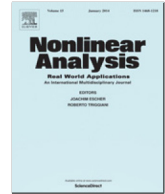




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Traveling waves for a reaction–diffusion–advection predator–prey model

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ABSTRACT

In this paper we study a reaction–diffusion–advection predator–prey model in a river. The existence of predator-invasion traveling wave solutions and prey-spread traveling wave solutions in the upstream and downstream directions is established and the corresponding minimal wave speeds are obtained. While some crucial improvements in theoretical methods have been established, the proofs of the existence and nonexistence of such traveling waves are based on Schauder's fixed-point theorem, LaSalle's invariance principle and Laplace transform. Based on theoretical results, we investigate the effect of the hydrological and biological factors on minimal wave speeds and hence on the spread of the prey and the invasion of the predator in the river. The linear determinacy of the predator–prey Lotka–Volterra system is compared with nonlinear determinacy of the competitive Lotka–Volterra system to investigate the mechanics of linear and nonlinear determinacy.

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1. Introduction

Various species and organisms live in media with a predominated unidirectional flow such as rivers and streams. Mathematical models, such as partial differential equations and integro-differential or integro-difference equations have been established to study the dynamics of populations of one or more species in streams or rivers (see e.g., [1–12]). One of the main goals is to understand how populations can persist in such a habitat when continuously subjected to a unidirectional flow (i.e., the “drift paradox”) and how the water flow influences spatial population spread and persistence. The studies also provide water management strategy for maintaining desired levels of ecosystem in rivers (i.e., the “instream flow needs”). Predator–prey systems are important components of ecosystems in river or stream environments. It is crucial to understand

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how the interacting preys and predators persist or spread when they are subjected to advective flows. Existing studies of predator–prey systems in rivers are few (see e.g., [3]) and have not theoretically analyzed the effect of the flow on persistence and spread (or invasion) of predator–prey systems.

In this paper we will study the following reaction–diffusion–advection predator–prey system:

$$\begin{cases} u_t = d_1 u_{xx} - b_1 u_x + u(r_1 - b_{11}u - b_{12}v), \\ v_t = d_2 v_{xx} - b_2 v_x + v(r_2 - b_{21}v + b_{22}u), \end{cases} \quad (1)$$

where $u(x, t)$ and $v(x, t)$ denote the densities of the prey and the predator at position $x \in \mathbb{R}$ and time t , respectively, d_1 and d_2 are diffusion constants of the prey and the predator, respectively, b_1 and b_2 are the advection rates of the prey and the predator, respectively, r_1 and r_2 are the growth rates of the prey and the predator, respectively, b_{11} and b_{21} and the density-dependent constants of the prey and the predator, respectively, b_{12} is the predation rate, b_{22} is the conversion rate. Parameters d_1, d_2, r_1 and b_{ij} ($i, j = 1, 2$) are positive constants; b_1, b_2 and r_2 are real numbers. When b_1 and b_2 have different signs, it means that the advective directions of the two species are not the same. For instance, if $b_2 > 0$ represents that the predator is subjected to the flow running from the left (upstream) to the right (downstream), then $b_1 < 0$ represents that the prey such as mayflies flies from the right (downstream) to the left (upstream). If r_2 is positive, then the predator has food sources other than the prey and can grow without the prey; if r_2 is negative, then r_2 essentially is a death rate of the predator and the predator only grows via consuming the prey.

Traveling wave solutions of partial differential equations have attracted increasing interest in recent years (see e.g., [13–30]). A traveling wave solution is a solution of the form

$$u(x, t) = \mathbf{U}(s), \quad v(x, t) = \mathbf{V}(s), \quad s = x + \tilde{c}t, \quad (2)$$

where \tilde{c} is the wave speed. It describes the translation of an invariant wave profile in the same direction at a constant speed. For biological models, traveling wave solutions can also show the invasion of species in the spatial habitat.

Various methods have been developed and applied to prove the existence of traveling wave solutions of different types of systems. The monotonic iteration method is powerful for monotonic systems [15,16]. The shooting method, proposed by Dunbar [13,14] and developed by Huang [17], is widely applied to prove the existence of traveling wave solutions for nonmonotonic systems [18–22]. The Schauder’s fixed-point theorem is also frequently used to prove the existence of traveling wave solutions for nonmonotonic systems [23–27]. Recently, Huang [31] proposed a geometric approach for some classes of nonmonotonic reaction–diffusion systems; Zhang et al. [30] and Fu et al. [32] developed methods based on the Schauder’s fixed-point theorem for nonmonotonic reaction–diffusion systems. The Harnack Inequality method was introduced into traveling waves to study the boundedness of traveling waves by Ducrot and Langlais [33]. However, different advection rates of the prey and the predator have not been considered in the theoretical studies of the minimal wave speeds of traveling waves for nonmonotonic systems. The effect of the water flow on persistence and extinction of predator–prey systems in rivers has been investigated in [3] by virtue of the approximation of traveling wave speeds for decoupled systems, but the theories of the spreading speeds or the minimal wave speeds of traveling waves of predator–prey systems in rivers have not been rigorously established due to the difficulty in mathematical analysis of nonmonotonic systems.

Model (1) is nonmonotonic and the advection coefficients b_1 and b_2 may be different. To derive the necessary and sufficient conditions for the existence of traveling wave solutions of model (1), we extend the methods in [30] for model (1) since different advection coefficients may result in a negative minimal wave speed, which can cause difficulties for the applications of the methods in [30]. Firstly, the upper–lower solutions in [30] must be improved to deal with the negative wave speed. Secondly, the non-triviality or positivity of traveling wave solutions with minimal wave speed for predator–prey models was rarely considered (e.g. [32,19,21,14,18,20]). This positivity of traveling wave solutions with minimal wave speed was confirmed

by Zhang [30] for a general noncooperative system but the proof method is not correct there. Li et al. [34] proved the positivity for a disease-transmission model via a Lyapunov function. However, it is difficult to construct a Lyapunov function for a complex model. In this paper, a general method (Lemma 3.9), which does not depend on the construction of a Lyapunov function, will be used to show this positivity and it can be applied to the general model in [30]. Thirdly, the boundedness of the ratio of the derivative of traveling wave solution to traveling wave solution is needed to show the persistence of traveling wave solutions in [30] or to apply the Lyapunov function [31]. The proof is lengthy to get this boundedness in [30,31]. In this paper, a simple result (Lemma 3.7) is established to show this boundedness and it can be applied to more complex models such as delayed models or models consisting of more than two equations. Actually, this lemma is a generalization of Harnack Inequality in [35] for a homogeneous elliptic operator on a bounded space domain, but the elliptic operator in Lemma 3.7 is nonhomogeneous and the space domain is unbounded.

The minimal wave speed of model (1) is said to be linearly determined or of linear determinacy if it is determined by the linearization of the predator equation of the corresponding ordinary differential equation system of traveling wave profiles at the invaded equilibrium. It is well-known that the minimal wave speed for some types of predator–prey models is linearly determined [13,14,18,19,17,24]. Recently, Zhang et al. [30] and Huang [31] have shown that the minimal wave speed for a reaction–diffusion system with predator–prey or susceptible–infective interaction is linearly determined. However, a model with different advection coefficients was not considered in [30] or [31]. In this paper we will show that the minimal wave speed for system (1) is of linear determinacy. We will also present the biological explanations of linear determinacy by comparing our results with those of the competitive Lotka–Volterra systems in [36–38]. It will be shown that there is a connection for the linear determinacy of the predator–prey Lotka–Volterra system and the competitive Lotka–Volterra system.

This paper is organized as follows. In Section 2, main theoretical results about minimal wave speeds are presented (without proofs). Section 3 is devoted to the proof of the first main theorem and Section 4 is devoted to the proof of the second main theorem. In Section 5, we provide the biological interpretation of the minimal wave speed and especially relate it to the predator’s invasion and the prey’s spread. In Section 6, we analyze the linear and nonlinear determinacy of the minimal wave speed and compare our results with previous results of models for interactive populations in [36–38]. A short discussion in Section 7 then completes the paper.

2. Main theoretical results

In this section, we present two main theorems in this paper. These theorems establish necessary and sufficient conditions for the existence of traveling wave solutions connecting the prey-only equilibrium to a predator-present (predator-only or coexistence) equilibrium and of traveling wave solutions connecting the predator-only equilibrium to the coexistence equilibrium. The minimal wave speeds of such traveling waves are obtained.

2.1. Nondimensionalization and equilibria of model (1)

We firstly simplify model (1) by decreasing the number of parameters. By introducing dimensionless variables as

$$\begin{aligned} \bar{u} &= \frac{b_{11}}{r_1}u, & \bar{v} &= \frac{b_{21}}{r_1}v, & \bar{t} &= r_1t, & \bar{x} &= \sqrt{\frac{r_1}{d_2}}x, \\ \gamma_1 &= \frac{b_{12}}{b_{21}}, & \gamma_2 &= \frac{b_{22}}{b_{11}}, & d &= \frac{d_1}{d_2}, & r &= \frac{r_2}{r_1}, & \alpha_1 &= \frac{b_1}{\sqrt{d_2r_1}}, & \alpha_2 &= \frac{b_2}{\sqrt{d_2r_1}}, \end{aligned} \tag{3}$$

system (1) can be written into

$$\begin{cases} \bar{u}_{\bar{t}} = d\bar{u}_{\bar{x}\bar{x}} - \alpha_1\bar{u}_{\bar{x}} + \bar{u}(1 - \bar{u} - \gamma_1\bar{v}), \\ \bar{v}_{\bar{t}} = \bar{v}_{\bar{x}\bar{x}} - \alpha_2\bar{v}_{\bar{x}} + \bar{v}(r - \bar{v} + \gamma_2\bar{u}), \end{cases} \tag{4}$$

where d, γ_1, γ_2 are positive, and α_1, α_2, r are real numbers.

System (4) admits the following three possible equilibria.

- The prey-only equilibrium $E_1(1, 0)$.
- The predator-only equilibrium $E_2(0, r)$ if $r > 0$.
- The unique coexistence equilibrium $E_3(\bar{u}^*, \bar{v}^*)$ with $\bar{u}^* = \frac{1-\gamma_1r}{1+\gamma_1\gamma_2}$ and $\bar{v}^* = \frac{r+\gamma_2}{1+\gamma_1\gamma_2}$, if and only if $-\gamma_2 < r < 1/\gamma_1$.

It is easy to show that if $r \leq -\gamma_2$, then E_1 is globally asymptotically stable for the corresponding non-spatial version of system (4):

$$\begin{cases} \bar{u}_{\bar{t}} = \bar{u}(1 - \bar{u} - \gamma_1\bar{v}), \\ \bar{v}_{\bar{t}} = \bar{v}(r - \bar{v} + \gamma_2\bar{u}), \end{cases} \tag{5}$$

which indicates that predators die out if no dispersion is incorporated in the model. Since our interest is in the spatial spread of both the prey and the predator, we assume the following condition throughout this paper.

(H1) $r > -\gamma_2$.

2.2. *Main results about the minimal wave speeds*

To present main theoretical results, the following notations are needed:

$$E^* = \begin{cases} E_3, & \text{if } -\gamma_2 < r < 1/\gamma_1, \\ E_2, & \text{if } r \geq 1/\gamma_1, \end{cases} \tag{6}$$

$$\begin{aligned} c^* &:= \bar{c} - \alpha_2, & c_{23}^* &:= \bar{c} - \alpha_1, \\ c_-^* &:= \bar{c} + \alpha_2, & c_{23-}^* &:= \bar{c} + \alpha_1, \end{aligned} \tag{6}$$

$$\bar{c} = 2\sqrt{r + \gamma_2}. \tag{7}$$

The following hypotheses are also needed for our theorems.

(H2) $c^* + \alpha_1 > 0$.

(H2) $c_-^* - \alpha_1 > 0$.

(H3) $r < 1/\gamma_1 - \gamma_2$.

Let

$$\bar{u}(\bar{x}, \bar{t}) = U(s), \quad \bar{v}(\bar{x}, \bar{t}) = V(s), \quad \text{where } s = \bar{x} + c\bar{t}. \tag{8}$$

The main theoretical results are as follows.

Theorem 2.1. *Assume (H1) holds.*

(i) If **(H2)** or **(H3)** is valid, system (4) has a positive traveling wave solution $(U(\bar{x} + c\bar{t}), V(\bar{x} + c\bar{t}))$ satisfying

$$(U(-\infty), V(-\infty)) = E_1 \quad \text{and} \quad (U(+\infty), V(+\infty)) = E^* \tag{9}$$

if and only if $c \geq c^*$.

(ii) **(H2)** or **(H3)** is valid, system (4) has a positive traveling wave solution $(U(\bar{x} - c\bar{t}), V(\bar{x} - c\bar{t}))$ satisfying

$$(U(-\infty), V(-\infty)) = E^* \quad \text{and} \quad (U(+\infty), V(+\infty)) = E_1 \tag{10}$$

if and only if $c \geq c^*_-$.

Theorem 2.2. Assume that **(H1)** holds and that both E_2 and E_3 exist, i.e. $0 < r < 1/\gamma_1$.

(i) System (4) has a positive traveling wave solution $(U(\bar{x} + c\bar{t}), V(\bar{x} + c\bar{t}))$ satisfying

$$(U(-\infty), V(-\infty)) = E_2 \quad \text{and} \quad (U(+\infty), V(+\infty)) = E_3 \tag{11}$$

if and only if $c \geq c^*_{23}$.

(ii) System (4) has a positive traveling wave solution $(U(\bar{x} - c\bar{t}), V(\bar{x} - c\bar{t}))$ satisfying

$$(U(-\infty), V(-\infty)) = E_3 \quad \text{and} \quad (U(+\infty), V(+\infty)) = E_2 \tag{12}$$

if and only if $c \geq c^*_{23-}$.

Remark 2.1. In **Theorems 2.1** and **2.2**, we assume the upstream of the river is on the left and the downstream is on the right, that is, the river flows from the left to the right. The waves in **Theorem 2.1** are called **predator-invasion traveling waves** since the state before invasions is $E_1(1, 0)$ where only preys exist and the state after invasions is E^* where predators persist (see **Fig. 1**). The waves in **Theorem 2.1(i)** are called upstream traveling waves, which indicates that the predator’s invasion is from the downstream to the upstream. The waves in **Theorem 2.1(ii)** are called downstream traveling waves, which indicates that the predator’s invasion is from the upstream to the downstream. Similarly, the waves in **Theorem 2.2** are called **prey-spread traveling waves** since the state before invasions is $E_2(0, r)$ where only predators exist and the state after invasions is $E_3(\bar{u}^*, \bar{v}^*)$ where preys persist. We also call the waves in **Theorem 2.2(i)** the upstream traveling waves, which corresponds to the fact that the prey is introduced from the downstream, and the waves in **Theorem 2.2(ii)** the downstream traveling waves, which corresponds to the fact that the prey is introduced from the upstream.

Note that the upstream traveling waves in **Theorem 2.1(i)** may not actually move to the upstream, i.e., predators may not really travel upstream because c^* may be negative due to the large advection parameter α_2 . Whether predators can travel upstream in **2.1(i)** depends on the sign of c^* .

Remark 2.2. It follows from **Theorem 2.1** that c^* is the **upstream minimal wave speed** and c^*_- is the **downstream minimal wave speed** of the predator-invasion traveling waves for (4). Moreover, by (2), (3) and (8), the predator’s **upstream minimal wave speed** of our original model (1) is

$$\bar{c}^* = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}}r_1 \right) - b_2};$$

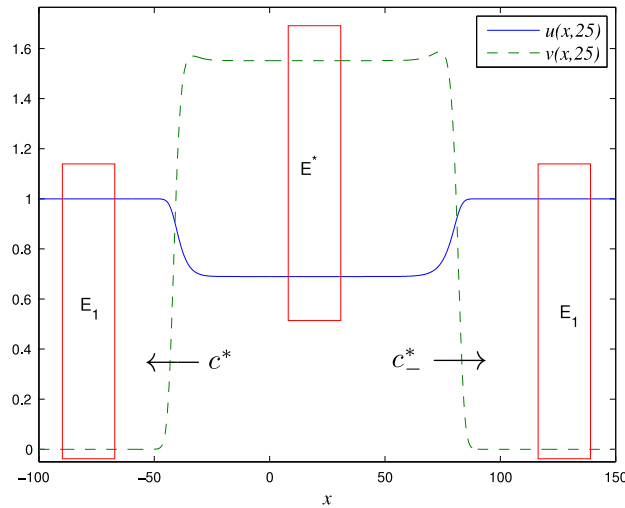


Fig. 1. The traveling of predators in model (4). The upstream is on the left and the downstream is on the right. The initial conditions are as follows: $\bar{u}(\bar{x}, 0) = 1, \bar{v}(\bar{x}, 0) = 0.2\chi_{[-1,1]}(\bar{x})$, where $\chi_{[-1,1]}(\bar{x})$ is the characteristic function of $[-1, 1]$. The parameters are assigned values as follows: $d = 1, r = 1, \gamma_1 = 0.2, \gamma_2 = 0.8, \alpha_1 = 0.3, \alpha_2 = 0.8$, where (H2) holds and $E^* = E_3$.

the predator’s **downstream minimal wave speed** of our original model (1) is

$$\tilde{c}_-^* = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)} + b_2.$$

Remark 2.3. It follows from Theorem 2.2 that c_{23}^* and c_{23-}^* are the **upstream minimal wave speed** and the **downstream minimal wave speed** of the prey-spread traveling waves for (4), respectively. By (2), (3) and (8), the prey’s **upstream minimal wave speed** of our original model (1) is

$$\tilde{c}_{23}^* = 2\sqrt{d_1 \left(r_1 - \frac{b_{12}}{b_{21}} r_2 \right)} - b_1;$$

the prey’s **downstream minimal wave speed** of model (1) is

$$\tilde{c}_{23-}^* = 2\sqrt{d_1 \left(r_1 - \frac{b_{12}}{b_{21}} r_2 \right)} + b_1.$$

3. Proof of Theorem 2.1

In this section we prove Theorem 2.1. Theorem 2.1(i) will be proved from Sections 3.1 to 3.5. The proof of Theorem 2.1(ii) will be converted to the proof of Theorem 2.1(i) by some transforms in Section 3.6. Therefore, we always suppose that one of (H2) and (H3) holds from Sections 3.1 to 3.5, and that one of (H2) and (H3) holds in Section 3.6.

Substituting (8) into (4) yields

$$\begin{cases} c_1 U' = dU'' + U(1 - U - \gamma_1 V), \\ c_2 V' = V'' + V(r - V + \gamma_2 U), \end{cases} \tag{13}$$

where

$$c_1 = c + \alpha_1, \quad c_2 = c + \alpha_2, \tag{14}$$

and $'$ denotes the derivative with respect to s . Thus, a traveling wave solution of (4) corresponds to a solution of (13).

3.1. Existence of traveling waves connecting E_1 when $c > c^*$

In this subsection we show the existence of positive solutions of (13) connecting E_1 , that is,

$$(U(-\infty), V(-\infty)) = E_1(1, 0), \tag{15}$$

when $c > c^*$. The existence in the case of $c > c^*$ is obtained by using Schauder’s fixed-point theorem. To apply Schauder’s fixed-point theorem an invariant cone will be constructed by a pair of upper–lower solutions.

Set

$$H(\lambda) = \lambda^2 - c_2\lambda + r + \gamma_2, \tag{16}$$

and

$$\lambda_1 = \frac{c_2 - \sqrt{c_2^2 - \bar{c}^2}}{2}, \quad \lambda_2 = \frac{c_2 + \sqrt{c_2^2 - \bar{c}^2}}{2},$$

where

$$\bar{c} = 2\sqrt{r + \gamma_2}$$

as defined in (7). Note that $H(\lambda)$ is the characteristic function of the linearization of the second equation of (13) at $E_1(1, 0)$ and that λ_1 and λ_2 are roots of $H(\lambda)$. Moreover, $H(\lambda_1 + \varepsilon) < 0$ if $0 < \varepsilon < (\lambda_2 - \lambda_1)/2$. In the following, we always assume $c > c^*$ (i.e., $c_2 > \bar{c}$) till Section 3.3.

Define

$$\begin{aligned} \bar{U}(s) &\equiv 1, & \bar{V}(s) &= \min\{e^{\lambda_1 s}, r + \gamma_2\}, \\ \underline{U}(s) &= \max\{1 - \sigma e^{\beta s}, \delta\}, & \underline{V}(s) &= \max\{e^{\lambda_1 s}(1 - M e^{\varepsilon s}), 0\}, \end{aligned} \tag{17}$$

where positive constants $\sigma, \beta, \varepsilon$ and M will be determined later and δ satisfies

$$\delta = \begin{cases} 0, & \text{if (H2) holds;} \\ 1 - \gamma_1(r + \gamma_2), & \text{if (H3) holds.} \end{cases}$$

We will prove in Lemmas 3.1–3.3 that $(\bar{U}(s), \bar{V}(s))$ and $(\underline{U}(s), \underline{V}(s))$ are a pair of upper–lower solutions of (13). In particular, these upper–lower solutions connect the invaded equilibrium E_1 at $s = -\infty$ since

$$(\bar{U}(-\infty), \bar{V}(-\infty)) = E_1, \quad (\underline{U}(-\infty), \underline{V}(-\infty)) = E_1.$$

Such idea of constructing upper–lower solutions in (17) was used in [39] for an integral equation and was developed in [30] for a nonmonotonic reaction–diffusion system. Note that (17) is a refinement of the upper–lower solutions in [30] if (H2) does not hold. This refinement can deal with the case with α_2 large.

Lemma 3.1. *The function $\bar{V}(s)$ satisfies inequality*

$$c_2 \bar{V}' \geq \bar{V}'' + \bar{V}(r + \gamma_2 - \bar{V})$$

for any $s \neq \bar{s} := \ln(r + \gamma_2)/\lambda_1$.

Proof. Firstly, consider the case $s < \bar{s}$, which implies $\bar{V}(s) = e^{\lambda_1 s}$. Then we have

$$\bar{V}'' - c_2 \bar{V}' + \bar{V}(r + \gamma_2 - \bar{V}) = (\lambda_1^2 - c_2 \lambda_1 + r + \gamma_2) \bar{V} - \bar{V}^2 = -\bar{V}^2 \leq 0.$$

If $s > \bar{s}$, then we have $\bar{V}(s) = r + \gamma_2$. It is obvious that the inequality in this lemma holds in such case. The proof is completed. \square

Lemma 3.2. *There exist positive constants σ (large enough) and β (small enough) such that function $\underline{U}(s)$ satisfies*

$$c_1 \underline{U}' \leq d \underline{U}'' + \underline{U}(1 - \underline{U} - \gamma_1 \bar{V})$$

for any $s \neq \underline{s}$, where

$$\underline{s} := \frac{1}{\beta} \ln \frac{1 - \delta}{\sigma} < 0.$$

Proof. Firstly, we set

$$0 < \beta < \lambda_1, \quad \sigma > \max \left\{ 1 - \delta, (r + \gamma_2)^{-\beta/\lambda_1} \right\},$$

which implies $\underline{s} < \min\{0, \bar{s}\}$.

We now assume **(H2)** holds, implying that $c_1 = c + \alpha_1 > 0$ since $c > c^*$. If $s > \underline{s}$, then $\underline{U}(s) = 0$ and the lemma holds. Assume $s < \underline{s}$, which implies $s < 0$, $\underline{U}(s) = 1 - \sigma e^{\beta s}$, $\bar{V}(s) = e^{\lambda_1 s}$. Set

$$\beta < \frac{c_1}{d}, \quad \sigma > \frac{\gamma_1}{(c_1 - d\beta)\beta}.$$

Then we have

$$\begin{aligned} -c_1 \underline{U}' + d \underline{U}'' + \underline{U}(1 - \underline{U} - \gamma_1 \bar{V}) &= c_1 \sigma \beta e^{\beta s} - d \sigma \beta^2 e^{\beta s} - \gamma_1 \underline{U} e^{\lambda_1 s} + \sigma \underline{U} e^{\beta s} \\ &= \left[c_1 \sigma \beta - d \sigma \beta^2 - \gamma_1 \underline{U} e^{(\lambda_1 - \beta)s} \right] e^{\beta s} + \sigma \underline{U} e^{\beta s} \\ &\geq [(c_1 - d\beta)\beta\sigma - \gamma_1] e^{\beta s} + \sigma \underline{U} e^{\beta s} \geq 0, \end{aligned}$$

where we have used the fact $c_1 > d\beta$ and $e^{(\lambda_1 - \beta)s} < 1$ due to $s < 0$ and $\beta < \lambda_1$.

Now assume **(H3)** holds. Set

$$\frac{\gamma_1}{\sigma} < \frac{\delta}{2}, \quad (d\beta - c_1)\beta < \frac{\delta}{2}, \quad (18)$$

which can be guaranteed by setting $\sigma > 2\gamma_1/\delta$ and letting β small enough. If $s > \underline{s}$, then $\underline{U}(s) = \delta = 1 - \gamma_1(r + \gamma_2)$ and

$$-c_1 \underline{U}' + d \underline{U}'' + \underline{U}(1 - \underline{U} - \gamma_1 \bar{V}) = \gamma_1 \underline{U}((r + \gamma_2) - \bar{V}) \geq 0.$$

If $s < \underline{s}$, then

$$\begin{aligned} -c_1 \underline{U}' + d \underline{U}'' + \underline{U}(1 - \underline{U} - \gamma_1 \bar{V}) &= \left[c_1 \sigma \beta - d \sigma \beta^2 - \gamma_1 \underline{U} e^{(\lambda_1 - \beta)s} + \sigma \underline{U} \right] e^{\beta s} \\ &\geq [(c_1 - d\beta)\beta\sigma - \gamma_1 + \sigma \underline{U}] e^{\beta s} \\ &\geq \sigma \left[(c_1 - d\beta)\beta - \frac{\gamma_1}{\sigma} + \delta \right] e^{\beta s} \geq 0, \end{aligned}$$

where the final inequality holds by (18). The proof is completed. \square

Lemma 3.3. *Assume $\varepsilon < \beta < \min\{\lambda_1, \lambda_2 - \lambda_1\}/2$. Then for $M > 0$ large enough, the function $\underline{V}(s)$ satisfies*

$$c_2 \underline{V}' \leq \underline{V}'' + \underline{V}(r - \underline{V} + \gamma_2 \underline{U})$$

for any $s \neq -\ln M/\varepsilon$.

Proof. It is clear that $\underline{U}(s) = \delta$ if and only if $s \geq \underline{s}$, that $\underline{V}(s) = 0$ if and only if $s \geq -\ln M/\varepsilon$, and that $-\ln M/\varepsilon < \underline{s}$ if and only if $M > (\frac{1-\delta}{\sigma})^{-\varepsilon/\beta}$. Assume $M > (\frac{1-\delta}{\sigma})^{-\varepsilon/\beta}$ in this proof. If $s > -\ln M/\varepsilon$, then $e^{\lambda_1 s}(1 - M e^{\varepsilon s}) < 0$, $\underline{V}(s) = 0$ and the inequality in Lemma 3.3 holds.

Now we consider the case $s < -\ln M/\varepsilon$ and set $M > 1$. Then $s < 0, s < \underline{s}$,

$$\underline{U}(s) = 1 - \sigma e^{\beta s} > 0, \quad \underline{V}(s) = e^{\lambda_1 s}(1 - Me^{\varepsilon s}) > 0.$$

To prove this lemma, it is enough to show

$$e^{-\lambda_1 s} [\underline{V}'' - c_2 \underline{V}' + \underline{V}(r - \underline{V} + \gamma_2 \underline{U})] \geq 0.$$

However, we have

$$\begin{aligned} & e^{-\lambda_1 s} [\underline{V}'' - c_2 \underline{V}' + \underline{V}(r - \underline{V} + \gamma_2 \underline{U})] \\ &= e^{-\lambda_1 s} [\underline{V}'' - c_2 \underline{V}' + (r + \gamma_2) \underline{V} + \gamma_2 (\underline{U} - 1) \underline{V} - \underline{V}^2] \\ &= \lambda_1^2 - M(\lambda_1 + \varepsilon)^2 e^{\varepsilon s} - c_2 \lambda_1 + c_2 M(\lambda_1 + \varepsilon) e^{\varepsilon s} + (r + \gamma_2)(1 - Me^{\varepsilon s}) \\ &\quad - \gamma_2 \sigma e^{\beta s}(1 - Me^{\varepsilon s}) - e^{\lambda_1 s}(1 - Me^{\varepsilon s})^2 \\ &= (\lambda_1^2 - c_2 \lambda_1 + r + \gamma_2) + M [-(\lambda_1 + \varepsilon)^2 + c_2(\lambda_1 + \varepsilon) - (r + \gamma_2)] e^{\varepsilon s} \\ &\quad - \gamma_2 \sigma e^{\beta s}(1 - Me^{\varepsilon s}) - e^{\lambda_1 s}(1 - Me^{\varepsilon s})^2 \\ &= [-MH(\lambda_1 + \varepsilon) - \gamma_2 \sigma(1 - Me^{\varepsilon s})e^{(\beta - \varepsilon)s} - (1 - Me^{\varepsilon s})^2 e^{(\lambda_1 - \varepsilon)s}] e^{\varepsilon s}. \end{aligned}$$

Thus we only need to show

$$-MH(\lambda_1 + \varepsilon) \geq \gamma_2 \sigma(1 - Me^{\varepsilon s})e^{(\beta - \varepsilon)s} + (1 - Me^{\varepsilon s})^2 e^{(\lambda_1 - \varepsilon)s}. \tag{19}$$

Since

$$0 \leq 1 - Me^{\varepsilon s} \leq 1, \quad 0 \leq e^{(\beta - \varepsilon)s} \leq 1, \quad 0 \leq e^{(\lambda_1 - \varepsilon)s} \leq 1,$$

it is sufficient to show

$$-MH(\lambda_1 + \varepsilon) \geq \gamma_2 \sigma + 1 \tag{20}$$

to prove (19). Since $H(\lambda_1 + \varepsilon) < 0$ by (16), inequality (20) holds if

$$M > -\frac{\gamma_2 \sigma + 1}{H(\lambda_1 + \varepsilon)}.$$

The proof is completed. \square

Remark 3.1. We can select suitable positive constants $\sigma, \beta, \varepsilon$ and M such that Lemmas 3.1–3.3 hold. Therefore, we always suppose the conditions for Lemmas 3.1–3.3 hold.

To apply Schauder’s fixed-point theorem, we will introduce a new norm in $C(\mathbb{R}, \mathbb{R}^2)$ and use functions in (17) to construct an invariant cone. Let μ be a positive constant which can be small enough. For $\Phi(s) = (\phi_1(s), \phi_2(s))$, define

$$|\Phi(\cdot)|_\mu = \max \left\{ \sup_{s \in \mathbb{R}} |\phi_1(s)| e^{-\mu|s|}, \sup_{s \in \mathbb{R}} |\phi_2(s)| e^{-\mu|s|} \right\}$$

and

$$B_\mu(\mathbb{R}, \mathbb{R}^2) = \{ \Phi(\cdot) \in C(\mathbb{R}, \mathbb{R}^2) : |\Phi(\cdot)|_\mu < +\infty \}.$$

We will find the traveling wave solutions in the following set:

$$\Gamma = \{ (U(\cdot), V(\cdot)) \in C(\mathbb{R}, \mathbb{R}^2) : \underline{U}(s) \leq U(s) \leq \bar{U}(s), \underline{V}(s) \leq V(s) \leq \bar{V}(s) \text{ for any } s \in \mathbb{R} \}.$$

Obviously, Γ is closed and convex in $B_\mu(\mathbb{R}, \mathbb{R}^2)$.

Let β_1 and β_2 be two positively large constants. System (13) can be changed into the following form:

$$\begin{cases} -dU'' + c_1U' + \beta_1U = H_1(U(\cdot), V(\cdot))(s), \\ -V'' + c_2V' + \beta_2V = H_2(U(\cdot), V(\cdot))(s), \end{cases} \quad (21)$$

where

$$\begin{aligned} H_1(U(\cdot), V(\cdot))(s) &= \beta_1U(s) + U(s)[1 - U(s) - \gamma_1V(s)], \\ H_2(U(\cdot), V(\cdot))(s) &= \beta_2V(s) + V(s)[r - V(s) + \gamma_2U(s)]. \end{aligned}$$

Let $\Lambda_{11} < 0 < \Lambda_{12}$ be the roots of

$$d\Lambda^2 - c_1\Lambda - \beta_1 = 0$$

and $\Lambda_{21} < 0 < \Lambda_{22}$ be the roots of

$$\Lambda^2 - c_2\Lambda - \beta_2 = 0.$$

Define $F = (F_1, F_2) : \Gamma \rightarrow C(\mathbb{R}, \mathbb{R}^2)$ by

$$\begin{aligned} F_1(U(\cdot), V(\cdot))(s) &= \frac{1}{d\Lambda_{11}} \left[\int_{-\infty}^s e^{\Lambda_{11}(s-t)} H_1(U, V)(t) dt + \int_s^{+\infty} e^{\Lambda_{12}(s-t)} H_1(U, V)(t) dt \right], \\ F_2(U(\cdot), V(\cdot))(s) &= \frac{1}{\Lambda_2} \left[\int_{-\infty}^s e^{\Lambda_{21}(s-t)} H_2(U, V)(t) dt + \int_s^{+\infty} e^{\Lambda_{22}(s-t)} H_2(U, V)(t) dt \right], \end{aligned} \quad (22)$$

where $\Lambda_1 = \Lambda_{12} - \Lambda_{11}$, $\Lambda_2 = \Lambda_{22} - \Lambda_{21}$. It is easy to verify that the fixed point of F in Γ is a nonnegative solution of system (13).

To show the existence of a fixed point of F in Γ , we first verify the conditions for application of Schauder's fixed-point theorem to F in the following two lemmas.

Lemma 3.4. $F(\Gamma) \subset \Gamma$ for positively large enough β_1 and β_2 .

Proof. Suppose $(U(\cdot), V(\cdot)) \in \Gamma$, that is

$$\underline{U}(s) \leq U(s) \leq 1, \quad \underline{V}(s) \leq V(s) \leq \bar{V}(s)$$

for any $s \in \mathbb{R}$. Then it is sufficient to prove

$$\underline{U}(s) \leq F_1(U(\cdot), V(\cdot))(s) \leq 1, \quad \underline{V}(s) \leq F_2(U(\cdot), V(\cdot))(s) \leq \bar{V}(s)$$

for any $s \in \mathbb{R}$.

For $\beta_2 \geq \gamma_2$, we have

$$\begin{aligned} H_2(U(\cdot), V(\cdot))(t) &= \beta_2V(t) + V(t)[r - V(t) + \gamma_2U(t)] \\ &\geq V(t)[\gamma_2 + r - \bar{V}(t) + \gamma_2U(t)] \\ &\geq V(t)[\gamma_2 + r - (\gamma_2 + r) + \gamma_2U(t)] \\ &\geq 0 \end{aligned}$$

for all $t \in \mathbb{R}$, which implies that $F_2(U(\cdot), V(\cdot))(s) \geq 0$ for all $s \in \mathbb{R}$. For $\beta_2 \geq r + 2\gamma_2$,

$$\frac{\partial}{\partial V} H_2(U(\cdot), V(\cdot)) = \beta_2 + r - 2V + \gamma_2U \geq \beta_2 + r - 2\bar{V} \geq \beta_2 + r - 2(r + \gamma_2) \geq 0.$$

Let $\beta_2 \geq r + 2\gamma_2$. By (H1), we have $\beta_2 \geq \gamma_2$. If $s \geq s_0 := -\ln M/\varepsilon$, then $\underline{V}(s) = 0$ and, hence, $F_2(U(\cdot), V(\cdot))(s) \geq \underline{V}(s)$. If $s < s_0$, then by Lemma 3.3, we have

$$\begin{aligned} -\underline{V}'' + c_2\underline{V}' + \beta_2\underline{V}(s) &\leq [\beta_2 + r - \underline{V}(s)]\underline{V}(s) + \gamma_2\underline{U}(s)\underline{V}(s) \\ &\leq [\beta_2 + r - V(s)]V(s) + \gamma_2U(s)V(s) \\ &= H_2(U, V)(s). \end{aligned}$$

This implies that

$$\begin{aligned} F_2(U(\cdot), V(\cdot))(s) &= \frac{1}{\Lambda_2} \left[\int_{-\infty}^s e^{\Lambda_{21}(s-t)} H_2(U, V)(t) dt + \int_s^{+\infty} e^{\Lambda_{22}(s-t)} H_2(U, V)(t) dt \right] \\ &\geq \frac{1}{\Lambda_2} \int_{-\infty}^s e^{\Lambda_{21}(s-t)} [-\underline{V}''(t) + c_2\underline{V}'(t) + \beta_2\underline{V}(t)] dt \\ &\quad + \frac{1}{\Lambda_2} \int_s^{s_0} e^{\Lambda_{22}(s-t)} [-\underline{V}''(t) + c_2\underline{V}'(t) + \beta_2\underline{V}(t)] dt \\ &\quad + \frac{1}{\Lambda_2} \int_{s_0}^{+\infty} e^{\Lambda_{22}(s-t)} [-\underline{V}''(t) + c_2\underline{V}'(t) + \beta_2\underline{V}(t)] dt \\ &= \frac{1}{\Lambda_2} \left(-\underline{V}'(s) - \Lambda_{21}\underline{V}(s) + c_2\underline{V}(s) + e^{\Lambda_{21}s}(-\Lambda_{21}^2 + c_2\Lambda_{21} + \beta_2) \int_{-\infty}^s e^{-\Lambda_{21}t}\underline{V}(t) dt \right) \\ &\quad + \frac{1}{\Lambda_2} \left(e^{\Lambda_{22}(s-s_0)}(-\underline{V}'(s_0 - 0) + c_2\underline{V}(s_0) - \Lambda_{22}\underline{V}(s_0)) + \underline{V}'(s) - c_2\underline{V}(s) + \Lambda_{22}\underline{V}(s) \right) \\ &\quad + \frac{e^{\Lambda_{22}s}}{\Lambda_2} \left((-\Lambda_{22}^2 + c_2\Lambda_{22} + \beta_2) \int_s^{s_0} e^{-\Lambda_{22}t}\underline{V}(t) dt \right) \\ &\quad + \frac{1}{\Lambda_2} \left(\underline{V}'(s_0 + 0) - c_2\underline{V}(s_0) + \Lambda_{22}\underline{V}(s_0) \right) \\ &\quad + e^{\Lambda_{22}s_0}(-\Lambda_{22}^2 + c_2\Lambda_{22} + \beta_2) \int_{s_0}^{\infty} e^{-\Lambda_{22}t}\underline{V}(t) dt \\ &= \underline{V}(s) + \frac{1}{\Lambda_2} e^{\Lambda_{22}(s-s_0)} [\underline{V}'(s_0 + 0) - \underline{V}'(s_0 - 0)] \\ &\geq \underline{V}(s), \end{aligned}$$

where we use the facts $\underline{V}(s) = e^{\lambda_1 s}(1 - Me^{\varepsilon s})$ for $s \leq s_0$, $\underline{V}(s) = 0$ for $s \geq s_0$, $\underline{V}'(s_0 + 0) = 0$, $\underline{V}'(s_0 - 0) \leq 0$, and the definitions of Λ_{21} , Λ_{22} and Λ_2 .

In conclusion, we have obtained that

$$F_2(U(\cdot), V(\cdot))(s) \geq \underline{V}(s)$$

for any $s \in \mathbb{R}$.

Similarly, it can be proved that

$$\underline{U}(s) \leq F_1(U(\cdot), V(\cdot))(s) \leq 1, \quad F_2(U(\cdot), V(\cdot))(s) \leq \overline{V}(s)$$

for any $s \in \mathbb{R}$. The proof is completed. \square

Lemma 3.5. For μ small enough, $F = (F_1, F_2) : \Gamma \rightarrow C(\mathbb{R}, \mathbb{R}^2)$ is continuous and compact with respect to the norm $|\cdot|_\mu$ in $B_\mu(\mathbb{R}, \mathbb{R}^2)$.

The proof of Lemma 3.5 is similar to those in [23,30], so we refer readers to [23,30].

We now establish the existence of traveling waves connecting E_1 when $c > c^*$ in Lemma 3.6.

Lemma 3.6. Let $c > c^*$ (i.e. $c_2 > \bar{c}$), then (13) has a positive solution $(U(s), V(s))$ satisfying

$$(U(-\infty), V(-\infty)) = E_1(1, 0), \quad U(s) < 1, \quad V(s) \leq r + \gamma_2$$

for any $s \in \mathbb{R}$.

Proof. Combination of Schauder's fixed-point theorem, Lemmas 3.4 and 3.5 implies that (13) has a nonnegative solution $(U(\cdot), V(\cdot)) \in \Gamma$ such that

$$(U(-\infty), V(-\infty)) \rightarrow (1, 0).$$

Let n be any fixed positive integer such that $n > \max\{-\underline{s}, \ln M/\varepsilon\}$, where $\underline{s}, \varepsilon$ and M are determined in Lemmas 3.2 and 3.3. Since $U(s) \geq \underline{U}(s)$ for all $s < \underline{s}$, we have $U(s) > 0$ for all $s \in [-n, n]$ by applying Harnack Inequality (refer to Theorem 2.1 in [40]) for the first equality of (13). It then follows that $U(s) > 0$ for all $s \in \mathbb{R}$ since n is any large positive integer. It can be similarly proved that $V(s) > 0$ for all $s \in \mathbb{R}$.

If $U(s_1) = 1$, then it follows that $U'(s_1) = 0, U''(s_1) \leq 0$ since $U(s) \leq 1$ for any $s \in \mathbb{R}$. From the first equation of (13) it can be inferred that $dU''(s_1) - \gamma_1 V(s_1) = 0$, a contradiction, which implies $U(s) < 1$ for any $s \in \mathbb{R}$. \square

3.2. Existence of traveling waves connecting E_1 and E^* when $c > c^*$

In this subsection we use LaSalle's invariance principle to show that the traveling wave solutions we obtained in Lemma 3.6 also connect E^* . To this end, we first give a lemma to show the boundedness of $|U'(s)/U(s)|$ and $|V'(s)/V(s)|$.

Lemma 3.7. Assume that $\psi(s) > 0$ for all $s \in \mathbb{R}$ and that $\psi(s)$ satisfies

$$\psi'' + p_1(s)\psi' + p_2(s)\psi + p_3(s) = 0, \quad s \in \mathbb{R},$$

where $|p_1(s)| \leq M_1$ and $|p_2(s)| \leq M_1$ for some positive constant M_1 and $p_3(s) \geq 0$. Then there exists positive constant M_2 depending only on M_1 such that

$$\left| \frac{\psi'(s)}{\psi(s)} \right| \leq M_2, \quad \text{for all } s \in \mathbb{R}.$$

Proof. Set $\varphi = \ln \psi, \psi = e^\varphi$. Substituting this transform into the equation $\psi(s)$ satisfies yields

$$\varphi'' + (\varphi')^2 + p_1(s)\varphi' + p_2(s) + p_3(s)e^{-\varphi} = 0.$$

It follows by setting $\varphi' = w$ that

$$w'(s) = -w^2(s) - p_1(s)w(s) - p_2(s) - p_3(s)e^{-\varphi}.$$

By the boundedness of p_1 and p_2 and positivity of p_3 , there exists $M_2 > 0$ depending only on M_1 such that $w' < 0$ for all $|w| \geq M_2$. Assume that $w(s_1) \leq -M_2$ for some $s_1 \in \mathbb{R}$. Then $w'(s) < 0$ and $w(s) \leq -M_2$ for all $s \geq s_1$. Note that $w(s) = \varphi'(s) = \psi'(s)/\psi(s)$. Then we have $\psi'(s)/\psi(s) \leq -M_2$ for all $s \geq s_1$, which implies that $\psi'(s) < 0$ for all $s \geq s_1$ since $\psi(s) > 0$. Therefore, $\psi(s) \rightarrow -\infty$ as $s \rightarrow \infty$, contradicting the fact that $\psi > 0$. Therefore, $w(s) \geq -M_2$ for all $s \in \mathbb{R}$. On the other hand, assume that $w(s_2) \geq M_2$ for some $s_2 \in \mathbb{R}$. Then since $w'(s_2) < 0$ we have $w(s) > M_2$ for $s < s_2$. Hence, $\psi'(s) > 0$ for all $s < s_2$. This implies that $\psi(s) \rightarrow -\infty$ as $s \rightarrow -\infty$, a contradiction to the fact $\psi > 0$. Therefore, $w(s) \leq M_2$ for all $s \in \mathbb{R}$. As a conclusion, we then have $w(s) \in [-M_2, M_2]$ for all $s \in \mathbb{R}$. \square

The following corollary follows from Lemma 3.7 and the boundedness of the traveling wave solution (U, V) .

Corollary 3.1. *There exist $M_u(c) > 0$ and $M_v(c) > 0$ such that the traveling wave solution (U, V) in Lemma 3.6 satisfies*

$$\left| \frac{U'(s)}{U(s)} \right| \leq M_u(c), \quad \left| \frac{V'(s)}{V(s)} \right| \leq M_v(c), \quad \forall s \in \mathbb{R}.$$

In addition, $M_u(c)$ and $M_v(c)$ can be chosen to be bounded on $c \in (c^*, c^* + 1]$.

Remark 3.2. In Section of Discussion, we will show how Lemma 3.7 is applied to more complex models.

Next we will construct a Lyapunov function and use LaSalle’s invariance principle to prove that the traveling wave solution $(U(s), V(s))$, obtained in Lemma 3.6, also connects the equilibrium E^* at $s = +\infty$.

Lemma 3.8. *If $c > c^*$, then (4) admits a positive traveling wave solution $(U(\bar{x} + c\bar{t}), V(\bar{x} + c\bar{t}))$ satisfying boundary condition (9).*

Proof. System (13) can be rewritten as

$$\begin{cases} U' = W, \\ dW' = c_1W - U(1 - U - \gamma_1V), \\ V' = Z, \\ Z' = c_2Z - V(r - V + \gamma_2U). \end{cases} \tag{23}$$

Denote $L = L_1(U, W, V, Z) + L_2(U, W, V, Z)$, where

$$\begin{aligned} L_1(U, W, V, Z) &= \gamma_2r(c_1U - dW), \\ L_2(U, W, V, Z) &= c_2V - Z + r\frac{Z}{V} - c_2r \ln V. \end{aligned}$$

Since the traveling wave solution $(U(s), V(s))$ satisfies (23), then simple calculations yield that the derivative of L_2 along traveling wave solution $(U(s), V(s))$ satisfies

$$\begin{aligned} \frac{dL_2}{ds} &= c_2V' - Z' + r\frac{Z' - c_2V'}{V} - r\frac{ZV'}{V^2} \\ &= \frac{c_2V' - Z'}{V}(V - r) - \frac{rZ^2}{V^2} \\ &= (r - V + \gamma_2U)(V - r) - \frac{rZ^2}{V^2}. \end{aligned}$$

Then we have

$$\begin{aligned} \frac{dL}{ds} &= \gamma_2rU(1 - U - \gamma_1V) + (r - V + \gamma_2U)(V - r) - \frac{rZ^2}{V^2} \\ &= \gamma_2rU(1 - \gamma_1V) - \gamma_2rU^2 - (r - V)^2 + \gamma_2U(V - r) - \frac{rZ^2}{V^2} \\ &= -\gamma_2UV(\gamma_1r - 1) - \gamma_2rU^2 - (r - V)^2 - \frac{rZ^2}{V^2}. \end{aligned}$$

Now suppose $\gamma_1r \geq 1$. From Lemma 3.6 and Corollary 3.1 it follows that $L(s)$ is bounded. It is clear that $L'(s) = 0$ if and only if $U(s) = Z(s) = 0$ and $V(s) = r$, and that the maximal invariant set of

$$\{(U, W, V, Z) : L'(s) = 0\}$$

consists of only one point, i.e. the equilibrium $(0, 0, r, 0)$. Then LaSalle’s invariance principle [41, Theorem 6.4] implies that the traveling wave solution $(U(s), V(s))$ in Lemma 3.6 satisfies

$$(U(+\infty), V(+\infty)) = E_2(0, r). \tag{24}$$

If $\gamma_1 r < 1$ is satisfied, we will construct the Lyapunov function as follows:

$$L_0 = \frac{\gamma_2}{\gamma_1} \left(c_1 U - dW + \frac{d\bar{u}^* W}{U} - c_1 \bar{u}^* \ln U \right) + c_2 V - Z + \frac{\bar{v}^* Z}{V} - c_2 \bar{v}^* \ln V.$$

It is easy to show that the derivative of L_0 along the traveling wave solution $(U(s), V(s))$ satisfies

$$\frac{dL_0}{ds} = -\frac{\gamma_2}{\gamma_1} (U - \bar{u}^*)^2 - \frac{\gamma_2 d\bar{u}^* W^2}{\gamma_1 U^2} - (V - \bar{v}^*)^2 - \frac{\bar{v}^* Z^2}{V^2}.$$

Similar to the proof for $\gamma_1 r \geq 1$, we can show that

$$(U(+\infty), V(+\infty)) = E_3(\bar{u}^*, \bar{v}^*).$$

In conclusion, we always have

$$(U(+\infty), V(+\infty)) = E^*.$$

Then applying Lemma 3.6 completes the proof of this lemma. \square

3.3. Existence of traveling waves when $c = c^*$

Lemma 3.9. (4) has a positive traveling wave solution $(U(\bar{x} + c^*t), V(\bar{x} + c^*t))$ satisfying boundary condition (9).

Proof. We first choose a positive constant u_0 such that

$$\max \left\{ -\frac{r}{\gamma_2}, \bar{u}^*, 0, 1 - \gamma_1 \frac{r + \gamma_2}{2 + \gamma_1 \gamma_2} \right\} < u_0 < 1, \tag{25}$$

where \bar{u}^* is defined in Section 2.1. This can be guaranteed by (H1) (i.e., $r + \gamma_2 > 0$) and

$$1 - \bar{u}^* = 1 - \frac{1 - \gamma_1 r}{1 + \gamma_1 \gamma_2} = \frac{\gamma_1 (r + \gamma_2)}{1 + \gamma_1 \gamma_2} > 0.$$

Note that

$$u_0 > 1 - \gamma_1 \frac{r + \gamma_2}{2 + \gamma_1 \gamma_2} \iff 1 - \gamma_1 \varrho < u_0,$$

where $\varrho := (r + \gamma_2 u_0)/2$.

Claim 1. Let $(U(s), V(s)), s \in \mathbb{R}$ be the bounded positive solution of (13) with $c_2 > \bar{c}$ in Corollary 3.1 where \bar{c} is defined in (7). Then we have

$$\liminf_{s \rightarrow +\infty} U(s) \leq u_0. \tag{26}$$

We assume, on the contrary, that

$$\liminf_{s \rightarrow +\infty} U(s) > u_0.$$

We first consider the case where $V(s)$ is not monotonic for large s , Then there exists a sequence $\{s_n\}_{n \in \mathbb{N}}$ with $s_n \rightarrow +\infty$ such that

$$V'(s_n) = 0, \quad V''(s_n) \geq 0, \quad \liminf_{s \rightarrow +\infty} V(s) = \lim_{n \rightarrow +\infty} V(s_n).$$

It follows from the second equality of (13) that

$$V(s_n) \geq r + \gamma_2 U(s_n) > r + \gamma_2 u_0 > \varrho \tag{27}$$

for all large n , which implies that $V(s) > \varrho$ and $1 - U(s) - \gamma_1 V(s) < 1 - u_0 - \gamma_1 \varrho < 0$. This, together with the first equality of (13), yields $U'(s) < 0$ for all large s , and hence, $U(s)$ is monotonic for large s . Therefore, it follows from the boundedness of U that $U(+\infty)$ ($\geq u_0$) exists and $U'(+\infty) = U''(+\infty) = 0$. Then by the first equality of (13) we obtain that $V(+\infty)$ exists and $V(+\infty) > \varrho > 0$. Now we suppose that $V(s)$ is monotonic for large s . Since V is bounded, $V(+\infty)$ exists. If $V(+\infty) = 0$, it follows that

$$r - V(s) + \gamma_2 U(s) \geq r - V(s) + \gamma_2 u_0 \geq \varrho > 0$$

for large s . By the monotonicity of $V(s)$, $V(s) \geq 0$, and $V(+\infty) = 0$, we can obtain $V'(s) \leq 0$ for large s . Then the second equality of (13) implies that $V''(s) < 0$ for large s . Thus there exists s_0 such that $V'(s) \leq V'(s_0) < 0$ for $s > s_0$, implying $V(+\infty) = -\infty$, a contradiction. In conclusion, we have shown $V(+\infty)$ exists and $V(+\infty) > 0$ whether $V(s)$ is monotonic or not for large s . Hence, $V'(+\infty) = V''(+\infty) = 0$ by the boundedness of $V(s)$ and $V'(s)$ on $s \in \mathbb{R}$. It then follows from the second equation of (13) that $r - V(+\infty) + \gamma_2 U(+\infty) = 0$, which implies the existence of $U(+\infty)$ and hence $U'(+\infty) = U''(+\infty) = 0$. The first equation of (13) then implies $1 - U(+\infty) - \gamma_1 V(+\infty) = 0$. This means that $(U(+\infty), V(+\infty))$ is the coexistence equilibrium $E_3(\bar{u}^*, \bar{v}^*)$, which contradicts the fact $U(+\infty) \geq u_0$ and assumptions in (25). The proof of Claim 1 is completed.

Let $\bar{c}_n := c^* + 1/n$ for positive integer n . By Lemma 3.6, there exists a positive solution $\Phi_n(\cdot) = (U_n(\cdot), V_n(\cdot)) \in \Gamma$ of system (13) with $c = \bar{c}_n$ such that

$$(U_n(-\infty), V_n(-\infty)) = (1, 0).$$

By Claim 1, we may assume by a translation that

$$U_n(0) = (1 + u_0)/2, \quad U_n(s) \geq (1 + u_0)/2, \quad \forall s < 0. \tag{28}$$

Corollary 3.1, Eqs. (13) and Arzela–Ascoli’s theorem imply that there exists a subsequence $\{\bar{c}_{n_k}\}$ such that $\{\Phi_{n_k}(\cdot)\}$ converges to a non-negative function $\Psi(\cdot) := (U(\cdot), V(\cdot))$ in function space $C_{loc}^2(\mathbb{R})$, where $\Psi(\cdot)$ satisfies

$$\begin{cases} (c^* + \alpha_1)U' = dU'' + U(1 - U - \gamma_1 V), \\ \bar{c}V' = V'' + V(r - V + \gamma_2 U), \end{cases}$$

with

$$U(0) = \frac{1 + u_0}{2}, \quad \frac{1 + u_0}{2} \leq U(s) \leq 1, \quad V(s) \geq 0, \quad \text{for all } s < 0. \tag{29}$$

Assume $V(s) = 0$ for all $s \in \mathbb{R}$ and we will get a contradiction in the following. Then $U(s)$ satisfies

$$(c^* + \alpha_1)U' = dU'' + U(1 - U). \tag{30}$$

Let a be a positive constant. Obviously, we have $U(0) > 0$ from (29). Then by using Harnack inequality [35, Section 6.4.3] on $[-a, a]$, it follows that $U(s) > 0$ for all $s \in [-a, a]$. We then obtain that $U(s) > 0$ for all $s \in \mathbb{R}$ since a is arbitrarily chosen. It follows from $0 < U(s) \leq 1$ for all $s \in \mathbb{R}$ that $U'(s^*) = 0$ if $U(s^*) = 1$. Since $U(s) \equiv 1$ is the unique solution of equation (30) with initial conditions $U(s^*) = 1, U'(s^*) = 0$ and we have $U(0) < 1$ by (29), it follows that $U(s) < 1$ for all $s \in \mathbb{R}$. Then (30) implies that $U(s)$ is monotonic in \mathbb{R} , and $U(-1) \geq U(0)$ (see (29)) furthermore implies that $U(s)$ is monotonically decreasing in \mathbb{R} and that $U(+\infty)$ exists. It is clear that $U(+\infty) = 0$. If (H2) holds, i.e. $c^* + \alpha_1 > 0$, then we have $U'(s) < 0, U''(s) < 0$, implying $U'(s) \leq U'(0) < 0$. It follows that $U(+\infty) = -\infty$, a contradiction. If (H3) holds, it follows that

$U_n(s) \geq \underline{U}(s) \geq \delta > 0$ for any n and any $s \in \mathbb{R}$, implying that $U(s) \geq \delta > 0$ for any $s \in [0, +\infty]$, a contradiction. Therefore, there exists s_0 such that $V(s_0) > 0$, and Harnack inequality furthermore yields $V(s) > 0$ for all $s \in \mathbb{R}$. Similar to the proof of [Claim 1](#), it can be shown that $(U(-\infty), V(-\infty))$ is an equilibrium. Since $U(-\infty) \geq u_0$ and u_0 satisfies [\(25\)](#), we obtain that $U(-\infty)$ cannot be 0 or \bar{u}^* , and hence, $(U(-\infty), V(-\infty)) = E_1(1, 0)$. Note that the inequality in [Corollary 3.1](#) and [Lemma 3.8](#) also hold in the case $c = c^*$. Then we have $(U(+\infty), V(+\infty)) = E^*$. \square

Remark 3.3. Actually, [Claim 1](#) can be directly proved by [Lemma 3.8](#). However, the proof of [Lemma 3.8](#) depends on the construction of a Lyapunov function, so that the proof of [Claim 1](#) also depends on the construction of a Lyapunov function. In most cases, it is difficult to construct a Lyapunov function. Hence, the proof of [Claim 1](#) in this paper can be used to prove the existence of positive traveling wave solutions with minimal wave speed c^* even if we cannot construct a Lyapunov function. Especially, the idea of the proof of [Claim 1](#) can be applied to the general model in [\[30\]](#).

3.4. Nonexistence of traveling waves when $c < c^*$

In this section we show the nonexistence of traveling wave solutions when $c < c^*$.

Lemma 3.10. *System [\(13\)](#) has no positive solutions $(U(s), V(s))$ satisfying [\(9\)](#) if $c < c^*$.*

Proof. We will prove this lemma by a contradiction. Suppose that [\(13\)](#) has a positive solution $(U(s), V(s))$ satisfying [\(9\)](#). It is evident that $c < c^*$ is equivalent to $c_2 < \bar{c} = 2\sqrt{r + \gamma_2}$. It is easy to show that the equilibrium $(1, 0, 0, 0)$ of [\(23\)](#) is hyperbolic. Then it follows by Stable Manifold Theorem in Perko [\[42\]](#) that there exists a positive constant ω such that

$$\sup_{s < 0} \{V(s)e^{-\omega s}\} < +\infty, \quad \sup_{s < 0} \{|V'(s)|e^{-\omega s}\} < +\infty, \quad \sup_{s < 0} \{|V''(s)|e^{-\omega s}\} < +\infty. \quad (31)$$

To continue the proof, we introduce the definition of *negative one-sided Laplace transform*:

$$\mathcal{V}(\lambda) = \mathcal{N}[V(\cdot)](\lambda) := \int_{-\infty}^0 e^{-\lambda s} V(s) ds$$

for $\lambda \geq 0$. By this definition we know that $\mathcal{V}(\lambda)$ is increasing on $[0, \lambda^*)$, where $\lambda^* = +\infty$ or $\lambda^* < +\infty$ with $\lim_{\lambda \rightarrow \lambda^*} \mathcal{V}(\lambda) = +\infty$. It follows from [\(31\)](#) that $\lambda^* \geq \omega$.

Note that [Corollary 3.1](#) actually holds for any real number c . It follows from [Corollary 3.1](#) that

$$\int_{-\infty}^0 e^{-\lambda \xi} |V'(\xi)| d\xi \leq M_v(c) \int_{-\infty}^0 e^{-\lambda \xi} V(\xi) d\xi < +\infty,$$

implying that $\int_{-\infty}^0 e^{-\lambda \xi} V'(\xi) d\xi$ is convergent. Then it follows from

$$[e^{-\lambda \xi} V(\xi)]' = e^{-\lambda \xi} V'(\xi) - \lambda e^{-\lambda \xi} V(\xi)$$

that

$$V(0) - e^{-\lambda s} V(s) = \int_s^0 e^{-\lambda \xi} V'(\xi) d\xi - \lambda \int_s^0 e^{-\lambda \xi} V(\xi) d\xi.$$

We obtain that $\lim_{s \rightarrow -\infty} e^{-\lambda s} V(s)$ exists since the right-hand side of above equality is convergent if $s = -\infty$. Then $\lim_{s \rightarrow -\infty} e^{-\lambda s} V(s) = 0$ since $\lim_{s \rightarrow -\infty} e^{-\lambda s} V(s) \neq 0$ implies that $\int_{-\infty}^0 e^{-\lambda s} V(s) ds$ is divergent. It can

be similarly shown that $\lim_{s \rightarrow -\infty} e^{-\lambda s} V'(s) = 0$. Then we can verify that $\mathcal{N}[\cdot]$ satisfies

$$\begin{aligned} \mathcal{N}[V'(\cdot)](\lambda) &= \lambda \mathcal{V}(\lambda) + V(0) - \lim_{s \rightarrow -\infty} e^{-\lambda s} V(s) \\ &= \lambda \mathcal{V}(\lambda) + V(0), \\ \mathcal{N}[V''(\cdot)](\lambda) &= \lambda^2 \mathcal{V}(\lambda) + \lambda V(0) + V'(0) - \lim_{s \rightarrow -\infty} e^{-\lambda s} V'(s) - \lambda \lim_{s \rightarrow -\infty} e^{-\lambda s} V(s) \\ &= \lambda^2 \mathcal{V}(\lambda) + \lambda V(0) + V'(0), \end{aligned} \tag{32}$$

for all $\lambda \in [0, \lambda^*)$.

The second equation of (13) can be restated as

$$L[V(\cdot)](s) = [\gamma_2(1 - U(s)) + V(s)]V(s)$$

where

$$L[V(\cdot)](s) := V''(s) - c_2 V'(s) + (\gamma_2 + r)V(s).$$

Define $\rho = \min\{H(\lambda) : \lambda \geq \omega\}$, where $H(\lambda)$ is defined in (16). It follows from condition $c_2 < \bar{c}$ that $\rho > 0$. Since (13) is autonomous, for any $a \in \mathbb{R}$, $(U(s - a), V(s - a))$ is also a solution of (13) satisfying $\lim_{s \rightarrow -\infty} U(s - a) = 1$ and $\lim_{s \rightarrow -\infty} V(s - a) = 0$. By using the fact $U(-\infty) = 1$ and $V(-\infty) = 0$ we can obtain that $1 - U(s)$ and $V(s)$ can be small enough when s is negatively large. We then can choose some $a_0 \in \mathbb{R}$ such that $(U(s - a_0), V(s - a_0))$ satisfies

$$\gamma_2(1 - U(s - a_0)) + V(s - a_0) < \frac{\rho}{2}, \quad \forall s \leq 0.$$

Consequently, without losing generality we can assume

$$\gamma_2(1 - U(s)) + V(s) < \frac{\rho}{2}$$

for all $s \leq 0$, which implies

$$L[V(\cdot)](s) \leq \frac{\rho}{2} V(s).$$

Applying the operator $\mathcal{N}[\cdot]$ to this inequality and using the properties of $\mathcal{N}[\cdot]$ in (32) yield that

$$\frac{\rho}{2} \mathcal{V}(\lambda) \geq \mathcal{N}[L[V(\cdot)](\cdot)](\lambda) = H(\lambda) \mathcal{V}(\lambda) + q(\lambda),$$

where

$$q(\lambda) = V'(0) + (\lambda - c_2)V(0).$$

Consequently, we have

$$\mathcal{H}(\lambda) := \left[H(\lambda) - \frac{\rho}{2} \right] \mathcal{V}(\lambda) + q(\lambda) \leq 0.$$

If $\lambda^* < +\infty$, then $\lim_{\lambda \rightarrow \lambda^*-} \mathcal{V}(\lambda) = +\infty$ and, therefore, $\lim_{\lambda \rightarrow \lambda^*-} \mathcal{H}(\lambda) = +\infty$, which is a contradiction. If $\lambda^* = +\infty$, we have that $\lim_{\lambda \rightarrow +\infty} \mathcal{H}(\lambda) = +\infty$ by the monotonicity of $\mathcal{V}(\lambda)$ and the definitions of $H(\lambda)$ and $q(\lambda)$, which is still a contradiction. The proof is completed. \square

3.5. Proof of Theorem 2.1(i)

The proof of Theorem 2.1(i) can be completed by combining Lemmas 3.8–3.10.

3.6. Proof of Theorem 2.1(ii)

Let $(U(\bar{x} - c\bar{t}), V(\bar{x} - c\bar{t}))$ be the positive traveling wave solutions of system (4) satisfying boundary condition (10). Substituting $(U(\xi), V(\xi)), \xi = \bar{x} - c\bar{t}$ into (4) yields

$$\begin{cases} (-c + \alpha_1)U' = dU'' + U(1 - U - \gamma_1 V), \\ (-c + \alpha_2)V' = V'' + V(r - V + \gamma_2 U), \end{cases} \quad (33)$$

where the derivative is with respect to ξ . By setting

$$\xi = -s, \quad \mathcal{U}(s) = U(\xi), \quad \mathcal{V}(s) = V(\xi),$$

we have

$$\begin{cases} (c - \alpha_1)\mathcal{U}' = d\mathcal{U}'' + \mathcal{U}(1 - \mathcal{U} - \gamma_1 \mathcal{V}), \\ (c - \alpha_2)\mathcal{V}' = V'' + \mathcal{V}(r - \mathcal{V} + \gamma_2 \mathcal{U}), \end{cases}$$

and

$$(\mathcal{U}(-\infty), \mathcal{V}(-\infty)) = E_1, \quad (\mathcal{U}(+\infty), \mathcal{V}(+\infty)) = E^*,$$

where the derivative is with respect to s . Then Theorem 2.1(ii) can be obtained from Theorem 2.1(i).

4. Proof of Theorem 2.2

We firstly give some notations:

$$\begin{aligned} \mu_1 &= \frac{c_1 - \sqrt{c_1^2 - \bar{c}_{23}^2}}{2d}, & \mu_2 &= \frac{c_1 + \sqrt{c_1^2 - \bar{c}_{23}^2}}{2d}, \\ P(\mu) &:= d\mu^2 - c_1\mu + 1 - \gamma_1 r, \end{aligned}$$

where $\bar{c}_{23} := 2\sqrt{d(1 - \gamma_1 r)}$. It is clear that μ_1 and μ_2 are roots of $P(\mu) = 0$. Define

$$\begin{aligned} \bar{U}(s) &= \min\{e^{\mu_1 s}, 1 - \gamma_1 r\}, & \bar{V}(s) &= r + \min\{\sigma e^{\beta s}, \gamma_2(1 - \gamma_1 r)\}, \\ \underline{U}(s) &= \max\{e^{\mu_1 s}(1 - M e^{\varepsilon s}), 0\}, & \underline{V}(s) &= r, \end{aligned} \quad (34)$$

where positive constants $\sigma, \beta, \varepsilon$ and M will be determined later. Note that most notations used in this section are same as those in Section 3, which, however, will not cause confusion since this section has no connections with Section 3 except the proof ideas.

Similar to the arguments in Section 3, we present the following three lemmas.

Lemma 4.1. *The function $\bar{U}(s)$ satisfies inequality*

$$c_1 \bar{U}' \geq d \bar{U}'' + \bar{U}(1 - \bar{U} - \gamma_1 \underline{V})$$

for any $s \neq \bar{s}_u := \ln(1 - \gamma_1 r)/\mu_1$.

Proof. Firstly, consider the case $s < \bar{s}_u$, which implies $\bar{U}(s) = e^{\mu_1 s}$. Then we have

$$d \bar{U}'' - c_1 \bar{U}' + \bar{U}(1 - \bar{U} - \gamma_1 \underline{V}) = (d\mu_1^2 - c_1\mu_1 + 1 - \gamma_1 r - \bar{U})e^{\mu_1 s} = -\bar{U}e^{\mu_1 s} \leq 0.$$

If $s > \bar{s}_u$, then we have $\bar{U}(s) = 1 - \gamma_1 r$. It is obvious that the inequality in this lemma holds. The proof is completed. \square

Lemma 4.2. *There exist positive constants σ (large enough) and β (small enough) such that function $\bar{V}(s)$ satisfies*

$$c_2\bar{V}' \geq \bar{V}'' + \bar{V}(r - \bar{V} + \gamma_2\bar{U})$$

for any $s \neq \bar{s}_v$, where

$$\bar{s}_v := \frac{1}{\beta} \ln \frac{\gamma_2(1 - \gamma_1 r)}{\sigma} < 0.$$

Proof. Firstly, we set

$$0 < \beta < \mu_1, \quad \sigma > \max \left\{ \gamma_2(1 - \gamma_1 r), \gamma_2(1 - \gamma_1 r)^{1-\beta/\mu_1} \right\},$$

which implies $\bar{s}_v < \min\{0, \bar{s}_u\}$.

If $s > \bar{s}_v$, then we have $\bar{V} = r + \gamma_2(1 - \gamma_1 r)$,

$$\begin{aligned} \bar{V}'' - c_2\bar{V} + \bar{V}(r - \bar{V} + \gamma_2\bar{U}) &= \bar{V}[-\gamma_2(1 - \gamma_1 r) + \gamma_2\bar{U}] \\ &\leq \bar{V}[-\gamma_2(1 - \gamma_1 r) + \gamma_2(1 - \gamma_1 r)] = 0. \end{aligned}$$

Assume $s < \bar{s}_v$, which implies $s < 0$, $\bar{U}(s) = e^{\mu_1 s}$, $\bar{V}(s) = r + \sigma e^{\beta s}$. Then we have

$$\bar{V}'' - c_2\bar{V} + \bar{V}(r - \bar{V} + \gamma_2\bar{U}) = (\sigma\beta^2 - c_2\sigma\beta)e^{\beta s} + \bar{V}(-\sigma e^{\beta s} + \gamma_2 e^{\mu_1 s}).$$

It is easy to show that

$$\frac{\gamma_2}{\sigma} e^{-\beta\bar{s}_v} e^{\mu_1\bar{s}_v} < \frac{1}{2} \iff \sigma > \gamma_2 2^{\beta/\mu_1} (1 - \gamma_1 r)^{1-\beta/\mu_1}.$$

By setting β small enough and σ large enough, we have

$$\begin{aligned} \frac{1}{\sigma e^{\beta s}} \left[\bar{V}'' - c_2\bar{V} + \bar{V}(r - \bar{V} + \gamma_2\bar{U}) \right] &= \beta(\beta - c_2) + \bar{V} \left(-1 + \frac{\gamma_2}{\sigma} e^{-\beta s} e^{\mu_1 s} \right) \\ &\leq \beta(\beta - c_2) + \bar{V} \left(-1 + \frac{1}{2} \right) \\ &\leq \frac{r}{2} - \frac{r}{2} = 0. \end{aligned}$$

Thus the proof is completed. \square

Lemma 4.3. *Assume $\varepsilon < \beta < \min\{\mu_1, \mu_2 - \mu_1\}/2$. Then for $M > 0$ large enough, the function $\underline{U}(s)$ satisfies*

$$c_1\underline{U}' \leq d\underline{U}'' + \underline{U}(1 - \underline{U} - \gamma_1\bar{V})$$

for any $s \neq \underline{s}_u := -\ln M/\varepsilon$.

Proof. It is clear that $\underline{U}(s) = 0$ if and only if $s \geq \underline{s}_u$, that $\bar{V} = r + \gamma_2(1 - \gamma_1 r)$ if and only if $s \geq \bar{s}_v$, and that $\underline{s}_u < \bar{s}_v$ if and only if

$$M > \left(\frac{\sigma}{\gamma_2(1 - \gamma_1 r)} \right)^{\varepsilon/\beta}.$$

Assume above inequality is satisfied and $M > 1$, implying $\underline{s}_u < \min\{0, \bar{s}_v\}$. If $s > \underline{s}_u$, then $\underline{U}(s) = 0$ and the inequality in Lemma 4.3 holds.

Now we consider the case $s < \underline{s}_u$. Then $s < 0$, $s < \bar{s}_v$, and

$$\underline{U}(s) = e^{\mu_1 s}(1 - M e^{\varepsilon s}) > 0, \quad \bar{V}(s) = r + \sigma e^{\beta s}.$$

To prove this lemma, it suffices to show

$$e^{-\mu_1 s} [d\underline{U}'' - c_1\underline{U}' + \underline{U}(1 - \underline{U} - \gamma_1\overline{V})] \geq 0.$$

However, we have

$$\begin{aligned} & e^{-\mu_1 s} [d\underline{U}'' - c_1\underline{U}' + \underline{U}(1 - \underline{U} - \gamma_1\overline{V})] \\ &= d\mu_1^2 - dM(\mu_1 + \varepsilon)^2 e^{\varepsilon s} - c_1\mu_1 + c_1M(\mu_1 + \varepsilon)e^{\varepsilon s} \\ &\quad + (1 - Me^{\varepsilon s})(1 - \gamma_1 r - \underline{U} - \gamma_1\sigma e^{\beta s}) \\ &= (d\mu_1^2 - c_1\mu_1 + 1 - \gamma_1 r) - M [d(\mu_1 + \varepsilon)^2 - c_1(\mu_1 + \varepsilon) + 1 - \gamma_1 r] e^{\varepsilon s} \\ &\quad - (1 - Me^{\varepsilon s})(\underline{U} + \gamma_1\sigma e^{\beta s}) \\ &= \left[-MP(\mu_1 + \varepsilon) - (1 - Me^{\varepsilon s})^2 e^{(\mu_1 - \varepsilon)s} - \gamma_1\sigma(1 - Me^{\varepsilon s})e^{(\beta - \varepsilon)s} \right] e^{\varepsilon s} \\ &\geq [-MP(\mu_1 + \varepsilon) - 1 - \gamma_1\sigma] e^{\varepsilon s}, \end{aligned}$$

where the final inequality holds since

$$0 \leq 1 - Me^{\varepsilon s} \leq 1, \quad 0 \leq e^{(\beta - \varepsilon)s} \leq 1, \quad 0 \leq e^{(\mu_1 - \varepsilon)s} \leq 1.$$

Because $P(\mu_1 + \varepsilon) < 0$ holds for any $0 < \varepsilon < \mu_2 - \mu_1$, setting

$$M > \frac{1 + \gamma_1\sigma}{-P(\mu_1 + \varepsilon)}$$

completes the proof. \square

Then we can prove [Theorem 2.2](#) by arguments completely similar to those in [Section 3](#). Actually, the proof of [Theorem 2.2](#) is simpler than that of [Theorem 2.1](#). The hypotheses **(H2)**, **(H3)** and **(H2)** are needed for the proof of [Theorem 2.1](#) for technical reasons, but are not needed for the proof of [Theorem 2.2](#). We conjecture that the hypotheses **(H2)**, **(H3)** and **(H2)** are not necessary for [Theorem 2.1](#) and leave this as a future problem.

5. Biological interpretations of the minimal wave speeds

In this section, we give some biological interpretations of [Theorems 2.1](#) and [2.2](#) for model [\(1\)](#).

By [\(3\)](#), the assumptions for model [\(1\)](#) are

- (H1)**: $r_2 b_{11} + r_1 b_{22} > 0$,
- (H2)**: $2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)} - b_2 + b_1 > 0$,
- (H2)**: $2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)} + b_2 - b_1 > 0$, and
- (H3)**: $\frac{r_2}{r_1} < \frac{b_{21}}{b_{12}} - \frac{b_{22}}{b_{11}}$.

The results in [Theorems 2.1](#) and [2.2](#) then become the following.

- Under **(H1)** and one of **(H2)** and **(H3)**, the predator’s upstream minimal wave speed of model [\(1\)](#) is

$$\tilde{c}^* = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)} - b_2.$$

- Under **(H1)** and one of **(H2)** and **(H3)**, the predator’s downstream minimal wave speed of model (1) is

$$\tilde{c}_-^* = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)} + b_2.$$

- Under **(H1)**, the prey’s upstream minimal wave speed and downstream minimal wave speed of model (1) are, respectively,

$$\tilde{c}_{23}^* = 2\sqrt{d_1 \left(r_1 - \frac{b_{12}}{b_{21}} r_2 \right)} - b_1$$

and

$$\tilde{c}_{23-}^* = 2\sqrt{d_1 \left(r_1 - \frac{b_{12}}{b_{21}} r_2 \right)} + b_1.$$

5.1. The predator’s invasion speed

The minimal wave speeds \tilde{c}^* and \tilde{c}_-^* are monotonically increasing with respect to the diffusion rate (d_2) and the growth rate (r_2) of the predator, the growth rate (r_1) of the prey, and the conversion rate (b_{22}); they are monotonically decreasing with respect to the density-dependent rate (b_{11}) of the prey. \tilde{c}^* decreases in the advection rate (b_2) of the predator but \tilde{c}_-^* increases in b_2 . The advection rate of the prey (b_1) is not involved in the formulas of \tilde{c}^* and \tilde{c}_-^* , but \tilde{c}^* and \tilde{c}_-^* rely on it since b_1 is in the conditions **(H2)** and **(H2)** which affect the existence of \tilde{c}^* and \tilde{c}_-^* . The predation rate (b_{12}) should be considered to be related to the conversion rate b_{22} in some sense. \tilde{c}^* and \tilde{c}_-^* do not depend on the diffusion rate of the prey (d_1) and the density-dependent rate (b_{21}) of the predator.

If the predator is a generalist ($r_2 > 0$), then the growth of the predator does not only depend on the prey, and hence, there is a chance for existence of a traveling wave connecting the prey-only equilibrium and the predator-only equilibrium. In this case, assumption **(H1)** is automatically true. If the predator is a specialist ($r_2 < 0$), then the growth of the predator only depends on the prey. Hence, the predator cannot exist without the prey and there might be traveling waves connecting the prey-only equilibrium and the coexistence equilibrium. In this case, **(H1)** is true provided that the growth rate of the predator r_2 is negatively small.

Note that

$$\bar{c} = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)}$$

is the minimal wave speed of traveling waves for (1) without advections (i.e., when $b_1 = b_2 = 0$). Therefore, if $\bar{c} > b_2 - b_1$, the assumption **(H2)** is true, and hence the minimal wave speed \tilde{c}^* of traveling waves for (1) can be defined. If $\bar{c} > b_1 - b_2$, then **(H2)** is true and \tilde{c}_-^* is defined. Here we do not require that the advection rates of the prey and the predator are the same (i.e., $b_1 = b_2$) or in the same direction (i.e., b_1 and b_2 have the same sign).

When the conversion rate $b_{22} = 0$, the predation of prey does not contribute to the growth of the predator. The prey system and the predator system are decoupled. The minimal wave speeds of (1) coincide with the minimal wave speeds of traveling waves for Fisher’s equation for the predator: $2\sqrt{d_2 r_2} \pm b_2$.

Note that $x = -\infty$ and $x = \infty$ represent the upstream end and the downstream end of the river, respectively. Then the traveling waves $(U(\bar{x} + c\bar{t}), V(\bar{x} + c\bar{t}))$ of (4) in Theorem 2.1 move to the upstream if $c > 0$ and to the downstream if $c < 0$. Since these traveling waves connect the prey-only equilibrium to a predator-present equilibrium, this corresponds to the situation where the predator invades from the downstream to the upstream of a river that is occupied by the prey at its carrying capacity. The wave profile of the traveling waves shows the resulted distributions of the prey and the predator in the river along such invasion. Therefore, when $\tilde{c}^* > 0$, the traveling wave $(\mathbf{U}(x + \tilde{c}^*t), \mathbf{V}(x + \tilde{c}^*t))$ of (1) moves to the upstream and the predator's invasion is successful; when $\tilde{c}^* < 0$, the traveling wave $(\mathbf{U}(x + \tilde{c}^*t), \mathbf{V}(x + \tilde{c}^*t))$ moves to the downstream so we expect both the prey and the predator to be washed to the downstream, and hence, the predator's invasion is not successful. Similarly, the traveling waves $(U(\bar{x} - c\bar{t}), V(\bar{x} - c\bar{t}))$ move to the downstream if $c > 0$ and correspond to the situation where the predator invades from the upstream to the downstream of a river that is occupied by the prey at its carrying capacity. If $b_2 > 0$, then $\tilde{c}_-^* > 0$ is always valid and hence such invasion is successful.

For partial differential equations for a single species such as Fisher's equation or for interacting populations such as cooperative or competitive models, it has been proved that the minimal wave speed of traveling waves coincides with the spreading speed, which is the rate at which a population asymptotically spreads in the spatial environment; see e.g., [43,44]. However, this has not been proved for predator-prey models, so we cannot say that our minimal wave speed \tilde{c}^* (\tilde{c}_-^*) is the spreading speed of (1) in the upstream (downstream) direction. As a result of the biological interpretation in the above paragraph, we use \tilde{c}^* (\tilde{c}_-^*) to represent the *upstream (downstream) invasion speed* of the predator in a river or stream environment, which also follows the same idea as in [3]. Then Theorem 2.1 coincides with the analysis in [3] and indicates that when the prey and the predator coexist in the stream, they spread at the same speed \tilde{c}^* in the upstream direction. However, our result also implies different information that this common invasion speed \tilde{c}^* does not only depend on the spread of the prey, but also on (or mainly on) the spread of the predator (see the diffusion (d_2), advection (b_2), growth (r_2) and conversion (b_{22}) in the expression of \tilde{c}^*). In particular, we consider the following situations.

- (a) When both the prey and the predator are subjected to the flow and the advection rates are the same, i.e., $b_1 = b_2 > 0$, (H2) follows from (H1). Thus, if $r_2 b_{11} + r_1 b_{22} > 0$, then the prey and the predator spread to the upstream at the speed \tilde{c}^* if $\tilde{c}^* > 0$ and only to the downstream if $\tilde{c}^* < 0$. This implies that in such a river (or a similar advective environment), a generalist (i.e., $r_2 > 0$) or a specialist with small death rate (i.e., $r_2 < 0$ but $|r_2|$ is small) can always spread with its prey at the same speed in the upstream direction. The relationship between \tilde{c}^* (and \tilde{c}_-^*) and the growth rate r_2 of the predator is shown in Fig. 2(a). In this example, the parameter values are $r_1 = 0.1$, $b_{11} = 0.05$, $b_{22} = 0.01$, $d_2 = 0.02$, $b_1 = 0.05$, and $b_2 = 0.05$; the assumptions (H1) and (H2) are valid provided that $r_2 > -0.02$. The prey and the predator will both be washed to the downstream if the predator is a specialist or if the predator is a generalist but does not rely much on other food sources ($r_2 < 0$ or $r_2 > 0$ but $|r_2|$ is small) since $\tilde{c}^* < 0$. The prey and the predator will both spread to the upstream if the predator is a generalist and greatly relies on other food sources (r_2 is positively large) since $\tilde{c}^* > 0$.
- (b) When the advection rates for the prey and the predator are not the same (i.e., $b_1 \neq b_2$) or even in opposite directions (i.e., $b_1 b_2 < 0$), under the condition $r_2 b_{11} + r_1 b_{22} > 0$, the prey and the predator will eventually spread at the same speed if $b_2 \leq b_1$ or $0 < b_2 - b_1 < \bar{c}$. This is not hard to understand. The prey may try to move to the opposite direction of the movement of the predator, but it will still be caught by the predator and proceed to the predators' moving direction eventually, provided that the prey's advection rate is small. For example, the mayfly flies to the upstream which results in a positive advection rate (i.e., $-b_1 > 0$) in (1), while its predator, say, some small fish, suffers a negative advection rate (i.e., $-b_2 < 0$) (see, e.g., [45–47]), but they will spread at the same rate to the upstream under suitable conditions. The

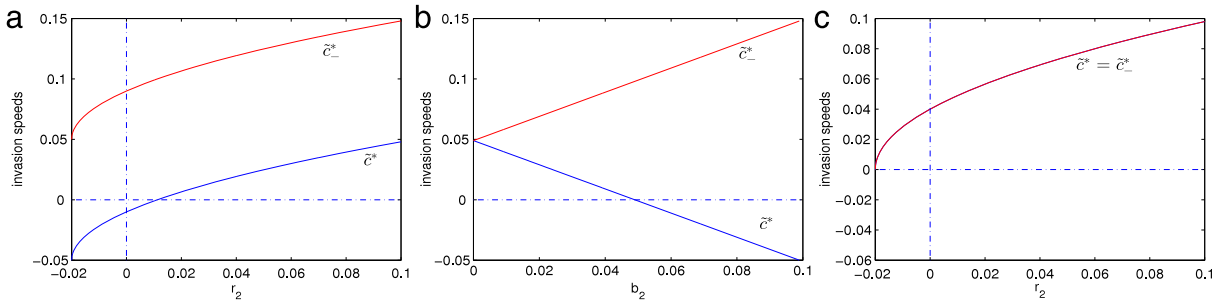


Fig. 2. The relationships between the predator-invasion minimal wave speeds of (1) and the growth rate of the predator r_2 and the advection rate b_2 , respectively. Parameter values are: (a) $r_1 = 0.1, b_{11} = 0.05, b_{22} = 0.01, d_2 = 0.02, b_1 = 0.05, b_2 = 0.05$; (b) $r_1 = 0.1, r_2 = 0.01, b_{11} = 0.05, b_{22} = 0.01, d_2 = 0.02, b_1 = 0.05$; (c) $r_1 = 0.1, b_{11} = 0.05, b_{22} = 0.01, d_2 = 0.02, b_1 = 0.05, b_2 = 0$.

relationship between \tilde{c}^* (and \tilde{c}_-) and the advection rate b_2 of the predator is shown in Fig. 2(b). In this example, the parameter values are $r_1 = 0.1, r_2 = 0.01, b_{11} = 0.05, b_{22} = 0.01, d_2 = 0.02$, and $b_1 = 0.05$; the assumption (H1) is obviously true and (H2) is true provided that $b_2 < 0.099$. We have the following observations in the case that the prey is subjected to the water flow (i.e., $b_1 > 0$) and the predator is a generalist. If the predator is also subjected to the flow with a large advection rate (i.e., $b_2 > 0$ and b_2 is large), then the prey and the predator will both be washed to the downstream as $\tilde{c}^* < 0$. If the predator is subjected to the flow with a small advection rate (i.e., $b_2 > 0$ and b_2 is small) or if the predator is able to intentionally move only to the upstream at a small rate (i.e., $b_2 < 0$ and $|b_2|$ is small), then the prey and the predator may spread to the upstream as $\tilde{c}^* > 0$. If the predator only drifts to the upstream at a large rate (i.e., $b_2 < 0$ and $|b_2|$ is large), then both the prey and the predator only spread to the upstream since the upstream invasion speed is positive ($\tilde{c}^* > 0$) but the downstream invasion speed is negative ($\tilde{c}_- < 0$).

(c) In the drift-feeding case as mentioned in [3], the predators are drift-feeders, who hold fixed positions in the water current and feed on invertebrates that are drifting by, we have $b_2 = 0$ and $b_1 > 0$. Then the upstream and downstream invasion speeds are $\tilde{c}^* = \tilde{c}_- = 2\sqrt{d_2(r_2 + b_{22}r_1/b_{11})}$ if (H1) holds. An example of the relationship between \tilde{c}^* and the growth rate r_2 of the predator in this case is shown in Fig. 2(c). Parameters are $r_1 = 0.1, b_{11} = 0.05, b_{22} = 0.01, d_2 = 0.02$, and $b_1 = 0.05$. It shows that if the predator is a generalist (i.e., $r_2 > 0$) or a specialist with sufficiently small death rate (i.e., $r_2 < 0$ but $|r_2|$ is small), then the prey and the predator both spread to the upstream and the invasion of the predator is still successful.

5.2. The prey’s spread speeds

The minimal wave speeds of the prey-spread traveling waves \tilde{c}_{23}^* and \tilde{c}_{23-}^* depend on all parameters of model (1) except diffusion rate (d_2) and the advection speed of the predator (b_2). Assumption (H1) is the only condition for the establishment of these speeds. Note that model (1) admits such traveling waves connecting a coexistence equilibrium to a predator-only equilibrium only when the predator is a generalist (i.e., $r_2 > 0$). The formulae of \tilde{c}_{23}^* and \tilde{c}_{23-}^* coincide with our intuition in the sense that they increase, and hence it is easier for the prey to spread, as the growth rate (r_1) and the diffusion rate (d_1) of the prey increase or the growth rate (r_2) of the predator decreases. Moreover, the higher the predation rate (b_{12}) the harder it is for the prey to survive and spread, but the higher the density-dependence rate (b_{21}) of the predator the easier it is for more prey to survive and spread as more predators die. The advection rate (b_1) of the prey, if positive, reduces the ability of the prey to spread to the upstream but helps the prey to spread

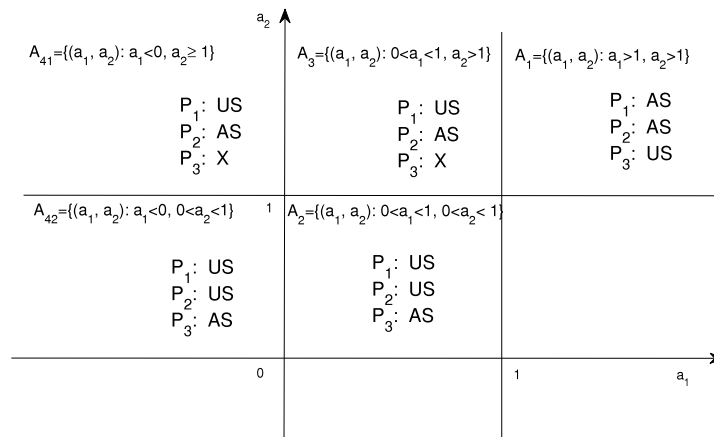


Fig. 3. Stability classification of equilibria for the ODE system corresponding to (35). “AS”: “asymptotically stable”; “US”: “unstable”; “x”: P_3 does not exist.

to the downstream. However, the movement of the predator (in terms of d_2 and b_2) does not influence the spread of the prey. This is because the prey is introduced into an environment where the predator originally occupies and the risk of predation is almost the same for the prey everywhere.

6. Biological explanation of linear and nonlinear determinacy

By (14) and (16) we know that the minimal wave speed $c = c^*$ of (4) is determined when $H(\lambda)$ admits a repeated root, which, together with Theorem 2.1(i), implies that the minimal wave speed of model (4) (or model (1)) is linearly determined. Linear determinacy has been previously studied for Lotka–Volterra models but mainly without advection. Therefore, in this section, in order to compare our results with previous results, we consider model (1) without advection

$$\begin{cases} u_t = d_1 u_{xx} + u(r_1 - b_{11}u - b_{12}v), \\ v_t = d_2 v_{xx} + v(r_2 - b_{21}v + b_{22}u), \end{cases} \quad (35)$$

to analyze the biological background of linear determinacy for Lotka–Volterra models by comparing Theorem 2.1(i) with the results in [36–38]. Note that we do not restrict b_{22} to be positive in this section, which indicates that system (35) is a predator–prey model if $b_{22} > 0$ and it is a competitive model if $b_{22} < 0$.

Let $P_1 = (u_1, 0)$, $P_2 = (0, v_2)$, and $P_3 = (p^*, q^*)$ be equilibria of (1), corresponding to equilibria E_1 , E_2 and E_3 of (4), respectively. Let

$$a_1 = -\frac{b_{22} r_1}{b_{11} r_2} \quad \text{and} \quad a_2 = \frac{b_{12} r_2}{b_{21} r_1}.$$

We classify the meaningful parameter range of a_1 and a_2 into subsets: A_1 , A_2 , A_3 , and $A_4 := A_{41} \cup A_{42}$ (see Fig. 3). The asymptotical stability of P_1, P_2 and P_3 for the ordinary differential equation system corresponding to (35) is given in Fig. 3 according to the range of parameters a_1 and a_2 .

Denote the minimal wave speed of system (35) by c^* if it exists. If $(a_1, a_2) \in A_1$, both P_1 and P_2 are asymptotically stable, and hence, the traveling wave connecting P_1 and P_2 is a bistable wave [36]. If $(a_1, a_2) \in A_2 \cup A_3$, it has been proved in Theorem 2.2 in [48] that, there exists a positive c^* such that system (35) has a traveling wave solution connecting P_1 and P^* with wave speed c if and only if $c \geq c^*$, where

$$P^* = \begin{cases} P_3, & \text{if } (a_1, a_2) \in A_2 \cup A_{42}; \\ P_2, & \text{if } (a_1, a_2) \in A_1 \cup A_3 \cup A_{41}. \end{cases} \quad (36)$$

It is easy to show that

$$c^* \geq \bar{c} := 2\sqrt{d_2 r_2 (1 - a_1)} = 2\sqrt{d_2 \left(r_2 + \frac{b_{22}}{b_{11}} r_1 \right)}.$$

If

$$c^* = \bar{c},$$

the minimum wave speed c^* is called to be **linearly determined** or to be of **linear determinacy**, and if

$$c^* > \bar{c},$$

the minimum wave speed is called to be **not linearly determined** or to be of **nonlinear determinacy** [36–38]. The linear determinacy of (35) in the case of $(a_1, a_2) \in A_2 \cup A_3$ is confirmed under some specific conditions [49–51, 38, 52, 44, 53]. However, Hosono [49] showed by numerical simulations that nonlinear determinacy may occur. Furthermore, Huang and Han [37] proved the nonlinear determinacy under certain limitation of parameters.

Remark 6.1. In the case of $a_1 < 0$, system (35) is a predator–prey system, a special case of (1). It follows from Remark 2.2 that the minimal wave speed of traveling wave solutions connecting P_1 and P^* of (35) with $a_1 < 0$ is given by $c^* = \bar{c}$. Hence, the minimum wave speed c^* of system (35) with $a_1 < 0$ is **linearly determined** or of **linear determinacy**.

We now restate the results in [36–38] as follows.

Lemma 6.1 ([36, 37]). *For any given constants $a_1 > 1, a_2 > 1$, there is a unique real number $c(a_1, a_2)$ such that (35) has a nonnegative traveling wave solution connecting P_1 and P_2 if and only if $c = c(a_1, a_2)$. Moreover, the following hold:*

- (a) $c(a_1, a_2)$ is differentiable with respect to a_1 and a_2 with $\frac{\partial c(a_1, a_2)}{\partial a_1} < 0$ and $\frac{\partial c(a_1, a_2)}{\partial a_2} > 0$.
- (b) If $d_1/d_2 = r_1/r_2$, then the bistable wave speed $c(a_2, a_2) = 0$ for all $a_2 > 1$.

Lemma 6.2 ([38, 37]).

- (a) Let $d_1/d_2 = r_1/r_2$ and $a_2 > 1$ be fixed. Let $c^*(a_1) = c^*$ be the minimum wave speed of traveling wave solutions connecting P_1 and P_2 of (35) for $0 < a_1 < 1$. Then there is a positive constant ε such that for all $a_1 \in [1 - \varepsilon, 1)$, $c^*(a_1) > \bar{c} = 2\sqrt{d_2 r_2 (1 - a_1)}$.
- (b) The minimal wave speed of (35) is linearly determined if

$$0 < a_1 < 1, \quad d_1/d_2 \leq 2, \quad r_1 a_1 a_2 / r_2 \leq (2 - d_1/d_2)(1 - a_1) + r_1/r_2. \tag{37}$$

It has been shown that the asymptotical spreading speed for (35) is identical to the minimum wave speed of traveling wave solutions connecting P_1 and P^* (see (36)) provided that $(a_1, a_2) \in A_2 \cup A_3$ [15, 44]. Thus the essence of linear determinacy is that the spreading speed is linearly determined and this fact will be used in the following discussion. We have the following conclusions about how and why the spreading speed or the minimal wave speed is determined by parameters a_1 and a_2 .

1. From (37), it follows that condition $a_1 a_2 > 1$ (i.e., $-b_{12} b_{22} > b_{11} b_{21}$) is necessary for nonlinear determinacy. This indicates that nonlinear determinacy can only occur if the interspecific competition

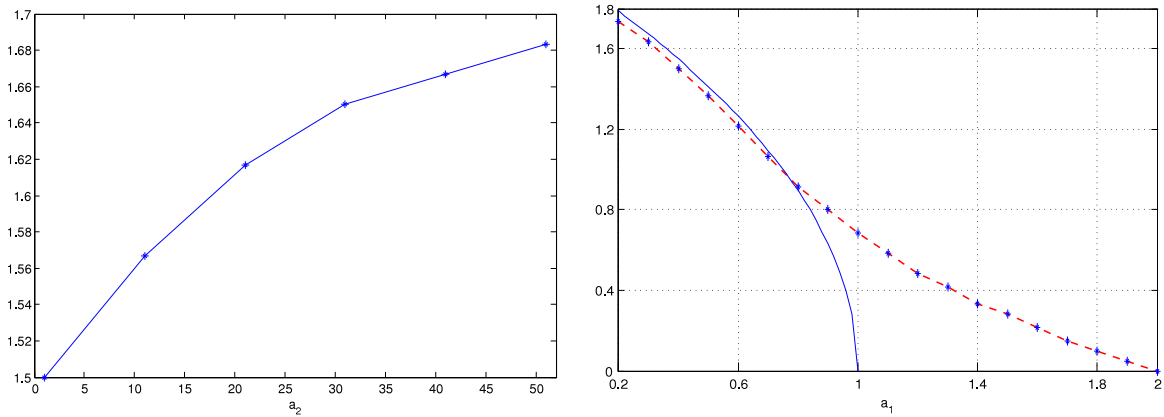


Fig. 4. The relationship between the simulated spreading speed and parameters a_1 and a_2 . “*” denotes the simulated spreading speed. Left: parameters: $a_1 = 0.4, d_1/d_2 = r_1/r_2 = 2$. Right: parameters: $a_2 = 2, d_1/d_2 = r_1/r_2 = 2$. The solid line in the right figure denotes $\bar{c} = 2\sqrt{d_2 r_2(1 - a_1)}$.

is stronger than the intraspecific competition, i.e., if the principle of competitive exclusion works [54]. Since $a_1 > 1$ and $a_2 > 1$ imply $-b_{22}/r_2 > b_{11}/r_1$ and $b_{12}/r_1 > b_{21}/r_2$, we call A_1 the strong-competition parameter area and A_2 the weak-competition parameter area. In addition A_4 (implying $a_1 a_2 < 0 < 1$) is the non-competition parameter area since population u has positive effect on v .

2. If $(a_1, a_2) \in A_1$ then Lemma 6.1 implies that there exists a unique wave speed $c(a_1, a_2)$, which decreases in $a_1 \in (1, +\infty)$ and increases in $a_2 \in (1, +\infty)$. See Fig. 4. Let $\chi := a_2 - a_1$ for $a_2 \geq a_1$. We then deduce that $c(a_1, a_2)$ is an increasing function in χ . As χ can serve as a measurement of the difference between these two populations’ competitive capacity, this indicates that larger difference of competitive capacity results in faster spreading speed (or invading speed). Thus, we may say that the spreading speed $c(a_1, a_2)$ is non-linearly determined if (a_1, a_2) belongs to strong-competition area A_1 .
3. According to Remark 6.1 and Lemma 6.2(b) the spreading speed is linearly determined if (a_1, a_2) belongs to weak-competition area A_2 or non-competition area A_4 . See the right figure of Fig. 4.
4. It follows from Lemma 6.2(a) that the spreading speed c^* is non-linearly determined if $(a_1, a_2) \in A_3$ but near the strong-competition parameter area A_1 , and c^* is linearly determined if $(a_1, a_2) \in A_3$ but near $A_2 \cup A_4$ (e.g. $a_1 a_2 < 1$) (see Figure Fig. 5). Therefore, A_3 is the transition parameter region from nonlinear to linear determinacy.

Based on above discussions we find that the basic reason for nonlinear determinacy lies in the strong interspecific competition. The minimal wave speed for predator–prey model (35) ($a_1 < 0, a_2 > 0$) is linearly determined since there is no mutual interspecific competition. We can also explain the linear determinacy for the predator–prey interaction in a more intuitive way. Assume that initially preys dominate the left part of the habitat and predators are introduced from the right part of the habitat. Predators then invade preys to the left and the density of preys decreases passively from u_1 to 0 because of the predator’s invasion (see Fig. 5). Therefore, we can say that the invasive speed of this system is controlled by predators. We set $u = u_1$ in the predator’s equation (i.e. the second equation of (35)) since the density of preys on the predator’s wave front can be approximated by its carrying capacity u_1 . The second equation of (35) with $u = u_1$ is a Fisher equation with the minimal wave speed $\bar{c} = 2\sqrt{d_2 r_2(1 - a_1)}$, which is equal to the minimal wave speed of model (35). This implies that the linear determinacy holds.

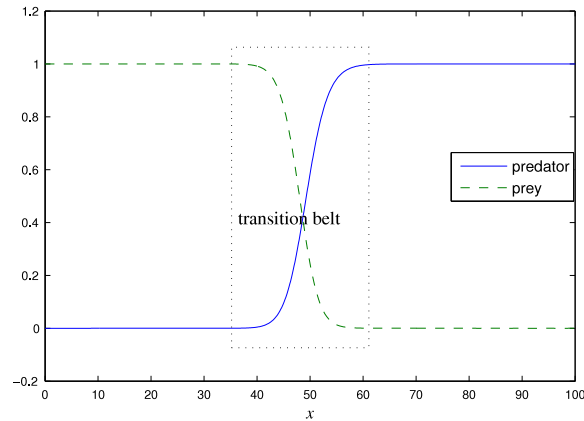


Fig. 5. The mechanics of linear determinacy of the minimal wave speed for predator–prey model (35) in the case of $a_1 < 0, a_2 > 1$ (i.e. $P^* = P_2$).

7. Discussion

In this paper, we obtain the sufficient and necessary conditions for the existence of the predator–invasion and the prey–spread traveling waves of the reaction–diffusion–advection predator–prey system (1) and assert linear determinacy of the minimal wave speed. We investigate the effect of parameters, especially the growth rate of the predator and the advection rate (or flow rate) of the predator on the minimal wave speed and hence on the spread of both species in an advective environment such as a river. It has been shown that the mechanics of linear determinacy is the same for the competitive Lotka–Volterra model with weak interspecific competition. We also show that the source of nonlinear determinacy lies in the strong interspecific competition.

For many spatial population models, it has been proved that the minimal wave speed of traveling waves coincides with the spreading speed, which is the asymptotic speed at which the population spreads in the direction the traveling waves spread to (see e.g., [43,6,44]). However, this has not been proved for the predator–prey models, with or without advection, due to the difficulty in theoretical analysis of nonmonotonic systems. In [3], the minimal wave speed of traveling waves was used to approximate the invasion speed of the species for predator–prey models in river environments. We adopt this idea in this paper and also use the minimal wave speed of traveling waves to approximate the invasion speed. This is biologically reasonable. The traveling wave solutions discussed in Theorem 2.1 connect the prey-only equilibrium to a predator–present (coexistence) equilibrium. Thus, they represent the invasion of the predator in an environment with the prey at its carrying capacity, and hence the wave speed in this work essentially represents the invasion speed of the predator. Theorem 2.1 shows that such invasion is successful in the upstream or downstream direction under certain conditions. If the predator is a specialist, then the invasion may result in coexistence of the prey and the predator; if the predator is a generalist, then the invasion may result in a predator-only situation where the predator coexists with its other food sources. The flow rate does negative effect on the upstream invasion but positive effect on the downstream invasion. Note that the result in Theorem 2.1 may be true when the two advection rates have different signs. A very special case where the predator is subjected to the flow effect and has an advection rate to the downstream direction but the prey is not subjected to the flow effect and has an advection rate to the upstream direction, may happen to some flies and their predators in rivers. In this case, when the advection rate for the prey is small enough, our result in Theorem 2.1 is still true. The traveling wave solutions discussed in Theorem 2.2 connect the predator-only equilibrium to a coexistence equilibrium. These waves particularly show the spread process of the prey in an environment

where the predator already exists. The results are straightforward in the sense that the preys can survive and spread when the conditions are good for them to grow and dispersal but not good for the predators.

As a potential future problem, it would be mathematically challenging but interesting to show whether the minimal wave speed of traveling waves coincides with the spreading speed for predator–prey models.

It is worthwhile to mention that the proofs of two main theorems are based on Schauder’s fixed-point theorem, LaSalle’s invariance principle and Laplace transform. In the applications of these methods, some improvements of theoretical methods are necessary such as the construction of upper–lower solutions, [Lemmas 3.7](#) and [3.9](#). Our methods are general enough to be applied to other models to establish the traveling waves. For instance, [Lemma 3.7](#) can also be applied to some models with time delay such as the following SI disease-transmission model with time delay:

$$\begin{cases} \frac{\partial S(x, t)}{\partial t} = d_1 \frac{\partial^2 S(x, t)}{\partial x^2} + B(1 - S(x, t)) - \beta S(x, t)I(x, t - \tau), \\ \frac{\partial I(x, t)}{\partial t} = d_2 \frac{\partial^2 I(x, t)}{\partial x^2} + \beta S(x, t)I(x, t - \tau) - \gamma I(x, t), \end{cases} \quad (38)$$

where all parameters are positive and τ is the latency of the infection in a vector. If $S(x, t) = S(\xi)$, $I(x, t) = I(\xi)$, $\xi = x + ct$ is a positive **bounded** traveling wave solution of [\(38\)](#), then it satisfies

$$\begin{cases} cS'(\xi) = d_1 S''(\xi) + B(1 - S(\xi)) - \beta S(\xi)I(\xi - c\tau), \\ cI'(\xi) = d_2 I''(\xi) + \beta S(\xi)I(\xi - c\tau) - \gamma I(\xi), \end{cases}$$

which is equivalent to

$$\begin{cases} d_1 S''(\xi) - cS'(\xi) + p_{21}(\xi)S(\xi) + B = 0, \\ d_2 I''(\xi) - cI'(\xi) - \gamma I(\xi) + p_{22}(\xi) = 0, \end{cases}$$

where

$$p_{21}(\xi) = -(B + \beta I(\xi - c\tau)), \quad p_{22}(\xi) = \beta S(\xi)I(\xi - c\tau) > 0.$$

Then applying [Lemma 3.7](#) implies

$$\left| \frac{S'(\xi)}{S(\xi)} \right| \leq \mathcal{M}, \quad \left| \frac{I'(\xi)}{I(\xi)} \right| \leq \mathcal{M}, \quad \forall \xi \in \mathbb{R}$$

for some positive constant \mathcal{M} . [Lemma 3.7](#) also can be applied to some models consisting of more than two equations [[55](#)].

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