

# Spatial-temporal dynamics of a Lotka-Volterra competition model with nonlocal dispersal under shifting environment

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## Abstract

We consider a competitive system with nonlocal dispersals in a 1-dimensional environment that is worsening with a constant speed, reflected by two shifting growth functions. By analyzing the spatial-temporal dynamics of the model system, we are able to identify certain ranges for the worsening speed  $c$ , respectively for (i) extinction of both species; (ii) extinction of one species but persistence of the other; (iii) persistence of both species. In the case of persistence of a species, it is achieved through spreading to the direction of favorable environment with certain speed(s), and some estimates of these speeds are also obtained. We also present some numeric simulation results which confirm our theoretical results, and in the mean time, motivate some challenging problems for future work.

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## 1. Introduction

In the real world, the habitat for a biological species is often temporally non-autonomous and spatially heterogeneous [39]. In addition to the seasonality and geographical differences, climate changes caused by global warming, industrialization and overdevelopment are also responsible for such a temporal-spatial heterogeneity. Climate changes naturally leads to changes of habitats for biological species. One may naturally wonder what impacts climate changes can have on the populations of various species, either when considering a single species, or when considering interacting species. There have been some field studies on such topics, for example, see [16,1,2,34,40] and the references therein.

There have also been some recent *quantitative* studies by *mathematical models* on the population dynamics of species, focusing on a special pattern of environment change, that is, shifting with constant speed. For example, to understand how species transfer their distribution over time and to predict whether the species can keep pace with the climate-induced range shifts in future, [6,17,43,20,28] adopted a practical approach of characterizing the habitats “on the move” by considering the growth rate  $r(t, x)$  of population to be dependent on time  $t$  and location  $x$  in the special form  $r(t, x) = r(x - ct)$ , reflecting the feature of environment shifting with constant speed  $c > 0$  toward the right direction. To explore the issue of species’ range distribution and spread with the varying habitat in response to the climate change, Li et al. [27] incorporated the aforementioned shifting pattern into the diffusive logistic equation, leading to the following equation

$$\partial_t u(t, x) = d \partial_{xx} u(t, x) + u(t, x) [r(x - ct) - u(t, x)], \quad (t, x) \in \mathbb{R}_+ \times \mathbb{R}, \quad (1)$$

where the growth function  $r(\cdot)$  is assumed to satisfy

- (A)  $r(\cdot)$  is continuous, nondecreasing, piecewise continuously differentiable with  $r(\pm\infty)$  finite and  $r(-\infty) < 0 < r(\infty)$ .

Assumption (A) combined with  $c > 0$  indicate that the region or habitat suitable for species growth is pushing to the right. The authors of [27] explored conditions for extinction and persistence of the species and the rightward spreading speed of the model (1) in the case of persistence. In recent work Hu et al. [23] investigated the spatial-temporal dynamics of (1) under the critical no-sign-change situation for the growth function:  $0 \leq r(-\infty) < r(\infty)$ . For slightly different content, Fang et al. [18] also derived a scalar equation of the form (1) from the classical SIS epidemic model to describe a pathogen’s population spread with the shifting host population.

For a model of the form (1), in addition to the species’ spreading speed in comparison with the speed of the environment shift, the feature of “shifting with given forced speed” represented by the moving frame allows one to explore the traveling wave solutions of the form  $u(t, x) = U(x - ct) = U(\xi)$  governed by a second order *non-autonomous* ODE with the moving coordinate  $\xi = x - ct$  as the independent variable. For the topic of traveling waves to (1) with assumption (A), the recent work from Hu and Zou [22] established its existence of forced extinction waves. By allowing different signs of  $c$ , Fang et al. [18] considered two scenarios: the favorable habitat is contracting ( $c > 0$ ) or expanding ( $c < 0$ ), and established the forced traveling waves for any  $c \in \mathbb{R}$  for the model (1). A more general version relative to (1) is the following reaction-diffusion equation

$$\partial_t u(t, x) = d \partial_{xx} u(t, x) + g(x - ct, u(t, x)), \quad (t, x) \in \mathbb{R}_+ \times \mathbb{R}. \quad (2)$$

The much earlier work [6] studied the traveling waves of (2) for the nonlinearity term  $g$  having support only on a finite interval, meaning that the environment was unfavorable outside a compact set and favorable inside. Later, Berestycki and Rossi [7] extended the results of [6] to higher dimensional space with more general type of  $g$ . Vo [35] removed the condition that *the favorable zone has compact support* in [6,7] and obtained similar results. More recently, Berestycki and Fang [9] have also investigated the forced waves of (2) when the nonlinearity reaction  $g(s, u)$  was asymptotically KPP type as  $s \rightarrow -\infty$ . The KPP type assumption means that there is no Allee effect. For models that consider the joint influences of Allee effect and climate change, we refer the reader to [32,10] and the references therein.

When studying phenotypical traits, Alfaro et al. [3] extended (1) to a more general equation by incorporating a nonlocal intra-species competition term and adopting the two dimensional spatial domain, leading to the following equation

$$\begin{aligned} \partial_t u(t, x, y) &= \Delta u(t, x, y) + \left[ r(x - ct, y) - \int_{\mathbb{R}} K(t, x, y, z) u(t, x, z) dz \right] \\ &\quad \times u(t, x, y), \quad (t, x, y) \in \mathbb{R}_+ \times \mathbb{R}^2, \\ u(0, x, y) &= u_0(x, y), \quad (x, y) \in \mathbb{R}^2. \end{aligned} \quad (3)$$

The authors determined a critical climate change speed such that the population could survive, spread or go to extinction under three scenarios of the growth function.

On the other hand, there are often more than one biological species sharing the same habitat and they typically compete for resources in the habitat. When the habitat experiences a shift in quality (due to, e.g., climate change), one would naturally wonder how such a shift with constant speed would interplay with the diffusions of the species and the competition between species to affect the population dynamics. In this regard, Potapov and Lewis [31] considered a Lotka-Volterra competition model in a domain with a moving range boundary, by which they obtained a critical patch size for each species to persist and spread. Later, Berestycki et al. [5] investigated the Lotka-Volterra competition model with both growth functions being “on the move” reflected by the form  $r_i(t, x) = r_i(x - ct)$ ,  $i = 1, 2$ , i.e., the following model system

$$\begin{cases} \partial_t u_1(t, x) = d_1 \partial_{xx} u_1(t, x) + u_1 [r_1(x - ct) - u_1 - a_1 u_2], \\ \partial_t u_2(t, x) = d_2 \partial_{xx} u_2(t, x) + u_2 [r_2(x - ct) - u_2 - a_2 u_1]. \end{cases} \quad (4)$$

They found that if the speed of the habitat edge exceeded the Fisher invasion speed of the advancing species, an expanding gap would occur. More recently, Zhang et al. [42] and Yuan et al. [41] also studied the spreading dynamics of such a Lotka-Volterra competition system with shifting growth functions, from different motivations and viewpoints, under the assumption that the growth functions  $r_1(\cdot)$  and  $r_2(\cdot)$  satisfied (A). The former focused on the persistence and extinction for two species, while the latter aimed at comparing the effect of different dispersal rates on the spatial-temporal dynamics for the two species when the habitat worsened with a constant speed.

As far as dispersion is concerned, in addition to random diffusion represented by the Laplacian in (1), (2), (3) and (4), for some species and under some circumstances, nonlocal dispersion is more plausible [25]. Since a population's vulnerability to climate change manifests an intricate relationship to its dispersal behavior, a nonlocal dispersal strategy can accommodate the intrinsic variability in individuals' capacity throughout a long range dispersion. Thus, under the worsening environment induced by climate change or global warming, among the key factors are how far individual animals or plant seeds can move, and how a species would evolve with a nonlocal dispersion strategy [26]. The long-range dispersion or nonlocal internal interactions widely exist in ecology and numerous data currently available have demonstrated these phenomena (e.g., see [13,11,24,12,4,15,14,33,19,21,8] and the references therein). Under a shifting effect in the growth rate, the recent work of Li et al. [29], Wang and Zhao [36] studied the persistence criterion and existence, uniqueness as well as stability of extinction wave for the following nonlocal dispersal population model in a shifting environment

$$\partial_t u(t, x) = d[(J * u)(t, x) - u(t, x)] + u(t, x)[r(x - ct) - u(t, x)], \quad (5)$$

where  $r(\cdot)$  was also assumed to satisfy (A) and  $(J * u)(t, x) = \int_{\mathbb{R}} J(x - y)u(t, y)dy$  with the kernel  $J(\cdot)$  satisfying the normative condition  $\int_{\mathbb{R}} J(s)ds = 1$ . Hence (5) is a result of replacing the random diffusion term  $d\partial_{xx}u(t, x)$  in (1) by the nonlocal dispersion term  $d[(J * u)(t, x) - u(t, x)]$  with  $d$  being the jumping rate.

Motivated by the aforementioned works, in this paper, we are interested in the spreading population dynamics of two competing species that adopt nonlocal dispersion strategy and face a shifting habitat. More precisely, we will consider the following Lotka-Volterra competition system

$$\begin{cases} \partial_t u_1(t, x) = d_1[(J_1 * u_1)(t, x) - u_1(t, x)] + u_1[r_1(x - ct) - u_1 - a_1 u_2], \\ \partial_t u_2(t, x) = d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + u_2[r_2(x - ct) - u_2 - a_2 u_1], \end{cases} \quad (6)$$

where  $(J_i * u_i)(t, x) = \int_{\mathbb{R}} J_i(x - y)u_i(t, y)dy$  and  $a_i, d_i > 0, i = 1, 2$ . Keeping in the same line as in [27,42,41,29], we will assume, throughout the paper, the following conditions on the growth functions  $r_i(\cdot)$  and the kernel functions  $J_i(\cdot)$  for  $i = 1, 2$ :

- (A1)  $r_i(x)$  is continuous and nondecreasing with  $-\infty < r_i(-\infty) < 0 < r_i(\infty) < \infty$ ;
- (A2)  $J_i \in C(\mathbb{R}, \mathbb{R}^+)$  is even with  $\int_{\mathbb{R}} J_i(y)dy = 1$ , and each  $\int_0^\infty J_i(y)e^{\mu y}dy$  converges for  $\mu > 0$ .

However, here we remove the common assumption that the nonlocal dispersal kernel is compactly supported (e.g., see [29]), and the resulting difficulty can be tackled by introducing a proper truncation function later.

The rest of this paper is organized as follows. In Section 2, we study the well-posedness including the existence and uniqueness of solution of (6), and establish a comparison principle for (6). In Section 3, we investigate criteria for extinction, persistence and displacement for the two competing species. In Section 4, we present some simulations to illustrate analytical results. We conclude the paper by Section 5 where we summarize our main results and discuss some possible future relevant project.

## 2. Existence, uniqueness and comparison principle

Consider the homogeneous kinetic system of the model system (6):

$$\begin{aligned} u_1'(t) &= u_1[r_1(\infty) - u_1 - a_1u_2], \\ u_2'(t) &= u_2[r_2(\infty) - u_2 - a_2u_1]. \end{aligned} \quad (7)$$

To ensure the existence of co-existence state to the system (7), we impose the following condition

$$r_1(\infty) > a_1r_2(\infty) \text{ and } r_2(\infty) > a_2r_1(\infty), \quad (8)$$

which implies  $a_1a_2 < 1$ . If (8) holds, then the co-existence equilibrium  $(u_1^*, u_2^*)$  exists and is stable, where

$$u_1^* = \frac{r_1(\infty) - a_1r_2(\infty)}{1 - a_1a_2}, \quad u_2^* = \frac{r_2(\infty) - a_2r_1(\infty)}{1 - a_1a_2}.$$

We now address the well-posedness of the Cauchy problem

$$\begin{cases} \partial_t u_1(t, x) = d_1[(J_1 * u_1)(t, x) - u_1(t, x)] + u_1[r_1(x - ct) - u_1 - a_1u_2], \\ \partial_t u_2(t, x) = d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + u_2[r_2(x - ct) - u_2 - a_2u_1], \\ u(0, x) := (u_1(0, x), u_2(0, x)) = (u_{10}(x), u_{20}(x)) =: u_0(x). \end{cases} \quad (9)$$

Let  $\mathbb{X} = \text{UC}(\mathbb{R}, \mathbb{R}^2) \cap L^\infty(\mathbb{R}, \mathbb{R}^2)$  be the set of all uniformly continuous and bounded vector functions from  $\mathbb{R}$  to  $\mathbb{R}^2$  equipped with the norm  $\|\phi\|_{\mathbb{X}} := \|\phi_1\| + \|\phi_2\|$ , where  $\|\phi_i\| := \sup_{x \in \mathbb{R}} |\phi_i(x)|$ . Denote  $\mathbb{X}_+ = \{\phi = (\phi_1, \phi_2) \in \mathbb{X} : (\phi_1, \phi_2)(x) \geq (0, 0) \text{ in } x \in \mathbb{R}\}$ . Then  $\mathbb{X}_+$  is a closed cone of  $\mathbb{X}$  and  $\mathbb{X}$  is a Banach lattice under the partial ordering induced by  $\mathbb{X}_+$ .

Consider the following auxiliary linear system

$$\partial_t u(t, x) = D \int_{\mathbb{R}} J(x - y)u(t, y)dy - Hu(t, x) \quad (10)$$

subjected to the initial data  $u(0, x) = \phi \in \mathbb{X}$ , where  $D = \text{diag}(d_1, d_2)$ ,  $J = \text{diag}(J_1, J_2)$ ,  $H = \text{diag}(h_1, h_2)$  and  $u = (u_1, u_2)$ . Obviously, (10) is a generalization of the linear part of (6) in the sense that when  $H = D$ , it reduces to (6). Define  $\mathcal{L}\phi = D \int_{\mathbb{R}} J(\cdot - y)\phi(y)dy - H\phi$ . Then the linear equations (10) with the initial data  $\phi \in \mathbb{X}$  can be rewritten as the abstract Cauchy problem

$$\frac{du(t)}{dt} = \mathcal{L}u(t), \quad u(0) = \phi \in \mathbb{X}.$$

Hence  $t \mapsto u(t) := e^{\mathcal{L}t}\phi$  with  $e^{\mathcal{L}t} = \sum_{l=0}^{\infty} \frac{(t\mathcal{L})^l}{l!}$  is the unique solution of (10). Since  $D$  and  $J$  are diagonal, the semigroup operator  $e^{\mathcal{L}t}\phi := u(t, \cdot)$  is order preserving on each component. Note that the solution of (10) satisfies the following integral equation

$$u(t, x) = e^{-Ht} \phi(x) + \int_0^t e^{-H(t-s)} D \int_{\mathbb{R}} J(x-y) u(s, y) dy ds. \quad (11)$$

Define  $J^{(0)}(x) = \delta(x)$ , the classic Dirac delta function and hence  $J^{(0)} * \phi = \phi$ . Recursively define  $J^{(l)} * \phi = J * [J^{(l-1)} * \phi]$  for  $l = 1, 2, \dots$ . Here  $J * \phi$  denotes the convolution defined by

$$[J * \phi](x) = \int_{\mathbb{R}} J(x-y) \phi(y) dy.$$

Then by iterating (11), the unique mild solution of (10) can be expressed as

$$u(t, x) = \left[ e^{\mathcal{L}t} \phi \right](x) = e^{-Ht} \sum_{l=0}^{\infty} \frac{(tD)^l}{l!} [J^{(l)} * \phi](x). \quad (12)$$

Let

$$\begin{aligned} f_1(x, u_1, u_2) &= u_1 [r_1(x) - u_1 - a_1 u_2], \\ f_2(x, u_1, u_2) &= u_2 [r_2(x) - u_2 - a_2 u_1]. \end{aligned}$$

For any  $0 \leq u_1, v_1 \leq r_1(\infty)$ ,  $0 \leq u_2, v_2 \leq r_2(\infty)$  and  $x \in \mathbb{R}$ , we have

$$|f_i(x, u_1, u_2) - f_i(x, v_1, v_2)| \leq \rho_i [|u_1 - v_1| + |u_2 - v_2|], \quad (13)$$

where  $\rho_i = 2r_i(\infty) - r_i(-\infty) + a_i [r_1(\infty) + r_2(\infty)]$ . Inequality (13) implies that  $f_i(x, u_1, u_2)$  is Lipschitz continuous in  $(u_1, u_2) \in [0, r_1(\infty)] \times [0, r_2(\infty)]$  for any  $x \in \mathbb{R}$  with  $i = 1, 2$ . Define

$$F_i(x, u_1, u_2) = \rho_i u_i + f_i(x, u_1, u_2), \quad i = 1, 2. \quad (14)$$

Then  $F_i(x, u_1, u_2)$  is nondecreasing in  $u_i \in [0, r_i(\infty)]$  for  $i = 1, 2$ . Let

$$\mathbb{X}_{r(\infty)} := \{(\phi_1, \phi_2) \in \mathbb{X} : (0, 0) \leq (\phi_1, \phi_2)(x) \leq (r_1(\infty), r_2(\infty)) \text{ in } \mathbb{R}\}.$$

Rewrite the Cauchy problem (9) as

$$\begin{cases} \partial_t u(t, x) = D(J * u)(t, x) - (D + \rho)u(t, x) + F(x - ct, u(t, x)), \\ u(0, \cdot) = u_0(\cdot) \in \mathbb{X}_{r(\infty)}, \end{cases} \quad (15)$$

where  $\rho = \text{diag}(\rho_1, \rho_2)$  and  $F = (F_1, F_2)$ . Choosing  $H = D + \rho$  in the definition of  $\mathcal{L}$ , the solution of (15) satisfies the integral equation by the variation of parameters

$$\begin{aligned} u(t, x) &= e^{\mathcal{L}t} u_0(x) + \int_0^t e^{\mathcal{L}(t-s)} F(x - cs, u(s, x)) ds \\ &=: [Gu](t, x). \end{aligned} \quad (16)$$

It follows that any solution of (9) can be seen as a fixed-point of the operator  $G$ , i.e.  $Gu = u$  in  $C(\mathbb{R}_+, \mathbb{X}_{r(\infty)})$ .

To address the existence and uniqueness of solution of (16), we first give the definition of the ordered upper and lower solutions for (16).

**Definition 2.1.** A pair of vector functions  $\tilde{u} = (\tilde{u}_1, \tilde{u}_2)$ ,  $\hat{u} = (\hat{u}_1, \hat{u}_2) \in C([0, \tau], \mathbb{X}_+)$  with  $\tau > 0$  are called ordered upper and lower solutions of (16) if  $(\tilde{u}_1, \tilde{u}_2) \geq (\hat{u}_1, \hat{u}_2) \geq (0, 0)$  and further satisfy

$$\begin{aligned} \tilde{u}_1(t, x) - [G(\tilde{u}_1, \hat{u}_2)]_1(t, x) &\geq 0 \geq \hat{u}_1(t, x) - [G(\hat{u}_1, \tilde{u}_2)]_1(t, x), \\ \tilde{u}_2(t, x) - [G(\hat{u}_1, \tilde{u}_2)]_2(t, x) &\geq 0 \geq \hat{u}_2(t, x) - [G(\tilde{u}_1, \hat{u}_2)]_2(t, x). \end{aligned} \quad (17)$$

**Remark 2.1.** If  $\tilde{u}, \hat{u} \in C([0, \tau] \times \mathbb{R}, \mathbb{R}^2)$  are  $C^1$  in  $t \in (0, \tau)$  with  $\tilde{u}(t, \cdot), \hat{u}(t, \cdot) \in \mathbb{X}_+$ , and for  $t \in (0, \tau)$  they satisfy

$$\begin{aligned} &\partial_t \tilde{u}_1 - d_1[(J_1 * \tilde{u}_1)(t, x) - \tilde{u}_1(t, x)] - f_1(x - ct, \tilde{u}_1, \hat{u}_2) \\ &\geq 0 \geq \partial_t \hat{u}_1 - d_1[(J_1 * \hat{u}_1)(t, x) - \hat{u}_1(t, x)] - f_1(x - ct, \hat{u}_1, \tilde{u}_2), \\ &\partial_t \tilde{u}_2 - d_2[(J_2 * \tilde{u}_2)(t, x) - \tilde{u}_2(t, x)] - f_2(x - ct, \hat{u}_1, \tilde{u}_2) \\ &\geq 0 \geq \partial_t \hat{u}_2 - d_2[(J_2 * \hat{u}_2)(t, x) - \hat{u}_2(t, x)] - f_2(x - ct, \tilde{u}_1, \hat{u}_2), \\ &\tilde{u}_i(0, x) \geq u_i(0, x) \geq \hat{u}_i(0, x), \quad x \in \mathbb{R}, i = 1, 2, \end{aligned}$$

then (17) holds (since  $e^{\mathcal{L}t}\mathbb{X}_+ \subset \mathbb{X}_+$  for all  $t \geq 0$ ), and hence  $\tilde{u}, \hat{u}$  are a pair of ordered upper and lower solutions of (9).

**Theorem 2.1.** If  $u_0 \in \mathbb{X}_{r(\infty)}$ , then the system (9) has a unique solution  $u(t, x)$  with  $u(0, x) = u_0(x)$  and  $u \in C(\mathbb{R}_+, \mathbb{X}_{r(\infty)})$ .

**Proof.** Let  $\tilde{u} \equiv (r_1(\infty), r_2(\infty))$ ,  $\hat{u} \equiv (0, 0)$ , then  $\tilde{u} \geq \hat{u}$  and it is easy to show  $\tilde{u}, \hat{u}$  are ordered upper and lower solutions of (16). Define

$$\begin{aligned} \bar{u}_1^{(k)}(t, x) &= e^{\mathcal{L}_1 t} u_{10}(x) + \int_0^t e^{\mathcal{L}_1(t-s)} F_1(x - cs, \bar{u}_1^{(k-1)}(s, x), \underline{u}_2^{(k-1)}(s, x)) ds, \\ \bar{u}_2^{(k)}(t, x) &= e^{\mathcal{L}_2 t} u_{20}(x) + \int_0^t e^{\mathcal{L}_2(t-s)} F_2(x - cs, \underline{u}_1^{(k-1)}(s, x), \bar{u}_2^{(k-1)}(s, x)) ds, \\ \underline{u}_1^{(k)}(t, x) &= e^{\mathcal{L}_1 t} u_{10}(x) + \int_0^t e^{\mathcal{L}_1(t-s)} F_1(x - cs, \underline{u}_1^{(k-1)}(s, x), \bar{u}_2^{(k-1)}(s, x)) ds, \\ \underline{u}_2^{(k)}(t, x) &= e^{\mathcal{L}_2 t} u_{20}(x) + \int_0^t e^{\mathcal{L}_2(t-s)} F_2(x - cs, \bar{u}_1^{(k-1)}(s, x), \underline{u}_2^{(k-1)}(s, x)) ds \end{aligned}$$

for  $k = 1, 2, \dots$ . Consider the corresponding sequences  $\{\bar{u}_1^{(k)}, \underline{u}_2^{(k)}\}$  and  $\{\underline{u}_1^{(k)}, \bar{u}_2^{(k)}\}$ , where  $(\bar{u}_1^{(0)}, \underline{u}_2^{(0)}) = (\tilde{u}_1, \hat{u}_2)$  and  $(\underline{u}_1^{(0)}, \bar{u}_2^{(0)}) = (\hat{u}_1, \tilde{u}_2)$ . We now show that

$$0 \leq \underline{u}_i^{(k)} \leq \underline{u}_i^{(k+1)} \leq \bar{u}_i^{(k+1)} \leq \bar{u}_i^{(k)} \leq r_i(\infty), \quad (18)$$

for  $k = 1, 2, \dots$  and  $i = 1, 2$ . By the iteration processes defined above and Definition 2.1, we obtain

$$\begin{aligned} \bar{u}_1^{(1)}(t, x) &\leq e^{\mathcal{L}_1 t} \tilde{u}_1(0, x) + \int_0^t e^{\mathcal{L}_1(t-s)} F_1(x - cs, \tilde{u}_1(s, x), \hat{u}_2(s, x)) ds \\ &\leq \tilde{u}_1(t, x) = \bar{u}_1^{(0)}(t, x) \end{aligned}$$

and

$$\begin{aligned} \underline{u}_2^{(1)}(t, x) &\geq e^{\mathcal{L}_2 t} \hat{u}_2(0, x) + \int_0^t e^{\mathcal{L}_2(t-s)} F_2(x - cs, \tilde{u}_1(s, x), \hat{u}_2(s, x)) ds \\ &\geq \hat{u}_2(t, x) = \underline{u}_2^{(0)}(t, x). \end{aligned}$$

A similar argument, using the property of  $(\hat{u}_1, \tilde{u}_2)$ , gives  $\underline{u}_1^{(1)} \geq \underline{u}_1^{(0)}$  and  $\bar{u}_2^{(1)} \leq \bar{u}_2^{(0)}$ . Note

$$\begin{aligned} &\bar{u}_1^{(1)}(t, x) - \underline{u}_1^{(1)}(t, x) \\ &= \int_0^t e^{\mathcal{L}_1(t-s)} [F_1(x - cs, \tilde{u}_1, \hat{u}_2) - F_1(x - cs, \hat{u}_1, \hat{u}_2)] ds \\ &\quad + \int_0^t e^{\mathcal{L}_1(t-s)} [F_1(x - cs, \hat{u}_1, \hat{u}_2) - F_1(x - cs, \hat{u}_1, \tilde{u}_2)] ds \geq 0. \end{aligned}$$

Similarly, we can show that  $\bar{u}_2^{(1)}(t, x) \geq \underline{u}_2^{(1)}(t, x)$ . An induction argument further leads to (18). Hence,  $\underline{u}_i(t, x) = \lim_{k \rightarrow \infty} \underline{u}_i^{(k)}(t, x)$  and  $\bar{u}_i(t, x) = \lim_{k \rightarrow \infty} \bar{u}_i^{(k)}(t, x)$  both exist and satisfy  $0 \leq \underline{u}_i(t, x) \leq \bar{u}_i(t, x) \leq r_i(\infty)$ ,  $i = 1, 2$ . Moreover, both  $\underline{u} = (\underline{u}_1, \underline{u}_2)$  and  $\bar{u} = (\bar{u}_1, \bar{u}_2)$  are in  $C(\mathbb{R}_+, \mathbb{X}_r(\infty))$  and satisfy

$$\begin{aligned} \bar{u}_1(t, x) &= e^{\mathcal{L}_1 t} u_{10}(x) + \int_0^t e^{\mathcal{L}_1(t-s)} F_1(x - cs, \bar{u}_1(s, x), \underline{u}_2(s, x)) ds, \\ \bar{u}_2(t, x) &= e^{\mathcal{L}_2 t} u_{20}(x) + \int_0^t e^{\mathcal{L}_2(t-s)} F_2(x - cs, \underline{u}_1(s, x), \bar{u}_2(s, x)) ds, \end{aligned}$$



$$\begin{aligned}
\underline{u}_1(t, x) &= e^{\mathcal{L}_1 t} u_{10}(x) + \int_0^t e^{\mathcal{L}_1(t-s)} F_1(x - cs, \underline{u}_1(s, x), \bar{u}_2(s, x)) ds, \\
\underline{u}_2(t, x) &= e^{\mathcal{L}_2 t} u_{20}(x) + \int_0^t e^{\mathcal{L}_2(t-s)} F_2(x - cs, \bar{u}_1(s, x), \underline{u}_2(s, x)) ds
\end{aligned} \tag{19}$$

by the Lebesgue's dominated convergence theorem. We next show that  $\bar{u}(t, x) = \underline{u}(t, x) = u(t, x)$  and hence (16) holds. Note that  $\|J_i^{(1)} * p_i\| = \|J_i * J_i^{(0)} * p_i\| = \|J_i * p_i\| = \|\int_{\mathbb{R}} J_i(y) p_i(\cdot - y) dy\| \leq \|p_i\|$ . Induction yields  $\|J_i^{(l)} * p_i\| \leq \|p_i\|$  for  $l = 0, 1, 2, \dots$ . By (12), we see that

$$\|e^{\mathcal{L}_i t} p_i\| \leq e^{-(d_i + \rho_i)t} \sum_{l=0}^{\infty} \frac{(d_i t)^l}{l!} \|p_i\| = e^{-(d_i + \rho_i)t} \cdot e^{d_i t} \|p_i\| = e^{-\rho_i t} \|p_i\|. \tag{20}$$

It follows from (19), (13), (14) and (20) that

$$\begin{aligned}
& |\bar{u}_1(t, x) - \underline{u}_1(t, x)| \\
& \leq \int_0^t e^{\mathcal{L}_1(t-s)} 2\rho_1 \left[ (\bar{u}_1(s, x) - \underline{u}_1(s, x)) + (\bar{u}_2(s, x) - \underline{u}_2(s, x)) \right] ds \\
& \leq 2\rho_1 \int_0^t e^{-\rho_1(t-s)} \left[ \|\bar{u}_1(s, \cdot) - \underline{u}_1(s, \cdot)\| + \|\bar{u}_2(s, \cdot) - \underline{u}_2(s, \cdot)\| \right] ds \\
& \leq 2\rho_1 \int_0^t e^{-\underline{\rho}(t-s)} \|\bar{u}(s, \cdot) - \underline{u}(s, \cdot)\|_{\mathbb{X}} ds,
\end{aligned}$$

where  $\underline{\rho} = \min\{\rho_1, \rho_2\}$ . Similarly, we have

$$|\bar{u}_2(t, x) - \underline{u}_2(t, x)| \leq 2\rho_2 \int_0^t e^{-\underline{\rho}(t-s)} \|\bar{u}(s, \cdot) - \underline{u}(s, \cdot)\|_{\mathbb{X}} ds.$$

Thus

$$e^{\underline{\rho} t} \|\bar{u}(t, \cdot) - \underline{u}(t, \cdot)\|_{\mathbb{X}} \leq 2(\rho_1 + \rho_2) \int_0^t e^{\underline{\rho} s} \|\bar{u}(s, \cdot) - \underline{u}(s, \cdot)\|_{\mathbb{X}} ds.$$

By the Gronwall's inequality, one must have  $\bar{u}(t, x) = \underline{u}(t, x)$ . Therefore, the Cauchy problem (9) has a unique solution  $u(t, x) = (u_1(t, x), u_2(t, x))$  satisfying  $0 \leq u_i(t, x) \leq r_i(\infty)$  for  $t > 0, x \in \mathbb{R}$  and  $i = 1, 2$ . The proof is complete.  $\square$

**Lemma 2.1** (Comparison principle). *The following statements hold.*

- (i) *Let  $v(t, x)$  and  $u(t, x)$  be a pair of upper and lower solutions of (9) and  $v(t, \cdot), u(t, \cdot) \in \mathbb{X}_{r(\infty)}$ . If  $v(0, x) \geq u(0, x)$ , then  $v(t, x) \geq u(t, x)$  for all  $t > 0$  and  $x \in \mathbb{R}$ .*
- (ii) *Let  $v(t, x), u(t, x)$  be two solutions of (9) with initial data  $v_0, u_0 \in \mathbb{X}_{r(\infty)}$ . If  $v_0(x) \geq u_0(x)$ , then  $v(t, x) \geq u(t, x)$  for all  $t > 0$  and  $x \in \mathbb{R}$ .*

**Proof.** To prove (i), we let  $T > 0$  be fixed and define  $\alpha = \max\{r_1(\infty)(1 + a_1), r_2(\infty)(1 + a_2)\}$ . For  $\varsigma > 0$ , denote  $w_1(t, x) = v_1(t, x) - u_1(t, x) + \varsigma e^{\alpha t}$  and  $w_2(t, x) = v_2(t, x) - u_2(t, x) + \varsigma e^{\alpha t}$ . We claim that  $(w_1(t, \cdot), w_2(t, \cdot)) \gg (0, 0)$  for  $t \in (0, T]$ . Assuming the claim is not true, define

$$t_* = \inf\{t : t \in [0, T], w_1(t, x) \leq 0 \text{ or } w_2(t, x) \leq 0 \text{ for some } x \in \mathbb{R}\}.$$

Then  $t_* > 0$  and the continuity implies  $w_1(t, x) > 0, w_2(t, x) > 0$  for  $t \in [0, t_*)$  and  $x \in \mathbb{R}$ . Note for  $t \in (0, t_*]$ ,

$$\begin{aligned} \partial_t w_1 &= \partial_t v_1(t, x) - \partial_t u_1(t, x) + \alpha \varsigma e^{\alpha t} \\ &\geq d_1[(J_1 * w_1)(t, x) - w_1(t, x)] + \alpha \varsigma e^{\alpha t} - a_1 u_1(u_2 - v_2) \\ &\quad + [r_1(x - ct) - (v_1 + u_1) - a_1 u_2](v_1 - u_1) \\ &\geq d_1[(J_1 * w_1)(t, x) - w_1(t, x)] + [r_1(x - ct) - (v_1 + u_1) - a_1 u_2] w_1 \\ &\quad + \varsigma e^{\alpha t} [\alpha - r_1(x - ct) + v_1 + u_1 + a_1 u_2 - a_1 u_1] \\ &\geq d_1[(J_1 * w_1)(t, x) - w_1(t, x)] + [r_1(x - ct) - (v_1 + u_1) - a_1 u_2] w_1. \end{aligned}$$

It then follows from [19, Proposition 2.1] that  $w_1(t, x) > 0$  for  $t \in [0, t_*]$  and  $x \in \mathbb{R}$ . In a similar way, we can show that  $w_2(t, x) > 0$  for  $t \in [0, t_*]$  and  $x \in \mathbb{R}$ . This is a contradiction, which implies that the claim holds. Hence,  $(w_1(t, \cdot), w_2(t, \cdot)) \gg (0, 0)$  for  $t \in (0, T]$ . Let  $\varsigma \rightarrow 0$ , we have  $v(t, \cdot) \geq u(t, \cdot)$  for  $t \in (0, T]$ . Since  $T > 0$  is arbitrariness, this proves (i).

(ii) is a special case of (i). The proof is complete.  $\square$

### 3. Extinction, persistence and displacement

For  $\mu > 0$ , we define

$$\tilde{\Delta}_i(x; \mu) = \frac{d_i \left[ \int_{\mathbb{R}} J_i(y) e^{\mu y} dy - 1 \right] + r_i(x) - a_i r_j(\infty)}{\mu}, \quad i \neq j \in \{1, 2\}.$$

Under (A1)-(A2) and (8), since  $r_i(x) - a_i r_j(\infty) > 0$  for large  $x > 0$ , one can easily verify that

$$\lim_{\mu \rightarrow 0^+} \tilde{\Delta}_i(x; \mu) = \infty \quad \text{and} \quad \lim_{\mu \rightarrow \infty} \tilde{\Delta}_i(x; \mu) = \infty, \quad \text{for large } x > 0.$$

This implies that for large  $x > 0$ , as function of  $\mu > 0$ ,  $\tilde{\Delta}_i(x, \mu)$  has at least one minimum. Note that

$$\partial_\mu \tilde{\Delta}_i(x; \mu) = \frac{1}{\mu} [\Phi_i(\mu) - \tilde{\Delta}_i(x; \mu)], \quad (21)$$

where

$$\Phi_i(\mu) = \frac{\partial}{\partial \mu} [\mu \tilde{\Delta}_i(x; \mu)] = d_i \int_{\mathbb{R}} J_i(y) y e^{\mu y} dy > 0.$$

Also note that

$$\partial_{\mu} [\mu^2 \partial_{\mu} \tilde{\Delta}_i(x; \mu)] = \partial_{\mu} [\mu (\Phi_i(\mu) - \tilde{\Delta}_i(x; \mu))] = \mu \Phi_i'(\mu) = \mu d_i \int_{\mathbb{R}} J_i(y) y^2 e^{\mu y} dy \geq 0,$$

meaning for large  $x > 0$ ,  $\mu^2 \partial_{\mu} \tilde{\Delta}_i(x; \mu)$  is nondecreasing in  $\mu > 0$  and hence,  $\partial_{\mu} \tilde{\Delta}_i(x; \mu)$  can have at most one positive zero for  $\mu$ . Combining the above arguments, we have shown that for large  $x > 0$ ,  $\tilde{\Delta}_i(x; \mu)$  admits exactly one (hence global) minimum  $\tilde{c}_i^*(x)$ , assuming that it is attained at  $\tilde{\mu}_i^*(x) > 0$ , that is,

$$\tilde{c}_i^*(x) = \inf_{\mu > 0} \tilde{\Delta}_i(x; \mu) = \tilde{\Delta}_i(x; \tilde{\mu}_i^*(x)) = \Phi_i(\tilde{\mu}_i^*(x)), \quad i = 1, 2. \quad (22)$$

Similarly (also see [29]), as for

$$\Delta_i(x; \mu) = \frac{d_i \left[ \int_{\mathbb{R}} J_i(y) e^{\mu y} dy - 1 \right] + r_i(x)}{\mu}, \quad i = 1, 2,$$

for large  $x > 0$ , there exists exactly one  $\mu_i^*(x) > 0$  such that

$$c_i^*(x) = \inf_{\mu > 0} \Delta_i(x; \mu) = \Delta_i(x; \mu_i^*(x)) \quad i = 1, 2. \quad (23)$$

In the sequel, we will see that the positive numbers  $c_i^*(\infty)$  and  $\tilde{c}_i^*(\infty)$  ( $i = 1, 2$ ) will play important roles in determining the spreading dynamics of (9). We start by the following result on the extinction of both species, caused by the *faster worsening speed of the environment* (i.e.,  $c > 0$  is large).

**Theorem 3.1.** Assume  $c > \max\{c_1^*(\infty), c_2^*(\infty)\}$  with  $c_i^*(\infty)$  defined in (23) by replacing  $x$  as  $\infty$ . Let  $u(t, x, u_0)$  be the unique solution of the Cauchy problem (9). If  $u_0 \in \mathbb{X}_{r(\infty)}$  has a compact support and  $\sup_{x \in \mathbb{R}} u_{i0}(x) < r_i(\infty)$ ,  $i = 1, 2$ , then for any  $\varepsilon > 0$ , there exists a  $T_0 > 0$  such that for all  $t \geq T_0$ ,  $u(t, x, u_0) \leq (\varepsilon, \varepsilon)$  for all  $x \in \mathbb{R}$ .

**Proof.** According to Theorem 2.1, we see that  $0 \leq u_i(t, x) \leq r_i(\infty)$  for  $t \geq 0$  and  $x \in \mathbb{R}$ . By [29, Theorem 4.5], the scalar equation

$$\partial_t w_i(t, x) = d_i [(J_i * w_i)(t, x) - w_i(t, x)] + w_i [r_i(x - ct) - w_i] \quad (24)$$

has a traveling wave front  $\psi_i(x - ct)$  with the profile function  $\psi_i(\cdot)$  nondecreasing and satisfying  $\psi_i(-\infty) = 0$  and  $\psi_i(\infty) = r_i(\infty)$ . Since  $u_{i0}(x)$  has a compact support and  $u_{i0}(x) < r_i(\infty)$  for all  $x \in \mathbb{R}$ , there exists a large enough number  $x_0 > 0$  such that  $\psi_i(x + x_0) > u_{i0}(x)$  for all  $x \in \mathbb{R}$ . Denote  $\tilde{u}_i(t, x) = \psi_i(x - ct + x_0)$  for all  $t \geq 0$  and  $x \in \mathbb{R}$ . We now show that  $(\tilde{u}_1(t, x), \tilde{u}_2(t, x))$

and  $(\hat{u}_1(t, x), \hat{u}_2(t, x)) = (0, 0)$  are a pair of ordered upper and lower solutions of (9). In fact, let  $z = x - ct + x_0$  and note that

$$\begin{aligned} \frac{\partial \tilde{u}_i(t, x)}{\partial t} &= -c\psi_i'(z) = d_i \left[ \int_{\mathbb{R}} J_i(y)\psi_i(z-y)dy - \psi_i(z) \right] \\ &\quad + \psi_i(z)[r_i(z) - \psi_i(z)] \\ &\geq d_i[(J_i * \tilde{u}_i)(t, x) - \tilde{u}_i(t, x)] + \tilde{u}_i[r_i(x - ct) - \tilde{u}_i] \end{aligned} \quad (25)$$

since  $r_i(\cdot)$  is nondecreasing. It follows from (25) that

$$\begin{aligned} &\partial_t \tilde{u}_1 - d_1[(J_1 * \tilde{u}_1)(t, x) - \tilde{u}_1(t, x)] - f_1(x - ct, \tilde{u}_1, \hat{u}_2) \\ &= \partial_t \tilde{u}_1 - d_1[(J_1 * \tilde{u}_1)(t, x) - \tilde{u}_1(t, x)] - \tilde{u}_1[r_1(x - ct) - \tilde{u}_1] \\ &\geq 0 = \partial_t \hat{u}_1 - d_1[(J_1 * \hat{u}_1)(t, x) - \hat{u}_1(t, x)] - f_1(x - ct, \hat{u}_1, \tilde{u}_2), \\ &\partial_t \tilde{u}_2 - d_2[(J_2 * \tilde{u}_2)(t, x) - \tilde{u}_2(t, x)] - f_2(x - ct, \hat{u}_1, \tilde{u}_2) \\ &= \partial_t \tilde{u}_2 - d_2[(J_2 * \tilde{u}_2)(t, x) - \tilde{u}_2(t, x)] - \tilde{u}_2[r_2(x - ct) - \tilde{u}_2] \\ &\geq 0 = \partial_t \hat{u}_2 - d_2[(J_2 * \hat{u}_2)(t, x) - \hat{u}_2(t, x)] - f_2(x - ct, \tilde{u}_1, \hat{u}_2). \end{aligned}$$

Also  $\tilde{u}_i(0, x) = \psi_i(x + x_0) > u_{i0}(x) \geq \hat{u}_i(0, x)$  for all  $x \in \mathbb{R}$ . Hence, by Remark 2.1,  $(\tilde{u}_1, \tilde{u}_2)$  and  $(0, 0)$  are a pair of ordered upper and lower solutions of (9). In view of the comparison principle, we obtain

$$u_i(t, x, u_0) \leq \tilde{u}_i(t, x) = \psi_i(x - ct + x_0) \quad \text{for all } t \geq 0 \text{ and } x \in \mathbb{R}.$$

For any  $\varepsilon > 0$ , since  $\psi_i(-\infty) = 0$ , we can pick a sufficiently large number  $M > 0$  such that  $\psi_i(-M + x_0) < \varepsilon$ . Thus the monotonicity of  $\psi_i$  yields that

$$u_i(t, x, u_0) \leq \psi_i(x - ct + x_0) \leq \psi_i(-M + x_0) < \varepsilon, \quad \forall t \geq 0, x \leq -M + ct. \quad (26)$$

Let  $v_i(t, x, u_0)$  be the unique solution of the following equation

$$\partial_t v_i(t, x) = d_i[(J_i * v_i)(t, x) - v_i(t, x)] + v_i[r_i(\infty) - v_i] \quad (27)$$

with  $v_i(0, x, u_0) = u_{i0}(x)$  for  $x \in \mathbb{R}$ . By Lutscher et al. [30, Theorem 3.2],  $c_i^*(\infty)$  is the spreading speed for (27). Therefore for any fixed  $c_i \in (c_i^*(\infty), c)$ , it must be  $\lim_{t \rightarrow \infty} \sup_{x \geq c_i t} v_i(t, x, u_0) = 0$ . Using a similar argument to the above, we can prove  $(v_1, v_2)$  and  $(0, 0)$  are a pair of ordered upper and lower solutions of (9). Then, by the comparison principle again, we know that  $\lim_{t \rightarrow \infty} \sup_{x \geq c_i t} u_i(t, x, u_0) = 0$ . Thus there exists some  $T_1 > 0$  such that

$$u_i(t, x, u_0) < \varepsilon \quad \text{for all } t \geq T_1 \text{ and } x \geq c_i t. \quad (28)$$

Let  $T_0 = \max\{T_1, M/(c - c_1), M/(c - c_2)\}$ , then  $-M + ct \geq c_i t$  for all  $t \geq T_0$ . This, together with (26) and (28) result in  $u_i(t, x, u_0) \leq \varepsilon$  for all  $t \geq T_0$  and  $x \in \mathbb{R}$ , completing the proof.  $\square$

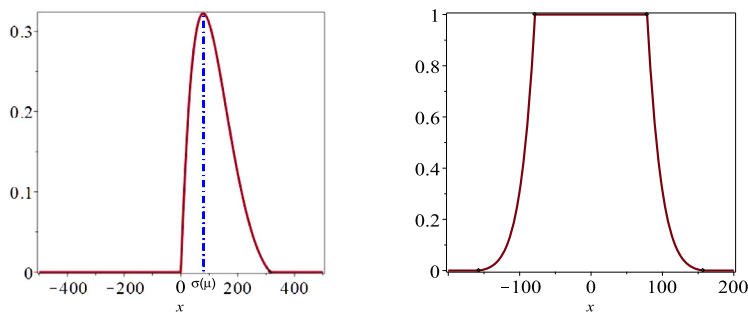


Fig. 1. Illustration of the function  $\eta(\mu; x)$  with parameters  $\mu = \gamma = 0.01$  in the left. The maximum of  $\eta(\mu; x)$  is obtained at  $x = \sigma(\mu)$  and  $0 \leq \eta \leq 1$ . Illustration of the symmetric cutoff function  $C(x)$  with parameters  $\mu = 0.05$  and  $\gamma = 0.01$  in the right.

Next, we show that if the environmental worsening speed is not so fast, then both two species can be persistent. To this end, we need some preparations. Denote

$$\tilde{c}^*(x) = \min\{\tilde{c}_1^*(x), \tilde{c}_2^*(x)\}, \quad (29)$$

where  $\tilde{c}_i^*(x)$  is defined in (22). We now introduce an auxiliary function which was first proposed by Weinberger [37]. For given  $\mu, \gamma > 0$ , let

$$\eta(\mu; x) = \begin{cases} e^{-\mu x} \sin(\gamma x), & 0 \leq x \leq \frac{\pi}{\gamma}, \\ 0, & \text{elsewhere.} \end{cases} \quad (30)$$

The function  $\eta(\mu; x)$  is continuous for all  $x$  and is  $C^2$  in  $x$  when  $x \neq 0, \pi/\gamma$ . The maximum of  $\eta(\mu; x)$  is obtained at  $x = \sigma(\mu) = \frac{1}{\gamma} \arctan(\frac{\gamma}{\mu})$  and  $\sigma(\mu)$  is strictly decreasing function of  $\mu$ . To give the readers some idea about this function, we plot it in Fig. 1 (left) with  $\mu = \gamma = 0.01$ . Let  $C(x) : \mathbb{R} \rightarrow [0, 1]$  be defined by

$$C(x) = \begin{cases} 1, & |x| \leq \frac{\pi}{4\gamma}, \\ e^{\frac{\mu\pi}{4\gamma}} e^{-\mu|x|} \sin(2\gamma|x|), & \frac{\pi}{4\gamma} \leq |x| \leq \frac{\pi}{2\gamma}, \\ 0, & |x| > \frac{\pi}{2\gamma}. \end{cases} \quad (31)$$

Obviously,  $C(x)$  is a continuous and symmetric cutoff function, see Fig. 1 (right) for  $C(x)$  with  $\mu = 0.05$  and  $\gamma = 0.01$ .

For  $\mu > 0$  and  $\gamma > 0$ , we further define

$$\begin{aligned} \Gamma_i(\mu, \gamma) &= \frac{d_i}{\gamma} \int_{\mathbb{R}} J_i(y) C(y) e^{\mu y} \sin(\gamma y) dy \\ &= \frac{d_i}{\gamma} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y) C(y) e^{\mu y} \sin(\gamma y) dy, \quad i = 1, 2. \end{aligned} \quad (32)$$

Since  $J_i$  and  $C$  are symmetric,  $\Gamma_i(\mu, \gamma)$  can be further expressed as

$$\Gamma_i(\mu, \gamma) = \frac{d_i}{\gamma} \int_0^{\frac{\pi}{2\gamma}} J_i(y) C(y) [e^{\mu y} - e^{-\mu y}] \sin(\gamma y) dy.$$

Thus  $\Gamma_i(\mu, \gamma) > 0$  and  $\Gamma_i(\mu, \gamma)$  is nondecreasing in  $\mu$ . Let  $\ell$  be so large that  $r_1(\ell) > a_1 r_2(\infty)$  and  $r_2(\ell) > a_2 r_1(\infty)$ . Define

$$\Psi_i(\gamma; \ell, \mu) = \frac{d_i \left[ \int_{\mathbb{R}} J_i(y) C(y) e^{\mu y} \cos(\gamma y) dy - 1 \right] + r_i(\ell) - a_i r_j(\infty)}{\mu}, \quad (33)$$

for  $i \neq j \in \{1, 2\}$  and  $c_{i\gamma}^*(\ell) = \inf_{\mu > 0} \Psi_i(\gamma; \ell, \mu)$ . Clearly,  $\Psi_i(\gamma; \ell, \mu) < \tilde{\Delta}_i(\ell; \mu)$  and  $\Psi_i(\gamma; \ell, \mu) \rightarrow \tilde{\Delta}_i(\ell; \mu)$  uniformly for  $\mu > 0$  in any bounded interval as  $\gamma \rightarrow 0^+$ . Furthermore, we have  $c_{i\gamma}^*(\ell) < \tilde{c}_i^*(\ell)$  and  $c_{i\gamma}^*(\ell) \rightarrow \tilde{c}_i^*(\ell)$  as  $\gamma \rightarrow 0^+$ .

Under (8),  $\tilde{c}^*(\infty)$  given by (29) is well-defined. Let  $c \in (0, \tilde{c}^*(\infty))$ . Then for  $\delta \in (0, [\tilde{c}^*(\infty) - c]/5)$ , let  $\ell_i > 0$  be large enough such that  $\tilde{c}_i^*(\ell_i) = \tilde{c}_i^*(\infty) - \delta$ , and let  $\gamma$  be sufficiently small so that  $\tilde{c}_i^*(\ell_i) - c_{i\gamma}^*(\ell_i) \leq \delta$ . We **claim** that there are  $\check{\mu}_i, \hat{\mu}_i \in (0, \tilde{\mu}_i^*(\ell_i))$  with  $\check{\mu}_i < \hat{\mu}_i$  such that

$$\Gamma_i(\check{\mu}_i, \gamma) = c + \delta \quad \text{and} \quad \Gamma_i(\hat{\mu}_i, \gamma) = c_{i\gamma}^*(\ell_i) - 2\delta,$$

where  $\Gamma_i$  is defined in (32). Indeed, we first note that

$$\begin{aligned} \Gamma_i(0, \gamma) &= 0 < c + \delta < \tilde{c}^*(\infty) - 4\delta \leq \tilde{c}_i^*(\infty) - 4\delta \\ &= \tilde{c}_i^*(\ell_i) - 3\delta \leq c_{i\gamma}^*(\ell_i) - 2\delta \leq \tilde{c}_i^*(\ell_i) - 2\delta < \tilde{c}_i^*(\ell_i). \end{aligned} \quad (34)$$

Since  $\tilde{\mu}_i^*(\ell_i)$  satisfies

$$\tilde{c}_i^*(\ell_i) = \tilde{\Delta}_i(\ell_i; \tilde{\mu}_i^*(\ell_i)) = \inf_{\mu > 0} \tilde{\Delta}_i(\ell_i; \mu),$$

thus we know  $\partial_\mu \tilde{\Delta}_i(\ell_i; \mu)|_{\mu=\tilde{\mu}_i^*(\ell_i)} = 0$ . By (21)

$$d_i \int_{\mathbb{R}} y J_i(y) e^{\tilde{\mu}_i^*(\ell_i)y} dy = \tilde{\Delta}_i(\ell_i; \tilde{\mu}_i^*(\ell_i)) = \tilde{c}_i^*(\ell_i). \quad (35)$$

It follows from (32) and (35) that

$$\begin{aligned} \lim_{\gamma \rightarrow 0^+} \Gamma_i(\tilde{\mu}_i^*(\ell_i), \gamma) &= \lim_{\gamma \rightarrow 0^+} d_i \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} y J_i(y) C(y) e^{\tilde{\mu}_i^*(\ell_i)y} \frac{\sin(\gamma y)}{\gamma y} dy \\ &= d_i \int_{-\infty}^{\infty} y J_i(y) e^{\tilde{\mu}_i^*(\ell_i)y} dy = \tilde{c}_i^*(\ell_i). \end{aligned} \quad (36)$$

Hence, for  $\gamma$  sufficiently small, based on the nondecreasing property of  $\Gamma_i$  with respect to  $\mu_i$  and (34)–(36), the **claim** holds.

**Lemma 3.1.** Assume (8) holds and  $c \in (0, \tilde{c}^*(\infty))$ . For  $\delta \in (0, [\tilde{c}^*(\infty) - c]/5)$ , let  $\ell_i > 0$  be large enough such that  $\tilde{c}_i^*(\ell_i) = \tilde{c}_i^*(\infty) - \delta$ , and let  $\gamma$  be sufficiently small so that  $\tilde{c}_i^*(\ell_i) - c_{i\gamma}^*(\ell_i) \leq \delta$ . Let  $0 < \check{\mu}_i < \hat{\mu}_i < \tilde{\mu}_i^*(\ell_i)$  satisfy  $\Gamma_i(\check{\mu}_i, \gamma) = c + \delta$  and  $\Gamma_i(\hat{\mu}_i, \gamma) = c_{i\gamma}^*(\ell_i) - 2\delta$ . Then for any  $\mu_i \in [\check{\mu}_i, \hat{\mu}_i]$  and small  $\beta_i > 0$ ,  $(r_1(\infty), r_2(\infty))$  and  $(W_1(t, x), W_2(t, x))$  are a pair of ordered upper and lower solutions of (6), where  $W_i(t, x) := \beta_i \eta(\mu_i; x - \ell_i - \Gamma_i(\mu_i, \gamma)t)$  with  $\eta$  given by (30). Moreover, if  $u_i(0, x) \geq W_i(0, x)$ , then  $u_i(t, x) \geq W_i(t, x)$  for all  $t > 0$  and  $x \in \mathbb{R}$ .

**Proof.** Indeed, we only need to show

$$\begin{aligned} \partial_t W_1 - d_1[(J_1 * W_1) - W_1] - W_1[r_1(x - ct) - W_1 - a_1 r_2(\infty)] &\leq 0, \\ \partial_t W_2 - d_2[(J_2 * W_2) - W_2] - W_2[r_2(x - ct) - W_2 - a_2 r_1(\infty)] &\leq 0. \end{aligned} \quad (37)$$

First, for  $x < \ell_i + \Gamma_i(\mu_i, \gamma)t$  or  $x > \ell_i + \Gamma_i(\mu_i, \gamma)t + \pi/\gamma$  with  $t > 0$ , one trivially has  $W_i(t, x) \equiv 0$ . Thus we only need to verify the case  $\ell_i + \Gamma_i(\mu_i, \gamma)t \leq x \leq \ell_i + \Gamma_i(\mu_i, \gamma)t + \pi/\gamma$  for  $t > 0$ . For this range, we have

$$W_i(t, x) = \beta_i e^{-\mu_i[x - \ell_i - \Gamma_i(\mu_i, \gamma)t]} \sin[\gamma(x - \ell_i - \Gamma_i(\mu_i, \gamma)t)], \quad (38)$$

$$\begin{aligned} \partial_t W_i(t, x) &= \beta_i \Gamma_i(\mu_i, \gamma) e^{-\mu_i[x - \ell_i - \Gamma_i(\mu_i, \gamma)t]} \\ &\times \{\mu_i \sin[\gamma(x - \ell_i - \Gamma_i(\mu_i, \gamma)t)] - \gamma \cos[\gamma(x - \ell_i - \Gamma_i(\mu_i, \gamma)t)]\}. \end{aligned} \quad (39)$$

Thus, for  $|y| \leq \pi/(2\gamma)$ ,  $t > 0$  and  $\ell_i + \Gamma_i(\mu_i, \gamma)t \leq x \leq \ell_i + \Gamma_i(\mu_i, \gamma)t + \pi/\gamma$ , there holds

$$W_i(t, x - y) \geq \beta_i e^{-\mu_i[x - y - \ell_i - \Gamma_i(\mu_i, \gamma)t]} \sin[\gamma(x - y - \ell_i - \Gamma_i(\mu_i, \gamma)t)], \quad (40)$$

and by (38) and (40), this further leads to

$$\begin{aligned} &\int_{\mathbb{R}} J_i(y) W_i(t, x - y) dy - W_i(t, x) \\ &\geq \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y) C(y) W_i(t, x - y) dy - W_i(t, x) \\ &\geq \beta_i e^{-\mu_i[x - \ell_i - \Gamma_i(\mu_i, \gamma)t]} \left\{ \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y) C(y) e^{\mu_i y} \sin[\gamma(x - y - \ell_i - \Gamma_i(\mu_i, \gamma)t)] dy \right. \\ &\quad \left. - \sin[\gamma(x - \ell_i - \Gamma_i(\mu_i, \gamma)t)] \right\}. \end{aligned} \quad (41)$$

By using  $\sin(a - b) = \sin a \cos b - \cos a \sin b$ , we get

$$\begin{aligned}
& \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \sin[\gamma(x-y-\ell_i-\Gamma_i(\mu_i, \gamma)t)]dy \\
&= \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \{ \sin[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \cos(\gamma y) \\
&\quad - \cos[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \sin(\gamma y) \} dy \\
&= \sin[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \cos(\gamma y) dy \\
&\quad - \cos[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \sin(\gamma y) dy.
\end{aligned} \tag{42}$$

To achieve (37), it is sufficient to verify

$$\begin{aligned}
& \mu_i \Gamma_i(\mu_i, \gamma) \sin[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \\
& \leq d_i \sin[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \left[ \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \cos(\gamma y) dy - 1 \right] \\
& \quad + \cos[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] \left[ \gamma \Gamma_i(\mu_i, \gamma) - d_i \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \sin(\gamma y) dy \right] \\
& \quad + \sin[\gamma(x-\ell_i-\Gamma_i(\mu_i, \gamma)t)] [r_i(x-ct) - W_i(t, x) - a_i r_j(\infty)]
\end{aligned} \tag{43}$$

because of (39), (41) and (42). According to (32),

$$\gamma \Gamma_i(\mu_i, \gamma) - d_i \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \sin(\gamma y) dy = 0.$$

Hence, (43) reduces to

$$\begin{aligned}
& \mu_i \Gamma_i(\mu_i, \gamma) \leq d_i \left[ \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y)C(y)e^{\mu_i y} \cos(\gamma y) dy - 1 \right] \\
& \quad + r_i(x-ct) - W_i(t, x) - a_i r_j(\infty),
\end{aligned}$$



due to the fact that  $\sin[\gamma(x - \ell_i - \Gamma_i(\mu_i, \gamma)t)] > 0$  for  $\ell_i + \Gamma_i(\mu_i, \gamma)t < x < \ell_i + \Gamma_i(\mu_i, \gamma)t + \pi/\gamma$ . For  $x = \ell_i + \Gamma_i(\mu_i, \gamma)t$  or  $x = \ell_i + \Gamma_i(\mu_i, \gamma)t + \pi/\gamma$ , inequality (43) holds trivially. Note  $r_i(x - ct) \geq r_i(\ell_i)$  and  $W_i(t, x) \leq \beta_i$ . Thus it is sufficient to prove

$$\beta_i \leq d_i \left[ \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_i(y) C(y) e^{\mu_i y} \cos(\gamma y) dy - 1 \right] + r_i(\ell_i) - a_i r_j(\infty) - \mu_i \Gamma_i(\mu_i, \gamma). \quad (44)$$

By (33) and (31), (44) is equivalent to

$$\beta_i \leq \mu_i [\Psi_i(\gamma; \ell_i, \mu_i) - \Gamma_i(\mu_i, \gamma)]. \quad (45)$$

Note  $\Gamma_i(\mu_i, \gamma) \leq \Gamma_i(\hat{\mu}_i, \gamma) = c_{i\gamma}^*(\ell_i) - 2\delta = \inf_{\mu_i > 0} \Psi_i(\gamma; \ell_i, \mu_i) - 2\delta$  and  $\mu_i \geq \check{\mu}_i$ . Hence, (45) holds if we choose  $\beta_i \leq 2\delta \check{\mu}_i$ . The proof is complete.  $\square$

**Theorem 3.2.** Assume (8) holds and suppose  $c \in (0, \tilde{c}^*(\infty))$ . Let  $u(t, x, u_0)$  be the unique solution of the Cauchy problem (9). If  $u_0 \in \mathbb{X}_{r(\infty)}$  and  $u_{i0}(x) > 0$  on a closed interval, then for any  $0 < \epsilon < (\tilde{c}^*(\infty) - c)/2$ , we have

$$\lim_{t \rightarrow \infty, x \in \mathcal{D}_t} (u_1(t, x), u_2(t, x)) = (u_1^*, u_2^*),$$

where  $\mathcal{D}_t = \{x \in \mathbb{R} : (c + \epsilon)t \leq x \leq (\tilde{c}^*(\infty) - \epsilon)t\}$ .

**Proof.** Since  $r_1(\infty) > a_1 r_2(\infty)$  and  $r_2(\infty) > a_2 r_1(\infty)$ , for  $\rho_i > 0$  ( $i = 1, 2$ ) given in (14), we can choose  $\delta, \beta_1, \beta_2, v_1, v_2 > 0$  sufficiently small such that

$$\begin{aligned} \delta &< \min \left\{ \frac{\tilde{c}^*(\infty) - c}{10}, \frac{r_1(\infty) - a_1 r_2(\infty)}{\tilde{\mu}_1^*(\infty)}, \frac{r_2(\infty) - a_2 r_1(\infty)}{\tilde{\mu}_2^*(\infty)} \right\}, \\ (1 - v_1)[\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)] &> \rho_1, \\ (1 - v_2)[\rho_2 + r_2(\infty) - \delta \tilde{\mu}_2^*(\infty) - \beta_2 - a_2 r_1(\infty)] &> \rho_2. \end{aligned} \quad (46)$$

Since  $u_{i0}(x) > 0$  on a closed interval, it follows from the strong monotonicity in [19, Proposition 2.2] that  $u_i(t, x) > 0$  for all  $t > 0$  and  $x \in \mathbb{R}$ . Choose  $0 < t_0 \leq \min\{\sigma(\check{\mu}_1)/c, \sigma(\check{\mu}_2)/c\}$  such that  $u_i(t_0, x) \geq \beta_i$  for  $x \in [\ell_i, \ell_i + 4\pi/\gamma]$  and set

$$\chi_i(0, x) = \begin{cases} \frac{\beta_i \eta(\check{\mu}_i; x - \ell_i)}{\eta(\check{\mu}_i; \sigma(\check{\mu}_i))}, & \ell_i \leq x \leq \ell_i + \sigma(\check{\mu}_i), \\ \beta_i, & \ell_i + \sigma(\check{\mu}_i) \leq x \leq \ell_i + \sigma(\hat{\mu}_i) + \frac{3\pi}{\gamma}, \\ \frac{\beta_i \eta(\hat{\mu}_i; x - \ell_i - \frac{3\pi}{\gamma})}{\eta(\hat{\mu}_i; \sigma(\hat{\mu}_i))}, & \ell_i + \sigma(\hat{\mu}_i) + \frac{3\pi}{\gamma} \leq x \leq \ell_i + \frac{4\pi}{\gamma}, \\ 0, & \text{elsewhere.} \end{cases}$$

It is easily seen that for  $0 \leq s \leq 2\pi/\gamma$ ,

$$\chi_i(0, x) \geq \frac{\beta_i}{\eta(\check{\mu}_i; \sigma(\check{\mu}_i))} \eta(\check{\mu}_i; x - \ell_i - s)$$

and

$$\chi_i(0, x) \geq \frac{\beta_i}{\eta(\hat{\mu}_i; \sigma(\hat{\mu}_i))} \eta(\hat{\mu}_i; x - \ell_i - 3\pi/\gamma + s).$$

Since  $u_i(t_0, x) \geq \beta_i \geq \chi_i(0, x)$  for  $x \in [\ell_i, \ell_i + 4\pi/\gamma]$ , by Lemma 3.1, it follows that for  $t \geq t_0$  and  $0 \leq s \leq 2\pi/\gamma$ ,

$$u_i(t, x) \geq \frac{\beta_i}{\eta(\check{\mu}_i; \sigma(\check{\mu}_i))} \eta(\check{\mu}_i; x - \ell_i - \Gamma_i(\check{\mu}_i, \gamma)(t - t_0) - s)$$

and

$$u_i(t, x) \geq \frac{\beta_i}{\eta(\hat{\mu}_i; \sigma(\hat{\mu}_i))} \eta(\hat{\mu}_i; x - \ell_i - \Gamma_i(\hat{\mu}_i, \gamma)(t - t_0) - 3\pi/\gamma + s).$$

Let  $\check{\Sigma}_i^{\ell_i}(t, t_0) = \ell_i + \Gamma_i(\check{\mu}_i, \gamma)(t - t_0) + \sigma(\check{\mu}_i)$  and  $\hat{\Sigma}_i^{\ell_i}(t, t_0) = \ell_i + \Gamma_i(\hat{\mu}_i, \gamma)(t - t_0) + \sigma(\hat{\mu}_i)$ . By similar induction arguments to those in [27, Theorem 2.2 (iii)], we can show that

$$u_i(t, x) \geq \chi_i(t - t_0, x), \quad \text{for all } t \geq t_0, \quad (47)$$

where

$$\chi_i(t - t_0, x) = \begin{cases} \frac{\beta_i \eta(\check{\mu}_i; x - \ell_i - \Gamma_i(\check{\mu}_i, \gamma)(t - t_0))}{\eta(\check{\mu}_i; \sigma(\check{\mu}_i))}, & \check{\Sigma}_i^{\ell_i}(t, t_0) - \sigma(\check{\mu}_i) \leq x \leq \check{\Sigma}_i^{\ell_i}(t, t_0), \\ \beta_i, & \check{\Sigma}_i^{\ell_i}(t, t_0) \leq x \leq \hat{\Sigma}_i^{\ell_i}(t, t_0) + \frac{3\pi}{\gamma}, \\ \frac{\beta_i \eta(\hat{\mu}_i; x - \ell_i - \Gamma_i(\hat{\mu}_i, \gamma)(t - t_0) - \frac{3\pi}{\gamma})}{\eta(\hat{\mu}_i; \sigma(\hat{\mu}_i))}, & \hat{\Sigma}_i^{\ell_i}(t, t_0) + \frac{3\pi}{\gamma} \leq x \leq \\ & \hat{\Sigma}_i^{\ell_i}(t, t_0) - \sigma(\hat{\mu}_i) + \frac{4\pi}{\gamma}, \\ 0, & \text{elsewhere.} \end{cases} \quad (48)$$

Let  $t_1 > t_0$  be sufficiently large. Then, for  $t > t_1$ , the solution  $(u_1(t, x), u_2(t, x))$  of (9) satisfies

$$\begin{aligned} u_1(t, x) &= [e^{\mathcal{L}_1(t-t_1)} u_1(t_1, \cdot)](x) \\ &\quad + \int_{t_1}^t [e^{\mathcal{L}_1(t-\theta)} F_1(\cdot - c\theta, u_1(\theta, \cdot), u_2(\theta, \cdot))](x) d\theta, \\ u_2(t, x) &= [e^{\mathcal{L}_2(t-t_1)} u_2(t_1, \cdot)](x) \\ &\quad + \int_{t_1}^t [e^{\mathcal{L}_2(t-\theta)} F_2(\cdot - c\theta, u_1(\theta, \cdot), u_2(\theta, \cdot))](x) d\theta, \end{aligned}$$

where  $F_i$  is defined in (14),  $i = 1, 2$ . According to (47), the positivity of  $e^{\mathcal{L}_i(t)}$  and the nondecreasing property of  $F_i$  with respect to  $u_i$ , we obtain for  $t > t_1$

$$\begin{aligned} u_1(t, x) &\geq [e^{\mathcal{L}_1(t-t_1)} \chi_1(t_1 - t_0, \cdot)](x) \\ &\quad + \int_{t_1}^t [e^{\mathcal{L}_1(t-\theta)} F_1(\cdot - c\theta, \chi_1(\theta - t_0, \cdot), u_2(\theta, \cdot))](x) d\theta, \\ u_2(t, x) &\leq [e^{\mathcal{L}_2(t-t_1)} r_2(\infty)](x) \\ &\quad + \int_{t_1}^t [e^{\mathcal{L}_2(t-\theta)} F_2(\cdot - c\theta, u_1(\theta, \cdot), r_2(\infty))](x) d\theta. \end{aligned} \quad (49)$$

Let  $[t_1]$  be the largest integer which is no more than  $t_1$ . For  $t \geq t_1$  and  $x$  satisfying

$$\check{\Sigma}_1^{\ell_1}(t, t_0) + [t_1]\pi/(2\gamma) \leq x \leq \hat{\Sigma}_1^{\ell_1}(t, t_0) + 3\pi/\gamma - [t_1]\pi/(2\gamma), \quad (50)$$

we have

$$\begin{cases} \chi_1(t - t_0, x) = \beta_1, \\ \chi_1(t - t_0, x - \sum_{i=1}^N x_i) = \beta_1, \quad x_i \in [-\pi/(2\gamma), \pi/(2\gamma)] \text{ for } N \in \{1, \dots, [t_1]\}. \end{cases} \quad (51)$$

In view of (12) and (51), we then further have

$$\begin{aligned} &[e^{\mathcal{L}_1(t-t_1)} \chi_1(t_1 - t_0, \cdot)](x) \\ &\geq e^{-(\rho_1+d_1)(t-t_1)} \sum_{l=0}^{[t_1]} \frac{[d_1(t-t_1)]^l}{l!} [J_1^{(l)} * \chi_1](t_1 - t_0, x) \\ &\geq e^{-(\rho_1+d_1)(t-t_1)} \left[ \chi_1(t_1 - t_0, x) + \frac{d_1(t-t_1)}{1!} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_1) \chi_1(t_1 - t_0, x - x_1) dx_1 + \right. \\ &\quad \left. \dots + \frac{(d_1(t-t_1))^{[t_1]}}{[t_1]!} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} \dots \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} \prod_{i=1}^{[t_1]} J_1(x_i) \chi_1(t_1 - t_0, x - \bar{x}_{[t_1]}) dx_1 \dots dx_{[t_1]} \right] \quad (52) \\ &= e^{-(\rho_1+d_1)(t-t_1)} \beta_1 \left[ 1 + \frac{d_1(t-t_1)}{1!} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_1) dx_1 + \dots \right. \\ &\quad \left. + \frac{(d_1(t-t_1))^{[t_1]}}{[t_1]!} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_1) dx_1 \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_2) dx_2 \dots \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_{[t_1]}) dx_{[t_1]} \right] \end{aligned}$$

$$\rightarrow e^{-\rho_1(t-t_1)} \beta_1 \left\{ 1 - e^{-d_1(t-t_1)} \sum_{i=[t_1]+1}^{\infty} \frac{[d_1(t-t_1)]^i}{i!} \right\}, \quad \text{as } \gamma \rightarrow 0^+$$

where  $\bar{x}_{[t_1]} = x_1 + x_2 + \cdots + x_{[t_1]}$ . Hence, for small  $v_1$  chosen as above, if  $t_1$  is sufficiently large and then  $\gamma := 1/t_1$  is so small, (52) implies

$$[e^{\mathcal{L}_1(t-t_1)} \chi_1(t_1 - t_0, \cdot)](x) \geq e^{-\rho_1(t-t_1)} \beta_1(1 - v_1). \quad (53)$$

Furthermore, for any  $\theta \in (t_1, t)$ , similar to (52), we get

$$\begin{aligned} & \left[ e^{\mathcal{L}_1(t-\theta)} F_1(\cdot - c\theta, \chi_1(\theta - t_0, \cdot), u_2(\theta, \cdot)) \right](x) \\ & \geq \left[ e^{\mathcal{L}_1(t-\theta)} F_1(\cdot - c\theta, \chi_1(\theta - t_0, \cdot), r_2(\infty)) \right](x) \\ & \geq e^{-(\rho_1+d_1)(t-\theta)} \sum_{l=0}^{[t_1]} \frac{[d_1(t-\theta)]^l}{l!} \left[ J_1^{(l)} * F_1 \right](x - c\theta, \chi_1(\theta - t_0, x), r_2(\infty)) \\ & \geq e^{-(\rho_1+d_1)(t-\theta)} \left[ F_1(x - c\theta, \chi_1(\theta - t_0, x), r_2(\infty)) + \frac{d_1(t-\theta)}{1!} \right. \\ & \quad \times \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} J_1(x_1) F_1(x - x_1 - c\theta, \chi_1(\theta - t_0, x - x_1), r_2(\infty)) dx_1 + \cdots \\ & \quad + \frac{(d_1(t-\theta))^{[t_1]}}{[t_1]!} \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} \cdots \int_{-\frac{\pi}{2\gamma}}^{\frac{\pi}{2\gamma}} \prod_{i=1}^{[t_1]} J_1(x_i) F_1(x - \bar{x}_{[t_1]} - c\theta, \\ & \quad \left. \chi_1(\theta - t_0, x - \bar{x}_{[t_1]}), r_2(\infty)) dx_1 \cdots dx_{[t_1]} \right]. \end{aligned} \quad (54)$$

Also for any  $t \geq t_1 > t_0$  and  $x$  satisfying (50), there holds

$$\begin{aligned} x - \sum_{i=1}^N x_i - ct & \geq \ell_1 + \Gamma_1(\check{\mu}_1, \gamma)(t - t_0) + \sigma(\check{\mu}_1) - ct \\ & = \ell_1 + (c + \delta)(t - t_0) + \sigma(\check{\mu}_1) - ct \\ & \geq \ell_1 - ct_0 + \sigma(\check{\mu}_1) \geq \ell_1, \end{aligned} \quad (55)$$

where we have used the fact that  $\Gamma_1(\check{\mu}_1, \gamma) = c + \delta$  and the choice of  $t_0$ . Besides, since  $\tilde{c}_1^*(\ell_1) = \tilde{c}_1^*(\infty) - \delta$ , we have

$$\begin{aligned} & \frac{d_1 \left[ \int_{\mathbb{R}} J_1(y) e^{\tilde{\mu}_1^*(\infty)y} dy - 1 \right] + r_1(\infty) - a_1 r_2(\infty)}{\tilde{\mu}_1^*(\infty)} - \delta \\ & \leq \tilde{\Delta}_1(\ell_1; \tilde{\mu}_1^*(\infty)) = \frac{d_1 \left[ \int_{\mathbb{R}} J_1(y) e^{\tilde{\mu}_1^*(\infty)y} dy - 1 \right] + r_1(\ell_1) - a_1 r_2(\infty)}{\tilde{\mu}_1^*(\infty)}. \end{aligned}$$

Hence  $r_1(\ell_1) \geq r_1(\infty) - \delta\tilde{\mu}_1^*(\infty)$ . It immediately follows from the nondecreasing property of  $r_1$  and (55) that

$$r_1\left(x - \sum_{i=1}^N x_i - c\theta\right) \geq r_1(\ell_1) \geq r_1(\infty) - \delta\tilde{\mu}_1^*(\infty) \quad (56)$$

for  $\theta \geq t_1$  and  $N \in \{1, \dots, [t_1]\}$ . From (48), (50) to (56) and with  $v_1$  chosen above, for any  $t \geq \theta \geq t_1$  and  $x$  satisfying (50), we have

$$\begin{aligned} & \left[ e^{\mathcal{L}_1(t-\theta)} F_1(\cdot - c\theta, \chi_1(\theta - t_0, \cdot), u_2(\theta, \cdot)) \right](x) \\ & \geq e^{-\rho_1(t-\theta)} \beta_1 [\rho_1 + r_1(\infty) - \delta\tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)] (1 - v_1). \end{aligned} \quad (57)$$

From (49) to (57), we obtain  $u_1(t, x) \geq \tilde{u}_1^{(1)}(t)$  and  $u_2(t, x) \leq \tilde{u}_2^{(1)}(t)$ , where

$$\begin{aligned} \tilde{u}_1^{(1)}(t) &= (1 - v_1) \beta_1 e^{-\rho_1(t-t_1)} + (1 - v_1) \\ & \quad \times \int_{t_1}^t e^{-\rho_1(t-\theta)} \beta_1 [\rho_1 + r_1(\infty) - \delta\tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)] d\theta, \\ \tilde{u}_2^{(1)}(t) &= r_2(\infty) e^{-\rho_2(t-t_1)} + \int_{t_1}^t e^{-\rho_2(t-\theta)} r_2(\infty) [\rho_2 - a_2 \beta_1] d\theta. \end{aligned} \quad (58)$$

For  $m \geq 2$ , we consider the following iterations scheme:

$$\begin{aligned} \tilde{u}_1^{(m)}(t) &= (1 - v_1) \beta_1 e^{-\rho_1(t-t_1)} + (1 - v_1) \int_{t_1}^t e^{-\rho_1(t-\theta)} E_1\left(\tilde{u}_1^{(m-1)}(\theta), \tilde{u}_2^{(m-1)}(\theta)\right) d\theta, \\ \tilde{u}_2^{(m)}(t) &= r_2(\infty) e^{-\rho_2(t-t_1)} + \int_{t_1}^t e^{-\rho_2(t-\theta)} E_2\left(\tilde{u}_1^{(m-1)}(\theta), \tilde{u}_2^{(m-1)}(\theta)\right) d\theta, \end{aligned} \quad (59)$$

where

$$\begin{aligned} & E_1\left(\tilde{u}_1^{(m-1)}(t), \tilde{u}_2^{(m-1)}(t)\right) \\ &= \tilde{u}_1^{(m-1)}(t) [\rho_1 + r_1(\infty) - \delta\tilde{\mu}_1^*(\infty) - \tilde{u}_1^{(m-1)}(t) - a_1 \tilde{u}_2^{(m-1)}(t)], \\ & E_2\left(\tilde{u}_1^{(m-1)}(t), \tilde{u}_2^{(m-1)}(t)\right) \\ &= \tilde{u}_2^{(m-1)}(t) [\rho_2 + r_2(\infty) - \tilde{u}_2^{(m-1)}(t) - a_2 \tilde{u}_1^{(m-1)}(t)]. \end{aligned} \quad (60)$$

By induction, we can further derive that for  $t \geq t_1$  large enough and  $x$  satisfying

$$\hat{\Sigma}_1^{\ell_1}(t, t_0) + m[t_1]\pi/(2\gamma) \leq x \leq \hat{\Sigma}_1^{\ell_1}(t, t_0) + 3\pi/\gamma - m[t_1]\pi/(2\gamma), \quad (61)$$

there holds

$$u_1(t, x) \geq \tilde{u}_1^{(m)}(t) \quad \text{and} \quad u_2(t, x) \leq \tilde{u}_2^{(m)}(t), \quad m \geq 1. \quad (62)$$

We next explore the asymptotic behavior of  $(\tilde{u}_1^{(m)}(t), \tilde{u}_2^{(m)}(t))$  as  $t \rightarrow \infty$ . We begin with  $(\tilde{u}_1^{(1)}(t), \tilde{u}_2^{(1)}(t))$ . Applying the L'Hospital's rule to (58), we know that  $\tilde{u}_1^{(1)}(\infty) := \lim_{t \rightarrow \infty} \tilde{u}_1^{(1)}(t)$  and  $\tilde{u}_2^{(1)}(\infty) := \lim_{t \rightarrow \infty} \tilde{u}_2^{(1)}(t)$  exist and are given by

$$\begin{aligned} \tilde{u}_1^{(1)}(\infty) &= \frac{1}{\rho_1} (1 - v_1) \beta_1 [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)], \\ \tilde{u}_2^{(1)}(\infty) &= \frac{1}{\rho_2} r_2(\infty) [\rho_2 - a_2 \beta_1]. \end{aligned} \quad (63)$$

Applying the L'Hospital's rule to (59), we inductively conclude that for  $m \geq 2$ ,  $\tilde{u}_1^{(m)}(\infty)$  and  $\tilde{u}_2^{(m)}(\infty)$  also exist and they satisfy the recursive relation:

$$\begin{aligned} \tilde{u}_1^{(m)}(\infty) &= \frac{1}{\rho_1} (1 - v_1) E_1 \left( \tilde{u}_1^{(m-1)}(\infty), \tilde{u}_2^{(m-1)}(\infty) \right), \\ \tilde{u}_2^{(m)}(\infty) &= \frac{1}{\rho_2} E_2 \left( \tilde{u}_1^{(m-1)}(\infty), \tilde{u}_2^{(m-1)}(\infty) \right). \end{aligned} \quad (64)$$

We next show that  $\tilde{u}_1^{(m)}(\infty)$  is increasing and  $\tilde{u}_2^{(m)}(\infty)$  is decreasing with respect to  $m$ . Firstly, (46) leads to  $\tilde{u}_1^{(1)}(\infty) > \beta_1$ . Obviously  $\tilde{u}_2^{(1)}(\infty) < r_2(\infty)$ . From (64) and (63), we then have

$$\begin{aligned} & \frac{\rho_1 [\tilde{u}_1^{(2)}(\infty) - \tilde{u}_1^{(1)}(\infty)]}{(1 - v_1)} \\ &= \tilde{u}_1^{(1)}(\infty) [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \tilde{u}_1^{(1)}(\infty) - a_1 \tilde{u}_2^{(1)}(\infty)] \\ & \quad - \beta_1 [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)] \\ &\geq \tilde{u}_1^{(1)}(\infty) [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \tilde{u}_1^{(1)}(\infty) - a_1 r_2(\infty)] \\ & \quad - \beta_1 [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - \beta_1 - a_1 r_2(\infty)] \geq 0, \end{aligned}$$

since  $u_1 [\rho_1 + r_1(\infty) - \delta \tilde{\mu}_1^*(\infty) - u_1 - a_1 r_2(\infty)]$  is nondecreasing in  $u_1 \in [0, r_1(\infty))$  (by (13)). Thus,  $\tilde{u}_1^{(2)}(\infty) \geq \tilde{u}_1^{(1)}(\infty)$ , and by induction,  $\tilde{u}_1^{(m)}(\infty)$  is increasing in  $m$ . Also

$$\begin{aligned} & \rho_2 [\tilde{u}_2^{(2)}(\infty) - \tilde{u}_2^{(1)}(\infty)] \\ &= \tilde{u}_2^{(1)}(\infty) [\rho_2 + r_2(\infty) - \tilde{u}_2^{(1)}(\infty) - a_2 \tilde{u}_1^{(1)}(\infty)] \\ & \quad - r_2(\infty) [\rho_2 - a_2 \beta_1] \\ &\leq r_2(\infty) [\rho_2 + r_2(\infty) - r_2(\infty) - a_2 \beta_1] - r_2(\infty) [\rho_2 - a_2 \beta_1] = 0, \end{aligned}$$

which implies  $\tilde{u}_2^{(2)}(\infty) \leq \tilde{u}_2^{(1)}(\infty)$ ; and by induction,  $\tilde{u}_2^{(m)}(\infty)$  is decreasing in  $m$ .

The monotonicity of  $\tilde{u}_1^{(m)}(\infty)$  and  $\tilde{u}_2^{(m)}(\infty)$  implies the limits of  $\tilde{u}_1^{(m)}(\infty)$  and  $\tilde{u}_2^{(m)}(\infty)$  as  $m \rightarrow \infty$  both exist. Letting  $m \rightarrow \infty$  in (64), and setting  $\lim_{m \rightarrow \infty} \tilde{u}_1^{(m)}(\infty) = u_1^\Delta$  and  $\lim_{m \rightarrow \infty} \tilde{u}_2^{(m)}(\infty) = u_2^\Delta$ , we get

$$\begin{aligned} u_1^\Delta &= u_1^* - \frac{\delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} - \frac{v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)}, \\ u_2^\Delta &= u_2^* + \frac{a_2 \delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} + \frac{a_2 v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)}, \end{aligned}$$

since it is easy to verify  $u_i^\Delta > 0$  ( $i = 1, 2$ ). Thus, for an arbitrary small  $\varsigma > 0$ , there exists some positive number  $m_1$  large enough such that

$$\begin{aligned} \tilde{u}_1^{(m_1)}(\infty) &\geq u_1^* - \frac{\delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} - \frac{v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)} - \varsigma, \\ \tilde{u}_2^{(m_1)}(\infty) &\leq u_2^* + \frac{a_2 \delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} + \frac{a_2 v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)} + \varsigma. \end{aligned} \quad (65)$$

Let  $m$  in (61) and (62) be replaced by this fixed  $m_1$ . Note that for any given  $0 < \epsilon < (\tilde{c}^*(\infty) - c)/2$ , we can select  $\delta$  small enough with  $\delta < \epsilon/4$ . Then, by Lemma 3.1, we have  $\Gamma_i(\check{\mu}_i, \gamma) = c + \delta < c + \epsilon/4$  and  $\Gamma_i(\hat{\mu}_i, \gamma) = c_{i\gamma}^*(\ell_i) - 2\delta \geq \tilde{c}_i^*(\ell_i) - 3\delta = \tilde{c}_i^*(\infty) - 4\delta > \tilde{c}_i^*(\infty) - \epsilon$ . Thus, for the above fixed  $m_1$  and below  $m_2$ , we can choose  $t \geq t_1$  sufficiently large such that for  $t \geq t_1$ , there holds

$$\begin{aligned} \check{\Sigma}_i^{\ell_i}(t, t_0) + m_i[t_1]\pi/(2\gamma) &= \ell_i + \Gamma_i(\check{\mu}_i, \gamma)(t - t_0) + \sigma(\check{\mu}_i) + m_i[t_1]\pi/(2\gamma) \\ &\leq (c + \epsilon)t < (\tilde{c}^*(\infty) - \epsilon)t \leq (\tilde{c}_i^*(\infty) - \epsilon)t \\ &\leq \ell_i + \Gamma_i(\hat{\mu}_i, \gamma)(t - t_0) + \sigma(\hat{\mu}_i) + 3\pi/\gamma - m_i[t_1]\pi/(2\gamma) \\ &= \hat{\Sigma}_i^{\ell_i}(t, t_0) + 3\pi/\gamma - m_i[t_1]\pi/(2\gamma). \end{aligned} \quad (66)$$

This implies for  $t \geq t_1$ , the spatial interval

$$\mathcal{H}_t = \left[ \check{\Sigma}_1^{\ell_1}(t, t_0) + m_1[t_1]\pi/(2\gamma), \hat{\Sigma}_1^{\ell_1}(t, t_0) + 3\pi/\gamma - m_1[t_1]\pi/(2\gamma) \right]$$

is non-empty and it indeed contains  $\mathcal{D}_t = \{x \in \mathbb{R} : (c + \epsilon)t \leq x \leq (\tilde{c}^*(\infty) - \epsilon)t\}$  as its subinterval. It follows from (62) and (65) that

$$\begin{aligned} \liminf_{t \rightarrow \infty, x \in \mathcal{D}_t} u_1(t, x) &\geq u_1^* - \frac{\delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} - \frac{v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)} - \varsigma, \\ \limsup_{t \rightarrow \infty, x \in \mathcal{D}_t} u_2(t, x) &\leq u_2^* + \frac{a_2 \delta \tilde{\mu}_1^*(\infty)}{1 - a_1 a_2} + \frac{a_2 v_1 \rho_1}{(1 - v_1)(1 - a_1 a_2)} + \varsigma. \end{aligned} \quad (67)$$

Similarly, with  $v_2, \beta_2, \rho_1, \rho_2, \delta$  chosen above, we can consider another iteration scheme:

$$\left\{ \begin{array}{l} \hat{u}_1^{(m)}(t) = r_1(\infty)e^{-\rho_1(t-t_1)} + \int_{t_1}^t e^{-\rho_1(t-\theta)} \hat{u}_1^{(m-1)}(\theta) \\ \quad \times \left[ \rho_1 + r_1(\infty) - \hat{u}_1^{(m-1)}(\theta) - a_1 \hat{u}_2^{(m-1)}(\theta) \right] d\theta, \quad m \geq 2, \\ \hat{u}_2^{(m)}(t) = (1-v_2)\beta_2 e^{-\rho_2(t-t_1)} + (1-v_2) \int_{t_1}^t e^{-\rho_2(t-\theta)} \hat{u}_2^{(m-1)}(\theta) \\ \quad \times \left[ \rho_2 + r_2(\infty) - \delta \tilde{\mu}_2^*(\infty) - \hat{u}_2^{(m-1)}(\theta) - a_2 \hat{u}_1^{(m-1)}(\theta) \right] d\theta, \quad m \geq 2; \\ \hat{u}_1^{(1)}(t) = r_1(\infty)e^{-\rho_1(t-t_1)} + \int_{t_1}^t e^{-\rho_1(t-\theta)} r_1(\infty) [\rho_1 - a_1 \beta_2] d\theta, \\ \hat{u}_2^{(1)}(t) = (1-v_2)\beta_2 e^{-\rho_2(t-t_1)} + (1-v_2) \int_{t_1}^t e^{-\rho_2(t-\theta)} \beta_2 \\ \quad \times \left[ \rho_2 + r_2(\infty) - \delta \tilde{\mu}_2^*(\infty) - \beta_2 - a_2 r_1(\infty) \right] d\theta. \end{array} \right.$$

By the same argument, we can show that when  $t_1$  is sufficiently large, there holds

$$u_1(t, x) \leq \hat{u}_1^{(m)}(t) \text{ and } u_2(t, x) \geq \hat{u}_2^{(m)}(t),$$

for  $t \geq t_1$  and  $x$  satisfying

$$\check{\Sigma}_2^{\ell_2}(t, t_0) + m[t_1]\pi/(2\gamma) \leq x \leq \hat{\Sigma}_2^{\ell_2}(t, t_0) + 3\pi/\gamma - m[t_1]\pi/(2\gamma). \quad (68)$$

We can also show that  $\hat{u}_1^{(m)}(\infty)$  and  $\hat{u}_2^{(m)}(\infty)$  exist and for arbitrary small  $\varsigma > 0$ , there exists  $m_2 > 0$  such that

$$\begin{aligned} \hat{u}_1^{(m_2)}(\infty) &\leq u_1^* + \frac{a_1 \delta \tilde{\mu}_2^*(\infty)}{1 - a_1 a_2} + \frac{a_1 v_2 \rho_2}{(1 - v_2)(1 - a_1 a_2)} + \varsigma, \\ \hat{u}_2^{(m_2)}(\infty) &\geq u_2^* - \frac{\delta \tilde{\mu}_2^*(\infty)}{1 - a_1 a_2} - \frac{v_2 \rho_2}{(1 - v_2)(1 - a_1 a_2)} - \varsigma. \end{aligned}$$

Moreover, in view of (66), the spatial interval defined by (68) is non-empty and contains  $\mathcal{D}_t$  as its subinterval when  $m$  is replaced by this fixed  $m_2$ . Hence, it leads to

$$\begin{aligned} \limsup_{t \rightarrow \infty, x \in \mathcal{D}_t} u_1(t, x) &\leq u_1^* + \frac{a_1 \delta \tilde{\mu}_2^*(\infty)}{1 - a_1 a_2} + \frac{a_1 v_2 \rho_2}{(1 - v_2)(1 - a_1 a_2)} + \varsigma, \\ \limsup_{t \rightarrow \infty, x \in \mathcal{D}_t} u_2(t, x) &\geq u_2^* - \frac{\delta \tilde{\mu}_2^*(\infty)}{1 - a_1 a_2} - \frac{v_2 \rho_2}{(1 - v_2)(1 - a_1 a_2)} - \varsigma. \end{aligned} \quad (69)$$



Finally, because  $\delta, v_1, v_2, \varsigma$  can be arbitrarily small, (67) and (69) actually imply

$$\begin{aligned} u_1^* &\leq \liminf_{t \rightarrow \infty, x \in \mathcal{D}_t} u_1(t, x) \leq \limsup_{t \rightarrow \infty, x \in \mathcal{D}_t} u_1(t, x) \leq u_1^*, \\ u_2^* &\leq \liminf_{t \rightarrow \infty, x \in \mathcal{D}_t} u_2(t, x) \leq \limsup_{t \rightarrow \infty, x \in \mathcal{D}_t} u_2(t, x) \leq u_2^*, \end{aligned}$$

and this completes the proof of the theorem.  $\square$

The next theorem identifies condition on the initial distributions and a traveling observer's speed (slower than  $c$  or faster than  $c_i^*(\infty)$ ) under which the species' population will eventually not be seen by the observer.

**Theorem 3.3.** *Let  $0 < c < \min\{c_1^*(\infty), c_2^*(\infty)\}$ . Then we have the following conclusions.*

- (i) *If  $u_0 \in \mathbb{X}_{r(\infty)}$  satisfies  $\sup_{x \in \mathbb{R}} u_{i0}(x) < r_i(\infty)$ ,  $i = 1, 2$  and  $u_0(x) \equiv 0$  for sufficiently large negative  $x$ , then for any small  $\kappa > 0$ ,*

$$\lim_{t \rightarrow \infty} \sup_{x \leq (c-\kappa)t} (u_1(t, x), u_2(t, x)) = (0, 0).$$

- (ii) *If  $u_0 \in \mathbb{X}_{r(\infty)}$  and  $u_0(x) \equiv 0$  for sufficiently large positive  $x$ , then for any small  $\varepsilon > 0$ ,*

$$\lim_{t \rightarrow \infty} \sup_{x \geq (c_i^*(\infty) + \varepsilon)t} (u_1(t, x), u_2(t, x)) = (0, 0).$$

**Proof.** (i) According to [29, Theorem 4.5], for any  $c > 0$ , the equation (24) has a nondecreasing positive traveling wave solution  $\psi_i(x - ct)$  with  $\psi_i(-\infty) = 0$  and  $\psi_i(\infty) = r_i(\infty)$ . Following the proofs of Theorem 3.1, we see that for any small  $\varepsilon > 0$ , there exists a large number  $M$  such that (26) holds. Notice that for any given  $\kappa > 0$ , there exists some  $T_2 > 0$  such that  $(c - \kappa)t \leq ct - M$  for all  $t \geq T_2$ . Thus, the conclusion follows from (26).

(ii) For any small  $\varepsilon > 0$ , let  $\mu_\varepsilon^i$  be the smallest positive root of  $\Delta_i(\infty; \mu) = c_i^*(\infty) + \frac{\varepsilon}{2}$ . Let  $\bar{u}_i(t, x) = q_i e^{-\mu_\varepsilon^i [x - \Delta_i(\infty; \mu_\varepsilon^i)t]}$  with  $q_i > 0$ , then it is a solution of the following linear equation

$$\partial_t v_i(t, x) = d_i [(J_i * v_i)(t, x) - v_i(t, x)] + r_i(\infty) v_i(t, x).$$

Choose  $q_i$  so large that  $u_{i0}(x) \leq \bar{u}_i(0, x) = q_i e^{-\mu_\varepsilon^i x}$  for all  $x$  since  $u_0(x) \equiv 0$  for sufficiently large positive  $x$ . By Remark 2.1, it is easy to see that  $(\bar{u}_1(t, x), \bar{u}_2(t, x))$  and  $(0, 0)$  are a pair of ordered upper and lower solutions of (9) for all  $t \geq 0$  and  $x \in \mathbb{R}$ . Hence, for  $x \geq (c_i^*(\infty) + \varepsilon)t = [\Delta_i(\infty; \mu_\varepsilon^i) + \frac{\varepsilon}{2}]t$ , there holds  $u_i(t, x) \leq q_i e^{-\mu_\varepsilon^i \frac{\varepsilon}{2}t}$ , leading to the conclusion, and the proof is completed.  $\square$

The following two theorems illustrate that replacement (or one species is invaded by the other) will happen if the environment worsening speed is medium.

**Theorem 3.4.** *Assume  $c_1^*(\infty) < c < c_2^*(\infty)$ . Let  $u(t, x, u_0)$  be the unique solution of the Cauchy problem (9) with  $u_0 \in \mathbb{X}_{r(\infty)}$ . If  $u_{10}(\cdot)$  has a compact support,  $\sup_{x \in \mathbb{R}} u_{10}(x) < r_1(\infty)$ , and*

$u_{20}(x) > 0$  on a closed interval, then for each  $0 < \varepsilon < [c_2^*(\infty) - c]/2$ , there exists a  $T_* > 0$  such that  $u_1(t, x) \leq \varepsilon$  for all  $t \geq T_*$  and  $x \in \mathbb{R}$ , and moreover  $\lim_{t \rightarrow \infty, x \in \mathcal{E}_t} u_2(t, x) = r_2(\infty)$ , where  $\mathcal{E}_t = \{x \in \mathbb{R} : (c + \varepsilon)t \leq x \leq (c_2^*(\infty) - \varepsilon)t\}$ .

**Proof.** By a similar argument to that in Theorem 3.1, we see that for any  $0 < \sigma < \varepsilon$  there exists a  $T_* > 0$  such that  $u_1(t, x) \leq \sigma$  for all  $t \geq T_*$  and  $x \in \mathbb{R}$ . Thus, for all  $t \geq T_*$  and  $x \in \mathbb{R}$ , we have

$$\partial_t u_2(t, x) \geq d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + u_2[r_2(x - ct) - u_2 - a_2\sigma]$$

and

$$\partial_t u_2(t, x) \leq d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + u_2[r_2(x - ct) - u_2].$$

Hence, the comparison principle implies that

$$v_2(t, x) \leq u_2(t, x, u_0) \leq w_2(t, x) \quad \text{for all } t \geq T_* \text{ and } x \in \mathbb{R},$$

where  $v_2(t, x)$  and  $w_2(t, x)$  is, respectively, solution of

$$\partial_t v_2(t, x) = d_2[(J_2 * v_2)(t, x) - v_2(t, x)] + v_2[r_2(x - ct) - a_2\sigma - v_2], \quad t > T_*,$$

$$v_2(T_*, x) = u_2(T_*, x, u_0) > 0,$$

and

$$\partial_t w_2(t, x) = d_2[(J_2 * w_2)(t, x) - w_2(t, x)] + w_2[r_2(x - ct) - w_2], \quad t > T_*,$$

$$w_2(T_*, x) = u_2(T_*, x, u_0) > 0.$$

From [29, Theorem 3.3] it follows that  $\lim_{t \rightarrow \infty, x \in \mathcal{E}_t} w_2(t, x) = r_2(\infty)$ . Denote

$$c_{2\sigma}^*(\infty) = \inf_{\mu > 0} \frac{d_2 \left[ \int_{\mathbb{R}} J_2(y) e^{\mu y} dy - 1 \right] + r_2(\infty) - a_2\sigma}{\mu}.$$

Applying [29, Theorem 3.3] to the equation for  $v_2$  defined above, then we have

$$\lim_{t \rightarrow \infty, x \in \mathcal{E}_t(\sigma)} v_2(t, x) = r_2(\infty) - a\sigma,$$

where  $\mathcal{E}_t(\sigma) = \{x \in \mathbb{R} : (c + \varepsilon)t \leq x \leq (c_{2\sigma}^*(\infty) - \varepsilon)t\}$ . Combining the above with the facts that  $c_{2\sigma}^*(\infty) < c_2^*(\infty)$ ,  $c_{2\sigma}^*(\infty) \rightarrow c_2^*(\infty)$ ,  $\mathcal{E}_t(\sigma) \rightarrow \mathcal{E}_t$  as  $\sigma \rightarrow 0^+$ , and noting that  $\sigma > 0$  can be arbitrary small, we are led to the conclusion. The proof is completed.  $\square$

In a parallel manner, we also have the following result.

**Theorem 3.5.** Assume  $c_2^*(\infty) < c < c_1^*(\infty)$ . Let  $u(t, x, u_0)$  be the unique solution of the Cauchy problem (9) with  $u_0 \in \mathbb{X}_{r(\infty)}$ . If  $u_{20}(\cdot)$  has a compact support,  $\sup_{x \in \mathbb{R}} u_{20}(x) < r_2(\infty)$ , and  $u_{10}(x) > 0$  on a closed interval, then for each  $0 < \varepsilon < [c_1^*(\infty) - c]/2$ , there exists a  $T^* > 0$  such that  $u_2(t, x) \leq \varepsilon$  for all  $t \geq T^*$  and  $x \in \mathbb{R}$ , and moreover  $\lim_{t \rightarrow \infty, x \in \mathcal{F}_t} u_1(t, x) = r_1(\infty)$ , where  $\mathcal{F}_t = \{x \in \mathbb{R} : (c + \varepsilon)t \leq x \leq (c_1^*(\infty) - \varepsilon)t\}$ .

#### 4. Numeric simulations

In this section, we present some numeric simulation results for the system (6) to demonstrate our analytic results. To be computable, we choose the following particular kernel function for both  $J_1$  and  $J_2$ :

$$J_2(x) = J_1(x) = \begin{cases} \frac{0.1}{2(1-e^{-1})} e^{-\frac{|x|}{10}}, & -10 \leq x \leq 10, \\ 0, & \text{elsewhere.} \end{cases}$$

Also, in the sequel we will use the following initial data:

$$u_1(0, x) = \begin{cases} 0.4 \sin(x - 20), & 20 \leq x \leq 20 + \pi, \\ 0, & \text{elsewhere,} \end{cases}$$

$$u_2(0, x) = \begin{cases} 0.8 \sin(x - 10), & 10 \leq x \leq 10 + \pi, \\ 0, & \text{elsewhere.} \end{cases}$$

For the two growth functions  $r_1$  and  $r_2$ , we first choose  $r_1(x - ct) = \frac{0.2}{\pi} \arctan(x - ct)$  and  $r_2(x - ct) = \frac{0.14}{\pi} \arctan(x - ct)$ . Then  $r_1(\infty) = 0.1$  and  $r_2(\infty) = 0.07$ . Now for  $a_1 = 0.12$ ,  $a_2 = 0.14$ ,  $d_1 = 1.3$ ,  $d_2 = 1.15$ , we can calculate to obtain

$$c_1^*(\infty) = \frac{1.3 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.1}{\mu} \Big|_{\mu \approx 0.07493} \approx 2.6041,$$

$$c_2^*(\infty) = \frac{1.15 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.07}{\mu} \Big|_{\mu \approx 0.06714} \approx 2.0438.$$

Now, if  $c = 2.8$ , then  $c > \max\{c_1^*(\infty), c_2^*(\infty)\}$ , a scenario that the environment worsens too fast and too severe ( $r_i(-\infty) < 0$ ), the numeric results presented in Fig. 2 (top left) show that both species will eventually go to extinction, agreeing with Theorem 3.1. However, if  $c = 2.2$ , then  $c_2^*(\infty) < c < c_1^*(\infty)$ . Then by Theorem 3.5,  $u_1$ -species will survive by spread toward the right at speed  $c_1^*(\infty)$  approaching the level  $r_1(\infty) = 0.1$ , while the  $u_2$ -species will eventually die out. See Fig. 2 (top right and bottom).

Next choose  $r_1(x - ct) = \frac{0.24}{\pi} \arctan(x - ct)$ ,  $r_2(x - ct) = \frac{0.16}{\pi} \arctan(x - ct)$  and  $a_1 = 0.28$ ,  $a_2 = 0.18$ ,  $d_1 = 1.3$ ,  $d_2 = 1.6$ . Then,  $r_1(\infty) - a_1 r_2(\infty) = 0.0976$ ,  $r_2(\infty) - a_2 r_1(\infty) = 0.0584$  and calculations give  $(u_1^*, u_2^*) \approx (0.103, 0.061)$  and

$$\tilde{c}_1^*(\infty) = \frac{1.3 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.0976}{\mu} \Big|_{\mu \approx 0.07408} \approx 2.5719,$$

$$\tilde{c}_2^*(\infty) = \frac{1.6 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.0584}{\mu} \Big|_{\mu \approx 0.05260} \approx 2.1929,$$

$$c_1^*(\infty) = \frac{1.3 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.12}{\mu} \Big|_{\mu \approx 0.08153} \approx 2.8597,$$

$$c_2^*(\infty) = \frac{1.6 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + 0.08}{\mu} \Big|_{\mu \approx 0.06117} \approx 2.5725.$$

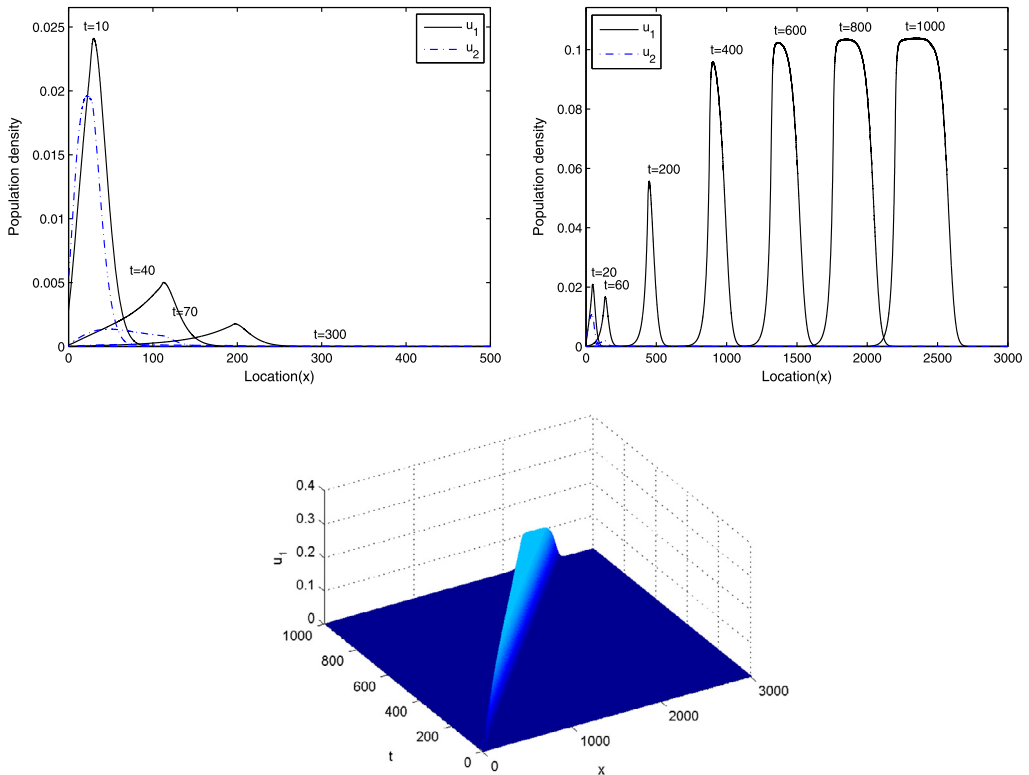


Fig. 2. In the top left, as  $c > \max\{c_1^*(\infty), c_2^*(\infty)\}$ , both two species become extinction eventually. In the top right, as  $c_2^*(\infty) < c < c_1^*(\infty)$ ,  $u_1$ -species will persist by spreading to the right with speed  $c_1^*(\infty)$ , while  $u_2$ -species will go to extinction. In the bottom, 3-D portrait shows that  $u_1$ -species persists by spreading to the right with the speed  $c_1^*(\infty) \approx 2.6$  and with the density approaching  $r_1(\infty) = 0.1$ .

Thus  $\tilde{c}^*(\infty) = \min\{\tilde{c}_1^*(\infty), \tilde{c}_2^*(\infty)\} \approx 2.19$  and  $c^*(\infty) = \min\{c_1^*(\infty), c_2^*(\infty)\} \approx 2.57$ . Now, if  $c = 1.8 < \tilde{c}^*(\infty)$ , Theorem 3.2 concludes that both species will persist through spreading to the right, and the numeric results confirm this conclusion, as shown in Fig. 3 (left).

## 5. Conclusion and discussion

We have analyzed the competitive system (6) with nonlocal dispersion and in a shifting environment reflected by the grow functions  $r_1(x - ct)$  and  $r_2(x - ct)$ . Our theoretical results show that under the “worsening” condition (A1) for these two growth functions and the standard condition (A2) for the two nonlocal dispersion kernels, the four composite parameters  $c_i^*(\infty)$  and  $\tilde{c}_i^*(\infty)$  ( $i = 1, 2$ ) play a crucial role in determining the spatial-temporal dynamics of the populations of two competing species. That is, (i) if the environment worsening speed  $c$  is very fast ( $c > \max\{c_1^*(\infty), c_2^*(\infty)\}$ ), then both species cannot survive in such a shifting of disastrous environment (noting that  $r_i(-\infty) < 0$ ,  $i = 1, 2$ ); (ii) if the worsening speed is small ( $c < \tilde{c}^*(\infty) := \min\{\tilde{c}_1^*(\infty), \tilde{c}_2^*(\infty)\}$ ), then both species will persist by spreading toward the right with a speed between  $c$  and  $c_i(\infty)$  for species  $i$  (see Theorems 3.2 and 3.3); (iii) when the worsening speed is medium-high, e.g.,  $c \in (c_1^*(\infty), c_2^*(\infty))$ , then species 1 will go to extinction while the species 2 will persist through spreading to the right (Theorem 3.4).

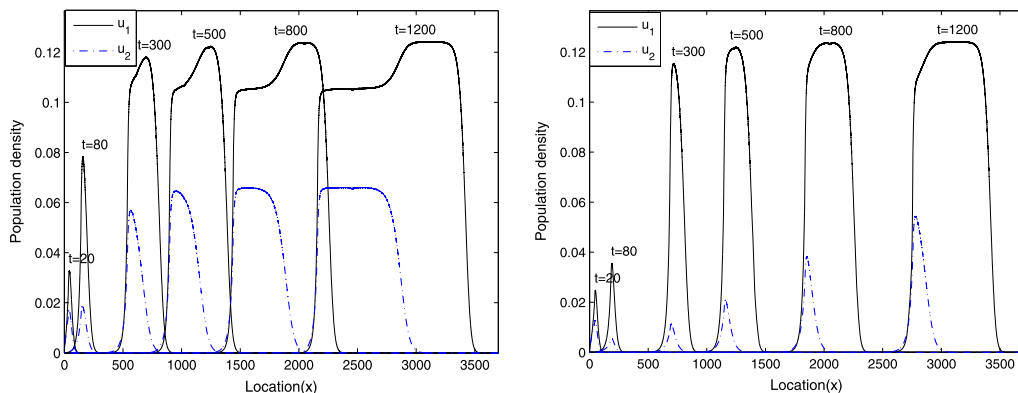


Fig. 3. In the left, as  $0 < c < \tilde{c}^*(\infty)$ , both species persist through spreading to the right. In the right, as  $\tilde{c}^*(\infty) < c < c^*(\infty)$ , both species can still persist through spreading to the right.

We point out that *even under homogeneous environment*, the results on spreading speed for a competitive Lotka-Volterra system with *nonlocal dispersal* are very limited. Hu et al. [21] considered a general multi-species system with nonlocal dispersal in homogeneous environment and obtained some abstract results, which can be applied to the following nonlocal dispersal Lotka-Volterra competition system with constant growth rates  $r_1, r_2 > 0$  that is pertinent to our model system (6):

$$\begin{cases} \partial_t p(t, x) = d_1[(J_1 * p)(t, x) - p(t, x)] + p[r_1 - p - a_1 q], \\ \partial_t q(t, x) = d_2[(J_2 * q)(t, x) - q(t, x)] + q[r_2 - q - a_2 p]. \end{cases} \quad (70)$$

Letting  $u_1 = p$ ,  $u_2 = r_2 - q$ , the system (70) is transformed into the cooperative system

$$\begin{cases} \partial_t u_1(t, x) = d_1[(J_1 * u_1)(t, x) - u_1(t, x)] + u_1[(r_1 - a_1 r_2) - u_1 + a_1 u_2], \\ \partial_t u_2(t, x) = d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + (r_2 - u_2)[a_2 u_1 - u_2], \end{cases} \quad (71)$$

when confined to  $u_i \in [0, r_i]$  with  $i = 1, 2$ , with the equilibrium  $(0, r_2)$  of (70) being transformed to the trivial equilibrium  $(0, 0)$  for (71). The linearization of (71) at  $(0, 0)$  is

$$\begin{cases} \partial_t u_1(t, x) = d_1[(J_1 * u_1)(t, x) - u_1(t, x)] + (r_1 - a_1 r_2)u_1, \\ \partial_t u_2(t, x) = d_2[(J_2 * u_2)(t, x) - u_2(t, x)] + a_2 r_2 u_1 - r_2 u_2. \end{cases} \quad (72)$$

The moment generating matrix of the time one solution map corresponding to (72) is given by  $e^{C_\mu}$  where

$$C_\mu = \begin{bmatrix} d_1[\int_{\mathbb{R}} J_1(y)e^{\mu y} dy - 1] + r_1 - a_1 r_2 & 0 \\ a_2 r_2 & d_2[\int_{\mathbb{R}} J_2(y)e^{\mu y} dy - 1] - r_2 \end{bmatrix}.$$

Let  $\gamma_1(\mu) = d_1[\int_{\mathbb{R}} J_1(y)e^{\mu y} dy - 1] + r_1 - a_1 r_2$  and  $\gamma_2(\mu) = d_2[\int_{\mathbb{R}} J_2(y)e^{\mu y} dy - 1] - r_2$ . By [21], the spreading speed of (72) is

$$\bar{c}_1 = \inf_{\mu > 0} \frac{\gamma_1(\mu)}{\mu} = \inf_{\mu > 0} \frac{d_1 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu y} dy - 1 \right] + r_1 - a_1 r_2}{\mu}. \quad (73)$$

The first part of [21, Theorem 4.1] has established the following

**Proposition 5.1.** *Let  $r_1 > a_1 r_2$  and  $\mu^*$  be the smallest positive number at which the infimum in (73) is attained. Assume that either*

(i)  *$\mu^*$  is finite and  $\int_{\mathbb{R}} J_2(y) e^{\mu^* y} dy$  is convergent, and*

$$\begin{aligned} & d_1 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu^* y} dy - 1 \right] + r_1 - a_1 r_2 \\ & \geq d_2 \left[ \int_{\mathbb{R}} J_2(y) e^{\mu^* y} dy - 1 \right] + r_2 [\max\{a_1 a_2, 1\} - 1] \end{aligned} \quad (74)$$

or

(ii)  *$\mu^* = \infty$ ,  $\int_{\mathbb{R}} J_i(y) e^{\mu y} dy$  is convergent for all  $\mu > 0$ , and there exists a sequence  $\mu_\sigma \rightarrow \infty$  such that for each  $\sigma$*

$$\begin{aligned} & d_1 \left[ \int_{\mathbb{R}} J_1(y) e^{\mu_\sigma y} dy - 1 \right] + r_1 - a_1 r_2 \\ & \geq d_2 \left[ \int_{\mathbb{R}} J_2(y) e^{\mu_\sigma y} dy - 1 \right] + r_2 [\max\{a_1 a_2, 1\} - 1] \end{aligned} \quad (75)$$

Then, the  $u_1$  component in system (70) will spread with speed  $\bar{c}_1$  given by (73).

Symmetrically, if  $r_2 > a_2 r_1$ , a  $\bar{c}_2$  corresponding to (73) can be obtained and statements parallel to those in the above proposition can be obtained for the spreading speed of the  $u_2$  component in (70), although this is not mentioned in [21]. If both  $r_1 > a_1 r_2$  and  $r_2 > a_2 r_1$  hold, then the last terms on the right sides of (74) and (75) disappear. We remark that verifying conditions in (74)–(75) is not trivial at all; comparing the magnitudes of  $\bar{c}_1$  and  $\bar{c}_2$  also remains an issue. There have been reports that different species even in a cooperative system can spread at different speeds (see [38]). Thus, *even under homogeneous environment*, spreading speed of a Lotka–Volterra competition system with nonlocal dispersal has not been completely understood. If  $r_i(x) \equiv r_i(\infty) =: r_i$  in (6), then the spreading speeds  $\bar{c}_i$  of model system (70) are indeed  $\bar{c}_i^*(\infty)$ ,  $i = 1, 2$ . As we have seen, for (70), because of the shifting nature, the shifting speed also comes into interplay, making problem more complicated.

Note that the competition coefficients  $a_1$  and  $a_2$  only affect  $\bar{c}_i^*(\infty)$  but have no impact on  $c_i^*(\infty)$ ,  $i = 1, 2$ ; also note that  $\bar{c}_i^*(\infty) \leq c_i^*(\infty)$ ,  $i = 1, 2$ . Thus, this is an obvious gap for  $c$  for which we are unable to obtain analytic results on the spatial-temporal dynamics of (6). However, numerical simulations suggest that when  $\bar{c}^*(\infty) < c < c^*(\infty) := \min\{c_1^*(\infty), c_2^*(\infty)\}$ , both

species can still persist through spreading to the right. For example, using the same parameter values as in the simulations for producing Fig. 3 (left) except for  $c$ , which is set to 2.3 (rather than 1.8), we obtain the numerical results given in Fig. 3 (right). It clearly shows that both species persist through spreading to the right. Analytically exploring the spatial-temporal dynamics of (6) when the worsening speed  $c$  falls into that gap  $(\tilde{c}^*(\infty), c^*(\infty))$  remains an interesting but challenging mathematical problem, and we leave it as a future work.

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## References

- [1] A new playing field: how climate change affects nature, Wildlife in a warming world, National Wildlife Federation, 2013.
- [2] J. Alexander, J. Diez, J. Levine, Novel competitors shape species' responses to climate change, *Nature* 525 (2015) 515–518.
- [3] M. Alfaro, H. Berestycki, G. Raoul, The effect of climate shift on a species submitted to dispersion, evolution, growth, and nonlocal competition, *SIAM J. Math. Anal.* 49 (1) (2017) 562–596.
- [4] P. Bates, G. Zhao, Existence, uniqueness and stability of the stationary solution to a nonlocal evolution equation arising in population dispersal, *J. Math. Anal. Appl.* 332 (2007) 428–440.
- [5] H. Berestycki, L. Desvillettes, O. Diekmann, Can climate change lead to gap formation?, *Ecol. Complex.* 20 (2014) 264–270.
- [6] H. Berestycki, O. Diekmann, C.J. Nagelkerke, P.A. Zegeling, Can a species keep pace with a shifting climate?, *Bull. Math. Biol.* 71 (2009) 399–429.
- [7] H. Berestycki, L. Rossi, Reaction-diffusion equations for population dynamics with forced speed. I. The case of the whole space, *Discrete Contin. Dyn. Syst., Ser. A* 21 (1) (2008) 41–67.
- [8] H. Berestycki, J. Coville, H. Vo, Persistence criteria for populations with non-local dispersion, *J. Math. Biol.* 72 (2016) 1693–1745.
- [9] H. Berestycki, J. Fang, Forced waves of the Fisher-KPP equation in a shifting environment, *J. Differ. Equ.* 264 (2018) 2157–2183.
- [10] J. Bouhoours, T. Giletti, Extinction and spreading of a species under the joint influence of climate change and a weak Allee effect: a two-patch model, *arXiv:1601.06589v1*, 2016.
- [11] M. Cain, B. Milligan, A. Strand, Long-distance seed dispersal in plant populations, *Am. J. Bot.* 87 (9) (2000) 1217–1227.
- [12] E. Chasseigne, M. Chaves, J.D. Rossi, Asymptotic behavior for nonlocal diffusion equations, *J. Math. Pures Appl.* 86 (2006) 271–291.
- [13] J. Clark, Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord, *Am. Nat.* 152 (2) (1998) 204–224.
- [14] C. Cortazar, M. Elgueta, J.D. Rossi, Nonlocal diffusion problems that approximate the heat equation with Dirichlet boundary conditions, *Isr. J. Math.* 170 (2009) 53–60.
- [15] J. Coville, J. Dávila, S. Martínez, Existence and uniqueness of solutions to a nonlocal equation with monostable nonlinearity, *SIAM J. Math. Anal.* 39 (2008) 1693–1709.
- [16] M. Deasi, D. Nelson, A quasispecies on a moving oasis, *Theor. Popul. Biol.* 67 (2005) 33–45.
- [17] J. Elith, M. Kearney, S. Phillips, The art of modelling range-shifting species, *Methods Ecol. Evol.* 1 (2010) 330–342.

- [18] J. Fang, Y. Lou, J. Wu, Can pathogen spread keep pace with its host invasion?, *SIAM J. Appl. Math.* 76 (2016) 1633–1657.
- [19] G. Hetzer, T. Nguyen, W. Shen, Coexistence and extinction in the Volterra-Lotka competition model with nonlocal dispersal, *Commun. Pure Appl. Anal.* 11 (2012) 1699–1722.
- [20] C. Hu, B. Li, Spatial dynamics for lattice differential equations with a shifting habitat, *J. Differ. Equ.* 259 (2015) 1967–1989.
- [21] C. Hu, Y. Kuang, B. Li, H. Liu, Spreading speeds and traveling wave solutions in cooperative integral-differential systems, *Discrete Contin. Dyn. Syst., Ser. B* 20 (2015) 1663–1684.
- [22] H. Hu, X. Zou, Existence of an extinction wave in the Fisher equation with a shifting habitat, *Proc. Am. Math. Soc.* 145 (2017) 4763–4771.
- [23] H. Hu, T. Yi, X. Zou, On spatial-temporal dynamics of Fisher-KPP equation with a shifting environment, *Proc. Am. Math. Soc.* (2019), in press.
- [24] V. Hutson, S. Martínez, K. Mischaikow, G.T. Vickers, The evolution of dispersal, *J. Math. Biol.* 47 (2003) 483–517.
- [25] C.-Y. Kao, Y. Lou, W. Shen, Random dispersal vs. non-local dispersal, *Discrete Contin. Dyn. Syst., Ser. A* 26 (2010) 551–596.
- [26] M.A. Lewis, N.G. Marculis, Z. Shen, Integrodifference equations in the presence of climate change: persistence criterion, travelling waves and inside dynamics, *J. Math. Biol.* 77 (2018) 1649–1687.
- [27] B. Li, S. Bewick, J. Shang, W. Fagan, Persistence and spread of a species with a shifting habitat edge, *SIAM J. Appl. Math.* 74 (5) (2014) 1397–1417.
- [28] B. Li, S. Bewick, M. Barnard, W. Fagan, Persistence and spreading speeds of integro-difference equations with an expanding or contracting habitat, *Bull. Math. Biol.* 78 (2016) 1337–1379.
- [29] W.-T. Li, J.-B. Wang, X.-Q. Zhao, Spatial dynamics of a nonlocal dispersal population model in a shifting environment, *J. Nonlinear Sci.* 28 (4) (2018) 1189–1219.
- [30] F. Lutscher, E. Pachepsky, M. Lewis, The effect of dispersal patterns on stream populations, *SIAM Rev.* 47 (2005) 749–772.
- [31] A. Potapov, M. Lewis, Climate and competition: the effect of moving range boundaries on habitat invasibility, *Bull. Math. Biol.* 66 (2004) 975–1008.
- [32] L. Roques, A. Roques, H. Berestycki, A. Kretschmar, A population facing climate change: joint influences of Allee effects and environmental boundary geometry, *Popul. Ecol.* 50 (2008) 215–225.
- [33] F. Schurr, O. Steinitz, R. Nathan, Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation, *J. Ecol.* 96 (4) (2008) 628–641.
- [34] D.A. Smale, T. Wernberg, Extreme climatic event drives range contraction of a habitat-forming species, *Proc. R. Soc. B* 280 (2013) 20122829.
- [35] H. Vo, Persistence versus extinction under a climate change in mixed environments, *J. Differ. Equ.* 259 (2015) 4947–4988.
- [36] J.-B. Wang, X.-Q. Zhao, Uniqueness and global stability of forced waves in a shifting environment, *Proc. Am. Math. Soc.* 147 (2019) 1467–1481.
- [37] H.F. Weinberger, Long-time behavior of a class of biological models, *SIAM J. Math. Anal.* 13 (1982) 353–396.
- [38] H.F. Weinberger, M.A. Lewis, B. Li, Analysis of linear determinacy for spread in cooperative models, *J. Math. Biol.* 45 (2002) 183–218.
- [39] C.F. Wu, D.M. Xiao, X.-Q. Zhao, Spreading speeds of a partially degenerate reaction-diffusion system in a periodic habitat, *J. Differ. Equ.* 255 (2013) 3983–4011.
- [40] H. Yin, A consistent poleward shift of the storm tracks in simulations of 21st century climate, *Geophys. Res. Lett.* 32 (2005) L18701.
- [41] Y. Yuan, Y. Wang, X. Zou, Spatial-temporal dynamics of a Lotka-Volterra competition model with a shifting habitat, *Discrete Contin. Dyn. Syst., Ser. B* (2019), in press.
- [42] Z. Zhang, W. Wang, J. Yang, Persistence versus extinction for two competing species under a climate change, *Nonlinear Anal., Model. Control* 22 (3) (2017) 285–302.
- [43] Y. Zhou, M. Kot, Discrete-time growth-dispersal models with shifting species ranges, *Theor. Ecol.* 4 (2011) 13–25.