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Asymptotic spreading of competition diffusion systems: The role of interspecific competitions

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This paper is concerned with the asymptotic spreading of competition diffusion systems, with the purpose of formulating the propagation modes of a co-invasion–coexistence process of two competitors. Using the comparison principle for competitive systems, some results on asymptotic spreading are obtained. Our conclusions imply that the interspecific competitions slow the invasion of one species and decrease the population densities in the coexistence domain. Therefore, the interspecific competitions play a negative role in the evolution of competitive communities.

Key words: Comparison principle; Co-invasion–coexistence; Competitive invaders

1 Introduction

Due to the limits on resources, e.g. light and water, competitive behaviour is inevitable in nature. In the evolution of populations, both interspecific and intraspecific competitions are universal, and there are many mathematical models describing these phenomena, such as the Lotka–Volterra [15, 31, 32] and Gilpin–Ayala competition systems [14]. The Lotka-Volterra competition diffusion system of two species takes the form

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1\Delta u(x,t) + r_1 u(x,t)\left[1 - u(x,t) - b_1 v(x,t)\right], \\ \dfrac{\partial v(x,t)}{\partial t} = d_2\Delta v(x,t) + r_2 v(x,t)\left[1 - v(x,t) - b_2 u(x,t)\right], \end{cases} \tag{1.1}$$

where $x \in \Omega \subset \mathbb{R}^n, t > 0$ and all the parameters are non-negative, and $u(x,t)$ and $v(x,t)$ can be thought of as the population densities at time t at location x of two competitors. It is clear that $(0,0)$ is a trivial equilibrium, and (1,0) and (0,1) are two spatially homogeneous equilibria of (1.1). Moreover, if $b_1, b_2 \in [0,1)$ or $b_1, b_2 \in (1,\infty)$, then (1.1) has a spatially homogeneous steady state $K = (k_1, k_2)$ defined by

$$K = \left(\frac{1-b_1}{1-b_1b_2}, \frac{1-b_2}{1-b_1b_2}\right).$$

In particular, if $b_1, b_2 \in [0,1)$, then K is a locally stable equilibrium of the corresponding kinetic system of (1.1).

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When Ω is a bounded domain in $\mathbb{R}^n$ and (1.1) is equipped with different boundary and initial value conditions, its dynamical properties have been widely studied (see [35, 38, 40]). If $\Omega = \mathbb{R}$, then one important issue is the propagation mode, e.g. [1, 8, 13, 17–19, 21–23, 25, 43, 46, 48]. In particular, the travelling wave solutions and asymptotic spreading, which describe interspecific exclusive phenomena (see [16]) and model the behaviour of a resident and an invading species in population dynamics, have been well investigated [13, 24, 48]. It should be noted that (1.1) is an essentially cooperative system when the interspecific exclusive process is considered, since the process involves the equilibrium $(0, 1)$ or $(1, 0)$, and the results in [48] for the cooperative evolutionary systems can be applied to (1.1) by combining the invariant region with a change of variables (see [24]). Recently, Huang and Han [19] proved that b_1, b_2 describing the interspecific competitions could affect the minimal wave speed of exclusive travelling wave solutions. Biologically, many historical records reflect the interspecific exclusive process between the resident and the invader, such as the competition between grey and red squirrels in United Kingdom (see [33]), we also refer to [39, Chapter 6] for some examples.

Other than the exclusive phenomena in competitive communities, there is evidence of a co-invasion–coexistence process of several competitors, modelling the expansion of geographic range of several plants in North America after the last ice age (16,000 years ago), we refer to [9] and [39, Chapter 7] for some records. Mathematically, $(0, 0)$ and (k_1, k_2) are involved when the co-invasion–coexistence process of (1.1) is studied. Such a co-invasion–coexistence process is totally different from an exclusive one from the viewpoint of monotone dynamical systems. More precisely, if we use the change of variables in [24] to obtain a formally cooperative system in the sense of standard partial order in $\mathbb{R}^2$, then the new interesting steady states, $(1, 0)$ and $(1 - k_1, k_2)$, are not ordered (regarding the importance of comparability of steady states in the theory of monotone semi-flows, see [40]). Recently, some investigators established the existence of travelling wave solutions of (1.1) connecting $(0, 0)$ with (k_1, k_2), which indicates that there is a transition zone moving from the steady state with no species to the steady state with the coexistence of all competitive species, see [1, 7, 20, 25, 26, 34, 43]. Due to the special form and asymptotic boundary conditions of travelling wave solutions in [1, 25, 27, 34, 43], it is clear that these travelling wave solutions represent the spatial invasion process from one unbounded domain to another.

If we model the simultaneous invasion of two competitors from a bounded domain into an unbounded domain (such as the examples in [39, Chapter 7]), then we must study the asymptotic spreading of (1.1) when the initial values have compact support. Similar to the study of travelling wave solutions, the methods for monotone semi-flows cannot be applied when the co-invasion–coexistence problem is concerned. Before the mathematical discussion, we first show some possible phenomena from the viewpoint of ecology. Motivated by experimental/statistical records about the role of interspecific competition (for example, see [5, 6] and [39, Chapter 7]), we intuitively believe that the interspecific competition (namely, $b_1 > 0$ and $b_2 > 0$) can *slow* the asymptotic spreading of one species compared with the case that the interspecific competition vanishes (namely, $b_1 = b_2 = 0$). We also conjecture that the population densities on the coexistence domain will be *smaller* than with vanishing interspecific competition, here coexistence means that

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the population densities of both species are bounded below by a small positive constant. In this paper, we shall first address these conjectures for (1.1).

In what follows, motivated by Lin *et al.* [28] but based on some significantly different estimates and techniques, we first establish some results on the asymptotic spreading for (1.1). These are proved by using the comparison principles appealing to the competition systems. In addition, we also study the possible generalisation of the corresponding delayed version of system (1.1) and more general competition diffusion systems which at least contain the Gilpin–Ayala type nonlinearity [14]. Our results also confirm our conjectures for these competition systems, namely, the interspecific competition may play a negative role in the evolution of competitive communities. For the corresponding delayed system of (1.1), we find that the bounded delays appearing in the interspecific competition terms have less effect on the asymptotic spreading speed of the species with the stronger ability to spread.

The rest of this paper is organised as follows. In Section 2, we give some notation and the main results for (1.1). To prove these results, some preliminaries are listed in Section 3. Section 4 is concerned with the proof of the main results. In the last section, we study the asymptotic spreading of some generalisations of competition system (1.1).

2 Main results

In this section, we shall state our main results for (1.1). For convenience, we first give some notation. Define C by

$$C = \{u(x)|u(x) : \mathbb{R} \to \mathbb{R}^2 \text{ is uniformly continuous and bounded}\}$$

equipped with the compact open topology. We also introduce the standard supremum norm $|\cdot|$ such that C is a complete metric space. Moreover, if $\mathbf{a} \leqslant \mathbf{b} \in \mathbb{R}^2$, then

$$C_{[\mathbf{a},\mathbf{b}]} = \{(u,v) : (u,v) \in C \text{ and } \mathbf{a} \leqslant (u(x), v(x)) \leqslant \mathbf{b} \text{ for all } x \in \mathbb{R}\}.$$

In order to formulate the asymptotic spreading of two competitors $(u(x,t), v(x,t))$ described by (1.1), we investigate the following initial value problem

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1 \Delta u(x,t) + r_1 u(x,t)\left[1 - u(x,t) - b_1 v(x,t)\right], \\ \dfrac{\partial v(x,t)}{\partial t} = d_2 \Delta v(x,t) + r_2 v(x,t)\left[1 - v(x,t) - b_2 u(x,t)\right], \\ (u(x,0), v(x,0)) = (u(x), v(x)) \in C_{[\mathbf{0},\mathbf{1}]}, \end{cases} \tag{2.1}$$

in which $(x,t) \in \mathbb{R} \times (0, +\infty)$.

Theorem 2.1 *Assume that $b_1, b_2 \in [0,1)$ satisfy*

$$d_1 r_1 (1 - b_1) > d_2 r_2. \tag{2.2}$$

Define positive constants as follows

$$c_1 = 2\sqrt{d_1 r_1},\ c_2 = 2\sqrt{d_2 r_2},\ c_3 = 2\sqrt{d_2 r_2 (1 - b_2)},\ c_4 = 2\sqrt{d_2 r_2 (1 - b_2(1 - b_1))}.$$

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If $u(x), v(x)$ have non-empty compact supports, then the solution $(u(x,t), v(x,t))$ of (2.1) is well defined for all $(x,t) \in \mathbb{R} \times (0,+\infty)$ and satisfies the following:

- **(i)** *For any given $\epsilon > 0$, $\lim_{t\to\infty} \sup_{|x|>(c_1+\epsilon)t} u(x,t) = \lim_{t\to\infty} \sup_{|x|>(c_2+\epsilon)t} v(x,t) = 0$;*
- **(ii)** *for any given $\epsilon \in (0, c_1)$, $\liminf_{t\to\infty} \inf_{|x|<(c_1-\epsilon)t} u(x,t) \geqslant 1 - b_1$;*
- **(iii)** *for any given $\epsilon > 0$, $\lim_{t\to\infty} \sup_{|x|>(c_4+\epsilon)t} v(x,t) = 0$ if $c_1 > c_2 + c_4$;*
- **(iv)** *for any given $\epsilon \in (0, \frac{c_1-c_2}{2})$, we have*

$$\liminf_{t\to\infty} \inf_{(c_2+\epsilon)t<|x|<(c_1-\epsilon)t} u(x,t) = \limsup_{t\to\infty} \sup_{(c_2+\epsilon)t<|x|<(c_1-\epsilon)t} u(x,t) = 1;$$

- **(v)** *for any given $\epsilon \in (0, c_3)$, we have*

$$\liminf_{t\to\infty} \inf_{|x|<(c_3-\epsilon)t} (u(x,t), v(x,t)) = \limsup_{t\to\infty} \sup_{|x|<(c_3-\epsilon)t} (u(x,t), v(x,t)) = (k_1, k_2).$$

To better understand the effect of interspecific competition, we also recall some well-known conclusions on the following classical Fisher equation

$$\begin{cases} \dfrac{\partial z(x,t)}{\partial t} = d\Delta z(x,t) + rz(x,t)\,[1 - z(x,t)]\,, \\ z(x,0) = z(x) \end{cases} \tag{2.3}$$

with $0 \leqslant z(x) \leqslant 1$, and $z(x)$ is a uniformly continuous function with non-empty compact support. By [2–4, 26, 44], the following result holds.

Lemma 2.2 *Assume that $z(x,t)$ is defined by (2.3). Then*

$$\lim_{t\to\infty} \inf_{|x|<(2\sqrt{dr}-\epsilon)t} z(x,t) = \lim_{t\to\infty} \sup_{|x|<(2\sqrt{dr}-\epsilon)t} z(x,t) = 1, \ \lim_{t\to\infty} \sup_{|x|>(2\sqrt{dr}+\epsilon)t} z(x,t) = 0$$

for any given $\epsilon \in (0, 2\sqrt{dr})$.

Remark 2.3 Theorem 2.1 and Lemma 2.2 imply that the interspecific competition does not slow the asymptotic spreading of $u(x,t)$ (see items (i) and (ii)), and the 'invasion frontier' of $u(x,t)$ seems to be ahead of the influence of $v(x,t)$ (see item (iv)). On the other hand, items (iii) and (v) of Theorem 2.1 indicate that the interspecific competition does slow the asymptotic spreading of v and reduce the population densities of u and v on the coexistence domain. Moreover, item (v) tells us that the eventual invasions of both competitors are successful, which is a co-invasion–coexistence process of two competitors. These results partially confirm our conjectures on the role of interspecific competitions.

Moreover, since the travelling wave solutions of (1.1) have been widely studied, we also give the following illustrations on Theorem 2.1 from the viewpoint of minimal wave speeds of travelling wave solutions. These speeds are often equal to the asymptotic speeds of spreading in many examples [2–4, 10, 22, 24, 26, 44, 48].

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Remark 2.4 Theorem 2.1 and Lemma 2.2 show that u leaves v behind after a long time and its invasion front is similar to that of single species described by the Fisher equation. Therefore, it is easy to understand the invasion speed of u is $2\sqrt{d_1 r_1}$, which is the minimal wave speed of invasion travelling wave solutions of (1.1) with $b_1 = 0$. At the same time, after a long time, v must invade the region already occupied by u. Note that u has a positive bound from the below on the region, then the invasion speed of v is less than $2\sqrt{d_2 r_2}$ since v encounters obstruction from u. But $u(x,t) \leqslant 1$ for all $(x,t) \in \mathbb{R} \times (0,\infty)$, so the asymptotic speed of spreading of v is no less than $2\sqrt{d_2 r_2 (1-b_2)}$, which is the possible minimal wave speed of travelling wave solutions connecting $(1,0)$ with (k_1,k_2) (see [24]). To better understand the problem, we also refer to [12] for the description of dynamics of solutions on bounded domains by travelling wave solutions, since only a bounded domain is in fact occupied by u and v at any fixed t.

3 Preliminaries

In this section, the initial value problem (2.1) will be analysed by the theory of reaction–diffusion systems [11, 35, 42, 50], abstract functional differential equations [29, 30, 37] and the operator semi-groups [36]. Denote C^+ as

$$C^+ = \{u : u \in C \text{ and } u(x) \geqslant 0 \text{ for all } x \in \mathbb{R}\}.$$

Let $\beta = 2(r_1 + r_2)$ and define

$$\begin{cases} [F_1(u,v)](x,t) = \beta u(x,t) + r_1 u(x,t)\,[1 - u(x,t) - b_1 v(x,t)]\,, \\ [F_2(u,v)](x,t) = \beta v(x,t) + r_2 v(x,t)\,[1 - v(x,t) - b_2 u(x,t)] \end{cases}$$

for $(u(x,t), v(x,t)) \in C_{[0,1]}$ with $t > 0$. Then $F_1(F_2)$ is monotone increasing in u (v) while decreasing in v (u).

For any given $(u(x), v(x)) \in C$ and $t > 0$, define $T(t) = (T_1(t), T_2(t)) : C \to C$ by

$$\begin{cases} T_1(t)u(x) = \dfrac{e^{-\beta t}}{\sqrt{4\pi d_1 t}} \displaystyle\int_{-\infty}^{\infty} e^{-\frac{(x-y)^2}{4d_1 t}} u(y)dy, \\ T_2(t)v(x) = \dfrac{e^{-\beta t}}{\sqrt{4\pi d_2 t}} \displaystyle\int_{-\infty}^{\infty} e^{-\frac{(x-y)^2}{4d_2 t}} v(y)dy. \end{cases} \tag{3.1}$$

Then $T(t) : C \to C$ is an analytic semi-group [36, 42] for any $t \geqslant 0$, and $T(t)$ is also a positive semi-group in the sense that $T(t) : C^+ \to C^+$ for all $t \geqslant 0$.

Lemma 3.1 *Assume that* $(u(x), v(x)) \in C_{[0,1]}$ *holds. Then* (2.1) *has a unique classical solution* $(u(x,t), v(x,t))$ *such that*

$$(u(x,t), v(x,t)) \in C_{[0,1]} \text{ for all } t \geqslant 0.$$

Furthermore, $(u(x,t), v(x,t))$ *also takes the form as follows*

$$\begin{cases} u(x,t) = T_1(t)u(x) + \displaystyle\int_0^t T_1(t-s)[F_1(u,v)](x,s)ds, \\ v(x,t) = T_2(t)v(x) + \displaystyle\int_0^t T_2(t-s)[F_2(u,v)](x,s)ds. \end{cases} \tag{3.2}$$

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Lemma 3.1 is clear by [29, 36, 42, 50], so here we omit the proof.

Definition 3.2 Assume that $(\overline{u}(x,t), \overline{v}(x,t)), (\underline{u}(x,t), \underline{v}(x,t)) \in C^+$ for $t \in [0, t')$. If $\overline{u}(x,t), \overline{v}(x,t), \underline{u}(x,t), \underline{v}(x,t)$ are differentiable in $t \in (0,t')$ and twice differentiable in $x \in \mathbb{R}$ such that

$$\begin{cases} \dfrac{\partial \overline{u}(x,t)}{\partial t} \geqslant d_1 \Delta \overline{u}(x,t) + r_1 \overline{u}(x,t)\left[1 - \overline{u}(x,t) - b_1 \underline{v}(x,t)\right], \\ \dfrac{\partial \overline{v}(x,t)}{\partial t} \geqslant d_2 \Delta \overline{v}(x,t) + r_2 \overline{v}(x,t)\left[1 - \overline{v}(x,t) - b_2 \underline{u}(x,t)\right], \\ \dfrac{\partial \underline{u}(x,t)}{\partial t} \leqslant d_1 \Delta \underline{u}(x,t) + r_1 \underline{u}(x,t)\left[1 - \underline{u}(x,t) - b_1 \overline{v}(x,t)\right], \\ \dfrac{\partial \underline{v}(x,t)}{\partial t} \leqslant d_2 \Delta \underline{v}(x,t) + r_2 \underline{v}(x,t)\left[1 - \underline{v}(x,t) - b_2 \overline{u}(x,t)\right], \\ (\underline{u}(x,0), \underline{v}(x,0)) \leqslant (u(x), v(x)) \leqslant (\overline{u}(x,0), \overline{v}(x,0)) \end{cases} \tag{3.3}$$

for all $x \in \mathbb{R}$ and $t \in (0,t')$, then $(\overline{u}(x,t), \overline{v}(x,t))$ and $(\underline{u}(x,t), \underline{v}(x,t))$ are a pair of **upper** and **lower solutions** of (2.1).

By the technique of upper and lower solutions and the theory of reaction–diffusion equations (see [11, 29, 30, 35, 42, 50]), we have the following comparison principle.

Lemma 3.3 *Assume that* $(\overline{u}(x,t), \overline{v}(x,t))$ *and* $(\underline{u}(x,t), \underline{v}(x,t))$ *are a pair of upper and lower solutions of* (2.1) *with* $x \in \mathbb{R}, t \in [0,t')$.

(i) $(\overline{u}(x,0), \overline{v}(x,0)) \geqslant (\underline{u}(x,0), \underline{v}(x,0))$ *holds for all* $x \in \mathbb{R}$ *implies that*

$$(\overline{u}(x,t), \overline{v}(x,t)) \geqslant (\underline{u}(x,t), \underline{v}(x,t)), x \in \mathbb{R}, t \in [0,t').$$

(ii) *The unique solution of* (2.1) *satisfies*

$$(\overline{u}(x,t), \overline{v}(x,t)) \geqslant (u(x,t), v(x,t)) \geqslant (\underline{u}(x,t), \underline{v}(x,t)), x \in \mathbb{R}, t \in [0,t').$$

(iii) *If* $(\overline{u}_1(x,t), \overline{v}_1(x,t))$ *and* $(\underline{u}_1(x,t), \underline{v}_1(x,t))$ *are another pair of upper and lower solutions of* (2.1) *with* $x \in \mathbb{R}, t \in [0,t')$, *then (i)-(ii) hold if we replace* $(\overline{u}(x,t), \overline{v}(x,t))$ *and* $(\underline{u}(x,t), \underline{v}(x,t))$ *by*

$$(\min\{\overline{u}(x,t), \overline{u}_1(x,t)\}, \min\{\overline{v}(x,t), \overline{v}_1(x,t)\})$$

and

$$(\max\{\underline{u}(x,t), \underline{u}_1(x,t)\}, \max\{\underline{v}(x,t), \underline{v}_1(x,t)\}),$$

respectively.

It is difficult to construct functions satisfying the smooth conditions in Definition 3.2. Therefore, we introduce the following weaker definition of super- and sub-solutions of (3.2).

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Definition 3.4 Assume that $(\overline{u}(x,t),\overline{v}(x,t)),(\underline{u}(x,t),\underline{v}(x,t)) \in C_{[0,1]}$ for $t \in [0,t')$ and are continuous for t in the sense of $|\cdot|$. If

$$\begin{cases} \overline{u}(x,t) \geqslant T_1(t-s)\overline{u}(x,s) + \int_s^t T_1(t-\theta)[F_1(\overline{u},\underline{v})](x,\theta)d\theta, \\ \overline{v}(x,t) \geqslant T_2(t-s)\overline{v}(x,s) + \int_s^t T_2(t-\theta)[F_2(\underline{u},\overline{v})](x,\theta)d\theta, \\ \underline{u}(x,t) \leqslant T_1(t-s)\underline{u}(x,s) + \int_s^t T_1(t-\theta)[F_1(\underline{u},\overline{v})](x,\theta)d\theta, \\ \underline{v}(x,t) \leqslant T_2(t-s)\underline{v}(x,s) + \int_s^t T_2(t-\theta)[F_2(\overline{u},\underline{v})](x,\theta)d\theta \end{cases} \tag{3.4}$$

for any $0 \leqslant s \leqslant t < t'$, then $(\overline{u}(x,t),\overline{v}(x,t))$ and $(\underline{u}(x,t),\underline{v}(x,t))$ are a pair of **super-** and **sub-solutions** of (3.1).

Due to the positivity of $T(t)$, we have the following comparison principle.

Lemma 3.5 *Assume that* $(\overline{u}(x,t),\overline{v}(x,t))$ *and* $(\underline{u}(x,t),\underline{v}(x,t))$ *are a pair of super- and sub-solutions of* (3.2) *for* $t \in [0,t')$*, respectively. Then*

$$(\overline{u}(x,t),\overline{v}(x,t)) \geqslant (u(x,t),v(x,t)) \geqslant (\underline{u}(x,t),\underline{v}(x,t))$$

for $x \in \mathbb{R}$ *and* $t \in [0,t')$*, in which* $(u(x,t),v(x,t))$ *is defined by* (2.1) *or* (3.2).

Before ending this section, we also give the following remark on the verification of super- and sub-solutions.

Remark 3.6 If some of $\overline{u},\overline{v},\underline{u}$ and $\underline{v}$, e.g. $\overline{u}$ is differentiable such that

$$\frac{\partial \overline{u}(x,t)}{\partial t} \geqslant d_1\Delta\overline{u}(x,t) + r_1\overline{u}(x,t)\left[1-\overline{u}(x,t)-b_1\underline{v}(x,t)\right], x \in \mathbb{R}, t \in (0,T),$$

then the positivity of $T(t)$ implies that

$$\overline{u}(x,t) \geqslant T_1(t-s)\overline{u}(x,s) + \int_s^t T_1(t-\theta)[F_1(\overline{u},\underline{v})](x,\theta)d\theta$$

for any $0 \leqslant s \leqslant t < T, x \in \mathbb{R}$ (see [29, 41]).

4 Proof of Theorem 2.1

In this section, we shall prove Theorem 2.1 step by step, throughout which the conditions of Theorem 2.1 are assumed to be satisfied.

Lemma 4.1 *Assume that* $\epsilon > 0$ *is given. Then*

$$\lim_{t\to\infty} \sup_{|x|>(c_1+\epsilon)t} u(x,t) = \lim_{t\to\infty} \sup_{|x|>(c_2+\epsilon)t} v(x,t) = 0.$$

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Proof Let $\overline{u}(x,t), \overline{v}(x,t)$ be defined as follows

$$\begin{cases} \dfrac{\partial \overline{u}(x,t)}{\partial t} = d_1 \Delta \overline{u}(x,t) + r_1 \overline{u}(x,t)\left[1 - \overline{u}(x,t)\right], \\ \overline{u}(x,0) = u(x), \end{cases}$$

$$\begin{cases} \dfrac{\partial \overline{v}(x,t)}{\partial t} = d_2 \Delta \overline{v}(x,t) + r_2 \overline{v}(x,t)\left[1 - \overline{v}(x,t)\right], \\ \overline{v}(x,0) = v(x). \end{cases}$$

Then $\overline{u}(x,t), \overline{v}(x,t)$ are well defined for $(x,t) \in \mathbb{R} \times (0,\infty)$. By Lemma 2.2, we obtain

$$\lim_{t\to\infty} \sup_{|x|>(c_1+\epsilon)t} \overline{u}(x,t) = \lim_{t\to\infty} \sup_{|x|>(c_2+\epsilon)t} \overline{v}(x,t) = 0$$

for any $\epsilon > 0$.

Take $\underline{u}(x,t) = \underline{v}(x,t) = 0$. Then Lemma 3.1 implies that $(\overline{u}(x,t), \overline{v}(x,t))$ and $(\underline{u}(x,t), \underline{v}(x,t))$ are a pair of upper and lower solutions of (2.1). Using Lemma 3.3, we have verified what we wanted.

At the same time, we also show another proof by constructing super- and sub-solutions. Let $\lambda_1 = \sqrt{r_1/d_1}, \lambda_2 = \sqrt{r_2/d_2}$ and

$$\overline{U}(x,t) = \min\{e^{\lambda_1(x+2\sqrt{d_1r_1}t+x_1)}, e^{\lambda_1(-x+2\sqrt{d_1r_1}t+x_1)}, 1\},$$
$$\overline{V}(x,t) = \min\{e^{\lambda_2(x+2\sqrt{d_2r_2}t+x_2)}, e^{\lambda_2(-x+2\sqrt{d_2r_2}t+x_2)}, 1\}$$

with large x_1, x_2 such that

$$\overline{U}(x,0) \geqslant u(x), \overline{V}(x,0) \geqslant v(x) \text{ for all } x \in \mathbb{R}.$$

Then it is easy to show that $(\overline{U}(x,t), \overline{V}(x,t))$ and $(\underline{u}(x,t), \underline{v}(x,t))$ are a pair of super- and sub-solutions of (2.1). By Lemma 3.5, the proof is complete. □

Lemma 4.2 *For any* $\epsilon < c_5 = 2\sqrt{d_1r_1(1-b_1)}$, $\liminf_{t\to\infty} \inf_{|x|<(c_5-\epsilon)t} u(x,t) \geqslant 1 - b_1$.

Proof Note that $v(x,t) \leqslant 1$ for any $(x,t) \in \mathbb{R} \times [0,\infty)$. Then

$$\frac{\partial u(x,t)}{\partial t} \geqslant d_1 \Delta u(x,t) + r_1 u(x,t)\left[1 - b_1 - u(x,t)\right] \tag{4.1}$$

for any $(x,t) \in \mathbb{R} \times (0,\infty)$. Since Definition 3.2 and Lemma 3.3 remain true if $b_1 = b_2 = 0$, then Lemma 2.2 implies $\liminf_{t\to\infty} \inf_{|x|<(c_5-\epsilon)t} u(x,t) \geqslant 1 - b_1$. The proof is complete. □

Lemma 4.3 *For any given* $\epsilon \in (0, c_1)$, $\liminf_{t\to\infty} \inf_{|x|<(c_1-\epsilon)t} u(x,t) > 0$.

Proof From Lemmas 4.1 and 4.2, for any $\epsilon' > 0$, we can fix $T_1 > 0$ large enough such that

(i) $\sup_{2|x|<(c_2+c_5)t}\{v(x,t)/u(x,t)\} < 2/(1-b_1)$;

(ii) $\sup_{2|x|\geqslant(2c_2+\epsilon)t} v(x,t) < \epsilon'$.

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In particular, let $\epsilon' > 0$ be small such that

$$2\sqrt{d_1 r_1(1 - b_1\epsilon')} > c_1 - \epsilon.$$

Then we have

$$\frac{\partial u(x,t)}{\partial t} \geqslant d_1 \Delta u(x,t) + r_1 u(x,t)\left[1 - b_1\epsilon' - (3 - b_1)u(x,t)/(1 - b_1)\right]$$

for all $t > T_1$ and $x \in \mathbb{R}$. Using Lemma 2.2, we complete the proof. □

Using the comparison principle, the following result of (2.3) is clear.

Lemma 4.4 *Let $\delta > 0, \kappa > 0$ be fixed constants and $z(x,t)$ be a solution of* (2.3). *Assume that $z(x) > \kappa$ for x satisfying $|x - x_0| \leqslant \delta$ with some $x_0 \in \mathbb{R}$. Then for any $\epsilon > 0$, there exists $T = T(\epsilon)$ such that $z(x_0, t) > 1 - \epsilon, t > T$.*

Using the lemma, we can further establish the following estimate.

Lemma 4.5 *For any given $\epsilon \in (0, c_1)$,* $\liminf_{t\to\infty} \inf_{|x|<(c_1-\epsilon)t} u(x,t) \geqslant 1 - b_1$.

Proof Let $2\varepsilon = (1 - b_1)/(3 - b_1)$. Then there exists $T_2 > 1$ such that

$$\inf_{|x| \leqslant (c_1 - \epsilon/4)t} u(x,t) > \varepsilon, t \geqslant T_2$$

by the proof of Lemma 4.3. In particular, we can choose $T_2 > 1$ large enough for the following.

Let $\delta \in (0, 1 - b_1)$ be a constant. If $|x| \leqslant (c_1 - \epsilon/2)T_2$, then there exists $T_3 > 0$ such that

$$\inf_{|x| \leqslant (c_1 - \epsilon/2)T_2} u(x,t) \geqslant 1 - b_1 - \delta, t > T_2 + T_3 \tag{4.2}$$

by Lemma 4.4. For each $t > T_2$, $u(x,t) > \varepsilon$ holds on a neighbourhood of $x = (c_1 - \epsilon/2)t$, since the radius of the neighbourhood is larger than $\epsilon t/4 > \epsilon/4$ for all $t > T_2$, then Lemma 4.4 further indicates that

$$u((c_1 - \epsilon/2)t, t + T_4) \geqslant 1 - b_1 - \delta, t > T_2 \tag{4.3}$$

for some $T_4 > 0$. Let $(c_1 - \frac{\epsilon}{2})t = (c_1 - \epsilon)s$, then $t \to \infty$ iff $s \to \infty$ and

$$t = \frac{c_1 - \epsilon}{c_1 - \frac{\epsilon}{2}} s.$$

Then (4.3) implies that

$$u\left((c_1 - \epsilon)s, \frac{c_1 - \epsilon}{c_1 - \frac{\epsilon}{2}} s + T_4\right) = u\left((c_1 - \epsilon)s, s + T_4 - \frac{\epsilon s}{2c_1 - \epsilon}\right) \geqslant 1 - b_1 - \delta, t > T_2. \tag{4.4}$$

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Let T_2 (independent of T_4) be large enough (if necessary, we choose T_2 again) such that

$$4T_4 < \frac{\epsilon T_2}{2c_1 - \epsilon}, \quad T_4 - \frac{\epsilon T_2}{2c_1 - \epsilon} < -T_4.$$

Applying (4.3) and (4.4), we obtain

$$\inf_{|x|=(c_1-\epsilon)t} u(x,t) \geqslant 1 - b_1 - \delta, t > T_2. \tag{4.5}$$

Similar to the verification of (4.5) and using (4.2), we have

$$\inf_{|x|\leqslant(c_1-\epsilon)t} u(x,t) \geqslant 1 - b_1 - \delta$$

for large t. Due to the arbitrary choice of δ, the proof is complete. □

Lemma 4.6 *For any given* $\epsilon > 0$, $\lim_{t\to\infty} \sup_{|x|>(c_4+\epsilon)t} v(x,t) = 0$ *if* $c_1 > c_2 + c_4$.

Proof It suffices to prove the result if $4\epsilon \in (0, c_5 - c_4)$. Let $\delta > 0$ be such that

$$\left(c_4 + \frac{\epsilon}{2}\right)^2 = 4d_2r_2(1 - b_2(1 - b_1 - \delta)).$$

Lemma 4.5 also indicates that there exist $T_5 > 0, N > 0$ such that

(a) $\inf_{|x|<(c_1-\frac{\epsilon}{4})t} u(x,t) \geqslant 1 - b_1 - \delta/2, t > T_5$;
(b) $(c_1 - c_2 - c_4 - \epsilon)T_5 > N - (c_1 - c_2 - c_4)$;
(c) $\frac{r_2b_2\delta}{2} \int_{-N}^{N} e^{-\frac{y^2}{4d_2s}} e^{-\lambda_4 y} dy \geqslant (r_2 + \beta)\left(\int_N^\infty + \int_{-\infty}^{-N}\right) e^{-\frac{y^2}{4d_2s}} e^{-\lambda_4 y} dy, s \in (0,1]$.

Define continuous functions

$$\overline{u}(x,t) = 1, \underline{u}(x,t) = w(x,t), \underline{v}(x,t) = 0,$$

in which $w(x,t)$ is given by

$$\begin{cases} \dfrac{\partial w(x,t)}{\partial t} = d_1\Delta w(x,t) + r_1 w(x,t)\left[1 - w(x,t) - b_1\overline{V}(x,t)\right], \\ w(x,0) = u(x) \end{cases}$$

with $\overline{V}(x,t)$ defined in the proof of Lemma 4.1. From Lemmas 4.1–4.5, we see that $w(x,t)$ satisfies the inequality (a) if $T_5 > 0$ is large.

Let λ_3 and λ_4 be fixed such that

$$\lambda_3 = \frac{c_2}{2d_2}\,(= \lambda_2), \quad \lambda_4 = \frac{c_4 + \frac{\epsilon}{2}}{2d_2}.$$

Construct a continuous function

$$\overline{v}(x,t) = \min\left\{e^{\lambda_3(\pm x + c_2 t) + t_3}, e^{\lambda_4\left(\pm x + \left(c_4 + \frac{\epsilon}{2}\right)t\right) + t_3}, 1\right\}$$

for $t_3 > 0$.

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We first prove that $(\overline{u},\overline{v})$ and $(\underline{u},\underline{v})$ are a pair of super- and sub-solutions of (1.1) if $t \in [T_5, T_5+1]$. Clearly, for each t, $c_2 > c_4$ implies that

$$\overline{v}(x,t) = e^{\lambda_3(x+c_2t)+t_3} \text{ as } -x \to \infty.$$

Let $t_3 > 0$ be large. Then, by Remark 3.6 and the definition of $\overline{V}(x,t)$, it is clear that $\overline{u}, \underline{u}, \underline{v}$ satisfy (3.4), and it suffices to prove the inequality for $\overline{v}$ in Definition 3.4.

Set

$$E(x,t) = T_2(t-s)\overline{v}(x,s) + \int_s^t T_2(t-\theta)\,[\beta\overline{v}(x,\theta) + r_2\overline{v}(x,\theta)\,[1-\overline{v}(x,\theta) - b_2\underline{u}(x,\theta)]]\,d\theta.$$

Then we only need to prove that

$$\overline{v}(x,t) \geqslant E(x,t) \tag{4.6}$$

if $T_5 \leqslant s \leqslant t \leqslant T_5+1$, and it is clear when $\overline{v}(x,t) = 1$. In fact, if $\overline{v}(x,t) = 1$, then

$$0 \leqslant \overline{v}(y,\theta) \leqslant 1, \underline{u}(y,\theta) \geqslant 0, y \in \mathbb{R}, \theta \in [s,t]$$

such that

$$\begin{aligned} E(x,t) &\leqslant T_2(t-s)\overline{v}(x,s) + \beta\int_s^t T_2(t-\theta)\overline{v}(x,\theta)d\theta \\ &\leqslant e^{-\beta(t-s)} + (1-e^{-\beta(t-s)}) \\ &= 1 = \overline{v}(x,t). \end{aligned}$$

We now prove (4.6) for $\overline{v}(x,t) = e^{\lambda_3(x+c_2t)+t_3}$ and for $\overline{v}(x,t) = e^{\lambda_4\left(x+\left(c_4+\frac{\epsilon}{2}\right)t\right)+t_3}$.
If $\overline{v}(x,t) = e^{\lambda_3(x+c_2t)+t_3}$, then the positivity of $\overline{u}$ and $\overline{v}$ implies that

$$\begin{aligned} E(x,t) &< T_2(t-s)\overline{v}(x,s) + \int_s^t T_2(t-\theta)\,[\beta\overline{v}(x,\theta) + r_2\overline{v}(x,\theta)]\,d\theta \\ &< \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}}\int_{\mathbb{R}} e^{-\frac{y^2}{4d(t-s)}}e^{\lambda_3(x-y+c_2s)+t_3}dy \\ &\quad + \int_s^t \frac{(\beta+r_2)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}}\int_{\mathbb{R}} e^{-\frac{y^2}{4d(t-\theta)}}e^{\lambda_3(x-y+c_2\theta)+t_3}dyd\theta \\ &= e^{\lambda_3(x+c_2t)+t_3}. \end{aligned}$$

If $\overline{v}(x,t) = e^{\lambda_4\left(x+\left(c_4+\frac{\epsilon}{2}\right)t\right)+t_3}$, then

$$\lambda_4\left(x+\left(c_4+\frac{\epsilon}{2}\right)t\right) < \lambda_3(x+c_2t).$$

According to the definitions of λ_3 and λ_4, we also have

$$-x < (c_2+c_4+\epsilon/2)t < (c_1-\epsilon/2)t,$$

which further implies that (a) holds.

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Since $\overline{v} > 0$, we also have

$$E(x,t) \leqslant \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y2}{4d_2(t-s)}} \overline{v}(x-y,s)\,dy + \int_s^t \frac{e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{\mathbb{R}} e^{-\frac{y2}{4d_2(t-\theta)}} [\beta\overline{v}(x-y,\theta) + r_2\overline{v}(x-y,\theta)(1-b_2\underline{u}(x-y,\theta))]\,dyd\theta.$$

From (b), we see that for each x with $\overline{v}(x,t) = e^{\lambda_4(x+(c_4+\frac{\epsilon}{2})t)+t_3}$ and $t \in [T_5, T_5+1]$,

$$w(y,s) \geqslant 1 - b_1 - \delta/2, y \in [x-N, x+N], s \in [T_5, T_5+1].$$

Therefore, (a) and (b) indicate that

$$\begin{aligned}
E(x,t) \leqslant{}& \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y2}{4d_2(t-s)}} e^{\lambda_4(x+(c_4+\frac{\epsilon}{2})t)+t_3}\,dy \\
&+ \int_s^t \frac{e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y2}{4d_2(t-\theta)}} \left[\beta e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} \right.\\
&\left. + r_2 e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3}(1-b_2 w(x-y,\theta))\right] dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_N^{\infty} e^{-\frac{y2}{4d_2(t-\theta)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\,dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-\infty}^{-N} e^{-\frac{y2}{4d_2(t-\theta)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\,dyd\theta \\
\leqslant{}& \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y2}{4d_2(t-s)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})s)+t_3}\,dy \\
&+ \int_s^t \frac{e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y2}{4d_2(t-\theta)}} \left[\beta e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\right. \\
&\left. + r_2 e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\left(1-b_2\left(1-b_1-\frac{\delta}{2}\right)\right)\right] dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_N^{\infty} e^{-\frac{y2}{4d_2(t-\theta)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\,dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-\infty}^{-N} e^{-\frac{y2}{4d_2(t-\theta)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\,dyd\theta \\
={}& \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y2}{4d_2(t-s)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})s)+t_3}\,dy \\
&+ \int_s^t \frac{(\beta+r_2(1-b_2(1-b_1-\delta)))\,e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y2}{4d_2(t-\theta)}} e^{\lambda_4(x-y+(c_4+\frac{\epsilon}{2})\theta)+t_3}\,dyd\theta
\end{aligned}$$

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$$
\begin{aligned}
&- \frac{r_2 b_2 \delta}{2} \int_s^t \frac{e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3}\, dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{N}^{\infty} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta \\
&+ \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-\infty}^{-N} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta.
\end{aligned}
$$

Since

$$
\begin{aligned}
&\frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y^2}{4d_2(t-s)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)s\right)+t_3} dy \\
&\quad + \int_s^t \frac{(\beta+r_2(1-b_2(1-b_1-\delta)))\, e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta \\
&\leqslant \frac{e^{-\beta(t-s)}}{\sqrt{4\pi d_2(t-s)}} \int_{\mathbb{R}} e^{-\frac{y^2}{4d_2(t-s)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)s\right)+t_3} dy \\
&\quad + \int_s^t \frac{(\beta+r_2(1-b_2(1-b_1-\delta)))\, e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{\mathbb{R}} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta \\
&= e^{\lambda_4\left(x+\left(c_3+\frac{\epsilon}{4}\right)t\right)+t_3},
\end{aligned}
$$

then (4.6) is true if

$$
\begin{aligned}
&\frac{r_2 b_2 \delta}{2} \int_s^t \frac{e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-N}^{N} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta \\
&\quad \geqslant \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{N}^{\infty} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta \\
&\quad\quad + \int_s^t \frac{(r_2+\beta)e^{-\beta(t-\theta)}}{\sqrt{4\pi d_2(t-\theta)}} \int_{-\infty}^{-N} e^{-\frac{y^2}{4d_2(t-\theta)}} e^{\lambda_4\left(x-y+\left(c_4+\frac{\epsilon}{2}\right)\theta\right)+t_3} dyd\theta
\end{aligned}
$$

and it suffices to prove that

$$
\frac{r_2 b_2 \delta}{2} \int_{-N}^{N} e^{-\frac{y^2}{4d_2 s}} e^{-\lambda_4 y} dy \geqslant (r_2+\beta)\left(\int_N^{\infty} + \int_{-\infty}^{-N}\right) e^{-\frac{y^2}{4d_2 s}} e^{-\lambda_4 y} dy \tag{4.7}
$$

for $s \in [0,1]$. From (c), we obtain (4.7) and complete the proof of (4.6) if $t \in [T_5, T_5+1]$.

By the comparison principle (Lemma 3.5), we obtain

$$
(\overline{u}(x,t), \overline{v}(x,t)) \geqslant (u(x,t), v(x,t)) \geqslant (\underline{u}(x,t), \underline{v}(x,t))
$$

for $x \in \mathbb{R}$ and $t \in [T_5, T_5+1]$.

Similarly, we can prove that

$$
(\overline{u}(x,t), \overline{v}(x,t)) \geqslant (u(x,t), v(x,t)) \geqslant (\underline{u}(x,t), \underline{v}(x,t))
$$

for $t \in [T_5+k, T_5+1+k]$ with $k \in \mathbb{N}$. The proof is complete. □

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For the 'frontier' of $u(x,t)$, we formulate it as follows.

Lemma 4.7 *For any given* $\epsilon \in (0, \frac{c_1-c_2}{2})$, $\lim_{t\to\infty,(c_2+\epsilon)t<|x|<(c_1-\epsilon)t} u(x,t) = 1$.

Proof By Lemma 4.3, there exists $u_* > 0$ such that

$$\liminf_{t\to\infty} \inf_{(c_2+\frac{\epsilon}{2})t<|x|<(c_1-\frac{\epsilon}{2})t} u(x,t) = u_* > 0, \qquad \limsup_{t\to\infty} \sup_{(c_2+\frac{\epsilon}{2})t<|x|} v(x,t) = 0. \tag{4.8}$$

Let $\{\epsilon_k\}_{k=1}^{\infty}$ be a sequence with

$$\frac{\epsilon}{2} = \epsilon_1 < \epsilon_2 < \cdots, \quad \lim_{k\to\infty} \epsilon_k = \epsilon.$$

Define $\{u_*^k\}_{k=1}^{\infty}$ by

$$\liminf_{t\to\infty} \inf_{(c_2+\epsilon_k)t<|x|<(c_1-\epsilon_k)t} u(x,t) = u_*^k \geqslant u_*.$$

Then it is easy to see that $1 \geqslant u_*^k \geqslant u_*^{k-1} \geqslant u_*, k = 2, 3, \ldots$, which further implies that there exists $1 \geqslant u^* \geqslant u_* > 0$ such that $\lim_{k\to\infty} u_*^k = u^*$ with

$$u^* \leqslant \liminf_{t\to\infty} \inf_{(c_2+\epsilon)t<|x|<(c_1-\epsilon)t} u(x,t).$$

By (4.8) and the standard definition of lim inf, (3.2) indicates that

$$u_*^k \geqslant \frac{\beta u_*^{k-1} + r_1 u_*^{k-1}(1-u_*^{k-1})}{\beta}. \tag{4.9}$$

In fact, let $\kappa > 0$ be a constant such that $2\kappa \in (0, u_*)$, then there exist $T > 0$ and $N > 0$ such that

$$\int_0^T \int_{-N}^{N} \frac{1}{\sqrt{4\pi ds}} e^{-\frac{y^2}{4ds}} dyds > 1 - \kappa.$$

Moreover, the definition of lim inf also indicates that for each $k \in \mathbb{N}$, there exists t_n^k satisfying $\lim_{n\to\infty} t_n^k = \infty$ such that

$$u(x_n^k, t_n^k) \leqslant u_*^k + \kappa$$

with

$$(c_2 + \epsilon_k)t_n^k < |x_n^k| < (c_1 - \epsilon_k)t_n^k.$$

At the same time, the monotonicity of ϵ_k implies that

$$\inf_{(c_2+\epsilon_{k-1})t<|x|<(c_1-\epsilon_{k-1})t} u(x,t) \geqslant u_*^{k-1} - \kappa$$

and

$$\sup_{(c_2+\epsilon_{k-1})t<|x|<(c_1-\epsilon_{k-1})t} v(x,t) \leqslant \kappa$$

if $t \in [t_n^k - T, t_n^k]$ and t_n^k is large. Moreover, if t_n^k is large, then

$$(\epsilon_k - \epsilon_{k-1})(t_n^k - T) > N.$$

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Let $n \to \infty$, then the monotonicity of F_1 indicates that

$$u_*^k + \kappa \geqslant \frac{\beta(u_*^{k-1} - \kappa) + (1-\kappa)(u_*^{k-1} - \kappa)(1 - (u_*^{k-1} - \kappa) - b_1\kappa)}{\beta}.$$

Due to the arbitrariness of κ, we obtain (4.9).

Let $k \to \infty$, then (4.9) implies that $u^* \geqslant 1$. In view of $u(x,t) \leqslant 1$, it is clear that $u^* = 1$. The proof is complete. □

Lemma 4.8 *For any given $\epsilon \in (0, c_3)$, $\lim_{t\to\infty} u(x,t) = k_1, \lim_{t\to\infty} v(x,t) = k_2$ with $|x| < (c_3 - \epsilon)t$.*

Proof Similar to the proof of Lemma 4.2, it is obvious that

$$\liminf_{t\to\infty} \inf_{|x|<(c_3-\frac{\epsilon}{2})t} v(x,t) > 0.$$

Then there exist $u_+ \geqslant u_- > 0, v_+ \geqslant v_- > 0$ such that

$$\liminf_{t\to\infty} \inf_{|x|<(c_3-\frac{\epsilon}{2})t} u(x,t) = u_-, \quad \liminf_{t\to\infty} \inf_{|x|<(c_3-\frac{\epsilon}{2})t} v(x,t) = v_-,$$
$$\limsup_{t\to\infty} \sup_{|x|<(c_3-\frac{\epsilon}{2})t} u(x,t) = u_+, \quad \limsup_{t\to\infty} \sup_{|x|<(c_3-\frac{\epsilon}{2})t} v(x,t) = v_+.$$

By a technique similar to that in the proof of Lemma 4.7 and the definitions of lim inf and lim sup, we obtain

$$\liminf_{t\to\infty} \inf_{|x|<(c_3-\epsilon)t} u(x,t) \geqslant k_1,\ 0 < \limsup_{t\to\infty} \sup_{|x|<(c_3-\epsilon)t} u(x,t) \leqslant k_1,$$
$$\liminf_{t\to\infty} \inf_{|x|<(c_3-\epsilon)t} v(x,t) \geqslant k_2,\ 0 < \limsup_{t\to\infty} \sup_{|x|<(c_3-\epsilon)t} v(x,t) \leqslant k_2,$$

and the result is clear. The proof is complete. □

According to the proof of Lemma 4.8, the following result is also evident.

Corollary 4.9 *Assume that $\underline{c} \geqslant c_3$ such that*

$$\liminf_{t\to\infty} \inf_{|x|<(\underline{c}-\epsilon)t} u(x,t) > 0, \quad \liminf_{t\to\infty} \inf_{|x|<(\underline{c}-\epsilon)t} v(x,t) > 0$$

for any given $\epsilon \in (0, \underline{c})$. Then

$$\liminf_{t\to\infty} \inf_{|x|<(\underline{c}-\epsilon)t} u(x,t) = \limsup_{t\to\infty} \sup_{|x|<(\underline{c}-\epsilon)t} u(x,t) = k_1,$$
$$\liminf_{t\to\infty} \inf_{|x|<(\underline{c}-\epsilon)t} v(x,t) = \limsup_{t\to\infty} \sup_{|x|<(\underline{c}-\epsilon)t} v(x,t) = k_2.$$

From these results, we can complete the proof of Theorem 2.1.

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5 Generalisations

In this section, we shall show the asymptotic spreading of a delayed version of system (1.1) and a more general competition diffusion system.

5.1 A delayed system

Consider the following initial value problem

$$\begin{cases} \dfrac{\partial p(x,t)}{\partial t} = d_1 \Delta p(x,t) + r_1 p(x,t)\left[1 - p(x,t) - b_1 q(x,t-\tau_1)\right], \\ \dfrac{\partial q(x,t)}{\partial t} = d_2 \Delta q(x,t) + r_2 q(x,t)\left[1 - q(x,t) - b_2 p(x,t-\tau_2)\right], \\ (p(x,s), q(x,s)) = (\phi(x,s), \psi(x,s)) \in C_{[\mathbf{0},\mathbf{1}]}, s \in [-\tau, 0], \end{cases} \tag{5.1}$$

in which $x \in \mathbb{R}, t > 0, \tau = \max\{\tau_1, \tau_2\}$ and $(\phi, \psi) \in C([-\tau, 0], C_{[\mathbf{0},\mathbf{1}]})$. For the initial value problem (5.1), there are many results on the existence of **mild solutions** and we refer to [29, 30, 37, 41, 45, 49]. The asymptotic spreading of p and q is formulated as follows.

Theorem 5.1 *Assume that* $0 \leqslant \tau_1, \tau_2 < \infty$ *and* $d_i, r_i, b_i, i = 1, 2$, *satisfy the assumptions in Theorem* 2.1. *Then the mild solution* $(p(x,t), q(x,t))$ *of* (5.1) *is well defined and unique for all* $x \in \mathbb{R}, t > 0$. *In particular, if* $\phi(x,s), \psi(x,s)$ *admit non-empty compact supports for all* $s \in [-\tau, 0]$, *then the results of Theorem* 2.1 *remain true when we replace* $(u(x,t), v(x,t))$ *by* $(p(x,t), q(x,t)), x \in \mathbb{R}, t > 0$.

Although the discussion of Theorem 5.1 is more complex than that of Theorem 2.1 due to the choice of the phase space, the comparison principle of (5.1) is similar to that of (2.1) and essentially the combination of the theory of abstract functional differential equations (see [29]) with the monotone dynamical systems (see [40]); see also [25, 30, 41, 47] for some related topics. Therefore, the proof of Theorem 5.1 is omitted here.

Remark 5.2 Comparing Theorem 2.1 with Theorem 5.1, we see that the delays in the interaction terms do not affect the asymptotic spreading of the species with stronger ability to spread. Note that the asymptotic spreading is an index describing the long-term behaviour of the system and the comparison principle of (5.1) is similar to that of (2.1), so Theorem 5.1 is obvious from Theorem 2.1 and $\lim_{t\to\infty} \frac{\tau_1}{t} = \lim_{t\to\infty} \frac{\tau_2}{t} = 0$. It is well known that the asymptotic speeds of spreading equal to the minimal wave speeds of travelling wave solutions in many models [26, 44, 48], and we refer to [25] for the role of inter-specific delays in the travelling wave solutions.

5.2 General competition systems

For the competitive diffusive systems defined on $\mathbb{R}$, one important result regarding travelling wave solutions was established by Tang and Fife [43]. More precisely, they

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considered the travelling wave solutions of the following system:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} = d_1 \Delta u(x,t) + u(x,t) f_1(u(x,t), v(x,t)), \\ \dfrac{\partial v(x,t)}{\partial t} = d_2 \Delta v(x,t) + v(x,t) f_2(u(x,t), v(x,t)), \end{cases} \tag{5.2}$$

and proved the existence of monotone travelling wave solutions connecting $(0,0)$ with its positive equilibrium. To state their results, we first give some assumptions on (5.2).

There exist $\widehat{u} > 0, \widehat{v} > 0$ such that $f_1(\widehat{u},\widehat{v}) = f_2(\widehat{u},\widehat{v}) = 0$.

(ii) Let $f_{11} = \frac{\partial f_1(u,v)}{\partial u}\Big|_{(u,v)=(\widehat{u},\widehat{v})}, f_{12} = \frac{\partial f_1(u,v)}{\partial v}\Big|_{(u,v)=(\widehat{u},\widehat{v})}, f_{21} = \frac{\partial f_2(u,v)}{\partial u}\Big|_{(u,v)=(\widehat{u},\widehat{v})}, f_{22} = \frac{\partial f_2(u,v)}{\partial v}\Big|_{(u,v)=(\widehat{u},\widehat{v})}$, then $f_{11}f_{22} > f_{12}f_{21}$.

(iii) $f_{11} < 0, f_{22} < 0$ and $f_{12} \leqslant 0, f_{21} \leqslant 0$.

(iv) If $u \in (0,\widehat{u}), v \in (0,\widehat{v})$, then $0 < f_1(u,v) < r_1, 0 < f_2(u,v) < r_2$, here $r_1 = f_1(0,0), r_2 = f_2(0,0)$.

Theorem 5.3 ([43]). *For each* $c \geqslant \max\{2\sqrt{d_1 r_1}, 2\sqrt{d_2 r_2}\}$, (5.2) *has a travelling wave solution*

$$u(x,t) = \phi(x+ct), v(x,t) = \psi(x+ct)$$

such that $(\phi(\xi),\psi(\xi))$ *is monotone for* $\xi \in \mathbb{R}$ *and satisfies*

$$\lim_{\xi\to-\infty}(\phi(\xi),\psi(\xi)) = (0,0), \lim_{\xi\to\infty}(\phi(\xi),\psi(\xi)) = (\widehat{u},\widehat{v}).$$

Because (5.2) is a competition system, we further assume that

(v) there exist $\overline{u} \geqslant \widehat{u}, \overline{v} \geqslant \widehat{v}$ such that $f_1(\overline{u},0) = f_2(0,\overline{v}) = 0$ and $f_1(u,0) > 0, f_2(0,v) > 0$ if $u \in (0,\overline{u}), v \in (0,\overline{v})$;

(vi) $\frac{\partial f_1(u,v)}{\partial u} \leqslant 0, \frac{\partial f_1(u,v)}{\partial v} \leqslant 0, \frac{\partial f_2(u,v)}{\partial u} \leqslant 0, \frac{\partial f_2(u,v)}{\partial v} \leqslant 0$ for all $u \in [0,\overline{u}], v \in [0,\overline{v}]$;

(vii) there exists $\underline{u} \in (0,\widehat{u}), \underline{v} \in (0,\widehat{v})$ such that $f_1(\underline{u},\overline{v}) = f_2(\overline{u},\underline{v}) = 0$ and $f_1(u,\overline{v}) > 0, f_2(\overline{u},v) > 0, u \in (0,\underline{u}), v \in (0,\underline{v})$.

(viii) If $\overline{x} \geqslant \underline{x} > 0$ and $\overline{y} \geqslant \underline{y} > 0$ satisfy

$$f_1(\overline{x},\underline{y}) \geqslant 0, f_1(\underline{x},\overline{y}) \leqslant 0, f_2(\underline{x},\overline{y}) \geqslant 0, f_2(\overline{x},\underline{y}) \leqslant 0,$$

then $\overline{x} = \underline{x} = \widehat{u}, \overline{y} = \underline{y} = \widehat{v}$.

Remark 5.4 Let $f_1 = 1 - u - b_1 v^{\alpha_1}, f_2 = 1 - v - b_1 u^{\alpha_2}$. Then the corresponding kinetic system of (5.2) is of special the Gilpin–Ayala type [14]. Clearly, if $b_1, b_2 \in [0,1)$ are small and $\alpha_1, \alpha_2 \in [1,\infty)$ hold, then (5.2) satisfies (i)–(viii).

To consider the asymptotic spreading of (5.2), we further suppose that

$$u(x,0) = u_0(x), v(x,0) = v_0(x). \tag{5.3}$$

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Then our main result in this section is presented as follows.

Theorem 5.5 *Assume that (i)–(viii) hold and*

$$d_1 f_1(0,\overline{v}) > d_2 r_2. \tag{5.4}$$

We further suppose that $u(x), v(x)$ *have non-empty compact supports, and* $u(x,t)$, $v(x,t)$ *are given by* (5.2) *and* (5.3) *respectively. Define constants*

$$c_1 = 2\sqrt{d_1 r_1}, c_2 = 2\sqrt{d_2 r_2}, c_3 = 2\sqrt{d_2 f_2(\overline{u},0)}, c_4 = 2\sqrt{d_2 f_2(\underline{u},0)}.$$

Then $u(x,t), v(x,t)$ *are well defined for all* $x \in \mathbb{R}, t > 0$, *and satisfy items (i)–(v) of Theorem* 2.1.

The proof of Theorem 5.5 is similar to that of Theorem 2.1, so we omit it here.

6 Conclusions

In this paper, we have studied the long-time behaviour of several competitive systems. These results model the co-invasion of two competitors. The co-invasion is not a cooperative process so that the well-known results established for monotone semi-flows cannot be applied. Using the comparison principle for competitive systems, we give some estimates of asymptotic spreading. Our results imply that the inter-specific competition can reduce the invasion speed of one species and two invaders may have different invasion speeds.

In particular, our results are independent of the sizes of the supports of the initial values. Very likely the asymptotic spreading depends on such sizes if (2.2) or (5.4) is removed. Moreover, we only give upper and lower bounds of spreading speed for $v(x,t)$ in Theorems 2.1 and 5.5. To obtain more precise results on $v(x,t)$, further investigations are needed.

Furthermore, Tang and Fife [43] proved the existence of monotone travelling wave solutions and conjectured the existence of non-monotone travelling wave solutions. Due to the desynchronized propagation speeds of two competitors formulated by Theorem 5.5, their conjecture seems to be true and we shall consider it in forthcoming papers.

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References

[1] Ahmad, S., Lazer, A. C. & Tineo, A. (2008) Traveling waves for a system of equations. *Nonlinear Anal.* **68**(12), 3909–3912.

https://doi.org/10.1017/S0956792512000198 Published online by Cambridge University Press

[2] Aronson, D. G. (1977) The asymptotic speed of propagation of a simple epidemic. In: W.E. Fitzgibbon & H. F. Walker (editors), *Nonlinear Diffusion*, Pitman, London, pp. 1–23.

[3] Aronson, D. G. & Weinberger, H. F. (1975) Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In: J. A. Goldstein (editor), *Partial Differential Equations and Related Topics*), Lecture Notes in Mathematics, Vol. 446, Springer, Berlin, Germany, pp. 5–49.

[4] Aronson, D. G. & Weinberger, H. F. (1978) Multidimensional nonlinear diffusion arising in population dynamics. *Adv. Math.* **30**(1), 33–76.

[5] Bengtsson, J. (1989) Interspecific competition increases local extinction rate in a metapopulation system. *Nature* **340**, 713–715.

[6] Bleasdale, J. K. A. (1956) Interspecific competition in higher plants. *Nature* **178**, 150–151.

[7] Chesson, P. (2000) General theory of competitive coexistence in spatially-varying environments. *Theor. Popul. Biol.* **58**, 211–237.

[8] Conley, C. & Gardner, R. (1984) An application of the generalized Morse index to travelling wave solutions of a competitive reaction diffusion model. *Indiana Univ. Math. J.* **33**(3), 319–343.

[9] Davis, M. B. (1981) Quaternary history and stability of forest communities. In: D.C. West, H. H. Shugart & D. B. Botkin (editors), *Forest Succession: Concepts and Applications*, Springer-Verlag, New York, pp. 132–153.

[10] Diekmann, O. (1979) Run for your life. A note on the asymptotic speed of propagation of an epidemic. *J. Differ. Equ.* **33**(1), 58–73.

[11] Fife, P. C. & Tang, M. (1981) Comparison principles for reaction–diffusion systems: Irregular comparison functions and applications to questions of stability and speed of propagation of disturbances. *J. Differ. Equ.* **40**(2), 168–185.

[12] Fusco, G., Hale, J. K. & Xun, J. (1996) Traveling waves as limits of solutions on bounded domain. *SIAM J. Math. Anal.* **27**(6), 1544–1558.

[13] Gardner, S. A. (1982) Existence and stability of traveling wave solutions of competition model: A degree theoretical approach. *J. Differ. Equ.* **44**(3), 343–364.

[14] Gilpin, M. & Ayala, F. (1973) Global models of growth and competition. *Proc. Nat. Acad. Sci. USA* **70**, 3590–3593.

[15] Goel, N. S., Maitra, S. C. & Montrol, E. W. (1971) On the Volterra and other nonlinear models of interacting populations. *Revs. Mod. Phys.* **43**, 231–276.

[16] Hardin, G. (1960) The competitive exclusion principle. *Science* **131**, 1292–1297.

[17] Hosono, Y. (1995) Travelling waves for a diffusive Lotka-Volterra competition model II. A geometric approach. *Forma* **10**(3), 235–257.

[18] Hosono, Y. (2003) Traveling waves for a diffusive Lotka-Volterra competition model I. Singular perturbations. *Discrete Contin. Dyn. Syst. Ser. B* **3**(1), 79–95.

[19] Huang, W. & Han, M. (2011) Non-linear determinacy of minimum wave speed for a Lotka-Volterra competition model. *J. Differ. Equ.* **251**(6), 1549–1561.

[20] Huston, M. A. & DeAngelis, D. L. (1994) Competition and coexistence: The effects of resource transport and supply rates. *Am. Nat.* **144**, 954–977.

[21] Kanel, J. I. & Zhou, L. (1996) Existence of wave front solutions and estimates of wave speed for a competition-diffusion system. *Nonlinear Anal.* **27**(5), 579–587.

[22] Kan-on, Y. (1995) Parameter dependence of propagation speed of traveling waves for competition-diffusion equations. *SIAM J. Math. Anal.* **26**(2), 340–363.

[23] Kan-on, Y. & Fang, Q. (1996) Stability of monotone travelling waves for competition-diffusion equations. *Japan J. Indust. Appl. Math.* **13**(2), 343–349.

https://doi.org/10.1017/S0956792512000198 Published online by Cambridge University Press

[24] Lewis, M. A., Li, B. & Weinberger, H. F. (2002) Spreading speed and linear determinacy for two-species competition models. *J. Math. Biol.* **45**(3), 219–233.

[25] Li, W.-T., Lin, G. & Ruan, S. (2006) Existence of travelling wave solutions in delayed reaction diffusion systems with applications to diffusion-competition systems. *Nonlinearity* **19**(6), 1253–1273.

[26] Liang, X. & Zhao, X. (2007) Asymptotic speeds of spread and traveling waves for monotone semi-flows with applications. *Comm. Pure Appl. Math.* **60**(1), 1–40.

[27] Lin, G., Li, W.-T. & Ma, M. (2010) Traveling wave solutions in delayed reaction diffusion systems with applications to multi-species models. *Discrete Contin. Dyn. Syst. Ser. B* **13**(3), 393–414.

[28] Lin, G., Li, W.-T. & Ruan, S. (2011) Spreading speeds and traveling waves in competitive recursion systems. *J. Math. Biol.* **62**(2), 165–201.

[29] Martin, R.-H. & Smith, H. L. (1990) Abstract functional differential equations and reaction–diffusion systems. *Trans. Am. Math. Soc.* **321**(1), 1–44.

[30] Martin, R. H. & Smith, H. L. (1991) Reaction–diffusion systems with the time delay: Monotonicity, invariance, comparison and convergence. *J. Reine. Angew. Math.* **413**, 1–35.

[31] May, R. M. (1973) *Stability and Complexity in Model Ecosystems*, Princeton University Press, Princeton, NJ.

[32] Murray, J. D. (1993) *Mathematical Biology,* Springer, New York, xiv+767 pp.

[33] Okubo, A., Maini, P. K., Williamson, M. H. & Murray, J. D. (1989) On the spatial spread of the grey squirrel in Britain. *Proc. R. Soc. Lond. B* **238**, 113–125.

[34] Pan, S. (2009) Traveling wave solutions in delayed diffusion systems via a cross iteration scheme. *Nonlinear Anal. Real World Appl.* **10**(5), 2807–2818.

[35] Pao, C. V. (1992) *Nonlinear Parabolic and Elliptic Equations*, Plenum, New York, xvi+777 pp.

[36] Pazy, A. (1983) *Semigroups of Linear Operators and Applications to Partial Differential Equations*. Springer-Verlag, New York, viii+279 pp.

[37] Ruan, S. & Wu, J. (1994) Reaction-diffusion systems with infinite delay. *Canad. Appl. Math. Quart.* **2**, 485–550.

[38] Ruan, S. & Zhao, X. (1999) Persistence and extinction in two species reaction-diffusion systems with delays. *J. Differ. Equ.* **156**(1), 71–92.

[39] Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*, Oxford University Press, Oxford, UK, xiii+205 pp.

[40] Smith, H. L. (1995) *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, AMS, Providence, RI, x+174 pp.

[41] Smith, H. L. & Zhao, X. (2000) Global asymptotic stability of travelling waves in delayed reaction-diffusion equations. *SIAM J. Math. Anal.* **31**(3), 514–534.

[42] Smoller, J. (1994) *Shock Waves and Reaction Diffusion Equations*, Springer-Verlag, New York, xxi+581 pp.

[43] Tang, M. M. & Fife, P. (1980) Propagating fronts for competing species equations with diffusion. *Arch. Ration. Mech. Anal.* **73**(1), 69–77.

[44] Thieme, H. R. & Zhao, X. (2003) Asymptotic speeds of spread and traveling waves for integral equations and delayed reaction diffusion models. *J. Differ. Equ.* **195**(2), 430–470.

[45] Travis, C. C. & Webb, G. F. (1974) Existence and stability for partial functional differential equations. *Trans. Am. Math. Soc.* **200**, 395–418.

[46] Volpert, A. I., Volpert, V. A. & Volpert, V. A. (1994) *Traveling Wave Solutions of Parabolic Systems* (Translations of Mathematical Monographs, 140), AMS, Providence, RI, xii+448 pp.

https://doi.org/10.1017/S0956792512000198 Published online by Cambridge University Press

[47] Wang, Z.-C., Li, W.-T. & Ruan, S. (2008) Travelling fronts in monostable equations with nonlocal delayed effects. *J. Dyn. Differ. Equ.* **20**(3), 573–603.

[48] Weinberger, H. F., Lewis, M. A. & Li, B. (2002) Analysis of linear determinacy for spread in cooperative models. *J. Math. Biol.* **45**(3), 183–218.

[49] Wu, J. (1996) *Theory and Applications of Partial Functional Differential Equations*, Springer-Verlag, New York, x+429 pp.

[50] Ye, Q., Li, Z., Wang, M. & Wu, Y. (2011) *Introduction to Reaction Diffusion Equations*, Science Press, Beijing, China, xvii+450 pp.

https://doi.org/10.1017/S0956792512000198 Published online by Cambridge University Press