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Spreading Speeds and Traveling Waves for Non-cooperative Reaction–Diffusion Systems

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Abstract Much has been studied on the spreading speed and traveling wave solutions for cooperative reaction–diffusion systems. In this paper, we shall establish the spreading speed for a large class of non-cooperative reaction–diffusion systems and characterize the spreading speed as the slowest speed of a family of non-constant traveling wave solutions. Our results are applied to a partially cooperative system describing interactions between ungulates and grass.

Keywords Traveling waves · Non-cooperative systems · Spreading speed · Reaction–diffusion systems

Mathematics Subject Classification (2000) Primary 35K45 · 35K57 · 35B40 · Secondary 92D25 · 92D40

1 Introduction

Fisher (1937) studied the nonlinear parabolic equation

$$w_t = w_{xx} + w(1 - w) \tag{1.1}$$

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for the spatial spread of an advantageous gene in a population and conjectured c^* to be the asymptotic speed of propagation of the advantageous gene. His results show that (1.1) has a traveling wave solution of the form $w(x+ct)$ if and only if $|c| \geq c^* = 2$. Kolmogorov et al. (1937) proved similar results with a more general model. Those pioneering works along with the paper by Aronson and Weinberger (1975, 1978) confirmed the conjecture of Fisher and established the speeding spreads for nonlinear parabolic equations. Lui (1989) established the theory of spreading speeds for cooperative recursion systems. In a series of papers, Lewis et al. (2002), Li et al. (2005), Weinberger et al. (2002, 2007) studied spreading speeds and traveling waves for more general cooperative recursion systems, and in particular, for quite general cooperative reaction–diffusion systems by analyzing traveling waves and the convergence of initial data to wave solutions. Related information can also be found in Fife (1979), Hadeler and Rothe (1975), Volpert et al. (1994) and Weinberger (1982).

However, due to various biological or physical constraints, many reaction–diffusion systems are not necessarily cooperative. Thieme (1979) showed that the asymptotic spreading speed of a model with nonmonotone growth functions can still be obtained by constructing monotone functions. Weinberger et al. (2009) discussed the reaction–diffusion model

$$
\begin{aligned}
\frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1[-\alpha - \delta u_1 + r_1 u_2],\\
\frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + u_2 r_2\big[1 - u_2 + h(u_1)\big],
\end{aligned}
\tag{1.2}
$$

where $d_1, \alpha, \delta, r_1, d_2, r_2$ are all positive parameters. This system describes the interaction between ungulates with linear density $u_1(x,t)$ and grass with linear density $u_2(x,t)$. The function $h(u_1)$ models the increase in the specific growth rate of the grass due to the presence of ungulates. When the density u_1 is small the net effect of ungulates is increasingly beneficial, but as the density increases above a certain value, the benefits decrease with increasing u_1. (1.2) is a partially cooperative two-species reaction–diffusion model, meaning that it is cooperative for small population densities but not for large ones. By employing comparison methods, Weinberger et al. (2009) established spreading speeds for (1.2). In Sect. 5, we take the nonmonotone Ricker function $u_1 e^{-u_1}$ as $h(u_1)$, which is simpler than that of Weinberger et al. (2009), and apply our main theorem (Theorem 2.1) to (1.2). The application of our general theorem allows us to characterize the spreading speed as the slowest speed of traveling wave solutions to (1.2), which is new and was not proved in Weinberger et al. (2009). Non-cooperative reaction–diffusion systems frequently occur in other biological systems such as epidermal wound healing (see Sherratt and Murray 1990, 1991; Dale et al. 1994). In a recent paper by Wang (2010), spreading speeds and traveling waves for a non-cooperative reaction–diffusion model of epidermal wound healing were established.

For related nonmonotone integro-difference equations, Hsu and Zhao (2008), and Li et al. (2009) extended the theory of spreading speed and established the existence of traveling wave solutions. Wang and Castillo-Chavez (2010) proved that a large class of nonmonotone integro-difference systems have spreading speeds and traveling wave solutions. Such an extension is largely based on the construction of two monotone operators with appropriate properties and fixed point theorems in Banach spaces. A similar method was also used in works by Ma (2007) and Wang (2009) to prove the existence of traveling wave solutions of nonmonotone reaction–diffusion equations.

In this paper, we shall establish the spreading speed for a general non-cooperative system (1.3) and characterize its spread speed as the slowest speed of a family of non-constant traveling wave solutions of (1.3). Our main theorem (Theorem 2.1) will be applied to (1.2) in Sect. 5.

We begin with some notation. We shall use $R, k, k^{\pm}, f, f^{\pm}, r, u, v$ to denote vectors in $\mathbb{R}^N$ or N-vector valued functions, and x, y, ξ the single variable in $\mathbb{R}$. Let $u = (u_i), v = (v_i) \in \mathbb{R}^N$; we write $u \geq v$ if $u_i \geq v_i$ for all i, and $u \gg v$ if $u_i > v_i$ for all i. A vector u is positive if $u \gg 0$. For any $r = (r_i) \gg 0, r \in \mathbb{R}^N$ let

$$[0, r] = \{u : 0 \leq u \leq r, u \in \mathbb{R}^N\} \subseteq \mathbb{R}^N$$

and

$$\mathcal{C}_r = \{u = (u_i) : u_i \in C(\mathbb{R}, \mathbb{R}), 0 \leq u_i(x) \leq r_i \text{ for } x \in \mathbb{R},\ i = 1, \dots, N\},$$

where $C(\mathbb{R}, \mathbb{R})$ is the set of all continuous functions from $\mathbb{R}$ to $\mathbb{R}$.

Consider the system of reaction–diffusion equations

$$u_t = Du_{xx} + f(u) \quad \text{for } x \in \mathbb{R},\ t \geq 0 \tag{1.3}$$

with

$$u(x, 0) = u_0(x) \quad \text{for } x \in \mathbb{R}, \tag{1.4}$$

where $u = (u_i)$, $D = \text{diag}(d_1, d_2, \dots, d_N)$, $d_i > 0$ for $i = 1, \dots, N$

$$f(u) = (f_1(u), f_2(u), \dots, f_N(u)),$$

and $u_0(x)$ is a bounded uniformly continuous function on $\mathbb{R}$. In this paper, by a solution we mean a continuous function u, which is twice continuously differentiable with respect to x or ξ and once continuously differentiable with respect to t, that satisfies an appropriate system of equations.

In order to deal with a non-cooperative system, we shall assume that there are two additional cooperative systems

$$u_t = Du_{xx} + f^+(u) \quad \text{for } x \in \mathbb{R},\ t \geq 0, \tag{1.5}$$

$$u_t = Du_{xx} + f^-(u) \quad \text{for } x \in \mathbb{R},\ t \geq 0, \tag{1.6}$$

where f^+ lies above and f^- below f. Such an assumption will enable us to make use of the corresponding results for cooperative systems in Lui (1989), Weinberger et al. (2002) to establish spreading speeds for (1.3).

(H1) (i) Assume that $D = \mathrm{diag}(d_1, d_2, \dots, d_N)$, $d_i > 0$ for $i = 1, \dots, N$. Let $k^+ = (k_i^+) \gg 0$ and $f : [0, k^+] \to \mathbb{R}^N$ be a continuous and twice piecewise continuously differentiable function. Assume that $\mathcal{C}_{k^+}$ is an invariant set of (1.3) in the sense that, for any given $u_0 \in \mathcal{C}_{k^+}$, the solution of (1.3) with the initial condition u_0 exists and remains in $\mathcal{C}_{k^+}$ for $t \in [0, \infty)$.

(ii) Let $0 \ll k^- = (k_i^-) \le k = (k_i) \le k^+$. Assume that there exists a continuous and twice piecewise continuously differentiable function $f^\pm = (f_i^\pm) : [0, k^+] \to \mathbb{R}^N$ such that for $u \in [0, k^+]$

$$f^-(u) \le f(u) \le f^+(u).$$

(iii) $f(0) = f(k) = 0$ and there is no other positive equilibrium of f between 0 and k. $f^\pm(0) = f^\pm(k^\pm) = 0$. There is no other positive equilibrium of $f^\pm$ between 0 and $k^\pm$. f has finite numbers of equilibria.

(iv) (1.5) and (1.6) are cooperative (i.e., $\partial_i f_j^\pm(u) \ge 0$ for $u \in [0, k^\pm]$, $i \ne j$).

(v) $f^\pm(u)$, $f(u)$ have the same Jacobian matrix $f'(0)$ at $u = 0$.

A traveling wave solution u of (1.3) is a solution of the form $u = u(x + ct)$, $u \in C(\mathbb{R}, \mathbb{R}^N)$. Substituting $u(x,t) = u(x + ct)$ into (1.3) and letting $\xi = x + ct$, we obtain the wave equation

$$Du''(\xi) - cu'(\xi) + f\big(u(\xi)\big) = 0 \quad \text{for } \xi \in \mathbb{R}. \tag{1.7}$$

Now if we look for a solution of the form $(u_i) = (\mathrm{e}^{\lambda\xi}\eta_\lambda^i)$, $\lambda > 0$, $\eta_\lambda = (\eta_\lambda^i) \gg 0$ for the linearization of (1.7) at the origin, we arrive at the system

$$\mathrm{diag}\big(d_i\lambda^2 - c\lambda\big)\eta_\lambda + f'(0)\eta_\lambda = 0,$$

which can be rewritten as the following eigenvalue problem:

$$\frac{1}{\lambda} A_\lambda \eta_\lambda = c\eta_\lambda, \tag{1.8}$$

where

$$A_\lambda = \big(a_\lambda^{i,j}\big) = \mathrm{diag}\big(d_i\lambda^2\big) + f'(0).$$

The matrix $f'(0)$ has nonnegative off-diagonal elements. In fact, there is a constant α such that $f'(0) + \alpha I$ has nonnegative entries, where I is the identity matrix.

By reordering the coordinates, we can assume that $f'(0)$ is in block lower triangular form, in which all the diagonal blocks are irreducible or 1 by 1 zero matrices. A matrix is irreducible if it is not similar to a lower triangular block matrix with two blocks via a permutation. From the Perron–Frobenius theorem any irreducible matrix A with nonnegative entries has a unique principal positive eigenvalue (which is the spectral radius of A, $\rho(A)$) with a corresponding principal eigenvector with strictly positive coordinates. For an irreducible matrix A with nonnegative off-diagonal elements, we shall call the eigenvalue $\rho(A + \alpha I) - \alpha$ of A, which has the same positive eigenvector, the principal eigenvalue of A (see, e.g., Horn and Johnson 1985; Weinberger et al. 2002). Let

$$\Psi(A) = \rho(A + \alpha I) - \alpha.$$

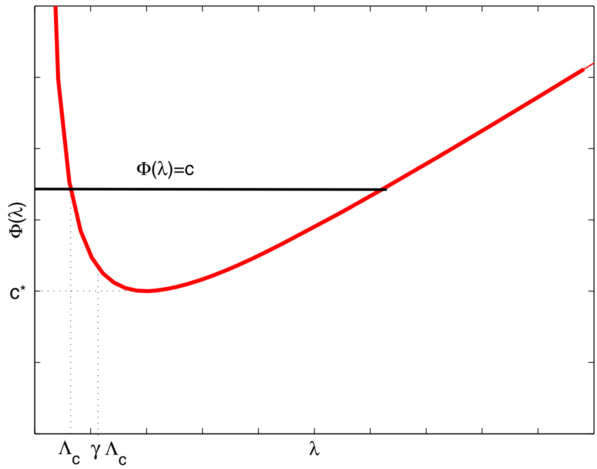

Fig. 1 (Color online) The *red curve* is $\Phi(\lambda)$. The minimum of $\Phi(\lambda)$ is c^*. For $c > c^*$, the left solution of $\Phi(\lambda) = c$ is Λ_c

Here $A + \alpha I$ is irreducible and nonnegative, and $\rho(A + \alpha I)$ is the spectral radius of $A + \alpha I$.

We shall need the following assumption (H2). Notice that (H2) is assumed for $\lambda = 0$ in Weinberger et al. (2002). However, with (H2), we are able to obtain better estimates for traveling solutions and the minimum speed c^*; see Lemma 1.1. As a result, the example in Sect. 5 requires a slightly stronger condition ($d_1 \geq d_2$) than that in Weinberger et al. (2009).

(H2) Assume that A_λ with irreducible blocks is in block lower triangular form. Further assume that its first diagonal block has the positive principal eigenvalue $\Psi(A_\lambda)$, and $\Psi(A_\lambda)$ is strictly larger than the principal eigenvalues of all other irreducible diagonal blocks for $\lambda > 0$. In addition, assume that there is a positive eigenvector $v_\lambda = (v_\lambda^i) \gg 0$ of A_λ corresponding to $\Psi(A_\lambda)$, and that v_λ is continuous with respect to λ for $\lambda > 0$.

Let

$$\Phi(\lambda) = \frac{1}{\lambda}\Psi(A_\lambda) > 0.$$

According to Lemma 1.1, we can expect the graph of Φ to appear as in Fig. 1. For the example in Sect. 5, Φ is a strictly convex function of λ and clearly satisfies Lemma 1.1.

Now we state Lemma 1.1, which shall enable us to calculate the minimum speed and give accurate asymptotic estimates of traveling solutions. Its proof is given in Appendix A.

Lemma 1.1 *Assume that* (H1)–(H2) *hold. Then*

(1) $\Phi(\lambda) \to \infty$ *as* $\lambda \to 0$;
(2) $\Phi(\lambda) \to \infty$ *as* $\lambda \to \infty$;
(3) $\Phi(\lambda)$ *is decreasing near* $\lambda = 0$ *and* $\lambda > 0$;
(4) $\Psi(A_\lambda)$ *is a convex function of* λ *for* $\lambda > 0$;
(5) $(\lambda^2\Phi'(\lambda))' = \lambda\frac{d^2\Psi(A_\lambda)}{d\lambda^2} \geq 0$;

(6) $\Phi'(\lambda)$ *changes sign at most once on* $(0,\infty)$;
(7) $\Phi(\lambda)$ *assumes its minimum*

$$c^* = \inf_{\lambda>0} \Phi(\lambda) > 0$$

at a finite λ.
(8) *For each* $c > c^*$, *there exist* $\Lambda_c > 0$ *and* $\gamma \in (1,2)$ *such that*

$$\Phi(\Lambda_c) = c, \qquad \Phi(\gamma\Lambda_c) < c.$$

That is,

$$\frac{1}{\Lambda_c} A_{\Lambda_c} \nu_{\Lambda_c} = \Phi(\Lambda_c)\nu_{\Lambda_c} = c\nu_{\Lambda_c}$$

and

$$\frac{1}{\gamma\Lambda_c} A_{\gamma\Lambda_c} \nu_{\gamma\Lambda_c} = \Phi(\gamma\Lambda_c)\nu_{\gamma\Lambda_c} < c\nu_{\gamma\Lambda_c},$$

where $\nu_{\Lambda_c} \gg 0$, $\nu_{\gamma\Lambda_c} \gg 0$ *are positive eigenvectors of* $\frac{1}{\Lambda_c}A_{\Lambda_c}$, $\frac{1}{\gamma\Lambda_c}A_{\gamma\Lambda_c}$ *corresponding to eigenvalues* $\Phi(\Lambda_c)$ *and* $\Phi(\gamma\Lambda_c)$, *respectively.*

Lemma 1.1 (1)–(3–6) is essentially due to Weinberger (1978) and Lui (1989). However, due to the fact that $f'(0)$ is only quasi-positive and the elements of A_λ are not necessarily log convex, some of its proofs here are different from those in Lui (1989). A theorem on the convexity of the dominant eigenvalue of matrices due to Cohen (1981) is used to show that $\Psi(A_\lambda)$ is a convex function of λ. Further, (2) and $c^* > 0$ in Lemma 1.1(7) are new, as Lui (1989) only establishes the existence of $c^* \geq 0$. Lemma 1.1(8) is new and is a direct consequence of (1)–(7).

There are two direct consequences of Lemma 1.1. First, it improves (Weinberger et al. 2002, Theorem 4.2), which will be used in this paper, by eliminating the case (b) in Weinberger et al. (2002, Theorem 4.2) because $c^* > 0$. Second, Lemma 1.1(8) will allow us to construct explicit lower solutions, therefore enabling us to obtain the asymptotic behavior of traveling solutions of (1.3).

In addition to (H1)–(H2), we also need assumption (H3), which only requires the nonlinearity to be less than its linearization along the particular function $\nu_\lambda e^{-\lambda x}$ (Weinberger et al. 2002). This means that the nonlinearity does not display an Allee effect for the particular function.

(H3) Assume that for any $\alpha > 0$, $\lambda > 0$

$$f^\pm(\alpha\nu_\lambda) \leq \alpha f'(0)\nu_\lambda, \quad \text{where } \nu_\lambda = (\nu_\lambda^i).$$

We now recall results on the spreading speeds in Weinberger et al. (2002) and Lui (1989). While Theorem 4.1 (Weinberger et al. 2002) holds for non-cooperative reaction–diffusion systems, it does require that the reaction–diffusion system have a single speed. In general, this condition is very difficult to verify. In the same section, for cooperative systems, Theorem 4.2 in Weinberger et al. (2002) provides sufficient conditions to have a single speed. The following theorem combines the results of

Theorems 4.1 and 4.2 in Weinberger et al. (2002), which can be a consequence of Theorems 3.1 and 3.2 for discrete-time recursions in Lui (1989).

Theorem 1.2 (Weinberger et al. 2002) *Assume* (H1)–(H3) *hold and* (1.3) *is* cooperative. *Then the following statements are valid.*

(i) *For any* $u_0 \in \mathcal{C}_k$ *with compact support, let* $u(x,t)$ *be the solution of* (1.3) *with* (1.4). *Then*

$$\lim_{t\to\infty} \sup_{|x|\geq ct} u(x,t) = 0, \quad \textit{for } c > c^*.$$

(ii) *For any strictly positive vector* $\omega \in \mathbb{R}^N$, *there is a positive* R_ω *with the property that if* $u_0 \in \mathcal{C}_k$ *and* $u_0 \geq \omega$ *on an interval of length* $2R_\omega$, *then the solution* $u(x,t)$ *of* (1.3) *with* (1.4) *satisfies*

$$\liminf_{t\to\infty} \inf_{|x|\leq tc} u(x,t) = k, \quad \textit{for } 0 < c < c^*.$$

In another paper Li et al. (2005), for *cooperative systems*, established that the slowest spreading speed c^* can always be characterized as the slowest speed of a family of traveling waves. These results describe the properties of spreading speed c^* for monotone systems. Based on these spreading results for cooperative systems, we will discuss analogous spreading speed results for non-cooperative systems.

2 Main Results

Our new contributions in this paper are to establish the asymptotic speed c^* (Theorem 2.1(i–ii)) for general non-cooperative reaction–diffusion systems (1.3), and further characterize the spreading speed as the speed of the slowest non-constant traveling wave solutions (Theorem 2.1(iii–v)). Note that, in the literature, the asymptotic speed and traveling wave solutions were largely discussed under different assumptions even for cooperative systems; see, e.g., Hsu and Zhao (2008), Li et al. (2005), Lui (1989), Weinberger et al. (2002). In this paper, we are able to identify the same assumptions (H1)–(H3) so that the two parts hold under the same assumptions. Therefore, our results provide a clear, coherent picture of the connection between the asymptotic speed c^* and traveling wave solutions.

Although the existence of traveling wave solutions for cooperative systems is known (see, e.g., Li et al. 2005), we shall prove the existence of traveling wave solutions for both cooperative and non-cooperative systems—our proofs for non-cooperative systems are based on those for cooperative systems. Further, we shall also be able to obtain the asymptotic behavior of the traveling wave solutions in terms of eigenvalues and eigenvectors for both cooperative and non-cooperative systems.

The following theorem contains our main results.

Theorem 2.1 *Assume that* (H1)–(H3) *hold. Then the following statements are valid.*

(i) *For any* $u_0 \in \mathcal{C}_k$ *with compact support, the solution* $u(x,t)$ *of* (1.3) *with* (1.4) *satisfies*

$$\lim_{t\to\infty}\sup_{|x|\geq tc} u(x,t)=0, \quad \textit{for } c>c^*.$$

(ii) *For any vector* $\omega\in\mathbb{R}^N$, $\omega\gg 0$, *there is a positive* R_ω *with the property that if* $u_0\in\mathcal{C}_k$ *and* $u_0\geq\omega$ *on an interval of length* $2R_\omega$, *then the solution* $u(x,t)$ *of* (1.3) *with* (1.4) *satisfies*

$$k^-\leq\liminf_{t\to\infty}\inf_{|x|\leq tc} u(x,t)\leq k^+, \quad \textit{for } 0<c<c^*.$$

(iii) *For each* $c>c^*$ (1.3) *admits a traveling wave solution* $u=u(x+ct)$ *such that* $0\ll u(\xi)\leq k^+, \xi\in\mathbb{R}$,

$$k^-\leq\liminf_{\xi\to\infty}u(\xi)\leq\limsup_{\xi\to\infty}u(\xi)\leq k^+$$

and

$$\lim_{\xi\to-\infty}u(\xi)\mathrm{e}^{-\Lambda_c\xi}=\nu_{\Lambda_c}. \tag{2.1}$$

If, in addition, (1.3) *is cooperative in* $\mathcal{C}_k$, *then* u *is nondecreasing on* $\mathbb{R}$.

(iv) *For* $c=c^*$ (1.3) *admits a non-constant traveling wave solution* $u=u(x+ct)$ *such that* $0\leq u(\xi)\leq k^+, \xi\in\mathbb{R}$.

(v) *For* $0<c<c^*$ (1.3) *does not admit a traveling wave solution* $u=u(x+ct)$ *with* $\liminf_{\xi\to\infty}u(\xi)\gg 0$ *and* $u(-\infty)=0$.

Remark 2.2 In many cases, $f^\pm$ can be taken as piecewise-defined functions consisting of f and appropriate constants as demonstrated in Sect. 5. In order to have a better estimate for the traveling wave solution u for non-cooperative systems, it is desirable to choose two functions $f^\pm$ which are close enough. The smallest monotone function above f and the largest monotone function below f are natural choices of $f^\pm$ if they satisfy other requirements, see Thieme (1979), Hsu and Zhao (2008), Li et al. (2009) for the discussion for scalar cases and Weinberger et al. (2009) for a partially cooperative reaction–diffusion system. Our construction of f^- in Sect. 5 is different than those in the previous papers.

Remark 2.3 The invariant set of (H1)(i) can often be established by the comparison principle (Theorem 3.1). In fact, for a given $u_0\in\mathcal{C}_{k^+}$, let $u(x,t)$ be the solution of (1.3) with the initial condition u_0. If we can choose appropriate f^-, f^+ so that $f^-(u)\leq f(u)\leq f^+(u)$ for all $u\in\mathbb{R}^N$, it follows that

$$k_t^+-Dk_{xx}^+-f^+\big(k^+\big)=0=u_t-Du_{xx}-f(u)\geq u_t-Du_{xx}-f^+(u)$$

and

$$0-D0-f^-(0)=0=u_t-Du_{xx}-f(u)\leq u_t-Du_{xx}-f^-(u).$$

The comparison principle (Theorem 3.1) implies that

$$0\leq u(x,t)\leq k^+ \quad \text{for } x\in\mathbb{R}, t>0.$$

Now according to Smoller (1994, Theorem 14.4) (1.3) (and also (1.5), (1.6)) has a solution u for $t \in [0, \infty)$ and $0 \le u \le k^+$ if the initial value u_0 is uniformly continuous on $\mathbb{R}$; see Sect. 5 for an example.

Remark 2.4 When (1.3) is cooperative in $\mathcal{C}_k$, we define $f^\pm = f$.

Remark 2.5 As indicated in Weinberger et al. (2002), if f is not defined everywhere, (H3) can be replaced by the following assumption.

(H3′) For each $\lambda > 0$, let $v^\pm = (\min\{k_i^\pm, \alpha\nu_\lambda^i\})$. Assume that for any $\alpha > 0$

$$f^\pm\bigl(v^\pm(x)\bigr) \le \alpha f'(0)\bigl(\nu_\lambda^i\bigr).$$

Theorem 2.1(i)–(ii) shall be proved in Sect. 3 and Theorem 2.1(iii)–(v) in Sect. 4.

3 The Asymptotic Spreading Speed

3.1 Comparison Principle

We state the following comparison theorem for cooperative systems of reaction–diffusion equations in Weinberger et al. (2009). The comparison principle is a consequence of the maximum principle (see, e.g., Protter and Weinberger 1984).

Theorem 3.1 *Let D be a positive definite diagonal matrix. Assume that $F = (F_j)$ is a vector-valued function in $\mathbb{R}^N$ that is continuous and piecewise continuously differentiable in $\mathbb{R}$ and the underlying system is cooperative in the sense that for each j, F_j is nondecreasing in all but the jth component. Suppose that $u(x,t)$, $v(x,t)$ satisfy*

$$u_t - Du_{xx} - F(u) \le v_t - Dv_{xx} - F(v). \tag{3.1}$$

If $u(x,t_0) \le v(x,t_0)$ for $x \in \mathbb{R}$, then

$$u(x,t) \le v(x,t) \quad \textit{for } x \in \mathbb{R}, t \ge t_0.$$

We are now able to prove parts (i) and (ii) of Theorem 2.1.

3.2 Proof of Parts (i) and (ii) of Theorem 2.1

Part (i). For a given $u_0 \in \mathcal{C}_k$ with compact support, let $u^+(x,t)$ be the solutions of (1.5) with the same initial condition u_0 as the solution u of (1.3). Then the comparison principle (Theorem 3.1) implies that $u^+(x,t) \in \mathcal{C}_{k^+}$,

$$u_t^+ - Du_{xx}^+ - f^+\bigl(u^+\bigr) = 0 = u_t - Du_{xx} - f(u) \ge u_t - Du_{xx} - f^+(u),$$

and

$$0 - D0 - f^-(0) = 0 = u_t - Du_{xx} - f(u) \le u_t - Du_{xx} - f^-(u).$$

Therefore, the comparison principle (Theorem 3.1) implies that

$$0 \le u(x,t) \le u^+(x,t) \quad \text{for } x \in \mathbb{R}, t > 0.$$

Thus for any $c > c^*$, it follows from Theorem 1.2(i) that

$$\lim_{t\to\infty} \sup_{|x|\ge tc} u^+(x,t) = 0,$$

and hence

$$\lim_{t\to\infty} \sup_{|x|\ge tc} u(x,t) = 0.$$

Part (ii). According to Theorem 1.2(ii), for any strictly positive constant ω, there is a positive R_ω (choose the larger one between the R_ω for (1.5) and the R_ω for (1.6)) with the property that if $u_0 \ge \omega$ on an interval of length $2R_\omega$, then the solutions $u^\pm(x,t)$ of (1.5) and (1.6) with the same initial value u_0 are in $\mathcal{C}_{k^+}$ and satisfy

$$\liminf_{t\to\infty} \inf_{|x|\le tc} u^\pm(x,t) = k^\pm, \quad \text{for } 0 < c < c^*.$$

As before we have

$$u_t^+ - Du_{xx}^+ - f^+\big(u^+\big) = 0 = u_t - Du_{xx} - f(u) \ge u_t - Du_{xx} - f^+(u)$$

and

$$u^- - Du_{xx}^- - f^-(u^-) = 0 = u_t - Du_{xx} - f(u) \le u_t - Du_{xx} - f^-(u).$$

Thus, the comparison principle (Theorem 3.1) implies that

$$u^-(x,t) \le u(x,t) \le u^+(x,t) \quad \text{for } x \in \mathbb{R}, t > 0.$$

Thus, for any $c < c^*$, it follows from Theorem 1.2(ii) that

$$\liminf_{t\to\infty} \inf_{|x|\le ct} u^\pm(x,t) = k^\pm,$$

and hence

$$k^- \le \liminf_{t\to\infty} \inf_{|x|\le ct} u(x,t) \le k^+.$$

4 The Characterization of c^* as the Slowest Speeds of Traveling Waves

4.1 Equivalent Integral Equations and Their Upper and Lower Solutions

In order to establish the existence of traveling wave solutions, we set up equivalent integral equations; this idea is discussed in standard textbooks for different equations. More recently, similar equivalent integral equations have also been used by a number of researchers; see, e.g., Wu and Zou (2001), Ma (2001, 2007) and Wang (2009). For convenience of analysis, in this paper and Wang (2009), both $\lambda_{1i}, \lambda_{2i}$ are chosen to be positive, and $-\lambda_{1i}, \lambda_{2i}$ are solutions of (4.1).

For $c > c^*$, the two solutions of the following equations:

$$d_i\lambda^2 - c\lambda - \beta = 0 \quad \text{for } i = 1, \dots, N \tag{4.1}$$

are $-\lambda_{1i}$ and λ_{2i}, where

$$\lambda_{1i} = \frac{-c + \sqrt{c^2 + 4\beta d_i}}{2d_i} > 0, \qquad \lambda_{2i} = \frac{c + \sqrt{c^2 + 4\beta d_i}}{2d_i} > 0.$$

We choose β sufficiently large so that

$$\begin{aligned} &\beta > \max\{|\partial_i f_j(x)|, x \in [0, k^+] \text{ for } i, j = 1, \dots, N\} > 0, \\ &\lambda_{2i} > \lambda_{1i} > 2\Lambda_c \quad \text{for } i = 1, \dots, N. \end{aligned} \tag{4.2}$$

Let $u = (u_i) \in \mathcal{C}_k$ and define an operator $\mathcal{T}[u] = (\mathcal{T}_i[u])$ by

$$\begin{aligned} \mathcal{T}_i[u](\xi) = \frac{1}{d_i(\lambda_{1i} + \lambda_{2i})} \biggl(&\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi - s)} H_i(u(s))\, \mathrm{d}s \\ &+ \int_{\xi}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi - s)} H_i(u(s))\, \mathrm{d}s \biggr), \end{aligned} \tag{4.3}$$

where

$$H_i(u(s)) = \beta u_i(s) + f_i(u(s)),$$

and $\mathcal{T}_i[u], i = 1, \dots, N$ is defined on $\mathbb{R}$ if $H_i(u), i = 1, \dots, N$ is a bounded continuous function. In fact, the following identity holds:

$$\begin{aligned} &\frac{1}{d_i(\lambda_{1i} + \lambda_{2i})} \left(\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi - s)} \beta\, \mathrm{d}s + \int_{\xi}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi - s)} \beta\, \mathrm{d}s \right) \\ &\quad = \frac{\beta}{d_i(\lambda_{1i} + \lambda_{2i})} \left(\frac{1}{\lambda_{1i}} + \frac{1}{\lambda_{2i}} \right) = \frac{\beta}{d_i(\lambda_{1i}\lambda_{2i})} \\ &\quad = 1. \end{aligned} \tag{4.4}$$

We shall show that a fixed point u of $\mathcal{T}$ or a solution of the equation

$$u(\xi) = \mathcal{T}[u](\xi) \quad \text{for } \xi \in \mathbb{R} \tag{4.5}$$

is a traveling wave solution of (1.3) in Lemma 4.1.

Lemma 4.1 *Assume that* (H1)–(H2) *hold. If $u \in \mathcal{C}_k$ is a fixed point of $\mathcal{T}[u]$,*

$$u(\xi) = \mathcal{T}[u](\xi) \quad \textit{for } \xi \in \mathbb{R},$$

then u is a solution of (1.7).

Proof Note that $H_i(u(s))$ are continuous functions on $\mathbb{R}$. Thus $\mathcal{T}[u](\xi)$ is defined and differentiable on $\mathbb{R}$. Direct calculations show that

$$\big(\mathcal{T}_i[u](\xi)\big)' = \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(-\lambda_{1i}\int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s)\big)\,ds \\ + \lambda_{2i}\int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s)\big)\,ds\bigg)$$

and

$$\big(\mathcal{T}_i[u](\xi)\big)'' = \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(\lambda_{1i}^2\int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s)\big)\,ds \\ + \lambda_{2i}^2\int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s)\big)\,ds \\ - \lambda_{1i}H_i\big(u(\xi)\big) - \lambda_{2i}H_i\big(u(\xi)\big)\bigg).$$

Noting that $-\lambda_{1i}, \lambda_{2i}$ are solutions of (4.1), one can evaluate the following expression:

$$\begin{aligned}
&\big(\mathcal{T}_i[u](\xi)\big)'' - c\big(\mathcal{T}_i[u](\xi)\big)' - \beta\mathcal{T}_i[u](\xi) \\
&= \frac{d_i\lambda_{1i}^2 + c\lambda_{1i}}{d_i(\lambda_{1i}+\lambda_{2i})}\int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s)\big)\,ds \\
&\quad + \frac{d_i\lambda_{2i}^2 - c\lambda_{2i}}{d_i(\lambda_{1i}+\lambda_{2i})}\int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s)\big)\,ds \\
&\quad - H_i\big(u(\xi)\big) - \beta\mathcal{T}[u](\xi) \\
&= \beta\mathcal{T}_i[u](\xi) - H_i\big(u(\xi)\big) - \beta\mathcal{T}_i[u](\xi) \\
&= -H_i\big(u(\xi)\big).
\end{aligned}$$

Now if $u(\xi) = \mathcal{T}[u](\xi)$ for $\xi \in \mathbb{R}$, then u is a solution of (1.7). □

We now define upper and lower solutions of (4.5), ϕ^+ and ϕ^-, which are only continuous on $\mathbb{R}$. Similar upper and lower solutions have been frequently used in the literature. See Diekmann (1978), Weinberger (1978), Lui (1989), Weinberger et al. (2002), Rass and Radcliffe (2003), Weng and Zhao (2006), and more recently, Ma (2007), Fang and Zhao (2009), Wang (2009), Wang and Castillo-Chavez (2010). In particular, it is believed that the vector-valued lower solutions of the form in this paper first appeared in Weng and Zhao (2006) for multi-type SIS epidemic models. We now define the upper and lower solutions for general reaction–diffusion systems, and we calculate the associated integrals to verify the validity of the upper and lower solutions.

Definition 4.2 A bounded continuous function $u = (u_i) \in C(\mathbb{R}, [0, \infty)^N)$ is an upper solution of (4.5) if

$$\mathcal{T}_i[u](\xi) \le u_i(\xi), \quad \text{for all } \xi \in \mathbb{R}, i = 1, \dots, N;$$

a bounded continuous function $u = (u_i) \in C(\mathbb{R}, [0, \infty)^N)$ is a lower solution of (4.5) if

$$\mathcal{T}_i[u](\xi) \ge u_i(\xi), \quad \text{for all } \xi \in \mathbb{R}, i = 1, \dots, N.$$

Let $c > c^*$ and consider the positive eigenvalue Λ_c and corresponding eigenvector $\nu_{\Lambda_c} = (\nu^i_{\Lambda_c})$ in Lemma 1.1 and $\gamma > 1, q > 1$. Define

$$\phi^+(\xi) = \big(\phi_i^+\big),$$

where

$$\phi_i^+ = \min\big\{k_i, \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi}\big\} \quad \text{for } i = 1, \dots, N, \xi \in \mathbb{R};$$

and

$$\phi^-(\xi) = (\phi_i^-),$$

$$\phi_i^- = \max\big\{0, \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} \mathrm{e}^{\gamma\Lambda_c \xi}\big\} \quad \text{for } i = 1, \dots, N, \xi \in \mathbb{R}.$$

It is clear that if $\xi \ge \frac{\ln \frac{k_i}{\nu^i_{\Lambda_c}}}{\Lambda_c}$, then $\phi_i^+(\xi) = k_i$, and if $\xi < \frac{\ln \frac{k_i}{\nu^i_{\Lambda_c}}}{\Lambda_c}$, then $\phi_i^+(\xi) = \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi}, i = 1, \dots, N$.

See Fig. 2 for the graphs of $\phi^\pm$. Similarly, if $\xi \ge \frac{\ln(q \frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})}{(1-\gamma)\Lambda_c}$, then $\phi_i^-(\xi) = 0$, and if $\xi < \frac{\ln(q \frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})}{(1-\gamma)\Lambda_c}$, then

$$\phi_i^-(\xi) = \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} \mathrm{e}^{\gamma\Lambda_c \xi} \quad \text{for } i = 1, \dots, N.$$

We choose $q > 1$ large enough so that

$$\frac{\ln(q \frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})}{(1-\gamma)\Lambda_c} < \frac{\ln \frac{k_i}{\nu^i_{\Lambda_c}}}{\Lambda_c} \quad \text{for } i = 1, \dots, N$$

and then

$$\phi_i^+(\xi) > \phi_i^-(\xi), \quad i = 1, \dots, N \text{ for } \xi \in \mathbb{R}.$$

For the lower solution, we need a restriction of γ. As in Wang (2009), for $\lambda > 0$ let

$$\big(M_i(\lambda)\big) = \beta \nu_\lambda - \lambda^2 D \nu_\lambda + A_\lambda \nu_\lambda$$

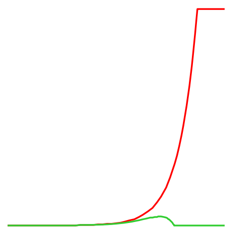

Fig. 2 (Color online) For each i, the curve above is ϕ_i^+ and the one below is ϕ_i^-

or

$$M_i(\lambda) = \beta\nu_\lambda^i - \nu_\lambda^i d_i \lambda^2 + \sum_{j=1}^{N} \nu_\lambda^j a_\lambda^{ij} \quad \text{for } i = 1, \dots, N, \tag{4.6}$$

where $\nu_\lambda = (\nu_\lambda^i)$ is the positive eigenvector of $\frac{1}{\lambda}A_\lambda$ in (1.8) corresponding to the principal eigenvalue $\Phi(\lambda)$. For $c > c^*$, recall that $\Phi(\Lambda_c) = c$. It follows that $\frac{1}{\Lambda_c}A_{\Lambda_c}\nu_{\Lambda_c} = \Phi(\Lambda_c)\nu_{\Lambda_c} = c\nu_{\Lambda_c}$ and

$$M_i(\Lambda_c) = \big(\beta - d_i\Lambda_c^2 + c\Lambda_c\big)\nu_{\Lambda_c}^i \quad \text{for } i = 1, \dots, N.$$

Because of (4.2), $M_i(\Lambda_c) > 0, i = 1, \dots, N$. Noting that $M_i(\lambda)$ is continuous with respect to λ, we can always choose a γ such that

$$1 < \gamma < 2, \quad M_i(\gamma\Lambda_c) > 0 \quad \text{for } i = 1, \dots, N. \tag{4.7}$$

We now state that ϕ^+ and ϕ^- are upper and lower solutions, respectively, of (4.5). The corresponding proofs will be given in Appendix B through careful analysis of the associated integrals.

Lemma 4.3 *Assume that* (H1)–(H3) *hold and* (1.3) *is cooperative. For any $c > c^*$, ϕ^+ defined above is an upper solution of* (4.5).

Lemma 4.4 *Assume that* (H1)–(H3) *hold and* (1.3) *is cooperative. Let γ satisfy* (4.7). *For any $c > c^*$, ϕ^- defined above is a lower solution of* (4.5) *if the constant q is sufficiently large.*

4.2 Proof of Theorem 2.1(iii) when (1.3) Is Cooperative

In this section, we assume that (1.3) is cooperative and prove Theorem 2.1(iii). In this case, $f^\pm = f$. Many results in this section are standard and are used to verify continuity and compactness of the operator. See, for example, Ma (2001, 2007) and Wang (2009). Define the following Banach space:

$$\mathcal{E}_\varrho = \Big\{u = (u_i) : u_i \in C(\mathbb{R}), \sup_{\xi\in\mathbb{R}} \big|u_i(\xi)\big|e^{-\varrho\xi} < \infty \text{ for } i = 1, \dots, N\Big\}$$

equipped with weighted norm

$$\|u\|_{\varrho} = \sum_{i=1}^{N} \sup_{\xi\in\mathbb{R}} \big|u_i(\xi)\big| e^{-\varrho\xi},$$

where $C(\mathbb{R})$ is the set of all continuous functions on $\mathbb{R}$ and ϱ is a positive constant such that $\varrho < \Lambda_c$. It follows that $\phi^+ \in \mathcal{E}_{\varrho}$ and $\phi^- \in \mathcal{E}_{\varrho}$. Consider the following set:

$$\mathcal{A} = \big\{u = (u_i) : u_i \in C(\mathbb{R}) \in \mathcal{E}_{\varrho}, \phi_i^-(\xi) \le u_i \le \phi_i^+(\xi) \text{ for } \xi \in \mathbb{R}, i = 1, \dots, N\big\}.$$

We shall prove the following lemma.

Lemma 4.5 *Assume that* (H1)–(H3) *hold and* $\partial_i f_j \ge 0, i \ne j$ *on* $[0, k]$. *Then* $\mathcal{T}$ *defined in* (4.3) *is monotone and therefore* $\mathcal{T}(\mathcal{A}) \subseteq \mathcal{A}$. *Furthermore*, $\mathcal{T}_i[u]$ *is nondecreasing if* $u \in \mathcal{A}$ *and all of* u_i *are nondecreasing.*

Proof Note that $H_i(u(\xi))$ and $\mathcal{T}[u](\xi)$ are bounded continuous functions on $\mathbb{R}$ if $u \in \mathcal{A}$. Note that $\beta > \max\{|\partial_i f_i(u)|, u \in [0, k], i = 1, \dots, N\} > 0$, $\partial_i g_j(u) \ge 0, u \in [0, k], i \ne j$. For any $u = (u_i), v = (u_i) \in \mathcal{A}$ with $u_i(\xi) \ge v_i(\xi)$ for $\xi \in \mathbb{R}$, we have, for $\xi \in \mathbb{R}$,

$$\begin{aligned} &H_i\big(u(\xi)\big) - H_i\big(v(\xi)\big) \\ &\quad = \beta\big(u_i(\xi) - v_i(\xi)\big) + \int_0^1 \frac{\partial f_i}{\partial u}\big(su(\xi) + (1-s)v(\xi)\big)\,ds\big(u(\xi) - v(\xi)\big) \ge 0. \end{aligned} \tag{4.8}$$

If $u \in \mathcal{A}$ and u_i are nondecreasing, we get, for $i = 1, \dots, N$, $\xi \in \mathbb{R}$ and $\xi_1 > 0$,

$$\begin{aligned} \mathcal{T}_i[u](\xi+\xi_1) - \mathcal{T}_i[u](\xi) &= \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(\int_{-\infty}^{\xi+\xi_1} e^{-\lambda_{1i}(\xi+\xi_1-s)} H_i\big(u(s)\big)\,ds \\ &\quad + \int_{\xi+\xi_1}^{\infty} e^{\lambda_{2i}(\xi+\xi_1-s)} H_i\big(u(s)\big)\,ds \\ &\quad - \int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s)\big)\,ds \\ &\quad - \int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s)\big)\,ds\bigg) \\ &= \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(\int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s+\xi_1)\big)\,ds \\ &\quad - \int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} H_i\big(u(s)\big)\,ds \\ &\quad + \int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s+\xi_1)\big)\,ds \\ &\quad - \int_{\xi}^{\infty} e^{\lambda_{2i}(\xi-s)} H_i\big(u(s)\big)\,ds\bigg). \end{aligned} \tag{4.9}$$

It follows from (4.8) that $\mathcal{T}_i[u](\xi+\xi_1) - \mathcal{T}_i[u](\xi) \ge 0$ for $\xi \in \mathbb{R}$ and $\xi_1 > 0$. □

Now we shall show that $\mathcal{T}[u]$ is continuous and maps a bounded set in $\mathcal{A}$ into a compact set.

Lemma 4.6 *Assume that* (H1)–(H3) *hold. Then* $\mathcal{T}:\mathcal{A}\to\mathcal{E}_\varrho$ *is continuous with the weighted norm* $\|\cdot\|_\varrho$.

Proof Let

$$L=\max\bigl\{\bigl|\partial_i f_j(u)\bigr|, u\in[0,k] \text{ for } i=1,\dots,N\bigr\}.$$

For any $u=(u_i)$, $v=(v_i)\in\mathcal{A}$, we have, for $\xi\in\mathbb{R}$,

$$\begin{aligned}
&\bigl|H_i\bigl(u(\xi)\bigr)-H_i\bigl(v(\xi)\bigr)\bigr|\mathrm{e}^{-\varrho\xi}\\
&\quad\le\beta\bigl|u_i(\xi)-v_i(\xi)\bigr|\mathrm{e}^{-\varrho\xi}+\left|\int_0^1\frac{\partial f_i}{\partial u}\bigl(su(\xi)+(1-s)v(\xi)\bigr)\,\mathrm{d}s\bigl(u(\xi)-v(\xi)\bigr)\right|\mathrm{e}^{-\varrho\xi}\\
&\quad\le(\beta+L)\|u-v\|_\varrho.
\end{aligned}\tag{4.10}$$

Thus, we obtain

$$\begin{aligned}
&\bigl|\mathcal{T}_i[u](\xi)-\mathcal{T}_i[v](\xi)\bigr|\mathrm{e}^{-\varrho\xi}\\
&\quad\le\frac{1}{(\lambda_{1i}+\lambda_{2i})}\biggl(\int_{-\infty}^{\xi}\mathrm{e}^{-\lambda_{1i}(\xi-s)}\bigl|H_i\bigl(u(s)\bigr)-H_i\bigl(v(s)\bigr)\bigr|\,\mathrm{d}s\\
&\qquad+\int_\xi^\infty\mathrm{e}^{\lambda_{2i}(\xi-s)}\bigl|H_i(u)(s)-H_i(v)(s)\bigr|\,\mathrm{d}s\biggr)\mathrm{e}^{-\varrho\xi}\\
&\quad\le\frac{(\beta+L)\|u-v\|_\varrho}{(\lambda_{1i}+\lambda_{2i})}\biggl(\int_{-\infty}^{\xi}\mathrm{e}^{-\lambda_{1i}(\xi-s)}\mathrm{e}^{\varrho s}\,\mathrm{d}s\\
&\qquad+\int_\xi^\infty\mathrm{e}^{\lambda_{2i}(\xi-s)}\mathrm{e}^{\varrho s}\,\mathrm{d}s\biggr)\mathrm{e}^{-\varrho\xi}\\
&\quad=\frac{\lambda_{1i}+\lambda_{2i}}{(\lambda_{1i}+\varrho)(\lambda_{2i}-\varrho)}\frac{(\beta+L)\|u-v\|_\varrho}{(\lambda_{1i}+\lambda_{2i})},
\end{aligned}\tag{4.11}$$

and

$$\bigl\|\mathcal{T}[u]-\mathcal{T}[v]\bigr\|_\varrho\le\frac{N(\beta+L)}{\min_i\{(\lambda_{1i}+\varrho)(\lambda_{2i}-\varrho)\}}\|u-v\|_\varrho.$$

Thus, $\mathcal{T}[u]$ is continuous. □

Lemma 4.7 *Assume that* (H1)–(H3) *hold. Then the set* $\mathcal{T}(\mathcal{A})$ *is relatively compact in* $\mathcal{E}_\varrho$.

Proof Let $\mathcal{N}_i=\max_{u\in\mathcal{A},\xi\in\mathbb{R}}H_i(u(\xi))<\infty$, $i=1,\dots,N$. Recall that

$$\frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl[\int_{-\infty}^{t}\mathrm{e}^{-\lambda_{1i}(t-s)}\,\mathrm{d}s+\int_t^\infty\mathrm{e}^{\lambda_{2i}(t-s)}\,\mathrm{d}s\biggr]=\frac{1}{\beta}.$$

If $u \in \mathcal{A}$, $\xi \in \mathbb{R}$, and $\delta > 0$ (without loss of generality), we have, for $i = 1, \dots, N$,

$$\begin{aligned}
&\mathcal{T}_i[u](\xi+\delta) - \mathcal{T}_i[u](\xi) \\
&\quad= \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(\int_{-\infty}^{\xi+\delta} \mathrm{e}^{-\lambda_{1i}(\xi+\delta-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s \\
&\qquad+ \int_{\xi+\delta}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi+\delta-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s \\
&\qquad- \int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s \\
&\qquad- \int_{\xi}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s\biggr) \\
&\quad= \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)}\bigl(\mathrm{e}^{-\lambda_{1i}\delta} H_i\bigl(u(s)\bigr) - H_i\bigl(u(s)\bigr)\bigr)\,\mathrm{d}s \\
&\qquad+ \int_{\xi}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi-s)}\bigl(\mathrm{e}^{\lambda_{2i}\delta} H_i\bigl(u(s)\bigr) - H_i\bigl(u(s)\bigr)\bigr)\,\mathrm{d}s \\
&\qquad+ \int_{\xi}^{\xi+\delta} \mathrm{e}^{-\lambda_{1i}(\xi+\delta-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s \\
&\qquad- \int_{\xi}^{\xi+\delta} \mathrm{e}^{\lambda_{2i}(\xi+\delta-s)} H_i\bigl(u(s)\bigr)\,\mathrm{d}s\biggr),
\end{aligned} \tag{4.12}$$

and

$$\begin{aligned}
\mathcal{T}_i[u](\xi+\delta) - \mathcal{T}_i[u](\xi)| &\le \max\bigl\{\bigl|\mathrm{e}^{-\lambda_{1i}\delta}-1\bigr|, \bigl|\mathrm{e}^{\lambda_{2i}\delta}-1\bigr|\bigr\}\frac{\mathcal{N}_i}{\beta} \\
&\quad+ \delta\frac{\mathcal{N}_i}{d_i(\lambda_{1i}+\lambda_{2i})} + \delta\mathrm{e}^{\lambda_{2i}\delta}\frac{\mathcal{N}_i}{d_i(\lambda_{1i}+\lambda_{2i})}.
\end{aligned}$$

Thus we establish that, for $i = 1, \dots, N$,

$$\lim_{\delta\to 0}\bigl(\mathcal{T}_i[u](\xi+\delta) - \mathcal{T}_i[u](\xi)\bigr) = 0, \quad \text{uniformly for all } u \in \mathcal{A}, \xi \in \mathbb{R}. \tag{4.13}$$

Take any sequence $(u^n) = (u_i^n) \in \mathcal{A}$ and let $v^n = (v_i^n) = \mathcal{T}[u^n]$. From Lemma 4.5 and (4.13), (v^n) is uniformly bounded on $\mathbb{R}$ and uniformly equicontinuous. For $I_m = [-m, m]$, $m \in \mathbb{N}$, by Ascoli's theorem and the standard diagonal process, we can construct subsequences (u^{n_m}) of (u^n) such that there is a function $v = (v_i)$, $v_i \in C(-\infty, \infty)$, $i = 1, \dots, N$ and $(v^{n_m} = \mathcal{T}[u^{n_m}])$ uniformly converges to v on each I_m for $m \in \mathbb{N}$. Now we need to show that $v \in \mathcal{A}$ and $\|v^{n_m} - v\|_\varrho \to 0$ as $n_m \to \infty$. By Lemma 4.5, $\phi_i^-(\xi) \le v_i(\xi) \le \phi_i^+(\xi)$, $i = 1, \dots, N$ for all $\xi \in \mathbb{R}$, and therefore $v \in \mathcal{A}$. Note that

$$\lim_{\xi\to\pm\infty}\bigl(\phi_i^+(\xi) - \phi_i^-(\xi)\bigr)\mathrm{e}^{-\varrho\xi} = 0 \quad \text{for } i = 1, \dots, N.$$

For any $\epsilon > 0$, we can find $K_0 > 0$ such that if $|\xi| > K_0$, then, for all $m \in \mathbb{N}$,

$$\left|v_i^{n_m}(\xi) - v_i\right| e^{-\varrho\xi} \le \left(\phi_i^+(\xi) - \phi_i^-(\xi)\right) e^{-\varrho\xi} < \epsilon \quad \text{for } i = 1, \ldots, N.$$

On the other hand, on $[-I_m, I_m]$, (v^{n_m}) uniformly converges to v. Thus there exists an $L > 0$ such that, for $n_m > L$,

$$\left|v_i^{n_m}(\xi) - v_i\right| e^{-\varrho\xi} < \epsilon \quad \text{for } \xi \in [-K_0, K_0], i = 1, \ldots, N.$$

Consequently, if $n_m > L$, the following inequality is true for all $\xi \in \mathbb{R}$:

$$\left|v_i^{n_m}(\xi) - v_i\right| e^{-\varrho\xi} < \epsilon \quad \text{for } i = 1, \ldots, N.$$

Thus $\|v^{n_m} - v\|_\varrho \to 0$ as $n_m \to \infty$. □

Now we are in a position to prove Theorem 2.1 when (1.3) is cooperative. Define the following iteration:

$$u^1 = \left(u_i^1\right) = \mathcal{T}\left[\phi^+\right], \qquad u^{n+1} = \left(u_i^n\right) = \mathcal{T}\left[u^n\right], \quad n > 1. \tag{4.14}$$

From Lemmas 4.3, 4.4, and 4.5, u^{n+1} is nondecreasing on $\mathbb{R}$, and

$$\phi_i^-(\xi) \le u_i^{n+1}(\xi) \le u_i^n(\xi) \le \phi_i^+(\xi) \quad \text{for } \xi \in \mathbb{R},\ n \ge 1, n = 1, \ldots, N.$$

By Lemma 4.7 and the monotonicity of (u^n), there is $u \in \mathcal{A}$ such that $\lim_{n\to\infty} \|u^n - u\|_\varrho = 0$. Lemma 4.6 implies that $\mathcal{T}[u] = u$. Furthermore, u is nondecreasing. It is clear that $\lim_{\xi\to-\infty} u_i(\xi) = 0, i = 1, \ldots, N$. Assume that $\lim_{\xi\to\infty} u_i(\xi) = k_i', i = 1, \ldots, N$, $k_i' > 0, i = 1, \ldots, N$ because of $u \in \mathcal{A}$. Applying the dominated convergence theorem to (4.3), we get $k_i' = \frac{1}{\beta}(\beta k_i' + f_i(k_1', \ldots, k_n'))$. By (H2), $k_i' = k_i$. Finally, note that

$$\nu_{\Lambda_c}^i \left(e^{\Lambda_c\xi} - q e^{\gamma\Lambda_c\xi}\right) \le u_i(\xi) \le \nu_{\Lambda_c}^i e^{\Lambda_c\xi} \quad \text{for } \xi \in \mathbb{R}.$$

We immediately obtain

$$\lim_{\xi\to-\infty} u_i(\xi) e^{-\Lambda_c\xi} = \nu_{\Lambda_c}^i \quad \text{for } i = 1, \ldots, N. \tag{4.15}$$

This completes the proof of Theorem 2.1(iii) when (1.3) is cooperative.

4.3 Proof of Theorem 2.1(iii)

Proof Theorem 2.1(iii) has been proved when (1.3) is cooperative in the last section. Now we need to prove it in the general case. In order to find traveling waves for (1.3), we will apply Schauder's fixed point theorem.

Let $u = (u_i) \in \mathcal{A}$ and define two integral operators

$$\mathcal{T}^\pm[u] = \left(\mathcal{T}_i^\pm[u]\right)$$

for f^- and f^+

$$\begin{aligned}\mathcal{T}_i^{\pm}[u](\xi) &= \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg[\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)} H_i^{\pm}\big(u(s)\big)\,\mathrm{d}s \\ &\quad + \int_{\xi}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi-s)} H_i^{\pm}\big(u(s)\big)\,\mathrm{d}s\bigg] \qquad (4.16)\end{aligned}$$

and

$$H_i^{\pm}\big(u(s)\big) = \beta u_i(s) + f_i^{\pm}\big(u(s)\big).$$

As in Sect. 4.2, both $\mathcal{T}^+$ and $\mathcal{T}^-$ are monotone. In view of Sect. 4.2 and the fact that f^- is nondecreasing, there exists a nondecreasing fixed point $u^- = (u_i^-)$ of $\mathcal{T}^-$ such that $\mathcal{T}^-[u^-] = u^-$, $\lim_{\xi\to\infty} u_i^-(\xi) = k_i^-$, $i = 1,\dots,N$, and $\lim_{\xi\to-\infty} u_i^-(\xi) = 0$, $i = 1,\dots,N$. Furthermore, $\lim_{\xi\to-\infty} u_i^-(\xi)\mathrm{e}^{-\Lambda_c\xi} = \nu_{\Lambda_c}^i$ for $i = 1,\dots,N$. According to Lemma 4.3, ϕ^+ (with k replaced by $k^{\pm}$) is also an upper solution of $\mathcal{T}^{\pm}$ because the proof of Lemma 4.3 is still valid if f is replaced by $f^{\pm}$. Let

$$\widetilde{\phi^+}(\xi) = \big(\widetilde{\phi_i^+}(\xi)\big),$$

where

$$\widetilde{\phi_i^+}(\xi) = \min\big\{k_i^+, \nu_{\Lambda_c}^i \mathrm{e}^{\Lambda_c\xi}\big\} \quad \text{for } i = 1,\dots,N,\ \xi\in\mathbb{R}.$$

It follows that $u_i^-(\xi) \le \widetilde{\phi_i^+}$ for $\xi\in\mathbb{R}$, $i = 1,\dots,N$. Now let

$$\mathcal{B} = \big\{u : u = (u_i)\in\mathcal{E}_\varrho, u^-(\xi) \le u(\xi) \le \widetilde{\phi^+}(\xi) \text{ for } \xi\in(-\infty,\infty)\big\}, \qquad (4.17)$$

where $\mathcal{E}_\varrho$ is defined in Sect. 4.2. It is clear that $\mathcal{B}$ is a bounded nonempty closed convex subset in $\mathcal{E}_\varrho$. Furthermore, we have, for any $u = (u_i)\in\mathcal{B}$,

$$u_i^- = \mathcal{T}_i^-[u^-] \le \mathcal{T}_i^-[u] \le \mathcal{T}_i[u] \le \mathcal{T}_i^+[u] \le \mathcal{T}_i^+\big[\widetilde{\phi^+}\big] \le \widetilde{\phi_i^+} \quad \text{for } i = 1,\dots,N.$$

Therefore, $\mathcal{T} : \mathcal{B}\to\mathcal{B}$. Note that the proofs of Lemmas 4.6 and 4.7 are valid if (1.3) is not cooperative. In the same way as in Lemmas 4.6 and 4.7, we can show that $\mathcal{T} : \mathcal{B}\to\mathcal{B}$ is continuous and maps bounded sets into compact sets. Therefore, the Schauder fixed point theorem shows that the operator $\mathcal{T}$ has a fixed point u in $\mathcal{B}$, which is a traveling wave solution of (1.3) for $c > c^*$. Since $u_i^-(\xi) \le u_i(\xi) \le \widetilde{\phi_i^+}(\xi)$, $\xi\in(-\infty,\infty)$, $i = 1,\dots,N$, it is easy to see that for $i = 1,\dots,N$, $\lim_{\xi\to-\infty} u_i(\xi) = 0$, $\lim_{\xi\to-\infty} u_i(\xi)\mathrm{e}^{-\Lambda_c\xi} = \nu_{\Lambda_c}^i$,

$$k^- \le \liminf_{\xi\to\infty} u(\xi) \le \limsup_{\xi\to\infty} u(\xi) \le k^+$$

and $0 < u_i^-(\xi) \le u_i(\xi) \le k_i^+$ for $\xi\in(-\infty,\infty)$. □

4.4 Proof of Theorem 2.1(iv)

Proof We adopt the limiting approach in Brown and Carr (1977) to prove Theorem 2.1(iv). For each $n \in \mathbb{N}$, choose $c_n > c^*$ such that $\lim_{n\to\infty} c_n = c^*$. According to Theorem 2.1(iii), for each c_n there is a traveling wave solution u_n of (1.3) such that

$$u_n = \mathcal{T}[u_n](\xi),$$

and

$$k^- \le \liminf_{\xi\to\infty} u_n(\xi) \le \limsup_{\xi\to\infty} u_n(\xi) \le k^+.$$

As it has shown in (4.12), (u_n) is equicontinuous and uniformly bounded on $\mathbb{R}$, and Ascoli's theorem implies that there is vector-valued continuous functions u on $\mathbb{R}$ and subsequences (u_{n_m}) of (u_n), such that

$$\lim_{m\to\infty} u_{n_m}(\xi) = u(\xi)$$

uniformly in ξ on any compact interval of $\mathbb{R}$. Further, in view of the dominated convergence theorem, we have

$$u = \mathcal{T}[u](\xi).$$

Here the underlying $\lambda_{1i}, \lambda_{2i}$ of $\mathcal{T}$ are dependent on c and continuous functions of c. Thus u is a traveling solution of (1.3) for $c = c^*$. Because of the translation invariance of u_n, we always can assume that the first component of $u_n(0)$ equals to a sufficiently small positive number for all n. Note that there are only finite number of equilibria. Consequently, u is a non-constant traveling solution of (1.3). □

4.5 Proof of Theorem 2.1(v)

Proof Suppose, by contradiction, that for some $c \in (0, c^*)$, (1.3) has a traveling wave $u(x,t) = u(x+ct)$ with $\liminf_{\xi\to\infty} u(\xi) \gg 0$ and $u(-\infty) = 0$. Thus $u(x,t) = u(x+ct)$ can be larger than a positive vector with arbitrary length. It follows from Theorem 2.1(ii) that

$$\liminf_{t\to\infty} \inf_{|x|\le ct} u(x,t) \ge k^- \gg 0, \quad \text{for } 0 < c < c^*.$$

Let $\hat{c} \in (c, c^*)$ and $x = -\hat{c}t$. Then

$$\lim_{t\to\infty} u\bigl(-(\hat{c}-c)t\bigr) = \lim_{t\to\infty} u(-\hat{c}t, t) \ge \liminf_{t\to\infty} \inf_{|x|\le t\hat{c}} u(x,t) \gg 0.$$

However,

$$\lim_{t\to\infty} u\bigl(-(\hat{c}-c)t\bigr) = u(-\infty) = 0,$$

which is a contradiction. □

5 An Example

Weinberger et al. (2009) established the spreading speed for (1.2) with $h(u_1)$ being unimodal on [0, 1] based on the spreading results for cooperative systems in Weinberger et al. (2002). Our choice of $h(u_1)$ is slightly different and simpler than the one in Weinberger et al. (2009).

Our new contribution to (1.2) is to characterize the spreading speed as the slowest speed of a family of non-constant traveling wave solutions of (1.2). One example of $h(u_1)$ in this paper is $h(u_1) = u_1 e^{-u_1}$. (1.2) has the two equilibria (0, 0), (0, 1) and the coexistence equilibrium. In order to study the invasion of the monoculture equilibrium (0, 1) by the first species, we introduce the new variables $w_1 = u_1$, $w_2 = u_2 - 1$; then (1.2) becomes

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= d_1 \Delta w_1 + w_1[r_1 - \alpha - \delta w_1 + r_1 w_2], \\ \frac{\partial w_2}{\partial t} &= d_2 \Delta w_2 + r_2(1 + w_2)\big[-w_2 + h(w_1)\big]. \end{aligned} \tag{5.1}$$

In this section, we make the following assumptions.

(H4) (i) Assume that h is continuously differentiable on $[0,\infty)$ and $h(0) = 0$, $h'(0) > 0$, $h(w_1) > 0$ for $w_1 \in (0,\infty)$. Also assume that there is a $w_m > 0$ and that h is increasing on $[0, w_m]$ and decreases on $[w_m,\infty)$ and $\lim_{w_1\to\infty} h(w_1) = 0$.

(ii) Assume that $\frac{h(w_1)}{w_1}$ is strictly decreasing on $(0,\infty)$.

(iii)

$$\big(h(w_1)\big)^2 + 4h(w_1) - 4h'(0)w_1 \le 0 \quad \text{for } w_1 \in [0,\infty). \tag{5.2}$$

(iv) $d_1, \alpha, \delta, r_1, d_2, r_2$ are all positive numbers. $d_1 \ge d_2$, $\alpha < r_1$, $k_1 > w_m$.

(v)

$$\delta \ge \frac{r_1 r_2 h'(0)}{r_1 + r_2 - \alpha}. \tag{5.3}$$

(H4)(i)–(ii) imply that

$$h(w_1) \le h'(0) w_1 \quad \text{for } w_1 \in [0,\infty). \tag{5.4}$$

We need to verify that $h(w_1) = w_1 e^{-w_1}$ satisfies (H4). $h(w_1) = w_1 e^{-w_1}$ achieves its maximum at $w_m = 1$, and is increasing on $[0, w_m]$ and decreasing on $[w_m,\infty)$. In addition, $h'(0) = 1$ and $h(w_1)/w_1 = e^{-w_1}$ is decreasing for $w_1 > 0$. It is easy to see that $e^x > x+1$ for $x > 0$ and $e^{-x} < \frac{1}{x+1}$ for $x > 0$. Thus, for $w_1 > 0$,

$$\begin{aligned}
&\big(h(w_1)\big)^2 + 4h(w_1) - 4h'(0)w_1 \\
&\quad \le \frac{w_1^2}{2w_1+1} + \frac{4w_1}{w_1+1} - 4w_1 \\
&\quad = \frac{w_1^2(w_1+1) + 4w_1(2w_1+1) - 4w_1(2w_1+1)(w_1+1)}{(2w_1+1)(w_1+1)} \\
&\quad = \frac{-7w_1^3 - 3w_1^2}{(2w_1+1)(w_1+1)} < 0.
\end{aligned} \tag{5.5}$$

We now demonstrate that Theorem 2.1 can be used to establish spreading speed and traveling wave solutions of the nonmonotone system (5.1). The following theorem contains the results for (5.1).

Theorem 5.1 *Assume that* (H4) *holds. Then the conclusions of Theorem* 2.1 *hold for* (5.1) *for the minimum speed* $c^* = 2\sqrt{(r_1-\alpha)d_1}$, $\Lambda_c = \frac{c-\sqrt{c^2-4d_1(r_1-\alpha)}}{2d_1} > 0$, *and* ν_{Λ_c}, *where* ν_λ *is defined in* (5.14).

Remark 5.2 If $w_m \ge k_1$, (5.1) is a cooperative system. As indicated in Remark 2.4, Theorem 5.1 can be proved by choosing $f^\pm$ to be f.

We now need to check that (H1), (H2), and (H3) hold for (5.1). In the nonnegative quadrant, (5.1) has two equilibria, (0, 0) and (k_1, k_2), where

$$\begin{aligned}
\alpha + \delta k_1 &= r_1 + r_1 h(k_1), \\
k_2 &= h(k_1).
\end{aligned} \tag{5.6}$$

We claim that (5.6) has only one positive solution. In fact, the first equation of (5.6) can be rewritten as

$$1 = \frac{r_1 - \alpha + r_1 h(k_1)}{\delta k_1}. \tag{5.7}$$

From (H4)(ii), $\frac{r_1-\alpha+r_1h(w_1)}{\delta w_1}$ is strictly decreasing from ∞ to 0 on $(0,\infty)$ and $1 = \frac{r_1-\alpha+r_1h(k_1)}{\delta k_1}$ has only one solution.

In order to use Theorem 2.1, we shall define the two monotone systems

$$h^+(w_1) = \begin{cases} h(w_1), & \text{for } 0 \le w_1 \le w_m, \\ h(w_m), & \text{for } w_1 \ge w_m, \end{cases}$$

and the corresponding cooperative system is

$$\begin{aligned}
\frac{\partial w_1}{\partial t} &= d_1 \Delta w_1 + w_1[r_1 - \alpha - \delta w_1 + r_1 w_2], \\
\frac{\partial w_2}{\partial t} &= d_2 \Delta w_2 + r_2(1+w_2)\big[-w_2 + h^+(w_1)\big].
\end{aligned} \tag{5.8}$$

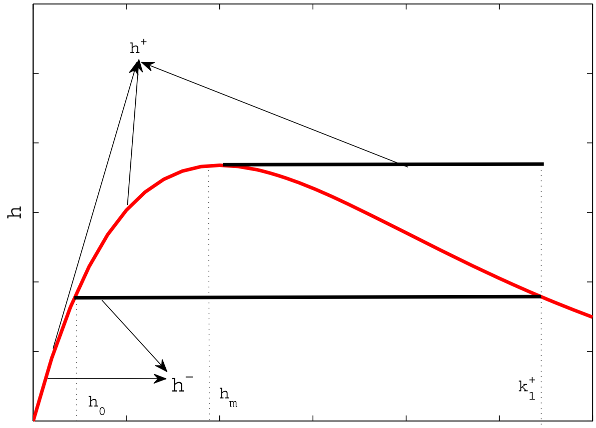

Fig. 3 (Color online) The construction of h^+ and h^-. The *red curve* is h

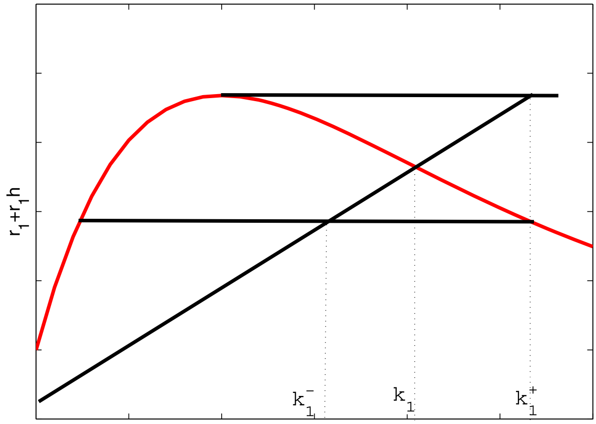

Fig. 4 (Color online) The intersections of $r_1 + r_1 h(w_1), r_1 + r_1 h^{\pm}(w_1)$ with the line $\alpha + \delta w_1$. The *red curve* is $r_1 + r_1 h$

In a similar manner, one can find that (5.8) has two equilibria, $(0,0)$ and (k_1^+, k_2^+), satisfying

$$\begin{aligned} \alpha + \delta k_1^+ &= r_1 + r_1 h^+\big(k_1^+\big), \\ k_2^+ &= h^+\big(k_1^+\big). \end{aligned} \tag{5.9}$$

Since $h^+ \geq h$, from the first equations of (5.6) and (5.9), it is easily seen that $k_1^+ \geq k_1$. In addition, since $k_1 > w_m$, we have $k_2^+ = h^+(k_1^+) = h(w_m) \geq h(k_1) = k_2$.

Now there is an $h_0 \in (0, w_m]$ such that $h(h_0) = h(k_1^+)$ and we define

$$h^-(w_1) = \begin{cases} h(w_1), & \text{for } 0 \leq w_1 \leq h_0, \\ h(k_1^+), & \text{for } w_1 > h_0. \end{cases}$$

Then

$$0 < h^-(w_1) \leq h(w_1) \leq h^+(w_1) \leq h'(0) w_1 \quad \text{for } w_1 \in \big(0, k_1^+\big].$$

The corresponding cooperative system for h^- is

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= d_1 \Delta w_1 + w_1[r_1 - \alpha - \delta w_1 + r_1 w_2], \\ \frac{\partial w_2}{\partial t} &= d_2 \Delta w_2 + r_2(1 + w_2)\big[-w_2 + h^-(w_1)\big]. \end{aligned} \tag{5.10}$$

In a similar manner, one can find that (5.10) has two equilibria, (0, 0) and (k_1^-, k_2^-), satisfying

$$\begin{aligned} \alpha + \delta k_1^- &= r_1 + r_1 h^-(k_1^-), \\ k_2^- &= h^-(k_1^-). \end{aligned} \tag{5.11}$$

Similarly, we have $k_1^- \le k_1$. Also see Fig. 3 and 4. In addition, by the definition of h^-, we have

$$k_2^- = h^-(k_1^-) \le h\big(k_1^+\big) \le h(k_1) = k_2.$$

Thus,

$$(0, 0) \ll (k_1^-, k_2^-) \le (k_1, k_2) \le \big(k_1^+, k_2^+\big).$$

As discussed in Remark 2.3, an invariance set for (5.1) can be established by the comparison principle (Theorem 3.1). First we can extend h, h^+ in (5.1) and (5.8) to zero for $w_1 < 0$. Let f, f^+ be the reaction terms in (5.1) and (5.8), respectively. Further, let f^- be the reaction terms in (5.10) with h being replaced by the constant zero function for all $w_1 \in \mathbb{R}$. From Remark 2.3, we can see that $\{(w_1, w_2) : 0 \le w_i \le k_i^+, i = 1, 2\}$ is an invariance set for (5.1). It is straightforward to check all other conditions of (H1)(i)–(v).

We now check that (H2) holds for (5.1). The linearization of (5.1) at the origin is

$$\begin{aligned} \frac{\partial w_1}{\partial t} &= d_1 \Delta w_1 + (r_1 - \alpha) w_1, \\ \frac{\partial w_2}{\partial t} &= d_2 \Delta w_2 + r_2\big(h'(0) w_1 - w_2\big). \end{aligned} \tag{5.12}$$

The matrix in (1.8) for (5.1) is

$$A_\lambda = \big(a_\lambda^{i,j}\big) = \begin{pmatrix} d_1\lambda^2 + r_1 - \alpha & 0 \\ r_2 h'(0) & d_2\lambda^2 - r_2 \end{pmatrix}. \tag{5.13}$$

Because $d_1 \ge d_2$ and $r_1 > \alpha$, the principal eigenvalue A_λ is $\Psi(A_\lambda) = d_1\lambda^2 + r_1 - \alpha$, which is a convex function of λ. Therefore,

$$\Phi(\lambda) = \frac{\Psi(A_\lambda)}{\lambda} = \frac{d_1\lambda^2 + r_1 - \alpha}{\lambda}$$

satisfies the results of Lemma 1.1. In fact, $\Phi(\lambda)$ is also a strictly convex function of λ. The minimum of $\Phi(\lambda)$ is $c^* = 2\sqrt{(r_1 - \alpha) d_1}$. For each $\lambda > 0$, the positive eigenvector of A_λ corresponding to $\Psi(\lambda)$ is

$$\nu_\lambda = \begin{pmatrix} \nu_\lambda^1 \\ \nu_\lambda^2 \end{pmatrix} = \begin{pmatrix} (d_1 - d_2)\lambda^2 + r_1 + r_2 - \alpha \\ r_2 h'(0) \end{pmatrix}. \tag{5.14}$$

For each $c > c^*$, the smaller positive solution of $\Phi(\lambda) = c$ is

$$\Lambda_c = \frac{c - \sqrt{c^2 - 4d_1(r_1 - \alpha)}}{2d_1}$$

in Lemma 1.1. Further, from (5.14) we can see that

$$\frac{\nu_\lambda^2}{\nu_\lambda^1} = \frac{r_2 h'(0)}{(d_1 - d_2)\lambda^2 + r_1 + r_2 - \alpha} = \frac{h'(0)}{\sigma},$$

where $\sigma = 1 + \frac{r_1 - \alpha + (d_1 - d_2)\lambda^2}{r_2} > 1$.

It remains to be seen that (H3) holds for (5.8). Let

$$(w_1, w_2) = \left(\theta, \theta \frac{h'(0)}{\sigma}\right) \gg (0, 0) \quad \text{for } \theta > 0.$$

Thus (H3) is equivalent to the following two inequalities:

$$w_1[r_1 - \alpha - \delta w_1 + r_1 w_2] \le (r_1 - \alpha) w_1,$$
$$r_2(1 + w_2)\big[-w_2 + h^+(w_1)\big] \le r_2\big(h'(0) w_1 - w_2\big)$$

or

$$\delta w_1 \ge r_1 w_2 \tag{5.15}$$

and

$$h'(0) w_1 + w_2^2 \ge h^+(w_1)(1 + w_2). \tag{5.16}$$

Therefore, the following equality suffices to verify (5.15):

$$\delta\theta \ge r_1 \theta \frac{h'(0)}{1 + \frac{r_1 - \alpha}{r_2}},$$

which is equivalent to (5.3).

In order to verify (5.16), following Weinberger et al. (2009), there always is a positive constant σ such that

$$w_2 = \frac{h'(0)}{\sigma} w_1.$$

We eliminate w_2 from (5.16) by using $w_2 = \frac{h'(0)}{\sigma} w_1$ and multiplying the resulting inequality by $\frac{\sigma^2}{h'(0)w_1}$ to obtain the equivalent inequality

$$\sigma^2 + h'(0)w_1 \geq \frac{\sigma^2 h^+(w_1)}{h'(0)w_1} + \sigma h^+(w_1).$$

Rearranging the terms produces

$$-\sigma^2\left(1 - \frac{h^+(w_1)}{h'(0)w_1}\right) + \sigma h^+(w_1) - h'(0)w_1 \leq 0 \quad \text{for } w_1 > 0. \tag{5.17}$$

Recall the definition that $h^+(w_1) = h(w_1)$ for $w_1 \leq w_m$ and $h^+(w_1) = h(w_m)$ for $w_1 > w_m$. Since the left side of (5.17) is decreasing in w_1 for $w_1 > w_m$, we only need to verify (5.17) for $w_1 \leq w_m$.

By the quadratic formula, the discriminant of the left side of (5.17) for $w_1 \leq w_m$ is

$$\big(h(w_1)\big)^2 - 4\left(1 - \frac{h(w_1)}{h'(0)w_1}\right)h'(0)w_1 = \big(h(w_1)\big)^2 + 4h(w_1) - 4h'(0)w_1,$$

which is nonpositive from (5.2). Thus the left side of (5.17) cannot have two real zeros. Note that $1 - \frac{h^+(w_1)}{h'(0)w_1} > 0$ for $w_1 > 0$. Since the left side of (5.17) is negative when $\sigma = 0$, the left side of (5.17) has to be nonpositive. In fact, (5.2) is one of the three possible conditions in Weinberger et al. (2009) to guarantee that (5.17) holds.

Because h^-, like h^+, is equal to h near the origin at $w_1 = 0$, the same proof shows that (H3) holds for (5.10).

In summary, we have verified (H1)–(H3) for (5.1) and completed the proof.

Appendix A

Proof of Lemma 1.1 We only need to prove those results different from Weinberger (1978), Lui (1989). The proof of the convexity of $\Psi(A_\lambda)$ is similar to that in Crooks (1996) for matrices with positive off-diagonal elements. It is easily seen that $\Psi(A_\lambda) = \rho(A_\lambda + \alpha I) - \alpha$ is a nondecreasing function of $\lambda > 0$ (Horn and Johnson 1985, Theorem 8.1.18). Further, a theorem on the convexity of the dominant eigenvalue of matrices due to Cohen (1981) states that for any positive diagonal matrices D_1, D_2 and $t \in (0, 1)$,

$$\Psi\big(tD_1 + (1-t)D_2 + f'(0)\big) \leq t\Psi\big(D_1 + f'(0)\big) + (1-t)\Psi\big(D_2 + f'(0)\big).$$

As before, $\Psi(A)$ is the principal eigenvalue of A. Now if $\alpha_1, \alpha_2 \in \mathbb{R}$ and $t \in (0, 1)$,

$$\big(t\alpha_1 + (1-t)\alpha_2\big)^2 \leq t\alpha_1^2 + (1-t)\alpha_2^2.$$

This implies that

$$\begin{aligned}\Psi(A_{t\lambda_1+(1-t)\lambda_2}) &= \Psi\big(\big(t\lambda_1+(1-t)\lambda_2\big)^2 D + f'(0)\big)\\ &\le \Psi\big(t\lambda_1^2 D + (1-t)\lambda_2^2 D + f'(0)\big)\\ &\le t\Psi\big(\lambda_1^2 D + f'(0)\big)\\ &\quad + (1-t)\Psi\big(\lambda_2^2 D + f'(0)\big)\\ &= t\Psi(A_{\lambda_1}) + (1-t)\Psi(A_{\lambda_2}).\end{aligned}$$

Since $\Psi(A_\lambda)$ is a simple root of the characteristic equation of an irreducible block, it can be shown that $\Psi(A_\lambda)$ is twice continuously differentiable on $\mathbb{R}$. Thus

$$\Psi''(\lambda) \ge 0$$

and a calculation shows that

$$\big[\lambda\Phi(\lambda)\big]' = \Psi'(\lambda),$$

$$\Phi'(\lambda) = \frac{1}{\lambda}\big[\Psi'(\lambda) - \Phi(\lambda)\big]$$

and

$$\big(\lambda^2\Phi'(\lambda)\big)' = \lambda\Psi''(\lambda) \ge 0.$$

(6) is a consequence of the above inequalities. As for (2), we need to prove that $\lim_{\lambda\to\infty}\frac{\Psi(A_\lambda)}{\lambda} = \infty$. In fact, there exists an $\epsilon > 0$ such that all diagonal elements of $D - \epsilon I$ are strictly positive. In view of the definition of Ψ, $\Psi(D-\epsilon I) > 0$ and we choose λ large enough so that

$$\begin{aligned}\Psi(A_\lambda) &= \Psi\big(D\lambda^2 + f'(0)\big)\\ &= \Psi\big((D-\epsilon I)\lambda^2 + \big(\epsilon\lambda^2 I + f'(0)\big)\big)\\ &\ge \Psi\big((D-\epsilon I)\lambda^2\big)\\ &= \lambda^2\Psi(D-\epsilon I).\end{aligned}$$

Thus $\lim_{\lambda\to\infty}\frac{\Psi(A_\lambda)}{\lambda} = \infty$. As we discussed before, (H2) implies the existence of positive eigenvector $\nu_\lambda \gg 0$ corresponding to $\Phi(A_\lambda)$. The first statement of (8) is a consequence of (1)–(7). The second statement of (8) is just a rephrase of the fact that $\nu_\lambda \gg 0$ is a eigenvector of $\frac{1}{\lambda}A_\lambda$ corresponding to eigenvalue $\Phi(A_\lambda)$ for $\lambda = \Lambda_c$ and $\gamma\Lambda_c$. □

Remark 6.1 It was suggested by one of the reviewers that the convexity of $\Psi(A_\lambda)$ can also be proved by the chain rule. Note that $\Psi(A_\lambda)$ is an increasing convex function of λ^2 and use the chain rule identity $\frac{d\Psi(A_\lambda)}{d\lambda} = 2\lambda\frac{d\Psi(A_\lambda)}{d(\lambda^2)}$ twice to see $\Psi''(A_\lambda) \ge 0$.

Appendix B

In this section, we provide a direct verification of Lemmas 4.3 and 4.4. Lower and upper solutions of the equivalent integral equations (4.5) play a central role in the construction of fixed points of the equivalent integral equations through monotone iterations. The lower and upper solutions give the asymptotic behavior of traveling wave solutions of (1.3).

Wu and Zou (2001, 2008) and Ma (2001, 2007) verify lower and upper solutions through differential equations, and then use them in monotone iterations of equivalent integral equations. While it was pointed out in Boumenir and Nguyen (2008) that the upper and lower solutions for differential equations are required to be smooth for delayed equations, Wang (2009) recently directly verified that ϕ^+ and ϕ^- are indeed lower and upper solutions through the equivalent integral equations for scalar equations, where the integrals and the two sides of (4.5) were calculated and compared. Clearly, in this way, the lower and upper solutions are not required to be smooth.

In this appendix, we shall directly verify that, for n-dimensional systems, ϕ^+ and ϕ^- are the lower and upper solutions of (4.5). Thus this appendix can be viewed as a continuation of Wang (2009) for the direct verification of non-smooth upper and lower solutions of the equivalent integral equations for n-dimensional systems.

Note that the proofs of two lemmas in Ma (2001, Lemmas 2.5, 2.6) can significantly simplify the verification of lower and upper solutions for the equivalent integral equations, although the conclusions of the two lemmas in Ma (2001) were about lower and upper solutions for differential equations (see Wang 2010, Sect. 6.1 for more details). As a result, we can always verify them in a much simpler way. Nevertheless, a direct verification can provide further evidence that ϕ^+ and ϕ^- are lower and upper solutions. In addition, by carefully analyzing eigenvalues and corresponding eigenvectors, we identify some identities and interesting relations among the parameters.

The results in this appendix are natural extensions of those by the author in Wang (2009) for scalar cases. To simplify our proofs, we first prove two identities (Lemmas 7.1, 7.2), which are the extension of the identities for scalar cases in Wang (2009). Their proofs are almost identical to those in Wang (2009), except that the eigenvector v^i_λ must be included.

Lemma 7.1 *Assume that* (H1)–(H2) *hold. Then, for each* $c > c^*$,

$$\frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\left(\frac{1}{\lambda_{1i}+\Lambda_c}+\frac{1}{\lambda_{2i}-\Lambda_c}\right)=v^i_{\Lambda_c}\quad \text{for } i=1,\dots,N. \tag{7.1}$$

Proof Recall that $\lambda_{2i} > \lambda_{1i} > 2\Lambda_c > \Lambda_c$. It follows that, $i = 1, \dots, N$,

$$\begin{aligned}
&\frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\left(\frac{1}{\lambda_{1i}+\Lambda_c}+\frac{1}{\lambda_{2i}-\Lambda_c}\right)\\
&\quad=\frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\frac{(\lambda_{1i}+\lambda_{2i})}{\lambda_{1i}\lambda_{2i}+(\lambda_{2i}-\lambda_{1i})\Lambda_c-\Lambda_c^2}\\
&\quad=\frac{M_i(\Lambda_c)}{d_i}\frac{1}{\frac{\beta}{d_i}+\frac{c}{d_i}\Lambda_c-\Lambda_c^2}\\
&\quad=M_i(\Lambda_c)\frac{1}{\beta+c\Lambda_c-d_i\Lambda_c^2}\\
&\quad=\frac{\beta\nu^i_{\Lambda_c}+\nu^i_{\Lambda_c}(c\Lambda_c-d_i\Lambda_c^2)}{\beta+c\Lambda_c-d_i\Lambda_c^2}\\
&\quad=\nu^i_{\Lambda_c}. \qquad (7.2)
\end{aligned}$$

□

Lemma 7.2 *Assume that* (H1)–H2) *hold and* γ *satisfies* (4.7). *Then, for each* $c > c^*$, $i = 1, \dots, N$,

$$\frac{M_i(\Lambda_c)}{(\lambda_{1i}+\Lambda_c)\nu^i_{\Lambda_c}}+\frac{M_i(\Lambda_c)}{(\lambda_{2i}-\Lambda_c)\nu^i_{\Lambda_c}}-\frac{M_i(\gamma\Lambda_c)}{(\lambda_{1i}+\gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}}-\frac{M_i(\gamma\Lambda_c)}{(\lambda_{2i}-\gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}}>0. \qquad (7.3)$$

Proof Since $\lambda_{2i} > \lambda_{1i} > 2\Lambda_c$, it follows that $\lambda_{2i} > \gamma\Lambda_c > \Lambda_c$. Lemma 1.1 ($\Phi(\gamma\Lambda_c) < c$) implies that, for $i = 1, \dots, N$,

$$\begin{aligned}
M_i(\gamma\Lambda_c)&=\beta\nu^i_{\gamma\Lambda_c}-\nu^i_{\gamma\Lambda_c}d_i(\gamma\Lambda_c)^2+\sum_{j=1,\dots,N}\nu^j_{\gamma\Lambda_c}a^{ij}_{\gamma\Lambda_c}\\
&=\big(\beta-d_i(\gamma\Lambda_c)^2+\Phi(\gamma\Lambda_c)\gamma\Lambda_c\big)\nu^i_{\gamma\Lambda_c}\\
&<\big(\beta-d_i(\gamma\Lambda_c)^2+c\gamma\Lambda_c\big)\nu^i_{\gamma\Lambda_c}. \qquad (7.4)
\end{aligned}$$

We also note that $M_i(\Lambda_c) = (\beta + c\Lambda_c - d_i\Lambda_c^2)\nu^i_{\Lambda_c}$. Thus, for $i = 1, \dots, N$, we have

$$\begin{aligned}
&\frac{M_i(\Lambda_c)}{(\lambda_{1i}+\Lambda_c)\nu^i_{\Lambda_c}}+\frac{M_i(\Lambda_c)}{(\lambda_{2i}-\Lambda_c)\nu^i_{\Lambda_c}}-\frac{M_i(\gamma\Lambda_c)}{(\lambda_{1i}+\gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}}-\frac{M_i(\gamma\Lambda_c)}{(\lambda_{2i}-\gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}}\\
&=\frac{(\lambda_{1i}+\lambda_{2i})M_i(\Lambda_c)}{(\lambda_{1i}\lambda_{2i}+(\lambda_{2i}-\lambda_{1i})\Lambda_c-\Lambda_c^2)\nu^i_{\Lambda_c}}\\
&\quad-\frac{(\lambda_{1i}+\lambda_{2i})M_i(\gamma\Lambda_c)}{(\lambda_{1i}\lambda_{2i}+(\lambda_{2i}-\lambda_{1i})\gamma\Lambda_c-(\gamma\Lambda_c)^2)\nu^i_{\gamma\Lambda_c}}
\end{aligned}$$

$$
\begin{aligned}
&= \frac{\frac{\sqrt{c^2+4\beta d_i}}{d_i} M_i(\Lambda_c)}{(\frac{\beta}{d_i} + \frac{c}{d_i}\Lambda_c - \Lambda_c^2)\nu^i_{\Lambda_c}} - \frac{\frac{\sqrt{c^2+4\beta d_i}}{d_i} M_i(\gamma\Lambda_c)}{(\frac{\beta}{d_i} + \frac{c}{d_i}\gamma\Lambda_c - (\gamma\Lambda_c)^2)\nu^i_{\gamma\Lambda_c}} \\
&= \frac{\sqrt{c^2+4\beta d_i} M_i(\Lambda_c)}{(\beta + c\Lambda_c - d_i\Lambda_c^2)\nu^i_{\Lambda_c}} - \frac{\sqrt{c^2+4\beta d_i} M_i(\gamma\Lambda_c)}{(\beta + c\gamma\Lambda_c - d_i(\gamma\Lambda_c)^2)\nu^i_{\gamma\Lambda_c}} \\
&= \sqrt{c^2+4\beta d_i}\left(\frac{M_i(\Lambda_c)}{(\beta + c\Lambda_c - d_i\Lambda_c^2)\nu^i_{\Lambda_c}} - \frac{M_i(\gamma\Lambda_c)}{(\beta + c\gamma\Lambda_c - d_i(\gamma\Lambda_c)^2)\nu^i_{\gamma\Lambda_c}}\right) \\
&= \sqrt{c^2+4\beta d_i}\left(1 - \frac{M_i(\gamma\Lambda_c)}{(\beta + c\gamma\Lambda_c - d_i(\gamma\Lambda_c)^2)\nu^i_{\gamma\Lambda_c}}\right) \\
&> 0.
\end{aligned}
\tag{7.5}
$$

This completes the proof. □

7.1 Proof of Lemma 4.3

The proof of Lemma 4.3 is almost identical to that in Wang (2009) for the scalar case, except that the eigenvector ν^i_λ must be included and delay terms are not present here.

Proof First, because of the assumption that (1.3) is cooperative and β is sufficiently large, H_i is monotone. Let $\xi_i^* = \frac{\ln \frac{k_i}{\nu^i_{\Lambda_c}}}{\Lambda_c}$, $i = 1, \dots, N$. Then $\phi_i^+(\xi) = k_i$ if $\xi \ge \xi_i^*$, and $\phi_i^+(\xi) = \nu^i_{\Lambda_c} e^{\Lambda_c \xi}$ if $\xi < \xi_i^*$, $i = 1, \dots, N$. Note that $\phi_i^+(\xi) \le \nu^i_{\Lambda_c} e^{\Lambda_c\xi}$, $\xi \in \mathbb{R}$. In view of (H1)–(H3), we have, for $\xi \le \xi_i^*$,

$$
\begin{aligned}
H_i\big(\phi^+(\xi)\big) &\le H_i\big(\nu^i_{\Lambda_c} e^{\Lambda_c\xi}\big) \\
&= \beta \nu^i_{\Lambda_c} e^{\Lambda_c\xi} + f_i\big(\nu^i_{\Lambda_c} e^{\Lambda_c\xi}\big) \\
&\le \beta \nu^i_{\Lambda_c} e^{\Lambda_c\xi} + \sum_{j=1}^n \partial_j f_i(0) \nu^i_{\Lambda_c} e^{\Lambda_c\xi} \\
&= M_i(\Lambda_c) e^{\Lambda_c\xi},
\end{aligned}
$$

where $M_i(\cdot)$ is defined in (4.6). For $\xi \ge \xi_i^*$, we have

$$
\begin{aligned}
H_i\big(\phi^+(\xi)\big) &\le \beta k_i + f_i(k) \\
&= \beta k_i.
\end{aligned}
$$

Thus, for $\xi \ge \xi_i^*$, $i = 1, \dots, N$, we obtain

$$
\begin{aligned}
\mathcal{T}_i\big[\phi^+\big](\xi) \le{}& \frac{M_i(\Lambda_c)}{d_i(\lambda_{1i} + \lambda_{2i})} \int_{-\infty}^{\xi_i^*} e^{-\lambda_{1i}(\xi - s)} e^{\Lambda_c s}\, ds \\
&+ \frac{1}{d_i(\lambda_{1i} + \lambda_{2i})} \left[\int_{\xi_i^*}^{\xi} e^{-\lambda_{1i}(\xi - s)} \beta k_i\, ds + \int_{\xi}^{\infty} e^{\lambda_{2i}(\xi - s)} \beta k_i\, ds\right].
\end{aligned}
\tag{7.6}
$$

Thus in view of (4.4), we add and subtract the term $\frac{\beta k_i}{d_i(\lambda_{1i}+\lambda_{2i})}\int_{-\infty}^{\xi_i^*} e^{-\lambda_{1i}(\xi-s)}\, ds$ at the left of (7.6). Now for $i=1,\ldots,N, \xi \geq \xi_i^*$, noting that $\nu_{\Lambda_c}^i e^{\Lambda_c \xi_i^*} = k_i$, (7.6) can be written as

$$
\begin{aligned}
\mathcal{T}_i[\phi^+](\xi) &\leq k_i + \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(M_i(\Lambda_c)\int_{-\infty}^{\xi_i^*} e^{-\lambda_{1i}(\xi-s)} e^{\Lambda_c s}\, ds \\
&\quad - \beta k_i \int_{-\infty}^{\xi_i^*} e^{-\lambda_{1i}(\xi-s)}\, ds\biggr) \\
&= k_i + \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(M_i(\Lambda_c)\frac{e^{-\lambda_{1i}\xi} e^{(\lambda_{1i}+\Lambda_c)\xi_i^*}}{\lambda_{1i}+\Lambda_c} - \beta k_i \frac{e^{-\lambda_{1i}\xi} e^{\lambda_{1i}\xi_i^*}}{\lambda_{1i}}\biggr) \\
&= k_i + \frac{k_i e^{-\lambda_{1i}\xi} e^{\lambda_{1i}\xi_i^*}}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(\frac{M_i(\Lambda_c)}{(\lambda_{1i}+\Lambda_c)\nu_{\Lambda_c}^i} - \frac{\beta}{\lambda_{1i}}\biggr) \\
&= k_i + \frac{k_i e^{-\lambda_{1i}\xi} e^{\lambda_{1i}\xi_i^*}}{d_i(\lambda_{1i}+\lambda_{2i})(\lambda_{1i}+\Lambda_c)\lambda_{1i}\nu_{\Lambda_c}^i}\bigl(\lambda_{1i}\bigl(M_i(\Lambda_c) - \nu_{\Lambda_c}^i\beta\bigr) - \nu_{\Lambda_c}^i \beta\Lambda_c\bigr).
\end{aligned}
\tag{7.7}
$$

Since $M_i(\Lambda_c) = \beta\nu_{\Lambda_c}^i - \nu_{\Lambda_c}^i d_i \Lambda_c^2 + c\Lambda_c \nu_{\Lambda_c}^i$, $i=1,\ldots,N$, we have, for $i=1,\ldots,N$,

$$
\begin{aligned}
&\lambda_{1i}\bigl(M_i(\Lambda_c) - \nu_{\Lambda_c}^i\beta\bigr) - \beta\nu_{\Lambda_c}^i\Lambda_c \\
&\quad = \nu_{\Lambda_c}^i \lambda_{1i}\bigl(c\Lambda_c - d_i\Lambda_c^2\bigr) - \beta\nu_{\Lambda_c}^i\Lambda_c \\
&\quad = \nu_{\Lambda_c}^i \frac{4\beta d_i}{2d_i(\sqrt{c^2+4\beta d_i}+c)}\bigl(c\Lambda_c - d_i\Lambda_c^2\bigr) - \beta\nu_{\Lambda_c}^i\Lambda_c \\
&\quad = \nu_{\Lambda_c}^i \frac{4\beta(c\Lambda_c - d_i\Lambda_c^2) - 2(\sqrt{c^2+4\beta d_i}+c)\beta\Lambda_c}{2(\sqrt{c^2+4\beta d_i}+c)} \\
&\quad = \nu_{\Lambda_c}^i \frac{2\beta\Lambda_c(2c - 2d_i\Lambda_c - \sqrt{c^2+4\beta d_i} - c)}{2(\sqrt{c^2+4\beta d_i}+c)} \\
&\quad = \nu_{\Lambda_c}^i \frac{2\beta\Lambda_c(c - 2d_i\Lambda_c - \sqrt{c^2+4\beta d_i})}{2(\sqrt{c^2+4\beta d_i}+c)} \\
&\quad < 0.
\end{aligned}
\tag{7.8}
$$

Combining (7.7) and (7.8), we see that, for $\xi \geq \xi_i^*$, $i=1,\ldots,N$,

$$
\mathcal{T}_i[\phi^+](\xi) \leq k_i. \tag{7.9}
$$

Similarly, noting $\nu_{\Lambda_c}^i e^{\Lambda_c\xi_i^*} = k_i$, one can see that, for $\xi \leq \xi_i^*$, $i=1,\ldots,N$,

$$
\mathcal{T}_i[\phi^+](\xi) \leq \frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\biggl(\int_{-\infty}^{\xi} e^{-\lambda_{1i}(\xi-s)} e^{\Lambda_c s}\, ds
$$

$$
\begin{aligned}
&+ \int_{\xi}^{\xi_i^*} \mathrm{e}^{\lambda_{2i}(\xi-s)} \mathrm{e}^{\Lambda_c s}\,\mathrm{d}s \biggr) + \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})} \int_{\xi_i^*}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi-s)} \beta k_i s \\
&= \frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})} \biggl(\frac{\mathrm{e}^{\Lambda_c \xi}}{\lambda_{1i}+\Lambda_c} + \frac{\mathrm{e}^{\Lambda_c \xi}}{\lambda_{2i}-\Lambda_c} \\
&\quad - \frac{\mathrm{e}^{\lambda_{2i}\xi} \mathrm{e}^{-(\lambda_{2i}-\Lambda_c)\xi_i^*}}{\lambda_{2i}-\Lambda_c} \biggr) + \frac{\beta k_i}{d_i(\lambda_{1i}+\lambda_{2i})} \frac{\mathrm{e}^{\lambda_{2i}\xi} \mathrm{e}^{-\lambda_{2i}\xi_i^*}}{\lambda_{2i}} \\
&= \frac{\mathrm{e}^{\Lambda_c \xi} M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})} \biggl(\frac{1}{\lambda_{1i}+\Lambda_c} + \frac{1}{\lambda_{2i}-\Lambda_c} \biggr) \\
&\quad + \frac{M_i(\Lambda_c)\mathrm{e}^{\lambda_{2i}\xi-\lambda_{2i}\xi_i^*}}{d_i(\lambda_{1i}+\lambda_{2i})} \biggl(\frac{-k_i}{(\lambda_{2i}-\Lambda_c)\nu_{\Lambda_c}^i} + \frac{\beta k_i}{M(\Lambda_c)\lambda_{2i}} \biggr).
\end{aligned} \tag{7.10}
$$

Since $M_i(\Lambda_c) = \beta \nu_{\Lambda_c}^i - \nu_{\Lambda_c}^i d_i \Lambda_c^2 + c\Lambda_c \nu_{\Lambda_c}^i$, $i = 1, \dots, N$, it is easy to see that, by choosing β sufficiently large if necessary,

$$
\begin{aligned}
\frac{-k_i}{(\lambda_{2i}-\Lambda_c)\nu_{\Lambda_c}^i} + \frac{\beta k_i}{M_i(\Lambda_c)\lambda_{2i}} &= k_i \frac{(-M_i(\Lambda_c) + \nu_{\Lambda_c}^i \beta)\lambda_{2i} - \Lambda_c \nu_{\Lambda_c}^i \beta}{\nu_{\Lambda_c}^i (\lambda_{2i}-\Lambda_c)\lambda_{2i} M_i(\Lambda_c)} \\
&= k_i \frac{\lambda_{2i}(\nu_{\Lambda_c}^i \Lambda_c^2 d_i - \nu_{\Lambda_c}^i \Lambda_c c) - \Lambda_c \nu_{\Lambda_c}^i \beta}{\nu_{\Lambda_c}^i (\lambda_{2i}-\Lambda_c)\lambda_{2i} M_i(\Lambda_c)} \\
&= k_i \nu_{\Lambda_c}^i \Lambda_c \frac{\lambda_{2i}(\Lambda_c d_i - c) - \beta}{\nu_{\Lambda_c}^i (\lambda_{2i}-\Lambda_c)\lambda_{2i} M_i(\Lambda_c)} \\
&= k_i \nu_{\Lambda_c}^i \Lambda_c \frac{\frac{c+\sqrt{c^2+4\beta d_i}}{2d_i}(\Lambda_c d_i - c) - \beta}{\nu_{\Lambda_c}^i (\lambda_{2i}-\Lambda_c)\lambda_{2i} M_i(\Lambda_c)} \\
&\le 0.
\end{aligned} \tag{7.11}
$$

Combining (7.1), (7.10), and (7.11) leads to, for $\xi \le \xi_i^*$, $i = 1, \dots, N$,

$$
\mathcal{T}_i\bigl[\phi^+\bigr](\xi) \le \nu_{\Lambda_c}^i \mathrm{e}^{\Lambda_c \xi}.
$$

And therefore, for $\xi \in \mathbb{R}$,

$$
\mathcal{T}_i\bigl[\phi^+\bigr](\xi) \le \phi_i^+(\xi) \quad \text{for } i = 1, \dots, N. \tag{7.12}
$$

This completes the proof of Lemma 4.3. □

We now need the following estimate on f, which is an application of Taylor's theorem for multivariable functions. Also see Wang (2009).

Lemma 7.3 *Assume that* (H1)–(H2) *hold. There exist positive constants* $b_{ij}, i, j = 1, \dots, N$ *such that*

$$f_i(u) \geq \sum_{j=1}^{N} \partial_j f_i(0) u_j - \sum_{j=1}^{N} b_{ij}(u_j)^2 \quad \textit{for } u = (u_i), u_i \in [0, k_i], i = 1, \dots, N.$$

7.2 Proof of Lemma 4.4

Again, the proof of Lemma 4.4 is almost identical to that in Wang (2009) for the scalar case, except that the eigenvector ν_λ^i must be included and delay terms are not present here.

Proof Let $\xi_i^* = \frac{\ln(q \frac{\nu^i_{\gamma\Lambda_c}}{\nu^i_{\Lambda_c}})}{(1-\gamma)\Lambda_c}, i = 1, \dots, N$. If $\xi \geq \xi_i^*$, $\phi_i^-(\xi) = 0$, and for $\xi < \xi_i^*$,

$$\phi_i^-(\xi) = \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} \mathrm{e}^{\gamma\Lambda_c \xi} \quad \text{for } i = 1, \dots, N.$$

Because of the assumption that (1.3) is cooperative and β is sufficiently large, H_i is monotone. For $\xi \in \mathbb{R}$, it follows that

$$H_i\big(\phi^-(\xi)\big) \geq H_i(0) = 0.$$

Thus, for $\xi \geq \xi_i^*$,

$$\mathcal{T}_i[\phi^-](\xi) \geq \phi_i^-(\xi) \quad \text{for } i = 1, \dots, N.$$

We now consider the case $\xi < \xi_i^*$. It is easy to see that

$$\nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi} \geq \phi_i^-(\xi) \geq \nu^i_{\Lambda_c} \mathrm{e}^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} \mathrm{e}^{\gamma\Lambda_c \xi} \quad \text{for } \xi \in \mathbb{R}, i = 1, \dots, N. \tag{7.13}$$

In view of Lemma 7.3, (7.13), and the definition of ν_λ, we have, for $\xi \in \mathbb{R}$, $i = 1, \dots, N$,

$$\begin{aligned} H_i\big(\phi^-(\xi)\big) &= \beta\phi_1^-(\xi) + f_i\big(\phi^-(\xi)\big) \\ &\geq \beta\phi_i^-(\xi) + \sum_{j=1}^{n} \partial_j f_i(0) \phi_j^-(\xi) - \sum_{j=1}^{n} b_{ij}\big(\phi_j^-(\xi)\big)^2 \\ &\geq M_i(\Lambda_c)\mathrm{e}^{\Lambda_c \xi} - q M_i(\gamma\Lambda_c)\mathrm{e}^{\gamma\Lambda_c \xi} - \widehat{M}_i \mathrm{e}^{2\Lambda_c \xi}, \end{aligned} \tag{7.14}$$

where $M_i(\cdot)$ is defined in (4.6) and

$$\widehat{M}_i = \sum_{j=1}^{n} b_{ij}\big(\nu^j_{\Lambda_c}\big)^2 > 0. \tag{7.15}$$

Now we are able to estimate $\mathcal{T}[\phi^-]$ for $\xi \le \xi^*, i = 1, \dots, N$:

$$\begin{aligned}
\mathcal{T}_i[\phi^-](\xi) \ge{}& \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)} M_i(\Lambda_c)\mathrm{e}^{\Lambda_c s}\,\mathrm{d}s \\
&- q\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)} M_i(\gamma\Lambda_c)\mathrm{e}^{\gamma\Lambda_c s}\,\mathrm{d}s \\
&- \widehat{M}_i\int_{-\infty}^{\xi} \mathrm{e}^{-\lambda_{1i}(\xi-s)} \mathrm{e}^{2\Lambda_c s}\,\mathrm{d}s \\
&+ \int_{\xi}^{\xi_i^*} \mathrm{e}^{\lambda_{2i}(\xi-s)} M_i(\Lambda_c)\mathrm{e}^{\Lambda_c s}\,\mathrm{d}s \\
&- q\int_{\xi}^{\xi_i^*} \mathrm{e}^{\lambda_{2i}(\xi-s)} M_i(\gamma\Lambda_c)\mathrm{e}^{\gamma\Lambda_c s}\,\mathrm{d}s \\
&- \widehat{M}_i\int_{\xi}^{\xi_i^*} \mathrm{e}^{\lambda_{2i}(\xi-s)} \mathrm{e}^{2\Lambda_c s}\,\mathrm{d}s\bigg) \\
={}& \frac{1}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg(\frac{M_i(\Lambda_c)\mathrm{e}^{\Lambda_c\xi}}{\lambda_{1i}+\Lambda_c} - q\frac{M_i(\gamma\Lambda_c)\mathrm{e}^{\gamma\Lambda_c\xi}}{\lambda_{1i}+\gamma\Lambda_c} \\
&- \widehat{M}_i\frac{\mathrm{e}^{2\Lambda_c\xi}}{\lambda_{1i}+2\Lambda_c} + \frac{\mathrm{e}^{\Lambda_c\xi_i^*-\lambda_{2i}\xi_i^*+\lambda_{2i}\xi} - \mathrm{e}^{\Lambda_c\xi}}{\Lambda_c-\lambda_{2i}} M_i(\Lambda_c) \\
&- q\frac{\mathrm{e}^{\gamma\Lambda_c\xi_i^*-\lambda_{2i}\xi_i^*+\lambda_{2i}\xi} - \mathrm{e}^{\gamma\Lambda_c\xi}}{\gamma\Lambda_c-\lambda_{2i}} M_i(\gamma\Lambda_c) \\
&- \widehat{M}_i\frac{\mathrm{e}^{2\Lambda_c\xi_i^*-\lambda_{2i}\xi_i^*+\lambda_{2i}\xi} - \mathrm{e}^{2\Lambda_c\xi}}{2\Lambda_c-\lambda_{2i}}\bigg).
\end{aligned} \tag{7.16}$$

Because $H_i(\phi^-(\xi)) \ge 0$, the term $\int_{\xi^*}^{\infty} \mathrm{e}^{\lambda_{2i}(\xi-s)} H_i(\phi^-(s))\,\mathrm{d}s$ of $\mathcal{T}_i[\phi^-]$ in (7.16) is ignored. In view of the identity (7.1), we can further simplify (7.16) as

$$\begin{aligned}
\mathcal{T}_i[\phi^-](\xi) \ge{}& \frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\left(\frac{1}{\lambda_{1i}+\Lambda_c} + \frac{1}{\lambda_{2i}-\Lambda_c}\right)\mathrm{e}^{\Lambda_c\xi} \\
&- \frac{M_i(\Lambda_c)}{d_i(\lambda_{1i}+\lambda_{2i})}\left(\frac{1}{\lambda_{1i}+\Lambda_c} + \frac{1}{\lambda_{2i}-\Lambda_c}\right)\frac{\nu_{\gamma\Lambda_c}^i}{\nu_{\Lambda_c}^i} q\mathrm{e}^{\gamma\Lambda_c\xi} \\
&+ \frac{\mathrm{e}^{\gamma\Lambda_c\xi}}{d_i(\lambda_{1i}+\lambda_{2i})}\bigg\{q\nu_{\gamma\Lambda_c}^i\bigg(\frac{M_i(\Lambda_c)}{(\lambda_{1i}+\Lambda_c)\nu_{\Lambda_c}^i} + \frac{M_i(\Lambda_c)}{(\lambda_{2i}-\Lambda_c)\nu_{\Lambda_c}^i} \\
&- \frac{M_i(\gamma\Lambda_c)}{(\lambda_{1i}+\gamma\Lambda_c)\nu_{\gamma\Lambda_c}^i} - \frac{M_i(\gamma\Lambda_c)}{(\lambda_{2i}-\gamma\Lambda_c)\nu_{\gamma\Lambda_c}^i}\bigg)
\end{aligned}$$

$$- \frac{\widehat{M}_i}{(\lambda_{1i} + 2\Lambda_c)} e^{(2-\gamma)\Lambda_c \xi} - \frac{M_i(\Lambda_c) e^{(\Lambda_c - \lambda_{2i})\xi^*}}{(\lambda_{2i} - \Lambda_c)} e^{(\lambda_{2i} - \gamma \Lambda_c)\xi}$$
$$- \frac{\widehat{M}_i}{(\lambda_{2i} - 2\Lambda_c)} e^{(2-\gamma)\Lambda_c \xi} \Bigg\}. \tag{7.17}$$

In (7.17), we subtract two terms to make a term $-\nu^i_{\gamma\Lambda_c} q e^{\gamma \Lambda_c \xi}$ and thus we need to add the terms. Recall that $\gamma \Lambda_c < 2\Lambda_c < \lambda_{2i}$. We ignore two positive terms $q \frac{M_i(\gamma\Lambda_c)}{(\lambda_{2i} - \gamma\Lambda_c) d_i (\lambda_{1i} + \lambda_{2i})} e^{(\gamma \Lambda_c - \lambda_{2i})\xi^* + \lambda_{2i}\xi}$ and $\frac{\widehat{M}_i}{(\lambda_{2i} - 2\Lambda_c) d_i (\lambda_{1i} + \lambda_{2i})} e^{(2\Lambda_c - \lambda_{2i})\xi^* + \lambda_{2i}\xi}$ in (7.17).

For $\xi \le \xi_i^*$, $e^{(2-\gamma)\Lambda_c \xi}, e^{(\lambda_{2i} - \gamma\Lambda_c)\xi}$ are bounded above. Because of the identity (7.1), (7.17) can be further simplified as, for $i = 1, \ldots, N$,

$$\mathcal{T}_i[\phi^-](\xi) \ge \nu^i_{\Lambda_c} e^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} e^{\gamma \Lambda_c \xi}$$
$$+ \frac{e^{\gamma\Lambda_c \xi}}{d_i(\lambda_{1i} + \lambda_{2i})} \Bigg\{ q \nu^i_{\gamma\Lambda_c} \Bigg(\frac{M_i(\Lambda_c)}{(\lambda_{1i} + \Lambda_c)\nu^i_{\Lambda_c}} + \frac{M_i(\Lambda_c)}{(\lambda_{2i} - \Lambda_c)\nu^i_{\Lambda_c}}$$
$$- \frac{M_i(\gamma\Lambda_c)}{(\lambda_{1i} + \gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}} - \frac{M_i(\gamma\Lambda_c)}{(\lambda_{2i} - \gamma\Lambda_c)\nu^i_{\gamma\Lambda_c}} \Bigg)$$
$$- \frac{\widehat{M}_i}{(\lambda_{1i} + 2\Lambda_c)} e^{(2-\gamma)\Lambda_c \xi_i^*} - \frac{M_i(\Lambda_c) e^{(\Lambda_c - \lambda_{2i})\xi_i^*}}{(\lambda_{2i} - \Lambda_c)} e^{(\lambda_{2i} - \gamma\Lambda_c)\xi_i^*}$$
$$- \frac{\widehat{M}_i}{(\lambda_{2i} - 2\Lambda_c)} e^{(2-\gamma)\Lambda_c \xi_i^*} \Bigg\}. \tag{7.18}$$

Finally, from (7.18) and Lemma 7.2, we conclude that there exists $q > 0$, which is independent of ξ, such that, for $\xi \le \xi_i^*$ and $i = 1, \ldots, N$,

$$\mathcal{T}_i[\phi^-](\xi) \ge \nu^i_{\Lambda_c} e^{\Lambda_c \xi} - q \nu^i_{\gamma\Lambda_c} e^{\gamma\Lambda_c \xi}. \tag{7.19}$$

And therefore, for $i = 1, \ldots, N$,

$$\mathcal{T}_i[\phi^-](\xi) \ge \phi_i^-(\xi) \quad \text{for } \xi \in \mathbb{R}.$$

This completes the proof. □

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