Asymptotic Spreading Fastened by Inter-Specific Coupled Nonlinearities: a Cooperative System

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Abstract

This paper is concerned with the asymptotic spreading of a Lotka-Volterra cooperative system. By using the theory of asymptotic spreading of nonautonomous equations, the asymptotic speeds of spreading of unknown functions formulated by a coupled system are estimated. Our results imply that the asymptotic spreading of one species can be significantly fastened by introducing a mutual species, which indicates the role of cooperation described by the coupled nonlinearities.

Keywords: Comparison principle; coupled nonlinearity; nonautonomous equation; complete spreading.

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1 Introduction

In this paper, we consider the propagation of the following diffusion system

\[
\begin{align*}
\frac{\partial u_1(t,x)}{\partial t} &= d_1 \Delta u_1(t,x) + r_1 u_1(t,x) \left[1 - u_1(t,x) + b_1 u_2(t,x)\right], \\
\frac{\partial u_2(t,x)}{\partial t} &= d_2 \Delta u_2(t,x) + r_2 u_2(t,x) \left[1 - u_2(t,x) + b_2 u_1(t,x)\right],
\end{align*}
\]  

in which \(u_1(t,x), u_2(t,x)\) denote the densities of two collaborators at time \(t > 0\) and location \(x \in \mathbb{R}\) in population dynamics, all the parameters are positive and \(b_1 b_2 < 1\) such that (1.1) has four spatial homogeneous steady states (for short, four equilibria)

\[(0, 0), (1, 0), (0, 1)\]

and \(K = (k_1, k_2)\) defined by

\[
(k_1, k_2) = \left(\frac{1 + b_1}{1 - b_1 b_2}, \frac{1 + b_2}{1 - b_1 b_2}\right).
\]

It is well known that \((k_1, k_2)\) is asymptotic stable while \((0, 0), (1, 0), (0, 1)\) are unstable in the corresponding spatial homogeneous system of (1.1).

Recently, Li et al. [11] have investigated the traveling wavefronts of (1.1) by using the theory established by Weinberger et al. [27], and the authors proved that the minimal wave speed of traveling wavefronts of (1.1) can be linearly determinate (see [4, 19]). In the modeling of population invasions (see Shigesada and Kawasaki [23] for many important historic records), the linear determinacy indicates that the minimal wave speed can be formulated by the parameters appearing in the system linearized at the invadable equilibrium which often is unstable in the corresponding kinetic system. In population dynamics, besides the minimal wave speeds of traveling wavefronts, the asymptotic speeds of spreading may also be linearly determinate, especially for the scalar equations, we refer to Aronson and Weinberger [1], van den Bosch [4], Diekmann [7, 8], Hsu and Zhao [10], Lui [16, 17], Mollison [19], Thieme [25], Thieme and Zhao [26] for some examples.

However, the nonlinearities in equations/systems often give expression to the inter- or intra-specific actions in population dynamics. Intuitively, the effect of nonlinearities should be reflected by many dynamical properties including the asymptotic speeds of spreading. Namely, the linear determinacy of minimal wave speed of traveling wavefronts and asymptotic speeds of spreading cannot be true for all nonlinear models. For autonomous scalar equations, a famous counter example of linear determinacy is

\[
\frac{\partial u(t, x)}{\partial t} = \Delta u(t, x) + u(t, x)(1 - u(t, x))(1 + \nu u(t, x)),
\]  

(1.2)
where $\nu > -1$ is a constant that does not appear in the following linearized system

$$\frac{\partial u(t,x)}{\partial t} = \Delta u(t,x) + u(t,x),$$

and we refer to Hadeler and Rothe [9] for precise results on its asymptotic speed of spreading, which is not linearly determinate for $\nu > 2$. Moreover, some results on asymptotic spreading have also been obtained for coupled diffusion systems with multi equilibria, which formulates the role of inter-specific coupled nonlinearities, see Lin et al. [15] and Weinberger et al. [28] for two examples of integral-difference equations, Lin [13] for a predator-prey reaction-diffusion system.

For reader’s convenience, we first give the following definition.

**Definition 1.1** Assume that $u(t,x)$ is a nonnegative function for $x \in \mathbb{R}$, $t > 0$. Then $c_*$ is called the asymptotic speed of spreading of $u(t,x)$ if

a) $\lim_{t \to \infty} \sup_{|x| > (c_* + \epsilon)t} u(t,x) = 0$ for any given $\epsilon > 0$;

b) $\liminf_{t \to \infty} \inf_{|x| < (c_* - \epsilon)t} u(t,x) > 0$ for any given $\epsilon \in (0, c_*)$.

Clearly, the asymptotic speed of spreading states the observed phenomena if an observer were to move to the right or left at a fixed speed [27]. Biologically, it also describes the speed at which the geographic range of the new population expands [10]. Therefore, it becomes a very important index formulating the spatial propagation of ecological communities. At the same time, it is possible that the asymptotic speed of spreading of a nonnegative function is not a positive constant in the above limit sense, see Berestycki et al. [3] for some examples. When the asymptotic speed of spreading is not a constant, its lower bounds and upper bounds in [2, Section 1.8] are still useful because these can describe and estimate the success of biological invasions.

If an irreducible cooperative system has just two equilibria in the interesting interval, it is very likely that all the unknown functions have the same asymptotic speed of spreading coincided with the linear determinacy, see some results by Liang and Zhao [12], Lui [16,17]. In particular, when (1.1) is concerned, Li et al. [11] Example 4.1] studied the propagation modes when one species is the aboriginal and the other is the invader, namely, the interesting interval is

$$[1,k_1] \times [0,k_2] \text{ or } [0,k_1] \times [1,k_2],$$

on which the system has no other equilibria, and can also be studied by [12,16,17].

In this paper, we consider the asymptotic spreading of (1.1) when both species are invaders, namely, $(0,0)$ will be the invadable equilibrium and the interesting interval will
be \([0, k_1] \times [0, k_2]\), on which (1.1) has four equilibria such that we cannot use the theory of [12, 16, 17]. To obtain some estimates on asymptotic spreading, the abstract results developed by Berestycki et al. [2] will be applied, and the lower bounds of asymptotic speeds of spreading will be estimated. More precisely, we first give some properties of \(u_1\), then we regard the second equation of (1.1) as a nonautonomous equation and establish some conclusions by [2]. Our results imply that: (1) The nonlinearities described the inter-specific actions may play an important role in asymptotic spreading such that the asymptotic spreading of one species is faster than the case that the inter-specific actions disappear; (2) It is necessary to use different indices to formulate the asymptotic spreading of each unknown functions if the system has multi equilibria. Moreover, our results answer the nonexistence of traveling wave solutions of (1.1), which also develops the theory of traveling wave solutions in Lin et al. [14].

In Section 2, we shall give some preliminaries, including a classical conclusion of Fisher equation and an important result established by Berestycki et al. [2]. Then we shall show some estimates on the asymptotic spreading of (1.1) if both species are invaders, which are also applied to the study of the corresponding traveling wave solutions. In the last section, further discussion is provided to illustrate our conclusions.

2 Preliminaries

We first present some results of the following Fisher’s equation

\[
\begin{aligned}
\frac{\partial z(t,x)}{\partial t} &= d\Delta z(t,x) + rz(t,x)\left[1 - \frac{z(t,x)}{K}\right], \\
z(0,x) &= z(x),
\end{aligned}
\]

(2.1)

in which all the parameters are positive and \(z(x) > 0\) is a uniform continuous and bounded function. Due to the theory of asymptotic spreading established by Aronson and Weinberger [1], we have the following result.

**Lemma 2.1** Assume that \(z(t,x)\) is defined by (2.1) and \(\epsilon \in (0, 2\sqrt{dr})\) holds. Then

\[
\lim_{t \to \infty} \inf_{|x| < (2\sqrt{dr} - \epsilon)t} z(t,x) = K.
\]

Moreover, if \(z(x)\) admits compact support, then

\[
\lim_{t \to \infty} \sup_{|x| > (2\sqrt{dr} + \epsilon)t} z(t,x) = 0.
\]

For (2.1), the following comparison principle is also true (see Ye and Li [29]).
Lemma 2.2 Assume that $\overline{z}(t,x) \geq 0, x \in \mathbb{R}, t > 0$, satisfies
\[
\begin{cases}
\frac{\partial \overline{z}(t,x)}{\partial t} \geq (\leq) d\Delta \overline{z}(t,x) + r \overline{z}(t,x) [1 - \overline{z}(t,x)/K], \\
\overline{z}(0,0) \geq (\leq) z(0).
\end{cases}
\]
Then $\overline{z}(t,x) \geq (\leq) z(t,x)$, where $z(t,x)$ is defined by (2.1).

For the system (1.1), we also give the following comparison principle (one also refers to Pao [21], Smoller [24], Ye and Li [29] for more details).

Lemma 2.3 Let $(u_1(t,x), u_2(t,x))$ be defined by
\[
\begin{cases}
\frac{\partial u_1(t,x)}{\partial t} = d_1 \Delta u_1(t,x) + r_1 u_1(t,x) [1 - u_1(t,x) + b_1 u_2(t,x)], \\
\frac{\partial u_2(t,x)}{\partial t} = d_2 \Delta u_2(t,x) + r_2 u_2(t,x) [1 - u_2(t,x) + b_2 u_1(t,x)], \\
u_1(0,x) = u_1(x), u_2(0,x) = u_2(x),
\end{cases}
\]
where $u_1(x) > 0, u_2(x) > 0$ are uniformly continuous and bounded. If $(z_1(t,x), z_2(t,x)) \geq (0,0)$ is uniformly continuous and bounded for $(t,x) \in (0, +\infty) \times \mathbb{R}$ and satisfies
\[
\begin{cases}
\frac{\partial z_1(t,x)}{\partial t} \geq (\leq) d_1 \Delta z_1(t,x) + r_1 z_1(t,x) [1 - z_1(t,x) + b_1 z_2(t,x)], \\
\frac{\partial z_2(t,x)}{\partial t} \geq (\leq) d_2 \Delta z_2(t,x) + r_2 z_2(t,x) [1 - z_2(t,x) + b_2 z_1(t,x)], \\
z_1(0,x) \geq (\leq) u_1(x), z_2(0,x) \geq (\leq) u_2(x).
\end{cases}
\]
Then $(z_1(t,x), z_2(t,x)) \geq (\leq) (u_1(t,x), u_2(t,x))$.

Now, we consider a nonautonomous equation as follows
\[
\begin{cases}
\frac{\partial u(t,x)}{\partial t} = d\Delta u(t,x) + f(t,x,u), \\
u(0,x) = u(x),
\end{cases}
\]
(2.2)
in which $f : \mathbb{R} \times \mathbb{R} \times \mathbb{R}^+ \to \mathbb{R}$ is assumed to be of class $C^{\delta/2, \delta}$ in $(t,x)$, locally in $u$, for a given $\delta \in (0,1)$. Moreover, $f$ is also locally Lipschitz continuous in $u$ and of class $C^1$ in $u \in [0, \beta]$ with $\beta > 0$ uniformly with respect to $(t,x) \in \mathbb{R} \times \mathbb{R}$, it is also supposed that $f(t,x,0) = 0$. Since (2.2) cannot generate a semiflow, the study of its asymptotic spreading is very hard. To formulate its asymptotic spreading, we first present some important definitions and results given by Berestycki et al. [2 Section 1.5].

Definition 2.4 We say that complete spreading occurs for a solution $u(t,x)$ of (2.2) if there is a function $t \to r(t) > 0$ such that $r(t) \to \infty$ as $t \to \infty$ and the family $(B_{r(t)})_{t \geq 0}$ is a family of propagation sets for $u$, that is
\[
\liminf_{t \to \infty} \left\{ \inf_{x \in B_{r(t)}} u(t,x) \right\} > 0,
\]
where \( B_r = \{ x \in \mathbb{R} : |x| < r \} \).

This definition, in fact, gives a description of the success of spatial spreading/invasion, which is similar to the second item of Definition 1.1. Since there are only two directions in \( \mathbb{R} \), we also show a specific case of Berestycki et al. [2, Definition 4] as follows.

**Definition 2.5** We say that a family \( (r(t))_{t \geq 0} \) of nonnegative real numbers is a family of asymptotic spreading radii for a solution \( u(t, x) \) of (2.2) if the family of segments \( ([-r(t), r(t)])_{t \geq 0} \) is a family of propagation sets for \( u(t, x) \), that is,

\[
\liminf_{t \to \infty} \left\{ \inf_{s \in [0, r(t)]} u(t, \pm s) \right\} > 0.
\]

**Definition 2.6** We say that a family \( (r(t))_{t \geq 0} \) is a family of admissible radii if \( (r(t))_{t \geq 0} \in C^{1+\delta/2}(\mathbb{R}^+, \mathbb{R}^+) \) and \( \sup_{t \geq 0} |r'(t)| < \infty \).

**Remark 2.7** If \( \liminf_{t \to \infty} r(t)/t \) exists and is positive, then it is a lower bounds of asymptotic speed of spreading. Such a definition is still useful because it can describe the phenomena of successful invasion, even if \( \lim_{t \to \infty} r(t)/t \) does not exist, see Berestycki et al. [2, Section 1.8] for the upper bounds of asymptotic speed of spreading.

For \( \phi \in C^{1,2}(\mathbb{R} \times \mathbb{R}) \), define

\[
L\phi = \frac{\partial \phi}{\partial t} - d\Delta \phi - f'_u(t, x, 0)\phi.
\]

Considering the generalized principal eigenvalue problem formulated by

\[
\lambda'_1 = \inf \{ \lambda \in \mathbb{R}, \exists \phi \in C^{1,2}(\mathbb{R} \times \mathbb{R}) \cap W^{1,\infty}(\mathbb{R} \times \mathbb{R}), \inf_{\mathbb{R} \times \mathbb{R}} \phi > 0, L\phi \leq \lambda \phi \},
\]

then \( \lambda'_1 < 0 \) implies that the equilibrium 0 is unstable and the following conclusion holds.

**Lemma 2.8 (2)** Assume that \( \lambda'_1 < 0 \) and there exists \( r(t) \) of admissible radii such that

\[
\liminf_{t \to \infty} u(t, \pm r(t)) > 0.
\]

Then

\[
\liminf_{t \to \infty} \left\{ \inf_{|x| \leq r(t)} u(t, x) \right\} > 0. \quad (2.3)
\]

**Lemma 2.9 (2)** Let \( u(t, x) \) be the solution of the Cauchy problem (2.2) associated with an initial datum \( u(x) > 0 \). Assume that \( \lambda'_1 < 0 \) holds and there exists \( r(t) \) of admissible radii such that

\[
\liminf_{R \to \infty} \left\{ \liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left( 4df'_u(t, x \pm r(t), 0) - (r'(t))^2 \right) \right\} \right\} > 0. \quad (2.4)
\]

Then (2.3) holds for \( u(t, x) \).
3 Main Results

In this section, we first prove the following result on asymptotic spreading.

**Theorem 3.1** Let \((u_1(t, x), u_2(t, x))\) be defined by

\[
\begin{cases}
\frac{\partial u_1(t, x)}{\partial t} = d_1 \Delta u_1(t, x) + r_1 u_1(t, x) [1 - u_1(t, x) + b_1 u_2(t, x)], \\
\frac{\partial u_2(t, x)}{\partial t} = d_2 \Delta u_2(t, x) + r_2 u_2(t, x) [1 - u_2(t, x) + b_2 u_1(t, x)], \\
u_1(0, x) = \phi_1(x), u_2(0, x) = \phi_2(x),
\end{cases}
\]  

in which \(\phi_1(x) > 0, \phi_2(x) > 0\) are uniformly continuous and bounded for \(x \in \mathbb{R}\). Suppose that \(d_1 r_1 > d_2 r_2\) holds. Then

\[
\lim_{t \to \infty} \inf_{|x| < ct} u_2(t, x) = \lim_{t \to \infty} \sup_{|x| < ct} u_2(t, x) = k_2 \quad (3.2)
\]

and

\[
\lim_{t \to \infty} \inf_{|x| < ct} u_1(t, x) = \lim_{t \to \infty} \sup_{|x| < ct} u_1(t, x) = k_1 \quad (3.3)
\]

for any \(c < c^* = \min\{2\sqrt{d_1 r_1}, 2\sqrt{d_2 r_2(1 + b_2)}\}\).

For the main condition of the theorem, we give the following remark.

**Remark 3.2** By [1], \(d_1 r_1 > d_2 r_2\) implies that \(u_1\) has stronger spreading ability than that of \(u_2\) if the inter-specific actions disappear in (3.1) (namely, \(b_1 = b_2 = 0\) in (3.1)).

Before verifying Theorem 3.1, we first prove several lemmas, through which the conditions of Theorem 3.1 will be imposed.

**Lemma 3.3** For all \(x \in \mathbb{R}, t > 0\), the Cauchy problem (3.1) admits a unique solution \((u_1(t, x), u_2(t, x))\) such that

\((0, 0) < (u_1(t, x), u_2(t, x)) \leq (E_1, E_2)\),

in which

\[
E_1 = \max \left\{ \sup_{x \in \mathbb{R}} \phi_1(x), k_1, \frac{k_1}{k_2} \sup_{x \in \mathbb{R}} \phi_2(x) \right\}, E_2 = \max \left\{ \sup_{x \in \mathbb{R}} \phi_2(x), k_2, \frac{k_2}{k_1} \sup_{x \in \mathbb{R}} \phi_1(x) \right\}.
\]

**Proof.** We prove the lemma by comparison principle. Clearly,

\[
r_1 E_1 (1 - E_1 + b_1 E_2) \leq 0, r_2 E_2 (1 - E_2 + b_2 E_1) \leq 0.
\]
Then \((E_1, E_2)\) is an upper solution while \((0, 0)\) is a lower solution of (3.1) for \((t, x) \in (0, +\infty) \times \mathbb{R}\). Therefore, Lemma 2.3 indicates that

\[
(0, 0) \leq (u_1(t, x), u_2(t, x)) \leq (E_1, E_2), \quad (t, x) \in (0, +\infty) \times \mathbb{R}.
\]

The strict inequalities are evident by the following two facts:

1. The heat operator has property of infinite propagation speed;
2. \(\phi_1(x), \phi_2(x)\) admit nonempty supports.

The proof is complete. \(\square\)

**Lemma 3.4** Define \(c_1 = 2\sqrt{d_1 r_1}\). Suppose that \(u_1(t, x)\) is defined by (3.1). Then

\[
\liminf_{t \to \infty} \inf_{|x| < ct} u_1(t, x) \geq 1 \tag{3.4}
\]

for any \(c < c_1\).

**Proof.** By Lemma 3.3, we see that

\[
\frac{\partial u_1(t, x)}{\partial t} \geq d_1 \Delta u_1(t, x) + r_1 u_1(t, x)[1 - u_1(t, x)], \quad x \in \mathbb{R}, t > 0.
\]

Then the result is evident by Lemmas 2.1 and 2.2. The proof is complete. \(\square\)

Let \(\beta > 0\) be a constant such that \(\beta u_1 + r_1 u_1[1 - u_1 + b_1 u_2], \beta u_2 + r_2 u_2[1 - u_2 + b_2 u_1]\) are monotone increasing if

\[
(0, 0) \leq (u_1, u_2) \leq (E_1, E_2).
\]

For \(t \geq 0\), define \(T(t) = (T_1(t), T_2(t))\) as follows

\[
\begin{align*}
T_1(t) u_1(x) &= \frac{e^{-\beta t}}{\sqrt{4\pi d_1 t}} \int_{-\infty}^{\infty} e^{-\frac{(x-y)^2}{4d_1 t}} u_1(y)dy, \\
T_2(t) u_2(x) &= \frac{e^{-\beta t}}{\sqrt{4\pi d_2 t}} \int_{-\infty}^{\infty} e^{-\frac{(x-y)^2}{4d_2 t}} u_2(y)dy.
\end{align*}
\]

Moreover, for \(t \geq 0, s \geq 0\), we still denote

\[
\begin{align*}
T_1(t) u_1(s, x) &= \frac{e^{-\beta t}}{\sqrt{4\pi d_1 t}} \int_{-\infty}^{\infty} e^{-\frac{(s-y)^2}{4d_1 t}} u_1(s, y)dy, \\
T_2(t) u_2(s, x) &= \frac{e^{-\beta t}}{\sqrt{4\pi d_2 t}} \int_{-\infty}^{\infty} e^{-\frac{(s-y)^2}{4d_2 t}} u_2(s, y)dy.
\end{align*}
\]
Let $X$ be defined as follows

$$X = \{ u : u \text{ is a bounded and uniformly continuous function from } \mathbb{R} \text{ to } \mathbb{R}^2 \},$$

which is a Banach space equipped with the supremum norm. Then $T(t) : X \to X$ is an analytic semigroup (see [6]). Denote

$$X^+ = \{ u : u \in X, u \geq 0 \}.$$

Then $T(t) : X^+ \to X^+$ is a positive semigroup. Using the standard theory of semigroup (see [22]), we have the following conclusion.

**Lemma 3.5** The unique solution of (3.1) can also be formulated by

$$
\begin{align*}
&u_1(t, x) = T_1(t) \phi_1(x) + \int_0^t T_1(t - s)[F_1(u_1, u_2)](s, x) ds, \\
u_2(t, x) = T_2(t) \phi_2(x) + \int_0^t T_2(t - s)[F_2(u_1, u_2)](s, x) ds,
\end{align*}
$$

(3.5)
in which $F_1(u_1, u_2) = \beta u_1 + r_1 u_1 [1 - u_1 + b_1 u_2]$, $F_2(u_1, u_2) = \beta u_2 + r_2 u_2 [1 - u_2 + b_2 u_1]$.

By above lemmas, we give the proof of Theorem 3.1 as follows.

**Proof.** Let $\bar{c} < c^*$ be fixed. By (3.4), we can choose $\epsilon > 0$ satisfying the following facts.

(A) There exists $T > 0$ such that

$$\inf_{|x| < (\bar{c} + 3c^*)t} u_1(t, x) > 1 - \epsilon \text{ for all } t > T. \quad (3.6)$$

(B) $4 \sqrt{d_2 r_2 (1 + b_2 (1 - \epsilon))} > \bar{c} + c^* > 2 \bar{c}$.

Define $r(t) = (\bar{c} + c^*) t / 2$. Then $r(t) \in C^\infty(\mathbb{R}^+, \mathbb{R}^+)$ such that Definition 2.6 is true. Moreover, $\lim_{t \to \infty} r(t) = \infty$ also implies that Definition 2.4 holds and a complete spreading of $u_1$ has been proved.

Denote

$$
\frac{\partial u_2(t, x)}{\partial t} = d_2 \Delta u_2(t, x) + r_2 u_2(t, x) [1 - u_2(t, x) + b_2 u_1(t, x)]
$$

$$= : d_2 \Delta u_2(t, x) + f(t, x, u_2), \quad (3.7)
$$
in which the definition of $f$ is clear. To apply Lemma 2.9, we encounter some difficulties since $f(t, x, u_2)$ has no definition if $t < 0$. So we define $f$ such that

$$f(t, x, u_2) = \begin{cases} f(t, x, u_2), t > 1, \\ g(t, x, u_2), t \in [0, 1], \\ r_2 u_2(1 - u_2), t < 0, \end{cases}$$

where $f(t, x, u_2)$ and $g(t, x, u_2)$ are defined as in (3.5).
in which \( g(t, x, u_2) = u_2 g_1(t, x, u_2) \) with
\[
r_2(1 - u_2) \leq g_1(t, x, u_2) \leq r_2(1 - u_2 + b_2 u_1), t \in [0, 1], x \in \mathbb{R}
\]
such that \( f \) satisfies the smooth condition of (2.2). Since \([0, 1]\) is a bounded interval, the existence of \( f \) or \( g \) is clear. Consider the following initial value problem
\[
\begin{cases}
  \frac{\partial z_2(t, x)}{\partial t} = d_2 \Delta z_2(t, x) + f(t, x, z_2), \\
  z_2(0, x) = z(x) > 0,
\end{cases}
\]
and
\[
\begin{cases}
  \frac{\partial z(t, x)}{\partial t} = d_2 \Delta z(t, x) + f(t, x, z), \\
  z(0, x) = z(x) > 0.
\end{cases}
\]
Then the comparison principle implies that
\[
z_2(t, x) \geq z(t, x), \ (t, x) \in (0, \infty) \times \mathbb{R}. \tag{3.8}
\]
Thus, it suffices to study
\[
\frac{\partial u_2(t, x)}{\partial t} = d_2 \Delta u_2(t, x) + f(t, x, u_2).
\]
Evidently, for any \((t, x) \in \mathbb{R} \times \mathbb{R}\), we have
\[
r_2 E_2 \geq f_{u_2}'(t, x, 0) \geq r_2. \tag{3.9}
\]
For the Fisher equation
\[
\frac{\partial u_2(t, x)}{\partial t} = d_2 \Delta u_2(t, x) + r_2 u_2(t, x) \left[ 1 - u_2(t, x) \right],
\]
we see that the corresponding \( \lambda_1' \) < 0 by Berestycki et al. [2, Section 1.5]. Then (3.9) implies that the corresponding \( \lambda_1' \) of (3.7) is also negative.

Therefore, we just need to verify that (2.4) is true. For any \( R > 0 \), we see that
\[
\liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left[ 4df'_{u_2}(t, x \pm r(t), 0) - (r'(t))^2 \right] \right\} = \liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left[ 4df'_{u_2}(t, x \pm r(t), 0) - \left( \frac{\vartheta + \epsilon^*}{2} \right)^2 \right] \right\} = \liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left[ 4dr_2(1 + b_2 u_1(t, x \pm r(t))) - \left( \frac{\vartheta + \epsilon^*}{2} \right)^2 \right] \right\}.
\]
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By the item (B), it is clear that (3.6) holds if \( t > 0 \) is large enough. Therefore,

\[
\liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left[ 4dr_2(1 + b_2u_1(t,x \pm r(t))) \right] - \left( \frac{\bar{c} + c^*}{2} \right)^2 \right\} \\
\geq 4dr_2(1 + b_2(1 - \epsilon)) - \left( \frac{\bar{c} + c^*}{2} \right)^2 > 0
\]

since \( R < -\frac{\bar{c} + c^*}{2}t \to \infty \) as \( t \to \infty \).

Note that \( 4dr_2(1 + b_2(1 - \epsilon)) - \left( \frac{\bar{c} + c^*}{2} \right)^2 \) is independent of \( R > 0 \), we also obtain that

\[
\liminf_{R \to \infty} \left\{ \liminf_{t \to \infty} \left\{ \inf_{|x| < R} \left[ 4dr_2'(t,x \pm r(t),0) - (r'(t))^2 \right] \right\} \right\} > 0.
\]

By Lemmas 2.8-2.9 and (3.8), if \( c = \bar{c} \), then

\[
\liminf_{t \to \infty} \inf_{|x| < ct} u_2(t,x) > 0.
\]

Due to the arbitrary of \( \bar{c} \), what we have done implies that

\[
\liminf_{t \to \infty} \inf_{|x| < ct} u_2(t,x) > 0, \quad \liminf_{t \to \infty} \inf_{|x| < ct} u_1(t,x) > 0
\]

for any \( c < c^* \).

It suffices to verify that (3.2) and (3.3) are also true for any fixed \( \bar{c} < c^* \). Let \( 2c_1 = \bar{c} + c^*, \ c_1 > c_2 > \cdots > c_n > c_{n+1} > \cdots, \lim_{n \to \infty} c_n = \bar{c} \), define positive constants

\[
\begin{align*}
\liminf_{t \to \infty} \inf_{|x| < c_n t} u_1(t,x) &= u_1^n, \quad \liminf_{t \to \infty} \inf_{|x| < c_n t} u_2(t,x) = u_2^n, \\
\limsup_{t \to \infty} \sup_{|x| < c_n t} u_1(t,x) &= \overline{u}_1^n, \quad \limsup_{t \to \infty} \sup_{|x| < c_n t} u_2(t,x) = \overline{u}_2^n.
\end{align*}
\]

and

\[
\begin{align*}
\liminf_{t \to \infty} \inf_{|x| < \bar{c} t} u_1(t,x) &= u_1, \quad \liminf_{t \to \infty} \inf_{|x| < \bar{c} t} u_2(t,x) = u_2, \\
\limsup_{t \to \infty} \sup_{|x| < \bar{c} t} u_1(t,x) &= \overline{u}_1, \quad \limsup_{t \to \infty} \sup_{|x| < \bar{c} t} u_2(t,x) = \overline{u}_2.
\end{align*}
\]

Clearly, these positive constants are well defined and satisfy

\begin{enumerate}
\item[(L1)] \( u_1^n, u_2^n \) are nondecreasing and \( u_1^n \leq u_1, u_2^n \leq u_2 \) for all \( n > 0 \);
\item[(L2)] \( \overline{u}_1^n, \overline{u}_2^n \) are nonincreasing and \( \overline{u}_1^n \geq u_1, \overline{u}_2^n \geq u_2 \) for all \( n > 0 \);
\item[(L3)] \( \lim_{n \to \infty} u_i^n \) and \( \lim_{n \to \infty} \overline{u}_i^n \) exist for \( i = 1, 2 \);
\item[(L4)] \( \lim_{n \to \infty} u_i^n \leq u_i \leq \lim_{n \to \infty} \overline{u}_i^n, i = 1, 2 \).
\end{enumerate}
For each $n \geq 1$, $t \to \infty$ implies that $(c_{n+1} - c_n)t \to \infty$. Using the positivity of the semigroup of $T(t)$ and the dominated convergence theorem for $t \to \infty$ in (3.5), we see that

$$u_{n+1}^0 \leq \frac{\beta u_n^0 + r_1 u_n^0 [1 - \beta u_1] + b_1 u_2^0]}{\beta}$$

by the monotonicity of $F_1$. Letting $n \to \infty$, we further obtain that

$$1 - \lim_{n \to \infty} u_{n+1}^0 + b_1 \lim_{n \to \infty} u_2^0 \geq 0.$$

In a similar way, we have

$$1 - \lim_{n \to \infty} u_1^n + b_1 \lim_{n \to \infty} u_2^n \leq 0,$$

$$1 - \lim_{n \to \infty} u_2^n + b_2 \lim_{n \to \infty} u_1^n \leq 0,$$

$$1 - \lim_{n \to \infty} u_2^n + b_2 \lim_{n \to \infty} u_1^n \geq 0,$$

and

$$\lim_{n \to \infty} u_1^n = \lim_{n \to \infty} u_2^n = k_1, \quad \lim_{n \to \infty} u_1^n = \lim_{n \to \infty} u_2^n = k_2.$$

From (L4), we obtain

$$u_1 = u_1 = k_1, \quad u_2 = u_2 = k_2.$$

Since $c$ is arbitrary, we complete the proof.

We now present three remarks to further illustrate our conclusion.

**Remark 3.6** If $d_1 = d_2, r_1 = r_2$, then Lin et al. [14] implies that (1.1) has a traveling wave solution connecting $(0, 0)$ with $(k_1, k_2)$ for any wave speed which is larger than $2\sqrt{d_1 r_1} = 2\sqrt{d_2 r_2}$. Therefore, if $0 < \phi_1(x) < k_1, 0 < \phi_2(x) < k_2$ admit compact supports, then the standard comparison principle states that the asymptotic speeds of spreading of two invasion species are not larger than $2\sqrt{d_1 r_1}$ (see the subsequent Propositions 3.9 and 3.10). By Lemma 3.4, the asymptotic speeds of spreading of both invasion species are $2\sqrt{d_1 r_1} = 2\sqrt{d_2 r_2}$.

**Remark 3.7** If $d_1 r_1 > d_2 r_2 k_2 = d_2 r_2 (1 + b_2) k_1$ holds and $0 < \phi_1(x) < k_1, 0 < \phi_2(x) < k_2$ admit compact supports, then $0 < u_i(t, x) \leq k_i$ and

$$\frac{\partial u_2(t, x)}{\partial t} \leq d_2 \Delta u_2(t, x) + r_2 u_2(t, x) [k_2 - u_2(t, x)].$$

Namely, $u_2$ is a lower solution of the following Cauchy problem

$$\left\{ \begin{array}{l}
\frac{\partial u_2(t, x)}{\partial t} = d_2 \Delta u_2(t, x) + r_2 u_2(t, x) [k_2 - u_2(t, x)], \\
w_2(0, x) = \phi_2(x).
\end{array} \right.$$
Then the comparison principle (Lemma 2.2) indicates that \( u_2(t, x) \leq w_2(t, x) \), and the upper bounds of asymptotic speed of spreading of \( u_2(t, x) \) is not larger than \( 2\sqrt{d_2r_2k_2} \) by Lemma 2.1. Recalling Lemma 3.4, the lower bounds of asymptotic speed of spreading of \( u_1(t, x) \) is larger than \( 2\sqrt{d_1r_1} \) such that two species have two distinct asymptotic speeds of spreading even if both of them are constants.

Remark 3.8 If \( 2\sqrt{d_2r_2} < 2\sqrt{d_1r_1} \leq 2\sqrt{d_2r_2(1 + b_2)} \) with \( d_1 = d_2 \) and \( 0 < \phi_1(x) < k_1, 0 < \phi_2(x) < k_2 \) admit compact supports, then Lin et al. [14] implies that the asymptotic speeds of spreading of both invasion species are less than \( 2\sqrt{d_1r_1} \) (see Propositions 3.9 and 3.10), and Theorem 3.1 indicates that the asymptotic speeds of spreading of both species are \( 2\sqrt{d_1r_1} \) such that the invasion of \( u_2 \) is fastened by \( u_1 \).

Before ending this section, we also apply our main result to the study of traveling wave solutions of (1.1).

Proposition 3.9 If (1.1) has a traveling wave solution \((u_1(t, x), u_2(t, x)) = (\psi_1(x + ct), \psi_2(x + ct))\) connecting \((0, 0)\) with \((k_1, k_2)\). Then the asymptotic speeds of spreading of \( u_1(t, x), u_2(t, x) \) are not larger than \( c \) if \( 0 < \phi_1(x) < k_1, 0 < \phi_2(x) < k_2 \) admit compact supports.

Proof. In the lemma, a traveling wave solution \((u_1(t, x), u_2(t, x)) = (\psi_1(x + ct), \psi_2(x + ct))\) connecting \((0, 0)\) with \((k_1, k_2)\) is formulated by

\[
\lim_{s \to -\infty} (\psi_1(s), \psi_2(s)) = (0, 0), \quad \lim_{s \to \infty} (\psi_1(s), \psi_2(s)) = (k_1, k_2),
\]

where \((\psi_1, \psi_2)\) is the wave profile and \(c\) is the wave speed.

For any \(\rho \in \mathbb{R}\), a traveling wave solution \((\psi_1(x + ct + \rho), \psi_2(x + ct + \rho))\) is also an entire solution (defined for all \(t \in \mathbb{R}\)) of the following Cauchy problem

\[
\begin{align*}
\frac{\partial u_1(t, x)}{\partial t} &= d_1 \Delta u_1(t, x) + r_1 u_1(t, x) [1 - u_1(t, x) + b_1 u_2(t, x)], \\
\frac{\partial u_2(t, x)}{\partial t} &= d_2 \Delta u_2(t, x) + r_2 u_2(t, x) [1 - u_2(t, x) + b_2 u_1(t, x)], \\
u_1(0, x) &= \psi_1(x + \rho), \quad u_2(0, x) = \psi_2(x + \rho).
\end{align*}
\]

Letting \(\rho\) large enough, then

\[
\psi_1(x + \rho) \geq \phi_1(x), \quad \psi_2(x + \rho) \geq \phi_2(x)
\]
since \(0 < \phi_1(x) < k_1, 0 < \phi_2(x) < k_2\) have compact supports. Now \((\psi_1(x + ct + \rho), \psi_2(x + ct + \rho))\) becomes an upper solution of (3.11). Then the comparison principle implies that

\[
\psi_1(x + ct + \rho) \geq u_1(t, x), \quad \psi_2(x + ct + \rho) \geq u_2(t, x)
\]

and the result is clear. \(\square\)
Proposition 3.10  Under the assumptions of Remark 3.6 or Remark 3.8, (1.1) has a traveling wave solution connecting (0, 0) with \((k_1, k_2)\) if \(c > \max\{2\sqrt{d_1 r_1}, 2\sqrt{d_2 r_2}\}\). Moreover, if \(d_1 \geq d_2, r_1 \geq r_2\), then (1.1) has a traveling wave solution connecting (0, 0) with \((k_1, k_2)\) if \(c > 2\sqrt{d_1 r_1}\). If \(c < 2\sqrt{d_1 r_1}\), then (1.1) has not a traveling wave solution connecting (0, 0) with \((k_1, k_2)\).

Proof. If \(c > \max\{2\sqrt{d_1 r_1}, 2\sqrt{d_2 r_2}\}\), then define 0 < \(\gamma_{i1} < \gamma_{i2}\) by

\[d_i \gamma_{i1}^2 - c \gamma_{i1} + r_i = d_i \gamma_{i2}^2 - c \gamma_{i2} + r_i = 0 \text{ for } i = 1, 2.
\]

By Lin et al. [14, Theorem 5.11], the lemma is true if \((\gamma_{11}, \gamma_{12}) \cap (\gamma_{21}, \gamma_{22})\) is nonempty, which is evident if Remark 3.6 or Remark 3.8 holds or \(d_1 \geq d_2\) and \(r_1 \geq r_2\) are true.

The nonexistence of traveling wave solutions is clear by Lemmas 2.1 and 3.4 and we omit the proof here. The proof is complete. □

4 Discussion

In ecological systems, the cooperative/symbiotic/mutualistic communities are very universal. For example, the role that insects, in particular bees, have in the fecundation of flowers, see Boucher [5]. Furthermore, Malchow et al. [18, Section 4.3.2] also introduced many examples. In population dynamics, the behavior of many cooperative kinetic systems is very simple: If a cooperative system admits only one positive equilibrium, then the equilibrium is asymptotic stable and the others are unstable. These mathematical results are very easy and can be found in many textbooks, we also refer to Malchow et al. [18], Murray [20]. In particular, if \(b_1 b_2 < 1\) in (1.1), then \((k_1, k_2)\) is stable and the phase plane of the corresponding kinetic system is very clear, see Murray [20, pp. 101]. Biologically, \((k_1, k_2) > (1, 1)\) implies that each species has increased its steady state population from its maximum value in isolation [20], which is achieved by inter-specific cooperation.

However, when the spatial-temporal structure is involved in cooperative systems, e.g., the spatial dispersal of plant and seeds (see Murray [20, Section 3.6]), its dynamical properties may be very complex since the process often involves the far-from-equilibrium dynamics. By Liang and Zhao [12], Lui [16, 17], if an irreducible cooperative system admits two steady states, it is very likely that different unknown functions have the same asymptotic speed of spreading. However, Remarks 3.6, 3.8 show that the complex propagation modes of evolutionary systems with multi equilibria since it is necessary to formulate the asymptotic spreading of different unknown functions by different indices. Note that the
number of steady states is determined by the nonlinearities, this certainly indicates the complex arising from the nonlinearities.

We now consider the linear determinacy problem. Because we consider the spatial invasion of two species, then one interesting equilibrium is $(0, 0)$ that is invadable. If the asymptotic speeds of spreading are linearly determinate, then the asymptotic speeds of spreading will be fully determined by $d_1, r_1, d_2, r_2$, which is impossible by Remarks 3.6-3.8. Therefore, our results show the effect of inter-specific cooperation from the following two factors: (1) asymptotic speed of spreading or its lower bounds of $u_2$ since $c^* > 2\sqrt{d_2 r_2}$ in Theorem 3.1 (2) eventual population densities on the coexistence domain because of $(k_1, k_2) > (1, 1)$.

In this paper, utilizing the theory established by Berestycki [2], we obtain some estimates of the asymptotic speeds of spreading, which partly shows the role of nonlinearity. Unfortunately, only the lower bounds and upper bounds of asymptotic speeds of spreading are obtained, precise results need further investigation.

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