INVASION DYNAMICS OF A DIFFUSIVE PIONEER-CLIMAX MODEL: MONOTONE AND NON-MONOTONE CASES

YUXIANG ZHANG*
School of Mathematics
Tianjin University, Tianjin 300350, China

SHIWANG MA
School of Mathematical Sciences and LPMC
Nankai University, Tianjin 300071, China

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Abstract. In this paper, we study the invasion dynamics of a diffusive pioneer-climax model in monotone and non-monotone cases. For parameter ranges in which the system admits monotone properties, we establish the existence of spreading speeds and their coincidence with the minimum wave speeds by monotone dynamical system theories. The linear determinacy of the minimum wave speeds is also studied by constructing suitable upper solutions. For parameter ranges in which the system is non-monotone, we further determine the existence of spreading speeds and traveling waves by the sandwich technique and upper-lower solution method. Our results generalize the existing results established under monotone assumptions to more general cases.

1. Introduction. In this work, we study the invasion dynamics of the following pioneer-climax model with diffusion

\[
\begin{aligned}
\frac{\partial u}{\partial t} &= D_1 \frac{\partial^2 u}{\partial x^2} + uf(c_{11}u + c_{12}v), \\
\frac{\partial v}{\partial t} &= D_2 \frac{\partial^2 v}{\partial x^2} + vg(c_{21}u + c_{22}v),
\end{aligned}
\]

(1)

which was proposed by Buchanan [5] to describe the growth and interaction between two species. Here \(u(t, x)\) and \(v(t, x)\) represent the population densities at time \(t \in [0, \infty)\) and location \(x \in (-\infty, \infty)\), respectively. The positive constants \(D_1\) and \(D_2\) are diffusion coefficients. It is assumed in (1) that the species’ per capita growth rates \(f\) and \(g\) are functions of the weighted total densities. The interaction matrix \(C := (c_{ij})_{2 \times 2}\) with \(c_{ij} > 0, i, j = 1, 2\) gives the weight distribution among species. An example of such type model is the well-studied Lotka-Volterra competition model, in which linearly decreasing fitness functions

\[
f(z) = r_1 - z, \quad g(w) = r_2 - w,
\]

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* Corresponding author: Yuxiang Zhang.
are assumed to describe the intra- and interspecific competition of two species for the same resources [12].

In an ecosystem, a population whose fitness is monotonically decreasing with density is called a “pioneer species”. An example of such species is the pine or poplar tree in a forest. According to [4, 5], the pioneer species thrive best at lower densities, and the fitness function is decreasing due to the effect of crowding and competing. Thus, in (1), the pioneer fitness function \( f \in C^1(\mathbb{R}) \) is assumed to satisfy

\[
f'(z) < 0 \text{ for } z \in \mathbb{R}, \quad f(z_0) = 0 \text{ for some } z_0 > 0.
\]

For example, it is suggested in [13] that some fish populations have exponential pioneer fitness in the form of

\[
f(z) = e^{r(1-z)} - a.
\]

However, not all species fall into this category. In contrast, a population whose fitness is monotonically increasing at lower densities, but it is decreasing at higher densities, is called a “climax species”. An example of such species is oak or maple tree in a forest. At lower densities, these species benefit from the presence of additional trees, but ultimately the individual reproduction decreases at higher densities due to the competition of resources. Hence, the fitness function \( g \) in (1) is assumed to be hump-shaped and there exist \( w_2 > w^* > w_1 > 0 \) such that \( g \in C^1(\mathbb{R}) \) satisfies

\[
g(w_1) = g(w_2) = 0, \quad g'(w) > 0 \text{ if } w < w^*, \quad g'(w) < 0 \text{ if } w > w^*.
\]

For example, the climax fitness in the form of

\[
g(w) = we^{r(1-w)} - a,
\]

was considered in [14, 15, 16]. We refer readers to Figure 1 for the general features of fitness functions \( f \) and \( g \).

![Figure 1. Typical fitness functions \( f \) and \( g \) in model (1).](image)

For the simplicity of notations, we consider the following equivalent non-dimensional system to (1):

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + uf(a_1 u + v), \\
\frac{\partial v}{\partial t} &= D \frac{\partial^2 v}{\partial x^2} + vg(u + a_2 v),
\end{align*}
\]

(2)
which is obtained by the following scaling

\[
\frac{1}{\sqrt{D_1}} x \to x, \quad c_{21} u \to u, \quad c_{12} v \to v, \quad \frac{c_{11}}{c_{21}} \to a_1, \quad \frac{c_{22}}{c_{12}} \to a_2, \quad \frac{D_2}{D_1} \to D.
\]

Throughout this work, we assume the parameters in (2) satisfy the following inequalities

\[
z_0 > \frac{w_2}{a_2}, \quad w_2 > \frac{z_0}{a_1} > w_1.
\] (3)

Under (3), we can verify that \(a_1 a_2 > 1\), which implies that the intraspecific interaction is stronger than the interspecific interaction. In this case, (2) admits a unique coexistence equilibrium \(E^* = (u^*, v^*)\), which is determined by the positive solution of

\[
\begin{align*}
    a_1 u + v &= z_0, \\
    u + a_2 v &= w_2.
\end{align*}
\] (4)

Solving (4), we get

\[
u^* = \frac{a_2 z_0 - w_2}{a_1 a_2 - 1}, \quad \frac{a_1 w_2 - z_0}{a_1 a_2 - 1}.
\]

By the properties of fitness functions \(f\) and \(g\), it is easy to calculate that system (2) always has the following axial equilibria

\[
E_0 = (0, 0), \quad E_1 = (0, \frac{w_1}{a_2}), \quad E_2 = (0, \frac{w_2}{a_2}), \quad E_3 = \left(\frac{z_0}{a_1}, 0\right).
\]

It is obvious that \(v^* < \frac{w_2}{a_2}\), and \(u^* < \frac{z_0}{a_1}\) (see Figure 2). For the location of nullclines and the structure of the constant equilibria of (2) with (3), we refer readers to Figure 2. Moreover, we can verify that the boundary equilibria \(E_2\) and \(E_3\) are unstable and the positive equilibrium \(E^*\) is globally attractive in the interior of \(\mathbb{R}_+^2\). For the rich dynamics and a complete categorization of the stability of the equilibria of the spatially homogeneous system of (2), we refer readers to [4, 17, 6, 14, 15, 16] and references therein.

Note that system (2) may be neither monotone nor mixed monotone for some parameter values, which makes the model analysis tricky due to the lack of comparison principle. Actually, the dynamics of (2) is quite rich and has not been completely understood. With different parameter values, the authors in [3] and [20] studied the existence of monostable/bistable traveling waves of (2) connecting boundary equilibria \(E_2\) and \(E_3\). Under assumptions (3), \(v^* \geq \frac{w_2}{a_2}\), and the convexity of function \(g\) on \([w_2, \infty)\), the existence of spreading speed and its linear determinacy are recently studied in [21]. Moreover, in the case of \(w^* \leq u^*\), the existence of spreading speed and traveling waves connecting \(E_3\) to \(E^*\) is also investigated in [21] and [23]. The assumptions in [21] and [23] are to make sure the fitness function \(g\) is monotonically decreasing for interested densities, and thus system (2) reduces to a competitive system. Then the monotone iteration method for traveling waves (see e.g. [22, 24]), and the theory for the linear determinacy of spreading speeds [7, 19] can be applied. However, in the case of \(v^* < \frac{w_2}{a_2}\) or \(w^* > u^*\), the theory for the monotone dynamical systems cannot be applied, since system (2) does not admit monotone properties for some interested densities.

The purpose of this work is further to study spreading speeds, the minimum wave speeds and their linear determinacy for system (2) with the following assumptions:

(H1) \(v^* > \frac{w_1}{a_2}\),

(H2) \(w^* < \frac{z_0}{a_1}\).
Figure 2. Nullclines and the structure of equilibria of (2) under (3).

In these cases, the fitness function $g$ is no longer monotonically decreasing for some interested population densities. We need to find new tools to determine the existence of spreading speeds and traveling waves. We first reconsider (2) with the assumption that $v^* \geq \frac{w_2}{a_2}$ such that (H1) is automatically satisfied. Using the general results established in [8], we know that (2) always admits a spreading speed and it is coincident with the minimum wave speed of monotone traveling waves connecting $E_2$ to $E^*$. Moreover, we figure out under which conditions the minimum wave speed is linearly determined. Our results extend [21, Theorem 3.1 and 4.2] with no additional convexity requirement on function $g$. Then we further consider the case that $w_1/a_2 < v^* < \frac{w_2}{a_2}$.

In this case, we show the existence of spreading speeds and traveling waves connecting $E_2$ to $E^*$ by constructing suitable auxiliary systems (see, for example, [10] and [18]). Furthermore, under condition (H2), we prove the existence of spreading speeds and traveling waves of (2) connecting $E_3$ to $E^*$, which generalizes [21, Theorem 3.2] and [23, Theorem 1] to more general cases.

The rest of this paper is organized as follows. In Section 2, we focus on the invasion dynamics of the pioneer species under (H1). We establish the existence of spreading speed and its coincidence with the minimum wave speed for traveling waves connecting $E_2$ to $E^*$. The linear determinacy of the minimum wave speed is determined by constructing suitable upper solutions. In Section 3, under (H2), we establish the existence of spreading speed and traveling waves connecting $E_3$ to $E^*$. 


At the end of this work, we present an example to show applications of our results, and a short conclusion finishes this paper.

2. Invasion of the pioneer species. In this section, we focus on the propagation dynamics of (2) under condition (H1). Let $\mathcal{C} := BC(\mathbb{R}, \mathbb{R}^2)$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$, and $\mathcal{C}_+ = \{(\psi_1, \psi_2) \in \mathcal{C} : \psi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$. It is easy to see that $\mathcal{C}_+$ is a nonempty closed cone of $\mathcal{C}$ and induces a partial order of $\mathcal{C}$. For any $\psi^1 = (\psi^1_1, \psi^1_2), \psi^2 = (\psi^2_1, \psi^2_2) \in \mathcal{C}$, we denote $\psi^1 \leq \psi^2$ if $\psi^2 - \psi^1 \in \mathcal{C}_+$ and $\psi^1 < \psi^2$ if $\psi^2 - \psi^1 \in \mathcal{C}_+ \setminus \{0\}$. For any vectors $a, b$ in $\mathbb{R}^2$, we define $a \leq (\leq) b$ similarly, and $a \ll b$ if $b - a \in int(\mathbb{R}_+^2)$. For any $b = (b_1, b_2) \in int(\mathbb{R}_+^2)$, we define $\mathcal{C}_b := \{(\psi_1, \psi_2) \in \mathcal{C} : 0 \leq \psi_1 \leq b_1, 0 \leq \psi_2 \leq b_2\}$, and $[0, b] := \{(x, y) \in \mathbb{R}_+^2 : 0 \leq x \leq b_1, 0 \leq y \leq b_2\}$.

For the convenience of mathematical analysis, we make the change of variables $u_1 = u$ and $v_1 = \frac{w_2}{a_2} - v$, then (2) converts to the following system
\[
\begin{align*}
\frac{\partial u_1}{\partial t} &= \frac{\partial^2 u_1}{\partial x^2} + u_1 f\left(\frac{w_2}{a_2} + a_1 u_1 - v_1\right) := \frac{\partial^2 u_1}{\partial x^2} + F(u_1, v_1), \\
\frac{\partial v_1}{\partial t} &= D \frac{\partial^2 v_1}{\partial x^2} - \left(\frac{w_2}{a_2} - v_1\right) g(w_2 + u_1 - a_2 v_1) := D \frac{\partial^2 v_1}{\partial x^2} + G(u_1, v_1),
\end{align*}
\]
where
\[
\begin{align*}
F(u_1, v_1) &= u_1 f\left(\frac{w_2}{a_2} + a_1 u_1 - v_1\right), \\
G(u_1, v_1) &= -\left(\frac{w_2}{a_2} - v_1\right) g(w_2 + u_1 - a_2 v_1).
\end{align*}
\]
Then equilibria $E_2$ and $E^*$ of (2) are transformed to
\[
E_2 = (0, 0), \quad E^* = (u^*, \frac{w_2}{a_2} - v^*),
\]
for (5), respectively. Note that $E_2 \ll E^*$ and there exists no other equilibrium between them. Then it suffices for us to study the existence of spreading speeds and traveling waves of (5) connecting $E_2$ to $E^*$. For the convenience of expression, we denote
\[
\mathcal{C}_{E^*} := \{(\psi_1, \psi_2) \in \mathcal{C} : 0 \leq \psi_1 \leq u^*, 0 \leq \psi_2 \leq \frac{w_2}{a_2} - v^*\},
\]
and
\[
[E_2, E^*] := \{(x, y) \in \mathbb{R}_+^2 : 0 \leq x \leq u^*, 0 \leq y \leq \frac{w_2}{a_2} - v^*\}.
\]

2.1. Spreading speed and invasion waves when $v^* \geq \frac{w^*}{a_2}$. We first consider the case that $v^* \geq \frac{w^*}{a_2}$, for which (H1) is automatically satisfied. For any $(x, y) \in [E_2, E^*]$, we observe that
\[
w_2 + x - a_2 y \geq w_2 - a_2 \left(\frac{w_2}{a_2} - v^*\right) = a_2 v^* \geq w^*.
\]
Then it follows that
\[
\begin{align*}
\frac{\partial F(x, y)}{\partial y} &= -xf\left(\frac{w_2}{a_2} + a_1 x - y\right) \geq 0, \\
\frac{\partial G(x, y)}{\partial x} &= -\frac{w_2}{a_2} - y)g'(w_2 + x - a_2 y) \geq 0,
\end{align*}
\]
which implies that (5) is cooperative in $\mathcal{C}_{E^*}$. Let $\{\Phi_t\}_{t \geq 0}$ be the solution semiflow associated with (5), then $\{\Phi_t\}_{t \geq 0}$ is order-preserving in $\mathcal{C}_{E^*}$ with $\Phi_t(E_2) = E_2$ and
Φ(t,E*) = E* for all t ≥ 0. Moreover, it is easy to observe that Φt is spatially translation and reflection invariant, continuous with respect to the compact open topology, and precompact in C(Ω). Thus, the conditions (A1)-(A5) in [8] are satisfied for each Φt with t > 0. Then by [8, Theorem 2.17], we know that there exists a real number c* > 0 such that c* is the spreading speed for solutions of (5) with initial functions having compact supports, which is summarized in the following result.

**Proposition 1.** Assume v* ≥ \( \frac{w_2}{a_2} \). Let \((u_1(t,x), v_1(t,x))\) be the unique solution of (5) with the initial data \((u_0(x), v_0(x)) \in C(Ω)\), then the following statements are valid:

(i) For any c > c*, if \(u_0(x)\) and \(v_0(x)\) are zero for x outside a bounded interval, then

\[
\lim_{t \to \infty, |x| > ct} u_1(t,x) = \lim_{t \to \infty, |x| > ct} v_1(t,x) = 0;
\]

(ii) For any 0 < c < c* and \(σ \in [0, E^*] \) with \(σ \gg 0\), if there is a positive number \(r_σ\) such that \((u_0(x), v_0(x)) \gg σ\) for x on an interval of length 2\(r_σ\), then

\[
\lim_{t \to \infty, |x| \leq ct} u_1(t,x) = u^*, \quad \lim_{t \to \infty, |x| \leq ct} v_1(t,x) = \frac{w_2}{a_2} - v^*.
\]

Moreover, by [8, Theorem 4.3 and 4.4], we further know that c* is also the minimum wave speed for monotone traveling waves of (5) connecting \(E_2\) to \(E^*\). A traveling wave solution of (5) connecting \(E_2\) to \(E^*\) is a bounded solution of (5) with the form \(u_1(t,x) = U(z), v_1(t,x) = V(z)\) with \(z = x + ct\) and the following asymptotic boundary conditions

\[
\begin{align*}
\lim_{z \to -\infty} U(z) = 0, & \quad \lim_{z \to \infty} U(z) = u^*, \\
\lim_{z \to -\infty} V(z) = 0, & \quad \lim_{z \to \infty} V(z) = \frac{w_2}{a_2} - v^*.
\end{align*}
\]

The constant \(c > 0\) is called the wave speed, and \(U, V\) are called the wave profiles. Then the following result is a direct consequence of [8, Theorem 4.3 and 4.4].

**Proposition 2.** Assume v* ≥ \( \frac{w_2}{a_2} \). Let c* be the spreading speed of (5) given in Proposition 1. Then the following statements are valid.

(i) For any \(c \geq c^*\), (5) has a traveling wave solution \((U(x + ct), V(x + ct))\) connecting \(E_2\) to \(E^*\) such that \(U(z)\) and \(V(z)\) are continuous and nondecreasing in \(z \in \mathbb{R}\).

(ii) For any \(0 < c < c^*\), (5) has no traveling wave solution connecting \(E_2\) to \(E^*\). That is, c* is the minimum wave speed of (5).

Note that, from the above two results, we do not have explicit formula for the calculation of the minimum wave speed c*, which is very important to estimate the spread of populations. We hope we could find suitable conditions under which the minimum wave speed c* is linearly determined. It is usually not obvious if the system cannot be linearly controlled as given in [8]. Linearizing (5) at \(E_2 = (0,0)\), we get the following linear system

\[
\begin{align*}
\frac{∂u_1}{∂t} = & \frac{∂^2 u_1}{∂x^2} + f\left(\frac{w_2}{a_2}\right)u_1,
\frac{∂v_1}{∂t} = & D\frac{∂^2 v_1}{∂x^2} - \frac{w_2}{a_2}g'(w_2)u_1 + w_2g'(w_2)v_1.
\end{align*}
\]

\(\text{(8)}\)
Substituting \((u_1(t,x), v_1(t,x)) = e^{\mu z}(\alpha_1, \alpha_2), \mu > 0\), to the right-hand side of (8), and letting \(x = 0\), we get the following matrix:

\[
C_\mu := \begin{pmatrix}
\mu^2 + f\left(\frac{w_2}{a_2}\right) & 0 \\
-\frac{w_2}{a_2}g'(w_2) & D\mu^2 + w_2g'(w_2)
\end{pmatrix},
\]

(9)

which is in Frobenius form and reducible. Let

\[
\lambda_1(\mu) := \mu^2 + f\left(\frac{w_2}{a_2}\right), \quad \lambda_2(\mu) := D\mu^2 + w_2g'(w_2),
\]

then following the idea as given in [19] and [11, Remark 2.3], we could define the linear speed \(c_0\) by

\[
c_0 := \inf_{\mu > 0} \frac{\lambda_1(\mu)}{\mu} = 2\sqrt{f\left(\frac{w_2}{a_2}\right)},
\]

provided \(\lambda_1(\bar{\mu}) > \lambda_2(\bar{\mu})\) with \(\bar{\mu} = \sqrt{f\left(\frac{w_2}{a_2}\right)}\), which is equivalent to the following inequality holds

\[
(2 - D)f\left(\frac{w_2}{a_2}\right) - w_2g'(w_2) > 0.
\]

(10)

Then it follows from [8] that \(c^* \geq c_0\). We say the minimum wave speed \(c^*\) is linearly determinate if \(c^* = c_0\), and it is nonlinearly determinate if \(c^* > c_0\).

Substituting \(u_1(t,x) = U(z), v_1(t,x) = V(z), z = x + ct\), to (5), we know that \(U(z)\) and \(V(z)\) satisfy the following wave profile equations:

\[
\begin{align*}
U''(z) - cU' + F(U, V) &= 0, \\
D V''(z) - cV' + G(U, V) &= 0.
\end{align*}
\]

(11)

Then by the ideas recently developed in [1] and [11], we can determine the linear determinacy of the minimum wave speed by constructing suitable upper solutions for (11) with \(c = c_0\). We first recall the definition of upper and lower solutions.

**Definition 2.1.** A vector function \(\phi(z) := (\bar{U}(z), \bar{V}(z))\) is called an upper solution of (11) if it is twice differentiable except at finitely many points on \(\mathbb{R}\), and satisfies the following inequalities

\[
\begin{align*}
\bar{U}'' - c\bar{U}' + F(\bar{U}, \bar{V}) &\leq 0, \\
D\bar{V}'' - c\bar{V}' + G(\bar{U}, \bar{V}) &\leq 0.
\end{align*}
\]

(12)

A lower solution \(\phi(z) := (\bar{U}(z), \bar{V}(z))\) of (11) can be similarly defined by reversing the inequalities in (12).

Following [11, Theorem 2.10] and the proof ideas as used in [11, Theorem 2.5], we have the following result for the linear determinacy of the minimum wave speed.

**Proposition 3.** Assume \(c^* \geq \frac{w_2}{a_2}\). For \(c = c_0\), if (11) admits a continuous and positive upper solution \((\bar{U}(z), \bar{V}(z))\) satisfying

\[
\lim_{z \to -\infty} (\bar{U}(z), \bar{V}(z)) = \mathcal{E}_2, \quad \liminf_{z \to -\infty} (\bar{U}(z), \bar{V}(z)) \gg \mathcal{E}_2,
\]

then the minimum wave speed \(c^*\) is linearly determinate, that is, \(c^* = c_0 = 2\sqrt{f\left(\frac{w_2}{a_2}\right)}\).

In order to find suitable upper solutions of (11) with \(c = c_0\), we substitute \((U, V)(z) = e^{\mu z}(\xi_1, \xi_2), \mu > 0\), to the linearization of (11) at \(\mathcal{E}_2\). We get

\[
M(\mu) \begin{pmatrix}
\xi_1 \\
\xi_2
\end{pmatrix} = 0,
\]

(13)
where the matrix $M(\mu)$ is given by
\[
M(\mu) = \begin{pmatrix}
\mu^2 - c\mu + f'\left(\frac{w_2}{a_2}\right) & 0 \\
-\frac{w_2}{a_2}g'(w_2) & D\mu^2 - c\mu + w_2g'(w_2)
\end{pmatrix}.
\] (14)

Let
\[
\Gamma_1(\mu, c) := \mu^2 - c\mu + f\left(\frac{w_2}{a_2}\right),
\]
\[
\Gamma_2(\mu, c) := D\mu^2 - c\mu + w_2g'(w_2).
\]

Then (13) admits nontrivial solutions if and only if
\[
\Gamma_1(\mu, c)\Gamma_2(\mu, c) = 0.
\]

For any $c > c_0$, we know that $\Gamma_1(\mu, c) = 0$ admits two positive roots $\mu_1(c) < \mu_2(c)$, which are given by
\[
\mu_1 := \mu_1(c) = \frac{c - \sqrt{c^2 - 4f(w_2/a_2)}}{2}, \quad \mu_2 := \mu_2(c) = \frac{c + \sqrt{c^2 - 4f(w_2/a_2)}}{2}.
\] (15)

When $c = c_0$, we have $\mu_1 = \mu_2 = \bar{\mu}$. Moreover, we can verify that $\mu_1(c)$ is decreasing and $\mu_2(c)$ is increasing in $c \in [c_0, \infty)$.

Now for any $z \in \mathbb{R}$, we define a continuous function
\[
\tilde{U}(z) = \begin{cases}
eu{ar{\mu}z}, & z < \bar{z}, \\
\nu^*, & z \geq \bar{z},
\end{cases}
\] (16)
where $\bar{z} := \ln\frac{\nu^*}{\bar{\mu}}$. Then we have the following result for the linear determinacy of the minimum wave speed.

**Theorem 2.2.** Assume $\nu^* \geq \frac{w_2}{a_2}$. Let $\tilde{U}(z)$ be given in (16). If there exists a continuous and positive function $\tilde{V}(z)$ satisfying $\tilde{V}(\infty) = 0$, $\lim_{z \to \infty} \tilde{V}(z) > 0$, $\tilde{V}(z) \leq a_1\tilde{U}(z)$ for $z < \bar{z}$, and $\tilde{V}(z) \leq \frac{1}{a_2}\tilde{U}(z)$ for $z \geq \bar{z}$ such that $(\tilde{U}, \tilde{V})(z)$ satisfies the second inequality of (12) with $c = c_0$, then $c^* = c_0$. In particular, if $D \leq 2$, the minimum wave speed $c^*$ is linearly determinate.

**Proof.** By Proposition 3, it is enough to check $(\tilde{U}, \tilde{V})(z)$ satisfies the first inequality of (12) with $c = c_0$ for any $z \neq \bar{z}$. If $z < \bar{z}$, we have $\tilde{U}(z) = e^{\bar{\mu}z}$, $\tilde{V}(z) \leq a_1\tilde{U}(z)$, and
\[
\tilde{U}'' - c_0\tilde{U}' + F(\tilde{U}, \tilde{V})
= e^{\bar{\mu}z}[\bar{\mu}^2 - c_0\bar{\mu} + f\left(\frac{w_2}{a_2} + a_1\tilde{U}(z) - \tilde{V}(z)\right)]
\leq e^{\bar{\mu}z}[\bar{\mu}^2 - c_0\bar{\mu} + f\left(\frac{w_2}{a_2}\right)] = 0.
\]
In the case of $z > \bar{z}$, we have $\tilde{U}(z) = \nu^*$, $\tilde{V}(z) \leq \frac{1}{a_2}\tilde{U}(z)$, and
\[
\tilde{U}'' - c_0\tilde{U}' + F(\tilde{U}, \tilde{V})
= \nu^* f\left(\frac{w_2}{a_2} + a_1\nu^* - \tilde{V}(z)\right)
\leq \nu^* f\left(\frac{w_2}{a_2} + a_1\nu^* - \frac{\nu^*}{a_2}\right)
\leq \nu^* f(z_0) = 0,
\]
where $a_1\nu^* + \nu^* = z_0$, $\nu^* + a_2\nu^* = w_2$ are used in the last inequality.

In particular, if $D \leq 2$, we define $\tilde{V}(z) = \frac{1}{a_2}\tilde{U}(z)$. It is easy to check that $\tilde{V}(z)$ satisfies $\tilde{V}(z) \leq a_1\tilde{U}(z)$ for $z \geq \bar{z}$, and $\tilde{V}(z) \leq a_1\tilde{U}(z)$ for $z < \bar{z}$ due to $a_1a_2 > 1$. 
Proposition 1 and Theorem 2.2 show that the spreading speed, and it is also the minimum wave speed \[21, \text{Theorem 4.2}\]. Our

spreading speed when the end of this work.

are decreasing and satisfy

\[
\frac{1}{a_2} e^{\bar{\mu} z} [D \bar{\mu}^2 - c_0 \bar{\mu}] - \frac{1}{a_2} (w_2 - e^{\bar{\mu} z}) g(w_2 + e^{\bar{\mu} z} - e^{\bar{\mu} z})
\]

\[
= \frac{1}{a_2} e^{\bar{\mu} z} [D \bar{\mu}^2 - c_0 \bar{\mu}]
\]

\[
= \frac{\bar{\mu}}{a_2} e^{\bar{\mu} z} (D - 2) f \left( \frac{w_2}{a_2} \right) \leq 0.
\]

If \( z > \bar{z} \), then \( \bar{U}(z) = u^* \), \( \bar{V}(z) = \frac{u^*}{a_2} \). By a direct computation, we know that

\[
D \bar{V}'' - c_0 \bar{V}' + G(\bar{U}, \bar{V}) = - \frac{1}{a_2} (w_2 - u^*) g(w_2 + u^* - u^*) = 0.
\]

Then Proposition 3 implies the result.

**Remark 1.** When \( D \leq 2 \) and \( v^* \geq \frac{w_2}{a_2} \), with the assumption that \( g \) is convex on \([w_2, \infty)\), it was shown in \[21, \text{Theorem 3.1}\] that (5) admits a linearly determined spreading speed, and it is also the minimum wave speed \[21, \text{Theorem 4.2}\]. Our

Proposition 1 and Theorem 2.2 show that the spreading speed \( c^* \) always exists for any \( D > 0 \), and it is linearly determined if \( D \leq 2 \). We extend \[21, \text{Theorem 3.1 and 4.2}\] with no requirement on the convexity of function \( g \). Thus, our results are applicable if \( g \) is a quadratic function, which as an example will be considered at the end of this work.

2.2. Spreading speed when \( \frac{w_1}{a_2} < v^* < \frac{w^*}{a_2} \). Now we are interested in the existence of spreading speed when \( v^* < \frac{w^*}{a_2} \) such that condition (H1) is satisfied, that is, we assume the following condition holds:

\( \text{(H1') } \frac{w_1}{a_2} < v^* < \frac{w^*}{a_2} \).

With condition (H1'), (5) does not satisfy the cooperative condition (6) for all \((x, y) \in [E_2, \mathcal{E}^*]\). Thus, we cannot use the theories for monotone dynamical systems as used in the last subsection to determine the existence of spreading speeds. Up to our best knowledge, this case has not been studied in literatures. In the following, we will appeal to the sandwich technique to determine the existence of spreading speeds.

From (H1'), we know that \( w_1 < a_2 v^* < w^* \). Since the function \( g \) is hump-shaped and get its maximum at \( w^* \), there exists a unique \( \bar{w} \in (w^*, w_2) \) such that \( g(a_2 v^*) = g(\bar{w}) \). Now we define two auxiliary functions

\[
\mathcal{g}(w) = \begin{cases} 
    g(w^*), & w \leq w^*, \\
    g(w), & w > w^*, 
\end{cases} \quad \mathcal{g}(w) = \begin{cases} 
    g(a_2 v^*), & w \leq \bar{w}, \\
    g(w), & w > \bar{w}. 
\end{cases}
\]

We refer readers to Figure 3 for the construction of \( \mathcal{g} \) and \( \bar{g} \). Then both \( \mathcal{g} \) and \( \bar{g} \) are decreasing and satisfy

\[
\mathcal{g}(w) \geq g(w) \geq \mathcal{g}(w), \text{ for } w \geq a_2 v^*,
\]

\[
\bar{g}(w) = \mathcal{g}(w) = g(w), \text{ for } w \geq \bar{w}.
\]
Then we define an upper system of (5) with function $g$ by
\[
\begin{cases}
\frac{\partial u_1}{\partial t} = \frac{\partial^2 u_1}{\partial x^2} + u_1 f\left(\frac{w_2}{a_2} + a_1 u_1 - v_1\right), \\
\frac{\partial v_1}{\partial t} = D \frac{\partial^2 v_1}{\partial x^2} - \left(\frac{w_2}{a_2} - v_1\right) g\left(w_2 + u_1 - a_2 v_1\right),
\end{cases}
\] (18)
and a lower system of (5) with function $\overline{g}$ by
\[
\begin{cases}
\frac{\partial u_1}{\partial t} = \frac{\partial^2 u_1}{\partial x^2} + u_1 f\left(\frac{w_2}{a_2} + a_1 u_1 - v_1\right), \\
\frac{\partial v_1}{\partial t} = D \frac{\partial^2 v_1}{\partial x^2} - \left(\frac{w_2}{a_2} - v_1\right) \overline{g}\left(w_2 + u_1 - a_2 v_1\right),
\end{cases}
\] (19)
By a simple calculation, we know that $E_2$, $E^*$ are still equilibria of (18) and (19), and also there is no other equilibrium between them. Moreover, due to the monotonicity of $g$ and $\overline{g}$, we know that both (18) and (19) are cooperative in $C_{E^*}$. Then we have the following result.

**Lemma 2.3.** Assume $D \leq 2$ and (H1'). Then (18) and (19) admit the same spreading speed $c^*$, which is linearly determinate and given by
\[c^* = c_0 = 2 \sqrt{f\left(\frac{w_2}{a_2}\right)}.
\]

**Proof.** Since (18) and (19) are cooperative in $C_{E^*}$, the similar results as given in Proposition 1 and Theorem 2.2 can be verified for (18) and (19), respectively. Note
that \( w_2 > \bar{w} \), and
\[
g(w) = \bar{g}(w) = g(w) \text{ for } w \geq \bar{w},
\]
which implies that (18) and (19) have the same linearization (8) at \( \mathcal{E}_2 \). Then Theorem 2.2 implies that (18) and (19) admit the same spreading speed \( c^* \), and it is linearly determinate if \( D \leq 2 \).

**Theorem 2.4.** Assume \( D \leq 2 \) and \((H1')\). Let \( c^* \) be given in Lemma 2.3, then \( c^* \) is the spreading speed of non-monotone system (5), which is also linearly determinate.

**Proof.** We use the dynamics of auxiliary systems (18) and (19) to prove the result. Let \((\bar{u}_1(t,x), \bar{v}_1(t,x))\), \((\bar{u}_2(t,x), \bar{v}_2(t,x))\), respectively, be the unique solution of system (18), (19) with the same initial data \((u_0(x), v_0(x))\) \(\in \mathcal{C}_\mathcal{E}_2\). Due to the inequalities given in (17), we know that \((\bar{u}_1(t,x), \bar{v}_1(t,x))\) is an upper solution, and \((\bar{u}_2(t,x), \bar{v}_2(t,x))\) is a lower solution of (5). By the comparison principle, we know that
\[
(\bar{u}_1(t,x), \bar{v}_1(t,x)) \leq (u_1(t,x), v_1(t,x)) \leq (\bar{u}_2(t,x), \bar{v}_2(t,x)) \text{ for } t \geq 0, x \in \mathbb{R}.
\]
Then it follows from Lemma 2.3 and statements (i)-(ii) in Proposition 1 that \( c^* \) is also the spreading speed of (5). The linear determinacy of \( c^* \) is easily observed due to the fact that systems (5), (18), (19) admit the same linearization at \( \mathcal{E}_2 \).

### 2.3. Invasion waves when \( \frac{a_1}{a_2} < v^* < \frac{a_2}{a_1} \)

Now we are interested in the existence of traveling waves of (5) connecting \( \mathcal{E}_2 \) to \( \mathcal{E}^* \) under condition \((H1')\). Since (5) is non-monotone in \( \mathcal{C}_\mathcal{E}_2 \), we will appeal to the standard upper-lower solution method to prove the existence of traveling waves.

Let \( c^* \) be given in Lemma 2.3 and \( \mu_1 \) be defined in (15) for \( c \geq c^* \). Then we choose positive number \( \varepsilon < \mu_1 \) small enough such that
\[
\Gamma_1(\mu_1 + \varepsilon, c) = (\mu_1 + \varepsilon)^2 - c(\mu_1 + \varepsilon) + f\left(\frac{w_2}{a_2}\right) < 0.
\]
For any \( z \in \mathbb{R} \), we define the following continuous and bounded functions
\[
P(z) = \min\{e^{\mu_1 z}, u^*\},
\]
\[
\bar{Q}(z) = \min\left\{ \frac{1}{a_2} e^{\mu_1 z}, \frac{w_2}{a_2} - v^* \right\},
\]
\[
P(z) = \max\{0, \frac{1}{a_2} (1 - M e^{\varepsilon z}) e^{\mu_1 z}\},
\]
\[
Q(z) = 0,
\]
where constant \( M > 1 \) is sufficiently large and will be determined later. In order to construct suitable lower solutions of (5), we first prove the existence of traveling waves for the lower system (19) for any \( c \geq c^* \).

For the convenience of expression, we denote functions \( \bar{G} \) in (19) as
\[
\bar{G}(u_1, v_1) := -\left( \frac{w_2}{a_2} - v_1 \right) \bar{g}(w_2 + u_1 - a_2 v_1).
\]
We similarly define \( \bar{G}(u_1, v_1) \) in (18) by replacing \( \bar{g} \) by \( g \). Substituting \( u_1(t,x) = P(z), \ ) v_1(t,x) = Q(z), z = x + ct, \) to (19), we know that \( P(z) \) and \( Q(z) \) satisfy the following equations
\[
\begin{cases}
P''(z) - cP'(z) + f(P,Q) = 0, \\
DQ''(z) - cQ'(z) + \bar{G}(P,Q) = 0.
\end{cases}
\tag{20}
\]
Then we have the following result, which is a specialization of [9, Theorem 2.2] for system (20).

**Proposition 4.** If system (20) has an upper solution \( \bar{\phi} \), and a lower solution \( \underline{\phi} \) in \( \mathcal{C}_E \), satisfying the following conditions:

1. \( \bar{\phi}, \underline{\phi} \in \mathcal{C}_E \);
2. \( \sup_{z \leq s} \bar{\phi}(z) \leq \underline{\phi}(s) \), for any \( s \in \mathbb{R} \);
3. for any \( z \in \mathbb{R} \), \( \bar{\phi}'(z+) \leq \underline{\phi}'(z-) \);
4. \( \underline{\phi}'(z+) \geq \bar{\phi}'(z-) \), for any \( z \in \mathbb{R} \),

then (20) admits a positive monotone solution \( \phi \in \mathcal{C}_E \), satisfying \( \phi(-\infty) = \mathcal{E}_2 \), \( \phi(\infty) = \mathcal{E}_* \), and \( \underline{\phi} \leq \phi \leq \bar{\phi} \).

**Lemma 2.5.** Let \( D \leq 2 \) and \( c > c^* \), then \((\bar{P}(z), \bar{Q}(z))\) satisfies the following inequalities

\[
\left\{ \begin{array}{l}
\bar{P}'' - c\bar{P}' + F(\bar{P}, \bar{Q}) \leq 0, \\
D\bar{Q}'' - c\bar{Q}' + G(\bar{P}, \bar{Q}) \leq 0,
\end{array} \right.
\]

for any \( z \neq z_1 := \frac{\ln u^*}{\mu_1} \).

**Proof.** Note that \( u^* + a_2 v^* = w_2 \). A simple calculation induces that if \( z < z_1 \),
\( \bar{P}(z) = e^{\mu_1 z} \), \( \bar{Q}(z) = \frac{1}{a_2} e^{\mu_1 z} \). Then we have

\[
\bar{P}'' - c\bar{P}' + F(\bar{P}, \bar{Q}) = e^{\mu_1 z}[\mu_1^2 - c\mu_1 + f(\frac{w_2}{a_2} + a_1 e^{\mu_1 z} - \frac{1}{a_2} e^{\mu_1 z})] \\
\leq e^{\mu_1 z}[\mu_1^2 - c\mu_1 + f(\frac{w_2}{a_2})] = 0.
\]

\[
D\bar{Q}'' - c\bar{Q}' + G(\bar{P}, \bar{Q})
= \frac{1}{a_2} e^{\mu_1 z}[D\mu_2^2 - c\mu_1] - \frac{1}{a_2} (w_2 - e^{\mu_1 z})g(w_2 + e^{\mu_1 z} - e^{\mu_1 z}) \\
= \frac{1}{a_2} e^{\mu_1 z}[D\mu_2^2 - c\mu_1] \\
= \frac{\mu_1}{a_2} e^{\mu_1 z}[D\sqrt{c^2 - 4f(w_2/a_2)} - c] \leq 0.
\]

In the case of \( z > z_1 \), then \( \bar{P}(z) = u^* \), \( \bar{Q}(z) = \frac{w_2}{a_2} - u^* \). By a direct computation, we know that

\[
\bar{P}'' - c\bar{P}' + F(\bar{P}, \bar{Q}) = u^* f(a_1 u^* + v^*) = u^* f(z_0) = 0.
\]

\[
D\bar{Q}'' - c\bar{Q}' + G(\bar{P}, \bar{Q}) = v^* g(u^* + a_2 v^*) = v^* g(w_2) = 0.
\]

Therefore, \( \bar{\phi}(z) := (\bar{P}(z), \bar{Q}(z)) \) is an upper solution of (20). \( \Box \)

**Lemma 2.6.** Let \( D \leq 2 \) and \( c > c^* \), then \((\bar{P}(z), \bar{Q}(z))\) satisfies the following inequalities

\[
\left\{ \begin{array}{l}
\bar{P}'' - c\bar{P}' + F(\bar{P}, \bar{Q}) \geq 0, \\
D\bar{Q}'' - c\bar{Q}' + G(\bar{P}, \bar{Q}) \geq 0,
\end{array} \right.
\]

for any \( z \neq z_2 := \frac{\ln(1/M)}{\varepsilon} \).
Proof. Choosing $M > 1$ large enough such that $z_2 < z_1$. When $z > z_2$, we know $P(z) = Q(z) = 0$, and the inequalities are obviously true. In the case of $z < z_2$, we have

$$ P(z) = \frac{1}{a_2}(1 - Me^{cz})e^{\mu_1 z}, \quad Q(z) = 0. $$

Note that $z < z_2 < 0$, then it follows that

$$ 0 < (1 - Me^{cz})e^{\mu_1 z} < 1. $$

Denote

$$ m := \min_{s \in [w_2/a_2, (w_2 + a_1)/a_2]} f'(s) < 0. $$

By a direct calculation, we get

$$ P'' - cP' + F(P, Q) = \frac{1}{a_2}e^{\mu_1 z}[\mu_1^2 - c\mu_1] - \frac{1}{a_2}Me^{(\mu_1 + \varepsilon)z}((\mu_1 + \varepsilon)^2 - c(\mu_1 + \varepsilon))] $$

$$ + \frac{1}{a_2}(1 - Me^{cz})e^{\mu_1 z}f\left(\frac{w_2}{a_2} + \frac{a_1}{a_2}(1 - Me^{cz})e^{\mu_1 z}\right) $$

$$ = \frac{1}{a_2}[e^{\mu_1 z}\Gamma_1(\mu_1, c) - Me^{(\mu_1 + \varepsilon)z}\Gamma_1(\mu_1 + \varepsilon, c) $$

$$ + (1 - Me^{cz})e^{\mu_1 z}(f\left(\frac{w_2}{a_2} + \frac{a_1}{a_2}(1 - Me^{cz})e^{\mu_1 z}\right) - f\left(\frac{w_2}{a_2}\right))]$$

$$ \geq \frac{1}{a_2}[-Me^{(\mu_1 + \varepsilon)z}\Gamma_1(\mu_1 + \varepsilon, c) + (1 - Me^{cz})e^{\mu_1 z}(m\frac{a_1}{a_2}(1 - Me^{cz})e^{\mu_1 z})]$$

$$ \geq \frac{1}{a_2}e^{(\mu_1 + \varepsilon)z}[\frac{-M}{a_2}\Gamma_1(\mu_1 + \varepsilon, c) + \frac{a_1}{a_2}e^{(\mu_1 + \varepsilon)z}]$$

$$ \geq \frac{1}{a_2}e^{(\mu_1 + \varepsilon)z}[\frac{-M}{a_2}\Gamma_1(\mu_1 + \varepsilon, c) + \frac{a_1}{a_2}] \geq 0. $$

provided $M$ large enough such that

$$ -M\Gamma_1(\mu_1 + \varepsilon, c) + \frac{a_1}{a_2} \geq 0. $$

Moreover, we have

$$ DQ'' - cQ' + F(P, Q) $$

$$ = -\frac{w_2}{a_2}g(w_2 + \frac{1}{a_2}(1 - Me^{cz})e^{\mu_1 z}) $$

$$ = -\frac{w_2}{a_2}g(w_2 + \frac{1}{a_2}(1 - Me^{cz})e^{\mu_1 z}) \geq 0. $$

This implies that $\bar{\phi}(z) := (P(z), Q(z))$ is a lower solution of (20). \hfill \Box

For any $c > c^*$, it is easy to check that $\phi$ and $\bar{\phi}$ given in Lemmas 2.5 and 2.6 satisfy conditions (1)-(4) of Proposition 4. Then we obtain the existence of monotone solutions of (20) for any $c > c^*$. For $c = c^*$, we can choose a sequence $c_n \in (c^*, c^* + 1]$ such that $c_n \to c^*$ as $n \to \infty$. Then a limiting argument as used in [2, 18] induces the existence of monotone solutions of (20) with $c = c^*$. Summarily, we get the following result.

**Proposition 5.** Assume $D \leq 2$ and (H1'). Then for any $c \geq c^*$, (20) admits a positive monotone solution $\phi_* \in C_{\mu}$ satisfying (7) and $\bar{\phi} \leq \phi_* \leq \bar{\phi}$. That is, the
lower system (19) admits a monotone traveling wave solution $\phi_*$ connecting $E_2$ to $E^*$ for any $c \geq c^*$.

Now we are in the position to prove the existence and nonexistence of traveling waves for non-monotone system (5). Equivalently, we need to investigate the existence of solutions for (11) with condition (7).

**Theorem 2.7.** Assume $D \leq 2$ and $(H1')$. Let $c^*$ be given in Lemma 2.3. Then the following statements are valid.

(i) For any $c \geq c^*$, (5) has a traveling wave solution $\phi^* \in C_{E^*}$ connecting $E_2$ to $E^*$.

(ii) For any $0 < c < c^*$, (5) has no traveling wave solution connecting $E_2$ to $E^*$. Equivalently, $c^*$ is the minimum wave speed of traveling waves connecting $E_2$ to $E^*$ for system (2).

**Proof.** For any $c \geq c^*$, let $\phi_*$ be the traveling wave solution of (19) determined in Proposition 5. By the comparison principle, we know that $\phi_*$ is a lower solution of (11). Moreover, we can check Lemma 2.5 is still true for any $c \geq c^*$ if we replace function $G$ by $\overline{G}$. Therefore, $\bar{\phi}$ is an upper solution of (11) as well, and $\phi_*(z) \leq \bar{\phi}(z)$ for any $z \in \mathbb{R}$. Now we define the set

$$\Pi = \{ \psi \in C_{E^*} : \phi_*(z) \leq \psi \leq \bar{\phi}(z), \forall z \in \mathbb{R} \}.$$  

It is clear that $\Pi$ is a bounded nonempty closed convex subset in $C_{E^*}$.

For constant $\beta > 0$ large enough, we define the operator $F : C \to C$

$$F(\phi)(z) = (F_1(\phi), F_2(\phi))(z), \forall \phi = (\phi_1, \phi_2) \in C, z \in \mathbb{R},$$

by

$$F_1(\phi)(z) = \frac{1}{(\lambda_{12} - \lambda_{11})} \left( \int_{-\infty}^{z} e^{\lambda_{11}(z-s)} + \int_{z}^{\infty} e^{\lambda_{12}(z-s)} \right) H_1(\phi)(s)ds,$$

$$F_2(\phi)(z) = \frac{1}{D(\lambda_{22} - \lambda_{21})} \left( \int_{-\infty}^{z} e^{\lambda_{21}(z-s)} + \int_{z}^{\infty} e^{\lambda_{22}(z-s)} \right) H_2(\phi)(s)ds,$$

where

$$\lambda_{11} = \frac{c - \sqrt{c^2 + 4\beta}}{2} < 0, \quad \lambda_{12} = \frac{c + \sqrt{c^2 + 4\beta}}{2} > 0,$$

$$\lambda_{21} = \frac{c - \sqrt{c^2 + 4D\beta}}{2D} < 0, \quad \lambda_{22} = \frac{c + \sqrt{c^2 + 4D\beta}}{2D} > 0,$$

and $H = (H_1, H_2) : C \to C$ is given by

$$H(\phi) = \left( \frac{F(\phi_1, \phi_2) + \beta \phi_1}{G(\phi_1, \phi_2) + \beta \phi_2} \right), \forall \phi := (\phi_1, \phi_2) \in C.$$

We also define operator $F^+$ and $H^+$ by replacing function $G$ by $\overline{G}$. Then $H^+$ is nonnegative and monotone in $C_{E^*}$ provided $\beta$ is large enough.

Note that a fixed point of operator $F$ in $C_{E^*}$ is a nonnegative and bounded solution of (11). From the monotonicity of $\overline{G}$ and $G$, we know that for any $\phi \in \Pi$, the following inequalities hold

$$0 \leq H^-(\phi) \leq H(\phi) \leq H^+(\phi) \leq H^+(E^*).$$

Then it follows that $F$ is well defined on $\Pi$, and satisfies $F\Pi \subseteq \Pi$ due to

$$\phi_* = F^-\phi_* \leq F^-\phi \leq F\phi \leq F^+\phi \leq F^+\phi \leq \phi, \forall \phi \in \Pi.$$

Moreover, by similar arguments as used in [23, Lemmas 5 and 7], we can check $F$ is continuous and compact on $\Pi$. Note that the continuity and compactness of $F$
does not depend on the monotonicity of function $G$. Therefore, the Schauder’s fixed point theorem shows that the operator $F$ admits a fixed point $\phi^* \in \Pi$, which is a traveling wave solution of (5) for $c \geq c^*$. Since

$$\phi_*(z) \leq \phi^*(z) \leq \phi(z), \forall z \in \mathbb{R},$$

and

$$\lim_{z \to -\infty} \phi_*(z) = \lim_{z \to -\infty} \phi^*(z) = \mathcal{E}_2, \quad \lim_{z \to -\infty} \phi_*(z) = \lim_{z \to -\infty} \phi^*(z) = \mathcal{E}^*,$$

we know that $\phi^*$ satisfies boundary condition (7).

Now we use the determined spreading speed theorem and a contradiction argument to prove the nonexistence of the traveling wave of (22) with speed $c \in (0, c^*)$. Assume, by contradiction, that there exists a traveling wave $\phi(x+ct)$ with some speed $c_1 \in (0, c^*)$ such that $\phi(-\infty) = \mathcal{E}_2$ and $\phi(\infty) = \mathcal{E}^*$. Then Theorem 2.4 and statements (i)-(ii) in Proposition 1 imply that

$$\lim_{t \to \infty} \phi(x+c_1t) = \lim_{t \to \infty} (\phi_1(x+c_1t), \phi_2(x+c_1t)) = \mathcal{E}^*, \quad \forall c \in (0, c^*).$$

Taking $c_2 \in (c_1, c^*)$, and letting $x = -c_2t$ in (21), then we have

$$\mathcal{E}_2 = \lim_{t \to \infty} \phi((c_1-c_2)t) = \mathcal{E}^*,$$

which is a contradiction. This completes the proof.

3. Invasion of the climax species. In this section, we consider the invasion dynamics of (2) under condition (H2). We use similar techniques as used in the last section to determine the existence of spreading speeds and traveling waves connecting $E_3$ to $E^*$. Here, we briefly present the corresponding results.

We first make the change of variables $u_2 = \frac{z_0}{a_1} - u$, $v_2 = v$, then (2) converts to

$$\begin{cases}
\frac{\partial u_2}{\partial t} = \frac{\partial^2 u_2}{\partial x^2} - \left(\frac{z_0}{a_1} - u_2\right)f(z_0 - a_1u_2 + v_2) := \frac{\partial^2 u_2}{\partial x^2} + F_1(u_2, v_2), \\
\frac{\partial v_2}{\partial t} = D\frac{\partial^2 v_2}{\partial x^2} + v_2g\left(\frac{z_0}{a_1} - u_2 + a_2v_2\right) := D\frac{\partial^2 v_2}{\partial x^2} + G_1(u_2, v_2),
\end{cases}$$

(22)

and the equilibria $E_3, E^*$ of (2) are transformed to

$$E_3 = (0, 0), \quad E^* = \left(\frac{z_0}{a_1} - u^*, v^*\right),$$

for (22). Note that $E_3 \ll E^*$, and there is no other equilibria of (22) between them. We denote

$$C_{E^*} := \{(\psi_1, \psi_2) \in \mathcal{C} : 0 \leq \psi_1 \leq \frac{z_0}{a_1} - u^*, \ 0 \leq \psi_2 \leq v^*\},$$

and

$$[E_3, E^*] := \{(x, y) \in \mathbb{R}^2_+ : 0 \leq x \leq \frac{z_0}{a_1} - u^*, \ 0 \leq y \leq v^*\}.$$

3.1. Spreading speed and invasion waves when $w^* \leq u^*$. We first consider the case that $w^* \leq u^*$ such that (H2) is satisfied due to $u^* < \frac{z_0}{a_1}$. We can verify that (22) is cooperative in $C_{E^*}$, and the general theories determined in [8] can be applied. Then (22) admits a spreading speed $\bar{c} > 0$, which is also the minimum wave speed for monotone traveling waves of (22) connecting $E_3$ and $E^*$. For any $c \geq \bar{c}$, substituting $u_2(t, x) = U(z), v_2(t, x) = V(z), z = x + ct$, to (22), we have

$$\begin{cases}
U''(z) - cU'(z) + F_1(U, V) = 0, \\
DV''(z) - cV'(z) + G_1(U, V) = 0,
\end{cases}$$

(23)
where \( \mathcal{U} \) and \( \mathcal{V} \) satisfy the following conditions

\[
\begin{align*}
\lim_{z \to -\infty} \mathcal{U}(z) &= 0, \quad \lim_{z \to \infty} \mathcal{U}(z) = \frac{z_0}{a_1} - u^*, \\
\lim_{z \to -\infty} \mathcal{V}(z) &= 0, \quad \lim_{z \to \infty} \mathcal{V}(z) = v^*.
\end{align*}
\]

As we did at subsection 2.1, we consider the linearization of (22) at \( z_0 \), which is given by

\[
\begin{align*}
\frac{\partial u_2}{\partial t} &= \frac{\partial^2 u_2}{\partial x^2} + z_0 f'(z_0) u_2 - \frac{z_0}{a_1} f'(z_0) v_2, \\
\frac{\partial v_2}{\partial t} &= D \frac{\partial^2 v_2}{\partial x^2} + g\left(\frac{z_0}{a_1}\right) v_2,
\end{align*}
\]

and the corresponding matrix:

\[
\tilde{C}_\nu := \begin{pmatrix} \nu^2 + \frac{z_0}{a_1} f'(z_0) & -\frac{z_0}{a_1} f'(z_0) \\ 0 & \nu D^2 + g\left(\frac{z_0}{a_1}\right) \end{pmatrix}.
\]

We define the linear speed \( \tilde{c}_0 \) for (22) as

\[
\tilde{c}_0 := \inf_{\nu > 0} \frac{D \nu^2 + g\left(\frac{z_0}{a_1}\right)}{\nu} = 2 \sqrt{D g\left(\frac{z_0}{a_1}\right)},
\]

where the infimum is obtained at \( \tilde{\nu} = \sqrt{D g\left(\frac{z_0}{a_1}\right)} \). Then we have a similar result as given in Proposition 3 for the linear determinacy of \( \tilde{c} \). In order to figure out explicit conditions for the linear determinacy of \( \tilde{c} \), we need to find suitable upper solution of (23) with \( c = \tilde{c}_0 \). For any \( z \in \mathbb{R} \), we define a continuous function

\[
\mathcal{V}(z) = \begin{cases} a_1 e^{\tilde{c}_0 z}, & z < \hat{z}, \\
v^*, & z \geq \hat{z}, \end{cases}
\]

where \( \hat{z} := \frac{1}{\tilde{c}_0} \ln\left(\frac{z_0}{a_1}\right) \). Then we have the following result.

**Theorem 3.1.** Assume \( v^* \leq u^* \). Let \( \mathcal{V}(z) \) be given in (26). If there exists a continuous and positive function \( \mathcal{U}(z) \) satisfying \( \mathcal{U}(\infty) = 0 \), \( \liminf_{z \to -\infty} \mathcal{U}(z) > 0 \), \( \mathcal{U}(z) \leq a_2 \mathcal{V}(z) \) for \( z < \hat{z} \), and \( \mathcal{U}(z) \leq \frac{1}{a_1} \mathcal{V}(z) \) for \( z \geq \hat{z} \) such that \( (\tilde{U}, \tilde{V})(z) \) satisfies the upper solution inequality of (23) for \( \mathcal{U} \) with \( c = \tilde{c}_0 \), then \( \tilde{c} = \tilde{c}_0 \). In particular, if \( D \geq \frac{1}{2} \), then the minimum wave speed \( \tilde{c} \) is linearly determinate.

**Proof.** For the first part of the result, it is enough for us to check \( (\tilde{U}(z), \tilde{V}(z)) \) satisfies the upper solution inequality of (23) for \( \mathcal{V} \) variable. For \( z < \hat{z} \), we have \( \tilde{V}(z) = a_1 e^{\tilde{c}_0 z} \), \( \mathcal{U}(z) \leq a_2 \mathcal{V}(z) \), and

\[
D \tilde{V}'' - \tilde{c}_0 \tilde{V}' + G_1(\tilde{U}, \tilde{V}) = a_1 e^{\tilde{c}_0 z} [D \tilde{U}'' - \tilde{c}_0 \tilde{U}' + g\left(\frac{z_0}{a_1}\right) - \tilde{U} + a_2 \tilde{V}] \\
\leq a_1 e^{\tilde{c}_0 z} [D \tilde{U}'' - \tilde{c}_0 \tilde{U}' + g\left(\frac{z_0}{c_{11}}\right)] = 0.
\]

If \( z > \hat{z} \), we have \( \tilde{V}(z) = v^* \), \( \tilde{U}(z) \leq \frac{1}{a_1} \tilde{V}(z) \), and

\[
D \tilde{V}'' - \tilde{c}_0 \tilde{V}' + G_1(\tilde{U}, \tilde{V}) = v^* g\left(\frac{z_0}{a_1}\right) - \tilde{U} + a_2 v^* = v^* g\left(\frac{v^*}{a_1}\right) - \tilde{U} \leq 0,
\]

where \( a_1 u^* + v^* = z_0, u^* + a_2 v^* = w_2 \) are used.
Now we construct the following two systems:

\[ \begin{align*}
\dot{u}'' - c_0 \dot{u}' + \Phi_1(\dot{u}, \dot{v}) &= e^{\beta z}[p^2 - c_0 p] - (\frac{z_0}{a_1} - e^{\beta z}) f(z_0 - a_1 e^{\beta z} + a_1 e^{\beta z}) \\
&= \nu e^{\beta z} (\dot{v} - c_0) \\
&= \nu e^{\beta z} \left( \frac{g(w_2/a_2)}{D} (1 - 2D) \right) \leq 0.
\end{align*} \]

If \( z > \hat{z} \), \( \bar{U}(z) = \frac{v^*}{a_1}, \bar{V}(z) = v^* \). Then we have

\[ \bar{U}'' - c_0 \bar{U}' + \Phi_1(\bar{U}, \bar{V}) = - \left( \frac{z_0}{a_1} - \frac{v^*}{a_1} \right) f(z_0 - v^* + v^*) = 0. \]

We complete the proof. \( \square \)

**Remark 2.** When \( D \geq \frac{1}{2} \) and \( w^* \leq u^* \), with the assumption that \( f \) is convex on \([z_0, \infty)\), the authors in [21, Theorem 3.2] showed that (22) admits a linearly determined spreading speed. Under the same conditions, the existence of traveling waves connecting \( E_3 \) and \( E^* \) was proved in [23, Theorem 1] by the Schauder’s fixed point theorem. Here, we extend the results in [21] and [23] with no requirement on the convexity of fitness function \( f \).

### 3.2. Spreading speed and invasion waves when \( u^* < w^* < \frac{z_0}{a_1} \)

Now we focus on the case that \( w^* > u^* \) such that condition (H2) holds. Equivalently, we assume the following condition holds:

\((H2') \; u^* < w^* < \frac{z_0}{a_1}\)

With condition \((H2')\), (22) is non-monotone in \( C_{E^*} \), and the existence of spreading speed and traveling waves connecting \( E_3 \) to \( E^* \) has not been studied. In order to use the sandwich technique, we further assume condition \((H2')\) holds such that

\[ g(u^*) > g \left( \frac{z_0}{a_1} \right). \tag{27} \]

It follows from the property of \( g \), we know that there exists a unique \( w^+ \in (w^*, \frac{z_0}{a_1}) \) such that \( g(u^*) = g(w^+) > g \left( \frac{z_0}{a_1} \right) \). Similarly, we define

\[ g^+(w) = \begin{cases} g(u^*), & w \leq w^*, \\ g(w), & w > w^*. \end{cases} \]

Then functions \( g^\pm \) are decreasing and satisfy

\[ g^-(w) \leq g(w) \leq g^+(w), \text{ for } w \geq u^*, \]

\[ g^-(w) = g^+(w) = g(w), \text{ for } w \geq w^+. \tag{28} \]

Now we construct the following two systems:

\[ \begin{align*}
\frac{\partial u_2}{\partial t} &= \frac{\partial^2 u_2}{\partial x^2} - (\frac{z_0}{a_1} - u_2) f(z_0 - a_1 u_2 + v_2), \\
\frac{\partial v_2}{\partial t} &= D \frac{\partial^2 v_2}{\partial x^2} + v_2 g^+(\frac{z_0}{a_1} - u_2 + a_2 v_2). \tag{29}
\end{align*} \]
and
\[
\begin{aligned}
\frac{\partial u_2}{\partial t} = \frac{\partial^2 u_2}{\partial x^2} - \left(\frac{z_0}{a_1} - u_2\right)f\left(z_0 - a_1u_2 + v_2\right), \\
\frac{\partial v_2}{\partial t} = D\frac{\partial^2 v_2}{\partial x^2} + v_2g\left(\frac{z_0}{a_1} - u_2 + a_2v_2\right).
\end{aligned}
\tag{30}
\]

By similar arguments as used in Lemma 2.3 and Theorem 2.4, we have the following result.

**Theorem 3.2.** Assume \( D \geq \frac{1}{2} \) and (H2) such that (27) holds. Then (29) and (30) admit the same spreading speed \( c \), which is linearly determinate and given by
\[
\bar{c} = \bar{c}_0 = 2\sqrt{Dg(z_0/a_1)}.
\]
Moreover, \( \bar{c} \) is also the linearly determined spreading speed of non-monotone system (22).

Now we are interested in the existence of traveling waves of (22) connecting \( E^*_3 \) to \( E^*_3 \), which corresponds to the traveling waves of (2) connecting the pioneer-only equilibrium \( E^*_3 \) to coexistence equilibrium \( E^*_3 \).

Denote functions \( G_1^+, G_1^- \) in (29) and (30), respectively, as
\[
G_1^+(u_2, v_2) := v_2g\left(\frac{z_0}{a_1} - u_2 + a_2v_2\right).
\]

Then for (30), we have wave equations
\[
\begin{aligned}
\mathcal{P}'(z) - c\mathcal{P}'(z) + F_1(P, Q) = 0, \\
D\mathcal{Q}'(z) - c\mathcal{Q}'(z) + G_1^-(P, Q) = 0.
\end{aligned}
\tag{31}
\]

Let \( \bar{c} \) be given in Theorem 3.2. For any \( c > \bar{c} \), we denote
\[
\nu_1 := \frac{c - \sqrt{c^2 - 4Dg(z_0/a_1)}}{2D} > 0,
\]

and define
\[
\bar{P}(z) = \min\{e^{\nu_1 z}, \frac{z_0}{a_1} - u^*\}, \\
\bar{Q}(z) = \min\{a_1e^{\nu_1 z}, v^*\}, \\
\overline{P}(z) = 0, \\
\overline{Q}(z) = \max\{a_1(1 - Me^{\nu_1 z})e^{\nu_1 z}, 0\}.
\]

Using similar arguments as used in Lemma 2.5 and 2.6, we verify that \( \bar{\varphi}(z) := (\bar{P}(z), \overline{Q}(z)) \) is an upper solution, and \( \varphi^*(z) := (\overline{P}(z), \overline{Q}(z)) \) is a lower solution of (31) provided \( M > 1 \) large enough and \( \varepsilon > 0 \) sufficiently small. Then the existence of monotone traveling waves of (30) for \( c > \bar{c} \) is a direct consequence of Proposition 4. For \( c = \bar{c} \), a limiting argument can be applied again to get the existence of monotone traveling waves of (30) connecting \( E^*_3 \) to \( E^*_3 \). Corresponding to Proposition 5, we have the following result.

**Proposition 6.** Assume \( D \geq \frac{1}{2} \) and (H2) such that (27) holds. Then for any \( c \geq \bar{c} \), the lower system (30) has a monotone traveling wave solution \( \varphi^* \) connecting \( E^*_3 \) to \( E^*_3 \) and satisfying \( \bar{\varphi} \leq \varphi^* \leq \bar{\varphi} \).

Now we denote \( \Omega = \{\psi \in C_{E^*_3} : \varphi^*(z) \leq \psi \leq \bar{\varphi}(z), \forall z \in \mathbb{R}\} \). We can use the same procedure as used in Theorem 2.7 to get the following result for the existence and nonexistence of traveling waves connecting \( E^*_3 \) to \( E^*_3 \) for (22).
Theorem 3.3. Assume $D \geq \frac{1}{2}$ and $(H'')$ such that (27) holds. Then the following statements are valid.

(i) For any $c \geq \bar{c}$, (22) has a traveling wave solution $\phi \in \mathcal{C}_Z$ connecting $E_3$ to $E^*$.

(ii) For any $0 < c < \bar{c}$, (22) has no traveling wave solution connecting $E_3$ to $E^*$.

Equivalently, $\bar{c}$ is the minimum wave speed of traveling waves connecting $E_3$ to $E^*$ for system (2).

4. Applications and conclusions. In this section, we give an example to show the applications of our theoretical results. We consider the linear pioneer fitness function

$$f(z) = z_0 - z,$$

and the quadratic climax fitness function

$$g(w) = (w_1 - w)(w - w_2),$$

where $z_0 > 0$ and $w_2 > w_1 > 0$. Then the fitness function $g$ does not satisfy the convexity assumption given in [21]. Substituting $f$ and $g$ to (2), we have the following model

$$\begin{align*}
\frac{\partial u}{\partial t} &= \frac{\partial^2 u}{\partial x^2} + u(z_0 - a_1u - v), \\
\frac{\partial v}{\partial t} &= D \frac{\partial^2 v}{\partial x^2} + v(w_1 - u - a_2v)(u + a_2v - w_2),
\end{align*}$$

(32)

In order to observe the evolution of populations and the possible pioneer invasion waves, we take $z_0 = 10, w_1 = \frac{1}{2}, w_2 = \frac{3}{2}, a_1 = 10, a_2 = \frac{1}{2}, D = 2$ in (32). Then we have $w^* = 1, u^* = \frac{3}{4}, v^* = \frac{7}{4}$, and the condition $(H'')$ holds. Theorems 2.4 and 2.7 show that (32) admits a spreading speed

$$c^* = 2\sqrt{f(\frac{w_2}{a_2})} = 2\sqrt{7},$$

and $c^*$ is the minimum wave speed of traveling waves connecting the climax-only equilibrium $E_2 = (0, 3)$ to the coexistence equilibrium $E^* = (\frac{2}{3}, \frac{5}{3})$. For numerical simulations, we truncate the infinity domain $\mathbb{R}$ to the finite interval $[-200, 200]$. In (a) and (b) of Fig. 4, we show the evolution of pioneer and climax species with a given initial data connecting $E_2$ and $E^*$. We observe that the solution finally run with the same shape at a constant speed as given in (c) and (d) of Fig. 4, which are possible wave profiles for $u$ and $v$. Here, we should point out that, at this moment, we have no good technique to prove the uniqueness and global stability of traveling waves due to the difficulty induced by the nonmonotonicity of fitness functions.

Similarly, to observe the climax invasion waves, we take $z_0 = 8, w_1 = \frac{1}{2}, w_2 = \frac{7}{2}, a_1 = \frac{5}{8}, a_2 = \frac{1}{4}, D = \frac{1}{2}$ in (32). Then we have $w^* = 2, u^* = \frac{3}{4}, v^* = 4$, and the condition $(H'')$ holds such that $g(u^*) = 2 > \frac{5}{4} = g(\frac{2w_2}{a_2})$. Theorems 3.2 and 3.3 imply that (32) admits a spreading speed

$$\bar{c} = 2\sqrt{Dg(\frac{2w_2}{a_2})} = \sqrt{5},$$

and $\bar{c}$ is the minimum wave speed of traveling waves connecting pioneer-only equilibrium $E_3 = (3, 0)$ to the coexistence equilibrium $E^* = (\frac{3}{2}, 4)$. For a given initial data connecting $E_3$ and $E^*$, we show the evolution of species in the last figure, and the possible climax invasion waves are observed.
In this paper, a diffusive pioneer-climax model is reconsidered for ranges of parameter values that may lead the system non-monotone. In the case of $v^* \geq \frac{w^*}{a_2}$ and $w^* \leq u^*$, we get the existence of spreading speeds and their coincidence with the minimum wave speeds by monotone dynamical system theories. By constructing suitable upper solutions, we further determine the linear determinacy of the minimum wave speeds. Once the minimum wave speeds are linearly determined, we further study the model under (H1') and (H2'), where the system is non-monotone. The sandwich technique and upper-lower solution method are applied to get the existence of spreading speeds and traveling waves. Our results extend the existing results established under monotone assumptions and convexity requirements on fitness functions.

Finally, we would like to mention that the dynamics of the pioneer-climax interaction model is quite rich. The system may admit strong invasion waves or bistable waves [3]. It is interesting to study the invasion dynamics of (2) under different parameter values. We believe that the techniques we used here can work for other parameter ranges in which the system does not admit monotone properties. We leave those interesting cases in the future works.

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Figure 5. The observed climax invasion waves for $u$ and $v$. 
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E-mail address: yx.zhang@tju.edu.cn
E-mail address: shiwangm@163.net