) = (u_0, v_0)$ .

Similarly, define the following orderings in  $Z$ :

$$(u_1, v_1) \leq_1 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \leq v_2, \quad (5.24)$$

$$(u_1, v_1) \leq_2 (u_2, v_2) \quad \text{if} \quad u_1 \leq u_2, v_1 \geq v_2. \quad (5.25)$$

We have

**Lemma 5.11.** (1) If  $(0, 0) \leq_1 (u_0, v_0)$ , then  $(0, 0) \leq_1 (u(t; u_0, v_0), v(t; u_0, v_0))$  for  $t > 0$  at which  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists.

(2) If  $(0, 0) \leq_1 (u_i, v_i)$  for  $i = 1, 2$  and  $(u_1, v_1) \leq_2 (u_2, v_2)$ , then  $(u(t; u_1, v_1), v(t; u_1, v_1)) \leq_2 (u(t; u_2, v_2), v(t; u_2, v_2))$  for  $t > 0$  at which both  $(u(t; u_1, v_1), v(t; u_1, v_1))$  and  $(u(t; u_2, v_2), v(t; u_2, v_2))$  exist.

**Corollary 5.12.** For any  $(u_0, v_0) \in Z^+ = X_P^+ \times Y_P^+$ ,  $(u(t; u_0, v_0), v(t; u_0, v_0))$  exists for all  $t > 0$ .

For any  $\delta > 0$ , (5.23) has a semi-trivial equilibrium  $(u^*, 0)$ , where  $u^* \in X_P$  is the unique positive equilibrium of

$$\frac{\partial u}{\partial t} = \mu \Delta u + u(a(x) - u), \quad x \in \mathbb{R}^N, \quad u(t, \cdot) \in X_P. \quad (5.26)$$

Also for any  $0 < \delta \ll 1$ , (5.23) has a semi-trivial equilibrium  $(0, v_{\delta, P}^*)$ , where  $v_{\delta, P}^* \in Y_P$  is the unique positive equilibrium of

$$\frac{\partial v}{\partial t} = K_{\delta, P} v - v + v(a(x) - v), \quad x \in \mathbb{R}^N, \quad v(t, \cdot) \in Y_P. \quad (5.27)$$

The main result of this subsection is

**Theorem 5.13.** Assume that  $a$  is a non-constant positive function and  $a \in C^3(\bar{D})$ . Then for  $0 < \delta \ll 1$ ,  $(u^*, 0)$  is unstable and  $(0, v_{\delta, P}^*)$  is stable.

First, we study the stability of  $(u^*, 0)$ . The linearized equation of (5.23) at  $(u^*, 0)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_1^*(x)u - u^*(x)v, & x \in \mathbb{R}^N, \\ \frac{\partial v}{\partial t} = K_{\delta, P} v - v + l_1^*(x)v, & x \in \mathbb{R}^N, \\ u(t, \cdot) \in X_P, \quad v(t, \cdot) \in Y_P, \end{cases} \quad (5.28)$$

where  $h_1^*(x) = a(x) - 2u^*(x)$  and  $l_1^*(x) = a(x) - u^*(x)$ .

**Lemma 5.14.** Suppose that  $a$  is a nonconstant function. When  $0 < \delta \ll 1$ ,  $\lambda_{NL, P}(\delta, l_1^*) > 0$  and  $(u^*, 0)$  is unstable.

*Proof.* Note that  $u^*$  satisfies

$$\mu \Delta u^* + l_1^*(x)u^* = 0, \quad x \in \mathbb{R}^N, \quad u^*(\cdot) \in X_P.$$

Hence we must have  $\max_{x \in \mathbb{R}^N} l_1^*(x) > 0$ . The rest of the proof is similar to that of Lemma 5.9.  $\square$

Next, we consider the stability of  $(0, v_{\delta, P}^*)$ . The linearized equation of (5.23) at  $(0, v_{\delta, P}^*)$  reads as follows:

$$\begin{cases} \frac{\partial u}{\partial t} = \mu \Delta u + h_2^*(x)u, & x \in \mathbb{R}^N, \\ \frac{\partial v}{\partial t} = K_{\delta, P} v - v - v_{\delta, P}^*(x)u + l_2^*(x)v, & x \in \mathbb{R}^N, \\ u(t, \cdot) \in X_P, \quad v(t, \cdot) \in Y_P, \end{cases} \quad (5.29)$$

where  $h_2^*(x) = a(x) - v_{\delta,P}^*(x)$  and  $l_2^*(x) = a(x) - 2v_{\delta,P}^*(x)$ .

**Lemma 5.15.** *Assume that  $a$  is a non-constant positive function and  $a \in C^3(\bar{\Omega})$ . When  $0 < \delta \ll 1$ ,  $\lambda_{R,P}(\mu, h_2^*) < 0$  and  $(0, v_{\delta,P}^*)$  is stable.*

*Proof.* The stability of  $(0, v_{\delta,P}^*)$  is determined by the principal eigenvalue of the eigenvalue problem

$$\mu \Delta \varphi + (a - v_{\delta,P}^*) \varphi = \lambda \varphi,$$

where  $\varphi$  is subject to periodic boundary condition. Let  $\lambda = \lambda_{R,P}(\mu, h_2^*)$  and  $\varphi$  be a positive eigenfunction associated to  $\lambda$ . Integrating the equation of  $\varphi$  in  $D$ , we have

$$\lambda = \frac{\int_D (a - v_{\delta,P}^*) \varphi}{\int_D \varphi}. \quad (5.30)$$

By Theorem 3.5,  $v_{\delta,P}^* \rightarrow a$  when  $\delta \rightarrow 0$ , we see that  $\lambda \rightarrow 0$ , so its corresponding eigenfunction (after suitable normalization) converges to 1 as  $\delta \rightarrow 0$ . Hence, by (5.30) and Theorem 3.5 (2) we have

$$\lim_{\delta \rightarrow 0} \frac{\lambda}{\delta^2} = \lim_{\delta \rightarrow 0} \frac{1}{|D|} \int_D \frac{a - v_{\delta,P}^*}{\delta^2} = -\frac{\mu \cdot \kappa}{|D|} \int_D \frac{\Delta a}{a},$$

where  $D = [0, p_1] \times [0, p_2] \times \cdots \times [0, p_N]$ . Since  $a$  is periodic in  $x_n$  with period  $p_n$  for  $n = 1, 2, \dots, N$ ,

$$\lim_{\delta \rightarrow 0} \frac{\lambda}{\delta^2} = -\frac{\mu \cdot \kappa}{|D|} \int_D \frac{|\nabla a|^2}{a^2} < 0,$$

provided that  $a$  is non-constant. This implies the stability of  $(0, v_{\delta,P}^*)$  for  $\delta > 0$  small.  $\square$

*Proof of Theorem 5.13.* It follows from Lemmas 5.14 and 5.15.  $\square$

## 6 Numerical Simulations

In the previous section, we do the local stability analysis of the solutions on three scenarios. The result suggests that, the species with non-local dispersal and small non-local interaction distance is preferred over random dispersal with zero Dirichlet and periodic boundary conditions. However, for zero Neumann boundary condition, the species with random dispersal can invade when rare versus the species with non-local dispersal and small non-local interaction. In order to know more about global dynamic behaviors of the solutions for general interaction distance  $\delta$  and effect of  $a(x)$ , we use simple finite difference method [8] to obtain the solution numerically. For simplicity, we choose  $D = (0, 1)$ ,  $\mu = \nu = 1$  and define an uniform grid of points  $x_j = j \cdot h$  where  $0 \leq j \leq N$  and  $N = \frac{1}{h}$ . The spacial discretization with second-order accuracy for the system of equations

$$\begin{cases} \frac{\partial u}{\partial t} &= \Delta u + u(a(x) - u - v) \\ \frac{\partial v}{\partial t} &= [K_{\delta, NP} v - v] + v(a(x) - u - v) \end{cases}$$

is

$$\begin{cases} \frac{\partial u}{\partial t}(t, x_i) &= \frac{u(t, x_{i+1}) - 2u(t, x_i) + u(t, x_{i-1}))}{h^2} + u(t, x_i) (a(x_i) - u(t, x_i) - v(t, x_i)) \\ \frac{\partial v}{\partial t}(t, x_i) &= [(K_{\delta, NP} v)_i - v(t, x_i)] + v(t, x_i) (a(x_i) - u(t, x_i) - v(t, x_i)) \end{cases}$$

for  $1 \leq i \leq N-1$  where the integration of the kernel  $(K_{\delta, NP}v)_i$  can be done by trapezoidal rule or Simpson's rule [19]. When we deal with nonlocal periodic dispersal,  $(K_{\delta, P}v)$  can be done in the similar way. We then integrate in time by using Matlab built-in function "solver" which was designed to solve system of ordinary differential equations. The boundary conditions for random dispersal need to be incorporated to the grid points  $x_0$  and  $x_N$ . The equilibrium results shown in the following figures are obtained when the difference between the solutions of two successive iterations is less than  $\epsilon = 1.e - 14$ .

### 6.1 Hostile surroundings: random vs non-local dispersal

First, we consider random dispersal versus nonlocal dispersal with hostile surroundings (5.1). We show the results for  $a(x) = 16(x^2(1-x)^2) + 0.5$  and  $a(x) = 16(x^2(1-x)^2) - 0.5$  in the first and second columns in Figure 1, respectively. We see that  $(0, v_{\delta, NP}^*)$  is stable no matter what  $a(x)$  is when  $\delta$  is small enough. When  $a(x) > 0$ ,  $v_{\delta, NP}^* \rightarrow a(x)$  for  $x$  away from the boundary as  $\delta \rightarrow 0$  (See Figure 1(a)). When  $a(x) < 0$  for some  $x \in D$ ,  $v_{\delta, NP}^* \rightarrow \max(a(x), 0)$  as  $\delta \rightarrow 0$  (See Figure 1(b)). From Figures 1(d) and 1(f), we observe that there exists a critical threshold  $\delta^*$  such that  $(u, v) = (0, 0)$  becomes the stable equilibrium for  $\delta > \delta^*$  and  $(0, v_{\delta, NP}^*)$  does not exist any more.

### 6.2 Neumann B.C. vs non-local dispersal with hostile surroundings

Second, we consider random dispersal with zero Neumann boundary condition versus non-local dispersal with hostile surroundings (5.9). Let  $a(x) = 16(x^2(1-x)^2) + 0.5$ . By Theorem 5.8, for small  $\delta$ , both  $(u^*, 0)$  and  $(0, v^*)$  are unstable and there is a positive equilibrium  $(u^{**}, v^{**}) \in X_N^{++} \times Y_{NP}^{++}$ . The results in Figures 2(a)-2(b) suggest that  $(u^{**}, v^{**})$  stable for small  $\delta$ . When  $\delta$  increase,  $(u^{**}, v^{**})$  disappears while  $(u^*, 0)$  becomes stable as shown in Figures 2(c) and 2(d). In Figure 3, we consider  $a(x) = 16(x^2(1-x)^2) - 0.5$ . Hence  $a(x) < 0$  for some  $x \in D$ . When  $\delta$  is small,  $(0, v_{\delta, NP}^*)$  is stable as shown in Figures 3(a)-3(b). Notice that this is very different from the case  $a(x) > 0$ . When  $\delta$  increases,  $(0, v_{\delta, NP}^*)$  becomes unstable and there is a stable positive equilibrium  $(u^{**}, v^{**})$  as shown in Figure 3(c) with  $\delta = 0.71$ . When  $\delta$  increases further,  $(u^{**}, v^{**})$  disappears and  $(u^*, 0)$  becomes stable as shown in Figure 3(d). As we can see from Figures 2 and 3, the zero Neumann boundary condition helps to compensate the disadvantage of the random dispersal.

### 6.3 Periodic environment: random vs non-local dispersal

The last example we demonstrate here is the random dispersal with periodic boundary condition versus nonlocal periodic dispersal (5.23). No matter what  $a(x)$  is and  $\delta$  is,  $(0, v_{\delta, P}^*)$  is stable as shown in Figures 4(a)-4(f). For  $a(x) > 0$ ,  $v_{\delta, P}^* \rightarrow a(x)$  as  $\delta \rightarrow 0$ . For  $a(x) < 0$  for some  $x \in D$ ,  $v_{\delta, NP}^* \rightarrow \max(a(x), 0)$  as  $\delta \rightarrow 0$ .

## 7 Discussions and future directions

We considered a mathematical model which consists of one reaction-diffusion equation and one integro-differential equation. The model describes two competing species that have the same population dynamics but two different dispersal strategies: the movement of

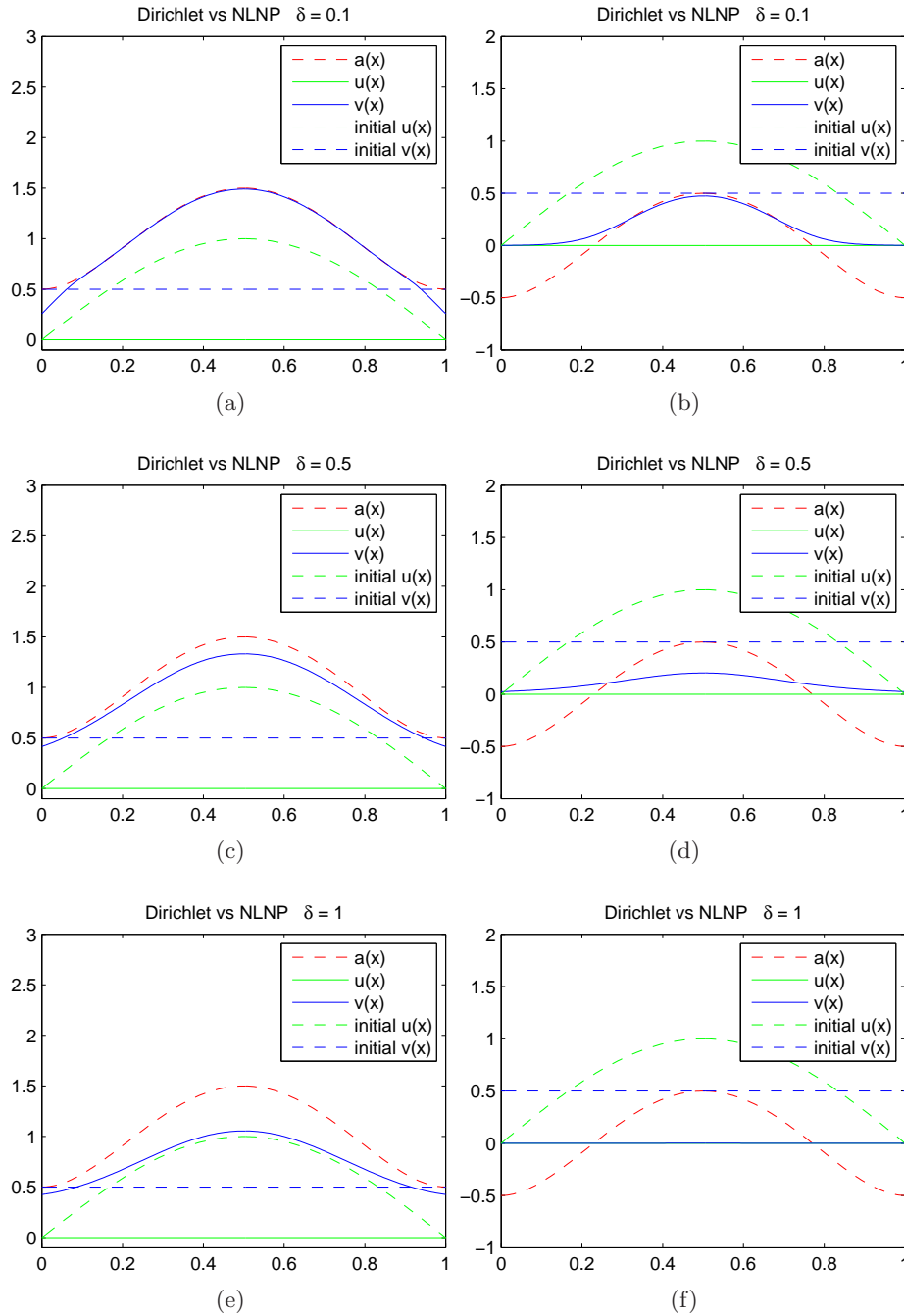


Figure 1: Dirichlet vs non-local: for different  $\delta$ . In the first column,  $a(x) = 16(x^2(1-x)^2) + 0.5$ . In the second column,  $a(x) = 16(x^2(1-x)^2) - 0.5$ . The grid size is  $dx = \frac{1}{200}$ .  $u_0(x) = \sin(\pi x)$ ,  $v_0(x) = 0.5$ , (a)-(b)  $\delta = 0.1$ , (c)-(d)  $\delta = 0.5$ , (e)-(f)  $\delta = 1$ .

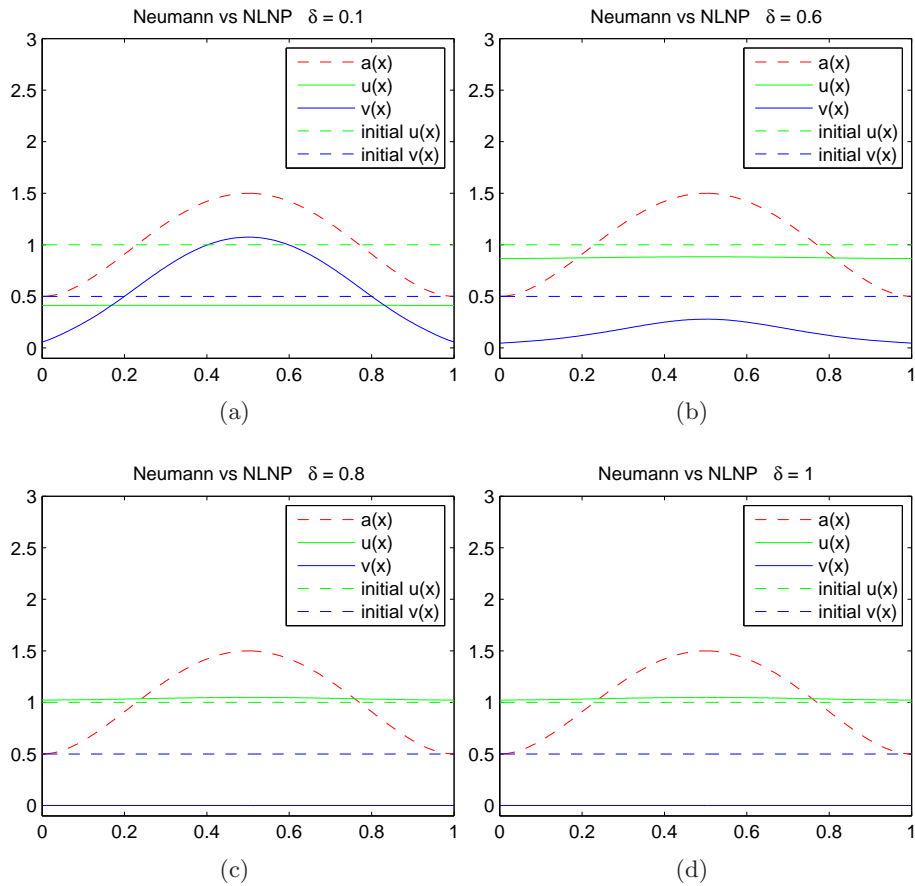


Figure 2: Neumann vs non-local: for different  $\delta$ . The grid size is  $dx = \frac{1}{200}$ .  $a(x) = 16(x^2(1-x)^2) + 0.5$ .  $u_0(x) = 1$ ,  $v_0(x) = 0.5$  (a)  $\delta = 0.1$ , (b)  $\delta = 0.6$ , (c)  $\delta = 0.8$ , (d)  $\delta = 1.0$ .

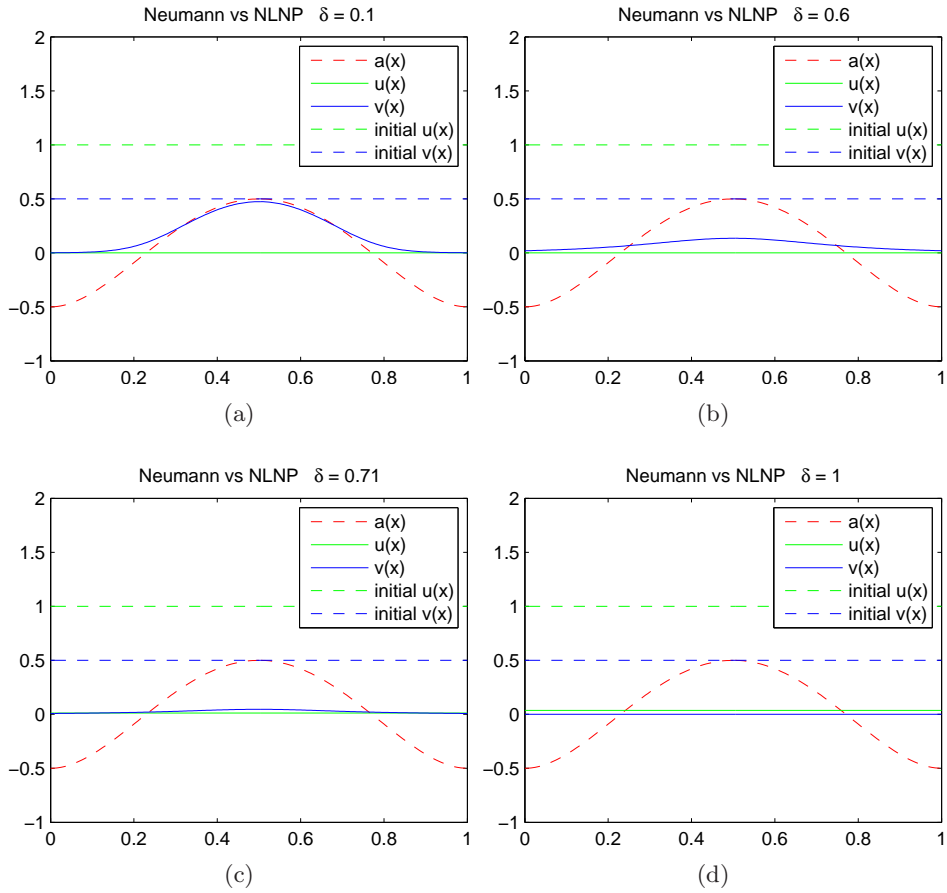


Figure 3: Neumann vs non-local: for different  $\delta$ . The grid size is  $dx = \frac{1}{200}$ .  $a(x) = 16(x^2(1-x)^2) - 0.5$ ,  $u_0(x) = 1$ ,  $v_0(x) = 0.5$ , (a)  $\delta = 0.1$ , (b)  $\delta = 0.6$ , (c)  $\delta = 0.71$ , (d)  $\delta = 1.0$ .

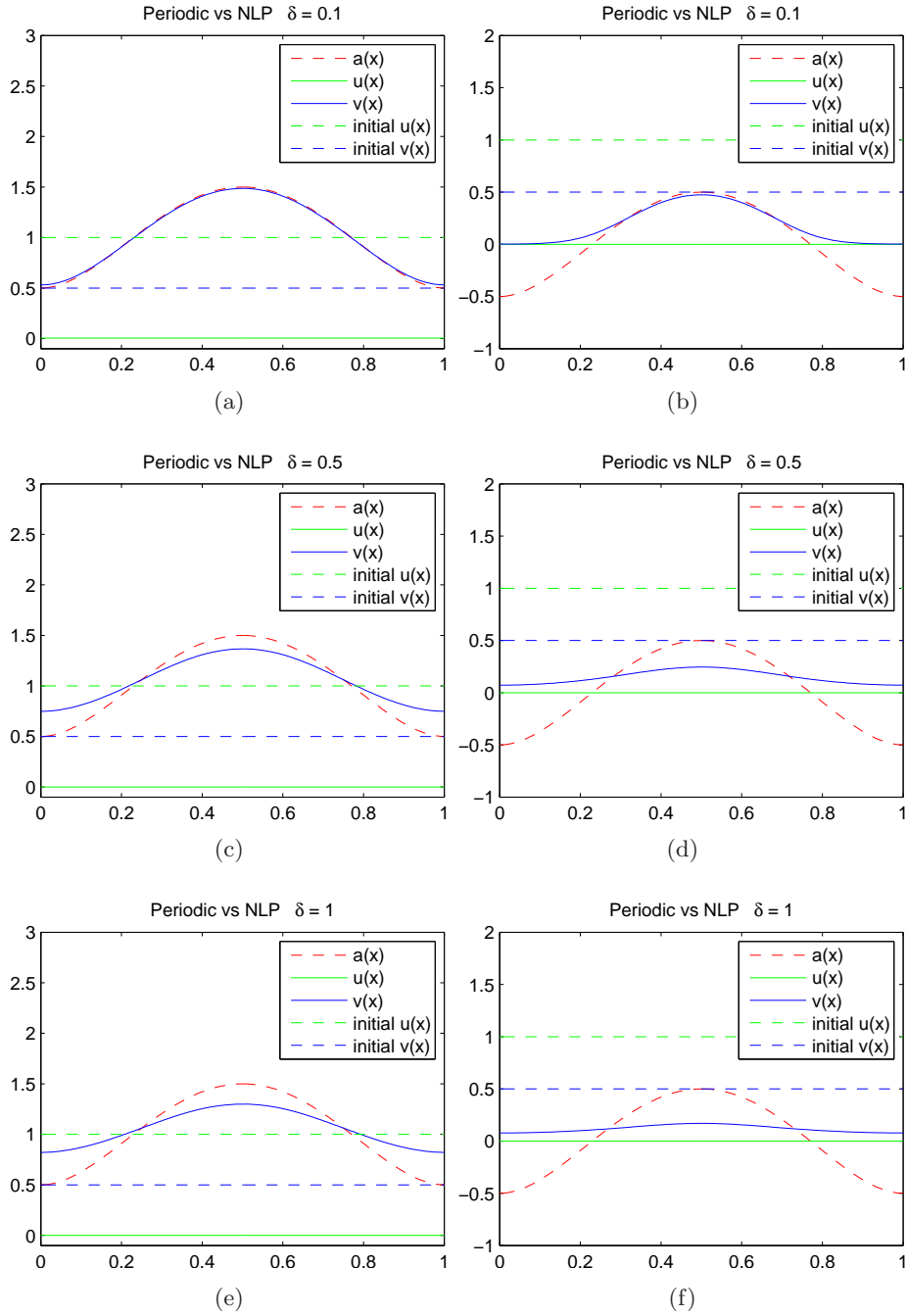


Figure 4: Periodic vs non-local periodic: for different  $\delta$ . In the first column,  $a(x) = 16(x^2(1-x)^2) + 0.5$ . In the second column,  $a(x) = 16(x^2(1-x)^2) - 0.5$ . The grid size is  $dx = \frac{1}{200}$ .  $u_0(x) = 1$ ,  $v_0(x) = 0.5$ , (a)-(b)  $\delta = 0.1$ , (c)-(d)  $\delta = 0.5$ , (e)-(f)  $\delta = 1.0$ . Interestingly, dynamics remains the same for all  $\delta$ .



one species is purely by random walk while the other species adopts a non-local dispersal strategy.

For both hostile surroundings and spatially periodic and heterogeneous environments we showed that the species with random dispersal can not invade when rare, while the species with non-local dispersal and small non-local interaction distance can always invade when rare. We conjecture that for hostile surroundings or spatially periodic and heterogeneous environments, the species with the non-local dispersal always wins, i.e., non-local dispersal is always preferred over random dispersal. This conjecture is strongly suggested by both our local stability analysis in Section 5 and the numerical results in Section 6. The numerical results further suggest that the selection for non-local dispersal seems to be very robust, irrelevant of the initial distribution of species, the non-local interaction distance, or the positivity of function  $a(x)$  (as long as  $a(x)$  is non-constant in the case of spatially periodic environments). The missing key in establishing the global stability of the semi-trivial equilibrium  $(0, v^*)$  is to show the non-existence of positive equilibria. Such mathematical problem appears to be non-standard and quite challenging as system (1.3) involves two different types of equations.

If the random dispersal strategy with the zero Neumann boundary condition is compared with non-local dispersal strategy with hostile surroundings, for the case when the intrinsic growth rate  $a(x)$  is positive and non-constant, each of the two species can invade when rare and both species can coexist, at least for small non-local interaction distance. The biological intuition is that for spatially heterogeneous environments, the zero-flux boundary condition can somehow help counterbalance the disadvantage caused by local dispersal. Interestingly, such biological reasoning is false for the case when  $a(x)$  changes sign, for which a new phenomenon occurs: the semi-trivial equilibrium  $(0, v^*)$  is stable for small  $\delta$ . If we regard the sub-domain  $\{x \in D : a(x) > 0\}$  as the source region and the sub-domain  $\{x \in D : a(x) < 0\}$  as the sink region, from these discussions we can predict that the dynamics of system (1.3) depend upon crucially on the source-sink population dynamics, at least for small non-local interaction distance  $\delta$ . We also plan to pursue along this line in future research.

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