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Global dynamics and spreading speeds for a partially degenerate system with non-local dispersal in periodic habitats

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This paper is concerned with the global dynamics and spreading speeds of a partially degenerate non-local dispersal system with monostable nonlinearity in periodic habitats. We first obtain the existence of the principal eigenvalue for a periodic eigenvalue problem with partially degenerate non-local dispersal. Then we study the coexistence and extinction dynamics. Finally, the existence and characterization of spreading speeds are considered. In particular, we show that the spreading speed is linearly determinate. Overall, we extend the existing results on global dynamics and spreading speeds for the degenerate reaction–diffusion system to the degenerate non-local dispersal case. The extension is non-trivial and meaningful.

Keywords: partially degenerate system; periodic habitat; non-local dispersal; global dynamics; spreading speeds

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1. Introduction

This paper is devoted to the study of global dynamics and spreading speeds of a general partially degenerate non-local dispersal system in periodic habitats:

$$\left.\begin{aligned}\frac{\partial u(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)u(t,y)\,\mathrm{d}y - u(t,x) + f(x,u,v),\\ \frac{\partial v(t,x)}{\partial t} &= g(x,u,v),\end{aligned}\right\} \tag{1.1}$$

where $u(t,x)$ and $v(t,x)$ are the densities of two species at time $t>0$ and location $x \in \mathbb{R}$ in an L-periodic habitat for some positive number L. In (1.1), the spatial migration of species u is formulated by the non-local dispersal operator, i.e. $\mathcal{N}u(t,x) = \int_{\mathbb{R}} J(x-y)u(t,y)\,\mathrm{d}y - u(t,x)$, which arises from the physics of long range effects and other disciplines and has significant use in population dynamics [5, 18, 27]. The dispersal kernel $J(\cdot)$ is a probability function satisfying the following hypothesis.

(J) $J \in \boldsymbol{C}^1(\mathbb{R}, \mathbb{R}_+)$ is compactly supported, $J(0) > 0$ and

$$\int_{\mathbb{R}} J(x)\,\mathrm{d}x = 1.$$

Note that the kernel J is not required to be symmetric in the above hypothesis. Obviously, asymmetric kernel functions describe some anisotropic dispersal process.

When $f(x,u,v) := -u+av$ and $g(x,u,v) := -bv+h(u)$ are independent of spatial variable x, system (1.1) is reduced to the following non-local dispersal human–environment–human epidemic model:

$$\left.\begin{aligned} \frac{\partial u(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)u(t,y)\,\mathrm{d}y - 2u(t,x) + av(t,x), \\ \frac{\partial v(t,x)}{\partial t} &= -bv(t,x) + h(u(t,x)). \end{aligned}\right\} \tag{1.2}$$

Under the extra assumption that J is symmetric, Zhang *et al.* [39] deal with multi-type entire solutions of system (1.1) for both monostable and bistable cases.

It is generally known that there is a close relationship between the non-local system (1.1) and the local version. In particular, let $J(x) = (1/\sigma)K(x/\sigma)$ with $\sigma > 0$, where $K(x)$ is a general mollification function with support $x \in [-1, 1]$. If $u(x)$ is smooth and $0 < \sigma \ll 1$, then the Taylor formula yields

$$\begin{aligned} &\int_{\mathbb{R}} J(x-y)u(y)\,\mathrm{d}y - u(x) \\ &\qquad = \int_{\mathbb{R}} \frac{1}{\sigma} K\left(\frac{x-y}{\sigma}\right)[u(y) - u(x)]\,\mathrm{d}y \\ &\qquad = \int_{\mathbb{R}} K(-z)[u(x+\sigma z) - u(x)]\,\mathrm{d}z \\ &\qquad = \frac{\sigma^2}{2}\int_{\mathbb{R}} K(-z)z^2\,\mathrm{d}z \frac{\partial^2 u(x)}{\partial x^2} + \sigma\int_{\mathbb{R}} K(-z)z\,\mathrm{d}z \frac{\partial u(x)}{\partial x} + o(\sigma^2). \end{aligned}$$

For simplicity, we define $D_1 = \frac{1}{2}\sigma^2 \int_{\mathbb{R}} K(-z)z^2\,\mathrm{d}z$ and $D_2 = \sigma \int_{\mathbb{R}} K(-z)z\,\mathrm{d}z$. Then system (1.1) can be viewed as an approximation of the classical reaction–diffusion system:

$$\left.\begin{aligned} \frac{\partial u(t,x)}{\partial t} &= D_1 \frac{\partial^2 u}{\partial^2 x} + D_2 \frac{\partial u}{\partial x} + f(x,u,v), \\ \frac{\partial v(t,x)}{\partial t} &= g(x,u,v). \end{aligned}\right\} \tag{1.3}$$

Note that $D_2 = 0$ if J is symmetric. We point out that systems similar to (1.3) with a homogeneous or heterogeneous reaction field have been widely studied in the last few years. In particular, Wu *et al.* [38] considered the travelling fronts and entire solutions of system (1.3) with $D_2 = 0$, $f(x,u,v) := -u + av$ and $g(x,u,v) := -bv + h(u)$, where $h(u)$ is a monostable term. For the general spatial periodic cooperative system (1.3), Wu *et al.* [37] studied the global dynamics and spreading speeds, while pulsating waves were investigated by Wang *et al.* [31] very recently.

With regard to the non-degenerate case, Kong *et al.* [19] recently investigated a two-species competition system with the same dispersal kernel in spatio-temporal periodic media:

$$\left.\begin{aligned}u_t &= \int_{\mathbb{R}^N} J(y-x)u(t,y)\,\mathrm{d}y - u(t,x) + u(a_1(t,x) - b_1(t,x)u - c_1(t,x)v),\\ v_t &= \int_{\mathbb{R}^N} J(y-x)v(t,y)\,\mathrm{d}y - v(t,x) + v(a_2(t,x) - b_2(t,x)u - c_2(t,x)v).\end{aligned}\right\} \quad (1.4)$$

Kong *et al*. investigated the spreading speeds and linear determinacy. In the case when the periodic dependence of the habitat in (1.4) is specifically only on the spatial variable, i.e. $a_k(t,x) = a_k(x)$, $b_k(t,x) = b_k(x)$ and $c_k(t,x) = c_k(x)$ for $k = 1, 2$, the coexistence and extinction dynamics were investigated by Hetzer *et al*. [14]. Very recently, Bao *et al*. [4] studied the existence, uniqueness and asymptotic stability of invasion travelling wave solutions. Note that both Bao *et al*. [4] and Kong *et al*. [19] transformed (1.4) into a cooperative system for further study.

The concept of spreading speeds was first introduced by Aronson and Weinberger [1–3] for reaction–diffusion equations, and has attracted much attention in recent years. The reader is referred to [6, 10, 11, 19, 21–25, 29, 30, 32–37] and the references therein for more details. All of these works indicate that spreading speed is an important ecological metric in a wide range of ecological and epidemiological applications, which can be used to study biological invasions and the spread of disease. There are two main approaches to dealing with the spreading speed. One is the construction method (see [23, 33]); the other is to employ the natural properties of the spreading speed and use the comparison principle, upper–lower solutions and the principal eigenvalue theory to establish the existence and characterization (see [19,29,30,37]). Generally speaking, the spreading speeds of a recursion with an order-preserving compact operator can be established by the former, while the latter is often used to handle some equations or systems in which the solution operator is non-compact and the nonlinearity is spatially inhomogeneous.

There are many phenomena in population biology, epidemiology and other disciplines that need to be modelled by partially degenerate dispersal systems such as (1.1) or (1.3), in which partial dispersal coefficients are zeros (see, for example, [7,12,20,26]). On the other hand, most real environments exhibit spatial heterogeneity, and periodic habitat is one of the useful approximations for understanding the effect of environmental heterogeneity on propagation phenomena. Based on the above considerations, the study of periodic degenerate dispersal system (1.1) is of both theoretical and practical value.

For the general partially degenerate non-local dispersal system (1.1), since the corresponding solution operator is non-compact and the reaction field is spatial periodic, we study the spreading speeds using the second method. Initially, we need to study the global dynamics of (1.1). To this end, we consider a periodic eigenvalue problem with partially degenerate non-local dispersal (see (2.8)), develop an appropriate comparison principle and investigate the positive periodic steady states. (It is important to note that the eigenvalue problem associated with non-degenerate system (1.4) cannot be applied to (2.8) directly, since the existence of the principal eigenvalue in (1.4) strictly depends on the uniformity of the two dispersal kernels. In fact, in our degenerate system (1.1) the two dispersal kernels are different, i.e. one is $J(\cdot)$ and the other is $\delta_0(\cdot)$ (the Dirac delta function).) Then we establish the existence of the spreading speed interval, and furthermore show using upper–lower linear control systems that this interval is a singleton with a specific computational formula. In other words, we shall extend the existing results on spreading speed for a partially degenerate reaction–diffusion system in periodic habitats. We point out that the spreading properties in periodic habitats originate from the propagating waves in periodic media; hence, we shall study spatial periodic travelling waves and some new types of entire solutions of (1.1) elsewhere.

We end this introduction with a series of hypotheses on the reaction field (f, g):

(F1) $f, g\colon \mathbb{R}\times\mathbb{R}_+\times\mathbb{R}_+ \to \mathbb{R}$ are $\boldsymbol{C}^2$ in $\boldsymbol{u} = (u, v)$, Hölder continuous and L-periodic in x, $f(x, 0, 0) = g(x, 0, 0) = 0$ and the partial derivatives of f, g up to second order with respect to u, v are all continuous and L-periodic in x, respectively;

(F2) there exists a positive vector $\boldsymbol{M} = (M_1, M_2)$ such that $f(x, \boldsymbol{M}) \leqslant 0$ and $g(x, \boldsymbol{M}) \leqslant 0$ for all $x \in \mathbb{R}$;

(F3) $f_v(x, u, v) > 0$ and $g_u(x, u, v) > 0$ for all $x \in \mathbb{R}$ and $(u, v) \in [0, M_1] \times [0, M_2]$, where f_w and g_w denote the partial derivatives of f and g with respect to w, respectively;

(F4) $\boldsymbol{F}(x, \boldsymbol{u}) := (f(x, \boldsymbol{u}), g(x, \boldsymbol{u}))$ is strictly subhomogeneous on $[0, M_1] \times [0, M_2]$ in the sense that $\boldsymbol{F}(x, \nu\boldsymbol{u}) > \nu\boldsymbol{F}(x, \boldsymbol{u})$ for all $x \in \mathbb{R}$, $\nu \in (0, 1)$ and $\boldsymbol{u} \in (0, M_1] \times (0, M_2]$.

The rest of this paper is organized as follows. In § 2, we prove some preliminary results including the comparison principle, the principal eigenvalue and linear evolution operators. Then the stationary solutions and global dynamics are considered in § 3. In § 4, we establish the existence of the spreading speed interval by sandwiching the original system (1.1) between two upper–lower linear control systems. Finally, in § 5, we prove that the spreading speed is a singleton combining the linear spectral theory and squeezing techniques.

2. Preliminaries

In this section, we introduce some notation and present preliminary results that will be very useful in later sections. First, we define some spaces. Let

$$X_p = \{w \in \boldsymbol{C}(\mathbb{R}, \mathbb{R}) \mid w(\cdot + L) = w(\cdot)\}$$

with the norm $\|w\|_{X_p} = \max_{x\in\mathbb{R}} |w(x)|$, and

$$X_p^+ = \{w \in X_p \mid w(x) \geqslant 0,\ \forall x \in \mathbb{R}\}$$

and

$$X_p^{++} = \{w \in X_p^+ \mid w(x) > 0,\ \forall x \in \mathbb{R}\}.$$

Let

$$X = \left\{w \in \boldsymbol{C}(\mathbb{R}, \mathbb{R}) \;\middle|\; w \text{ is uniformly continuous on } \mathbb{R} \text{ and } \sup_{x\in\mathbb{R}} |w(x)| < \infty\right\}$$

with the norm $\|w\|_X = \sup_{x\in\mathbb{R}} |w(x)|$ and

$$X^+ = \{w \in X \mid w(x) \geqslant 0,\ \forall x \in \mathbb{R}\} \quad \text{and} \quad X^{++} = \left\{w \in X^+ \;\middle|\; \inf_{x\in\mathbb{R}} w(x) > 0\right\}.$$

For $u_1, u_2 \in X$, we define $u_1 \leqslant (\ll)\, u_2$ if $u_2 - u_1 \in X^+(X^{++})$. Moreover, for $\boldsymbol{u}_1 = (u_1, v_1)$ and $\boldsymbol{u}_2 = (u_2, v_2)$, we write $\boldsymbol{u}_1 \leqslant (\ll)\, \boldsymbol{u}_2$ if and only if $u_1 \leqslant (\ll)\, u_2$ and $v_1 \leqslant (\ll)\, v_2$. For a constant $0 \ll r$, we define $[0, r]_X = \{w \in X : 0 \leqslant w(x) \leqslant r,\ \forall x \in \mathbb{R}\}$ and $(0, r]_X = \{w \in X : 0 < w(x) \leqslant r,\ \forall x \in \mathbb{R}\}$. For given $\rho \geqslant 0$, let

$$X_\rho = \{(u, v) \in \boldsymbol{C}(\mathbb{R}, \mathbb{R}^2) \mid (\mathrm{e}^{-\rho|\cdot|}u(\cdot), \mathrm{e}^{-\rho|\cdot|}v(\cdot)) \in X \times X\}$$

be equipped with the norm $\|(u, v)\|_{X_\rho} = \sup_{x\in\mathbb{R}} \mathrm{e}^{-\rho|x|}(|u(x)| + |v(x)|)$. Obviously, $X_0 = X \times X$.

For any given $(u_0, v_0) \in X^+ \times X^+$, we consider the initial-value problem:

$$\left.\begin{aligned} \frac{\partial u(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)u(t,y)\,\mathrm{d}y - u(t,x) + f(x,u,v), \quad x \in \mathbb{R},\ t > 0, \\ \frac{\partial v(t,x)}{\partial t} &= g(x,u,v), \quad x \in \mathbb{R},\ t > 0, \\ u(0,x) &= u_0(x), \quad v(0,x) = v_0(x), \quad x \in \mathbb{R}. \end{aligned}\right\} \tag{2.1}$$

According to [16, lemmas 2.1 and 2.2], the fundamental solution of the Cauchy problem

$$\left.\begin{aligned} \frac{\partial u(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)u(t,y)\,\mathrm{d}y - u(t,x), \\ u(0,x) &= u_0(x) \in X, \end{aligned}\right\} \tag{2.2}$$

can be decomposed as $S(t, x) = \mathrm{e}^{-t}\delta_0(x) + K_t(x)$, where δ_0 denotes the Delta function and

$$K_t(x) = \int_{\mathbb{R}} (\exp(t(\hat{J}(\xi) - 1)) - \mathrm{e}^{-t})\mathrm{e}^{\mathrm{i}x\xi}\,\mathrm{d}\xi$$

satisfies $\|K_t(x)\|_{L^1(\mathbb{R})} \leqslant 2$ for any $t > 0$, and here $\hat{J}(\xi)$ is the Fourier transformation of J. Thus, the solution of (2.2) can be written as $(S * u_0)(t, x)$. It then follows that (2.1) can be written in the following integral form:

$$\begin{aligned} u(t,x;\boldsymbol{u}_0) &= \int_{\mathbb{R}} S(t,y)u_0(x-y)\,\mathrm{d}y \\ &\quad + \int_0^t \int_{\mathbb{R}} S(t-s,x-y) f(y, u(s,y;\boldsymbol{u}_0), v(s,y;\boldsymbol{u}_0))\,\mathrm{d}y\,\mathrm{d}s, \\ v(t,x;\boldsymbol{u}_0) &= v_0 + \int_0^t g(x, u(s,x;\boldsymbol{u}_0), v(s,x;\boldsymbol{u}_0))\,\mathrm{d}s, \end{aligned}$$

where $\boldsymbol{u}_0 = (u_0, v_0)$.

2.1. The well-posedness of solutions

We first consider the existence, uniqueness and invariance of solutions of (2.1) in $[0, M_1] \times [0, M_2]$.

Theorem 2.1. *For any initial value $\boldsymbol{u}_0 = (u_0, v_0) \in [0, M_1]_X \times [0, M_2]_X$, (2.1) admits a unique mild solution $(u(t, \cdot; \boldsymbol{u}_0), v(t, \cdot; \boldsymbol{u}_0))$ with $(u(0, \cdot; \boldsymbol{u}_0), v(0, \cdot; \boldsymbol{u}_0)) = (u_0, v_0)$, and $(u(t, \cdot; \boldsymbol{u}_0), v(t, \cdot; \boldsymbol{u}_0)) \in [0, M_1]_X \times [0, M_2]_X$ for all $t \geqslant 0$.*

Proof. The proof is similar to [37, theorem 2.1] and we omit the details here. □

Now we are ready to present a comparison principle for system (1.1). To do this, we recall the concept of upper–lower solutions.

HYPOTHESIS 2.2. *A pair of continuous functions* $(u(t,x),v(t,x))$ *on* $[0,\tau)\times\mathbb{R}$ *is called an upper solution of (1.1) if both* $\partial u/\partial t$ *and* $\partial v/\partial t$ *exist, are continuous on* $[0,\tau)\times\mathbb{R}$*, and satisfy*

$$\frac{\partial u(t,x)}{\partial t}\geqslant\int_{\mathbb{R}}J(x-y)u(t,y)\,\mathrm{d}y-u(t,x)+f(x,u,v),\qquad\frac{\partial v(t,x)}{\partial t}\geqslant g(x,u,v),$$

and called a lower solution of (1.1) if both $\partial u/\partial t$ *and* $\partial v/\partial t$ *exist, are continuous on* $[0,\tau)\times\mathbb{R}$*, and satisfy*

$$\frac{\partial u(t,x)}{\partial t}\leqslant\int_{\mathbb{R}}J(x-y)u(t,y)\,\mathrm{d}y-u(t,x)+f(x,u,v),\qquad\frac{\partial v(t,x)}{\partial t}\leqslant g(x,u,v),$$

for $t\in[0,\tau]$ *and* $x\in\mathbb{R}$.

LEMMA 2.3.

(i) *Suppose that* $(\bar{u}(t,x),\bar{v}(t,x))$ *is a bounded upper solution of (1.1) on* $[0,\tau]$ *and* $(\underline{u}(t,x),\underline{v}(t,x))$ *is a bounded lower solution of (1.1) on* $[0,\tau]$*. If* $\underline{u}(0,x)\leqslant\bar{u}(0,x)$ *and* $\underline{v}(0,x)\leqslant\bar{v}(0,x)$ *for all* $x\in\mathbb{R}$*, then*

$$\underline{u}(t,x)\leqslant\bar{u}(t,x),\quad\underline{v}(t,x)\leqslant\bar{v}(t,x)$$

for all $x\in\mathbb{R}$ *and* $t\in[0,\tau]$.

(ii) *For every* $(u_0,v_0)\in X^+\times X^+$, $(u(t,\cdot;u_0,v_0),v(t,\cdot;u_0,v_0))$ *exists for all* $t\geqslant 0$.

Proof.
(i) Set

$$\tilde{u}(t,x)=\mathrm{e}^{Kt}(\bar{u}(t,x)-\underline{u}(t,x)),\qquad\tilde{v}(t,x)=\mathrm{e}^{Kt}(\bar{v}(t,x)-\underline{v}(t,x)),$$

where K is a positive constant to be determined later. Then $(\tilde{u}(t,x),\tilde{v}(t,x))$ satisfies

$$\begin{aligned}\frac{\partial\tilde{u}(t,x)}{\partial t}&\geqslant\int_{\mathbb{R}}J(x-y)\tilde{u}(t,y)\,\mathrm{d}y+[-1+K+f_u(x,\tilde{u}^*,\tilde{v}^*)]\tilde{u}\\&\quad+f_v(x,\tilde{u}^*,\tilde{v}^*)\tilde{v},\quad x\in\mathbb{R},\\\frac{\partial\tilde{v}(t,x)}{\partial t}&\geqslant g_u(x,\tilde{u}^{**},\tilde{v}^{**})\tilde{u}+[K+g_v(x,\tilde{u}^{**},\tilde{v}^{**})]\tilde{v},\quad x\in\mathbb{R},\end{aligned}$$

where $\tilde{u}^*=\tilde{u}^*(t,x)$, $\tilde{u}^{**}=\tilde{u}^{**}(t,x)$ are between $\underline{u}(t,x)$ and $\bar{u}(t,x)$, while $\tilde{v}^*=\tilde{v}^*(t,x)$, $\tilde{v}^{**}=\tilde{v}^{**}(t,x)$ are between $\underline{v}(t,x)$ and $\bar{v}(t,x)$.

By (F3) we have

$$f_v(x,\tilde{u}^*,\tilde{v}^*)>0,\qquad g_u(x,\tilde{u}^{**},\tilde{v}^{**})>0.$$

At the same time, we can choose sufficiently large $K>0$ such that

$$-1+K+f_u(x,\tilde{u}^*,\tilde{v}^*)>0,\qquad K+g_v(x,\tilde{u}^{**},\tilde{v}^{**})>0.$$

By the boundedness of the upper–lower solutions and (F1), we can define

$$p_0 = \max_{x\in\mathbb{R}}\{f_v(x,\tilde{\boldsymbol{u}}^*), g_u(x,\tilde{\boldsymbol{u}}^{**}), -1+K+f_u(x,\tilde{\boldsymbol{u}}^*), K+g_v(x,\tilde{\boldsymbol{u}}^{**})\} > 0,$$

where $\tilde{\boldsymbol{u}}^* = (\tilde{u}^*, \tilde{v}^*)$ and $\tilde{\boldsymbol{u}}^{**} = (\tilde{u}^{**}, \tilde{v}^{**})$.

Let $\tau_0 = \min\{\tau, 1/2(1+2p_0)\}$. We now claim that $\tilde{u}(t,x) \geqslant 0$ and $\tilde{v}(t,x) \geqslant 0$ for all $x \in \mathbb{R}$ and $t \in [0,\tau_0]$. Assume by contradiction that there are some $x_0 \in \mathbb{R}$ and $t_0 \in [0,\tau_0]$ such that $\tilde{u}(t_0,x_0) < 0$ or $\tilde{v}(t_0,x_0) < 0$. Set

$$\tilde{u}_{\inf} = \inf_{t\in[0,\tau_0],x\in\mathbb{R}} \tilde{u}(t,x), \qquad \tilde{v}_{\inf} = \inf_{t\in[0,\tau_0],x\in\mathbb{R}} \tilde{v}(t,x).$$

Then $\tilde{u}_{\inf} < 0$ or $\tilde{v}_{\inf} < 0$, and we can further assume that $\tilde{u}_{\inf} \leqslant \tilde{v}_{\inf}$ without loss of generality. Note that there are some sequences $\{x_n\}_{n\in N^+} \subset \mathbb{R}$ and $\{t_n\}_{n\in N^+} \subset (0,\tau_0]$ such that

$$\tilde{u}(t_n,x_n) \to \tilde{u}_{\inf} \quad \text{as } n \to +\infty.$$

Then a direct calculation implies that

$$\begin{aligned}
&\tilde{u}(t_n,x_n) - \tilde{u}(0,x_n)\\
&\quad\geqslant \int_0^{t_n}\biggl[\int_{\mathbb{R}} J(x_n-y)\tilde{u}(t,y)\,\mathrm{d}y + (-1+K+f_u(x_n,\tilde{\boldsymbol{u}}^*))\tilde{u}(t,x_n)\\
&\qquad\qquad + f_v(x_n,\tilde{\boldsymbol{u}}^*)\tilde{v}(t,x_n)\biggr]\mathrm{d}t\\
&\quad\geqslant \int_0^{t_n}\biggl[\int_{\mathbb{R}} J(x_n-y)\tilde{u}_{\inf}\,\mathrm{d}y + p_0\tilde{u}_{\inf} + p_0\tilde{v}_{\inf}\biggr]\mathrm{d}t\\
&\quad\geqslant (1+2p_0)\tilde{u}_{\inf}t_n \geqslant (1+2p_0)\tilde{u}_{\inf}\tau_0.
\end{aligned}$$

Noting that $\tilde{u}(0,x_n) = \bar{u}(0,x_n) - \underline{u}(0,x_n) \geqslant 0$ and then letting $n \to +\infty$ in the above inequality, we can obtain

$$\tilde{u}_{\inf} \geqslant (1+2p_0)\tilde{u}_{\inf}\tau_0 > \tilde{u}_{\inf}.$$

This is a contradiction, and so our claim is true.

Furthermore, through similar arguments we have $\tilde{u}(t,x) \geqslant 0$ and $\tilde{v}(t,x) \geqslant 0$ for all $x \in \mathbb{R}$ and $t \in [\tau_0, \min\{\tau, 2\tau_0\}]$. By induction, we have $\tilde{u}(t,x) \geqslant 0$ and $\tilde{v}(t,x) \geqslant 0$ for all $x \in \mathbb{R}$ and $t \in [0,\tau]$, i.e.

$$\underline{u}(t,x) \leqslant \bar{u}(t,x) \quad \text{and} \quad \underline{v}(t,x) \leqslant \bar{v}(t,x) \quad \text{for all } x \in \mathbb{R} \text{ and } t \in [0,\tau].$$

(ii) By (F2), there exists $\boldsymbol{M} = (M_1, M_2)$ such that

$$(u_0(x), v_0(x)) \leqslant (M_1, M_2), \quad f(x,\boldsymbol{M}) \leqslant 0 \quad \text{and} \quad g(x,\boldsymbol{M}) \leqslant 0.$$

Define $(u_{\boldsymbol{M}}(t,x), v_{\boldsymbol{M}}(t,x)) \equiv (M_1, M_2)$ for all $(t,x) \in [0,\infty) \times \mathbb{R}$. Then $(u_{\boldsymbol{M}}, v_{\boldsymbol{M}})$ is an upper solution of (1.1) on $[0,\infty)$. Let $I(u_0,v_0) \subset \mathbb{R}$ be the maximal interval for existence of the solution $(u(t,x;u_0,v_0), v(t,x;u_0,v_0))$ of (1.1). Moreover, in view of (i) and $(u_0,v_0) \in X^+ \times X^+$, we have

$$(0,0) \leqslant (u(t,x;u_0,v_0), v(t,x;u_0,v_0)) \leqslant (M_1, M_2)$$

for $t \in I(u_0,v_0) \cap [0,\infty)$ and $x \in \mathbb{R}$. It then follows easily that $[0,\infty) \subset I(u_0,v_0)$, and $(u(t,\cdot;u_0,v_0), v(t,\cdot;u_0,v_0))$ exists for all $t \geqslant 0$. □

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Now we show the continuous dependence of solutions with respect to the initial values.

LEMMA 2.4. *If* (u_k, v_k), $(u_0, v_0) \in X^+ \times X^+$ *satisfy* $\|(u_k, v_k)\|_{X_\rho} \leqslant C$ *for some* $C > 0$ *and* $k = 0, 1, 2, \dots,$ *and* $(u_k(x), v_k(x)) \to (u_0(x), v_0(x))$ *as* $k \to \infty$ *uniformly for* x *in bounded subsets of* $\mathbb{R}$*, then*

$$(u(t, x; u_k, v_k), v(t, x; u_k, v_k)) \to (u(t, x; u_0, v_0), v(t, x; u_0, v_0)) \quad \text{as } k \to \infty$$

uniformly for (t, x) *in bounded subsets of* $[0, \infty) \times \mathbb{R}$.

Proof. Let $u^k(t, x) = u(t, x; u_k, v_k) - u(t, x; u_0, v_0)$ and $v^k(t, x) = v(t, x; u_k, v_k) - v(t, x; u_0, v_0)$. Then we have

$$\begin{aligned} \frac{\partial u^k}{\partial t} &= \int_{\mathbb{R}} J(x-y) u^k(t, y)\,\mathrm{d}y - u^k(t, x) + f_u(x, \tilde{u}, \tilde{v}) u^k + f_v(x, \tilde{u}, \tilde{v}) v^k, \\ \frac{\partial v^k}{\partial t} &= A v^k + g_u(x, \hat{u}, \hat{v}) u^k + (g_v(x, \hat{u}, \hat{v}) - A) v^k, \end{aligned}$$

where $\tilde{u}(t, x)$ and $\hat{u}(t, x)$ are between $u(t, x; u_0, v_0)$ and $u(t, x; u_k, v_k)$, while $\tilde{v}(t, x)$ and $\hat{v}(t, x)$ are between $v(t, x; u_0, v_0)$ and $v(t, x; u_k, v_k)$ and $A > 0$ is a constant. Note that

$$(\mathcal{N}, A)(u, v) = \left(\int_{\mathbb{R}} J(x-y) u(t, y)\,\mathrm{d}y - u, Av \right)$$

is a bounded linear operator, and $f_u(x, \tilde{u}, \tilde{v})$, $f_v(x, \tilde{u}, \tilde{v})$, $g_u(x, \hat{u}, \hat{v})$ and $g_v(x, \hat{u}, \hat{v})$ are bounded on $\mathbb{R} \times [0, M_1] \times [0, M_2]$; for simplicity we denote these by $\tilde{f}_u$, $\tilde{f}_v$, $\hat{g}_u$ and $\hat{g}_v$, respectively. Hence, there are some $M > 0$ and $\omega > 0$ such that

$$\|\mathrm{e}^{(\mathcal{N}, A)t}\|_{X_\rho} \leqslant M \mathrm{e}^{\omega t} \quad \text{and} \quad |\tilde{f}_u|, |\tilde{f}_v|, |\hat{g}_u|, |\hat{g}_v - A| \leqslant M.$$

Note that $(u^k(0, \cdot), v^k(0, \cdot)) = (u_k(\cdot) - u_0(\cdot), v_k(\cdot) - v_0(\cdot)) \in X_\rho$ and

$$\begin{aligned} &(u^k(t, \cdot), v^k(t, \cdot)) \\ &\quad = \mathrm{e}^{(\mathcal{N}, A)t} (u^k(0, \cdot), v^k(0, \cdot)) \\ &\qquad + \int_0^t \mathrm{e}^{(\mathcal{N}, A)(t-s)} (\tilde{f}_u u^k(s, \cdot) + \tilde{f}_v v^k(s, \cdot), \hat{g}_u u^k(s, \cdot) + (\hat{g}_v - A) v^k(s, \cdot))\,\mathrm{d}s. \end{aligned}$$

Thus,

$$\begin{aligned} \|(u^k(t, \cdot), v^k(t, \cdot))\|_{X_\rho} &\leqslant M \mathrm{e}^{\omega t} \|(u^k(0, \cdot), v^k(0, \cdot))\|_{X_\rho} \\ &\quad + M^2 \int_0^t \mathrm{e}^{\omega(t-s)} \|(u^k(s, \cdot), v^k(s, \cdot))\|_{X_\rho}\,\mathrm{d}s. \end{aligned}$$

Now, Gronwall's inequality yields

$$\|(u^k(t, \cdot), v^k(t, \cdot))\|_{X_\rho} \leqslant M \mathrm{e}^{(\omega + M^2)t} \|(u^k(0, \cdot), v^k(0, \cdot))\|_{X_\rho}.$$

Observe that $\|(u^k(0, \cdot), v^k(0, \cdot))\|_{X_\rho} \to 0$ as $k \to \infty$. It then follows that

$$(u^k(t, x), v^k(t, x)) \to (0, 0) \quad \text{as } k \to \infty$$

uniformly for (t,x) in bounded subsets of $[0,\infty)\times\mathbb{R}$, and so we complete the proof. $\square$

Due to spatial heterogeneity, for any $z\in\mathbb{R}$ we shall consider the space-shifted system of (1.1):

$$\left.\begin{aligned}\frac{\partial u(t,x)}{\partial t}=\int_{\mathbb{R}}J(x-y)u(t,y)\,\mathrm{d}y-u(t,x)+f(x+z,u,v),\quad x\in\mathbb{R},\ t>0,\\ \frac{\partial v(t,x)}{\partial t}=g(x+z,u,v),\quad x\in\mathbb{R},\ t>0.\end{aligned}\right\}\tag{2.3}$$

Similarly, it follows from general semigroup theory (see [28]) that (2.3) has a unique mild solution $\boldsymbol{u}(t,x;\boldsymbol{u}_0,z)$ with $\boldsymbol{u}(0,x;\boldsymbol{u}_0,z)=\boldsymbol{u}_0(x)$ for every $\boldsymbol{u}_0\in[\mathbf{0},\boldsymbol{M}]_X$.

Remark 2.5. Lemmas 2.3 and 2.4 also hold for the space-shifted system (2.3).

2.2. A principal eigenvalue problem

Linearizing (2.1) at $\mathbf{0}=(0,0)$, we have

$$\left.\begin{aligned}\frac{\partial\hat{u}}{\partial t}&=\int_{\mathbb{R}}J(x-y)\hat{u}(t,y)\,\mathrm{d}y-\hat{u}+f_u(x,\mathbf{0})\hat{u}+f_v(x,\mathbf{0})\hat{v},\\ \frac{\partial\hat{v}}{\partial t}&=g_u(x,\mathbf{0})\hat{u}+g_v(x,\mathbf{0})\hat{v},\quad x\in\mathbb{R},\ t>0.\end{aligned}\right\}\tag{2.4}$$

Since two off-diagonal entries of the matrix

$$D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})=\begin{pmatrix}f_u(x,\mathbf{0}) & f_v(x,\mathbf{0})\\ g_u(x,\mathbf{0}) & g_v(x,\mathbf{0})\end{pmatrix}\tag{2.5}$$

are strictly positive for all $x\in\mathbb{R}$ by (F3), we can further choose some sufficiently large $\alpha>0$ such that $D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})+\alpha\boldsymbol{I}$ is strictly positive. Let

$$\beta=\min\left\{\min_{x\in\mathbb{R}}\{D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})+\alpha\boldsymbol{I}\}_{ij}\colon 1\leqslant i,j\leqslant 2\right\}>0.$$

Note that

$$\boldsymbol{F}^{\mathrm{T}}(x,\boldsymbol{u})=\boldsymbol{F}^{\mathrm{T}}(x,\mathbf{0})+D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})\boldsymbol{u}^{\mathrm{T}}+o(|\boldsymbol{u}|).$$

It then follows that, for any given $\epsilon\in(0,1)$, there exists $\delta=\delta(\epsilon)>0$ such that

$$\boldsymbol{F}^{\mathrm{T}}(x,\boldsymbol{u})\geqslant\boldsymbol{F}^{\mathrm{T}}(x,\mathbf{0})+D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})\boldsymbol{u}^{\mathrm{T}}-\beta\boldsymbol{\epsilon}^{\mathrm{T}}|\boldsymbol{u}|\quad\text{for all }\boldsymbol{u}\in[0,\delta]\times[0,\delta],$$

where $\boldsymbol{\epsilon}=(\epsilon,\epsilon)$. In view of

$$|\boldsymbol{u}|\leqslant u+v\leqslant\frac{1}{\beta}\{(D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})+\alpha\boldsymbol{I})\boldsymbol{u}^{\mathrm{T}}\}_i,\quad i=1,2,$$

and $\boldsymbol{F}^{\mathrm{T}}(x,\mathbf{0})=\mathbf{0}^{\mathrm{T}}$, we have

$$\boldsymbol{F}^{\mathrm{T}}(x,\boldsymbol{u})\geqslant D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})\boldsymbol{u}^{\mathrm{T}}-\epsilon(D_{\boldsymbol{u}}\boldsymbol{F}(x,\mathbf{0})+\alpha\boldsymbol{I})\boldsymbol{u}^{\mathrm{T}}\quad\text{for all }\boldsymbol{u}\in[0,\delta]\times[0,\delta],$$

which is equivalent to

$$\left.\begin{aligned} f(x,u,v) &\geqslant [(1-\epsilon)f_u(x,0,0)-\epsilon\alpha]u+(1-\epsilon)f_v(x,0,0)v,\\ g(x,u,v) &\geqslant (1-\epsilon)g_u(x,0,0)u+[(1-\epsilon)g_v(x,0,0)-\epsilon\alpha]v \end{aligned}\right\} \tag{2.6}$$

for $(u,v)\in[0,\delta]\times[0,\delta]$.

Consider the following linear system:

$$\left.\begin{aligned} \frac{\partial\hat{u}}{\partial t} &= \int_{\mathbb{R}} J(x-y)\hat{u}(t,y)\,\mathrm{d}y-\hat{u}+[(1-\epsilon)f_u(x,0,0)-\epsilon\alpha]\hat{u}\\ &\qquad\qquad +(1-\epsilon)f_v(x,0,0)\hat{v},\\ \frac{\partial\hat{v}}{\partial t} &= (1-\epsilon)g_u(x,0,0)\hat{u}+[(1-\epsilon)g_v(x,0,0)-\epsilon\alpha]\hat{v}. \end{aligned}\right\} \tag{2.7}$$

For any given $\mu\in\mathbb{R}\backslash\{0\}$, letting $(\hat{u}(t,x),\hat{v}(t,x))=\exp(-\mu(x-\lambda/\mu)t)(\phi(x),\varphi(x))$, we then obtain the following periodic eigenvalue problem:

$$\left.\begin{aligned} \int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\phi(y)\,\mathrm{d}y-\phi(x)+a_{11}^{\epsilon}(x)\phi(x)+a_{12}^{\epsilon}(x)\varphi(x) &= \lambda(\mu,\epsilon)\phi(x),\\ a_{21}^{\epsilon}(x)\phi(x)+a_{22}^{\epsilon}(x)\varphi(x) &= \lambda(\mu,\epsilon)\varphi(x),\\ \phi(\cdot),\ \varphi(\cdot)\in X_p, \end{aligned}\right\} \tag{2.8}$$

where

$$\begin{aligned} a_{11}^{\epsilon}(x) &= (1-\epsilon)f_u(x,0,0)-\epsilon\alpha, & a_{12}^{\epsilon}(x) &= (1-\epsilon)f_v(x,0,0)>0,\\ a_{21}^{\epsilon}(x) &= (1-\epsilon)g_u(x,0,0)>0, & a_{22}^{\epsilon}(x) &= (1-\epsilon)g_v(x,0,0)-\epsilon\alpha. \end{aligned}$$

Note that $a_{ij}^{\epsilon}(x)\in X_p$ by (F1), $1\leqslant i,j\leqslant 2$. For convenience, we set $\lambda=\lambda(\mu,\epsilon)$ and $\bar{a}_{ij}(\epsilon)=\max_{x\in\mathbb{R}}a_{ij}^{\epsilon}(x)$, while $\underline{a}_{ij}(\epsilon)=\min_{x\in\mathbb{R}}a_{ij}^{\epsilon}(x)$. In addition, we give the following hypotheses:

(H1) $\bar{a}_{11}(\epsilon)\leqslant\bar{a}_{22}(\epsilon)+1$ and $a_{22}^{\epsilon}(x)\equiv\bar{a}_{22}(\epsilon)$ for all $x\in\mathbb{R}$.

(H2) $\underline{a}_{11}(\epsilon)\geqslant\bar{a}_{22}(\epsilon)+1$.

The following theorem gives some sufficient conditions for the existence of a principal eigenvalue of (2.8).

Theorem 2.6. *Assume that either (H1) or (H2) holds. Then, for any $\mu\in\mathbb{R}$, (2.8) has a geometrically simple eigenvalue $\lambda^*(\mu,\epsilon)$ with a pair of strongly positive and L-periodic eigenfunctions $(\phi^*(x,\mu;\epsilon),\varphi^*(x,\mu;\epsilon))\in X_p^{++}\times X_p^{++}$.*

Proof. For all $\lambda>\bar{a}_{22}(\epsilon)$, we define a linear operator $\mathcal{L}_\lambda$ by

$$(\mathcal{L}_\lambda\phi)(x)=\int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\phi(y)\,\mathrm{d}y-\phi(x)+\left[a_{11}^{\epsilon}(x)+\frac{a_{12}^{\epsilon}(x)a_{21}^{\epsilon}(x)}{\lambda-a_{22}^{\epsilon}(x)}\right]\phi(x).$$

Now, for any given $\mu\in\mathbb{R}$ and $\lambda>\bar{a}_{22}(\epsilon)$, we consider the following eigenvalue problem:

$$\left.\begin{aligned} (\mathcal{L}_\lambda\phi)(x):=(J_\mu\phi)(x)-\phi(x)+A_\lambda^{\epsilon}(x)\phi(x) &= \Lambda(\lambda)\phi(x),\\ \phi(x)\in X_p^{++},\ x\in\mathbb{R}, \end{aligned}\right\} \tag{2.9}$$

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where

$$(J_\mu\phi)(x) = \int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\phi(y)\,\mathrm{d}y \quad \text{and} \quad A^\epsilon_\lambda(x) := a^\epsilon_{11}(x) + \frac{a^\epsilon_{12}(x)a^\epsilon_{21}(x)}{\lambda - a^\epsilon_{22}(x)} \in X_p.$$

Following Shen and Zhang [29], we first introduce a compact and positive operator $U_{\theta,\lambda}$ associated with J_μ. Specifically, for given $\theta > -1 + \bar{A}_\lambda(\epsilon)$ with $\bar{A}_\lambda(\epsilon) = \max_{x\in\mathbb{R}} A^\epsilon_\lambda(x)$, define

$$(U_{\theta,\lambda}v)(x) = \int_{\mathbb{R}} \frac{J(x-y)\mathrm{e}^{\mu(x-y)}v(y)}{\theta + 1 - A^\epsilon_\lambda(y)}\,\mathrm{d}y.$$

From [29, proposition 3.1], the spectral radius of $U_{\theta,\lambda}$ provides a useful tool for the investigation of those eigenvalues of $\mathcal{L}_\lambda$ that are greater than $-1+\bar{A}_\lambda(\epsilon)$. Since $A^\epsilon_\lambda(x) \in X_p$ satisfies the 'flatness condition' (see [30, (H4)]) by (F1), by [30, theorem B′(3)], (2.9) admits a principal eigenvalue $\varLambda(\lambda)$ for all $\mu \in \mathbb{R}$ and $\lambda > \bar{a}_{22}(\epsilon)$. Moreover, by [29, proposition 3.2], we have $\varLambda(\lambda) > -1 + \bar{A}_\lambda(\epsilon)$ for all $\lambda > \bar{a}_{22}(\epsilon)$. It follows from [8, proposition 1.1] or [9, proposition 3.8] that $\varLambda(\lambda)$ is a continuous and strictly decreasing function on $(\bar{a}_{22}(\epsilon), +\infty)$.

Next, we plan to find some $\lambda_0 > \bar{a}_{22}(\epsilon)$ such that $-1 + A^\epsilon_{\lambda_0}(x) \geqslant \lambda_0$, i.e.

$$-1 + a^\epsilon_{11}(x) + \frac{a^\epsilon_{12}(x)a^\epsilon_{21}(x)}{\lambda_0 - a^\epsilon_{22}(x)} \geqslant \lambda_0, \quad x \in \mathbb{R}, \tag{2.10}$$

which is equivalent to

$$\lambda_0^2 - [a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1]\lambda_0 + a^\epsilon_{22}(x)(a^\epsilon_{11}(x) - 1) - a^\epsilon_{12}(x)a^\epsilon_{21}(x) \leqslant 0 \quad \text{for all } x \in \mathbb{R}. \tag{2.11}$$

Note that, by direct computation, we have

$$\begin{aligned}\Delta^\epsilon(x) &:= [a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1]^2 - 4[a^\epsilon_{11}(x)a^\epsilon_{22}(x) - a^\epsilon_{22}(x) - a^\epsilon_{12}(x)a^\epsilon_{21}(x)] \\ &= [(a^\epsilon_{11}(x) - a^\epsilon_{22}(x)) - 1]^2 + 4a^\epsilon_{12}(x)a^\epsilon_{21}(x) \\ &> 0 \quad \text{for all } x \in \mathbb{R}. \end{aligned} \tag{2.12}$$

On the other hand, we denote the larger root of the corresponding quadratic equation of (2.11) by λ_0^+. Then, for all $x \in \mathbb{R}$,

$$\begin{aligned}\lambda_0^+ &= \frac{a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1 + \sqrt{\Delta^\epsilon(x)}}{2} \\ &> \frac{a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1 + \sqrt{[(a^\epsilon_{11}(x) - a^\epsilon_{22}(x)) - 1]^2}}{2} \\ &= \frac{a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1 + |a^\epsilon_{11}(x) - a^\epsilon_{22}(x) - 1|}{2}.\end{aligned}$$

If (H1) holds, then

$$\lambda_0^+ > \frac{a^\epsilon_{11}(x) + a^\epsilon_{22}(x) - 1 - a^\epsilon_{11}(x) + a^\epsilon_{22}(x) + 1}{2} = a^\epsilon_{22}(x) \equiv \bar{a}_{22}(\epsilon), \tag{2.13}$$

and if (H2) holds, then

$$\lambda_0^+ > \frac{a_{11}^\epsilon(x) + a_{22}^\epsilon(x) - 1 + a_{11}^\epsilon(x) - a_{22}^\epsilon(x) - 1}{2} = a_{11}^\epsilon(x) - 1 \geqslant \underline{a}_{11}(\epsilon) - 1 \geqslant \bar{a}_{22}(\epsilon). \tag{2.14}$$

Obviously, (2.12) and (2.13) or (2.14) ensure the existence of $\lambda_0 > \bar{a}_{22}(\epsilon)$ satisfying (2.10). Furthermore, we have

$$\Lambda(\lambda_0) > -1 + \bar{A}_{\lambda_0}(\epsilon) \geqslant -1 + A_{\lambda_0}^\epsilon(x) \geqslant \lambda_0.$$

Define $G(\lambda) := \Lambda(\lambda) - \lambda$. Then $G(\lambda)$ is a continuous and strictly decreasing function on $(\bar{a}_{22}(\epsilon), +\infty)$. Note that $G(\lambda_0) > 0$ and $G(\lambda) \leqslant \Lambda(\lambda_0) - \lambda < 0$ for all $\lambda \geqslant \Lambda(\lambda_0)$. Then the intermediate-value theorem implies that there exists $\lambda^* > \lambda_0$ such that $G(\lambda^*) = 0$. Since $G(\lambda)$ is strictly decreasing, λ^* is the unique zero of $G(\lambda)$ on $(\bar{a}_{22}(\epsilon), +\infty)$. It then follows that $\Lambda(\lambda) > \lambda$ for all $\lambda \in (\bar{a}_{22}(\epsilon), \lambda^*)$, and $\Lambda(\lambda^*) = \lambda^*$ and $\Lambda(\lambda) < \lambda$ for all $\lambda > \lambda^*$. This indicates that λ^* is the principal eigenvalue of $\mathcal{L}_{\lambda^*}$, and hence there is a strongly positive and L-periodic function $\phi^*(x, \mu; \epsilon)$ such that $\mathcal{L}_{\lambda^*}\phi^*(x, \mu; \epsilon) = \lambda^*\phi^*(x, \mu; \epsilon)$. Let $\varphi^*(x, \mu; \epsilon) = (\lambda^* - a_{22}^\epsilon(x))^{-1} a_{21}^\epsilon(x)\phi^*(x, \mu; \epsilon)$. Then $\varphi^*(x, \mu; \epsilon) \in X_p^{++}$, since $\lambda^* > \bar{a}_{22}(\epsilon)$ and $a_{21}^\epsilon(x) > 0$ for all $x \in \mathbb{R}$. Thus, λ^* is the principal eigenvalue of (2.8) with a pair of strongly positive and L-periodic eigenfunctions $(\phi^*(x, \mu; \epsilon), \varphi^*(x, \mu; \epsilon))$, and we complete the proof. □

REMARK 2.7. In this subsection, we introduced a small parameter, $\epsilon \in (0, 1)$, with a view to constructing a lower linear control system. The idea comes from Wu *et al*. [37]. This is very important in order for us to study the spreading speed of system (1.1). Of course, theorem 2.6 holds when we set $\epsilon = 0$. In fact, there is no need to do this when we consider only a periodic eigenvalue problem and study the coexistence and extinction dynamics of system (1.1).

2.3. Evolution operators and principal eigenvalues

Consider the following non-local linear evolution system:

$$\left.\begin{aligned} \frac{\partial \breve{u}(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\breve{u}(t,y)\,\mathrm{d}y - \breve{u}(t,x) + a_{11}^\epsilon(x)\breve{u} + a_{12}^\epsilon(x)\breve{v}, \\ \frac{\partial \breve{v}(t,x)}{\partial t} &= a_{21}^\epsilon(x)\breve{u} + a_{22}^\epsilon(x)\breve{v}, \end{aligned}\right\} \tag{2.15}$$

where $t > 0$, $x \in \mathbb{R}$ and $\mu \in \mathbb{R}$. Note that (2.15) reduces to (2.7) when $\mu = 0$. Let $\boldsymbol{\Phi}(t; \mu, \epsilon)$ be the solution operator of (2.15), i.e.

$$\boldsymbol{\Phi}(t; \mu, \epsilon) = (\breve{u}(t, \cdot; \breve{u}_0, \breve{v}_0, \mu, \epsilon), \breve{v}(t, \cdot; \breve{u}_0, \breve{v}_0, \mu, \epsilon)),$$

and let $\boldsymbol{\Phi}^p(t; \mu, \epsilon)\colon X_p \times X_p \to X_p \times X_p$ be defined by

$$\boldsymbol{\Phi}^p(t; \mu, \epsilon) = \boldsymbol{\Phi}(t; \mu, \epsilon)|_{X_p \times X_p} \quad \text{for } t \geqslant 0,\ \mu \in \mathbb{R} \text{ and small } \epsilon \geqslant 0.$$

Let $r(\boldsymbol{\Phi}^p(1; \mu, \epsilon))$ and $\sigma(\boldsymbol{\Phi}^p(1; \mu, \epsilon))$ be the spectral radius and the spectrum of $\boldsymbol{\Phi}^p(1; \mu, \epsilon)$, respectively.

Now, we give two lemmas that follow from [13, theorems 1.5.2 and 1.5.3] and [29, proposition 3.3].

LEMMA 2.8. *The principal eigenvalue $\lambda^*(\mu,\epsilon)$ of (2.8) exists if and only if $r(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$ is a simple eigenvalue of $\boldsymbol{\Phi}^p(1;\mu,\epsilon)$ with a pair of eigenfunctions in $X_p^{++}\times X_p^{++}$, and $|\lambda| < r(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$ for every $\lambda\in\sigma(\boldsymbol{\Phi}^p(1;\mu,\epsilon))\setminus\{r(\boldsymbol{\Phi}^p(1;\mu,\epsilon))\}$. Furthermore, if $\lambda^*(\mu,\epsilon)$ exists, then $\lambda^*(\mu,\epsilon)=\ln r(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$.*

Now, we shall derive an alternative expression for $\boldsymbol{\Phi}(1;\mu,\epsilon)$. For given $\breve{\boldsymbol{u}}_0 := (\breve{u}_0,\breve{v}_0)\in X\times X$ and $\mu\in\mathbb{R}$, let $\hat{\breve{\boldsymbol{u}}}_0(x)=\mathrm{e}^{-\mu x}\breve{\boldsymbol{u}}_0(x)$. It then follows that, for all $t\geqslant 0$,

$$[\boldsymbol{\Phi}(t;0,\epsilon)\hat{\breve{\boldsymbol{u}}}_0](x)=\mathrm{e}^{-\mu x}[\boldsymbol{\Phi}(t;0,\epsilon)\breve{\boldsymbol{u}}_0(x)](x). \tag{2.16}$$

Observe that, for $x\in\mathbb{R}$, there are bounded non-negative measures $m_{ij}(x;y,\mathrm{d}y)$ such that

$$[\boldsymbol{\Phi}(1;0,\epsilon)\hat{\breve{\boldsymbol{u}}}_0]_i(x)=\sum_{j=1}^{2}\int_{\mathbb{R}}\hat{\breve{\boldsymbol{u}}}_{0j}(y)m_{ij}(x;y,\mathrm{d}y),\quad i=1,2, \tag{2.17}$$

where $\hat{\breve{\boldsymbol{u}}}_{01}(\cdot)=\hat{\breve{u}}_0(\cdot)$ and $\hat{\breve{\boldsymbol{u}}}_{02}(\cdot)=\hat{\breve{v}}_0(\cdot)$. At the same time, we can easily obtain that

$$m_{ij}(x-L;y,\mathrm{d}y)=m_{ij}(x;y+L,\mathrm{d}y),\quad 1\leqslant i,j\leqslant 2. \tag{2.18}$$

Consequently, by (2.16) and (2.17), we have

$$[\boldsymbol{\Phi}(1;\mu,\epsilon)\breve{\boldsymbol{u}}_0]_i(x)=\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\breve{\boldsymbol{u}}_{0j}(y)m_{ij}(x;y,\mathrm{d}y),\quad i=1,2, \tag{2.19}$$

where $\breve{\boldsymbol{u}}_{01}(\cdot)=\breve{u}_0(\cdot)$ and $\breve{\boldsymbol{u}}_{02}(\cdot)=\breve{v}_0(\cdot)$.

LEMMA 2.9. *For every $\breve{\boldsymbol{u}}_0=(\breve{u}_0,\breve{v}_0)\in X_p^{++}\times X_p^{++}$ and $i=1,2$,*

$$\begin{aligned}\inf_{x\in\mathbb{R}}\frac{1}{\breve{\boldsymbol{u}}_{0i}(x)}&\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\breve{\boldsymbol{u}}_{0j}(y)m_{ij}(x;y,\mathrm{d}y)\\ &\leqslant r(\boldsymbol{\Phi}^p(1;\mu,\epsilon))\\ &\leqslant \sup_{x\in\mathbb{R}}\frac{1}{\breve{\boldsymbol{u}}_{0i}(x)}\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\breve{\boldsymbol{u}}_{0j}(y)m_{ij}(x;y,\mathrm{d}y).\end{aligned}$$

Next, we shall introduce truncated operators of $\boldsymbol{\Phi}^p(1;\mu,\epsilon)$, which are very useful to establish the spreading speed of (2.1). In particular, let $\chi(s)\colon\mathbb{R}\to[0,1]$ be a smooth function satisfying the following:

$$\chi(s)=\begin{cases}1 & \text{for } |s|\leqslant 1,\\ 0 & \text{for } |s|\geqslant 2.\end{cases}$$

For a given $B>0$, define $\boldsymbol{\Phi}_B(1;\mu,\epsilon)\colon X\times X\to X\times X$ by

$$[\boldsymbol{\Phi}_B(1;\mu,\epsilon)\breve{\boldsymbol{u}}_0]_i(x)=\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\breve{\boldsymbol{u}}_{0j}(y)\chi\left(\frac{|y-x|}{B}\right)m_{ij}(x;y,\mathrm{d}y),\quad i=1,2, \tag{2.20}$$

and $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon)\colon X_p\times X_p\to X_p\times X_p$ by $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon)=\boldsymbol{\Phi}_B(1;\mu,\epsilon)|_{X_p\times X_p}$.

The space-shifted system of (2.15) is

$$\left.\begin{aligned}\frac{\partial \breve{u}(t,x)}{\partial t} &= \int_{\mathbb{R}} J(x-y)e^{\mu(x-y)}\breve{u}(t,y)\,dy - \breve{u}(t,x) + a_{11}^{\epsilon}(x+z)\breve{u} + a_{12}^{\epsilon}(x+z)\breve{v},\\ \frac{\partial \breve{v}(t,x)}{\partial t} &= a_{21}^{\epsilon}(x+z)\breve{u} + a_{22}^{\epsilon}(x+z)\breve{v},\end{aligned}\right\} \tag{2.21}$$

where $t>0$ and $x,z\in\mathbb{R}$. Let $\boldsymbol{\Phi}(t;\mu,\epsilon,z)$ be the solution operator of (2.21) and let $\boldsymbol{\Phi}^p(t;\mu,\epsilon,z)=\boldsymbol{\Phi}(t;\mu,\epsilon,z)|_{X_p\times X_p}$. Similarly, define $\boldsymbol{\Phi}_B(1;\mu,\epsilon,z)\colon X\times X\to X\times X$ by

$$[\boldsymbol{\Phi}_B(1;\mu,\epsilon,z)\breve{\boldsymbol{u}}_0]_i(x) = \sum_{j=1}^{2}\int_{\mathbb{R}} e^{\mu(x+z-y)}\breve{\boldsymbol{u}}_{0j}(y-z)\chi\left(\frac{|y-x-z|}{B}\right)m_{ij}(x+z;y,dy) \tag{2.22}$$

with $i=1,2$ and $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon,z)=\boldsymbol{\Phi}_B(1;\mu,\epsilon,z)|_{X_p\times X_p}$. Using the same method as [29, lemma 3.3] we can check that

$$\|\boldsymbol{\Phi}_B^p(1;\mu,\epsilon,z)-\boldsymbol{\Phi}^p(1;\mu,\epsilon,z)\|_{X_p\times X_p}\to 0 \quad \text{as } B\to\infty \tag{2.23}$$

uniformly for μ in bounded sets and $z\in\mathbb{R}$.

We now prove some properties of the principal eigenvalue $\lambda^*(\mu,\epsilon)$ of (2.8).

Theorem 2.10. *Let $\lambda^*(\mu,\epsilon)$ be the principal eigenvalue of (2.8). Then the following statements hold.*

(i) *$\lambda^*(\mu,\epsilon)$ is convex in $\mu\in\mathbb{R}$. Moreover, if $J(\cdot)$ is symmetric, then $\lambda^*(-\mu,\epsilon)=\lambda^*(\mu,\epsilon)$ for all $\mu\in\mathbb{R}$ and small $\epsilon\geqslant 0$.*

(ii) *If $\lambda^*(0,\epsilon)>0$, then there exists μ^* such that $\inf_{\mu>0}\lambda^*(\mu,\epsilon)/\mu=\lambda^*(\mu^*,\epsilon)/\mu^*$.*

Proof.
(i) We shall prove the convexity using the idea from [29, theorem A(2)] (see also [9, proposition 3.3] or [37, theorem 3.3]). By lemma 2.8, $r(\boldsymbol{\Phi}^p(1;\mu^k,\epsilon))$ is a simple eigenvalue of $\boldsymbol{\Phi}^p(1;\mu^k,\epsilon)$ with a pair of eigenfunctions $(\phi^*(x,\mu^k;\epsilon),\varphi^*(x,\mu^k;\epsilon))\in X_p^{++}\times X_p^{++}$, $k=1,2$, which combine with (2.19) to imply

$$\begin{aligned}r(\boldsymbol{\Phi}^p(1;\mu^k,\epsilon)) &= \frac{[\boldsymbol{\Phi}^p(1;\mu^k,\epsilon)\boldsymbol{\psi}]_i(x)}{\boldsymbol{\psi}_i(x,\mu^k;\epsilon)}\\ &= \frac{1}{\boldsymbol{\psi}_i(x,\mu^k;\epsilon)}\sum_{j=1}^{2}\int_{\mathbb{R}} e^{\mu^k(x-y)}\boldsymbol{\psi}_j(y,\mu^k;\epsilon)m_{ij}(x;y,dy), \quad i=1,2,\end{aligned}$$

where $\boldsymbol{\psi}(x,\mu^k;\epsilon)$ is a two-dimensional vector defined by

$$\boldsymbol{\psi}(x,\mu^k;\epsilon)=(\phi^*(x,\mu^k;\epsilon),\varphi^*(x,\mu^k;\epsilon)).$$

For given $\varrho \in [0,1]$, let $\tilde{\boldsymbol{\psi}}_i(x,\mu^{12};\epsilon) := \boldsymbol{\psi}_i^{\varrho}(x,\mu^1;\epsilon)\boldsymbol{\psi}_i^{1-\varrho}(x,\mu^2;\epsilon)$. Then the Hölder inequality yields

$$
\begin{aligned}
&[r(\boldsymbol{\Phi}^p(1;\mu^1,\epsilon))]^{\varrho}[r(\boldsymbol{\Phi}^p(1;\mu^2,\epsilon))]^{1-\varrho}\\
&\quad = \left[\frac{1}{\boldsymbol{\psi}_i(x,\mu^1;\epsilon)}\sum_{j=1}^{2}\int_{\mathbb{R}} \mathrm{e}^{\mu^1(x-y)}\boldsymbol{\psi}_j(y,\mu^1;\epsilon)m_{ij}(x;y,\mathrm{d}y)\right]^{\varrho}\\
&\qquad \times \left[\frac{1}{\boldsymbol{\psi}_i(x,\mu^2;\epsilon)}\sum_{j=1}^{2}\int_{\mathbb{R}} \mathrm{e}^{\mu^2(x-y)}\boldsymbol{\psi}_j(y,\mu^2;\epsilon)m_{ij}(x;y,\mathrm{d}y)\right]^{1-\varrho}\\
&\quad \geqslant \sum_{j=1}^{2}\int_{\mathbb{R}}\left[\frac{\mathrm{e}^{\mu^1(x-y)}\boldsymbol{\psi}_j(y,\mu^1;\epsilon)}{\boldsymbol{\psi}_i(x,\mu^1;\epsilon)}\right]^{\varrho}\left[\frac{\mathrm{e}^{\mu^2(x-y)}\boldsymbol{\psi}_j(y,\mu^2;\epsilon)}{\boldsymbol{\psi}_i(x,\mu^2;\epsilon)}\right]^{1-\varrho} m_{ij}(x;y,\mathrm{d}y)\\
&\quad = \sum_{j=1}^{2}\int_{\mathbb{R}}\frac{\mathrm{e}^{[\varrho\mu^1+(1-\varrho)\mu^2](x-y)}\tilde{\boldsymbol{\psi}}_j(x,\mu^{12};\epsilon)}{\tilde{\boldsymbol{\psi}}_i(x,\mu^{12};\epsilon)}m_{ij}(x;y,\mathrm{d}y) \quad \text{for all } x\in\mathbb{R}.
\end{aligned}
$$

On the other hand, according to lemma 2.9, we have

$$
\begin{aligned}
&[r(\boldsymbol{\Phi}^p(1;\mu^1,\epsilon))]^{\varrho}[r(\boldsymbol{\Phi}^p(1;\mu^2,\epsilon))]^{1-\varrho}\\
&\quad \geqslant \sup_{x\in\mathbb{R}}\frac{1}{\tilde{\boldsymbol{\psi}}_i(x,\mu^{12};\epsilon)}\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{[\varrho\mu^1+(1-\varrho)\mu^2](x-y)}\tilde{\boldsymbol{\psi}}_j(x,\mu^{12};\epsilon)m_{ij}(x;y,\mathrm{d}y)\\
&\quad \geqslant r(\boldsymbol{\Phi}^p(1;\varrho\mu^1+(1-\varrho)\mu^2,\epsilon)),
\end{aligned}
$$

which further implies that

$$
\ln[r(\boldsymbol{\Phi}^p(1;\mu^1,\epsilon))]^{\varrho}[r(\boldsymbol{\Phi}^p(1;\mu^2,\epsilon))]^{1-\varrho} \geqslant \ln r(\boldsymbol{\Phi}^p(1;\varrho\mu^1+(1-\varrho)\mu^2,\epsilon)).
$$

Again by lemma 2.8, we obtain that

$$
\varrho\lambda^*(\mu^1,\epsilon)+(1-\varrho)\lambda^*(\mu^2,\epsilon) \geqslant \lambda^*(\varrho\mu^1+(1-\varrho)\mu^2,\epsilon)
$$

for any $\varrho\in[0,1]$, and this gives that $\lambda^*(\mu,\cdot)$ is convex.

We next show that $\lambda^*(-\mu,\cdot)=\lambda^*(\mu,\cdot)$ under the extra assumption that $J(\cdot)$ is symmetric. Indeed, from the proof of theorem 2.6, $\lambda^*(\mu,\cdot)$ is the principal eigenvalue of $\mathcal{L}_{\lambda^*,\mu}$. Here, we denote $\mathcal{L}_{\lambda^*}$ by $\mathcal{L}_{\lambda^*,\mu}$ in order to emphasize the dependence of $\mathcal{L}_{\lambda^*}$ on the parameter μ. We can easily check that $\mathcal{L}_{\lambda^*,-\mu}$ is the adjoint operator of $\mathcal{L}_{\lambda^*,\mu}$. Then $\lambda^*(-\mu,\cdot)$ is the principal eigenvalue of $\mathcal{L}_{\lambda^*,\mu}$, and hence we have $\lambda^*(\mu,\cdot)=\lambda^*(-\mu,\cdot)$ by the uniqueness of the principal eigenvalue.

(ii) By the proof of theorem 2.6 we have

$$
\begin{aligned}
\lambda^*(\mu,\epsilon)\phi^*(x,\mu;\epsilon) &= \int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\phi^*(y,\mu;\epsilon)\,\mathrm{d}y\\
&\quad -\phi^*(x,\mu;\epsilon)+a_{11}^{\epsilon}(x)\phi^*(x,\mu;\epsilon)+\frac{a_{12}^{\epsilon}(x)a_{21}^{\epsilon}(x)}{\lambda^*(\mu,\epsilon)-a_{22}^{\epsilon}(x)}\phi^*(x,\mu;\epsilon),
\end{aligned}
$$

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which combines with the facts $a_{12}^\epsilon(x)a_{21}^\epsilon(x) > 0$ and $\lambda^*(\mu,\epsilon) > a_{22}^\epsilon(x)$ for all $x \in \mathbb{R}$ to imply

$$\lambda^*(\mu,\epsilon)\phi^*(x,\mu;\epsilon) \geqslant \int_{\mathbb{R}} J(x-y)\mathrm{e}^{\mu(x-y)}\phi^*(y,\mu;\epsilon)\,\mathrm{d}y - \phi^*(x,\mu;\epsilon) + a_{11}^\epsilon(x)\phi^*(x,\mu;\epsilon).$$

Moreover, by [9, proposition 3.8(i)], we get

$$\lambda^*(\mu,\epsilon) \geqslant \int_{\mathbb{R}} J(y)\mathrm{e}^{\mu y}\,\mathrm{d}y - 1 + \underline{a}_{11}(\epsilon).$$

By (J), we may assume that $\operatorname{supp}(J) = [-\delta_0^1 - \varrho_0, \delta_0^2 + \varrho_0]$, where δ_0^1, δ_0^2 and ϱ_0 are some positive constants. Then there exist $\theta_0 > 0$ such that

$$J(x) \geqslant \theta_0 > 0 \quad \text{for } x \in [-\delta_0^1, \delta_0^2].$$

This implies that

$$\lambda^*(\mu,\epsilon) \geqslant \theta_0 \int_{-\delta_0^1}^{\delta_0^2} \mathrm{e}^{\mu y}\,\mathrm{d}y - 1 + \underline{a}_{11}(\epsilon) = \theta_0 \frac{\mathrm{e}^{\delta_0^2\mu} - \mathrm{e}^{-\delta_0^1\mu}}{\mu} - 1 + \underline{a}_{11}(\epsilon),$$

and so

$$\frac{\lambda^*(\mu,\epsilon)}{\mu} \geqslant \theta_0\left(\frac{\mathrm{e}^{\delta_0^2\mu}}{\mu^2} - \frac{1}{\mu^2\mathrm{e}^{\delta_0^1\mu}}\right) + \frac{-1 + \underline{a}_{11}(\epsilon)}{\mu}.$$

Note that $\mathrm{e}^{\delta_0^2\mu}/\mu^2 \to \infty$ as $\mu \to \infty$. Thus, we have $\lambda^*(\mu,\epsilon)/\mu \to \infty$ as $\mu \to \infty$. In addition, by $\lambda^*(0,\epsilon) > 0$, we have $\lambda^*(\mu,\epsilon)/\mu \to \infty$ as $\mu \to 0$. Hence, there exists μ^* such that

$$\inf_{\mu>0} \frac{\lambda^*(\mu,\epsilon)}{\mu} = \frac{\lambda^*(\mu^*,\epsilon)}{\mu^*},$$

and the proof is complete. □

Let $\lambda_B^*(\mu,\epsilon) = \ln r_B(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$, and let $r_B(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$ be the spectral radius of $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon)$. We have the following result, which is a straightforward consequence of [29, theorem 3.1].

Lemma 2.11. *Suppose that (2.8) admits a principal eigenvalue $\lambda^*(\mu,\epsilon)$ for all $\mu \in \mathbb{R}$, that $\lambda^*(0,\epsilon) > 0$ and that*

$$\frac{\lambda^*(\mu^*,\epsilon)}{\mu^*} < \frac{\lambda^*(\mu^*+l_0,\epsilon)}{\mu^*+l_0} \quad \textit{for some } l_0 > 0.$$

Then the following statements hold.

(i) *There exists $B_0 > 0$ such that, for each $B \geqslant B_0$ and $|\mu| \leqslant \mu^* + l_0$, $r_B(\boldsymbol{\Phi}^p(1;\mu,\epsilon))$ is a simple eigenvalue of $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon)$ with an eigenfunction $(\phi_B^*(x,\mu;\epsilon), \varphi_B^*(x,\mu;\epsilon)) \in X_p^{++} \times X_p^{++}$. Also, $\lambda_B^*(0,\epsilon) > 0$ and*

$$\frac{\lambda_B^*(\mu^*,\epsilon)}{\mu^*} < \frac{\lambda_B^*(\mu^*+l_0,\epsilon)}{\mu^*+l_0}.$$

(ii) *For each $B \geqslant B_0$, $\lambda_B^*(\mu,\epsilon)$ is convex in μ for $|\mu| \leqslant \mu^* + l_0$.*

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(iii) *For a given* $B \geqslant B_0$, *define*

$$\mu_B^* = \inf\left\{\tilde{\mu} \colon \frac{\lambda_B^*(\tilde{\mu},\epsilon)}{\tilde{\mu}} = \inf_{\mu\in(0,\mu^*+l_0]} \frac{\lambda_B^*(\mu,\epsilon)}{\mu}\right\}.$$

Then we have the following:

(a) $\mu_B^* > 0$ *and* $\partial\lambda_B^*(\mu,\epsilon)/\partial\mu < \lambda_B^*(\mu,\epsilon)/\mu$ *for* $\mu \in (0,\mu_B^*)$;

(b) *for each* $\varepsilon_0 > 0$, *there exists* $\mu_{\varepsilon_0} > 0$ *such that, for* $\mu \in (\mu_{\varepsilon_0},\mu_B^*)$,

$$-\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu} < -\frac{\lambda_B^*(\mu_B^*,\epsilon)}{\mu_B^*} + \varepsilon_0;$$

(c) $\lim_{B\to\infty} \lambda_B^*(\mu_B^*,\epsilon)/\mu_B^* = \lambda^*(\mu^*,\epsilon)/\mu^*$.

3. Stationary solutions and global dynamics

In this section, we shall consider the stationary problem of (1.1):

$$\left.\begin{aligned}\int_{\mathbb{R}} J(x-y)u(y)\,\mathrm{d}y - u(x) + f(x,u,v) = 0, \quad x\in\mathbb{R},\\ g(x,u,v) = 0, \quad x\in\mathbb{R}.\end{aligned}\right\} \tag{3.1}$$

We first define a space $\tilde{X}_p$ by

$$\tilde{X}_p = \{w \colon \mathbb{R}\to\mathbb{R} \mid w \text{ is bounded Lebesgue measurable and } w(x+L) = w(x)\}$$

with the norm

$$\|w\|_{\tilde{X}_p} = \sup_{x\in\mathbb{R}} |w(x)|.$$

Let $\tilde{X}_p^+ = \{w \in \tilde{X}_p \mid w \geqslant 0,\ \forall x \in \mathbb{R}\}$. Then the interior of $\tilde{X}_p^+$, denoted by $\tilde{X}_p^{++}$, is not empty, and $\tilde{X}_p^{++} = \{w \in \tilde{X}_p^+ \mid w(x) > 0,\ \forall x\in\mathbb{R}\}$. Observe that $X_p \subseteq \tilde{X}_p$.

Now, we introduce the part metric in $\tilde{X}_p^{++}\times\tilde{X}_p^{++}$. In fact, for any $(u_i,v_i) \in \tilde{X}_p^{++}\times\tilde{X}_p^{++}$ with $i = 1,2$, we can always find some $\gamma > 1$ such that $(u_1,v_1)/\gamma \leqslant (u_2,v_2) \leqslant \gamma(u_1,v_1)$. Define

$$d[(u_1,v_1),(u_2,v_2)] = \inf\left\{\ln\gamma \;\middle|\; \gamma \geqslant 1, \frac{1}{\gamma}(u_1,v_1) \leqslant (u_2,v_2) \leqslant \gamma(u_1,v_1)\right\}$$

for any $(u_i,v_i) \in \tilde{X}_p^{++}\times\tilde{X}_p^{++}$ with $i = 1,2$. Obviously, $d[(u_1,v_1),(u_1,v_1)] = 0$ and $d[(u_1,v_1),(u_2,v_2)] = d[(u_2,v_2),(u_1,v_1)]$. Note that if there exists a sequence $\gamma_n \to \gamma$ satisfying $\gamma_n \geqslant 1$ and $(u_1,v_1)/\gamma_n \leqslant (u_2,v_2) \leqslant \gamma_n(u_1,v_1)$, then $(u_1,v_1)/\gamma \leqslant (u_2,v_2) \leqslant \gamma(u_1,v_1)$. Thus,

$$d[(u_1,v_1),(u_2,v_2)] = \min\left\{\ln\gamma \;\middle|\; \gamma \geqslant 1, \frac{1}{\gamma}(u_1,v_1) \leqslant (u_2,v_2) \leqslant \gamma(u_1,v_1)\right\}.$$

Repeating the procedure for the proof of lemma 2.3(ii), we obtain that, for every $(u_0,v_0) \in \tilde{X}_p^+\times\tilde{X}_p^+$, $(u(t,\cdot;u_0,v_0), v(t,\cdot;u_0,v_0))$ also exist for all $t \geqslant 0$, and for convenience we denote them by $\boldsymbol{Q}(t)(u_0,v_0)(x) = (Q_1(t),Q_2(t))(u_0,v_0)(x)$. Note that lemma 2.4 is also valid when we choose an initial value in $\tilde{X}_p^+\times\tilde{X}_p^+$.

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Lemma 3.1. *For any two elements* $(u_0^1, v_0^1), (u_0^2, v_0^2) \in \tilde{X}_p^{++} \times \tilde{X}_p^{++}$ *with* $(u_0^1, v_0^1) \neq (u_0^2, v_0^2)$*,* $d[\boldsymbol{Q}(t)(u_0^1, v_0^1), \boldsymbol{Q}(t)(u_0^2, v_0^2)]$ *is strictly decreasing as* t *increases.*

Proof. For any given $(u_0^1, v_0^1), (u_0^2, v_0^2) \in \tilde{X}_p^{++} \times \tilde{X}_p^{++}$ with $(u_0^1, v_0^1) \neq (u_0^2, v_0^2)$, let $\gamma > 1$ be such that $(u_0^1, v_0^1)/\gamma \leqslant (u_0^2, v_0^2) \leqslant \gamma(u_0^1, v_0^1)$. Then, by lemma 2.3(i), $\boldsymbol{Q}(t)(u_0^2, v_0^2) \leqslant \boldsymbol{Q}(t)(\gamma(u_0^1, v_0^1))$ for $t > 0$. Let

$$(u(t), v(t)) := \gamma \boldsymbol{Q}(t)(u_0^1, v_0^1) = (\gamma Q_1(t), \gamma Q_2(t))(u_0^1, v_0^1).$$

By (F4) and $1/\gamma \in (0, 1)$, we have

$$\begin{aligned} f(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) &= f(x, u(t)/\gamma, v(t)/\gamma) > (1/\gamma) f(x, u(t), v(t)), \\ g(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) &= g(x, u(t)/\gamma, v(t)/\gamma) > (1/\gamma) g(x, u(t), v(t)). \end{aligned}$$

Then we have

$$\begin{aligned} \frac{\partial u(t)(x)}{\partial t} &= \int_{\mathbb{R}} J(x-y) u(t)(y)\,\mathrm{d}y - u(t)(x) + \gamma f(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) \\ &= \int_{\mathbb{R}} J(x-y) u(t)(y)\,\mathrm{d}y - u(t)(x) + f(x, u(t), v(t)) \\ &\quad + \gamma f(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) - f(x, u(t), v(t)) \\ &> \int_{\mathbb{R}} J(x-y) u(t)(y)\,\mathrm{d}y - u(t)(x) + f(x, u(t), v(t)) \end{aligned}$$

and

$$\begin{aligned} \frac{\partial v(t)(x)}{\partial t} &= \gamma g(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) \\ &= g(x, u(t), v(t)) + \gamma g(x, Q_1(t)(u_0^1, v_0^1), Q_2(t)(u_0^1, v_0^1)) - g(x, u(t), v(t)) \\ &> g(x, u(t), v(t)). \end{aligned}$$

Thus, $\boldsymbol{Q}(t)(\gamma(u_0^1, v_0^1)) \ll \gamma \boldsymbol{Q}(t)(u_0^1, v_0^1)$. Similarly, $(1/\gamma)\boldsymbol{Q}(t)(u_0^1, v_0^1) \ll \boldsymbol{Q}(t)(u_0^1/\gamma, v_0^1/\gamma)$. Hence, $(1/\gamma)\boldsymbol{Q}(t)(u_0^1, v_0^1) \ll \boldsymbol{Q}(t)(u_0^2, v_0^2) \ll \gamma \boldsymbol{Q}(t)(u_0^1, v_0^1)$. This implies that

$$d[\boldsymbol{Q}(t)(u_0^1, v_0^1), \boldsymbol{Q}(t)(u_0^2, v_0^2)] < d[(u_0^1, v_0^1), (u_0^2, v_0^2)]$$

for any $t > 0$. Then the proof is complete. □

Observe that when $v(t, x) \equiv 0$ (1.1) reduces to

$$u_t(t, x) = \int_{\mathbb{R}} J(x-y) u(t, y)\,\mathrm{d}y - u(t, x) + \hat{f}(x, u), \tag{3.2}$$

and when $u(t, x) \equiv 0$ (1.1) reduces to

$$v_t(t, x) = \hat{g}(x, v), \tag{3.3}$$

where $\hat{f}(x, u) = f(x, u, 0)$ and $\hat{g}(x, v) = g(x, 0, v)$. Note that the global dynamics of (3.2) have been studied in [9, 17, 29]. For (3.3), we can easily verify that if $\max_{x \in \mathbb{R}} \hat{g}_v(x, 0) < 0$, then, for any $v_0 \in [0, M_2]_{X_p}$, $\lim_{t \to \infty} v(t, x; v_0) = 0$. If $\max_{x \in \mathbb{R}} \hat{g}_v(x, 0) > 0$, then $\lim_{t \to \infty} v(t, x; v_0) = v_*(x)$ for every $v_0 \in (0, M_2]_{X_p}$, where $v_* \in X_p^{++}$ satisfies $g(x, v_*(x)) = 0$ for all $x \in \mathbb{R}$. We next investigate the coexistence and extinction dynamics of (1.1).

THEOREM 3.2. *Assume that the condition in theorem 2.6 holds for all small* $\epsilon \geqslant 0$. *Let* $\boldsymbol{u}(t,\cdot;\boldsymbol{u}_0) := (u(t,\cdot;\boldsymbol{u}_0), v(t,\cdot;\boldsymbol{u}_0))$ *be the unique solution of (2.1) through* $\boldsymbol{u}_0 := (u_0, v_0)$ *and* $\lambda_0^* := \lambda^*(0,0)$. *Then the following conclusions hold.*

(i) *If* $\lambda_0^* < 0$, *then for any* $\boldsymbol{u}_0 \in [\boldsymbol{0}, \boldsymbol{M}]_{X_p}$, *we have* $\lim_{t\to+\infty} \boldsymbol{u}(t,\cdot;\boldsymbol{u}_0) = \boldsymbol{0}$ *uniformly for* $x \in \mathbb{R}$.

(ii) *If* $\lambda_0^* > 0$, *then there is a unique continuous steady state* $\boldsymbol{u}^*(x) = (u^*(x), v^*(x)) \in X_p^{++} \times X_p^{++}$ *that is globally asymptotically stable, i.e. for any* $(u_0, v_0) \in (0, M_1]_{X_p} \times (0, M_2]_{X_p}$ *we have* $\lim_{t\to+\infty} \boldsymbol{u}(t,x;\boldsymbol{u}_0) = \boldsymbol{u}^*(x)$.

Proof.
(i) According to (F1) and (F4), we have $\boldsymbol{F}^{\mathrm{T}}(x,u) \leqslant D_{\boldsymbol{u}}\boldsymbol{F}(x,0)\boldsymbol{u}^{\mathrm{T}}$ for all $x \in \mathbb{R}$ and $\boldsymbol{u} \in [\boldsymbol{0}, \boldsymbol{M}]$ (see [40, lemma 2.3.2]). Let $(\phi^*(x), \varphi^*(x)) := (\phi^*(x,0;0), \varphi^*(x,0;0))$ be the eigenpair corresponding to λ_0^* and then choose some $\rho_0 > 0$ such that $(0,0) \leqslant (u_0(x), v_0(x)) \leqslant \rho_0(\phi^*(x), \varphi^*(x))$. Note that (2.4) is an upper control system of (2.1) and $\rho_0 \mathrm{e}^{\lambda_0^* t}(\phi^*(x), \varphi^*(x))$ is a solution of (2.4). If $\lambda_0^* < 0$, the comparison principle yields that $(0,0) \leqslant (u(t,x;\boldsymbol{u}_0), v(t,x;\boldsymbol{u}_0)) \leqslant \rho_0 \mathrm{e}^{\lambda_0^* t}(\phi^*(x), \varphi^*(x)) \to (0,0)$ as $t \to +\infty$ and then lemma 3.1(i) follows.

(ii) We first show the existence of a positive steady state solution by upper–lower solutions method. By (F2), let $(u^+, v^+) \equiv (M_1, M_2)$. Then we have

$$\int_{\mathbb{R}} J(x-y)u^+(y)\,\mathrm{d}y - u^+(x) + f(x, u^+, v^+) \leqslant 0 \quad \text{and} \quad g(x, u^+, v^+) \leqslant 0,$$

which implies that $\boldsymbol{Q}(t)(u^+, v^+) \leqslant (u^+, v^+)$ for $0 < t \ll 1$ and thus $\boldsymbol{Q}(t_1)(u^+, v^+) \geqslant \boldsymbol{Q}(t_2)(u^+, v^+)$ for any $t_2 > t_1 > 0$. Thus, there exists $(u^*, v^*) \in \tilde{X}_p^+ \times \tilde{X}_p^+$ such that $\lim_{t\to\infty} \boldsymbol{Q}(t)(u^+, v^+)(x) = (u^*, v^*)(x)$ for all $x \in \mathbb{R}$. Furthermore, for any $t > 0$ and $x_0 \in \mathbb{R}$, $\limsup_{x\to x_0}(u^*, v^*)(x) \leqslant \limsup_{x\to x_0} \boldsymbol{Q}(t)(u^+, v^+)(x)$. By lemma 2.4(ii),

$$\lim_{t\to\infty} \boldsymbol{Q}(t)(u^+, v^+)(x_0) = (u^*, v^*)(x_0)$$

and

$$\limsup_{x\to x_0} \boldsymbol{Q}(t)(u^+, v^+)(x) = \boldsymbol{Q}(t)(u^+, v^+)(x_0).$$

Therefore, $\limsup_{x\to x_0}(u^*, v^*)(x) \leqslant (u^*, v^*)(x_0)$, and then $\boldsymbol{u}^*(x) = (u^*(x), v^*(x))$ is upper semi-continuous. Note that, for any $t, s > 0$,

$$\begin{aligned} Q_1(t+s)(u^+, v^+) &- Q_1(t)(u^+, v^+) \\ &= \int_0^s \biggl[\int_{\mathbb{R}} J(x-y)Q_1(t+\tau)(u^+, v^+)(y)\,\mathrm{d}y - Q_1(t+\tau)(u^+, v^+)(x) \\ &\qquad + f(x, Q_1(t+\tau)(u^+, v^+), Q_2(t+\tau)(u^+, v^+)) \biggr] \mathrm{d}\tau \end{aligned} \tag{3.4}$$

and

$$\begin{aligned} Q_2(t+s)(u^+, v^+) &- Q_2(t)(u^+, v^+) \\ &= \int_0^s g(x, Q_1(t+\tau)(u^+, v^+), Q_2(t+\tau)(u^+, v^+))\,\mathrm{d}\tau. \end{aligned} \tag{3.5}$$

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Letting $t \to \infty$ in (3.4) and (3.5), Lebesgue's dominated convergence theorem implies that

$$\left.\begin{aligned}\int_{\mathbb{R}} J(x-y)u^*(y)\,\mathrm{d}y - u^*(x) + f(x,u^*,v^*) = 0, \quad x\in\mathbb{R},\\ g(x,u^*,v^*) = 0, \quad x\in\mathbb{R},\end{aligned}\right\} \tag{3.6}$$

which indicates that $\boldsymbol{Q}(t)(u^*,v^*) \equiv (u^*,v^*) \in \tilde{X}_p^+ \times \tilde{X}_p^+$.

Since $\lambda_0^* > 0$, $(0,0)$ is unstable and we claim that there exist $(0,0) < (u^-,v^-) \ll (1,1)$ and $T>0$ such that $\boldsymbol{Q}(T)(u^-,v^-) \geqslant (u^-,v^-)$. In fact, let $(\phi^*(x,0;\epsilon), \varphi^*(x,0;\epsilon))$ be an eigenfunction corresponding to $\lambda^*(0,\epsilon)$. By the continuity of $\lambda^*(0,\epsilon)$ on ϵ, we get there exists ϵ_0 such that $\lambda^*(0,\epsilon) > 0$ for $0 \leqslant \epsilon \leqslant \epsilon_0$. Note that by (2.6) it is not difficult to verify that if $(u_0,v_0) \in \tilde{X}_p^+ \times \tilde{X}_p^+$ and $(0,0) \leqslant (u(t,x;u_0,v_0), v(t,x;u_0,v_0)) \leqslant (\delta,\delta)$ for $0 \leqslant t \leqslant t_0$ and $x \in \mathbb{R}$, then

$$(u(t,x;u_0,v_0), v(t,x;u_0,v_0)) \geqslant \boldsymbol{\Phi}(t;0,\epsilon)(u_0,v_0)(x)$$

for $0 \leqslant \epsilon \leqslant \epsilon_0$, $0 \leqslant t \leqslant t_0$ and $x \in \mathbb{R}$. Let

$$(u^-,v^-) = (\eta_1\phi^*(x,0;\epsilon), \eta_2\varphi^*(x,0;\epsilon))$$

with

$$(\eta_1,\eta_2) < \left(\frac{\delta}{\max_{x\in\mathbb{R},\epsilon\in[0,\epsilon_0]}\phi^*(x,0;\epsilon)}, \frac{\delta}{\max_{x\in\mathbb{R},\epsilon\in[0,\epsilon_0]}\varphi^*(x,0;\epsilon)}\right).$$

Note that $\boldsymbol{\Phi}(t;0,\epsilon)(u^-,v^-)(x) = \mathrm{e}^{\lambda^*(0,\epsilon)t}(\eta_1\phi^*(x,0;\epsilon), \eta_2\varphi^*(x,0;\epsilon))$. Thus,

$$(u(t,x;u^-,v^-), v(t,x;u^-,v^-)) \geqslant \mathrm{e}^{\lambda^*(0,\epsilon)t}(\eta_1\phi^*(x,0;\epsilon), \eta_2\varphi^*(x,0;\epsilon)) \geqslant (u^-,v^-)$$

for $0 \leqslant \epsilon \leqslant \epsilon_0$, $0 \leqslant t \leqslant t_0$ and $x \in \mathbb{R}$. Then, by lemma 2.3,

$$(u(t,x;u^-,v^-), v(t,x;u^-,v^-)) \geqslant (u^-,v^-) \quad \text{for } t \geqslant 0.$$

This yields that our claim is correct. We then have $\boldsymbol{Q}(nT)(u^-,v^-) \geqslant \boldsymbol{Q}((n-1)T)(u^-,v^-)$ for $n = 1,2,\ldots$. Hence, there exists $(u_*,v_*) \in \tilde{X}_p^{++} \times \tilde{X}_p^{++}$ such that $\lim_{n\to\infty}\boldsymbol{Q}(nT)(u^-,v^-) = (u_*,v_*)$. We can further obtain that $\boldsymbol{Q}(nT)(u_*,v_*) \equiv (u_*,v_*)$ and $\liminf_{x\to x_0}(u_*,v_*)(x) \geqslant (u_*,v_*)(x_0)$, i.e. $(u_*,v_*)(x)$ is lower semi-continuous.

Obviously, $d[\boldsymbol{Q}(nT)(u_*,v_*), \boldsymbol{Q}(nT)(u^*,v^*)] = d[(u_*,v_*),(u^*,v^*)]$ and $(0,0) < (u_*,v_*) \leqslant (u^*,v^*) \leqslant (M_1,M_2)$. Hence, (u_*,v_*), $(u^*,v^*) \in \tilde{X}_p^{++} \times \tilde{X}_p^{++}$. However, according to lemma 3.1, if $(u_*,v_*) \neq (u^*,v^*)$, there must be

$$d[\boldsymbol{Q}(nT)(u_*,v_*), \boldsymbol{Q}(nT)(u^*,v^*)] < d[(u_*,v_*),(u^*,v^*)],$$

which is a contradiction. Therefore, $(u_*,v_*) = (u^*,v^*) =: \boldsymbol{u}^* \in \tilde{X}_p^{++} \times \tilde{X}_p^{++}$ is both upper and lower semi-continuous and $\boldsymbol{Q}(t)\boldsymbol{u}^* = \boldsymbol{u}^*$. Then $\boldsymbol{u}^*$ is a continuous steady state and so $\boldsymbol{u}^* \in X_p^{++} \times X_p^{++}$.

Next, we prove that $\boldsymbol{u}^*$ is globally asymptotically stable. For any $(u_0,v_0) \in (0,M_1]_{X_p} \times (0,M_2]_{X_p}$, we can always find the above (u^-,v^-) and (u^+,v^+) such that $(u^-,v^-) \leqslant (u_0,v_0) \leqslant (u^+,v^+)$ and $(u^*,v^*) \leqslant (u^+,v^+)$. By lemma 2.3(i), we obtain that

$$\boldsymbol{Q}(t)(u^-,v^-) \leqslant \boldsymbol{Q}(t)(u_0,v_0) \leqslant \boldsymbol{Q}(t)(u^+,v^+) \quad \text{and} \quad \boldsymbol{Q}(t)(u^+,v^+) \geqslant (u^*,v^*).$$

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Since $\lim_{t\to\infty} \boldsymbol{Q}(t)(u^-, v^-) = \lim_{t\to\infty} \boldsymbol{Q}(t)(u^+, v^+) = (u^*, v^*)$, we obtain

$$\lim_{t\to\infty} \boldsymbol{Q}(t)(u_0, v_0) = (u^*, v^*)$$

by the squeezing technique. Hence, (u^*, v^*) is globally asymptotically stable and the uniqueness holds. □

REMARK 3.3. Assume that $\lambda_0^* > 0$. Then, for any constant vector $\boldsymbol{m} \in (0, M_1]_{X_p} \times (0, M_2]_{X_p}$, we have

$$\lim_{t\to\infty} (u(t, x; \boldsymbol{m}, z), v(t, x; \boldsymbol{m}, z)) = (u^*(x + z), v^*(x + z))$$

uniformly in $x, z \in \mathbb{R}$.

4. Spreading speed intervals

From now on, we always assume that (2.8) admits a principal eigenvalue $\lambda^*(\mu, \epsilon)$ for all $\mu \in \mathbb{R}$ and small $\epsilon \geqslant 0$, $\lambda_0^* := \lambda^*(0, 0) > 0$ and $(u^*, v^*) \in X_p^{++} \times X_p^{++}$ is the unique positive and globally asymptotically stable equilibrium solution. We shall obtain a spreading speed interval for (2.1) and then investigate its basic properties.

Set $u^*_{\text{inf}} := \inf_{x\in\mathbb{R}} u^*(x)$ and $v^*_{\text{inf}} := \inf_{x\in\mathbb{R}} v^*(x)$ and then define

$$X_1^+ = \Big\{ u \in X^+ \;\Big|\; \sup_{x\in\mathbb{R}} u(x) < u^*_{\text{inf}},\ \liminf_{x\to-\infty} u(x) > 0 \text{ and } u(x) = 0,\ \forall x \gg 1 \Big\}$$

and

$$X_2^+ = \Big\{ v \in X^+ \;\Big|\; \sup_{x\in\mathbb{R}} v(x) < v^*_{\text{inf}},\ \liminf_{x\to-\infty} v(x) > 0 \text{ and } v(x) = 0,\ \forall x \gg 1 \Big\}.$$

HYPOTHESIS 4.1. *Assume that $(u(t, x; \boldsymbol{u}_0), v(t, x; \boldsymbol{u}_0))$ is the solution of Cauchy problem (2.1) through $\boldsymbol{u}_0 = (u_0, v_0)$. Let*

$$C_{\text{inf}} = \Big\{ c\colon \forall \boldsymbol{u}_0 \in X_1^+ \times X_2^+,\ \liminf_{x\leqslant ct,\, t\to\infty} (u(t, x; \boldsymbol{u}_0) - u^*(x), v(t, x; \boldsymbol{u}_0) - v^*(x)) = (0, 0) \Big\}$$

and

$$C_{\text{sup}} = \Big\{ c\colon \forall \boldsymbol{u}_0 \in X_1^+ \times X_2^+,\ \limsup_{x\geqslant ct,\, t\to\infty} [u^2(t, x; \boldsymbol{u}_0) + v^2(t, x; \boldsymbol{u}_0)] = 0 \Big\}.$$

Define

$$c^*_{\text{inf}} = \begin{cases} \sup\{c\colon c \in C_{\text{inf}}\} & \text{if } C_{\text{inf}} \neq \emptyset, \\ -\infty & \text{if } C_{\text{inf}} = \emptyset \end{cases}$$

and

$$c^*_{\text{sup}} = \begin{cases} \inf\{c\colon c \in C_{\text{sup}}\} & \text{if } C_{\text{sup}} \neq \emptyset, \\ \infty & \text{if } C_{\text{sup}} = \emptyset. \end{cases}$$

Then $[c^*_{\text{inf}}, c^*_{\text{sup}}]$ is called the spreading speed interval for (2.1).

Let $\eta(s)$ be the function defined by $\eta(s) = \frac{1}{2}(1 + \tanh \frac{1}{2}s)$ for $s \in \mathbb{R}$. Observe that, for all $s \in \mathbb{R}$,

$$\eta'(s) = \eta(s)(1-\eta(s)) \quad \text{and} \quad \eta''(s) = \eta(s)(1-\eta(s))(1-2\eta(s)).$$

Without loss of generality, we may assume that $f(x,u,v) = g(x,u,v) = 0$ for all $u \ll 0$ or $v \ll 0$. Otherwise, let $\zeta(u,v) \in C^\infty(\mathbb{R}^2)$ satisfy

$$\zeta(u,v) = \begin{cases} 1 & \text{for } u \geqslant 0 \text{ and } v \geqslant 0, \\ 0 & \text{for } u \ll 0 \text{ or } v \ll 0. \end{cases}$$

Then we replace $f(x,u,v)$ and $g(x,u,v)$ by $f(x,u,v)\zeta(u,v)$ and $g(x,u,v)\zeta(u,v)$, respectively. Hence, we may also assume that there exist $u_- < 0$ and $v_- < 0$ such that $[u_-,0] \times [v_-,0]$ is positively invariant for the solution operator of (2.1).

Lemma 4.2. *Let $\boldsymbol{\alpha}^\pm = (\alpha_1^\pm, \alpha_2^\pm)$ be given constant vectors satisfying $u_- \leqslant \alpha_1^- \leqslant 0 \ll \alpha_1^+ \leqslant u^*_{\text{inf}}$ and $v_- \leqslant \alpha_2^- \leqslant 0 \ll \alpha_2^+ \leqslant v^*_{\text{inf}}$. Then there exists $C_0 > 0$ such that, for every $C \geqslant C_0$ and $z \in \mathbb{R}$, the following conclusions hold.*

(i) *Let $u_1^\pm(t,x;z) = u(t,x;\boldsymbol{\alpha}^\pm,z)\eta(x+Ct) + u(t,x;\boldsymbol{\alpha}^\mp,z)[1-\eta(x+Ct)]$ and $v_1^\pm(t,x;z) = v(t,x;\boldsymbol{\alpha}^\pm,z)\eta(x+Ct) + v(t,x;\boldsymbol{\alpha}^\mp,z)[1-\eta(x+Ct)]$. Then (u_1^+,v_1^+) and (u_1^-,v_1^-) are the upper and lower solutions of (2.3) on $[0,\infty)$, respectively.*

(ii) *Let $u_2^\pm(t,x;z) = u(t,x;\boldsymbol{\alpha}^\mp,z)\eta(x-Ct) + u(t,x;\boldsymbol{\alpha}^\pm,z)[1-\eta(x-Ct)]$ and $v_2^\pm(t,x;z) = v(t,x;\boldsymbol{\alpha}^\mp,z)\eta(x-Ct) + v(t,x;\boldsymbol{\alpha}^\pm,z)[1-\eta(x-Ct)]$. Then (u_2^+,v_2^+) and (u_2^-,v_2^-) are the upper and lower solutions of (2.3) on $[0,\infty)$, respectively.*

Proof. Here we prove only that (u_1^+,v_1^+) with $z=0$ is an upper solution of (2.3); the other conclusions can be obtained similarly. For convenience, we write $(u_1^+(t,x), v_1^+(t,x))$ for $(u_1^+(t,x;0), v_1^+(t,x;0))$.

Set $s = x + Ct$, $p(t,x) = u(t,x;\alpha^+) - u(t,x;\alpha^-)$ and $q(t,x) = v(t,x;\alpha^+) - v(t,x;\alpha^-)$. Then a direct computation yields

$$\begin{aligned}
&\frac{\partial u_1^+}{\partial t} - \left[\int_{\mathbb{R}} J(x-y)u_1^+(t,y)\,\mathrm{d}y - u_1^+(t,x)\right] - f(x,u_1^+,v_1^+) \\
&\quad = \eta'(s)\left[Cp(t,x) - \int_{\mathbb{R}} J(x-y)p(t,y)\frac{\eta(y+Ct)-\eta(x+Ct)}{\eta'(x+Ct)}\,\mathrm{d}y\right] \\
&\qquad + \eta(s)[f(x,u(t,x;\alpha^+),v(t,x;\alpha^+)) - f(x,u(t,x;\alpha^-),v(t,x;\alpha^-))] \\
&\qquad - [f(x,u(t,x;\alpha^-)+\eta(s)p(t,x), v(t,x;\alpha^-)+\eta(s)q(t,x)) \\
&\qquad\qquad - f(x,u(t,x;\alpha^-),v(t,x;\alpha^-))] \\
&\quad = \eta'(s)\left[Cp(t,x) - \int_{\mathbb{R}} J(x-y)p(t,y)\frac{\eta(y+Ct)-\eta(x+Ct)}{\eta'(x+Ct)}\,\mathrm{d}y\right] \\
&\qquad + \eta(s)\int_0^1 [f_u(x,u(t,x;\alpha^-)+rp(t,x), v(t,x;\alpha^-)+rq(t,x))p(t,x) \\
&\qquad\qquad + f_v(x,u(t,x;\alpha^-)+rp(t,x), v(t,x;\alpha^-)+rq(t,x))q(t,x)]\,\mathrm{d}r
\end{aligned}$$

$$
\begin{aligned}
&- \int_0^1 [f_u(x, u(t,x;\alpha^-) + r\eta(s)p(t,x), v(t,x;\alpha^-) + r\eta(s)q(t,x))\eta(s)p(t,x) \\
&\qquad + f_v(x, u(t,x;\alpha^-) + r\eta(s)p(t,x), v(t,x;\alpha^-) \\
&\qquad\qquad + r\eta(s)q(t,x))\eta(s)q(t,x)]\,\mathrm{d}r \\
&= \eta'(s)\biggl\{Cp(t,x) - \int_{\mathbb{R}} J(x-y)p(t,y)\frac{\eta(y+Ct)-\eta(x+Ct)}{\eta'(x+Ct)}\,\mathrm{d}y \\
&\qquad + p(t,x)\int_0^1 r[f_{uu}(x,u^*,v^*)p + f_{uv}(x,u^{**},v^{**})q]\,\mathrm{d}r \\
&\qquad + q(t,x)\int_0^1 r[f_{vu}(x,u_*,v_*)p + f_{vv}(x,u_{**},v_{**})q]\,\mathrm{d}r\biggr\},
\end{aligned}
$$

where u^*, u^{**}, u_*, u_{**} are between $u(t,x;\alpha^-)+rp(t,x)$ and $u(t,x;\alpha^-)+r\eta(s)p(t,x)$, while v^*, v^{**}, v_*, v_{**} are between $v(t,x;\alpha^-)+rq(t,x)$ and $v(t,x;\alpha^-)+r\eta(s)q(t,x)$. By remark 2.5 and the definition of $\eta(s)$, there exist $K_i > 0$ $(i = 1,2,3)$ such that

$$
\begin{aligned}
&p(t,x) \geqslant K_1, \quad q(t,x) \geqslant K_2 \quad \text{for all } x \in \mathbb{R},\ t \geqslant 0, \\
&\left|\frac{\eta(y+Ct)-\eta(x+Ct)}{\eta'(x+Ct)}\right| \leqslant K_3 \quad \text{for all } x, y \in \mathbb{R},\ t \geqslant 0, \\
&\qquad\qquad \text{with } |x-y| \leqslant \max\{\delta_0^1+\varrho_0, \delta_0^2+\varrho_0\},
\end{aligned}
$$

where $[-\delta_0^1-\varrho_0, \delta_0^2+\varrho_0] =: \mathrm{supp}(J)$. It follows that there exists C_1 such that

$$
\frac{\partial u_1^+}{\partial t} - \biggl[\int_{\mathbb{R}} J(x-y)u_1^+(t,y)\,\mathrm{d}y - u_1^+(t,x)\biggr] - f(x,u_1^+,v_1^+) \geqslant 0 \quad \text{for } C \geqslant C_1.
$$

On the other hand,

$$
\begin{aligned}
&\frac{\partial v_1^+}{\partial t} - g(x,u_1^+,v_1^+) \\
&\quad = C\eta'(s)q(t,x) + \eta(s)[g(x,u(t,x;\alpha^+),v(t,x;\alpha^+)) - g(x,u(t,x;\alpha^-),v(t,x;\alpha^-))] \\
&\qquad - [g(x,u(t,x;\alpha^-)+\eta(s)p(t,x), v(t,x;\alpha^-) \\
&\qquad\qquad + \eta(s)q(t,x)) - g(x,u(t,x;\alpha^-),v(t,x;\alpha^-))].
\end{aligned}
$$

Similarly to the above discussion, we can further prove that there exists $C_2 > 0$ such that, for every $C \geqslant C_2$, $\partial v_1^+/\partial t - g(x,u_1^+,v_1^+) \geqslant 0$ and then we complete the proof. □

We may now obtain the following two results, which are analogous to [15, lemmas 3.4 and 3.5].

Lemma 4.3.

(i) *If there exists* $(u^+,v^+) \in X_1^+ \times X_2^+$ *such that*

$$
\liminf_{x\leqslant ct,\, t\to\infty} (u(t,x;u^+,v^+,z) - u^*(x+z), v(t,x;u^+,v^+,z) - v^*(x+z)) = (0,0)
$$

uniformly in $z \in \mathbb{R}$, *then* $c \leqslant c^*_{\mathrm{inf}}$.

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(ii) *If* $c < c^*_{\inf}$, *then for every* $(u^0, v^0) \in X_1^+ \times X_2^+$ *we have*

$$\liminf_{x \leqslant ct,\, t\to\infty} (u(t,x;u^0,v^0,z) - u^*(x+z), v(t,x;u^0,v^0,z) - v^*(x+z)) = (0,0)$$

uniformly in $z \in \mathbb{R}$.

LEMMA 4.4.

(i) *If there exists* $(u^+, v^+) \in X_1^+ \times X_2^+$ *such that*

$$\limsup_{x \geqslant ct,\, t\to\infty} [u^2(t,x;u^+,v^+,z) + v^2(t,x;u^+,v^+,z)] = 0$$

uniformly in $z \in \mathbb{R}$, *then* $c \geqslant c^*_{\sup}$.

(ii) *If* $c > c^*_{\sup}$, *then for every* $(u^0, v^0) \in X_1^+ \times X_2^+$ *we have*

$$\limsup_{x \geqslant ct,\, t\to\infty} [u^2(t,x;u^0,v^0,z) + v^2(t,x;u^0,v^0,z)] = 0$$

uniformly in $z \in \mathbb{R}$.

THEOREM 4.5. $[c^*_{\inf}, c^*_{\sup}]$ *is a finite spreading speed interval.*

Proof. Let $\boldsymbol{\alpha}^{\pm} = (\alpha_1^{\pm}, \alpha_2^{\pm})$ be given constant vectors satisfying the conditions in lemma 4.2. There exists $(u^+(x), v^+(x)) \in X_1^+ \times X_2^+$ such that

$$\begin{aligned}(u_2^+(0,x;z), v_2^+(0,x;z)) &= (\alpha_1^-\eta(x) + \alpha_1^+(1-\eta(x)), \alpha_2^-\eta(x) + \alpha_2^+(1-\eta(x))) \\ &\geqslant (u^+(x), v^+(x)).\end{aligned}$$

Then, by the comparison principle and lemma 4.2, we have

$$\begin{aligned}u_2^+(t,x;z) &= u(t,x;\boldsymbol{\alpha}^-,z)\eta(x-C_0t) + u(t,x;\boldsymbol{\alpha}^+,z)[1-\eta(x-C_0t)] \\ &\geqslant u(t,x;u^+,v^+,z), \\ v_2^+(t,x;z) &= v(t,x;\boldsymbol{\alpha}^-,z)\eta(x-C_0t) + v(t,x;\boldsymbol{\alpha}^+,z)[1-\eta(x-C_0t)] \\ &\geqslant v(t,x;u^+,v^+,z).\end{aligned}$$

In particular, let $\alpha_1^- = \alpha_2^- = 0$. For each $\tilde{C}_1 \geqslant C_0$, the fact that $\eta(\infty) = 1$ yields

$$\begin{aligned}0 &\leqslant \limsup_{x \geqslant \tilde{C}_1 t,\, t\to\infty} [u^2(t,x;u^+,v^+,z) + v^2(t,x;u^+,v^+,z)] \\ &\leqslant \limsup_{x \geqslant \tilde{C}_1 t,\, t\to\infty} [(u_2^+)^2(t,x;z) + (v_2^+)^2(t,x;z)] \\ &= \limsup_{x \geqslant \tilde{C}_1 t,\, t\to\infty} [u^2(t,x;0,0,z) + v^2(t,x;0,0,z)] \\ &= 0.\end{aligned}$$

It then follows by lemma 4.4(i) that $c^*_{\sup} \leqslant \tilde{C}_1$.

On the other hand, there exists $(\tilde{u}^+, \tilde{v}^+) \in X_1^+ \times X_2^+$ such that

$$\begin{aligned}(u_1^-(0,x;z), v_1^-(0,x;z)) &= (\alpha_1^+\eta(x) + \alpha_1^-(1-\eta(x)), \alpha_2^+\eta(x) + \alpha_2^-(1-\eta(x))) \\ &\leqslant (\tilde{u}^+(x), \tilde{v}^+(x)).\end{aligned}$$

Using the comparison principle and lemma 4.2 again, we have

$$\begin{aligned}u_1^-(t,x;z) &= u(t,x;\boldsymbol{\alpha}^-,z)\eta(x+C_0t)+u(t,x;\boldsymbol{\alpha}^+,z)[1-\eta(x+C_0t)]\\ &\leqslant u(t,x;\tilde{u}^+,\tilde{v}^+,z),\\ v_1^-(t,x;z) &= v(t,x;\boldsymbol{\alpha}^-,z)\eta(x+C_0t)+v(t,x;\boldsymbol{\alpha}^+,z)[1-\eta(x+C_0t)]\\ &\leqslant v(t,x;\tilde{u}^+,\tilde{v}^+,z).\end{aligned}$$

Then, for each $\tilde{C}_2 < -C_0$, combining the above with $\eta(-\infty)=0$, we obtain

$$\begin{aligned}&\liminf_{x\leqslant \tilde{C}_2 t,\, t\to\infty}(u(t,x;\tilde{u}^+,\tilde{v}^+,z)-u^*(x+z),v(t,x;\tilde{u}^+,\tilde{v}^+,z)-v^*(x+z))\\ &\quad\geqslant \liminf_{x\leqslant \tilde{C}_2 t,\, t\to\infty}(u_1^-(t,x;z)-u^*(x+z),v_1^-(t,x;z)-v^*(x+z))\\ &\quad= \liminf_{x\leqslant \tilde{C}_2 t,\, t\to\infty}(u(t,x;\alpha_1^+,\alpha_2^+,z)-u^*(x+z),v_1^-(t,x;\alpha_1^+,\alpha_2^+,z)-v^*(x+z))\\ &\quad=(0,0).\end{aligned}$$

At the same time, as $(\tilde{u}^+,\tilde{v}^+)\ll(u^*_{\text{inf}},v^*_{\text{inf}})$, we can further obtain that

$$\begin{aligned}&\liminf_{x\leqslant \tilde{C}_2 t,\, t\to\infty}(u(t,x;\tilde{u}^+,\tilde{v}^+,z)-u^*(x+z),v(t,x;\tilde{u}^+,\tilde{v}^+,z)-v^*(x+z))\\ &\quad\leqslant \liminf_{x\leqslant \tilde{C}_2 t,\, t\to\infty}(u(t,x;u^*_{\text{inf}},v^*_{\text{inf}},z)-u^*(x+z),v(t,x;u^*_{\text{inf}},v^*_{\text{inf}},z)-v^*(x+z))\\ &\quad=(0,0).\end{aligned}$$

According to the above discussion, combining this result with lemma 4.3(i) yields $c^*_{\text{inf}}\geqslant \tilde{C}_2$. Hence, $[c^*_{\text{inf}},c^*_{\text{sup}}]$ is a finite spreading speed interval and the proof is complete. □

Let

$$\tilde{X}_i^+=\Big\{\psi_0\in X_i^+\ \Big|\ \liminf_{x\to-\infty}\psi_0(x)>0,\ \ \limsup_{x\to\infty}\psi_0(x)=0\Big\},\quad i=1,2.$$

LEMMA 4.6. *Let $c\in\mathbb{R}$ and $(u_0,v_0)\in\tilde{X}_1^+\times\tilde{X}_2^+$. If there exist T_0 and $(0,0)\ll(\varrho_1^0,\varrho_2^0)\ll(u^*_{\text{inf}},v^*_{\text{inf}})$ such that*

$$\liminf_{x\leqslant cnT_0,\ n\to\infty}(u(nT_0,x;u_0,v_0,z),v(nT_0,x;u_0,v_0,z))\geqslant(\varrho_1^0,\varrho_2^0) \tag{4.1}$$

uniformly in $z\in\mathbb{R}$, where $n\in\mathbb{N}$, then, for every $c'<c$,

$$\liminf_{x\leqslant c't,\, t\to\infty}(u(t,x;u_0,v_0,z)-u^*(x+z),v(t,x;u_0,v_0,z)-v^*(x+z))=(0,0)$$

uniformly in $z\in\mathbb{R}$.

Proof. For given $c'<c$, by (4.1) there exists $n_0\in\mathbb{N}$ such that

$$(u(nT_0,x+y;u_0,v_0,z),v(nT_0,x+y;u_0,v_0,z))\geqslant(\tfrac{1}{2}\varrho_1^0,\tfrac{1}{2}\varrho_1^0) \tag{4.2}$$

for $z\in\mathbb{R}$, $n\geqslant n_0$, $x\leqslant(c-c')nT_0$ and $y\leqslant c'nT_0$. Let $(\tilde{u}_0(\cdot),\tilde{v}_0(\cdot))\equiv(\tfrac{1}{2}\varrho_1^0,\tfrac{1}{2}\varrho_1^0)$. By remark 2.5, for every $\varepsilon>0$, there exists $n_1\geqslant n_0$ such that

$$(u(t,x;\tilde{u}_0,\tilde{v}_0,z),v(t,x;\tilde{u}_0,\tilde{v}_0,z))\geqslant(u^*(x+z)-\varepsilon,v^*(x+z)-\varepsilon) \tag{4.3}$$

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for $t \geqslant n_1T_0$ and $x, z \in \mathbb{R}$. For a given $B > 1$, suppose that $(\tilde{u}_B(\cdot), \tilde{v}_B(\cdot)) \in [0, \frac{1}{2}\varrho_1^0]_X \times [0, \frac{1}{2}\varrho_2^0]_X$, which satisfies $(\tilde{u}_B(x), \tilde{v}_B(x)) = (\frac{1}{2}\varrho_1^0, \frac{1}{2}\varrho_1^0)$ for $x \leqslant B-1$ and $(\tilde{u}_B(x), \tilde{v}_B(x)) = (0,0)$ for $x \geqslant B$. By the continuous dependence of the solution on the initial value (see lemma 2.4), we have

$$(u(t,0;\tilde{u}_B,\tilde{v}_B,z), v(t,0;\tilde{u}_B,\tilde{v}_B,z)) \to (u(t,0;\tilde{u}_0,\tilde{v}_0,z), v(t,0;\tilde{u}_0,\tilde{v}_0,z)) \quad \text{as } B \to \infty \tag{4.4}$$

uniformly in $z \in \mathbb{R}$. Then, combining (4.3) and (4.4), there exists $B_0 > 1$ such that, for each $B \geqslant B_0$,

$$(u(t,0;\tilde{u}_B,\tilde{v}_B,z), v(t,0;\tilde{u}_B,\tilde{v}_B,z)) \geqslant (u^*(z) - 2\varepsilon, v^*(z) - 2\varepsilon) \tag{4.5}$$

for $n_1T_0 \leqslant t \leqslant (n_1+1)T_0$ and $z \in \mathbb{R}$. Note that $(c-c')nT_0 \to \infty$ as $n \to \infty$. Thus, there exists $n_2 \geqslant n_1$ such that

$$(c-c')nT_0 \geqslant B_0 + c'(n_1+1)T_0 \quad \text{for } n \geqslant n_2. \tag{4.6}$$

Now, we claim that

$$\begin{aligned}(u(nT_0, y+x+c'nT_0+c'T_1; u_0, v_0, z), v(nT_0, y+x+c'nT_0+c'T_1; u_0, v_0, z))\\ \geqslant (\tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y)) \quad \text{for } x \leqslant 0,\ T_1 \in [n_1T_0, (n_1+1)T_0],\ n \geqslant n_2,\ y \in \mathbb{R}.\end{aligned} \tag{4.7}$$

In fact, if $y \leqslant B_0$, then $(\tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y)) \leqslant (\tilde{u}_0(y), \tilde{v}_0(y))$, and, for all $x \leqslant 0$, $n_1T_0 \leqslant T_1 \leqslant (n_1+1)T_0$, $n \geqslant n_2$, we can obtain from (4.6) that

$$y + x + c'nT_0 + c'T_1 \leqslant B_0 + 0 + c'nT_0 + c'(n_1+1)T_0 \leqslant cnT_0.$$

It then follows from (4.2) that

$$\begin{aligned}(u(nT_0, y+x+c'nT_0+c'T_1; u_0, v_0, z), v(nT_0, y+x+c'nT_0+c'T_1; u_0, v_0, z))\\ \geqslant (\tfrac{1}{2}\varrho_1^0, \tfrac{1}{2}\varrho_1^0) = (\tilde{u}_0(y), \tilde{v}_0(y)) \geqslant (\tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y)).\end{aligned}$$

On the other hand, when $y \geqslant B_0$, $(\tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y)) = (0,0)$. Thus, the claim is true.

Next fix $n \geqslant n_2$ and $(n+n_1)T_0 \leqslant t \leqslant (n+n_1+1)T_0$. Let $T_1 = t - nT_0$. By (4.7) and (4.5), we have

$$\begin{aligned}&(u(t, x+c't; u_0, v_0, z), v(t, x+c't; u_0, v_0, z))\\ &\quad = (u(T_1, x+c't; u(nT_0, y; u_0, v_0, z), v(nT_0, y; u_0, v_0, z), z),\\ &\qquad\qquad v(T_1, x+c't; u(nT_0, y; u_0, v_0, z), v(nT_0, y; u_0, v_0, z), z))\\ &\quad = (u(T_1, 0; u(nT_0, y+Y_x; u_0, v_0, z), v(nT_0, y+Y_x; u_0, v_0, z), z+x+c't),\\ &\qquad\qquad v(T_1, 0; u(nT_0, y+Y_x; u_0, v_0, z), v(nT_0, y+Y_x; u_0, v_0, z), z+x+c't))\\ &\quad \geqslant (u(T_1, 0; \tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y), z+x+c't), v(T_1, 0; \tilde{u}_{B_0}(y), \tilde{v}_{B_0}(y), z+x+c't))\\ &\quad \geqslant (u^*(z+x+c't) - 2\varepsilon, v^*(z+x+c't) - 2\varepsilon),\end{aligned}$$

where $Y_x = x + c'nT_0 + c'T_1$ and $x \leqslant 0$. Thus, we have

$$(u(t, x; u_0, v_0, z), v(t, x; u_0, v_0, z)) \geqslant (u^*(z+x) - 2\varepsilon, v^*(z+x) - 2\varepsilon)$$

for $x \leqslant c't$, $z \in \mathbb{R}$ and $t \geqslant (n_1+n_2)T_0$. Then the arbitrariness of ε leads to the lemma. □

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5. Spreading speeds

First define

$$c^*(1) = \inf_{\mu>0} \frac{\lambda^*(\mu,0)}{\mu} \quad \text{and} \quad c^*(-1) = \inf_{\mu>0} \frac{\lambda^*(-\mu,0)}{\mu}.$$

The following theorem shows that $c^*(1)$ and $c^*(-1)$ are the rightward and leftward spreading speeds of (2.1), respectively.

THEOREM 5.1. *The following statements are valid.*

(i) $c^*(1)$ *and* $c^*(-1)$ *are the rightward and leftward spreading speeds of (2.1). Moreover,* $c^*(1) + c^*(-1) > 0$*.*

(ii) *For every* $(u_0, v_0) \in X_1^+ \times X_2^+$ *and* $c > \max\{c^*(1), c^*(-1)\}$*,*

$$\limsup_{|x|\geqslant ct,\, t\to\infty} [u^2(t,x;u_0,v_0,z)+v^2(t,x;u_0,v_0,z)] = 0 \text{ uniformly in } z \in \mathbb{R}. \quad (5.1)$$

(iii) *For every* $(u_0, v_0) \in X_1^+ \times X_2^+$ *and* $c < \min\{c^*(1), c^*(-1)\}$*,*

$$\liminf_{|x|\leqslant ct,\, t\to\infty} (u(t,x;u_0,v_0,z) - u^*(x+z), v(t,x;u_0,v_0,z) - v^*(x+z)) = (0,0) \quad (5.2)$$

uniformly in $z \in \mathbb{R}$*.*

Proof.
(i) We prove only that $c^*(1)$ is a rightward spreading speed, since we can obtain that $c^*(-1)$ is a leftward spreading speed by the change of variable $U(t,x) = u(t,-x)$ and repeating the same procedure.

To begin with, we show that $c^*_{\sup} \leqslant c^*(1)$. Let $(\phi^*(x,\mu), \varphi^*(x,\mu)) \in X_p^{++} \times X_p^{++}$ be a principal eigenfunction of (2.8) corresponding to $\lambda^*(\mu,0)$. Set $c' = \lambda^*(\mu,0)/\mu$ with $\mu > 0$. Similar to the proof of theorem 3.2 (i), we can choose $\tilde{\rho} > 0$ satisfying $(u_0,v_0) \leqslant \tilde{\rho} e^{-\mu x}(\phi^*(x,\mu), \varphi^*(x,\mu))$ such that

$$(0,0) \leqslant (u(t,x;u_0,v_0), v(t,x;u_0,v_0)) \leqslant \tilde{\rho} e^{-\mu(x-c't)}(\phi^*(x,\mu), \varphi^*(x,\mu)).$$

Thus, for each $c > c'$, we have

$$\limsup_{x\geqslant ct,\, t\to\infty} [u^2(t,x;u_0,v_0,z) + v^2(t,x;u_0,v_0,z)] = 0.$$

We then have $c^*_{\sup} \leqslant c' = \lambda^*(\mu,0)/\mu$ for any $\mu > 0$, and so $c^*_{\sup} \leqslant c^*(1)$.

Next we prove that $c^*_{\inf} \geqslant \inf_{\mu>0} \lambda^*(\mu,\epsilon)/\mu$. This procedure can be handled as in step 2 of the proof of [37, theorem 4.1] coupled with lemmas 2.11, 4.6 and 4.3(i). For completeness, we give the following rough outline of the proof process.

Choose $B \gg 1$ such that lemma 2.11 holds. Observe that if $\boldsymbol{u}_0 = (u_0,v_0) \in X^+ \times X^+$ is so small that $(0,0) \leqslant (u(t,x;\boldsymbol{u}_0,z), v(t,x;\boldsymbol{u}_0,z)) \leqslant (\delta,\delta)$ for $t \in [0,1]$, $x,z \in \mathbb{R}$, then by (2.6) we have

$$(u(t,x;\boldsymbol{u}_0,z), v(t,x;\boldsymbol{u}_0,z)) \geqslant [\boldsymbol{\Phi}(1;0,\epsilon,z)\boldsymbol{u}_0](x) \geqslant [\boldsymbol{\Phi}_B(1;0,\epsilon,z)\boldsymbol{u}_0](x). \quad (5.3)$$

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In view of lemma 2.11, $r_B(\boldsymbol{\Phi}^p(1;\mu,\epsilon,0))$ is a simple eigenvalue of $\boldsymbol{\Phi}_B^p(1;\mu,\epsilon,0)$ with an eigenfunction $(\phi_B^*(x,\mu;\epsilon),\varphi_B^*(x,\mu;\epsilon))\in X_p^{++}\times X_p^{++}$ for $|\mu|\leqslant\mu^*+l_0$.

By lemma 2.11(c), for each $\varepsilon_1>0$, there exists $B>0$ such that

$$-\frac{\lambda_B^*(\mu_B^*,\epsilon)}{\mu_B^*}\leqslant-\frac{\lambda^*(\mu^*,\epsilon)}{\mu^*}+\varepsilon_1. \tag{5.4}$$

For the above ε_1, by lemma 2.11(b), there exists $\mu_{\varepsilon_1}>0$ such that, for $\mu\in(\mu_{\varepsilon_1},\mu_B^*)$,

$$-\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}<-\frac{\lambda_B^*(\mu_B^*,\epsilon)}{\mu_B^*}+\varepsilon_1. \tag{5.5}$$

We now fix $\mu\in(\mu_{\varepsilon_1},\mu_B^*)$. By lemma 2.11(a),

$$\lambda_B^*(\mu,\epsilon)-\mu\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}>0. \tag{5.6}$$

Let

$$(\kappa_B^1(x,\mu;\epsilon),\kappa_B^2(x,\mu;\epsilon))=\left(\frac{1}{\phi_B^*(x,\mu;\epsilon)}\frac{\partial\phi_B^*(x,\mu;\epsilon)}{\partial\mu},\frac{1}{\varphi_B^*(x,\mu;\epsilon)}\frac{\partial\varphi_B^*(x,\mu;\epsilon)}{\partial\mu}\right).$$

Define $\boldsymbol{w}=(w^1,w^2)$ by

$$w^i(s,x)=\begin{cases}\varepsilon_2\boldsymbol{\psi}_B^i(x,\mu;\epsilon)\mathrm{e}^{-\mu s}\sin\gamma[s-\kappa_B^i(x,\mu;\epsilon)], & 0\leqslant s-\kappa_B^i(x,\mu;\epsilon)\leqslant\pi/\gamma,\\ 0, & \text{otherwise},\end{cases} \tag{5.7}$$

where ε_2 and γ are sufficiently small positive numbers and $(\boldsymbol{\psi}_B^1,\boldsymbol{\psi}_B^2)=(\phi_B^*,\varphi_B^*)$. Let

$$\begin{aligned}\tau_B^i(\gamma,z)=\frac{1}{\gamma}\tan^{-1}\Bigg(\Bigg(\sum_{j=1}^2\int_{\mathbb{R}}&\boldsymbol{\psi}_B^j(y,\mu;\epsilon)\mathrm{e}^{-\mu(y-z)}\chi\left(\frac{|y-z|}{B}\right)\\&\times\sin\gamma[-(y-z)+\kappa_B^j(y,\mu;\epsilon)]m_{ij}(z;y,\mathrm{d}y)\Bigg)\\&\times\Bigg(\sum_{j=1}^2\int_{\mathbb{R}}\boldsymbol{\psi}_B^j(y,\mu;\epsilon)\mathrm{e}^{-\mu(y-z)}\chi\left(\frac{|y-z|}{B}\right)\\&\times\cos\gamma[-(y-z)+\kappa_B^j(y,\mu;\epsilon)]m_{ij}(z;y,\mathrm{d}y)\Bigg)^{-1}\Bigg).\end{aligned}$$

Similarly to Wu *et al*. [37], by the Lebesgue dominated convergence theorem, we can obtain that

$$\lim_{\gamma\to0}\tau_B^i(\gamma,z)=\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}+\kappa_B^i(z,\mu;\epsilon)$$

uniformly for $z\in\mathbb{R}$.

Choose $\gamma>0$ so small that

$$\gamma(B+|\tau_B^i(\gamma,z)|+|\kappa_B^j(y,\mu;\epsilon)|)<\pi, \tag{5.8}$$

$$\kappa_B^i(z,\mu;\epsilon)-\tau_B^i(\gamma,z)<-\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}+\varepsilon_1\quad\text{for all } y,z\in\mathbb{R},\ 1\leqslant i,j\leqslant2. \tag{5.9}$$

Set $\boldsymbol{w}^*(x;s,z) = \boldsymbol{w}(x+s-\kappa_B^i(x,\mu;\epsilon)+\tau_B^i(\gamma,z),x+z)$. If $0 \leqslant s-\kappa_B^i(x,\mu;\epsilon) \leqslant \pi/\gamma$ and $|y-z| \leqslant B$, then combining this result with (5.8) yields

$$\begin{aligned}-\frac{\pi}{\gamma} &\leqslant -B - |\tau_B^i(\gamma,z)| - |\kappa_B^j(y,\mu;\epsilon)| \\ &\leqslant y-z+s-\kappa_B^i(z,\mu;\epsilon)+\tau_B^i(\gamma,z)-\kappa_B^j(y,\mu;\epsilon) \\ &\leqslant B+\frac{\pi}{\gamma}+|\tau_B^i(\gamma,z)|+|\kappa_B^j(y,\mu;\epsilon)| \\ &\leqslant \frac{2\pi}{\gamma}.\end{aligned}$$

When $P := y-z+s-\kappa_B^i(x,\mu;\epsilon)+\tau_B^i(\gamma,z)-\kappa_B^j(y,\mu;\epsilon) \in [-\pi/\gamma,0)\cup(\pi/\gamma,2\pi/\gamma]$, we have $\sin(\gamma P) \leqslant 0$. Moreover, via (5.7), we get

$$\begin{aligned}w_*^j(y-z;s,z) &= w^j(y-z+s-\kappa_B^i(x,\mu;\epsilon)+\tau_B^i(\gamma,z),y) \\ &\geqslant \varepsilon_2 \boldsymbol{\psi}_B^j(y,\mu;\epsilon)\mathrm{e}^{-\mu P}\sin(\gamma P).\end{aligned} \tag{5.10}$$

Choose ε_2 so small that $(0,0) \leqslant (u(t,x;\boldsymbol{w}_*(\cdot;s,z),z), v(t,x;\boldsymbol{w}_*(\cdot;s,z),z)) \leqslant (\delta,\delta)$ for all $t \in [0,1]$ and $x,z \in \mathbb{R}$. Let $\zeta_B^i(z,\mu,\gamma;\epsilon) = -\kappa_B^i(z,\mu;\epsilon)+\tau_B^i(\gamma,z)$. Then we write $P = y-z+s+\zeta_B^i(z,\mu,\gamma;\epsilon)-\kappa_B^j(y,\mu;\epsilon)$, and by (5.3), (2.22) and (5.10), for $0 \leqslant s-\kappa_B^i(x,\mu;\epsilon) \leqslant \pi/\gamma$,

$$\begin{aligned}&(u(1,0;\boldsymbol{w}_*(\cdot;s,z),z), v(1,0;\boldsymbol{w}_*(\cdot;s,z),z)) \\ &\quad \geqslant [\boldsymbol{\Phi}_B(1;0,\epsilon,z)\boldsymbol{w}_*](0) \\ &\quad = \sum_{j=1}^{2}\int_{\mathbb{R}} w_*^j(y-z;s,z)\chi\left(\frac{|y-z|}{B}\right)(m_{1j}(z;y,\mathrm{d}y), m_{2j}(z;y,\mathrm{d}y)) \\ &\quad \geqslant \sum_{j=1}^{2}\int_{\mathbb{R}} \varepsilon_2\boldsymbol{\psi}_B^j(y,\mu;\epsilon)\mathrm{e}^{-\mu P}\sin(\gamma P)\chi\left(\frac{|y-z|}{B}\right)(m_{1j}(z;y,\mathrm{d}y), m_{2j}(z;y,\mathrm{d}y)).\end{aligned}$$

Through a similar computational process with [37], we can obtain

$$(u(1,0;\boldsymbol{w}_*(\cdot;s,z),z), v(1,0;\boldsymbol{w}_*(\cdot;s,z),z)) \geqslant (w^1(s,z), w^2(s,z)) \tag{5.11}$$

for $0 \leqslant s-\kappa_B^i(x,\mu;\epsilon) \leqslant \pi/\gamma$. According to the definition of $w^i(s,z)$, it further follows that (5.11) holds for all $s \in \mathbb{R}$.

Let $\bar\kappa = \max_{1\leqslant i\leqslant 2,\ z\in\mathbb{R}} \kappa_B^i(z,\mu;\epsilon)$ and define $\bar{\boldsymbol{w}} = (\bar w^1, \bar w^2)$ with

$$\bar w^i(s,x) = \begin{cases} w^i(\bar s_i(x),x) & \text{if } s \leqslant \bar s_i(x)-\pi/\gamma-\bar\kappa, \\ w^i(s+\pi/\gamma+\bar\kappa,x) & \text{if } s \geqslant \bar s_i(x)-\pi/\gamma-\bar\kappa,\end{cases}$$

where $\bar s_i(x)$ is the maximum point of $w^i(\cdot,x)$ on $\mathbb{R}$. Set

$$\bar{\boldsymbol{w}}_*(x;s,z) = \bar{\boldsymbol{w}}(x+s-\kappa_B^i(z,\mu;\epsilon)+\tau_B^i(\gamma,z),x+z).$$

Then we can easily verify $(u(1,0;\bar{\boldsymbol{w}}_*(\cdot;s,z),z), v(1,0;\bar{\boldsymbol{w}}_*(\cdot;s,z),z)) \geqslant (\bar w^1(s,z), \bar w^2(s,z))$. Let $\boldsymbol{w}_0(x;z) = \bar{\boldsymbol{w}}(x,x+z)$. Note that $\bar{\boldsymbol{w}}(s,x)$ is non-increasing in s.

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Hence, combining (5.4), (5.5) and (5.9), we have

$$\begin{aligned}
&(u(1,x;\boldsymbol{w}_0(\cdot;z),z),v(1,x;\boldsymbol{w}_0(\cdot;z),z))\\
&\quad=(u(1,0;\boldsymbol{w}_0(\cdot+x;z),x+z),v(1,0;\boldsymbol{w}_0(\cdot+x;z),x+z))\\
&\quad=(u(1,0;\bar{\boldsymbol{w}}_*(\cdot;x+\kappa_B^i(x+z,\mu;\epsilon)-\tau_B^i(\gamma,x+z),x+z),x+z),\\
&\qquad\qquad v(1,0;\bar{\boldsymbol{w}}_*(\cdot;x+\kappa_B^i(x+z,\mu;\epsilon)-\tau_B^i(\gamma,x+z),x+z),x+z))\\
&\quad\geqslant(\bar{w}^1(x+\kappa_B^i(x+z,\mu;\epsilon)-\tau_B^i(\gamma,x+z),x+z),\\
&\qquad\qquad\qquad \bar{w}^2(x+\kappa_B^i(x+z,\mu;\epsilon)-\tau_B^i(\gamma,x+z),x+z))\\
&\quad\geqslant\left(\bar{w}^1\left(x-\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}+\varepsilon_1,x+z\right),\bar{w}^2\left(x-\frac{\partial\lambda_B^*(\mu,\epsilon)}{\partial\mu}+\varepsilon_1,x+z\right)\right)\\
&\quad\geqslant(\bar{w}^1(x-\lambda_B^*(\mu_B^*,\epsilon)/\mu_B^*+2\varepsilon_1,x+z),\bar{w}^2(x-\lambda_B^*(\mu_B^*,\epsilon)/\mu_B^*+2\varepsilon_1,x+z))\\
&\quad\geqslant(\bar{w}^1(x-\lambda^*(\mu^*,\epsilon)/\mu^*+3\varepsilon_1,x+z),\bar{w}^2(x-\lambda^*(\mu^*,\epsilon)/\mu^*+3\varepsilon_1,x+z))\\
&\quad\geqslant(w_0^1(x-\tilde{c}^*;z+\tilde{c}^*),w_0^2(x-\tilde{c}^*;z+\tilde{c}^*)),
\end{aligned}$$

where $\tilde{c}^*=\lambda^*(\mu^*,\epsilon)/\mu^*-3\varepsilon_1$. Furthermore, we have

$$\begin{aligned}
&(u(2,x;\boldsymbol{w}_0(\cdot;z),z),v(2,x;\boldsymbol{w}_0(\cdot;z),z))\\
&\qquad\geqslant(u(1,x;\boldsymbol{w}_0(\cdot-\tilde{c}^*;z+\tilde{c}^*),z),v(1,x;\boldsymbol{w}_0(\cdot-\tilde{c}^*;z+\tilde{c}^*),z))\\
&\qquad=(u(1,x-\tilde{c}^*;\boldsymbol{w}_0(\cdot;z+\tilde{c}^*),z+\tilde{c}^*),v(1,x-\tilde{c}^*;\boldsymbol{w}_0(\cdot;z+\tilde{c}^*),z+\tilde{c}^*))\\
&\qquad\geqslant(\bar{w}^1(x-2\tilde{c}^*,z+2\tilde{c}^*),\bar{w}^2(x-2\tilde{c}^*,z+2\tilde{c}^*)).
\end{aligned}$$

By induction, we get

$$(u(n,x;\boldsymbol{w}_0(\cdot;z),z),v(n,x;\boldsymbol{w}_0(\cdot;z),z))\geqslant(\bar{w}^1(x-n\tilde{c}^*,z+n\tilde{c}^*),\bar{w}^2(x-n\tilde{c}^*,z+n\tilde{c}^*))$$

for $z\in\mathbb{R}$ and $n\geqslant 1$. This, together with lemmas 4.6 and 4.3(i) implies that $\tilde{c}^*=\lambda^*(\mu^*,\epsilon)/\mu^*-3\varepsilon_1\leqslant c^*_{\inf}$, and we can further obtain that $\lambda^*(\mu^*,\epsilon)/\mu^*\leqslant c^*_{\inf}$ by the arbitrariness of ε_1.

From the above discussion, we indeed have

$$\inf_{\mu>0}\frac{\lambda^*(\mu,\epsilon)}{\mu}\leqslant c^*_{\inf}\leqslant c^*_{\sup}\leqslant c^*(1)\quad\text{for all small }\epsilon\geqslant 0.$$

We then get that $c^*_{\inf}=c^*_{\sup}=c^*(1)$ by letting $\epsilon\to 0$.

Now we prove $c^*(1)+c^*(-1)>0$. By theorem 2.10(ii), there exist $\mu_1,\mu_2>0$ such that

$$c^*(1)=\frac{\lambda^*(\mu_1,0)}{\mu_1}\quad\text{and}\quad c^*(-1)=\frac{\lambda^*(-\mu_2,0)}{\mu_2}.$$

Let $\vartheta=\mu_1/(\mu_1+\mu_2)$. Then $(1-\vartheta)\mu_1=\vartheta\mu_2$ and $\vartheta\in(0,1)$. In view of theorem 2.10(i), $\lambda^*(\mu,0)$ is convex in $\mu\in\mathbb{R}$. Then we have

$$\begin{aligned}
c^*(1)+c^*(-1)&=\frac{\lambda^*(\mu_1,0)}{\mu_1}+\frac{\lambda^*(-\mu_2,0)}{\mu_2}\\
&=\frac{1}{\vartheta\mu_2}[(1-\vartheta)\lambda^*(\mu_1,0)+\vartheta\lambda^*(-\mu_2,0)]
\end{aligned}$$

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$$\geqslant \frac{1}{\vartheta\mu_2}\lambda^*((1-\vartheta)\mu_1 - \vartheta\mu_2, 0)$$
$$= \frac{1}{\vartheta\mu_2}\lambda_0^*$$
$$> 0.$$

(ii), (iii) We can prove (5.1) and (5.2) by similar arguments to those in [30, theorem E] and combining lemmas 2.6(ii) and 2.4(ii) so we omit the details here. Then we complete the proof of this theorem. □

REMARK 5.2. If the non-local dispersal kernel J is symmetric, then $c^*(1) = c^*(-1)$.

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