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Non-linear determinacy of minimum wave speed for a Lotka–Volterra competition model

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ABSTRACT

For a reaction–diffusion system that serves as a 2-species Lotka–Volterra diffusive competition model, suppose that the corresponding reaction system has one stable boundary equilibrium and one unstable boundary equilibrium. Then it is well known that there exists a positive number c^*, called the minimum wave speed, such that, for each c larger than or equal to c^*, the reaction–diffusion system has a positive traveling wave solution of wave speed c connecting these two equilibria if and only if $c \geqslant c^*$. It has been shown that the minimum wave speed for this system is identical to another important quantity – the asymptotical speed of population spread towards the stable equilibrium. Hence to find the minimum wave speed c^* not only is of the interest in mathematics but is of the importance in application. It has been conjectured that the minimum wave speed can be determined by studying the eigenvalues of the unstable equilibrium, called the linear determinacy. In this paper we will show that the conjecture on the linear determinacy is not true in general.

1. Introduction

Consider a classical diffusive Lotka–Volterra competition model

$$u_t = d_1 \Delta u + r_1 u(1 - b_{11}u - b_{12}v),$$
$$v_t = d_2 \Delta v + r_2(1 - b_{21}v - b_{22}u),$$

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where $u(x,t)$ and $v(x,t)$ denote the population densities of species u and v at a position $x \in \mathbb{R}^n$ and time t, and Δ is the Laplace operator. For $i = 1, 2$, d_i and r_i are diffusion coefficients and linear birth rates; $1/b_{i1}$ are carrying capacities; and b_{i2} are competition coefficients for species u and v, respectively. By scaling variables and time [2], the above model can be transformed to a simpler, dimensionless system

$$\begin{aligned} u_t &= \Delta u + u(1 - u - a_1 v), \\ v_t &= d\Delta v + r(1 - v - a_2 u), \end{aligned} \tag{1.1}$$

where d, r, a_1 and a_2 are positive constants. It is clear that Eq. (1.1) always has two boundary equilibria $E_1 = (1,0)$ and $E_2 = (0,1)$. The convergence of solutions to one of equilibria E_1 and E_2 implies the competitive exclusion of one species. In this paper, we consider a mono-stable case in the sense that for the corresponding reaction system, one E_i's $(i = 1,2)$ is stable and the other is unstable. Without loss of generality, we assume that E_1 is stable and E_2 is unstable. This is equivalent to assuming that

$$a_1 < 1, \qquad a_2 > 1. \tag{1.2}$$

A biologically and mathematically interesting question is the asymptotical speed of population spread towards to the stable equilibrium point E_1. It has been proved in [6,7] that for Eq. (1.1), the asymptotical speed of population spread is identical to the minimum wave speed of traveling wave solutions connecting equilibria E_2 and E_1. Suppose the space variable $x \in \mathbb{R}^n$ in Eq. (1.1). Then a traveling wave solution of Eq. (1.1) connecting the equilibria E_2 and E_1 is a solution of the form

$$\begin{aligned} &u(x,t) = U(k \cdot x + ct), \qquad v(x,t) = V(k \cdot x + ct), \\ &\big(U(-\infty), V(-\infty)\big) = E_2, \qquad \big(U(\infty), V(\infty)\big) = E_1. \end{aligned} \tag{1.3}$$

Here the number c is the wave speed and $k \in \mathbb{R}^n$ is a unit vector denoting the direction of the wave propagation. It is well known (Theorem 4.2 in [10]) that there is a positive number c^* such that Eq. (1.1) has a nonnegative traveling wave solution of the form (1.3) if and only if $c \geqslant c^*$. In addition, a nonnegative traveling wave solution (1.3) is monotone increasing whenever it exists. Hence the number c^* is called a minimum wave speed.

A straightforward substitution yields that the functions $U(s)$ and $V(s)$ with $s = x + ct$ satisfy the system of differential equations

$$\begin{aligned} c\dot{U} &= \ddot{U} + U(1 - U - a_1 V), \\ c\dot{V} &= d\ddot{V} + rV(1 - V - a_2 U). \end{aligned} \tag{1.4}$$

If $(U(t), V(t))$ is a nonnegative solution such that $(U(t), V(t))$ converges to the unstable equilibrium point $E_2 = (0,1)$ as $t \to -\infty$, then it is necessary that the linearization of Eq. (1.4) at E_2 has a real, nonnegative eigenvalue. This is equivalent to the condition $c \geqslant 2\sqrt{1 - a_1}$ following a direct computation. Therefore we conclude that

$$c^* \geqslant 2\sqrt{1 - a_1}.$$

On the other hand, motivated by the result on minimum wave speed for Fisher's equation and by using a heuristic argument, Murray [8] and Okubo et al. [9] further conjectured that

$$c^* = 2\sqrt{1 - a_1}. \tag{1.5}$$

Since Murray and Okubo's conjecture is based on the linearization of (1.4) at the unstable equilibrium point $E_2 = (0, 1)$, if (1.5) holds, we say that the minimum wave speed is linearly determined, or it is of *linear determinacy*. Indeed, Murray and Okubo's conjecture has been confirmed for some cases [1,2,4–6]. However, it also has been indicated numerically in [2] that the conjecture might be false for some other cases. This naturally raises a question on the equality (1.5). Another reason that one may doubt the validity of (1.5) is that the right-hand sided of (1.5) is independent of the diffusion coefficient d, birth rate r and the competition coefficient a_2 of the competing species. In this paper we shall provide examples of Eq. (1.1) for which the conjecture (1.5) does not hold. That is, the minimum wave speed cannot be linearly determined in general.

This paper is organized as follows. Sections 2 and 3 are developed to establish some preliminary lemmas and auxiliary results that will be used in Section 4. In Section 4 we give a complete proof of the main theorem of this paper that shows that for certain range of parameters in Eq. (1.1) the corresponding minimum wave speed c^* is strictly large than $2\sqrt{1-a_1}$.

2. Auxiliary results

A traveling wave solution of (1.3) is said to be mono-stable if E_2 is unstable and E_1 is stable. A traveling wave solution of (1.3) is bistable if both equilibria E_1 and E_2 are stable (i.e. $a_1 > 1$ and $a_2 > 1$). It is known that, unlike the mono-stable wave, the wave speed for the bistable wave of Eq. (1.1) is unique [3]. However, we shall point out that actually there is connection between the minimum wave speed for mono-stable wave and wave speed for a bistable wave. The purpose of this section is to provide some results for bistable traveling wave of (1.1) that will be used later to study the minimum wave speed of mono-stable waves.

For the bistable wave we have the following known result [3].

Theorem 2.1. *For any given constants $a_1 > 1$, $a_2 > 1$, there is a unique real number $c(a_1, a_2)$ such that Eq. (1.1) has a nonnegative traveling wave solution $(U(s), V(s))$ of form (1.3) if and only if $c = c(a_1, a_2)$. Moreover, the following hold:*

1. *The nonnegative traveling wave solution $(U(\cdot), V(\cdot)) = (U(a_1, a_2)(\cdot), V(a_1, a_2)(\cdot))$ is unique (up to a time translation). In addition, $U(t)$ is strictly increasing and $V(t)$ is strictly decreasing.*
2. *$c(a_1, a_2)$ and $(U(a_1, a_2)(\cdot), V(a_1, a_2)(\cdot))$ are differentiable with respect to a_1 and a_2 for $a_1 > 1$, $a_2 > 1$.*
3. *Let $A_{\{a_1,a_2\}} : W^{2,2}(\mathbb{R}, \mathbb{R}^2) \to L^2(\mathbb{R}, \mathbb{R}^2)$ be the variational operator of (1.4) corresponding to the traveling wave solution $(U, V) = (U(a_1, a_2)(\cdot), V(a_1, a_2)(\cdot))$, i.e.*

$$A_{\{a_1,a_2\}}(\eta, \xi)(t) = \begin{bmatrix} \ddot{\eta}(t) - c\dot{\eta}(t) + [1 - 2U(t) - a_1 V(t)]\eta(t) - a_1 U(t)\xi(t) \\ d\ddot{\xi}(t) - c\dot{\xi}(t) - ra_2 V(t)\eta(t) + r[1 - 2V(t) - a_2 U(t)]\xi(t) \end{bmatrix},$$

where $c = c(a_1, a_2)$. Then zero is a simple eigenvalue of the operator $A_{\{a_1,a_2\}}$ and its adjoint operator $A^*_{\{a_1,a_2\}}$. Moreover, the eigenfunction $(\eta^*(\cdot), \xi^*(\cdot)) \in W^{2,2}(\mathbb{R}, \mathbb{R}^2)$ of the operator $A^*_{\{a_1,a_2\}}$ corresponding to zero eigenvalue can be chosen such that $\eta^*(t) > 0$ and $\xi^*(t) < 0$ for all $t \in \mathbb{R}$. Here for any $(u, v), (\eta, \xi) \in W^{2,2}(\mathbb{R}, \mathbb{R}^2)$,

$$\big\langle (\eta, \xi), A_{\{a_1,a_2\}}(u, v)\big\rangle = \big\langle A^*_{\{a_1,a_2\}}(\eta, \xi), (u, v)\big\rangle$$

with $\langle\cdot,\cdot\rangle$ being defined by

$$\big\langle (\eta, \xi), (u, v)\big\rangle = \int_{\mathbb{R}} \big[\eta(t)u(t) + \xi(t)v(t)\big]\, dt$$

for $(u, v), (\eta, \xi) \in L^2(\mathbb{R}, \mathbb{R}^2)$.

By Theorem 2.1 we have the following corollary that shows the relation between the bistable wave speed $c(a_1, a_2)$ and the parameters a_1 and a_2.

Corollary 2.2. *Fix $d > 0$ and $r > 0$, the unique bistable wave speed $c(a_1, a_2)$ (for $a_1 > 1$ and $a_2 > 1$) is differentiable with respect to a_1 and a_2, in addition,*

$$\frac{\partial c(a_1, a_2)}{\partial a_1} < 0, \qquad \frac{\partial c(a_1, a_2)}{\partial a_2} > 0.$$

Proof. For $a_1 > 1$ and $a_2 > 1$, define $F : W^{2,2}(\mathbb{R}, \mathbb{R}^2) \times \mathbb{R} \times (1, \infty) \times (1, \infty) \to L^2(\mathbb{R}, \mathbb{R}^2)$ by

$$F(u, v, c, a_1, a_2) = \begin{bmatrix} \ddot{u} - c\dot{u} + u[1 - u - a_1 v] \\ d\ddot{v} - c\dot{v} + rv(1 - a_2 u - v) \end{bmatrix}. \tag{2.1}$$

Let $U(t) = U(a_1, a_2)(t)$ and $V(t) = V(a_1, a_2)(t)$ be the traveling wave solution of (1.4) connecting equilibria E_2 and E_1, and let $c = c(a_1, a_2)$ be the corresponding wave speed. Then

$$F\big(U(a_1, a_2), V(a_1, a_2), c(a_1, a_2), a_1, a_2\big) \equiv 0, \quad \text{for all } a_1 > 1,\ a_2 > 1. \tag{2.2}$$

By Theorem 2.1 $U(a_1, a_2)$, $V(a_1, a_2)$ and $c(a_1, a_2)$ are differentiable with respect to a_1. Differentiating (2.2) with respect to a_1, and using definition of operator $A_{\{a_1,a_2\}}$ given in part 2 of Theorem 2.1 we obtain

$$A_{\{a_1,a_2\}}\left(\frac{\partial U(a_1, a_2)}{\partial a_1}, \frac{\partial V(a_1, a_2)}{\partial a_1}\right) = \begin{bmatrix} \frac{\partial c(a_1,a_2)}{\partial a_1}\dot{U}(a_1, a_2) + U(a_1, a_2)V(a_1, a_2) \\ \frac{\partial c(a_1,a_2)}{\partial a_1}\dot{V}(a_1, a_2) \end{bmatrix}. \tag{2.3}$$

Let $(\eta^*(\cdot), \xi^*(\cdot))$ be the eigenfunction of the operator $A^*_{\{a_1,a_2\}}$ corresponding to zero eigenvalue. From (2.3) and a straightforward computation it follows that

$$\begin{aligned}
&\frac{\partial c(a_1, a_2)}{\partial a_1}\int_{\mathbb{R}}\big[\eta^*(t)\dot{U}(a_1, a_2)(t) + \xi^*(t)\dot{V}(a_1, a_2)(t)\big]\,dt + \int_{\mathbb{R}}\eta^*(t)U(a_1, a_2)(t)V(a_1, a_2)(t)\,dt \\
&= \left\langle \big(\eta^*, \xi^*\big), A_{\{a_1,a_2\}}\left(\frac{\partial U(a_1, a_2)}{\partial a_1}, \frac{\partial V(a_1, a_2)}{\partial a_1}\right)\right\rangle \\
&= \left\langle \left(\frac{\partial U(a_1, a_2)}{\partial a_1}, \frac{\partial V(a_1, a_2)}{\partial a_1}\right), A^*_{\{a_1,a_2\}}\big(\eta^*, \xi^*\big)\right\rangle \\
&= \left\langle \left(\frac{\partial U(a_1, a_2)}{\partial a_1}, \frac{\partial V(a_1, a_2)}{\partial a_1}\right), 0\right\rangle \\
&= 0.
\end{aligned} \tag{2.4}$$

Since $\eta^*(t)$ and $\dot{U}(a_1, a_2)(t)$ are positive, $\xi^*(t)$ and $\dot{V}(a_1, a_2)(t)$ are negative, and $U(a_1, a_2)(t)$ and $V(a_1, a_2)(t)$ are positive, by (2.4) we deduce that

$$\frac{\partial(a_1, a_2)}{\partial a_1} = -\frac{\int_{\mathbb{R}}\eta^*(t)U(a_1, a_2)(t)V(a_1, a_2)(t)\,dt}{\int_{\mathbb{R}}[\eta^*(t)\dot{U}(a_1, a_2)(t) + \xi^*(t)\dot{V}(a_1, a_2)(t)]\,dt} < 0.$$

With the same computation one easily sees that

$$\frac{\partial c(a_1, a_2)}{\partial a_2} > 0. \qquad \square$$

3. Preliminary lemmas

In this section we shall establish a few lemmas that is needed to construct examples of Eq. (1.1) for which the minimum wave speed cannot be linearly determined, i.e. for which we have

$$c^* > \sqrt{1-a_1}.$$

For convenience of discussion we transform (1.4) to a monotone system by letting $W = 1 - V$. Then U and W satisfy the system

$$\begin{aligned} c\dot{U} &= \ddot{U} + U\big[1 - U - a_1(1 - W)\big], \\ c\dot{W} &= d\ddot{W} + r(1 - W)(a_2 U - W) \end{aligned} \tag{3.1}$$

with the boundary condition

$$\big(U(-\infty), W(-\infty)\big) = (0,0) = 0, \qquad \big(U(\infty), W(\infty)\big) = (1,1). \tag{3.2}$$

It is well known that (3.1) is a monotone system. Also it is clear that Eq. (1.4) has a nonnegative solution connecting E_2 and E_1 if and only if (3.1) and (3.2) has a nonnegative solution $(U(\cdot), W(\cdot))$ connecting the equilibria $(0,0)$ and $(1,1)$.

Now let us consider a special bistable case of (3.1) in which $a_1 = a_2 > 1$ and $d = r$.

Lemma 3.1. *If $d = r$, then the bistable wave speed $c(a_2, a_2) = 0$ for all $a_2 > 1$.*

Proof. First we let $d = r = 1$ and let $c = c(a_2, a_2)$ be the corresponding wave speed. By Theorem 2.1, Eq. (3.1) has a strictly increasing solution $(U(s), V(s))$ satisfying the boundary condition (3.2). Let

$$U_1(t) = 1 - W(-t), \qquad W_1(t) = 1 - U(-t), \quad t \in \mathbb{R}.$$

Then, by a straightforward computation we obtain

$$\begin{aligned} c\dot{U}_1(t) = c\dot{W}(-t) &= \ddot{W}(-t) + \big[1 - W(-t)\big]\big[a_2 U(-t) - W(-t)\big] \\ &= -\big[\ddot{U}_1(t) + U_1(t)\big(1 - U_1(t) - a_2\big[1 - W_1(t)\big]\big)\big]. \end{aligned}$$

So that

$$-c\dot{U}_1 = \ddot{U}_1 + U_1\big(1 - U_1 - a_2[1 - W_1]\big). \tag{3.3}$$

Similarly, one is able to show that

$$-c\dot{W}_1 = \ddot{W}_1 + (1 - W_1)(a_2 U_1 - W_1). \tag{3.4}$$

Moreover, by the definitions of U_1 and W_1 it is easy to see that

$$\big(U_1(-\infty), W_1(-\infty)\big) = (0,0), \qquad \big(U_1(\infty), W_1(\infty)\big) = (1,1). \tag{3.5}$$

That is, both $(U(t), W(t))$ and $(U_1(t), W_1(t))$ are nonnegative solutions of (3.1)–(3.2) for $d = r = 1$ and $a_1 = a_2$. The uniqueness of bistable wave speed therefore implies that $c = -c = c(a_2, a_2)$. Thus we must have $c(a_2, a_2) = 0$. Hence we have, for $d = r = 1$,

$$0 = \ddot{U} + U\big[1 - U - a_2(1 - W)\big],$$
$$0 = d\ddot{W} + r(1 - W)(a_2 U - W). \tag{3.6}$$

One therefore sees that (3.6) is valid for all $d = r$. That is, $c(a_1, a_2) = 0$ for all $d = r$. □

Lemma 3.2. *Let $d > 0$, $r > 0$, $\beta_1 > 0$, $\beta_2 > 0$, $c_1 < c_2$, and $0 < \lambda_1 < \lambda_2$ be constants. Suppose that there are functions $W_i(t)$, $U_i(t)$, $i = 1, 2$, such that $W_i(t)$ is positive and increasing, and satisfies*

$$d\ddot{W}_i(t) - c_i\dot{W}_i(t) + r\big(1 - W_i(t)\big)\big(\beta_i U_i(t) - W_i(t)\big) = 0, \quad t \in \mathbb{R},$$
$$W_i(t) \to 0 \quad \text{as } t \to -\infty, \tag{3.7}$$

and

$$U_i(t) = h_i e^{\lambda_i t} + o\big(e^{\lambda_i t}\big) \quad \text{as } t \to -\infty, \tag{3.8}$$

where h_i, $i = 1, 2$, are positive constants. Then there exists a constant T such that

$$U_1(t) > U_2(t), \qquad W_1(t) > W_2(t), \quad t \in (-\infty, T]. \tag{3.9}$$

Proof. The existence of T for which (3.9) holds for the functions $U_1(t)$ and $U_2(t)$ is trivial. To show the inequality (3.9) for the functions $W_1(t)$ and $W_2(t)$, we pick a small positive constant ϵ. For $i = 1, 2$, we rewrite the equation in (3.7) as

$$d\ddot{W}_i - c_i\dot{W}_i - r_i W_i = -g_i(t), \tag{3.10}$$

where

$$r_1 = r(1 + \epsilon), \qquad r_2 = r(1 - \epsilon),$$
$$g_1(t) = r\beta_1 U_1(t) + rW_1(t)\big[\epsilon - \big(\beta_1 U_1(t) - W_1(t)\big)\big],$$
$$g_2(t) = r\beta_2 U_2(t) - rW_2(t)\big[\epsilon + \big(\beta_2 U_2(t) - W_2(t)\big)\big]. \tag{3.11}$$

Let $-\alpha_i$ and μ_i be the negative and positive roots of the quadratic equation

$$d\lambda^2 - c_i\lambda - r_i = 0,$$

respectively. That is,

$$\alpha_i = \frac{-c_i + \sqrt{c_i^2 + 4dr_i}}{2d}, \qquad \mu_i = \frac{c_i + \sqrt{c_i^2 + 4dr_i}}{2d}.$$

Recall that $c_1 < c_2$ and notice that the function $y(c) = c + \sqrt{c^2 + 4dr}$ is increasing with respect to c. It follows that

$$c_1 + \sqrt{c_1^2 + 4dr} < c_2 + \sqrt{c_2^2 + 4dr}.$$

Hence, if $\epsilon > 0$ is sufficiently small, we have

$$\mu_1 = \frac{c_1 + \sqrt{c_1^2 + 4dr(1+\epsilon)}}{2d} < \frac{c_2 + \sqrt{c_2^2 + 4dr(1-\epsilon)}}{2d} = \mu_2. \tag{3.12}$$

From the assumptions that $U_i(t) \to 0$, $W_i(t) \to 0$ as $t \to -\infty$, $\lambda_1 < \lambda_2$, the expressions (3.8) and (3.11) it follows that there is a T_1 such that

$$\begin{aligned} \beta_2 U_2(t) &< \beta_1 U_1(t), \quad t \in (-\infty, T_1], \\ g_1(t) &\geqslant r\beta_1 U_1(t), \quad t \in (-\infty, T_1], \\ g_2(t) &\leqslant r\beta_1 U_2(t), \quad t \in (-\infty, T_1]. \end{aligned} \tag{3.13}$$

Applying the variation-of-parameters formula to Eq. (3.10) we arrive at

$$\begin{aligned} W_i(t) = {}& \frac{1}{d(\alpha_i + \mu_i)} \left[\int_{T_1}^{t} e^{-\alpha_i(t-s)} g_i(s)\, ds - \int_{T_1}^{t} e^{\mu_i(t-s)} g_i(s)\, ds \right] \\ & + m_i e^{-\alpha_i(t-T_1)} + k_i e^{\mu_i(t-T_1)}, \end{aligned} \tag{3.14}$$

where the constants m_i and k_i satisfy

$$m_i + k_i = W_i(T_1), \qquad -\alpha_i m_i + \mu_i k_i = \dot{W}_i(T_1).$$

The last equations yield that

$$k_i = \frac{\alpha_i W_i(T_1) + \dot{W}_i(T_1)}{\alpha_i + \mu_i} > 0, \quad i = 1, 2. \tag{3.15}$$

Also one is able to verify that $W_i(t) \to 0$ as $t \to -\infty$ implies that

$$m_i e^{\alpha_i T_1} = \frac{1}{d(\alpha_i + \mu_i)} \int_{-\infty}^{T_1} e^{\alpha_i s} g_i(s)\, ds. \tag{3.16}$$

Upon a substitution of (3.16) into (3.14) we obtain

$$W_i(t) = \frac{1}{d(\alpha_i + \mu_i)} \left[\int_{-\infty}^{t} e^{-\alpha_i(t-s)} g_i(s)\, ds + \int_{t}^{T_1} e^{\mu_i(t-s)} g_i(s)\, ds \right] + k_i e^{\mu_i(t-T_1)}. \tag{3.17}$$

Thus from (3.8), (3.13) and (3.17) if follows that, for $t \leqslant T_1$,

$$\begin{aligned} W_1(t) &\geqslant \frac{1}{d(\alpha_1 + \mu_1)} \left[\int_{-\infty}^{t} e^{-\alpha_1(t-s)} r\beta_1 U_1(s)\, ds + \int_{t}^{T_1} e^{\mu_1(t-s)} r\beta_1 U_1(s)\, ds \right] + k_1 e^{\mu_1(t-T_1)}, \\ W_2(t) &\leqslant \frac{1}{d(\alpha_2 + \mu_2)} \left[\int_{-\infty}^{t} e^{-\alpha_2(t-s)} r\beta_2 U_2(s)\, ds + \int_{t}^{T_1} e^{\mu_2(t-s)} r\beta_2 U_2(s)\, ds \right] + k_2 e^{\mu_2(t-T_1)}. \end{aligned} \tag{3.18}$$

By (3.8), (3.13) and inequality $\mu_1 < \mu_2$ we easily deduce that

$$\int_{-\infty}^{t} e^{-\alpha_i(t-s)} r\beta_i U_i(s)\,ds = \frac{rh_i\beta_i}{\alpha_i+\lambda_i} e^{\lambda_i t} + o\left(e^{\lambda_i t}\right) \quad \text{as } t \to -\infty,$$

$$\int_{t}^{T_1} e^{\mu_1(t-s)} r\beta_1 U_1(s)\,ds \geqslant \int_{t}^{T_1} e^{\mu_2(t-s)} r\beta_2 U_2(s)\,ds, \quad t \leqslant T_1. \tag{3.19}$$

From the inequalities $\lambda_1 < \lambda_2$, $\mu_1 < \mu_2$, (3.8), (3.15), (3.18), and (3.19) it therefore follows that there is a $T \leqslant T_1$ such that

$$W_1(t) > W_2(t), \quad t \in (-\infty, T]. \qquad \square \tag{3.20}$$

Corollary 3.3. *Let $a_2 > 1$, $c_1 < c_2$, and $1 \leqslant b_1 \leqslant b_2$. If $(U_i(t), W_i(t))$, $i = 1, 2$, are monotone increasing functions satisfying*

$$\ddot{U}_i - c_i\dot{U}_i + U_i\left[1 - U_i - b_i(1 - W_i)\right] = 0,$$
$$d\ddot{W}_i - c_i\dot{W}_i + r(1 - W_i)(a_2U_i - W_i) = 0,$$
$$\left(U_i(-\infty), W_i(-\infty)\right) = (0, 0), \qquad \left(U_i(\infty), W_i(\infty)\right) = (1, 1). \tag{3.21}$$

Then there are real numbers T_1 and T_2 such that

$$U_1(t) > U_2(t), \qquad W_1(t) > W_2(t) \quad \text{for all } t \in (-\infty, T_1] \cup [T_2, \infty). \tag{3.22}$$

Proof. For $i = 1, 2$, the first equation of (3.21) yields that

$$\ddot{U}_i - c_i\dot{U}_i + (1 - b_i)U_i = o\left(\left|U_1(t)\right|\right) \quad \text{as } t \to -\infty.$$

Hence $U_i(t) > 0$ and $U_i(t) \to 0$ as $t \to -\infty$ imply that

$$U_i(t) = h_i e^{\lambda_i t} + o\left(e^{\lambda_i t}\right) \quad \text{as } t \to -\infty, \tag{3.23}$$

where

$$\lambda_1 = \frac{c_1 + \sqrt{c_1^2 + 4(b_1 - 1)}}{2} < \frac{c_2 + \sqrt{c_2^2 + 4(b_2 - 1)}}{2} = \lambda_2$$

and h_i is a positive constant for $i = 1, 2$. It therefore follows from Lemma 3.2 that there is a number T_1 such that

$$U_1(t) > U_2(t), \qquad W_1(t) > W_2(t), \quad t \in (-\infty, T_1]. \tag{3.24}$$

To show the above inequality for sufficiently large t, we let

$$X_1(t) = 1 - W_2(-t), \qquad Y_1(t) = 1 - U_2(-t),$$
$$X_2(t) = 1 - W_1(-t), \qquad Y_2(t) = 1 - U_1(-t). \tag{3.25}$$

Then $X_i(t)$, $Y_i(t)$ are monotone increasing with

$$\big(X_i(-\infty), Y_i(-\infty)\big) = (0,0), \qquad \big(X_i(\infty), Y_i(\infty)\big) = (1,1).$$

Moreover, one is able to verify that $(X_i(t), Y_i(t))$ satisfies the equations

$$\begin{aligned} d\ddot{X}_i - \hat{c}_i\dot{X}_i + rX_i\big[1 - X_i - a_2(1-Y_i)\big] &= 0,\\ \ddot{Y}_i - \hat{c}_i\dot{Y}_i + (1-Y_i)(\beta_i X_i - Y_i) &= 0, \end{aligned} \tag{3.26}$$

where $\hat{c}_1 = -c_2 < -c_1 = \hat{c}_2$ and $\beta_1 = b_2$, $\beta_2 = b_1$. Arguing in the same way as above we conclude that there is a number T_2 such that

$$X_1(t) > X_2(t), \qquad Y_1(t) > Y_2(t), \quad t \in (-\infty, -T_2].$$

By the definitions of X_i and Y_i given in (3.25) and above inequalities we therefore deduce that

$$U_1(t) > U_2(t), \qquad W_1(t) > W_2(t), \quad t \in [T_2, \infty). \qquad \square \tag{3.27}$$

Lemma 3.4. *For fixed $a_1 > 0$, $a_2 > 0$, $d > 0$, $r > 0$, and $c \in \mathbb{R}$, if there exist two pairs of positive functions $(U_i(t), W_i(t))$ satisfying the following conditions: for all $t \in \mathbb{R}$,*

$$\begin{gathered} \ddot{U}_1(t) - c\dot{U}_1(t) + U_1(t)\big[1 - U_1(t) - a_1\big(1 - W_1(t)\big)\big] \geqslant 0,\\ d\ddot{W}_1(t) - c\dot{W}_1(t) + r\big(1 - W_1(t)\big)\big(a_2U_1(t) - W_1(t)\big) \geqslant 0,\\ \ddot{U}_2(t) - c\dot{U}_2(t) + U_2(t)\big[1 - U_2(t) - a_1\big(1 - W_2(t)\big)\big] \leqslant 0,\\ d\ddot{W}_2(t) - c\dot{W}_2(t) + r\big(1 - W_2(t)\big)\big(a_2U_2(t) - W_2(t)\big) \leqslant 0,\\ U_1(t) \leqslant U_2(t), \qquad W_1(t) \leqslant W_2(t),\\ \big(U_i(-\infty), W_i(-\infty)\big) = (0,0), \qquad \big(U_i(\infty), W_i(\infty)\big) = (1,1), \end{gathered} \tag{3.28}$$

then the system

$$\begin{aligned} \ddot{U} - c\dot{U} + U\big[1 - U - a_1(1-W)\big] &= 0,\\ d\ddot{W} - c\dot{W} + r(1-W)(a_2U - W) &= 0 \end{aligned} \tag{3.29}$$

has a positive solution $(U(t), W(t))$ with

$$\big(U_i(-\infty), W_i(-\infty)\big) = (0,0), \qquad \big(U_i(\infty), W_i(\infty)\big) = (1,1).$$

Proof. Note that (3.29) is a monotone system and (U_1, W_1) and (U_2, W_2) are lower and upper solutions of (3.29), respectively. The lemma therefore is a direct consequence of the monotone iteration approach. $\square$

Lemma 3.5. *Let $a_2 > 1$ be fixed. Suppose that the system*

$$\begin{aligned} \ddot{U} + U\big[1 - U - (1-W)\big] &= 0,\\ d\ddot{W} + r(1-W)(a_2U - W) &= 0 \end{aligned} \tag{3.30}$$

has a monotone increasing solution $(U_0(t), W_0(t))$ *connecting* $(0,0)$ *and* $(1,1)$. *Then for all* $a_1 > 1$, $c(a_1, a_2) < 0$, *where* $c(a_1, a_2)$ *is the bistable wave speed of Eq.* (1.1) *defined in Theorem* 2.1.

Proof. Suppose on contrary that there is an $a_1 > 1$ such that $c(a_1, a_2) \geqslant 0$. Fix an $a_1^0 \in (1, a_1)$. Then $\frac{\partial c(a_1,a_2)}{\partial a_1} < 0$ (by Corollary 2.2) implies that $c = c(a_1^0, a_2) > 0$. Let (Uc, W_c) be the corresponding monotone traveling wave solution of Eq. (3.1) connecting $(0,0)$ and $(1,1)$. Then, since $\dot{U}_c(t) \geqslant 0$, $\dot{W}_c(t) \geqslant 0$ for all $t \in \mathbb{R}$, we have

$$\begin{aligned} &\ddot{U}_c + U_c\big[1 - U_c - a_1^0(1 - W_c)\big] \geqslant \ddot{U}_c - c\dot{U}_c + U_c\big[1 - U_c - a_1^0(1 - W_c)\big] = 0, \\ &d\ddot{W}_c + r(1 - W_c)(a_2U_c - W_c) \geqslant d\ddot{W}_c - c\dot{W}_c + r(1 - W_c)(a_2U_c - W_c) = 0. \end{aligned} \tag{3.31}$$

Hence (U_c, W_c) is a lower solution of the system

$$\begin{aligned} &\ddot{U} + U\big[1 - U - a_1^0(1 - W)\big] = 0, \\ &d\ddot{W} + r(1 - W)(a_2U - W) = 0. \end{aligned} \tag{3.32}$$

Moreover, by the assumption on (U_0, W_0) and the inequalities of $a_1^0 > 1$ and $1 - W_0(t) \geqslant 0$ for all $t \in \mathbb{R}$ we have

$$\begin{aligned} &\ddot{U}_0 + U_0\big[1 - U_0 - a_1^0(1 - W_0)\big] \leqslant \ddot{U}_0 + U_0\big[1 - U_0 - (1 - W_0)\big] = 0, \\ &d\ddot{W}_0 + r(1 - W_0)(a_2U_0 - W_0) = 0. \end{aligned} \tag{3.33}$$

It follows that (U_0, W_0) is an upper solution of (3.32). By identifying $c_1 = 0$, $c_2 = c = c(a_1^0, a_2) > 0$, $b_1 = 1 < a_1^0 = b_2$, $(U_1, W_1) = (U_0, W_0)$ and $(U_2, W_2) = (U_c, W_c)$ in Lemma 3.2, it therefore follows from Corollary 3.3 that there is a $T > 0$ such that

$$U_0(t) > U_c(t), \qquad W_0(t) > W_c(t), \quad t \in (-\infty, -T] \cup [T, \infty).$$

Since $U_0(t)$ and $W_0(t)$ are monotone increasing and (3.32) is autonomous, without loss of generality, otherwise by a translation if necessary, we can suppose

$$U_0(t) \geqslant U_c(t), \qquad W_0(t) \geqslant W_c(t), \quad t \in \mathbb{R}. \tag{3.34}$$

Thus from Lemma 3.4 it follows that the system

$$\begin{aligned} &\ddot{U} + U\big[1 - U - a_1^0(1 - W)\big] = 0, \\ &d\ddot{W} + r(1 - W)(a_2U - W) = 0 \end{aligned} \tag{3.35}$$

has a positive solution connecting $(0,0)$ and $(1,1)$. Hence Theorem 2.1 implies that $c(a_1^0, a_2) = 0$, which contradicts the fact that $c = c(a_1^0, a_2) > 0$. $\square$

Corollary 3.6. *Let* $a_2 > 1$ *be fixed. Then the system* (3.30) *has no monotone increasing solution connecting* $(0,0)$ *and* $(1,1)$.

Proof. Suppose in opposite that (3.30) does have a monotone increasing solution $(U_0(t), W_0(t))$ connecting $(0,0)$ and $(1,1)$. Then from Lemma 3.5 it follows that $c(a_1, a_2) < 0$ for all $a_1 > 1$. In particular, one has $c(a_2, a_2) < 0$. But this contradicts Lemma 3.1. $\square$

4. Non-linear determinacy of minimum wave speed

Now we are ready to show that the minimum wave speed for Eq. (1.1) cannot always be linearly determined. To be specific, we have the following theorem.

Theorem 4.1. *Let $d = r$ and $a_2 > 1$ be fixed in Eq. (1.1). Let $c^*(a_1) = c^*$ be the minimum wave speed for $a_1 < 1$. Then there is an $\epsilon > 0$ such that for all $a_1 \in [1-\epsilon, 1)$,*

$$c^*(a_1) > 2\sqrt{1-a_1}.$$

Proof. Suppose the theorem is not true. Then there is a sequence $\{a_1^n\}$ of real numbers with

$$\lim_{n\to\infty} a_1^n = 1 \quad \text{and} \quad \lim_{n\to\infty} c_n^* = \lim_{n\to\infty} 2\sqrt{1-a_1^n} = 0, \tag{4.1}$$

where $c_n^* = c^*(a_1^n)$. Note that c_n^* is the minimum wave speed. Hence for each n, if we let $c_n = c_n^* + \frac{1}{n}$, then there are monotone increasing functions $U_n(t)$, $W_n(t)$ such that

$$\big(U_n(-\infty), W_n(-\infty)\big) = (0,0), \qquad \big(U_n(\infty), W_n(\infty)\big) = (1,1) \tag{4.2}$$

and

$$\begin{aligned} c_n\dot{U}_n &= \ddot{U}_n + U_n\big(1 - U_n - a_1^n[1-W_n]\big), \\ c_n\dot{W}_n &= d\ddot{W}_n + d(1-W_n)(a_2U_n - W_n). \end{aligned} \tag{4.3}$$

It is apparent that

$$c_n \to 0 \quad \text{as } n \to \infty. \tag{4.4}$$

We shall show that $\{(U_n(t), W_n(t))\}$ has a convergent subsequence that converges to a function $(U_0(t), W_0(t))$ uniformly for t in any bounded subset of $\mathbb{R}$. To this end we first show that $\{(\dot{U}_n(t), \dot{W}_n(t))\}$ is uniformly bounded. Since (4.3) is an autonomous system, without loss of generality (otherwise by a translation if necessary) we can suppose that $U_n(0) = \frac{1}{2}$ for all n. We rewrite the first equation of (4.3) as

$$\ddot{U}_n = \dot{U}_n - \big[(1-c_n)\dot{U}_n(t) + h_n(t)\big], \tag{4.5}$$

with $h_n(t) = U_n(t)(1 - U_n(t) - a_1^n[1 - W_n(t)])$. Hence

$$\begin{aligned} \dot{U}_n(t) &= \int_t^\infty e^{t-s}\big[(1-c_n)\dot{U}_n(s) + h_n(s)\big]\,ds \\ &= -(1-c_n)U_n(t) + \int_t^\infty e^{t-s}\big[(1-c_n)U_n(s)\,ds + h_n(s)\big]\,ds. \end{aligned} \tag{4.6}$$

It is obvious that there is an $M > 0$ such that

$$\big|(1-c_n)U_n(s) + h_n(s)\big| \leqslant M \quad \text{for } n = 1, 2, \ldots,\ s \in \mathbb{R}. \tag{4.7}$$

(4.6) and (4.7) yield that

$$\left|\dot{U}_n(t)\right| \leqslant 1 + c_n + M \quad \text{for } n = 1, 2, \ldots,\ t \in \mathbb{R}. \tag{4.8}$$

(4.8) implies that $\{U_n(t)\}$ is equicontinuous. Apparently the equicontinuity of $\{W_n(t)\}$ follows the same argument. By Ascoli–Arzelá theorem, for each positive integer m, there is a subsequence of $\{(U_n(t), W_n(t))\}$ that is convergent uniformly on the interval $[-m, m]$. One therefore concludes that there exist a subsequence $\{(U_{n_k}(t), W_{n_k}(t))\}$ of $\{(U_n(t), W_n(t))\}$ and a function $(U_0(t), W_0(t))$ such that $\{(U_{n_k}(t), W_{n_k}(t))\}$ converges to $(U_0(t), W_0(t))$ uniformly for t in any bounded interval of $\mathbb{R}$. Without loss of generality we suppose that

$$\big(U_n(t), W_n(t)\big) \to \big(U_0(t), W_0(t)\big) \quad \text{as } n \to \infty \tag{4.9}$$

uniformly for t in any bounded subset of $\mathbb{R}$. We rewrite the first equation of (4.3) as

$$\ddot{U}_n - c_n\dot{U}_n - U_n = -\big[U_n + U_n\big(1 - U_n - a_1^n[1 - W_n]\big)\big]. \tag{4.10}$$

Then applying the variation-of-constant formula we obtain

$$U_n(t) = \frac{1}{\alpha_n + \mu_n}\left[\int_0^t e^{-\alpha_n(t-s)} f_n(s)\,ds - \int_0^t e^{\mu_n(t-s)} f_n(s)\,ds\right] + \nu_n e^{-\alpha_n t} + \zeta_n e^{\mu_n t}, \tag{4.11}$$

where

$$\alpha_n = \frac{-c_n + \sqrt{(c_n)^2 + 4}}{2}, \qquad \mu_n = \frac{c_n + \sqrt{(c_n)^2 + 4}}{2},$$
$$f_n(t) = U_n(t) + U_n(t)\big(1 - U_n(t) - a_1^n\big[1 - W_n(t)\big]\big), \tag{4.12}$$

and the constants ν_n and ζ_n satisfy

$$\nu_n + \zeta_n = U_n(0), \qquad -\alpha_n\nu_n + \mu_n\zeta_n = \dot{U}_n(0). \tag{4.13}$$

Notice that both $\{U_n(0)\}$ and $\{\dot{U}_n(0)\}$ are bounded sequences. So that the sequences $\{\nu_n\}$ and $\{\zeta_n\}$ are bounded. Hence, without loss of generality, we suppose

$$\nu_n \to \nu_0 \in \mathbb{R}, \qquad \zeta_n \to \zeta_0 \in \mathbb{R} \quad \text{as } n \to \infty. \tag{4.14}$$

By passing limit in (4.11) as $n \to \infty$ and with the use of (4.9), (4.12) and (4.14) we therefore arrive at

$$U_0(t) = \frac{1}{2}\left[\int_0^t e^{-(t-s)} f_0(s)\,ds - \int_0^t e^{(t-s)} f_0(s)\,ds\right] + \nu_0 e^{-t} + \zeta_0 e^{t} \tag{4.15}$$

with

$$f_0(s) = U_0(s) + U_0(s)\big(1 - U_0(s) - \big[1 - W_0(s)\big]\big). \tag{4.16}$$

(4.15) and (4.16) immediately yield that

$$\ddot{U}_0 + U_0\big(1 - U_0 - [1 - W_0]\big) = 0, \quad t \in \mathbb{R}. \tag{4.17}$$

Similarly one is able to deduce that

$$d\ddot{W}_0 + r(1 - W_0)(a_2U_0 - W_0) = 0, \quad t \in \mathbb{R}. \tag{4.18}$$

Recall that for each n, $(U_n(t), W_n(t))$ is monotone increasing. It follows that both U_0 and W_0 are monotone increasing functions and $0 \leqslant U_0(t) \leqslant 1$, $0 \leqslant W_0(t) \leqslant 1$. Hence $(U_0(-\infty), W_0(-\infty))$ and $(U_0(\infty), W_0(\infty))$ exist and are equilibria of the system (4.17)–(4.18). Moreover, the equality $U_n(0) = \frac{1}{2}$ for all n implies that $U_0(0) = \frac{1}{2}$. It follows that $U_0(-\infty) \leqslant \frac{1}{2} \leqslant U_0(\infty)$. We then are able to conclude that $(U_0(-\infty), W_0(-\infty)) = (0,0)$ and $(U_0(\infty), W_0(\infty)) = (1,1)$. That is, the system (3.30) has a monotone increasing solution connecting $(0,0)$ and $(1,1)$, which is in contradiction with Corollary 3.6. □

5. A short discussion

For the minimum wave speed of mono-stable traveling wave solutions of the system (1.1), most of work done is to find a sufficient condition on the parameters that implies the linear determinacy, or the equality (1.5). For example, Lewis, Li and Weinberger [5] showed that (1.5) holds provided that

$$d \leqslant 2 \quad \text{and} \quad \frac{r + (d-2)(1-a_1)}{a_2 r} > a_1. \tag{5.1}$$

Recently, Huang [4] proved the equality (1.5) under a weaker condition

$$\frac{r + (d-2)(1-a_1)}{a_2 r} \geqslant \max\left\{a_1, \frac{d-2}{2|d-1|}\right\}, \tag{5.2}$$

which allows $d \geqslant 2$. Note that (5.1) and (5.2) are the same if $d < 2$. All parameters play role in the condition (5.1) or (5.2). It is unknown what should be the minimum wave speed c^* if the condition (5.2) fails. Further research should be carried out to find an algebraic, or analytic expression of minimum wave speed c^* that is clearly of great interest both in mathematics and in application.

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