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On the conjecture for the pushed wavefront to the diffusive Lotka–Volterra competition model

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Abstract
This paper concerns ecological invasion phenomenon of species based on the diffusive Lotka–Volterra competition model. We investigate the spreading speed (or the minimal wave speed of traveling waves) selection to the model and concentrate on the conjecture raised by Roques et al. (J Math Biol 71(2):465–489, 2015). By using an abstract implicit function theorem in a weighted functional space coupled with a perturbation technique, we not only prove this conjecture, but also show that the fast decay behavior of the first species is necessary and sufficient for the nonlinear speed selection of the whole system. This may lead to further significant results on the answer to the original Hosono's conjecture, a problem that has been outstanding for more than twenty years.

Keywords Lotka–Volterra · Competition · Pulled and pushed waves · Speed selection

Mathematics Subject Classification 35K57 · 35B20 · 92D25

1 Introduction

Biodiversity of a specific ecosystem creates a competitive scene of different species. Growth of competitive species can be studied based on the characteristics of competition strength (Kolar and Lodge 2001; Lonsdale 1999), environmental resources (Sher and Hyatt 1999), or by considering these factors together (Shea and Chesson

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2002). Ecological competition also appears evidently in biological invasions. Interaction between invasive and resident species leads to ecological equilibrium so that they can coexist or only one of them wins the competition and survives (Amarasekare 2003; Tang and Fife 1980). Indeed, species dispersal has a significant impact to the population growth in competition so that when populations spread they encounter others (Mack et al. 2000). Mathematically, logistic equation describes the population growth of a single species. By including interspecific competition and the dispersal factors, invasion spreading and its speed can be described by traveling wave solutions of the diffusive Lotka–Volterra competition model,

$$\begin{aligned} \phi_t &= d_1\phi_{xx} + r_1\phi\left(1 - \frac{\phi}{k_1} - l_1\psi\right), \\ \psi_t &= d_2\psi_{xx} + r_2\psi\left(1 - l_2\phi - \frac{\psi}{k_2}\right), \end{aligned} \tag{1.1}$$

subjected to $\phi(x, 0) = \phi_0(x)$ and $\psi(x, 0) = \psi_0(x)$. Here $\phi(x, t)$ and $\psi(x, t)$ are the population densities at time t and location x; d_1 and d_2 are the diffusion coefficients; r_1 and r_2 are the net birth rates; l_1 and l_2 are the competition coefficients; k_1 and k_2 are the carrying capacities which include the intraspecific competition. Based on this model, Okubo et al. (1989) successfully studied the dynamics of the externally introduced gray squirrels and the indigenous red squirrels in Britain.

By letting

$$d = \frac{d_1}{d_2}, \quad r = \frac{r_2}{r_1}, \quad a_1 = l_1k_2, \quad a_2 = l_2k_1,$$
$$u(x, t) = \frac{\phi(x, t)}{k_1}, \text{ and } v(x, t) = 1 - \frac{\psi(x, t)}{k_2},$$

the time-space transformation

$$\sqrt{r_1/d_1}\, x \to x \text{ and } r_1t \to t$$

leads to a cooperative system

$$\begin{aligned} u_t &= u_{xx} + u(1 - a_1 - u + a_1v), \\ v_t &= dv_{xx} + r(1 - v)(a_2u - v), \end{aligned} \tag{1.2}$$

subjected to $u(x, 0) = u_0(x)$ and $v(x, 0) = v_0(x)$. In this work, we assume that the invasive species ϕ outcompetes the resident ψ, that is, the condition

$$0 \le a_1 < 1 < a_2 \tag{1.3}$$

is satisfied. Under this condition, equilibria of the system (1.2) inside $[0, 1] \times [0, 1]$ are only $(0, 0)$, $(0, 1)$, and $(1, 1)$. In the absence of diffusion, standard linear stability analysis implies that $(1, 1)$ is stable and $(0, 0)$ is unstable (see e.g. Kan-on 1997). Back to the original system, the state $(0, k_2)$, which corresponds to $(u, v) = (0, 0)$, means that only species ψ is present with the value of its carrying capacity. If it is invaded by species with density ϕ, then it will be excluded to the state $(k_1, 0)$, which corresponds to $(u, v) = (1, 1)$.

Biologically, competitive exclusion and spatial dispersal result in a wave propagation phenomenon. To describe the spreading of the invasive species into the resident one, we consider traveling wave solutions of (1.2) in the form

$$(u, v)(x, t) = (U, V)(z), \; z = x - ct,$$

which connects $(1, 1)$ and $(0, 0)$, for some constant $c \geq 0$ that is called the wave speed. Indeed, the system satisfied by (U, V) reads

$$\begin{aligned} &U'' + cU' + U(1 - a_1 - U + a_1 V) = 0, \\ &dV'' + cV' + r(1 - V)(a_2 U - V) = 0, \\ &(U, V)(-\infty) = (1, 1), \; (U, V)(\infty) = (0, 0). \end{aligned} \tag{1.4}$$

For the behavior of the wave profile of the nonlinear system (1.4) near the equilibrium point $(0, 0)$, by linearizing the system around $(0, 0)$, we get the following system

$$\begin{aligned} &U'' + cU' + U(1 - a_1) = 0, \\ &dV'' + cV' + r(a_2 U - V) = 0, \end{aligned} \tag{1.5}$$

where the first equation is de-coupled from the system. Since we require that U tends to zero as $z \to \infty$, obviously the solution U has the behavior

$$U(z) \sim C_1 e^{-\mu_1(c) z}, \quad \text{as } z \to \infty, \tag{1.6}$$

or

$$U(z) \sim C_2 e^{-\mu_2(c) z}, \quad \text{as } z \to \infty, \tag{1.7}$$

with positive constants C_1 and C_2, where μ_1 and μ_2 are given by

$$\mu_1(c) = \frac{c - \sqrt{c^2 - 4(1 - a_1)}}{2}, \quad \mu_2(c) = \frac{c + \sqrt{c^2 - 4(1 - a_1)}}{2} \tag{1.8}$$

for $c > c_0 = 2\sqrt{1 - a_1}$. Here, μ_1 and μ_2 are real and monotonic in c with $\mu_1(c) < \mu_2(c)$. For more details we refer readers to Appendix A of (Alhasanat and Ou 2019a). A similar behavior was also derived by Okubo et al. (1989) and Roques et al. (2015).

Define

$$c^* = \inf\{c : (1.4) \text{ has a positive monotone solution}\}.$$

Results of (Kan-on 1997; Liang and Zhao 2007; Li et al. 2005; Volpert et al. 1994) imply the existence of $c^* > 0$. The value of c^* is equal to the asymptotic spreading speed which describes how the invasive species spread into the resident species (Roques et al. 2015). By a standard linearization of the system about (0, 0), we can show that $c^* \geq c_0 = 2\sqrt{1-a_1}$, where c_0 is the minimal wave speed of the linearized system. If $c^* = c_0$, then we say that the minimal wave speed is *linearly selected*, and the wavefront with this speed is called a pulled front; if $c^* > c_0$, then the minimal wave speed is *nonlinearly selected* and the wavefront with the speed c^* is called a pushed front.

The speed selection problem of the system (1.4), under the condition (1.3), is widely investigated. While many sufficient conditions on the parameters for both linear and nonlinear selections are established (Alhasanat and Ou 2019b, a; Hosono 1998; Hozler and Scheel 2012; Huang and Han 2011; Huang 2010; Lewis et al. 2002), the so-called Hosono conjecture raised by Hosono (1998) has remained unsolved.

To further study this problem, based on numerical computations, recently Roques et al. (2015) raised another important conjecture for the key feature of wave front U in terms of its decay behavior in the case of nonlinear speed selection.

Conjecture 1 (Conjecture 1 of (Roques et al. 2015)) *For $d, r > 0$, assume that the minimal wave speed of the system (1.4), under the condition (1.3), is nonlinearly selected and $(U^*, V^*)(z)$ is the solution of the system with the minimal speed c^*. Then, $u(t,x) = U(x - c^*t)$ is a fast decay wave, i.e., $U(z)$ decays to 0 at the rate*

$$U(z) \sim Ce^{-\mu_2(c^*)z}, \quad \text{as } z \to \infty, \quad z = x - c^*t,$$

where C is a positive constant and

$$\mu_2(c^*) = \frac{c^* + \sqrt{(c^*)^2 - 4(1-a_1)}}{2}.$$

This conjecture claims that the pushed wavefront U decays at infinity in a fast manner $e^{-\mu_2(c^*)z}$ instead of the slow convergence rate $e^{-\mu_1(c^*)z}$ that seems to be taken for all waves with speed $c > c_0$. Some related facts were discussed by Roques et al. (2015) based on the validity of the result in this conjecture. As far as we know, there has been no rigourous proof on it. In the present paper, we work on this conjecture. By way of an abstract implicit function theorem in a weighted functional space coupled with a perturbation technique, this conjecture is successfully proved, and we also show that the fast decay behavior of the pushed wavefront U is necessary and sufficient for the nonlinear speed selection. This will help to further develop significant results on a possible answer to the original Hosono conjecture, a problem that has been outstanding for more than twenty years.

The rest of the paper is organized as follows. In Sect. 2, we present and prove our main results, the necessity and sufficiency of the condition in Conjecture 1 for two cases: $d > 0$ and $d = 0$. Conclusions are presented in Sect. 3.

2 Main results

The following theorem is a necessary and sufficient condition for the nonlinear selection of the minimal speed. Its necessity part provides an answer to Conjecture 1.

Theorem 2.1 *When $d > 0$, the minimal wave speed c^* of (1.4), under the condition (1.3), is nonlinearly selected if and only if there exists $\bar{c} > c_0$ so that the function $U(x - \bar{c}t)$ in the solution $(U, V)(x - \bar{c}t)$ of (1.4) satisfies*

$$U(z) \sim C_2 e^{-\mu_2(\bar{c})z}, \quad z \to \infty, \quad z = x - \bar{c}t, \tag{2.1}$$

for some constant $C_2 > 0$. Furthermore, $\bar{c} = c^*$.

Proof From the above section, $U(z)$ has the behavior in (1.6)–(1.7) for $c \geq c_0$. In this theorem we shall prove that $c^* > c_0$ if and only if $U(z)$, when $c = c^*$, has the fast decay rate $e^{-\mu_2(c^*)(z)}$ as $z \to \infty$.

For the sufficiency, let the solution $(\overline{U}, \overline{V})(z)$ of (1.4), when $c = \bar{c} > c_0$, exist with

$$\overline{U}(z) \sim C_2 e^{-\mu_2(\bar{c})z}, \quad z \to \infty, \quad z = x - \bar{c}t, \tag{2.2}$$

for some constant $C_2 > 0$. We shall prove that there is no traveling wave of (1.4) for $c \in [c_0, \bar{c})$. Assume, to the contrary, there exists a monotone traveling wave solution $(U, V)(x - ct)$ to the original system (1.2) with the initial conditions

$$u(x, 0) = U(x) \quad \text{and} \quad v(x, 0) = V(x),$$

for some c in $(c_0, \bar{c})$. Definitely (U, V) satisfies (1.4). In particular, U satisfies (1.6) or (1.7). In view of (2.2) and the monotonicity of $\mu_i(c)$, $i = 1, 2$, we have $\overline{U}(z) \leq U(z)$ when $z \to \infty$. On the other hand, when $z \to -\infty$, we assume that $U(z) \sim 1 - Ke^{\lambda z}$ for some positive constants K and λ. After the substitution, we can always show that λ is decreasing with respect to c. Hence, for $\bar{c} > c$, we have $\overline{U}(z) \leq U(z)$ when $z \to -\infty$. Initially at $t = 0$, by shifting if necessary, we can assume that $\overline{U}(x) \leq U(x)$ for all x. In the second equation of the system (1.4), the term $r(1 - V)(a_2 U - V)$ is monotone with respect to U. By comparison, the solution V is monotone with respect to U. Hence, we obtain $(\overline{U}, \overline{V})(x) \leq (U, V)(x)$, for all x. Since $(\overline{U}, \overline{V})(x - \bar{c}t)$ is a solution to the system (1.2) with the initial data $(\overline{U}, \overline{V})(x)$, and by comparison, we have

$$\overline{U}(x - \bar{c}t) \leq U(x - ct), \tag{2.3}$$

$$\overline{V}(x - \bar{c}t) \leq V(x - ct), \tag{2.4}$$

for all $(x, t) \in (-\infty, \infty) \times (0, \infty)$. Fix $\bar{z} = x - \bar{c}t$ to have $\overline{U}(\bar{z}) > 0$. Furthermore, we have

$$U(x - ct) = U(\bar{z} + (\bar{c} - c)t) \sim U(\infty) = 0 \text{ as } t \to \infty.$$

By the above comparison in (2.3), we conclude that $\overline{U}(\bar{z}) \leq 0$, which is a contradiction. Hence, there is no traveling wave solution to (1.4) when $c_0 < c < \bar{c}$. Finally, in our contrary assumption, if $c = c_0$, then traveling waves exist if and only if $c \geq c_0$. Naturally there exists a traveling wave with speed c in $(c_0, \bar{c})$. The above argument follows to derive a contradiction. Therefore, no traveling wave solution of (1.4) exists when $c_0 \le c < \bar{c}$ and $c^* = \bar{c}$ is nonlinearly selected.

For the necessity, from the nonlinear system (1.4), we first transform it into an integral system. For this purpose, let α be large enough so that the functions

$$F(U, V) = \alpha U + U(1 - a_1 - U + a_1 V)$$

and

$$G(U, V) = \alpha V + r(1 - V)(a_2 U - V)$$

are nondecreasing in U and V, respectively. Introducing F and G in the system (1.4) gives

$$\begin{aligned} U'' + cU' - \alpha U &= -F(U, V), \\ dV'' + cV' - \alpha V &= -G(U, V). \end{aligned} \tag{2.5}$$

Define constants $\lambda_1^{\pm}$ and $\lambda_2^{\pm}$ as

$$\begin{aligned} \lambda_1^- &= \frac{-c - \sqrt{c^2 + 4\alpha}}{2} < 0, \quad \lambda_1^+ = \frac{-c + \sqrt{c^2 + 4\alpha}}{2} > 0, \\ \lambda_2^- &= \frac{-c - \sqrt{c^2 + 4\alpha d}}{2d} < 0, \quad \lambda_2^+ = \frac{-c + \sqrt{c^2 + 4\alpha d}}{2d} > 0. \end{aligned} \tag{2.6}$$

One can apply the variation-of-parameters to get the integral form of (2.5) as

$$\begin{aligned} U(z) &= T_1(F(U, V))(z), \\ V(z) &= T_2(G(U, V))(z), \end{aligned} \tag{2.7}$$

where

$$T_1(F)(z) = \frac{1}{\lambda_1^+ - \lambda_1^-} \left\{ \int_{-\infty}^{z} e^{\lambda_1^-(z-s)} F(U, V)(s) ds + \int_{z}^{\infty} e^{\lambda_1^+(z-s)} F(U, V)(s) ds \right\},$$
$$T_2(G)(z) = \frac{1}{d(\lambda_2^+ - \lambda_2^-)} \left\{ \int_{-\infty}^{z} e^{\lambda_2^-(z-s)} G(U, V)(s) ds + \int_{z}^{\infty} e^{\lambda_2^+(z-s)} G(U, V)(s) ds \right\}.$$

Now, assume that the minimal speed c^* of (1.4) is nonlinearly selected. We proceed to prove (2.1). To the contrary, assume that the solution $(U, V) = (U^*, V^*)(z)$, at $c = c^*$, satisfies

$$U^*(z) \sim C_1 e^{-\mu_1(c^*)z}, \quad z \to \infty, \quad z = x - c^* t,$$

for some $C_1 > 0$. Define

$$\omega(z) = \frac{1}{1 + \delta \exp((\mu_1(c_\delta) - \mu_1(c^*))z)},$$

for $0 < \delta \ll 1$, and $c_\delta = c^* - \delta$. Also, let

$$\overline{U}(z) = U^*(z)\omega(z), \quad \overline{V}(z) = V^*(z).$$

For small δ, $\overline{U}(z)$ is close to $U^*(z)$ but with a different decay behavior. To get a contradiction, we shall prove the existence of $W_1, W_2 \in C_0$, where C_0 is defined by $\{u \in C(-\infty, \infty) : u(\pm\infty) = 0\}$, so that

$$(U, V) = (U_\delta, V_\delta) = (\overline{U} + W_1, \overline{V} + W_2),$$

is a solution to the problem (1.4) (or (2.7)) with speed $c_\delta = c^* - \delta < c^*$. Equations for W_1 and W_2 can be derived by substituting this into the integral system (2.7), and using the relation $(U^*, V^*) = (T_1(F^*), T_2(G^*))$, where $F^* = F(U^*, V^*)$ and $G^* = G(U^*, V^*)$. This gives

$$W_1 = T_1(F_0) + F_\omega + T_1(F_\delta) + T_1(F_h), \tag{2.8}$$
$$W_2 = T_2(G_0) + T_2(G_\delta) + T_2(G_h), \tag{2.9}$$

where

$$\begin{aligned}
F_0 &= F_0(W) = \alpha W_1 + (1 - a_1 - 2U^* + a_1 V^*)W_1 + a_1 U^* W_2,\\
F_\omega &= T_1(\omega F^*) - \omega T_1(F^*),\\
F_\delta &= (-\bar{U} + 2W_1 - a_1 W_2)(U^* - \overline{U}),\\
F_h &= W_1(-W_1 + a_1 W_2),\\
G_0 &= G_0(W) = ra_2(1 - V^*)W_1 + \alpha W_2 + r(-1 - a_2 U^* + 2V^*)W_2,\\
G_\delta &= ra_2(-1 + V^* + W_2)(U^* - \overline{U}),\\
G_h &= rW_2(-a_2 W_1 + W_2).
\end{aligned}$$

We can easily show that F_ω, $T_1(F_\delta)$ and $T_2(G_\delta)$ are of $O(\delta)$ when $\delta \to 0$.

The linear operator

$$T(W) = \begin{pmatrix} T_1(F_0(W)) \\ T_2(G_0(W)) \end{pmatrix}, \quad W = (W_1, W_2), \tag{2.10}$$

is compact and strongly positive, and has a simple principal eigenvalue $\lambda = 1$ with the associated positive eigenfunction $\alpha^*(z) = (\frac{d}{dz}(-U^*), \frac{d}{dz}(-V^*))$ via the Krein-Rutman Theorem. Indeed, $\alpha^*(z)$ is a fixed point to the linear problem $W = T(W)$, which is equivalent to

$$\begin{aligned}
&W_1'' + c^* W_1' + (1 - a_1 - 2U^* + a_1 V^*)W_1 + a_1 U^* W_2 = 0,\\
&dW_2'' + c^* W_2' + ra_2(1 - V^*)W_1 + r(-1 - a_2 U^* + 2V^*)W_2 = 0.
\end{aligned}$$

To remove this eigenfunction from C_0, we define a weighted functional space $\mathcal{U}$ as

$$\mathcal{U} = \{u(\xi) \in C_0 : ue^{\mu_1(c_\delta)\xi} = o(1) \text{ as } \xi \to \infty\}.$$

For the space $\mathcal{U} \times C_0$, the eigenvector $\alpha^*(z)$ is not inside, i.e., T has no eigenvalue $\lambda = 1$ for (W_1, W_2) in $\mathcal{U} \times C_0$. This means that $I - T$ has a bounded inverse in $\mathcal{U} \times C_0$, where I is the identity operator. By the inverse function theorem in the abstract space $\mathcal{U} \times C_0$, there exists a small positive number δ_0 so that the problem (2.8)–(2.9) has a solution $W = (W_1, W_2)$, for any $\delta \in [0, \delta_0)$. As such, it follows that we have a positive solution (U_δ, V_δ) to the traveling wave problem (1.4) with $c_\delta < c^*$, which contradicts the definition of the minimal wave speed. The proof is complete. □

We are wondering if this result is also valid for the special case when $d = 0$. Indeed, the operator associated to the V-equation may not be compact or strongly positive, and the method in the proof of Theorem 2.1 can not be directly applied. However, in such a case, the system reads

$$\begin{aligned} &U'' + cU' + U(1 - a_1 - U + a_1 V) = 0, \\ &cV' + r(1 - V)(a_2 U - V) = 0, \\ &(U, V)(-\infty) = (1, 1), \ \ (U, V)(\infty) = (0, 0), \end{aligned} \tag{2.11}$$

and an explicit formula of V in the second nonlinear equation can be found in terms of U. Hence, the system can be reduced into a single equation. By working on this new equation, the result in the above theorem can be proved for $d = 0$ as well. We shall show this by providing the following theorem.

Theorem 2.2 *When $d = 0$, the minimal wave speed c^* of (2.11), under the condition (1.3) is nonlinearly selected if and only if there exists $\bar{c} > c_0$ so that the wavefront solution $U = U(x - \bar{c}t)$ satisfies*

$$U(z) \sim C_2 e^{-\mu_2(\bar{c})z}, \quad z \to \infty, \quad z = x - \bar{c}t,$$

for some constant $C_2 > 0$. Furthermore, $\bar{c} = c^*$.

Proof By the same work as that of (Alhasanat and Ou 2019b), the formula of $V(z)$ from the second equation in (2.11) is given by

$$V(U)(z) = \frac{ra_2 \int_z^\infty \mu(s)U(s)ds}{c\mu(z) + ra_2 \int_z^\infty \mu(s)U(s)ds}, \tag{2.12}$$

where

$$\mu(y) = \exp\left(\frac{r}{c}\int_0^y (a_2 U(\tau) - 1)d\tau\right).$$

This reduces (2.11) into a non-local equation

$$\begin{cases} U'' + cU' + U(1 - a_1 - U + a_1 V(U)) = 0, \\ U(-\infty) = 1, \quad U(\infty) = 0, \end{cases} \tag{2.13}$$

where $V(U)$ is given in (2.12).

Now, a similar comparison argument to that for $d > 0$ can be applied to prove the sufficiency of the condition in this theorem. For the necessity, an integral equation can be generated from the first equation of (2.13). Hence, both parts of the previous case, $d > 0$, can be carried out with this new operator to get the result for $d = 0$. This completes the proof. □

3 Conclusions

The minimal wave speed of traveling waves for the diffusive Lotka–Volterra competition model describes the ecological invasion of a resident species by an invasive species. Unfortunately, there is no explicit formula for this speed. However, we have obtained the speed selection mechanism (linear or nonlinear) under the assumption that invaders outcompetes residents, i.e., condition (1.3). Conjecture 1 of (Roques et al. 2015) was successfully proved (see Theorem 2.1). The sufficiency of the condition in the conjecture was provided as well. Also, the problem without diffusion of the resident species has been considered. By reducing the problem into a single equation, we have extended our result for this special case (see Theorem 2.2).

Biologically, in an invasion system of two species with competition exclusion and spatial dispersal, our rigorous result discloses the inside dynamics of the spreading of invasive wave. Its linear system provides the basic pulled speed that is determined by the leading edge of the solution. However, the invasive species can propagate with a faster (pushed or nonlinear) speed as long as it can spatially increases its population density with a faster rate. The resident species will response to this invasion and dies out spatially with the same faster propagation speed.

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