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Spreading speeds of a partially degenerate reaction–diffusion system in a periodic habitat ☆

Chufen Wu [a,b], Dongmei Xiao [b], Xiao-Qiang Zhao [c,*]

[a] Department of Mathematics, Foshan University, Foshan 528000, PR China
[b] Department of Mathematics, Shanghai Jiao Tong University, Shanghai 200240, PR China
[c] Department of Mathematics and Statistics, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada

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ABSTRACT

This paper is devoted to the study of the spreading speeds of a partially degenerate reaction–diffusion system with monostable nonlinearity in a periodic habitat. We first obtain sufficient conditions for the existence of principal eigenvalues in the case where solution maps of the associated linear systems lack compactness, and prove a threshold type result on the global dynamics for the periodic initial value problem. Then we establish the existence and computational formulae of spreading speeds for the general initial value problem. It turns out that the spreading speed is linearly determinate.

1. Introduction

The spatial dynamics of populations in homogeneous or heterogeneous habitats is a central topic in biology and ecology, and the spreading speed of populations is a crucial quantity in the study of biological invasions and disease spread, which has attracted a lot of attentions both theoretically

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* Corresponding author.
E-mail addresses: chufenwu@126.com (C. Wu), xiaodm@sjtu.edu.cn (D. Xiao), zhao@mun.ca (X.-Q. Zhao).

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and empirically; see [1–5,7,10–13,15–17,19,24,26,31–33], and references therein. Homogeneity and heterogeneity are concepts referring to qualitatively uniform and varying habitats for populations, respectively. Most real environments exhibit more complex patterns than strict periodicity, but the main characteristics of many landscapes can be captured well by this assumption. For example, the growth and spread of an invading species in a forest which consists of trees planted in periodic rows when the population density does not vary in the direction of the rows [27]. In order to model the growth and spread of benthic-pelagic population in a river, Lutscher, Lewis and McCauley [20] partitioned the river into the flowing water (or pelagic) zone and the storage (or benthic) zone, and proposed the following partially degenerate reaction–diffusion system in a periodic habitat with piecewise constant coefficient functions, which corresponds to a river with a series of pools and riffles:

$$\begin{aligned} \frac{\partial u_1}{\partial t}(t,x) &= \frac{1}{a(x)}\frac{\partial}{\partial x}\left(d(x)a(x)\frac{\partial u_1}{\partial x}\right) - \frac{q}{a(x)}\frac{\partial u_1}{\partial x} + k(x)(u_2-u_1), \\ \frac{\partial u_2}{\partial t}(t,x) &= p(x)(u_1-u_2) + \left[f(x)-u_2\right]u_2, \end{aligned} \tag{1.1}$$

where $u_1(t,x)$ and $u_2(t,x)$ are the densities of pelagic and benthic individuals, respectively, $a(x)$ is the cross-sectional areas of flowing zone, $d(x)$ is the diffusion rate, q is the advective flux, $k(x)$ and $p(x)$ are two exchange rates, $f(x)$ is the growth rate, and

$$a(x), d(x), f(x), k(x), p(x) = \begin{cases} 1, 1, 1, k_1, p_1, & x \in (0, l_1) + L\mathbb{Z}, \\ a_2, d_2, f_2, k_2, p_2, & x \in (l_1, L) + L\mathbb{Z}. \end{cases}$$

By analyzing the effects of heterogeneity on the persistence and spread of populations in a riverine habitat, Lutscher et al. obtained implicit formulae for the persistence boundary and the dispersion relation of the wave speed for model (1.1). However, the question of the existence of a spreading speed of system (1.1) remains unresolved.

The purpose of the present work is to study spreading speeds of a more general partially degenerate reaction–diffusion system in a periodic habitat:

$$\begin{aligned} \frac{\partial u_1}{\partial t}(t,x) &= \frac{\partial}{\partial x}\left(D_1(x)\frac{\partial u_1}{\partial x}\right) + D_2(x)\frac{\partial u_1}{\partial x} + f(x,u_1,u_2), \\ \frac{\partial u_2}{\partial t}(t,x) &= g(x,u_1,u_2), \end{aligned} \tag{1.2}$$

where $u_1(t,x)$ and $u_2(t,x)$ are the densities of two species at time t and location x in an L-periodic habitat for some positive number L. The coefficient functions and reaction functions of system (1.2) satisfy the following conditions:

(A1) $D_1 \in C^{1+\nu}(\mathbb{R})$, $D_2 \in C^{\nu}(\mathbb{R})$, $D_i(x+L) = D_i(x)$, $\forall i = 1,2$, $x \in \mathbb{R}$, where $C^{\nu}(\mathbb{R})$ is the space of Hölder continuous functions with exponent $\nu \in (0,1)$. The differential operator $\frac{\partial}{\partial x}(D_1(x)\frac{\partial}{\partial x}) + D_2(x)\frac{\partial}{\partial x}$ is uniformly elliptic, i.e., there exists a positive number β_0 such that $D_1(x) \geqslant \beta_0$, $\forall x \in \mathbb{R}$.

(A2) $f, g : \mathbb{R} \times \mathbb{R}^2_+ \to \mathbb{R}^2$, $f(x,u)$ and $g(x,u)$ are C^2 in u, Hölder continuous and L-periodic in x, $f(x,0) = g(x,0) = 0$, and the partial derivatives of f, g up to order 2 with respect to u_1, u_2 are all continuous and L-periodic in x, respectively.

(A3) There exists a positive vector $M = (M_1, M_2)$ such that

$$f(x,M) \leqslant 0 \quad \text{and} \quad g(x,M) \leqslant 0, \quad \forall x \in \mathbb{R}.$$

(A4) $f_{u_2}(x,u_1,u_2) > 0$, $g_{u_1}(x,u_1,u_2) > 0$, $\forall x \in \mathbb{R}$, $u \in [0,M_1] \times [0,M_2]$, where f_q denotes the partial derivative of f with respect to q.

(A5) $F(x,u) := (f(x,u), g(x,u))$ is strictly subhomogeneous on $[0, M_1] \times [0, M_2]$ in the sense that $F(x, \nu u) > \nu F(x,u)$, $\forall x \in \mathbb{R}$, $\nu \in (0,1)$, $u \in [0, M_1] \times [0, M_2]$ with $u_i > 0$ for all $i = 1, 2$.

By the differentiability of $D_1(x)$, we can reduce system (1.2) to the following simple form:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_1(x)\frac{\partial^2 u_1}{\partial x^2} + D_0(x)\frac{\partial u_1}{\partial x} + f(x, u_1, u_2), \\ \frac{\partial u_2}{\partial t} &= g(x, u_1, u_2), \quad t > 0,\ x \in \mathbb{R}, \end{aligned} \tag{1.3}$$

where $D_0(x) = D_1'(x) + D_2(x)$.

Since there is no diffusion term in the second equation of (1.3), the solution maps $Q(t)$ of system (1.3) are not compact with respect to the compact open topology. Therefore, we cannot use the theory of spreading speeds and traveling waves developed by Weinberger [31]. More precisely, the map $Q(t)$ does not satisfy the compactness assumption [31, Hypothesis 2.1vi]. Besides, more restrictive conditions on reaction terms are needed to show that $Q(t)$ is an α-contraction with respect to the Kuratowski measure of non-compactness. So we may not expect to apply the abstract results in Liang and Zhao [19] to study the spreading speed for the model system (1.3).

The spreading properties in periodic habitats originate from the propagating waves in periodic media, see, e.g., [10,11,34,2,23,24] and references therein. In terms of ecological applications, there are numerous publications exploring biological invasions and range expansion in heterogeneous landscapes, see, e.g., [27,28,16,17,4] and references therein. Weinberger [31] studied the spreading speed and traveling waves for a recursion with a periodic order-preserving compact operator, which can be regarded as a general model of time evolution in population genetics or population ecology in a periodic habitat (see also [32]). Recently, Shen and Zhang [26] investigated the spreading speed for a nonlocal dispersal equation in a periodic habitat. Differently from the construction of spreading speeds in [30,31,19], they developed a new approach to spreading speeds (see also [15]) to overcome the difficulty induced by the non-compactness of solution operators. We will study the global dynamics and spreading speeds of system (1.3) by combining the theory of monotone dynamical systems and the ideas in [26]. To characterize the spreading speed for system (1.3), we need to use the principal eigenvalues of a class of degenerate elliptic eigenvalue problems subject to the periodic boundary condition. Note that the celebrated Krein–Rutman theorem and its generalization [25] do not apply to our current case. We will show the existence of such principal eigenvalues by appealing to the theory recently developed by Wang and Zhao [29].

The rest of this paper is organized as follows. In Section 2, we present some preliminary results on the well-posedness of solutions, the comparison principle, the principal eigenvalue, global dynamics for a periodic initial value problem, and linear evolution operators. In Section 3, we prove the existence of the spreading speed interval by sandwiching the given system (1.3) in between two appropriate linear systems, which can provide upper and lower bounds for spreading speeds. In Section 4, we show that the spreading speed interval is a singleton by employing the linear spectral theory, squeezing techniques and the arguments modified from [21,30,31,18,26]. At the end of Section 4, we also apply our analytic results to model (1.1) to give computational formulae of spreading speeds.

2. Preliminaries

In this section, we introduce some notations and present preliminary results which will be used in later sections.

Let $\mathcal{C} = BC(\mathbb{R}, \mathbb{R}^2)$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$. Clearly, any vectors in $\mathbb{R}^2$ can be regarded as an element in $\mathcal{C}$. For $u = (u_1, u_2)$, $v = (v_1, v_2) \in \mathcal{C}$, we write $u \geqslant v$ ($u \gg v$) provided $u_i(x) \geqslant v_i(x)$ ($u_i(x) > v_i(x)$), $\forall i = 1, 2$, $x \in \mathbb{R}$, and $u > v$ provided $u \geqslant v$ but $u \neq v$. For a constant $r \gg 0$, we define $[0, r] := \{u \in \mathbb{R}^2\colon\ 0 \leqslant u \leqslant r\}$ and $[0, r]_{\mathcal{C}} := \{u \in \mathcal{C}\colon\ 0 \leqslant u(x) \leqslant r$, $\forall x \in \mathbb{R}\}$. It is easy to see that $\mathcal{C}_+ = \{u \in \mathcal{C}\colon\ u(x) \geqslant 0,\ \forall x \in \mathbb{R}\}$ is a positive cone of $\mathcal{C}$.

We equip $\mathcal{C}$ with the compact open topology. Moreover, we define a norm $|\cdot|_{\mathcal{C}}$ by

$$|u|_{\mathcal{C}} = \sum_{k=1}^{\infty} \frac{1}{2^k} \max_{|x|\leqslant k} \bigl|u(x)\bigr|, \quad \forall u \in \mathcal{C},$$

where $|\cdot|$ denotes the usual norm in $\mathbb{R}^2$. It follows that $(\mathcal{C}, |\cdot|_{\mathcal{C}})$ is a normed space.

Let $d_c(\cdot,\cdot)$ be the distance induced by the norm $|\cdot|_{\mathcal{C}}$. Then the topology in the metric space $(\mathcal{C}, d_c)$ is the same as the compact open topology in $\mathcal{C}$. Besides, $([0,r]_{\mathcal{C}}, d_c)$ is a complete metric space.

For any given $\phi = (\phi_1, \phi_2) \in \mathcal{C}$, we consider the following initial value problem:

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} = D_1(x)\frac{\partial^2 u_1}{\partial x^2} + D_0(x)\frac{\partial u_1}{\partial x} + f(x, u_1, u_2),\\
&\frac{\partial u_2}{\partial t} = g(x, u_1, u_2), \quad t > 0,\ x \in \mathbb{R},\\
&u_i(0,x) = \phi_i(x), \quad i = 1, 2,\ x \in \mathbb{R}.
\end{aligned} \tag{2.1}$$

Let $G(t,x,y)$ be the Green function associated with the linear equation

$$\frac{\partial u_1}{\partial t} = D_1(x)\frac{\partial^2 u_1}{\partial x^2} + D_0(x)\frac{\partial u_1}{\partial x}, \quad t > 0,\ x \in \mathbb{R}. \tag{2.2}$$

Then Eq. (2.2) generates a linear semigroup $\ell_1(t)$ on $BC(\mathbb{R},\mathbb{R})$, which is defined by

$$\bigl[\ell_1(t)\phi_1\bigr](x) = \int_{\mathbb{R}} G(t,x,y)\phi_1(y)\,\mathrm{d}y, \quad \forall \phi_1 \in BC(\mathbb{R},\mathbb{R}),\ t > 0,\ x \in \mathbb{R}. \tag{2.3}$$

It follows that Eq. (2.1) can be written as the following integral form:

$$\begin{aligned}
&u_1(t,\cdot;\phi) = \ell_1(t)\phi_1 + \int_0^t \ell_1(t-s) f\bigl(\cdot, u_1(s,\cdot;\phi), u_2(s,\cdot;\phi)\bigr)\,\mathrm{d}s,\\
&u_2(t,\cdot;\phi) = \phi_2 + \int_0^t g\bigl(\cdot, u_1(s,\cdot;\phi), u_2(s,\cdot;\phi)\bigr)\,\mathrm{d}s,
\end{aligned}$$

or equivalently,

$$u(t,\cdot;\phi) = \ell(t)\phi + \int_0^t \ell(t-s) F\bigl(\cdot, u_1(s,\cdot;\phi), u_2(s,\cdot;\phi)\bigr)\,\mathrm{d}s,$$

where I is an identity operator and

$$\bigl[F(\phi)\bigr](x) = F\bigl(x,\phi(x)\bigr) = \begin{pmatrix} f(x,\phi_1(x),\phi_2(x)) \\ g(x,\phi_1(x),\phi_2(x)) \end{pmatrix}, \qquad \ell(t) = \begin{pmatrix} \ell_1(t) & 0 \\ 0 & I \end{pmatrix}.$$

2.1. The well-posedness of solutions

We consider the existence, uniqueness, invariance of solutions of (2.1) in $[0, M]_{\mathcal{C}}$.

Theorem 2.1. *For any initial data $\phi \in [0, M]_{\mathcal{C}}$, system (2.1) admits a unique mild solution $u(t, \cdot; \phi)$ defined on $[0, \infty)$ with $u(0, \cdot; \phi) = \phi$, and $u(t, \cdot; \phi) \in [0, M]_{\mathcal{C}}$ for all $t \geqslant 0$.*

Proof. By the mean value theorem, there exist constants $\alpha_i, \beta_i > 0$, $i = 1, 2$ such that

$$\begin{aligned} f(x, u_1, u_2) - f(x, v_1, v_2) &\geqslant -\alpha_1(u_1 - v_1) + \beta_2(u_2 - v_2), \\ g(x, u_1, u_2) - g(x, v_1, v_2) &\geqslant \beta_1(u_1 - v_1) - \alpha_2(u_2 - v_2), \end{aligned} \tag{2.4}$$

for all $u, v \in [0, M]$ with $u \geqslant v$. According to (2.4), for any $\phi \in [0, M]_{\mathcal{C}}$ and any small $h > 0$, we have

$$\phi(x) + h\big[F(\phi)\big](x) = \begin{pmatrix} \phi_1(x) + hf(x, \phi_1(x), \phi_2(x)) \\ \phi_2(x) + hg(x, \phi_1(x), \phi_2(x)) \end{pmatrix} \geqslant \begin{pmatrix} (1 - h\alpha_1)\phi_1(x) \\ (1 - h\alpha_2)\phi_2(x) \end{pmatrix} \geqslant 0,$$

and

$$\begin{aligned} \phi(x) + h\big[F(\phi)\big](x) &= \begin{pmatrix} \phi_1 - M_1 + M_1 + h[f(x, \phi_1, \phi_2) - f(x, M_1, \phi_2) + f(x, M_1, \phi_2)] \\ \phi_2 - M_2 + M_2 + h[g(x, \phi_1, \phi_2) - g(x, \phi_1, M_2) + g(x, \phi_1, M_2)] \end{pmatrix} \\ &\leqslant \begin{pmatrix} (1 - h\alpha_1)(\phi_1 - M_1) + M_1 + hf(x, M_1, \phi_2) \\ (1 - h\alpha_2)(\phi_2 - M_2) + M_2 + hg(x, \phi_1, M_2) \end{pmatrix} \leqslant M. \end{aligned}$$

Therefore, $\phi + hF(\phi) \in [0, M]_{\mathcal{C}}$, which in turn implies that

$$\lim_{h \to 0^+} \frac{1}{h} \operatorname{dist}\big(\phi + hF(\phi); [0, M]_{\mathcal{C}}\big) = 0, \quad \forall \phi \in [0, M]_{\mathcal{C}}.$$

By [22, Corollary 4] with $K = [0, M]_{\mathcal{C}}$, $S(t, s) = \ell(t - s)$, $B(t, \phi) = F(\phi)$, it follows that system (2.1) admits a unique mild solution $u(t, \cdot; \phi)$ on $[0, \infty)$ with $u(0, \cdot; \phi) = \phi$, and $u(t, \cdot; \phi) \in [0, M]_{\mathcal{C}}$ for all $t \geqslant 0$. □

To establish the comparison principle for system (2.1), we recall the concept of upper and lower solutions.

Definition 2.1. A function $v(t, \cdot)$ is called an upper solution (a lower solution) of (2.1) on $[0, b)$ with $b > 0$ if

$$v(t, \cdot) \geqslant (\leqslant)\, \ell(t)\phi + \int_0^t \ell(t - s) F\big(\cdot, v_1(s, \cdot), v_2(s, \cdot)\big)\, ds, \quad \forall t \in [0, b).$$

Lemma 2.1. *Let $w(t, \cdot), v(t, \cdot) \in [0, M]_{\mathcal{C}}$ be a pair of upper and lower solutions of (2.1) on $[0, \infty)$, respectively. If $w(0, \cdot) \geqslant v(0, \cdot)$, then $w(t, \cdot) \geqslant v(t, \cdot)$ for all $t \geqslant 0$. Furthermore, if $w(0, \cdot) > v(0, \cdot)$, then $w(t, \cdot) \gg v(t, \cdot)$ for all $t > 0$.*

Proof. We first show that $F(\phi)$ is quasi-monotone on $[0, M]_{\mathcal{C}}$ in the sense that

$$\lim_{h \to 0^+} \frac{1}{h} \operatorname{dist}\big(\phi - \psi + h\big[F(\phi) - F(\psi)\big]; \mathcal{C}_+\big) = 0, \tag{2.5}$$

for all $\phi, \psi \in [0, M]_{\mathcal{C}}$ with $\phi \geqslant \psi$. In fact, by (2.4), for any small $h > 0$, we have

$$\phi - \psi + h\big[F(\phi) - F(\psi)\big] \geqslant \begin{pmatrix} (1 - h\alpha_1)(\phi_1 - \psi_1) \\ (1 - h\alpha_2)(\phi_2 - \psi_2) \end{pmatrix} \geqslant 0,$$

which indicates that (2.5) is valid. Since $v_0 := v(0, x) \leqslant w(0, x) =: w_0$ for all $x \in \mathbb{R}$, we see from [22, Corollary 5] that

$$0 \leqslant v(t, \cdot) \leqslant u(t, \cdot; v_0) \leqslant u(t, \cdot; w_0) \leqslant w(t, \cdot) \leqslant M, \quad \forall t \geqslant 0.$$

Let $m(t, x) = w(t, x) - v(t, x)$. Substituting m in (2.1) and using (2.4), we get

$$\frac{\partial m_1}{\partial t} \geqslant D_1(x)\frac{\partial^2 m_1}{\partial x^2} + D_0(x)\frac{\partial m_1}{\partial x} - \alpha_1 m_1 + \beta_2 m_2, \qquad \frac{\partial m_2}{\partial t} \geqslant \beta_1 m_1 - \alpha_2 m_2.$$

If $m_1(0, x) \not\equiv 0$ on $\mathbb{R}$, by integrating, we obtain

$$m_1(t, x) \geqslant \int_{\mathbb{R}} e^{-\alpha_1 t} G(t, x, y) m_1(0, y)\, dy > 0, \quad \forall t > 0,$$

which in turn yields that

$$m_2(t, x) \geqslant e^{-\alpha_2 t} m_2(0, x) + \int_0^t e^{-\alpha_2(t-s)} \beta_1 m_1(s, x)\, ds > 0, \quad \forall t > 0, \tag{2.6}$$

where $G(t, x, y)$ is a fundamental solution of (2.3). On the other side, if $m_2(0, x) \not\equiv 0$, then we see from (2.6) that $m_2(t, x) \not\equiv 0$, $\forall t \geqslant 0$, $x \in \mathbb{R}$. Thus, we also have

$$m_1(t, x) \geqslant \int_0^t \int_{\mathbb{R}} e^{-\alpha_1(t-s)} G(t - s, x, y) \beta_2 m_2(s, y)\, dy\, ds > 0.$$

Again, by using (2.6), we know that $m_2(t, x) > 0$, $\forall t > 0$, $x \in \mathbb{R}$. $\square$

Lemma 2.2. *Let $\tilde{u}$, $\tilde{g}$, $\tilde{h}$ be nonnegative and continuous functions defined on $[0, \infty)$. If*

$$\tilde{u}(t) \leqslant \tilde{g}(t) + \tilde{h}(t)\left[\int_0^t \tilde{u}(s)\, ds + \int_0^t \tilde{h}(s)\left(\int_0^s \tilde{u}(\sigma)\, d\sigma\right) ds\right], \quad \forall t \in [0, \infty),$$

then we have

$$\tilde{u}(t) \leqslant \tilde{g}(t) + \tilde{h}(t)\left[\int_0^t \left(\tilde{g}(s) + \tilde{h}(s) \int_0^s 2\tilde{g}(\sigma) e^{\int_\sigma^s 2\tilde{h}(\eta)\, d\eta}\, d\sigma\right) ds\right], \quad \forall t \in [0, \infty). \tag{2.7}$$

Proof. Let $\tilde{v}(t)=\int_0^t \tilde{u}(s)\,\mathrm{d}s+\int_0^t \tilde{h}(s)(\int_0^s \tilde{u}(\sigma)\,\mathrm{d}\sigma)\,\mathrm{d}s$. Then $\tilde{u}(t)\leqslant \tilde{g}(t)+\tilde{h}(t)\tilde{v}(t)$ and

$$\begin{aligned}\tilde{v}'(t)&=\tilde{u}(t)+\tilde{h}(t)\int_0^t \tilde{u}(\sigma)\,\mathrm{d}\sigma\\&\leqslant \tilde{g}(t)+\tilde{h}(t)\left[\tilde{v}(t)+\int_0^t\big(\tilde{g}(\sigma)+\tilde{h}(\sigma)\tilde{v}(\sigma)\big)\,\mathrm{d}\sigma\right].\end{aligned}\tag{2.8}$$

Set $\tilde{w}(t)=\tilde{v}(t)+\int_0^t[\tilde{g}(\sigma)+\tilde{h}(\sigma)\tilde{v}(\sigma)]\,\mathrm{d}\sigma$. It then follows from (2.8) that

$$\tilde{w}(t)\geqslant \tilde{v}(t)\quad\text{and}\quad \tilde{v}'(t)\leqslant \tilde{g}(t)+\tilde{h}(t)\tilde{w}(t).\tag{2.9}$$

On the other hand, by (2.9), we get

$$\tilde{w}'(t)=\tilde{v}'(t)+\tilde{g}(t)+\tilde{h}(t)\tilde{v}(t)\leqslant 2\tilde{g}(t)+2\tilde{h}(t)\tilde{w}(t).$$

Since $\tilde{w}(0)=\tilde{v}(0)=0$, it holds $\tilde{w}(t)\leqslant \int_0^t 2\tilde{g}(\sigma)\mathrm{e}^{\int_\sigma^t 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma$. Substituting this inequality in (2.9) and integrating it from 0 to t leads to

$$\tilde{v}(t)\leqslant \int_0^t\left[\tilde{g}(s)+\tilde{h}(s)\int_0^s 2\tilde{g}(\sigma)\mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma\right]\mathrm{d}s.$$

Hence, $\tilde{u}(t)\leqslant \tilde{g}(t)+\tilde{h}(t)\int_0^t[\tilde{g}(s)+\tilde{h}(s)\int_0^s 2\tilde{g}(\sigma)\mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma]\,\mathrm{d}s$. □

Let $Q(t)\phi=u(t,\cdot;\phi)=(u_1(t,\cdot;\phi),u_2(t,\cdot;\phi))$, $t\geqslant 0$, be the solution maps generated by (2.1). Then $Q(t):[0,M]_{\mathcal{C}}\to[0,M]_{\mathcal{C}}$ satisfies that $Q(0)=I$ and $Q(t)\circ Q(s)=Q(t+s)$ for all $t,s\geqslant 0$. The subsequent result shows that $\{Q(t)\}_{t\geqslant 0}$ is a continuous-time semiflow on $[0,M]_{\mathcal{C}}$.

Lemma 2.3. *$Q(t)\phi$ is continuous in $(t,\phi)\in[0,\infty)\times[0,M]_{\mathcal{C}}$ with respect to the compact open topology.*

Proof. By Theorem 2.1, for any given $\phi\in[0,M]_{\mathcal{C}}$, $Q(t)\phi$ is continuous in $t\in[0,\infty)$ with respect to the compact open topology. We first prove the following two claims.

Claim 1. *For any $\epsilon>0$ and $t_0>0$, there exist $\delta(\epsilon,t_0),\kappa(\epsilon,t_0)>0$ such that for any $z\in\mathbb{R}$, if $u^o,w^o\in[0,M]_{\mathcal{C}}$ with $|u^o(x)-w^o(x)|<\delta$, $\forall x\in[z-\kappa,z+\kappa]$, then $|u(t,z;u^o)-u(t,z;w^o)|<\epsilon$, $\forall t\in[0,t_0]$.*

By the spatial translation invariance of system (2.1), it suffices to prove the claim for the case of $z=0$. First consider the case where $u^o\geqslant w^o$. Let $v(t,x)=u(t,x;u^o)-u(t,x;w^o)$. Then Lemma 2.1 implies that $v(t,x)\geqslant 0$. Note that

$$\begin{aligned}&F\big(x,u\big(t,x;u^o\big)\big)-F\big(x,u\big(t,x;w^o\big)\big)\\&\quad=\int_0^1 D_uF\big(x,u\big(t,x;w^o\big)+s\big[u\big(t,x;u^o\big)-u\big(t,x;w^o\big)\big]\big)\,\mathrm{d}s\cdot v(t,x).\end{aligned}\tag{2.10}$$

Then $v(t,x)=(v_1(t,x),v_2(t,x))$ satisfies

$$\begin{aligned}
\frac{\partial v_1}{\partial t} &= D_1(x)\frac{\partial^2 v_1}{\partial x^2} + D_0(x)\frac{\partial v_1}{\partial x} + a_1(t,x)v_1 + a_2(t,x)v_2, \\
\frac{\partial v_2}{\partial t} &= b_1(t,x)v_1 + b_2(t,x)v_2,
\end{aligned}$$

where

$$\begin{aligned}
a_i(t,x) &= \int_0^1 f_{u_i}\big(x, u\big(t,x;w^o\big) + s\big[u\big(t,x;u^o\big) - u\big(t,x;w^o\big)\big]\big)\,\mathrm{d}s, \\
b_i(t,x) &= \int_0^1 g_{u_i}\big(x, u\big(t,x;w^o\big) + s\big[u\big(t,x;u^o\big) - u\big(t,x;w^o\big)\big]\big)\,\mathrm{d}s, \quad i = 1,2.
\end{aligned}$$

Integrating the above system, one has

$$\begin{aligned}
v_1(t,\cdot) &= \ell_1(t)v_1(0,\cdot) + \int_0^t \ell_1(t-s)\big[a_1(s,\cdot)v_1(s,\cdot) + a_2(s,\cdot)v_2(s,\cdot)\big]\,\mathrm{d}s, \\
v_2(t,\cdot) &= v_2(0,\cdot)\mathrm{e}^{\int_0^t b_2(\eta,\cdot)\,\mathrm{d}\eta} + \int_0^t b_1(\sigma,\cdot)v_1(\sigma,\cdot)\mathrm{e}^{\int_\sigma^t b_2(\eta,\cdot)\,\mathrm{d}\eta}\,\mathrm{d}\sigma,
\end{aligned} \tag{2.11}$$

where $\ell_1(t)$ is defined in (2.3). After a substitution, we arrive at

$$\begin{aligned}
v_1(t,\cdot) = {} & \ell_1(t)v_1(0,\cdot) + \int_0^t \ell_1(t-s)a_1(s,\cdot)v_1(s,\cdot)\,\mathrm{d}s + \int_0^t \ell_1(t-s)a_2(s,\cdot) \\
& \times \left[v_2(0,\cdot)\mathrm{e}^{\int_0^s b_2(\eta,\cdot)\,\mathrm{d}\eta} + \int_0^s b_1(\sigma,\cdot)v_1(\sigma,\cdot)\mathrm{e}^{\int_\sigma^s b_2(\eta,\cdot)\,\mathrm{d}\eta}\,\mathrm{d}\sigma\right]\mathrm{d}s.
\end{aligned} \tag{2.12}$$

Let $\Omega := [0,\infty) \times \mathbb{R}$ and define $\bar{\gamma} = \max\{\sup_{(t,x)\in\Omega}|a_i(t,x)|, \sup_{(t,x)\in\Omega}|b_i(t,x)|,\ i = 1,2\}$. In view of (2.12) and the fact that $\|\ell_1(t)\| \leqslant 1$, $\forall t \geqslant 0$, we obtain

$$\begin{aligned}
v_1(t,\cdot) \leqslant {} & \big\|\ell_1(t)\big\|v_1(0,\cdot) + \bar{\gamma}\int_0^t \big\|\ell_1(t-s)\big\|v_1(s,\cdot)\,\mathrm{d}s \\
& + \bar{\gamma}\int_0^t \big\|\ell_1(t-s)\big\|\left[v_2(0,\cdot)\mathrm{e}^{\bar{\gamma}s} + \bar{\gamma}\int_0^s v_1(\sigma,\cdot)\mathrm{e}^{\bar{\gamma}(s-\sigma)}\,\mathrm{d}\sigma\right]\mathrm{d}s \\
\leqslant {} & v_1(0,\cdot) + \bar{\gamma}\int_0^t v_1(s,\cdot)\,\mathrm{d}s + \bar{\gamma}\int_0^t v_2(0,\cdot)\mathrm{e}^{\bar{\gamma}s}\,\mathrm{d}s + \bar{\gamma}^2\int_0^t\int_0^s v_1(\sigma,\cdot)\mathrm{e}^{\bar{\gamma}s}\,\mathrm{d}\sigma\,\mathrm{d}s \\
\leqslant {} & v_1(0,\cdot) + v_2(0,\cdot)\big(\mathrm{e}^{\bar{\gamma}t} - 1\big) + \bar{\gamma}\mathrm{e}^{\bar{\gamma}t}\left[\int_0^t v_1(s,\cdot)\,\mathrm{d}s + \int_0^t \bar{\gamma}\mathrm{e}^{\bar{\gamma}s}\int_0^s v_1(\sigma,\cdot)\,\mathrm{d}\sigma\,\mathrm{d}s\right], \quad \forall t \geqslant 0.
\end{aligned}$$

Let $\tilde{u}(t) = v_1(t,0)$, $\tilde{g}(t) = v_1(0,0) + v_2(0,0)(\mathrm{e}^{\bar{\gamma}t} - 1)$, $\tilde{h}(t) = \bar{\gamma}\mathrm{e}^{\bar{\gamma}t}$ and $t_0 > 0$ be given. Using (2.7) in Lemma 2.2, we have

$$\begin{aligned} v_1(t,0) &\leqslant \tilde{g}(t) + \tilde{h}(t)\left[\int_0^t \left(\tilde{g}(s) + \tilde{h}(s)\int_0^s 2\tilde{g}(\sigma)\mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma\right)\mathrm{d}s\right] \\ &\leqslant \tilde{g}(t) + \tilde{g}(t)\tilde{h}(t)\int_0^t \left(1 + 2\tilde{h}(s)\int_0^s \mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma\right)\mathrm{d}s \\ &= \tilde{g}(t)\left[1 + \tilde{h}(t)\int_0^t \left(1 + 2\tilde{h}(s)\int_0^s \mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma\right)\mathrm{d}s\right] \\ &\leqslant \tilde{g}(t_0)(1+\gamma_0), \quad \forall t \in [0,t_0], \end{aligned} \tag{2.13}$$

where $\gamma_0 = \tilde{h}(t_0)\int_0^{t_0}[1 + 2\tilde{h}(s)\int_0^s \mathrm{e}^{\int_\sigma^s 2\tilde{h}(\eta)\,\mathrm{d}\eta}\,\mathrm{d}\sigma]\,\mathrm{d}s$. By (2.11) and (2.13), we also have

$$\begin{aligned} v_2(t,0) &\leqslant v_2(0,0)\mathrm{e}^{\bar{\gamma}t_0} + \bar{\gamma}\int_0^t v_1(\sigma,0)\mathrm{e}^{\bar{\gamma}(t-\sigma)}\,\mathrm{d}\sigma \\ &\leqslant \mathrm{e}^{\bar{\gamma}t_0}\left[v_2(0,0) + \tilde{g}(t_0)(1+\gamma_0)\right], \quad \forall t \in [0,t_0]. \end{aligned} \tag{2.14}$$

So, for any $\epsilon > 0$, there exist $\delta(\epsilon, t_0) = \frac{\epsilon}{\mathrm{e}^{\bar{\gamma}t_0}[1+\mathrm{e}^{\bar{\gamma}t_0}(1+\gamma_0)]}$ and $\kappa(\epsilon, t_0)$ such that if $v(0,x) < \boldsymbol{\delta} := (\delta,\delta)$, $\forall x \in [-\kappa,\kappa]$, then employing (2.13) and (2.14), we obtain

$$u(t,0;u^o) - u(t,0;w^o) = v(t,0) < \boldsymbol{\delta}\mathrm{e}^{\bar{\gamma}t_0}\left[1 + \mathrm{e}^{\bar{\gamma}t_0}(1+\gamma_0)\right] = \boldsymbol{\epsilon}, \quad \forall t \in [0,t_0].$$

Now consider the case where $u^o \not\geqslant w^o$. Set

$$\bar{u}^o(x) = \max\{u^o(x), w^o(x)\}, \qquad \underline{u}^o(x) = \min\{u^o(x), w^o(x)\}, \quad \forall x \in \mathbb{R}.$$

Then $u(t,x;\underline{u}^o) \leqslant u(t,x;u^o)$, $u(t,x;w^o) \leqslant u(t,x;\bar{u}^o)$, $\forall t \geqslant 0$, $x \in \mathbb{R}$. It turns out that

$$\left|u(t,x;u^o) - u(t,x;w^o)\right| \leqslant u(t,x;\bar{u}^o) - u(t,x;\underline{u}^o), \quad \forall t \geqslant 0,\ x \in \mathbb{R}.$$

Repeating the above steps, we conclude that Claim 1 holds for this case.

Claim 2. *For any $t_0 > 0$, $Q(t)\phi$ is continuous in ϕ uniformly for $t \in [0,t_0]$.*

Fix $\psi \in [0,M]_{\mathcal{C}}$ and $t_0 > 0$. For any $\epsilon > 0$, according to Claim 1, there are δ, κ such that

$$\left|u(t,z;\phi) - u(t,z;\psi)\right| < \epsilon/2, \quad \forall t \in [0,t_0], \tag{2.15}$$

provided that $|\phi(x) - \psi(x)| < \delta$, $\forall z \in \mathbb{R}$, $x \in [z-\kappa, z+\kappa]$. Choose $k_1 > 0$ so large that $\sum_{k=k_1}^{\infty} 2^{-k}|M| < \epsilon/2$ and let $\delta_1 = 2^{-(k_1+\kappa)}\delta$. For any $\phi \in [0,M]_{\mathcal{C}}$ with $d_c(\phi,\psi) < \delta_1$, we have $\max_{|x|\leqslant k_1+\kappa}|\phi(x) - \psi(x)| < 2^{(k_1+\kappa)}\delta_1 = \delta$. It follows from (2.15) that

$$\left|u(t,z;\phi) - u(t,z;\psi)\right| < \epsilon/2, \quad \forall t \in [0,t_0],\ z \in [-k_1,k_1].$$

Consequently, if $d_c(\phi,\psi)<\delta_1$, then

$$d_c\big(Q(t)\phi, Q(t)\psi\big)=\sum_{k=1}^{k_1}\frac{1}{2^k}\max_{|x|\leqslant k}\big|u(t,x;\phi)-u(t,x;\psi)\big|+\sum_{k=k_1+1}^{\infty}\frac{1}{2^k}\max_{|x|\leqslant k}\big|u(t,x;\phi)-u(t,x;\psi)\big|$$
$$\leqslant\frac{\epsilon}{2}\sum_{k=1}^{\infty}\frac{1}{2^k}+\sum_{k=k_1}^{\infty}\frac{1}{2^k}|M|<\epsilon,$$

which shows that Claim 2 holds true.

For any $t,t_1\geqslant 0$ and $\phi,\varphi\in[0,M]_{\mathcal{C}}$, we have

$$\big|Q_t(\phi)-Q_{t_1}(\varphi)\big|_{\mathcal{C}}\leqslant\big|Q_t(\phi)-Q_t(\varphi)\big|_{\mathcal{C}}+\big|Q_t(\varphi)-Q_{t_1}(\varphi)\big|_{\mathcal{C}}.$$

This, together with the continuity of $Q_t(\varphi)$ in t and Claim 2, implies that $Q_t(\phi)$ is continuous at (t_1,φ). □

2.2. A principal eigenvalue problem

Linearizing (2.1) at the zero solution, we obtain

$$\begin{aligned}\frac{\partial\bar u_1}{\partial t}&=D_1(x)\frac{\partial^2\bar u_1}{\partial x^2}+D_0(x)\frac{\partial\bar u_1}{\partial x}+f_{u_1}(x,0)\bar u_1+f_{u_2}(x,0)\bar u_2,\\ \frac{\partial\bar u_2}{\partial t}&=g_{u_1}(x,0)\bar u_1+g_{u_2}(x,0)\bar u_2,\quad t>0,\ x\in\mathbb{R}.\end{aligned}\tag{2.16}$$

Since two off-diagonal entries of the matrix

$$D_uF(x,0)=\begin{pmatrix}f_{u_1}(x,0) & f_{u_2}(x,0)\\ g_{u_1}(x,0) & g_{u_2}(x,0)\end{pmatrix}$$

are positive for all $x\in\mathbb{R}$, we can fix an $\alpha>0$ such that the matrix $D_uF(x,0)+\alpha I$ is strictly positive. Let $\underline{b}=\min\{\min_{x\in\mathbb{R}}\{D_uF(x,0)+\alpha I\}_{ij}\colon\ 1\leqslant i,j\leqslant 2\}$. Note that

$$F(x,u)=F(x,0)+D_uF(x,0)\cdot u+o\big(|u|\big).$$

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

$$F(x,u)\geqslant F(x,0)+D_uF(x,0)\cdot u-\underline{b}\boldsymbol{\varepsilon}|u|,\quad\forall u\in[0,\boldsymbol{\delta}],$$

where $\boldsymbol{\delta}=(\delta,\delta)$ and $\boldsymbol{\varepsilon}=(\varepsilon,\varepsilon)$. Since $|u|\leqslant u_1+u_2\leqslant\frac{1}{\underline{b}}\{(D_uF(x,0)+\alpha I)u\}_i$, $i=1,2$, we obtain

$$F(x,u)\geqslant F(x,0)+D_uF(x,0)\cdot u-\varepsilon\big(D_uF(x,0)+\alpha I\big)u,\quad\forall u\in[0,\boldsymbol{\delta}],$$

which is equivalent to

$$\begin{aligned}f(x,u_1,u_2)&\geqslant\big(f_1^{\varepsilon}(x,0)-\varepsilon\alpha\big)u_1+f_2^{\varepsilon}(x,0)u_2,\quad\forall u\in[0,\boldsymbol{\delta}],\\ g(x,u_1,u_2)&\geqslant g_1^{\varepsilon}(x,0)u_1+\big(g_2^{\varepsilon}(x,0)-\varepsilon\alpha\big)u_2,\quad\forall u\in[0,\boldsymbol{\delta}],\end{aligned}\tag{2.17}$$

with $f_i^{\varepsilon}(x,0):=(1-\varepsilon)f_{u_i}(x,0)$, $g_i^{\varepsilon}(x,0):=(1-\varepsilon)g_{u_i}(x,0)$, $i=1,2$.

Now we consider the linear system

$$\frac{\partial \underline{u}_1}{\partial t} = D_1(x)\frac{\partial^2 \underline{u}_1}{\partial x^2} + D_0(x)\frac{\partial \underline{u}_1}{\partial x} + \big(f_1^\varepsilon(x,0) - \varepsilon\alpha\big)\underline{u}_1 + f_2^\varepsilon(x,0)\underline{u}_2,$$
$$\frac{\partial \underline{u}_2}{\partial t} = g_1^\varepsilon(x,0)\underline{u}_1 + \big(g_2^\varepsilon(x,0) - \varepsilon\alpha\big)\underline{u}_2. \tag{2.18}$$

For any given $\mu \in \mathbb{R}$, letting $\underline{u}(t,x) = \mathrm{e}^{-\mu x}\upsilon(t,x)$ in (2.18), we see that $\upsilon(t,x) = (\upsilon_1(t,x), \upsilon_2(t,x))$ satisfies

$$\frac{\partial \upsilon_1}{\partial t} = D_1(x)\frac{\partial^2 \upsilon_1}{\partial x^2} + \big[D_0(x) - 2\mu D_1(x)\big]\frac{\partial \upsilon_1}{\partial x} + \big[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x)\big]\upsilon_1 + a_{12}^\varepsilon(x)\upsilon_2,$$
$$\frac{\partial \upsilon_2}{\partial t} = a_{21}^\varepsilon(x)\upsilon_1 + a_{22}^\varepsilon(x)\upsilon_2, \tag{2.19}$$

where $a_{11}^\varepsilon(x) = f_1^\varepsilon(x,0) - \varepsilon\alpha$, $a_{12}^\varepsilon(x) = f_2^\varepsilon(x,0)$, $a_{21}^\varepsilon(x) = g_1^\varepsilon(x,0)$, $a_{22}^\varepsilon(x) = g_2^\varepsilon(x,0) - \varepsilon\alpha$. Letting $\upsilon(t,x) = \mathrm{e}^{\lambda t}\xi(x)$, we then have the following periodic eigenvalue problem:

$$D_1(x)\xi_1''(x) + \big[D_0(x) - 2\mu D_1(x)\big]\xi_1'(x) + \big[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x)\big]\xi_1(x)$$
$$+ a_{12}^\varepsilon(x)\xi_2(x) = \lambda\xi_1(x), \quad x \in \mathbb{R},$$
$$a_{21}^\varepsilon(x)\xi_1(x) + a_{22}^\varepsilon(x)\xi_2(x) = \lambda\xi_2(x), \quad x \in \mathbb{R},$$
$$\xi_i(x+L) = \xi_i(x), \quad \forall x \in \mathbb{R},\ i = 1,2. \tag{2.20}$$

In what follows, we will add some parameters in the bracket of a value or function in order to emphasize its dependence on these parameters. For example, we write the eigenvalue λ of (2.20) as $\lambda(\mu,\varepsilon)$.

Let $\bar{a}_{22}(\varepsilon) = \max_{x\in\mathbb{R}} a_{22}^\varepsilon(x)$. Then there is $x_0 \in \mathbb{R}$ such that $\bar{a}_{22}(\varepsilon) = a_{22}^\varepsilon(x_0)$.

Theorem 2.2. *Assume that $a_{22}^\varepsilon(x) = \bar{a}_{22}(\varepsilon)$, $\forall x \in U_{\delta_0}(x_0)$, for some $\delta_0 > 0$, where $U_{\delta_0}(x_0) := (x_0 - \delta_0, x_0 + \delta_0)$. Then for any $\mu \in \mathbb{R}$, (2.20) has a geometrically simple eigenvalue $\lambda(\mu,\varepsilon)$ with a strongly positive and L-periodic eigenfunction $\zeta(x,\mu;\varepsilon)$.*

Proof. Without loss of generality, assume that $x_0 \in (0,L)$. We can further restrict δ_0 so small that $\bar{U}_{\delta_0}(x_0) := [x_0 - \delta_0, x_0 + \delta_0] \subset (0,L)$. Then $A := \min_{x\in\bar{U}_{\delta_0}(x_0)} a_{12}^\varepsilon(x)a_{21}^\varepsilon(x) > 0$. Let $\mu \in \mathbb{R}$ be given. According to [29, Section 2], we define a linear operator $\mathscr{L}_\lambda$ by

$$(\mathscr{L}_\lambda\xi_1)(x) = D_1(x)\xi_1''(x) + \big[D_0(x) - 2\mu D_1(x)\big]\xi_1'(x)$$
$$+ \left[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x) + \frac{a_{12}^\varepsilon(x)a_{21}^\varepsilon(x)}{\lambda - a_{22}^\varepsilon(x)}\right]\xi_1(x), \quad \forall\lambda > \bar{a}_{22}(\varepsilon).$$

Let λ_1 be the principal eigenvalue of the elliptic eigenvalue problem with the Dirichlet boundary condition:

$$D_1(x)\xi_1''(x) + \big[D_0(x) - 2\mu D_1(x)\big]\xi_1'(x)$$
$$+ \big[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x)\big]\xi_1(x) = \lambda\xi_1(x), \quad x \in U_{\delta_0}(x_0),$$
$$\xi_1(x_0 - \delta_0) = \xi_1(x_0 + \delta_0) = 0$$

with a positive eigenfunction $\zeta_1^\diamond(x,\mu;\varepsilon)$ on $U_{\delta_0}(x_0)$. Set

$$\lambda' := \frac{\lambda_1 + \bar{a}_{22}(\varepsilon) + \sqrt{[\lambda_1 - \bar{a}_{22}(\varepsilon)]^2 + 4A}}{2}.$$

Since $A > 0$, we have $\lambda' > \frac{\lambda_1 + \bar{a}_{22}(\varepsilon) + |\lambda_1 - \bar{a}_{22}(\varepsilon)|}{2}$. If $\lambda_1 > \bar{a}_{22}(\varepsilon)$, then

$$\lambda' > \frac{\lambda_1 + \bar{a}_{22}(\varepsilon) + \lambda_1 - \bar{a}_{22}(\varepsilon)}{2} = \lambda_1 > \bar{a}_{22}(\varepsilon);$$

while if $\lambda_1 \leqslant \bar{a}_{22}(\varepsilon)$, then

$$\lambda' > \frac{\lambda_1 + \bar{a}_{22}(\varepsilon) + \bar{a}_{22}(\varepsilon) - \lambda_1}{2} = \bar{a}_{22}(\varepsilon).$$

Hence, we have $\lambda' > \bar{a}_{22}(\varepsilon)$. It follows that

$$\left(\mathscr{L}_{\lambda'}\zeta_1^\diamond\right)(x) \geqslant \lambda_1\zeta_1^\diamond(x) + \frac{A}{\lambda' - \bar{a}_{22}(\varepsilon)}\zeta_1^\diamond(x) = \left(\lambda_1 + \frac{A}{\lambda' - \bar{a}_{22}(\varepsilon)}\right)\zeta_1^\diamond(x) = \lambda'\zeta_1^\diamond(x),$$

for all $x \in U_{\delta_0}(x_0)$. Define a continuous function $\xi_1^o(x)$ on $[0,L]$ by

$$\xi_1^o(x) = \begin{cases} \zeta_1^\diamond(x), & \text{if } x \in \bar{U}_{\delta_0}(x_0), \\ 0, & \text{if } x \in [0,L]\backslash\bar{U}_{\delta_0}(x_0). \end{cases}$$

Clearly, $\xi_1^o(0) = \xi_1^o(L)$, and $\xi_1^o(x)$ can be extended to a continuous and L-periodic function on $\mathbb{R}$. It is easy to see that $(\mathscr{L}_{\lambda'}\xi_1^o)(x) \geqslant \lambda'\xi_1^o(x)$, $\forall x \in [0,L]\backslash\{x_0 \pm \delta_0\}$. It then follows that $e^{\lambda' t}\xi_1^o(x)$ is a lower solution of the integral form of $u_t = \mathscr{L}_{\lambda'}u$ subject to the L-periodic boundary condition. By [29, Theorem 2.3 and Remark 2.3], (2.20) has a geometrically simply eigenvalue $\lambda(\mu,\varepsilon)$ with a nonnegative eigenfunction $\zeta(x,\mu;\varepsilon)$. Using the parabolic system associated with (2.20) and the condition that $a_{12}^\varepsilon(x) > 0$ and $a_{21}^\varepsilon(x) > 0$, it easily follows that $\zeta(x,\mu;\varepsilon)$ is strongly positive on $\mathbb{R}$. $\square$

Theorem 2.3. *Let λ^* be the principal eigenvalue of the eigenvalue problem with the Dirichlet boundary condition:*

$$\begin{aligned} &D_1(x)\xi_1''(x) + D_0(x)\xi_1'(x) + a_{11}^\varepsilon(x)\xi_1(x) = \lambda\xi_1(x), \quad x \in (0,L), \\ &\xi_1(0) = \xi_1(L) = 0. \end{aligned} \tag{2.21}$$

Assume that $\lambda^* > \bar{a}_{22}(\varepsilon)$. Then for any $\mu \in \mathbb{R}$, (2.20) has a geometrically simple eigenvalue $\lambda(\mu,\varepsilon)$ with a strongly positive and L-periodic eigenfunction $\zeta(x,\mu;\varepsilon)$.

Proof. Let $\bar{a}_{22}(\varepsilon) = a_{22}^\varepsilon(x_0)$ for some $x_0 \in (0,L)$. For any given $\mu \in \mathbb{R}$, we consider

$$\begin{aligned} &D_1(x)\xi_1''(x) + \left[D_0(x) - 2\mu D_1(x)\right]\xi_1'(x) \\ &\quad + \left[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x)\right]\xi_1(x) = \lambda\xi_1(x), \quad x \in (0,L), \\ &\xi_1(0) = \xi_1(L) = 0. \end{aligned} \tag{2.22}$$

Let $\xi_1^*(x)$ be the eigenfunction of (2.21) corresponding to λ^*. It is easy to check that $e^{\mu x}\xi_1^*(x)$ satisfies (2.22) with $\lambda = \lambda^*$. The uniqueness of the principal eigenvalue of (2.22) indicates that λ^* is also a principal eigenvalue of (2.22). Let λ_n^μ be the principal eigenvalue of (2.22) with $(0, L)$ replaced by $(\frac{1}{n}, L - \frac{1}{n})$, $\forall n > \frac{1}{L}$. Since $\lim_{n\to\infty} \lambda_n^\mu = \lambda^* > \bar{a}_{22}(\varepsilon)$, we can fix an $n_0 > \frac{1}{L}$ such that $\lambda_{n_0}^\mu > \bar{a}_{22}(\varepsilon)$. Let $\xi_1^{n_0}(x)$ be the eigenfunction corresponding to $\lambda_{n_0}^\mu$, and define

$$\zeta_1^o(x) = \begin{cases} \xi_1^{n_0}(x), & \text{if } x \in [\frac{1}{n_0}, L - \frac{1}{n_0}], \\ 0, & \text{if } x \in [0, L] \backslash [\frac{1}{n_0}, L - \frac{1}{n_0}]. \end{cases}$$

Then $\zeta_1^o(x)$ satisfies (2.22) with $\lambda = \lambda_{n_0}^\mu$ for all $x \in [0, L] \backslash \{\frac{1}{n_0}, L - \frac{1}{n_0}\}$. It follows that $\lambda_p^\mu \geqslant \lambda_{n_0}^\mu > \bar{a}_{22}(\varepsilon)$, where λ_p^μ is the principal eigenvalue of the following eigenvalue problem with periodic boundary condition:

$$D_1(x)\xi_1''(x) + \left[D_0(x) - 2\mu D_1(x)\right]\xi_1'(x) + \left[\mu^2 D_1(x) - \mu D_0(x) + a_{11}^\varepsilon(x)\right]\xi_1(x) = \lambda\xi_1(x), \quad x \in \mathbb{R},$$
$$\xi_1(x + L) = \xi_1(x), \quad \forall x \in \mathbb{R}.$$

Let $s(a_{22}^\varepsilon(x))$ be the spectral bound of the multiplication operator a_{22}^ε, which is defined by $(a_{22}^\varepsilon \cdot u)(x) = a_{22}^\varepsilon(x)u(x)$, $\forall x \in \mathbb{R}$. Since $\lambda_p^\mu > \bar{a}_{22}(\varepsilon) = s(a_{22}^\varepsilon(x))$, it follows from [29, Corollary 2.4 and Remark 2.3] that (2.20) has a geometrically simple eigenvalue $\lambda(\mu, \varepsilon)$ with a strongly positive and L-periodic eigenfunction $\zeta(x, \mu; \varepsilon)$. □

2.3. The periodic initial value problem

Let $\mathcal{P} = PC(\mathbb{R}, \mathbb{R}^2)$ be the Banach space of all L-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ with the maximum norm $|\cdot|_{\mathcal{P}}$. Then $\mathcal{P}_+ = \{\phi \in \mathcal{P}\colon\ \phi(x) \geqslant 0,\ \forall x \in \mathbb{R}\}$ is a positive cone of $\mathcal{P}$, and $(\mathcal{P}, \mathcal{P}_+)$ is a strongly ordered Banach space. Define $[0, M]_{\mathcal{P}} = \{u \in \mathcal{P}\colon\ 0 \leqslant u \leqslant M\}$.

Theorem 2.4. *Assume that the condition in Theorem 2.2 or 2.3 holds for all small $\varepsilon \geqslant 0$. Let $u(t, x; \phi)$ be the unique solution of (2.1) through ϕ and $\lambda_0 := \lambda(0, 0)$. Then the following statements are valid:*

(1) *If $\lambda_0 < 0$, then for any $\phi \in [0, M]_{\mathcal{P}}$, we have $\lim_{t\to\infty} u(t, x; \phi) = 0$ uniformly for $x \in \mathbb{R}$.*
(2) *If $\lambda_0 > 0$ and $g_{u_2}(x, u) < 0$, $\forall (x, u) \in [0, L] \times [0, M]$, then there is a unique positive L-periodic steady state $u^*(x)$ such that for any $\phi \in [0, M]_{\mathcal{P}} \backslash \{0\}$, we have $\lim_{t\to\infty} u(t, x; \phi) = u^*(x)$ uniformly for $x \in \mathbb{R}$.*

Proof. (1) Since $F(\cdot, u)$ is strictly subhomogeneous in u and $F(\cdot, 0) = 0$, it then follows that (see, e.g., [35, Lemma 2.3.2])

$$F(x, u) \leqslant D_u F(x, 0) \cdot u, \quad \forall x \in \mathbb{R},\ u \in [0, M]. \tag{2.23}$$

Let $\zeta(x) = \zeta(x, 0; 0)$ be the positive and L-periodic eigenfunction corresponding to λ_0 and choose $\rho_0 > 0$ so that $0 \leqslant \phi(x) \leqslant \rho_0\zeta(x)$. Notice that $\rho_0 e^{\lambda_0 t}\zeta(x)$ is a solution of (2.16). Therefore, if $\lambda_0 < 0$, we deduce from (2.23) and the comparison principle that

$$0 \leqslant u(t, x; \phi) \leqslant \rho_0 e^{\lambda_0 t}\zeta(x), \quad \forall t \geqslant 0,\ x \in \mathbb{R}.$$

This implies that $\lim_{t\to\infty} u(t, x; \phi) = 0$ uniformly for $x \in \mathbb{R}$.

(2) By Lemma 2.1, we see that the solution map $Q(t)$ is strongly monotone on $[0, M]_{\mathcal{P}}$. In view of assumptions (A4) and (A5), it easily follows from the arguments in [9, Theorem 2.2] that for each $t > 0$, $Q(t)$ is strictly subhomogeneous on $[0, M]_{\mathcal{P}}$ in the sense that $Q(t)(\nu\phi) > \nu Q(t)\phi$ for all $\nu \in (0, 1)$ and $\phi \in [0, M]_{\mathcal{P}}$ with $\phi \gg 0$. Under the additional assumption on g_{u_2}, we can find $r_0 < 0$ such that $g_{u_2}(x, u) \leqslant r_0$, $\forall (x, u) \in [0, L] \times [0, M]$. By similar arguments to those in [13, Lemma 4.1], we see

that for any $\phi \in [0, M]_{\mathcal{P}}$, the forward orbit $\gamma^+(\phi) := \{Q(t)\phi \colon t \geqslant 0\}$ is asymptotically compact in the sense that for any sequence $t_n \to \infty$, there exists a subsequence t_{n_k} such that $Q(t_{n_k})\phi$ converges in $\mathcal{P}$ as $k \to \infty$. Let $\omega(\phi)$ be the omega limit set of $\gamma^+(\phi)$. It then follows that $\omega(\phi)$ is nonempty, compact and invariant for the semiflow $Q(t)$. Since $\lim_{\varepsilon\to 0} \lambda(0,\varepsilon) = \lambda_0 > 0$, we can fix a small number $\varepsilon > 0$ such that $\lambda(0,\varepsilon) > 0$. Let $\delta = \delta(\varepsilon) > 0$ be defined as in Section 2.2 so that (2.17) holds. Now we prove the following two claims.

Claim 1. $\limsup_{t\to\infty} |Q(t)\phi|_{\mathcal{P}} \geqslant \delta$ *for all* $\phi \in [0, M]_{\mathcal{P}} \setminus \{0\}$.

Suppose for contradiction that $\limsup_{t\to\infty} |Q(t)\phi_0|_{\mathcal{P}} < \delta$ for some $\phi_0 \in [0, M]_{\mathcal{P}} \setminus \{0\}$. Then there exists $t_0 > 0$ such that $u(t, x; \phi_0) < \boldsymbol{\delta} := (\delta, \delta)$, $\forall x \in \mathbb{R}$, $t \geqslant t_0$. Since $u(t_0, \cdot; \phi_0) \gg 0$ in $\mathcal{P}$, there exists small $\rho > 0$ such that $u(t_0, x; \phi_0) \geqslant \rho e^{\lambda(0,\varepsilon)t_0} \zeta(x; \varepsilon)$, $\forall x \in \mathbb{R}$. Note that $\rho e^{\lambda(0,\varepsilon)t} \zeta(x; \varepsilon)$ is a solution of linear system (2.18). In view of (2.17) and the comparison principle, we have $u(t, x; \phi_0) \geqslant \rho e^{\lambda(0,\varepsilon)t} \zeta(x; \varepsilon)$, $\forall x \in \mathbb{R}$, $t \geqslant t_0$. Letting $t \to \infty$, we see that $u(t, x; \phi_0)$ is unbounded, a contradiction.

Claim 2. $\omega(\phi) \subset \mathrm{Int}(\mathcal{P}_+)$ *for all* $\phi \in [0, M]_{\mathcal{P}} \setminus \{0\}$.

Let $\phi \in [0, M]_{\mathcal{P}} \setminus \{0\}$ be given. By Claim 1, we see that the set $\mathcal{A} := \{0\}$ is an isolated invariant set for the semiflow $Q(t)$ and $\omega(\phi) \not\subset \mathcal{A}$. Thus, the Butler–McGehee lemma (see, e.g., [6, Lemma 2.1] and its generalization [35, Lemma 1.2.7]) implies that $\omega(\phi) \cap \mathcal{A} = \emptyset$, and hence, $\omega(\phi) \subset [0, M]_{\mathcal{P}} \setminus \{0\}$. By the strong monotonicity of $Q(t)$ and the invariance of $\omega(\phi)$ for $Q(t)$, it easily follows that $\omega(\phi) \subset \mathrm{Int}(\mathcal{P}_+)$.

Let $t_0 > 0$ be fixed. Then $Q(t_0)$ is strongly monotone and strictly subhomogeneous on $[0, M]_{\mathcal{P}}$. Note that $\omega(\phi)$ is a compact and invariant set for $Q(t_0)$. It then follows from Claim 2 and [35, Theorem 2.3.2] with $K = \omega(\phi)$ that $Q(t_0)$ has a fixed point $u^* \gg 0$ such that $\omega(\phi) = \{u^*\}$, $\forall \phi \in [0, M]_{\mathcal{P}} \setminus \{0\}$. Since $Q(t)\omega(\phi) = \omega(\phi)$ for all $t \geqslant 0$, we see that u^* is a positive equilibrium of the semiflow $Q(t)$. Consequently, the conclusion in statement (2) holds true. $\square$

Due to the spatial heterogeneity, for any $z \in \mathbb{R}$, we consider the space shifted equation of (2.1):

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= D_1(x+z)\frac{\partial^2 u_1}{\partial x^2} + D_0(x+z)\frac{\partial u_1}{\partial x} + f(x+z, u_1, u_2), \\ \frac{\partial u_2}{\partial t} &= g(x+z, u_1, u_2), \quad t > 0, \ x \in \mathbb{R}. \end{aligned} \tag{2.24}$$

It is once again a consequence of the semigroup theory that (2.24) has a unique mild solution $u(t, x; \phi, z)$ with $u(0, x; \phi, z) = \phi(x)$ for every $\phi \in [0, M]_{\mathcal{C}}$.

Remark 2.1. Assume that the conditions in Theorem 2.4(2) hold. Then for any constant vector $\gamma \in [0, M] \setminus \{0\}$, we have $\lim_{t\to\infty} u(t, x; \gamma, z) = u^*(x+z)$ uniformly in $x, z \in \mathbb{R}$.

2.4. Evolution operators and principal eigenvalues

Note that for each $\upsilon^o \in \mathcal{C}$, linear system (2.19) admits a unique mild solution $\upsilon(t, \cdot; \upsilon^o)$ with $\upsilon(0, \cdot) = \upsilon^o$, and $\upsilon(t, \cdot; \upsilon^o) \in \mathcal{C}$, $\forall t \geqslant 0$. In addition, the comparison principle holds for (2.19).

Let $\Phi(t; \mu, \varepsilon)$ be the solution operator of (2.19), i.e., $\Phi(t; \mu, \varepsilon)\upsilon^o = \upsilon(t, \cdot; \upsilon^o, \mu, \varepsilon)$, and $\Phi_p(t; \mu, \varepsilon) : \mathcal{P} \to \mathcal{P}$ be defined by $\Phi_p(t; \mu, \varepsilon) = \Phi(t; \mu, \varepsilon)|_{\mathcal{P}}$. We will now derive an alternative expression for $\Phi(t; \mu, \varepsilon)$ when $t = 1$. For given $\upsilon^o \in \mathcal{C}$ and $\mu \in \mathbb{R}$, let $\underline{u}^o(x) = e^{-\mu x}\upsilon^o(x)$. It then follows that

$$\big[\Phi(t; 0, \varepsilon)\underline{u}^o\big](x) = e^{-\mu x}\big[\Phi(t; \mu, \varepsilon)\upsilon^o\big](x), \quad \forall t \geqslant 0, \ x \in \mathbb{R}, \ \upsilon^o \in \mathcal{C}.$$

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

$$\big[\Phi(1; 0, \varepsilon)\underline{u}^o\big]_i(x) = \sum_{j=1}^{2} \int_{\mathbb{R}} \underline{u}_j^o(y)\, m_{ij}(x; y, \mathrm{d}y), \quad 1 \leqslant i, j \leqslant 2.$$

Consequently,

$$\big[\Phi(1; \mu, \varepsilon)\upsilon^o\big]_i(x) = \sum_{j=1}^{2} \int_{\mathbb{R}} \mathrm{e}^{\mu(x-y)} \upsilon_j^o(y)\, m_{ij}(x; y, \mathrm{d}y), \quad 1 \leqslant i, j \leqslant 2. \tag{2.25}$$

To establish the spreading speed of (2.1), certain suitable truncated operators of $\Phi(1; \mu, \varepsilon)$ are used. To see this, let $\chi(s) : \mathbb{R} \to [0, 1]$ be a smooth function given by

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

So right now, by (2.25) and the compactly supported property of $\chi(s)$, we can fix a positive number ϱ, and define $\Phi^\varrho(1; \mu, \varepsilon) : \mathcal{C} \to \mathcal{C}$ as

$$\big[\Phi^\varrho(1; \mu, \varepsilon)\upsilon^o\big]_i(x) = \sum_{j=1}^{2} \int_{\mathbb{R}} \mathrm{e}^{\mu(x-y)} \upsilon_j^o(y) \chi\left(\frac{|y-x|}{\varrho}\right) m_{ij}(x; y, \mathrm{d}y), \quad 1 \leqslant i, j \leqslant 2,$$

and $\Phi_p^\varrho(1; \mu, \varepsilon) : \mathcal{P} \to \mathcal{P}$ by $\Phi_p^\varrho(1; \mu, \varepsilon) = \Phi^\varrho(1; \mu, \varepsilon)|_{\mathcal{P}}$.

The space shifted equation of (2.19) is

$$\begin{aligned} \frac{\partial \upsilon_1}{\partial t} &= D_1(x+z)\frac{\partial^2 \upsilon_1}{\partial x^2} + \big[D_0(x+z) - 2\mu D_1(x+z)\big]\frac{\partial \upsilon_1}{\partial x} \\ &\quad + \big[\mu^2 D_1(x+z) - \mu D_0(x+z) + a_{11}^\varepsilon(x+z)\big]\upsilon_1 + a_{12}^\varepsilon(x+z)\upsilon_2, \\ \frac{\partial \upsilon_2}{\partial t} &= a_{21}^\varepsilon(x+z)\upsilon_1 + a_{22}^\varepsilon(x+z)\upsilon_2. \end{aligned} \tag{2.26}$$

Let $\Phi(t; \mu, \varepsilon, z)$ be the solution operator of (2.26) and $\Phi_p(t; \mu, \varepsilon, z) = \Phi(t; \mu, \varepsilon, z)|_{\mathcal{P}}$. Similarly, define $\Phi^\varrho(1; \mu, \varepsilon, z) : \mathcal{C} \to \mathcal{C}$ as

$$\big[\Phi^\varrho(1; \mu, \varepsilon, z)\upsilon^o\big]_i(x) = \sum_{j=1}^{2} \int_{\mathbb{R}} \mathrm{e}^{\mu(x+z-y)} \upsilon_j^o(y-z) \chi\left(\frac{|y-x-z|}{\varrho}\right) m_{ij}(x+z; y, \mathrm{d}y), \tag{2.27}$$

for $1 \leqslant i, j \leqslant 2$, and $\Phi_p^\varrho(1; \mu, \varepsilon, z) = \Phi^\varrho(1; \mu, \varepsilon, z)|_{\mathcal{P}}$. Then it is easy to check that

$$\big\|\Phi_p^\varrho(1; \mu, \varepsilon, z) - \Phi_p(1; \mu, \varepsilon, z)\big\|_{\mathcal{P}} \to 0 \quad \text{as } \varrho \to \infty$$

uniformly for μ in bounded sets and $z \in [0, L]$.

Let $r(\mu, \varepsilon) := r(\Phi_p(1; \mu, \varepsilon))$ and $\sigma(\Phi_p(1; \mu, \varepsilon))$ be the spectral radius and the spectrum of $\Phi_p(1; \mu, \varepsilon)$, respectively. Then the following two results can be derived directly from [14, Theorems 1.5.2 and 1.5.3], [8, Theorems 3.6 and 4.3] and [26, Proposition 3.3].

Lemma 2.4. *The principal eigenvalue $\lambda(\mu,\varepsilon)$ of (2.20) exists if and only if $r(\mu,\varepsilon)$ is a simple eigenvalue of $\Phi_p(1;\mu,\varepsilon)$ with a strongly positive eigenfunction in $\mathcal{P}_+$, and for each $\tilde r(\mu,\varepsilon)\in\sigma(\Phi_p(1;\mu,\varepsilon))\backslash\{r(\mu,\varepsilon)\}$, we have $|\tilde r|<r(\mu,\varepsilon)$. Furthermore, if $\lambda(\mu,\varepsilon)$ exists, then $\lambda(\mu,\varepsilon)=\ln r(\mu,\varepsilon)$.*

Lemma 2.5. *For each $\upsilon^o\in\operatorname{Int}(\mathcal{P}_+)$,*

$$\inf_{x\in\mathbb{R}}\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\upsilon_j^o(y)\,m_{ij}(x;y,\mathrm{d}y)}{\upsilon_i^o(x)} \leqslant r(\mu,\varepsilon)\leqslant\sup_{x\in\mathbb{R}}\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\upsilon_j^o(y)\,m_{ij}(x;y,\mathrm{d}y)}{\upsilon_i^o(x)},\quad i=1,2.$$

Theorem 2.5. *Let $\lambda(\mu,\varepsilon)$ be the principal eigenvalue of (2.20). Then the following two statements are valid*:

(1) *$\lambda(\mu,\varepsilon)$ is convex in μ.*
(2) *If $\lambda(0,\varepsilon)>0$, then there exists $\mu^*>0$ such that $\inf_{\mu>0}\frac{\lambda(\mu,\varepsilon)}{\mu}=\frac{\lambda(\mu^*,\varepsilon)}{\mu^*}$.*

Proof. (1) By Lemma 2.4, $r(\mu,\varepsilon)$ is an eigenvalue of $\Phi_p(1;\mu,\varepsilon)$ with a strongly positive eigenfunction $\zeta(x,\mu)$, which combine with (2.25) to imply

$$r(\mu,\varepsilon)=\frac{[\Phi_p(1;\mu,\varepsilon)\zeta]_i(x)}{\zeta_i(x,\mu)}=\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\zeta_j(y,\mu)\,m_{ij}(x;y,\mathrm{d}y)}{\zeta_i(x,\mu)},\quad i=1,2.$$

Similarly, $r(\bar\mu,\varepsilon)=\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\bar\mu(x-y)}\bar\zeta_j(y,\mu)\,m_{ij}(x;y,\mathrm{d}y)/\bar\zeta_i(x,\mu)$. For given $\nu\in[0,1]$ and each i, letting $\tilde\zeta_i=\zeta_i^{\nu}\bar\zeta_i^{1-\nu}$ and using Hölder inequality, we obtain

$$\begin{aligned}
&\big[r(\mu,\varepsilon)\big]^{\nu}\big[r(\bar\mu,\varepsilon)\big]^{1-\nu}\\
&=\left[\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\mu(x-y)}\zeta_j(y,\mu)\,m_{ij}(x;y,\mathrm{d}y)}{\zeta_i(x,\mu)}\right]^{\nu}\left[\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{\bar\mu(x-y)}\bar\zeta_j(y,\mu)\,m_{ij}(x;y,\mathrm{d}y)}{\bar\zeta_i(x,\mu)}\right]^{1-\nu}\\
&\geqslant\sum_{j=1}^{2}\int_{\mathbb{R}}\left[\frac{\mathrm{e}^{\mu(x-y)}\zeta_j(y,\mu)}{\zeta_i(x,\mu)}\right]^{\nu}\left[\frac{\mathrm{e}^{\bar\mu(x-y)}\bar\zeta_j(y,\mu)}{\bar\zeta_i(x,\mu)}\right]^{1-\nu}m_{ij}(x;y,\mathrm{d}y)\\
&=\sum_{j=1}^{2}\int_{\mathbb{R}}\frac{\mathrm{e}^{[\nu\mu+(1-\nu)\bar\mu](x-y)}\tilde\zeta_j(y,\mu)}{\tilde\zeta_i(x,\mu)}m_{ij}(x;y,\mathrm{d}y),\quad\forall x\in\mathbb{R}.
\end{aligned}$$

By Lemma 2.5, we have

$$\begin{aligned}
\big[r(\mu,\varepsilon)\big]^{\nu}\big[r(\bar\mu,\varepsilon)\big]^{1-\nu}&\geqslant\sup_{x\in\mathbb{R}}\frac{\sum_{j=1}^{2}\int_{\mathbb{R}}\mathrm{e}^{[\nu\mu+(1-\nu)\bar\mu](x-y)}\tilde\zeta_j(y,\mu)\,m_{ij}(x;y,\mathrm{d}y)}{\tilde\zeta_i(x,\mu)}\\
&\geqslant r\big(\nu\mu+(1-\nu)\bar\mu,\varepsilon\big).
\end{aligned}$$

This shows that $\ln[r(\mu,\varepsilon)]^{\nu}[r(\bar\mu,\varepsilon)]^{1-\nu}\geqslant\ln r(\nu\mu+(1-\nu)\bar\mu,\varepsilon)$. By Lemma 2.4 again, $\nu\lambda(\mu,\varepsilon)+(1-\nu)\lambda(\bar\mu,\varepsilon)\geqslant\lambda(\nu\mu+(1-\nu)\bar\mu,\varepsilon)$, $\forall\nu\in[0,1]$. Hence, $\lambda(\mu,\varepsilon)$ is convex in μ.

(2) Since $a_{12}^{\varepsilon}(x)>0$ and $\zeta(x,\mu)\gg 0$, we see from (2.20) that

$$\frac{\lambda(\mu,\varepsilon)}{\mu}\geqslant\frac{D_1(x)\zeta_1''(x)}{\zeta_1(x)\mu}+\zeta_1'(x)\frac{D_0(x)-2\mu D_1(x)}{\zeta_1(x)\mu}+\mu D_1(x)-D_0(x)+\frac{1}{\mu}a_{11}^{\varepsilon}(x).$$

Letting $\mu \to \infty$, we get $\frac{\lambda(\mu,\varepsilon)}{\mu} \to \infty$ due to $D_1(x)$ having the positive lower bound, which, together with the convexity of $\lambda(\mu,\varepsilon)$ in μ and $\lim_{\mu\to 0}\frac{\lambda(\mu,\varepsilon)}{\mu} = \infty$, leads to the conclusion. $\square$

Let $r^{\varrho}(\mu,\varepsilon) := r(\Phi_p^{\varrho}(1;\mu,\varepsilon))$ and $\lambda^{\varrho}(\mu,\varepsilon) := \ln r^{\varrho}(\mu,\varepsilon)$. As a straightforward consequence of [26, Theorem 3.1], we have the following result.

Lemma 2.6. *Assume that (2.20) admits a principal eigenvalue $\lambda(\mu,\varepsilon)$ for $\mu \in \mathbb{R}$, that $\lambda(0,\varepsilon) > 0$, and that $\frac{\lambda(\mu^*,\varepsilon)}{\mu^*} < \frac{\lambda(\mu^*+l_0,\varepsilon)}{\mu^*+l_0}$ for some $l_0 > 0$. Then the following statements are valid:*

(1) *There exists $\varrho_0 > 0$ such that for each $\varrho \geqslant \varrho_0$ and $|\mu| \leqslant \mu^* + l_0$, $r^{\varrho}(\mu,\varepsilon)$ is a simple eigenvalue of $\Phi_p^{\varrho}(1;\mu,\varepsilon)$ with a strongly positive eigenfunction $\zeta^{\varrho}(x,\mu;\varepsilon)$. Also, $\lambda^{\varrho}(0,\varepsilon) > 0$ and $\frac{\lambda^{\varrho}(\mu^*,\varepsilon)}{\mu^*} < \frac{\lambda^{\varrho}(\mu^*+l_0,\varepsilon)}{\mu^*+l_0}$.*
(2) *For each $\varrho \geqslant \varrho_0$, $\lambda^{\varrho}(\mu,\varepsilon)$ is convex in μ for $|\mu| \leqslant \mu^* + l_0$.*
(3) *For a given $\varrho \geqslant \varrho_0$, define*

$$\mu_{\varrho}^* = \inf\left\{\tilde{\mu}\colon \frac{\lambda^{\varrho}(\tilde{\mu},\varepsilon)}{\tilde{\mu}} = \inf_{\mu\in(0,\mu^*+l_0]}\frac{\lambda^{\varrho}(\mu,\varepsilon)}{\mu}\right\}.$$

Then we have
(i) *$\mu_{\varrho}^* > 0$ and $\frac{\partial\lambda^{\varrho}(\mu,\varepsilon)}{\partial\mu} < \frac{\lambda^{\varrho}(\mu,\varepsilon)}{\mu}$ for $\mu \in (0,\mu_{\varrho}^*)$.*
(ii) *For each $\epsilon_0 > 0$, there exists $\mu_{\epsilon_0} > 0$ such that for $\mu \in (\mu_{\epsilon_0},\mu_{\varrho}^*)$,*

$$-\frac{\partial\lambda^{\varrho}(\mu,\varepsilon)}{\partial\mu} < -\frac{\lambda^{\varrho}(\mu_{\varrho}^*,\varepsilon)}{\mu_{\varrho}^*} + \epsilon_0.$$

(iii) $\lim_{\varrho\to\infty}\frac{\lambda^{\varrho}(\mu_{\varrho}^*,\varepsilon)}{\mu_{\varrho}^*} = \frac{\lambda(\mu^*,\varepsilon)}{\mu^*}$.

3. Spreading speed intervals

From now on, we always assume that the principal eigenvalue $\lambda(\mu,\varepsilon)$ exists for all $\mu \in \mathbb{R}$ and small $\varepsilon \geqslant 0$, $\lambda(0,0) > 0$, and the conclusion in Theorem 2.4(2) holds. In this section, we first obtain a spread speed interval $[c_{\inf}^*, c_{\sup}^*]$ of system (2.1), and then establish its basic properties.

For convenience, for given $u^o, u(t,\cdot) \in \mathcal{C}$ and $c \in \mathbb{R}$, set

$$\liminf_{x\to-\infty} u^o(x) = \lim_{r\to-\infty}\inf_{x\leqslant r} u^o(x), \qquad \limsup_{x\to\infty} u^o(x) = \lim_{r\to\infty}\sup_{x\geqslant r} u^o(x),$$

and

$$\liminf_{t\to\infty,\, x\leqslant ct} u(t,x) = \liminf_{t\to\infty}\inf_{x\leqslant ct} u(t,x), \qquad \limsup_{t\to\infty,\, x\geqslant ct} u(t,x) = \limsup_{t\to\infty}\sup_{x\geqslant ct} u(t,x).$$

Let $u_{\inf}^* := \inf_{x\in\mathbb{R}} u^*(x)$ and define

$$\mathcal{C}_+^* = \left\{u \in \left[0,u^*\right]_{\mathcal{C}}\colon u \ll u_{\inf}^*,\ \liminf_{x\to-\infty} u(x) > 0,\ u(x) = 0,\ \forall x \geqslant x_1 \text{ for some } x_1 \in \mathbb{R}\right\}.$$

Definition 3.1 *(Spreading speed interval).* Let

$$C_{\inf}^* = \left\{c\colon \forall u^o \in \mathcal{C}_+^*,\ \liminf_{t\to\infty,\, x\leqslant ct}\left[u\left(t,x;u^o\right) - u^*(x)\right] = 0\right\}$$

and

$$C^*_{\sup} = \Big\{c\colon \forall u^o \in \mathcal{C}^*_+,\ \limsup_{t\to\infty,\, x\geqslant ct} u\big(t,x;u^o\big)=0\Big\}.$$

Define

$$c^*_{\inf} = \sup\big\{c\colon c \in C^*_{\inf}\big\}, \qquad c^*_{\sup} = \inf\big\{c\colon c\in C^*_{\sup}\big\}.$$

We call $[c^*_{\inf}, c^*_{\sup}]$ as the spread speed interval of (2.1).

Let $\eta(s)$ be the function defined by

$$\eta(s) = \frac{1}{2}\left(1+\tanh\frac{s}{2}\right), \quad s\in\mathbb{R}.$$

Note that

$$\eta'(s) = \eta(s)\big(1-\eta(s)\big) > 0, \quad s\in\mathbb{R}.$$

Without loss of generality, we can assume that there exists a vector $u^- \ll 0$ in $\mathbb{R}^2$ such that $f(x,u)$ and $g(x,u)$ are defined for all $u\in[u^-,\infty)$, $f(x,u^-)\geqslant 0$ and $g(x,u^-)\geqslant 0$ for all $x\in\mathbb{R}$, and the condition (A4) holds for all $u\in[u^-,M]$. It then follows that $[u^-,0]_{\mathcal{C}}$ is positively invariant for the semiflow $\{Q(t)\}_{t\geqslant 0}$.

Lemma 3.1. *Let $\alpha^\pm$ be given constant vectors with $u^- \leqslant \alpha^- \leqslant 0 \ll \alpha^+ \leqslant u^*_{\inf}$. Then there is $C_0>0$ such that for every $C\geqslant C_0$ and $z\in\mathbb{R}$, the following statements are valid*:

(1) *Let $v^\pm(t,x;z) = u(t,x;\alpha^\pm,z)\eta(x+Ct) + u(t,x;\alpha^\mp,z)[1-\eta(x+Ct)]$. Then v^+ and v^- are upper and lower solutions of (2.24) on $[0,\infty)$.*

(2) *Let $w^\pm(t,x;z) = u(t,x;\alpha^\mp,z)\eta(x-Ct) + u(t,x;\alpha^\pm,z)[1-\eta(x-Ct)]$. Then w^+ and w^- are upper and lower solutions of (2.24) on $[0,\infty)$.*

Proof. We only prove $v^+(t,x;z)$ with $z=0$ is an upper solution of (2.24), the proof of other statements is virtually identical. We write $v^+(t,x)$ for $v^+(t,x;0)$.

Set $s=x+Ct$ and $w(t,x)=u(t,x;\alpha^+)-u(t,x;\alpha^-)$. Since $v^+(t,x)=u(t,x;\alpha^+)\eta(s)+u(t,x;\alpha^-)\times[1-\eta(s)]$, we obtain

$$\begin{aligned}
&\frac{\partial v_1^+}{\partial t} - D_1(x)\frac{\partial^2 v_1^+}{\partial x^2} - D_0(x)\frac{\partial v_1^+}{\partial x} - f\big(x, v_1^+, v_2^+\big)\\
&\quad = \eta'(s)\big\{\big[C - D_1(x)\big(1-2\eta(s)\big) - D_0(x)\big]w_1(t,x) - 2D_1(x)w_{1x}\big\} + \varLambda,
\end{aligned}\tag{3.1}$$

with $\varLambda := \eta(s)[f(x,u(t,x;\alpha^+)) - f(x,u(t,x;\alpha^-))] + f(x,u(t,x;\alpha^-)) - f(x,v^+)$.

By using (2.10), we get

$$f\big(x,u\big(t,x;\alpha^+\big)\big) - f\big(x,u\big(t,x;\alpha^-\big)\big) = \sum_{i=1}^{2}\int_0^1 f_{u_i}\big(x,u\big(t,x;\alpha^-\big)+rw(t,x)\big)w_i(t,x)\,\mathrm{d}r, \tag{3.2}$$

and

$$f\big(x,u\big(t,x;\alpha^-\big)\big)-f\big(x,v^+\big)=-\big[f\big(x,u\big(t,x;\alpha^-\big)+\eta(s)w(t,x)\big)-f\big(x,u\big(t,x;\alpha^-\big)\big)\big]$$
$$=-\sum_{i=1}^{2}\int_0^1 f_{u_i}\big(x,u\big(t,x;\alpha^-\big)+r\eta(s)w(t,x)\big)\eta(s)w_i(t,x)\,\mathrm{d}r. \tag{3.3}$$

We obtain from (3.2) and (3.3) that

$$\begin{aligned}\Lambda&=\sum_{i=1}^{2}\eta w_i\int_0^1\big[f_{u_i}\big(x,u\big(t,x;\alpha^-\big)+rw(t,x)\big)-f_{u_i}\big(x,u\big(t,x;\alpha^-\big)+r\eta(s)w(t,x)\big)\big]\,\mathrm{d}r\\
&=\eta'(s)w_1\int_0^1 r\big[f_{u_1u_1}\big(x,u_r(t,x)\big)w_1+f_{u_1u_2}\big(x,u_r(t,x)\big)w_2\big]\,\mathrm{d}r\\
&\quad+\eta'(s)w_2\int_0^1 r\big[f_{u_2u_1}\big(x,\tilde u_r(t,x)\big)w_1+f_{u_2u_2}\big(x,\tilde u_r(t,x)\big)w_2\big]\,\mathrm{d}r,\end{aligned}\tag{3.4}$$

where $u_r(t,x)$, $\tilde u_r(t,x)$ are between $u(t,x;\alpha^-)$ and $u(t,x;\alpha^+)$.

Combining (3.1) with (3.4), we derive that

$$\begin{aligned}&\frac{\partial v_1^+}{\partial t}-D_1(x)\frac{\partial^2 v_1^+}{\partial x^2}-D_0(x)\frac{\partial v_1^+}{\partial x}-f\big(x,v_1^+,v_2^+\big)\\
&\quad=\eta'(s)\Bigg\{\big[C-D_1(1-2\eta)-D_0\big]w_1-2D_1w_{1x}+w_2^2\int_0^1 f_{u_2u_2}(x,\tilde u_r)r\,\mathrm{d}r\\
&\qquad+w_1\int_0^1 r\big[f_{u_1u_1}(x,u_r)w_1+f_{u_1u_2}(x,u_r)w_2+f_{u_2u_1}(x,\tilde u_r)w_2\big]\,\mathrm{d}r\Bigg\}.\end{aligned}$$

By Remark 2.1 and a prior estimates for parabolic equations, there exist $\gamma_1,\gamma_2>0$ such that $w_1(t,x)\geqslant\gamma_1$ and $|w_{1x}(t,x)|\leqslant\gamma_2$ for all $t\geqslant 0$, $x\in\mathbb{R}$. Therefore there is $C_1>0$ such that for $C\geqslant C_1$, $\frac{\partial v_1^+}{\partial t}-D_1(x)\frac{\partial^2 v_1^+}{\partial x^2}-D_0(x)\frac{\partial v_1^+}{\partial x}-f(x,v_1^+,v_2^+)\geqslant 0$. By the same procedure, there exists $C_2>0$ such that for $C\geqslant C_2$, $\frac{\partial v_2^+}{\partial t}-g(x,v_1^+,v_2^+)\geqslant 0$. $\square$

Lemma 3.2. *The following statements are valid*:

(1) *If there exists $u^+\in\mathcal{C}_+^*$ such that*

$$\liminf_{t\to\infty,\,x\leqslant ct}\big[u\big(t,x;u^+,z\big)-u^*(x+z)\big]=0\quad\textit{uniformly in } z\in\mathbb{R},$$

then $c\leqslant c^*_{\inf}$.

(2) *If $c<c^*_{\inf}$, then for every $u^0\in\mathcal{C}_+^*$, we have*

$$\liminf_{t\to\infty,\,x\leqslant ct}\big[u\big(t,x;u^0,z\big)-u^*(x+z)\big]=0\quad\textit{uniformly in } z\in\mathbb{R}.$$

Proof. The proof is analogous to [15, Lemma 3.4]. □

Lemma 3.3. *The following statements are valid*:

(1) *If there exists* $u^+ \in \mathcal{C}_+^*$ *such that*

$$\limsup_{t\to\infty,\, x\geqslant ct} u\big(t,x;u^+,z\big)=0 \quad \textit{uniformly in } z\in\mathbb{R},$$

then $c \geqslant c_{\sup}^*$.

(2) *If* $c > c_{\sup}^*$, *then for every* $u^0 \in \mathcal{C}_+^*$, *we have*

$$\limsup_{t\to\infty,\, x\geqslant ct} u\big(t,x;u^0,z\big)=0 \quad \textit{uniformly in } z\in\mathbb{R}.$$

Proof. This can be proved in a similar way to [15, Lemma 3.5]. □

Theorem 3.1. $[c_{\inf}^*, c_{\sup}^*]$ *is a finite interval.*

Proof. Let α^- and α^+ be the given constant vectors with $u^- \leqslant \alpha^- < 0 \ll \alpha^+ < u_{\inf}^*$. Then there is $u^+ \in \mathcal{C}_+^*$ such that

$$w^+(0,x;z)=\alpha^-\eta(x)+\alpha^+\big[1-\eta(x)\big]\geqslant u^+(x), \quad \forall x,z\in\mathbb{R}.$$

It follows from the comparison principle and Lemma 3.1 that

$$\begin{aligned} w^+(t,x;z)&=u\big(t,x;\alpha^-,z\big)\eta(x-C_0t)+u\big(t,x;\alpha^+,z\big)\big[1-\eta(x-C_0t)\big]\\ &\geqslant u\big(t,x;u^+,z\big), \quad \forall t\geqslant 0,\ x,z\in\mathbb{R}. \end{aligned}$$

For each $C_1 > C_0$, the fact that $\eta(\infty)=1$ implies

$$\begin{aligned} 0\leqslant \limsup_{t\to\infty,\, x\geqslant C_1t} u\big(t,x;u^+,z\big) &\leqslant \limsup_{t\to\infty,\, x\geqslant C_1t} w^+(t,x;z)\\ &= \limsup_{t\to\infty,\, x\geqslant C_1t} u(t,x;0,z)=0. \end{aligned}$$

Thus, we have

$$\limsup_{t\to\infty,\, x\geqslant C_1t} u\big(t,x;u^+,z\big)=0 \quad \text{uniformly in } z\in\mathbb{R}.$$

By Lemma 3.3(1), it follows that $c_{\sup}^* \leqslant C_1$.

Since $u^- \leqslant \alpha^- < 0 \ll \alpha^+ < u_{\inf}^*$, there exists $\tilde{u}^+ \in \mathcal{C}_+^*$ such that

$$v^-(0,x;z)=\alpha^-\eta(x)+\alpha^+\big[1-\eta(x)\big]\leqslant \tilde{u}^+(x), \quad \forall x,z\in\mathbb{R}.$$

By the comparison principle and Lemma 3.1 again, we have

$$\begin{aligned} v^-(t,x;z)&=u\big(t,x;\alpha^-,z\big)\eta(x+C_0t)+u\big(t,x;\alpha^+,z\big)\big[1-\eta(x+C_0t)\big]\\ &\leqslant u\big(t,x;\tilde{u}^+,z\big), \quad \forall t\geqslant 0,\ x,z\in\mathbb{R}. \end{aligned}$$

Then for each $C_2 < -C_0$, the fact that $\eta(-\infty) = 0$, together with Remark 2.1, implies that

$$\begin{aligned}\liminf_{t\to\infty,\, x\leqslant C_2 t}\big[u\big(t,x;\tilde{u}^+,z\big) - u^*(x+z)\big] &\geqslant \liminf_{t\to\infty,\, x\leqslant C_2 t}\big[v^-(t,x;z) - u^*(x+z)\big] \\ &= \liminf_{t\to\infty,\, x\leqslant C_2 t}\big[u\big(t,x;\alpha^+,z\big) - u^*(x+z)\big] = 0,\end{aligned}$$

for all $t \geqslant 0$, $x, z \in \mathbb{R}$. On the other side, since $\tilde{u}^+ \ll u^*_{\inf}$, the comparison principle and Remark 2.1 give rise to

$$\liminf_{t\to\infty,\, x\leqslant C_2 t}\big[u\big(t,x;\tilde{u}^+,z\big) - u^*(x+z)\big] \leqslant \liminf_{t\to\infty,\, x\leqslant C_2 t}\big[u\big(t,x;u^*_{\inf},z\big) - u^*(x+z)\big] = 0$$

for all $t \geqslant 0$, $x, z \in \mathbb{R}$. Therefore, we obtain

$$\liminf_{t\to\infty,\, x\leqslant C_2 t}\big[u\big(t,x;\tilde{u}^+,z\big) - u^*(x+z)\big] = 0 \quad \text{uniformly in } z \in \mathbb{R}.$$

In view of Lemma 3.2(1), $c^*_{\inf} \geqslant C_2$. So, to summarize, $[c^*_{\inf}, c^*_{\sup}]$ is a finite interval. □

Lemma 3.4. *Let $c \in \mathbb{R}$ and $u^o \in [0, u^*]_C$ be given. If there exist $T_0 > 0$ and $0 \ll \delta^o \leqslant u^*_{\inf}$ such that*

$$\liminf_{n\to\infty,\, x\leqslant cnT_0} u\big(nT_0, x; u^o, z\big) \geqslant \delta^o \quad \textit{uniformly in } z \in \mathbb{R}, \tag{3.5}$$

then for each $c' < c$,

$$\liminf_{t\to\infty,\, x\leqslant c't}\big[u\big(t,x;u^o,z\big) - u^*(x+z)\big] = 0 \quad \textit{uniformly in } z \in \mathbb{R}.$$

Proof. First, by (3.5), there is $n_0 \in \mathbb{N}$ such that

$$u\big(nT_0, x; u^o, z\big) \geqslant \delta^o/2 \quad \text{for } n \geqslant n_0,\ x \leqslant cnT_0,\ z \in \mathbb{R}. \tag{3.6}$$

Let $\tilde{u}^o(x) \equiv \delta^o/2$. According to Remark 2.1, for each $\epsilon > 0$, there exists $n_1 \geqslant n_0$ such that

$$u\big(t,x;\tilde{u}^o,z\big) \geqslant u^*(x+z) - \epsilon \quad \text{for } t \geqslant n_1 T_0,\ x, z \in \mathbb{R}. \tag{3.7}$$

Fixing $\varrho > 1$, let $\tilde{u}^\varrho \in [0, \frac{\delta^o}{2}]_C$ be such that $\tilde{u}^\varrho(x) = \delta^o/2$ for $x \leqslant \varrho - 1$ and $\tilde{u}^\varrho(x) = 0$ for $x \geqslant \varrho$. Notice the obvious point $\tilde{u}^\varrho \to \tilde{u}^o$ as $\varrho \to \infty$. We infer from Lemma 2.3 that

$$u\big(t,0;\tilde{u}^\varrho,z\big) \to u\big(t,0;\tilde{u}^o,z\big) \quad \text{as } \varrho \to \infty, \text{ uniformly in } z \in \mathbb{R}. \tag{3.8}$$

Hence, one concludes from (3.8) and then (3.7) that there exists $\varrho_o > 1$ such that for each $\varrho \geqslant \varrho_o$,

$$u\big(t,0;\tilde{u}^\varrho,z\big) \geqslant u^*(z) - 2\epsilon \quad \text{for } n_1 T_0 \leqslant t \leqslant (n_1+1)T_0,\ z \in \mathbb{R}. \tag{3.9}$$

For given $c' < c$, observe that $(c - c')nT_0 \to \infty$ as $n \to \infty$. Thus, there is $n_2 \geqslant n_1$ such that

$$(c - c')nT_0 \geqslant \varrho_o + c'(n_1+1)T_0, \quad \text{for } n \geqslant n_2. \tag{3.10}$$

This, together with (3.6), implies that

$$u\big(nT_0, s+x+c'nT_0+c'\tau; u^o, z\big) \geqslant \tilde{u}^{\varrho_o}(s),$$
$$\forall x \leqslant 0,\ \tau \in \big[n_1T_0, (n_1+1)T_0\big],\ n \geqslant n_2,\ s \in \mathbb{R}. \tag{3.11}$$

Indeed, if $s \leqslant \varrho_o$, then $\tilde{u}^{\varrho_o}(s) \leqslant \tilde{u}^o(s)$, and for all $x \leqslant 0$, $n_1T_0 \leqslant \tau \leqslant (n_1+1)T_0$, $n \geqslant n_2$, by (3.10), we get

$$s+x+c'nT_0+c'\tau \leqslant \varrho_o + 0 + c'nT_0 + c'(n_1+1)T_0 \leqslant cnT_0.$$

It follows from (3.6) that

$$u\big(nT_0, s+x+c'nT_0+c'\tau; u^o, z\big) \geqslant \delta^o/2 = \tilde{u}^o(s) \geqslant \tilde{u}^{\varrho_o}(s).$$

On the other hand, if $s \geqslant \varrho_o$, then $\tilde{u}^{\varrho_o}(s) \equiv 0$. Thus, (3.11) holds true for all $s \in \mathbb{R}$.

Given $n \geqslant n_2$ and $(n+n_1)T_0 \leqslant t < (n+n_1+1)T_0$. Let $\tau = t - nT_0$. By (3.11) and (3.9), we get

$$\begin{aligned} u\big(t, x+c't; u^o, z\big) &= u\big(\tau, x+c't; u\big(nT_0, \cdot; u^o, z\big), z\big) \\ &= u\big(\tau, 0; u\big(nT_0, \cdot + x + c'nT_0 + c'\tau; u^o, z\big), z+x+c't\big) \\ &\geqslant u\big(\tau, 0; \tilde{u}^{\varrho_o}(\cdot), z+x+c't\big) \\ &\geqslant u^*\big(z+x+c't\big) - 2\epsilon, \quad \forall x \leqslant 0. \end{aligned}$$

Thus, we have

$$u\big(t, x; u^o, z\big) \geqslant u^*(z+x) - 2\epsilon, \quad \forall x \leqslant c't,\ t \geqslant (n_1+n_2)T_0,\ z \in \mathbb{R},$$

which implies the desired conclusion. □

4. Spreading speeds

In this section, we first characterize spreading speeds, and then show that system (2.1) admits the propagation features.

Theorem 4.1. *There exist $c_+^* = \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}$ and $c_-^* = \inf_{\mu>0} \frac{\lambda(-\mu,0)}{\mu}$, being the rightward and leftward spreading speeds of (2.1). Further, $c_+^* + c_-^* > 0$.*

Proof. We split the proof into five steps.

Step 1. To prove that $c_{\sup}^* \leqslant \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}$. Let $\zeta(x,\mu)$ be a principal eigenfunction of (2.20) corresponding to $\lambda(\mu,0)$. Then $\rho e^{-\mu(x-c't)}\zeta(\mu,x)$ is a solution of (2.16) with $c' = \lambda(\mu,0)/\mu$ and any $\mu, \rho > 0$. For any $u^o \in \mathcal{C}_+^*$, choose $\tilde{\rho} > 0$ such that $u^o \leqslant \tilde{u}^o := \tilde{\rho} e^{-\mu x}\zeta(\mu,x) \leqslant u_{\inf}^*$. It follows from the comparison principle and (2.23) that

$$u\big(t, x; u^o\big) \leqslant u\big(t, x; \tilde{u}^o\big) \leqslant \tilde{\rho} e^{-\mu(x-c't)}\zeta(\mu,x).$$

Hence,

$$\limsup_{t\to\infty,\, x\geqslant ct} u\big(t, x; u^o\big) = 0 \quad \text{for each } c > c'.$$

By Lemma 3.3(1), $c_{\sup}^* \leqslant \frac{\lambda(\mu,0)}{\mu}$ for any $\mu > 0$, and hence, $c_{\sup}^* \leqslant \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}$.

Step 2. To prove that $c^*_{\inf} \geqslant \inf_{\mu>0} \frac{\lambda(\mu,\varepsilon)}{\mu}$. Choose $\varrho \gg 1$ such that Lemma 2.6 holds. Note that if $u^o \in \mathcal{C}_+$ is so small that $0 \leqslant u(t,x;u^o,z) \leqslant \delta$, $\forall t \in [0,1]$, $x,z \in \mathbb{R}$. In view of (2.17), we then get

$$u\big(t,x;u^o,z\big) \geqslant \big[\Phi(1;0,\varepsilon,z)u^o\big](x) \geqslant \big[\Phi^\varrho(1;0,\varepsilon,z)u^o\big](x), \quad \forall x,z \in \mathbb{R}. \tag{4.1}$$

Here $\Phi(t;\mu,\varepsilon,z)$ is the solution operator of (2.26) and $\Phi^\varrho(1;\mu,\varepsilon,z)$ is the truncated operator of $\Phi(1;\mu,\varepsilon,z)$ given in (2.27). Let $r^\varrho(\mu,\varepsilon)$ be the spectral radius of $\Phi^\varrho_p(1;\mu,\varepsilon,0)$ and $\lambda^\varrho(\mu,\varepsilon) = \ln r^\varrho(\mu,\varepsilon)$. By Lemma 2.6(1), $r^\varrho(\mu,\varepsilon)$ is an eigenvalue of $\Phi^\varrho_p(1;\mu,\varepsilon,0)$ with a strongly positive eigenfunction $\zeta^\varrho(x,\mu;\varepsilon)$ for $|\mu| \leqslant \mu^* + l_0$.

By Lemma 2.6(3)(iii), for each $\epsilon_1 > 0$, there exists $\varrho > 0$ such that

$$-\frac{\lambda^\varrho(\mu^*_\varrho,\varepsilon)}{\mu^*_\varrho} \leqslant -\frac{\lambda(\mu^*,\varepsilon)}{\mu^*} + \epsilon_1. \tag{4.2}$$

For the above $\epsilon_1 > 0$, by Lemma 2.6(3)(ii), there is $\mu_{\epsilon_1} > 0$ such that

$$-\frac{\partial \lambda^\varrho(\mu,\varepsilon)}{\partial \mu} < -\frac{\lambda^\varrho(\mu^*_\varrho,\varepsilon)}{\mu^*_\varrho} + \epsilon_1, \quad \forall \mu \in \big(\mu_{\epsilon_1},\mu^*_\varrho\big). \tag{4.3}$$

In the following, we fix $\mu \in (\mu_{\epsilon_1},\mu^*_\varrho)$. In terms of Lemma 2.6(3)(i), we see that

$$\lambda^\varrho(\mu,\varepsilon) - \mu \frac{\partial \lambda^\varrho(\mu,\varepsilon)}{\partial \mu} > 0. \tag{4.4}$$

Let $\kappa^\varrho_i(z,\mu;\varepsilon) = \frac{1}{\zeta^\varrho_i(z,\mu;\varepsilon)} \frac{\partial \zeta^\varrho_i(z,\mu;\varepsilon)}{\partial \mu}$, $i = 1,2$. Define $v = (v_1,v_2)$ with

$$v_i(s,x) = \begin{cases} \epsilon_2 \zeta^\varrho_i(x,\mu;\varepsilon) e^{-\mu s} \sin\gamma[s - \kappa^\varrho_i(x,\mu;\varepsilon)], & 0 \leqslant s - \kappa^\varrho_i(x,\mu;\varepsilon) \leqslant \frac{\pi}{\gamma}, \\ 0, & \text{otherwise}, \end{cases} \tag{4.5}$$

where ϵ_2 and γ are sufficiently small positive numbers. Let τ^ϱ_i be defined by

$$\tau^\varrho_i(\gamma,z) = \frac{1}{\gamma} \tan^{-1} \frac{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) \sin\gamma[-(y-z) + \kappa^\varrho_j(y,\mu;\varepsilon)] m_{ij}(z;y,dy)}{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) \cos\gamma[-(y-z) + \kappa^\varrho_j(y,\mu;\varepsilon)] m_{ij}(z;y,dy)}.$$

By Lebesgue dominated convergence theorem, we have

$$\begin{aligned} &\lim_{\gamma\to 0} \tau^\varrho_i(\gamma,z) \\ &\quad = \lim_{\gamma\to 0} \frac{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) \frac{\sin\gamma[-(y-z)+\kappa^\varrho_j(y,\mu;\varepsilon)]}{\gamma} m_{ij}(z;y,dy)}{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) \cos\gamma[-(y-z) + \kappa^\varrho_j(y,\mu;\varepsilon)] m_{ij}(z;y,dy)} \\ &\quad = \frac{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) [-(y-z) + \kappa^\varrho_j(y,\mu;\varepsilon)] m_{ij}(z;y,dy)}{\sum_{j=1}^2 \int_\mathbb{R} \zeta^\varrho_j(y,\mu;\varepsilon) e^{-\mu(y-z)} \chi(\frac{|y-z|}{\varrho}) m_{ij}(z;y,dy)} \end{aligned}$$

$$
\begin{aligned}
&= \frac{\sum_{j=1}^{2}\int_{\mathbb{R}} \frac{\partial}{\partial\mu}[\zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}]\chi(\frac{|y-z|}{\varrho})\, m_{ij}(z;y,\mathrm{d}y)}{r^{\varrho}(\mu,\varepsilon)\zeta_i^{\varrho}(z,\mu;\varepsilon)} \\
&= \frac{\frac{\partial}{\partial\mu}[\sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}\chi(\frac{|y-z|}{\varrho})\, m_{ij}(z;y,\mathrm{d}y)]}{r^{\varrho}(\mu,\varepsilon)\zeta_i^{\varrho}(z,\mu;\varepsilon)} \\
&= \frac{\frac{\partial}{\partial\mu}[r^{\varrho}(\mu,\varepsilon)\zeta_i^{\varrho}(z,\mu;\varepsilon)]}{r^{\varrho}(\mu,\varepsilon)\zeta_i^{\varrho}(z,\mu;\varepsilon)} \\
&= \frac{\partial\lambda^{\varrho}(\mu,\varepsilon)}{\partial\mu} + \kappa_i^{\varrho}(z,\mu;\varepsilon) \quad \text{uniformly for } z\in\mathbb{R}.
\end{aligned}
$$

Choose $\gamma > 0$ so small that

$$\gamma\big(\varrho + \big|\tau_i^{\varrho}(\gamma,z)\big| + \big|\kappa_j^{\varrho}(y,\mu;\varepsilon)\big|\big) < \pi \quad \text{and} \tag{4.6}$$

$$\kappa_i^{\varrho}(z,\mu;\varepsilon) - \tau_i^{\varrho}(\gamma,z) < -\lambda_{\mu}^{\varrho}(\mu,\varepsilon) + \epsilon_1, \quad \forall y,z\in\mathbb{R},\ 1\leqslant i,j\leqslant 2. \tag{4.7}$$

Set

$$\upsilon^*(x;s,z) = v\big(x+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z),\, x+z\big). \tag{4.8}$$

If $0\leqslant s-\kappa_i^{\varrho}(z,\mu;\varepsilon)\leqslant \frac{\pi}{\gamma}$ and $|y-z|\leqslant\varrho$, then by (4.6),

$$
\begin{aligned}
-\frac{\pi}{\gamma} &\leqslant -\varrho - \big|\tau_i^{\varrho}(\gamma,z)\big| - \big|\kappa_j^{\varrho}(y,\mu;\varepsilon)\big| \\
&\leqslant y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z)-\kappa_j^{\varrho}(y,\mu;\varepsilon) \\
&\leqslant \varrho + \frac{\pi}{\gamma} + \big|\tau_i^{\varrho}(\gamma,z)\big| + \big|\kappa_j^{\varrho}(y,\mu;\varepsilon)\big| \\
&\leqslant \frac{2\pi}{\gamma}.
\end{aligned}
$$

If $y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z)-\kappa_j^{\varrho}(y,\mu;\varepsilon)$ belongs to $[-\frac{\pi}{\gamma},0)$ or $(\frac{\pi}{\gamma},\frac{2\pi}{\gamma}]$, then

$$\sin\gamma\big[y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z)-\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\leqslant 0.$$

Therefore, by (4.8) and then via (4.5), we always get

$$
\begin{aligned}
\upsilon_j^*(y-z;s,z) &= v_j\big(y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z),\, y\big) \\
&\geqslant \epsilon_2\zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu[y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z)]} \\
&\quad \times \sin\gamma\big[y-z+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z)-\kappa_j^{\varrho}(y,\mu;\varepsilon)\big].
\end{aligned} \tag{4.9}
$$

Choose ϵ_2 sufficiently small such that

$$0\leqslant u\big(t,x;\upsilon^*(\cdot;s,z),z\big)\leqslant\boldsymbol{\delta}, \quad \forall t\in[0,1],\ x,z\in\mathbb{R}.$$

Let $\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon) := -\kappa_i^{\varrho}(z,\mu;\varepsilon) + \tau_i^{\varrho}(\gamma,z)$. Then according to (4.1), (2.27) and (4.9), for $0 \leqslant s - \kappa_i^{\varrho}(z,\mu;\varepsilon) \leqslant \frac{\pi}{\gamma}$, we obtain

$$\begin{aligned} u_i\big(1,0;\upsilon^*(\cdot;s,z),z\big) &\geqslant \big[\Phi^{\varrho}(1;0,\varepsilon,z)\upsilon^*\big]_i(0) \\ &= \sum_{j=1}^{2}\int_{\mathbb{R}} \upsilon_j^*(y-z;s,z)\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y) \\ &\geqslant \epsilon_2 \mathrm{e}^{-\mu[s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)]}\sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}\chi\left(\frac{|y-z|}{\varrho}\right) \\ &\quad \times \sin\gamma\big[y-z+s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)-\kappa_j^{\varrho}(y,\mu;\varepsilon)\big] m_{ij}(z;y,\mathrm{d}y). \end{aligned}$$

By means of $\sin(A-B) = \sin A\cos B - \cos A\sin B$, we get

$$\begin{aligned} &\sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}\chi\left(\frac{|y-z|}{\varrho}\right) \\ &\qquad \times \sin\gamma\big[y-z+s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)-\kappa_j^{\varrho}(y,\mu;\varepsilon)\big] m_{ij}(z;y,\mathrm{d}y) \\ &\quad = \sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}\cos\gamma\big[-(y-z)+\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y) \\ &\qquad \times \big\{\sin\gamma\big[s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)\big]-\cos\gamma\big[s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)\big]\tan\big(\gamma\tau_i^{\varrho}\big)\big\} \\ &\quad = \sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}\cos\gamma\big[-(y-z)+\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y) \\ &\qquad \times \sin\gamma\big[s-\kappa_i^{\varrho}(z,\mu;\varepsilon)\big]\sec\big(\gamma\tau_i^{\varrho}\big). \end{aligned}$$

Thus, we obtain

$$\begin{aligned} u_i\big(1,0;\upsilon^*(\cdot;s,z),z\big) &\geqslant \epsilon_2 \mathrm{e}^{-\mu[s+\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)]}\sin\gamma\big[s-\kappa_i^{\varrho}(z,\mu;\varepsilon)\big]\sec\big(\gamma\tau_i^{\varrho}\big) \\ &\quad \times \sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)} \\ &\quad \times \cos\gamma\big[-(y-z)+\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y) \\ &= \mathrm{e}^{-\mu\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)}\frac{v_i(s,z)}{\zeta_i^{\varrho}(z,\mu;\varepsilon)}\sec\big(\gamma\tau_i^{\varrho}\big)\sum_{j=1}^{2}\int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)} \\ &\quad \times \cos\gamma\big[-(y-z)+\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y). \end{aligned}$$

By (4.4), we see that

$$\lim_{\gamma\to 0} \mathrm{e}^{-\mu\eta_i^{\varrho}(z,\mu,\gamma;\varepsilon)} \frac{\sec(\gamma\tau_i^{\varrho})}{\zeta_i^{\varrho}(z,\mu;\varepsilon)} \sum_{j=1}^{2} \int_{\mathbb{R}} \zeta_j^{\varrho}(y,\mu;\varepsilon)\mathrm{e}^{-\mu(y-z)}$$
$$\times \cos\gamma\big[-(y-z)+\kappa_j^{\varrho}(y,\mu;\varepsilon)\big]\chi\left(\frac{|y-z|}{\varrho}\right) m_{ij}(z;y,\mathrm{d}y)$$
$$= \mathrm{e}^{-\mu\lambda_\mu^{\varrho}(\mu,\varepsilon)} r^{\varrho}(\mu,\varepsilon) = \mathrm{e}^{-\mu\lambda_\mu^{\varrho}(\mu,\varepsilon)+\lambda^{\varrho}(\mu,\varepsilon)} > 1.$$

It then follows that for $0 \leqslant s-\kappa_i^{\varrho}(z,\mu;\varepsilon) \leqslant \frac{\pi}{\gamma}$,

$$u_i\big(1,0;\upsilon^*(\cdot;s,z),z\big) \geqslant v_i(s,z).$$

By the definition of $v_i(s,z)$, it follows that the above inequality is true for all $s\in\mathbb{R}$. Now let $\bar\kappa = \max_{1\leqslant i\leqslant 2,\, z\in\mathbb{R}} \kappa_i^{\varrho}(z,\mu;\varepsilon)$ and define $\bar v = (\bar v_1, \bar v_2)$ with

$$\bar v_i(s,x) = \begin{cases} v_i(\bar s_i(x),x), & s \leqslant \bar s_i(x) - \frac{\pi}{\gamma} - \bar\kappa, \\ v_i(s+\frac{\pi}{\gamma}+\bar\kappa, x), & s \geqslant \bar s_i(x) - \frac{\pi}{\gamma} - \bar\kappa, \end{cases}$$

where $\bar s_i(x)$ is the maximum point of $v_i(\cdot,x)$ on $\mathbb{R}$. Let

$$\bar\upsilon^*(x;s,z) = \bar v\big(x+s-\kappa_i^{\varrho}(z,\mu;\varepsilon)+\tau_i^{\varrho}(\gamma,z), x+z\big).$$

Then it is easy to verify $u_i(1,0;\bar\upsilon^*(\cdot;s,z),z) \geqslant \bar v_i(s,z)$. Put $\tilde\upsilon^o(x;z) = \bar v(x,x+z)$. Since $\bar v(s,x)$ is non-increasing in s, we obtain

$$\begin{aligned} u_i\big(1,x;\tilde\upsilon^o(\cdot;z),z\big) &= u_i\big(1,0;\tilde\upsilon^o(\cdot+x;z),x+z\big) \\ &= u_i\big(1,0;\bar\upsilon^*\big(\cdot;x+\kappa_i^{\varrho}(x+z,\mu;\varepsilon)-\tau_i^{\varrho}(\gamma,x+z),x+z\big),x+z\big) \\ &\geqslant \bar v_i\big(x+\kappa_i^{\varrho}(x+z,\mu;\varepsilon)-\tau_i^{\varrho}(\gamma,x+z),x+z\big) \\ &\geqslant \bar v_i\big(x-\lambda_\mu^{\varrho}(\mu,\varepsilon)+\epsilon_1,x+z\big) \quad \big(\text{by (4.7)}\big) \\ &\geqslant \bar v_i\big(x-\lambda^{\varrho}\big(\mu_\varrho^*,\varepsilon\big)/\mu_\varrho^*+2\epsilon_1,x+z\big) \quad \big(\text{by (4.3)}\big) \\ &\geqslant \bar v_i\big(x-\lambda\big(\mu^*,\varepsilon\big)/\mu^*+3\epsilon_1,x+z\big) \quad \big(\text{by (4.2)}\big) \\ &= \tilde\upsilon_i^o\big(x-\tilde c^*;z+\tilde c^*\big) \quad \text{with } \tilde c^* = \lambda\big(\mu^*,\varepsilon\big)/\mu^* - 3\epsilon_1. \end{aligned}$$

Thus, we have

$$\begin{aligned} u_i\big(2,x;\tilde\upsilon^o(\cdot;z),z\big) &\geqslant u_i\big(1,x;\tilde\upsilon^o\big(\cdot-\tilde c^*;z+\tilde c^*\big),z\big) \\ &= u_i\big(1,x-\tilde c^*;\tilde\upsilon^o\big(\cdot;z+\tilde c^*\big),z+\tilde c^*\big) \\ &\geqslant \tilde\upsilon_i^o\big(x-2\tilde c^*;z+2\tilde c^*\big), \quad \forall z\in\mathbb{R}. \end{aligned}$$

By induction, we finally get

$$u_i\big(n,x;\tilde\upsilon^o(\cdot;z),z\big) \geqslant \tilde\upsilon_i^o\big(x-n\tilde c^*;z+n\tilde c^*\big), \quad \forall z\in\mathbb{R}.$$

By Lemma 3.4 and then Lemma 3.2(1), $\tilde c^* \leqslant c^*_{\inf}$, namely, $\lambda(\mu^*,\varepsilon)/\mu^* - 3\epsilon_1 \leqslant c^*_{\inf}$. Since ϵ_1 is arbitrary, we must have $\inf_{\mu>0} \frac{\lambda(\mu,\varepsilon)}{\mu} \leqslant c^*_{\inf}$.

Step 3. To prove that $c_+^* = \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}$. Combining steps 1 and 2, we have

$$\inf_{\mu>0} \frac{\lambda(\mu,\varepsilon)}{\mu} \leqslant c_{\inf}^* \leqslant c_{\sup}^* \leqslant \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}.$$

Letting $\varepsilon \to 0$, we see that $c_{\inf}^* = c_{\sup}^* =: c_+^* = \inf_{\mu>0} \frac{\lambda(\mu,0)}{\mu}$.

Step 4. To prove that $c_-^* = \inf_{\mu>0} \frac{\lambda(-\mu,0)}{\mu}$. By the change of variable $w(t,x) = u(t,-x)$ and continue the above procedure, we see that c_-^* is the spreading speed of the resulting equation for w. Hence, $c_-^* = \inf_{\mu>0} \frac{\lambda(-\mu,0)}{\mu}$.

Step 5. To prove that $c_+^* + c_-^* > 0$. There exist $\mu_1, \mu_2 > 0$ such that $c_+^* = \frac{\lambda(\mu_1,0)}{\mu_1}$ and $c_-^* = \frac{\lambda(-\mu_2,0)}{\mu_2}$. Let $\nu = \frac{\mu_1}{\mu_1+\mu_2}$. Then $\nu \in (0,1)$ and $(1-\nu)\mu_1 = \nu\mu_2$. Since $\lambda(\mu,0)$ is convex in μ, we get

$$\begin{aligned} c_+^* + c_-^* &= \frac{\lambda(\mu_1,0)}{\mu_1} + \frac{\lambda(-\mu_2,0)}{\mu_2} \\ &= \frac{1}{\nu\mu_2}\bigl[(1-\nu)\lambda(\mu_1,0) + \nu\lambda(-\mu_2,0)\bigr] \\ &\geqslant \frac{1}{\nu\mu_2}\lambda\bigl((1-\nu)\mu_1 - \nu\mu_2, 0\bigr) = \frac{1}{\nu\mu_2}\lambda(0,0) > 0. \qquad \square \end{aligned}$$

Theorem 4.2. *Let c_+^* and c_-^* be defined as in Theorem 4.1. Then the following statements are valid*:

(1) *For any $c < c_+^*$ and $c' < c_-^*$, if $u^o \in [0,u^*]_C$ with $u^o \not\equiv 0$, then*

$$\liminf_{t\to\infty,\ -c't \leqslant x \leqslant ct} \bigl[u\bigl(t,x;u^o,z\bigr) - u^*(x+z)\bigr] = 0 \quad \textit{uniformly in } z \in \mathbb{R}.$$

(2) *If $u^o \in [0,u^*]_C$ has compact support and satisfies $u^o(x) \ll u_{\inf}^*$ for all $x \in \mathbb{R}$, then for each $c > c_+^*$ and $c' > c_-^*$, $\limsup_{t\to\infty,\, x\geqslant ct} u(t,x;u^o,z) = 0$ and $\limsup_{t\to\infty,\, x\leqslant -c't} u(t,x;u^o,z) = 0$ uniformly in $z \in \mathbb{R}$.*

Proof. If $u^o \in [0,u^*]_C$ with $u^o \not\equiv 0$, then $u(t,x;u^o) \gg 0$ for any $t > 0$. Fix a $t_0 > 0$. Then for any given $r > 0$, we have $u(t_0,x;u^o) \geqslant \min_{|x|\leqslant r} u(t_0,x;u^o) \gg 0$ for all $|x| \leqslant r$. Now take $u(t_0,x;u^o)$ as a new initial data and the conclusions can be obtained by using the similar arguments to those in [26, Theorem D] except that r_σ may not be chosen to be independent of σ. In fact, since $Q(t)$ is subhomogeneous, we are able to use an analogous manner to that in [21, Proposition 3.3] or in [18, Corollary 2.16] to show that r_σ can be chosen to be independent of σ. $\square$

To finish this section, we apply our analytic results to the benthic-pelagic population model (1.1). Although the piecewise constant coefficient functions in (1.1) are not Hölder continuous, one may choose a sequence of smooth and L-periodic functions to approximate such a coefficient function. By a limiting process, we may carry the analytic results over to the case of model (1.1). Thus, we compute two spreading speeds by directly using the piecewise constant functions in model (1.1).

Linearizing (1.1) at the trivial solution $u = 0$ and recalling d, a, f, k, p are piecewise constant functions, we obtain

$$\begin{aligned} \frac{\partial u_1}{\partial t}(t,x) &= d\frac{\partial^2 u_1}{\partial x^2} - \frac{q}{a}\frac{\partial u_1}{\partial x} + ku_2 - ku_1, \\ \frac{\partial u_2}{\partial t}(t,x) &= pu_1 + (f-p)u_2, \quad x \in (0,L). \end{aligned}$$

According to (2.20), we have the following eigenvalue problem associated with (1.1):

$$d\xi_1''(x) - \left[\frac{q}{a} + 2\mu d\right]\xi_1'(x) + \left[d\mu^2 + \frac{q}{a}\mu - k\right]\xi_1(x) + k\xi_2(x) = \lambda\xi_1(x), \quad x \in (0, L),$$
$$p\xi_1(x) + [f - p]\xi_2(x) = \lambda\xi_2(x), \quad x \in (0, L), \qquad \xi_i(0) = \xi_i(L), \quad i = 1, 2.$$

For convenience, we use the subscripts 1 and 2 to denote the value of the coefficient functions on the good and bad patches, respectively, i.e., a_1 and a_2 and so on. On the bad patches, the growth rate becomes a death rate, hence $f_2 < 0$. Assume that the remaining parameters are positive and $f_1 < p_1$ on the good patches. Then it is easy to check that (1.1) satisfies our assumptions (A3)–(A5). Straightforward calculations show that $\lambda = \lambda(\mu)$ can be determined implicitly by the following expression:

$$\Psi^+(\mu, \lambda) = 0,$$

where

$$\Psi^+(\mu, \lambda) = \cosh\left(\mu L + \frac{q}{2}\left(l_1 + \frac{L - l_1}{a_2 d_2}\right)\right) - \cosh\big(\Lambda_1(\lambda) l_1\big)\cosh\big(\Lambda_2(\lambda)(L - l_1)\big)$$
$$- \sinh\big(\Lambda_1(\lambda) l_1\big)\sinh\big(\Lambda_2(\lambda)(L - l_1)\big)\frac{\Lambda_1^2(\lambda) + (d_2 a_2)^2 \Lambda_2^2(\lambda)}{2a_2 d_2 \Lambda_1(\lambda)\Lambda_2(\lambda)},$$
$$\Lambda_1(\lambda) = \sqrt{\lambda - g_1 + q^2/4}, \qquad \Lambda_2(\lambda) = \sqrt{(\lambda - g_2)/d_2 + q^2/\big(4a_2^2 d_2^2\big)},$$

and g_1, g_2 are defined as the values on the good and bad patches of $g = \frac{k(f-\lambda)}{p-f+\lambda}$. Let

$$\Psi^-(\mu, \lambda) = \Psi^+(-\mu, \lambda).$$

By Theorems 2.2, 2.5 and 4.1, it follows that the rightward and leftward spreading speeds of system (1.1) can be computed as

$$c_+^* = \frac{\lambda(\mu_1)}{\mu_1}, \qquad c_-^* = \frac{\lambda(-\mu_2)}{\mu_2},$$

where μ_1 satisfies $\Psi^+(\mu_1, \lambda(\mu_1)) = 0$ and $\frac{\lambda(\mu_1)}{\mu_1} = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu}$, and μ_2 satisfies $\Psi^-(\mu_2, \lambda(-\mu_2)) = 0$ and $\frac{\lambda(-\mu_2)}{\mu_2} = \inf_{\mu>0} \frac{\lambda(-\mu)}{\mu}$.

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References

[1] K. Bencala, R. Walters, Simulation of solute transport in a mountain pool-and-riffle stream: A transient storage model, Water Resour. Res. 19 (3) (1983) 718–724.
[2] H. Berestycki, F. Hamel, Front propagation in periodic excitable media, Comm. Pure Appl. Math. 55 (2002) 949–1032.
[3] H. Berestycki, F. Hamel, N. Nadirashvili, The speed of propagation for KPP type problems: I. Periodic framework, J. Eur. Math. Soc. 7 (2005) 173–213.
[4] H. Berestycki, F. Hamel, L. Roques, Analysis of the periodically fragmented environment model: II. Biological invasions and pulsating traveling fronts, J. Math. Pures Appl. 84 (2005) 1101–1146.
[5] H. Berestycki, F. Hamel, G. Nadin, Asymptotic spreading in heterogeneous diffusive excitable media, J. Funct. Anal. 255 (2008) 2146–2189.

[6] G. Butler, P. Waltman, Persistence in dynamical systems, J. Differential Equations 63 (1986) 255–263.
[7] D. DeAngelis, M. Loreau, D. Neergaard, P. Mulholland, E. Marzolf, Modelling nutrient-periphyton dynamics in streams: The importance of transient storage zones, Ecol. Model. 80 (1995) 149–160.
[8] K.-H. Föster, B. Nagy, Local spectral radii and Collatz–Wielandt numbers of monic operator polynomials with nonnegative coefficients, Linear Algebra Appl. 268 (1998) 41–57.
[9] H. Freedman, X.-Q. Zhao, Global asymptotics in some quasimonotone reaction–diffusion systems with delays, J. Differential Equations 137 (1997) 340–362.
[10] M. Freidlin, On wavefront propagation in periodic media, in: Stochastic Analysis and Applications, in: Adv. Probab. Relat. Top., vol. 7, Dekker, New York, 1984, pp. 147–166.
[11] J. Gärtner, M. Freidlin, On the propagation of concentration waves in periodic and random media, Soviet Math. Dokl. 20 (1979) 1282–1286.
[12] J. Guo, F. Hamel, Front propagation for discrete periodic monostable equations, Math. Ann. 335 (2006) 489–525.
[13] S.-B. Hsu, F.-B. Wang, X.-Q. Zhao, Dynamics of a periodically pulsed bio-reactor model with a hydraulic storage zone, J. Dynam. Differential Equations 23 (2011) 817–842.
[14] D. Henry, Geometric Theory of Semilinear Parabolic Equations, Lecture Notes in Math., vol. 840, Springer-Verlag, Berlin, 1981.
[15] J. Huang, W. Shen, Speeds of spread and propagation for KPP models in time almost and space periodic media, SIAM J. Appl. Dyn. Syst. 8 (2009) 790–821.
[16] N. Kinezaki, K. Kawasaki, F. Takasu, N. Shigesada, Modeling biological invasions into periodically fragmented environments, Theor. Popul. Biol. 64 (2003) 291–302.
[17] N. Kinezaki, K. Kawasaki, N. Shigesada, Spatial dynamics of invasion in sinusoidally varying environments, Popul. Ecol. 48 (2006) 263–270.
[18] X. Liang, X.-Q. Zhao, Asymptotic speeds of spread and traveling waves for monotone semiflows with applications, Comm. Pure Appl. Math. 60 (2007) 1–40; Comm. Pure Appl. Math. 61 (2008) 137–138 (Erratum).
[19] X. Liang, X.-Q. Zhao, Spreading speeds and traveling waves for abstract monostable evolution systems, J. Funct. Anal. 259 (2010) 857–903.
[20] F. Lutscher, M.A. Lewis, E. McCauley, Effects of heterogeneity on spread and persistence in rivers, Bull. Math. Biol. 68 (2006) 2129–2160.
[21] R. Lui, Biological growth and spread modeled by systems of recursions, Math. Biosci. 93 (1989) 269–312.
[22] H. Martin, H. Smith, Abstract functional differential equations and reaction–diffusion systems, Trans. Amer. Math. Soc. 321 (1990) 1–44.
[23] G. Nadin, Reaction–diffusion equations in space–time periodic media, C. R. Acad. Sci. Paris Sér. I 345 (2007) 489–493.
[24] G. Nadin, Traveling fronts in space–time periodic media, J. Math. Pures Appl. 92 (2009) 232–262.
[25] R.D. Nussbaum, Eigenvectors of nonlinear positive operator and the linear Krein–Rutman theorem, in: E. Fadell, G. Fournier (Eds.), Fixed Point Theory, in: Lecture Notes in Math., vol. 886, Springer, New York, Berlin, 1981, pp. 309–331.
[26] W. Shen, A. Zhang, Spreading speeds for monostable equations with nonlocal dispersal in space periodic habitats, J. Differential Equations 249 (2010) 747–795.
[27] N. Shigesada, K. Kawasaki, E. Teramoto, Traveling periodic waves in heterogeneous environments, Theor. Popul. Biol. 30 (1986) 143–160.
[28] N. Shigesada, K. Kawasaki, Biological Invasions: Theory and Practice, Oxford University Press, Oxford, 1997.
[29] W. Wang, X.-Q. Zhao, Basic reproduction numbers for reaction–diffusion epidemic models, SIAM J. Appl. Dyn. Syst. 11 (2012) 1652–1673.
[30] H.F. Weinberger, Long-time behavior of a class of biological models, SIAM J. Math. Anal. 13 (1982) 353–396.
[31] H.F. Weinberger, On spreading speeds and traveling waves for growth and migration models in a periodic habitat, J. Math. Biol. 45 (2002) 511–548.
[32] H.F. Weinberger, K. Kawasaki, N. Shigesada, Spreading speeds of spatially periodic integro-difference models for populations with nonmonotone recruitment functions, J. Math. Biol. 57 (2008) 387–411.
[33] P. Weng, X.-Q. Zhao, Spatial dynamics of a nonlocal and delayed population model in a periodic habitat, Discrete Contin. Dyn. Syst. Ser. A 29 (2011) 343–366.
[34] J. Xin, Existence and nonexistence of traveling waves and reaction–diffusion front propagation in periodic media, J. Stat. Phys. 73 (1993) 893–926.
[35] X.-Q. Zhao, Dynamical Systems in Population Biology, Springer, New York, 2003.