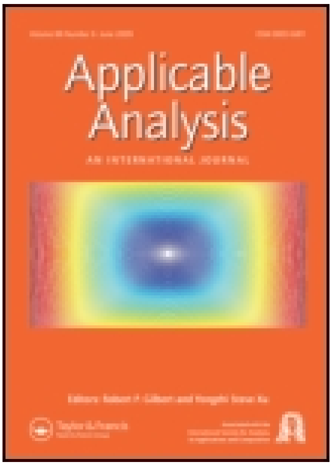

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Minimal wave speed and spread speed of competing pioneer and climax species

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In this article, for a diffusive population model describing interaction of pioneer-climax species, we explore the issues of spreading speed, linear determinacy and traveling wave fronts. Applying the theory developed by Weinberger et al. [J. Math. Biol. 2002;45:183–218], we identify some ranges of model parameters within which, the model is shown to have a single spreading speed which is linearly determinate and coincides with the corresponding minimal speed for the traveling wave fronts connecting two relevant equilibria, one being a boundary equilibrium and the other being a coexistence equilibrium.

Keywords: single spreading speed; linear determinacy; traveling wave front; reaction-diffusion system; pioneer and climax species

AMS Subject Classifications: 35K57; 34C12; 92D25

1. Introduction

In Buchanan [1], a reaction-diffusion system was proposed to model the interaction of a pioneer species and a climax species. Assuming random dispersion for the two species, the model system is given by

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} = D_1 \dfrac{\partial^2 u(t,x)}{\partial x^2} + u(t,x) f(c_{11}u(t,x) + c_{12}v(t,x)), \\ \dfrac{\partial v(t,x)}{\partial t} = D_2 \dfrac{\partial^2 v(t,x)}{\partial x^2} + v(t,x) g(c_{21}u(t,x) + c_{22}v(t,x)). \end{cases} \tag{1.1}$$

Here, $u(t,x)$ and $v(t,x)$ represent the population densities of the pioneer and climax species, respectively, at time t and location x, the positive constants D_1 and D_2 are the diffusion coefficients for the respective species, and the interacting matrix $C = (c_{ij})_{2\times 2}$ gives the weight distribution of resources among the two species. To reflect the nature of pioneer and climax species, the two fitness functions $f,\ g \in C^1(\mathbb{R})$ are assumed to satisfy

$$f'(z) < 0 \quad \text{for } z \in \mathbb{R}, \quad f(z_0) = 0 \quad \text{for some } z_0 > 0,\ f \text{ is concave up on } [z_0, \infty).$$

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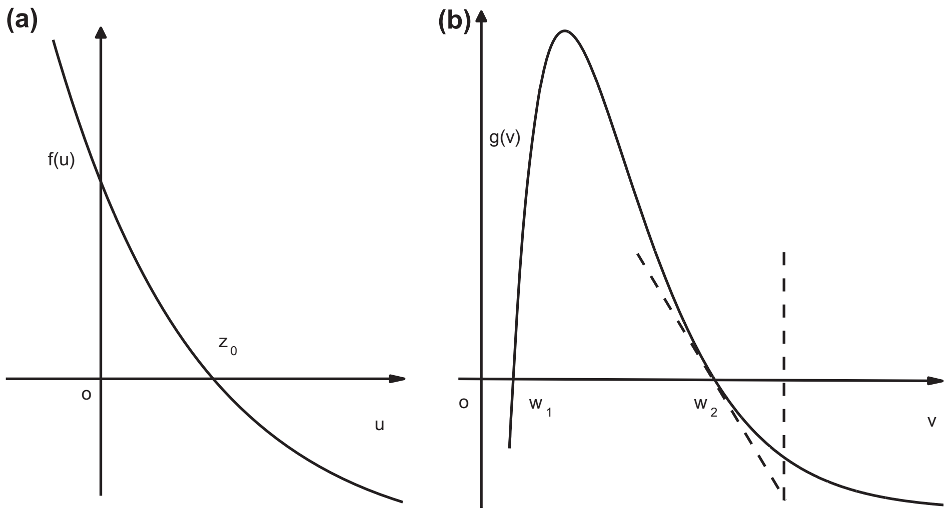

Figure 1. Typical fitness functions for pioneer species and climax species.

and

$$\begin{cases} g(w_1) = g(w_2) = 0, \quad \text{where } 0 < w_1 < w_2; \\ (w^* - w)g'(w) > 0 \text{ when } w > 0 \text{ and } w \neq w^* \text{ for some } w^* \in (w_1, w_2); \\ g(w) \text{ is concave up on } [w_2, +\infty). \end{cases}$$

The conditions on f simply indicate that the u species thrives best at lower densities and thus, is a good candidate for pioneering (hence, the name "pioneer"); while the conditions on g assume that the v species attains the maximal fitness at an intermediate-weighted density w^* (hence, the name "climax"). These features are depicted in Figure 1. Examples of f and g satisfying the above conditions include $f(u) = e^{r(1-u)} - a$ (see, e.g. [2]), $f(u) = \frac{r}{(1+bu)^p} - a$ (see, e.g. [3]), and $g(u) = ue^{r(1-u)} - a$ (see, e.g. [4–7]).

When ignoring the spatial factor, an ordinary differential equation version of (1.1) is obtained by dropping the diffusion terms in (1.1). It turns out that the dynamics of the ODE version can be very rich, due to the complicated structure of the equilibria of the ODE system (number of the equilibria and their various distributions). For details on the dynamics of the corresponding ODE model, a reader is referred to [4,7–11] and the references therein. In particular, Buchanan [8] gave a nice summary of the ODE model.

When considering (1.1) in a bounded spatial domain, Buchanan [1] observed that Turing instability can occur. That is, the diffusion may destroy the stability of an spatially homogeneous steady state, leading to the formation of spatially heterogeneous patterns. Almost simultaneously, Brown et al. [12] also studied (1.1) but for $x \in (-\infty, \infty)$. By using a singular perturbation approach, Brown et al. [12] established existence of traveling wave front for (1.1) that connects two boundary equilibria. Such a traveling wave front accounts for transition from one mono-culture steady state to another mono-culture steady state, implying that within some range of model parameters, a spatial domain initially occupied by the pioneer species will be eventually taken over by the climax species with a certain speed. Yuan and Zou [13] further explored (1.1) for $x \in (-\infty, \infty)$, and they found that within some other range of model parameters, the existence of co-invasive traveling wave fronts that connect the pioneer-invasion-only equilibrium with a coexistence equilibrium is also possible and this should be attributed to mild competition.

For a reaction-diffusion system with the spatial variable $x \in (-\infty, \infty)$, another important topic is the spreading speed, which is different from but closely related to the speed of traveling wave front. See [14–16] for details of this concept. A natural question in this regard for a system is that when there are more than one species in interaction, will different species spread by different spreading speeds? Li et al. [17] and Weinberger et al. [18] have observed that it sometimes happens, even in cooperative systems, that different species spread at different speeds, so that there is the slowest speed and the fastest speed; while it is also possible for a system to have a single spreading speed, meaning that all species spread at the same rate (see [14–16]). It turns out that under some conditions on the nonlinearities, the slowest spreading speed coincides with the minimal speed of the traveling wave fronts, see [17,19] and the references therein.

In the context of spreading speed, in the case of a single speed for all species, there is an issue of how to determine or calculate this speed c^*. Linearizing the nonlinear system under consideration at an unstable equilibrium leads to a linear system which also has a single spreading speed $\bar{c}$. If $c^* = \bar{c}$, then the nonlinear system is said to be *linearly determinate*. The so-called "linear conjecture" in this context refers to a statement of belief that under some conditions, a nonlinear system is linearly determinate. It has been shown that the linear determinacy does not hold in general and conditions are needed for it to hold (see, e.g. [18,20–22]). When a system describing the interactions of two species allows anomalous speeds, for the slowest and fastest spreading speeds, there is also the issue of linear determinacy. In addition to the recent works mentioned above, the earlier works [23–27] also have good coverage on this topic.

For the reaction-diffusion model (1.1) with $x \in (-\infty, \infty)$, the above issues have not been addressed in the literature, and this constitutes the purpose of this paper. In other words, we shall discuss, in the rest of the paper, single or multiple spreading speeds and the linear determinacy for the spreading speed(s), as well as the minimal wave speed for traveling wave fronts related to the co-invasion of the two species for the model (1.1). In Section 2, we do some preparation by identifying certain ranges of the model parameters within which, we are able to address the issues. This is mainly due to the nice structure of the equilibria within these ranges of the parameters. In Section 3, we show the existence of single spreading speed for the two species and confirm its linear determinacy, within the parameter ranges sorted out in Section 2. In Section 4, we show that the single spreading speed indeed coincides with the minimal speed of the traveling wave fronts of (1.1) connecting two relevant equilibria.

2. Preliminaries

Note that a re-scaling transforms system (1.1) into

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} = D_1 \dfrac{\partial^2 u(t,x)}{\partial x^2} + u(t,x) f(c_{11} u(t,x) + v(t,x)), \\ \dfrac{\partial v(t,x)}{\partial t} = D_2 \dfrac{\partial^2 v(t,x)}{\partial x^2} + v(t,x) g(u(t,x) + c_{22} v(t,x)), \end{cases} \tag{2.1}$$

which has the same dynamics as (1.1), and thus in the following, we shall consider (2.1) only.

By the properties of the fitness functions f and g, we can easily see that (2.1) has the following equilibria:

$$E_0 = (0, 0), \quad E_1 = \left(0, \frac{w_1}{c_{22}}\right), \quad E_2 = \left(0, \frac{w_2}{c_{22}}\right), \quad E_3 = \left(\frac{z_0}{c_{11}}, 0\right),$$

regardless of the values of the parameters. In addition, the coexistence equilibria are obtained by solving either

$$c_{11}u + v = z_0, \quad u + c_{22}v = w_1, \tag{2.2}$$

or

$$c_{11}u + v = z_0, \quad u + c_{22}v = w_2 \tag{2.3}$$

for positive solutions. Denote the possible positive solution of (2.2) by (u^+, v^+) and the possible positive solution of (2.3) by (u^*, v^*). Directly solving gives

$$u^+ = \frac{c_{22}z_0 - w_1}{c_{11}c_{22} - 1}, \quad v^+ = \frac{c_{11}w_1 - z_0}{c_{11}c_{22} - 1},$$
$$u^* = \frac{c_{22}z_0 - w_2}{c_{11}c_{22} - 1}, \quad v^* = \frac{c_{11}w_2 - z_0}{c_{11}c_{22} - 1}.$$

For convenience of discussion, we need the following assumptions:

(H1) $z_0 > \frac{w_2}{c_{22}}, \quad w_1 < \frac{z_0}{c_{11}} < w_2;$
(H2) $z_0 > \frac{w_2}{c_{22}}, \quad \frac{z_0}{c_{11}} < w_1.$

We point out that either (H1) or (H2) implies $c_{11}c_{22} > 1$. In fact, if (H1) holds, then we have

$$z_0c_{22} > w_2 \ \Rightarrow\ c_{11}z_0c_{22} > c_{11}w_2 > z_0 \ \Rightarrow\ c_{11}c_{22} > 1;$$

if (H2) holds, then we have

$$z_0c_{22} > w_2 \ \Rightarrow\ c_{11}z_0c_{22} > c_{11}w_2 > c_{11}w_1 > z_0 \ \Rightarrow\ c_{11}c_{22} > 1.$$

Noting that $w_1 < w_2$, it is obvious that under (H1), $E^* = (u^*, v^*)$ exists with $u^* < z_0/c_{11}$; while under (H2), in addition to $E^* = (u^*, v^*)$, there is the other coexistence equilibrium $E^+ = (u^+, v^+)$. Also note that under the assumption (H1), we have $f(\frac{w_2}{c_{22}}) > 0$ and $g(\frac{z_0}{c_{11}}) > 0$; while under the assumption (H2), we have $f(\frac{w_2}{c_{22}}) > 0$ and $g(\frac{z_0}{c_{11}}) < 0$.

We shall also consider two additional assumptions to restrict E^* to a desirable region:

(A1) $\frac{w^*}{c_{22}} \le v^*$;
(A2) $w^* \le u^*$.

Clearly, (A2) is impossible under (H2), so we only have three possible cases: (H1)–(A1), (H2)–(A1), and (H1)–(A2), which are depicted in Figures 2–4.

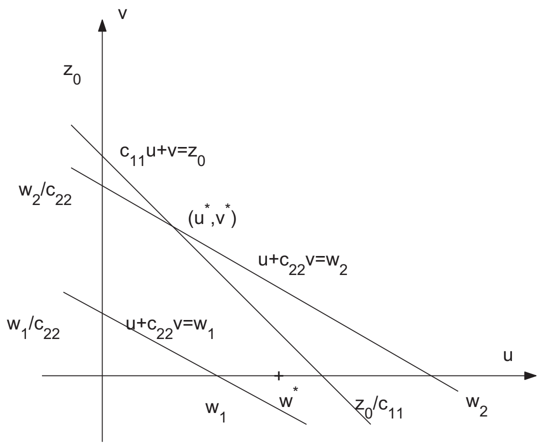

Figure 2. Structure of equilibria of (2.1) under (H1)–(A1).

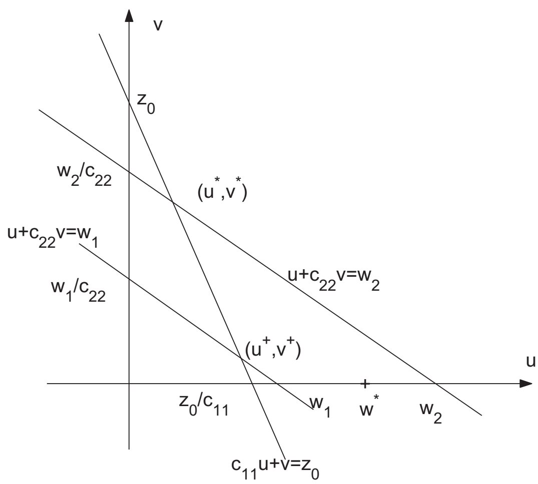

Figure 3. Structure of equilibria of (2.1) under (H2)–(A1).

(I) Assume that either (H1)–(A1) or (H2)–(A1) hold. Let $p = u$ and $q = \frac{w_2}{c_{22}} - v$. Then (2.1) is transformed to

$$\begin{cases} \dfrac{\partial p}{\partial t} = d_1 \dfrac{\partial^2 p}{\partial x^2} + p\, f\left(\dfrac{w_2}{c_{22}} + c_{11} p - q\right) =: d_1 \dfrac{\partial^2 p}{\partial x^2} + F_1(p, q), \\ \dfrac{\partial q}{\partial t} = d_2 \dfrac{\partial^2 q}{\partial x^2} - \left(\dfrac{w_2}{c_{22}} - q\right)\, g(w_2 + p - c_{22} q) =: d_2 \dfrac{\partial^2 q}{\partial x^2} + F_2(p, q). \end{cases} \tag{2.4}$$

The $u - v$ region given by $u + c_{22} v \geq w^*$ and $0 \leq v \leq \frac{w_2}{c_{22}}$ is transformed to the $p - q$ region given by $w_2 + p - c_{22} q = u + c_{22} v \geq w^*$ and $0 \leq q \leq w_{22}/c_{22}$. In this region,

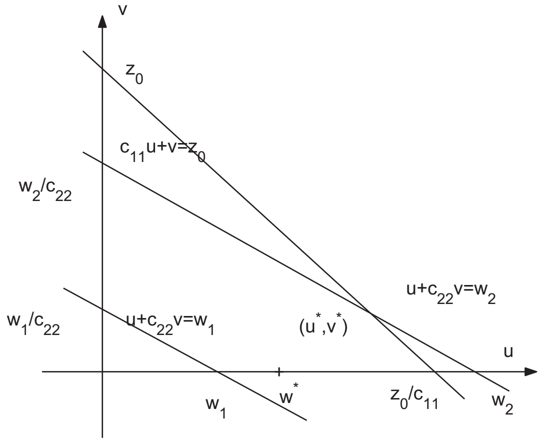

Figure 4. Structure of equilibria of (2.1) under (H1)–(A2).

$F_1(p,q) = f(\frac{w_2}{c_{22}} + c_{11}p - q)$ is increasing in q and $g(w_2 + p - c_{22}q)$ is decreasing in p and hence $F_2(p,q) = -(\frac{w_2}{c_{22}} - q)\, g(w_2 + p - c_{22}q)$ is increasing in p, meaning that (2.4) is cooperative.

By the above transformation, the equilibria $E_0,\ E_1,\ E_2,\ E_3,\ E^*$ are transformed, respectively, to

$$\hat{E}_0 = \left(0, \frac{w_2}{c_{22}}\right), \quad \hat{E}_1 = \left(0, \frac{w_2 - w_1}{c_{22}}\right), \quad \hat{E}_2 = (0,0),$$

$$\hat{E}_3 = \left(\frac{z_0}{c_{11}}, \frac{w_2}{c_{22}}\right), \quad \hat{E}^* = \left(u^*, \frac{w_2}{c_{22}} - v^*\right)$$

in the $p - q$ plane. Although E^+ also exists under (H2) and is transformed to $\hat{E}^+ = (u^+, \frac{w_2}{c_{22}} - v^+)$, but this is outside the parallelepiped with vertices $\hat{E}_2$ and $\hat{E}^*$. In other words, under either (H1)–(A1) or (H2)–(A1), $\hat{E}_2$ and $\hat{E}^*$ are ordered in the $p-q$ plane and there is no other equilibrium between $\hat{E}_2$ and $\hat{E}^*$.

(II) Next, assume that (H1)–(A2) hold. Let $p = \frac{z_0}{c_{11}} - u$ and $q = v$. Then, (2.1) is transformed to the following system

$$\begin{cases} \dfrac{\partial p}{\partial t} = d_1 \dfrac{\partial^2 p}{\partial x^2} - \left(\dfrac{z_0}{c_{11}} - p\right) f(z_0 - c_{11}p + q), \\ \dfrac{\partial q}{\partial t} = d_2 \dfrac{\partial^2 q}{\partial x^2} + q\, g\left(\dfrac{z_0}{c_{11}} - p + c_{22}q\right). \end{cases} \tag{2.5}$$

In this case, E^+ does not exist and the other equilibria $E_0,\ E_1,\ E_2,\ E_3,\ E^*$ are transformed respectively to

$$\bar{E}_0 = \left(\frac{z_0}{c_{11}}, 0\right), \quad \bar{E}_1 = \left(\frac{z_0}{c_{11}}, \frac{w_1}{c_{22}}\right), \quad \bar{E}_2 = \left(\frac{z_0}{c_{11}}, \frac{w_2}{c_{22}}\right),$$

$$\bar{E}_3 = (0, 0), \quad \bar{E}^* = \left(\frac{z_0}{c_{11}} - u^*, v^*\right),$$

with $\bar{E}_3$ and $\bar{E}^*$ being ordered and there is no other equilibrium between $\bar{E}_3$ and $\bar{E}^*$. Moreover, between $\bar{E}_3$ and $\bar{E}^*$ (i.e. $0 \le p \le \frac{z_0}{c_{11}} - u^*, 0 \le q \le v^*$), $-(\frac{z_0}{c_{11}} - p) f(z_0 - c_{11} p + q)$ is increasing in q and $q\, g(\frac{z_0}{c_{11}} - p + c_{22} q)$ is increasing in p, meaning that (2.5) is cooperative. It is worth emphasizing that $u^* > w^*$ is an important condition that guarantees the cooperative property of the system (2.5), and which is also a technical condition in [13] for establishing the existence of traveling wave fronts that connect the monoculture equilibrium E_3 and the coexistence equilibrium E^*.

In the sequel, we will apply the theoretical results developed in [28] to investigate the existence of a single spreading speed for the two species and the linear determinacy of this speed under either (H1)–(A1) or (H2)–(A1) or (H1)–(A2). To this end, we will follow the notations on equilibria for this purpose in [28] by letting

$$\theta := (0,0) = \begin{cases} \hat{E}_2 & \text{when considering (2.4); under } (H1)\text{–}(A1) \text{ or } (H2)\text{–}(A1); \\ \bar{E}_3 & \text{when considering (2.5); under } (H1)\text{–}(A2); \end{cases}$$

$$\beta := \begin{cases} \hat{E}^* & \text{when considering (2.4); under } (H1)\text{–}(A1) \text{ or } (H2)\text{–}(A1); \\ \bar{E}^* & \text{when considering (2.5). under } (H1)\text{–}(A2); \end{cases}$$

3. Single spreading speed and linear determinacy

First, let us assume either (H1)–(A1) or (H2)–(A1) hold and consider (2.4). The linearization of (2.4) at the equilibrium $\theta = (0, 0)$ is

$$\begin{cases} \dfrac{\partial p}{\partial t} = d_1 \dfrac{\partial^2 p}{\partial x^2} + f\left(\dfrac{w_2}{c_{22}}\right) p, \\ \dfrac{\partial q}{\partial t} = d_2 \dfrac{\partial^2 q}{\partial x^2} - \dfrac{w_2}{c_{22}} g'(w_2) p + w_2 g'(w_2) q. \end{cases} \tag{3.1}$$

Let $\mathbf{F} = (F_1, F_2)$. The Jacobian matrix in the linear system (3.1) is

$$D\mathbf{F}(\theta) = \begin{pmatrix} f\left(\dfrac{w_2}{c_{22}}\right) & 0 \\ -\dfrac{w_2}{c_{22}} g'(w_2) & w_2 g'(w_2) \end{pmatrix}.$$

which obviously has the Frobenius form (see, e.g. [28]).

To apply the results in [28], we need the following matrix

$$C_\mu = \begin{pmatrix} d_1 \mu^2 + f\left(\dfrac{w_2}{c_{22}}\right) & 0 \\ -\dfrac{w_2}{c_{22}} g'(w_2) & d_2 \mu^2 + w_2 g'(w_2) \end{pmatrix}$$

which is referred to as the coefficient matrix for (3.1) in [28].

The following proposition is a specialization of Theorem 4.2 in [28] for system (2.4):

PROPOSITION 3.1 *Suppose the system* (2.4) *has the following properties:*

(i) $\theta = (0, 0)$ *and* $\beta = (k_1, k_2)$ *are equilibria with* $k_i > 0, i = 1, 2$, *and there is no other constant equilibrium* (ω_1, ω_2) *such that* $0 < \omega_i \le k_i, i = 1, 2$.

(ii) *The system is cooperative.*
(iii) *The reaction term in* (2.4) *does not explicitly depend on* x *and* t.
(iv) *The growth functions* F_1 *and* F_2 *are continuous and piecewise continuously differentiable for* $(0, 0) \leq (p, q) \leq (k_1, k_2)$ *and differentiable at* $(0, 0)$.
(v) *The principal eigenvalue* $\gamma_1(\mu)$ *of the first diagonal block for* C_μ *and the principal eigenvalue* $\gamma_2(\mu)$ *of the second diagonal block for* C_μ *satisfy* $\gamma_1(0) > 0$, $\gamma_1(0) > \gamma_2(0)$, *and the* $(2, 1)$ *element of* C_0 *is positive.*
(vi) *There is a* $\bar{\mu} \in (0, \infty)$ *such that* $\inf_{\mu>0}\{\Phi(\mu)\} = \Phi(\bar{\mu})$ *and* $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$, *where* $\Phi(\mu) := \frac{\gamma_1(\mu)}{\mu}$.
(vii) *For any* $\rho > 0$, $\mathbf{F}(\rho\zeta(\bar{\mu})) \leq \rho D\mathbf{F}(\theta)\zeta(\bar{\mu})$, *where* $\zeta(\mu) = (\zeta_1(\mu), \zeta_2(\mu))$ *is the eigenvector corresponding to* $\gamma_1(\mu)$.

Then, system (2.4) *has a single spreading speed* c^* *and it is linearly determinate. Moreover, the speed is indeed equal to* $\Phi(\bar{\mu})$.

We are now in the position to state and prove the first main result.

THEOREM 3.1 *Assume that either* (H1)–(A1) *or* (H2)–(A1) *holds. If*

(C1) $\frac{d_2}{d_1} \leq 2$,

then system (2.4) *has a single spreading speed* c^* *and it is linearly determinate, with the speed being given by*

$$c^* = 2\sqrt{d_1 f\left(\frac{w_2}{c_{22}}\right)}.$$

Proof By the preparations in Section 2, the conditions (i)–(iv) in the above proposition are easily verified for (2.4). The principal eigenvalues of the first diagonal block and the second block are

$$\gamma_1(\mu) = d_1\mu^2 + f\left(\frac{w_2}{c_{22}}\right), \quad \gamma_2(\mu) = d_2\mu^2 + w_2 g'(w_2) \tag{3.2}$$

respectively. The eigenvector corresponding to $\gamma_1(\mu)$ is $\zeta(\mu) = (\zeta_1(\mu), \zeta_2(\mu))$, where

$$\begin{aligned} \zeta_1(\mu) &= \gamma_1(\mu) - \gamma_2(\mu) = (d_1 - d_2)\mu^2 + \left[f\left(\frac{w_2}{c_{22}}\right) - w_2 g'(w_2)\right], \\ \zeta_2(\mu) &= -\frac{w_2}{c_{22}} g'(w_2) > 0. \end{aligned} \tag{3.3}$$

Thus, by the properties of f and g, we have

$$\gamma_1(0) = f\left(\frac{w_2}{c_{22}}\right) > 0 > w_2 g'(w_2) = \gamma_2(0). \tag{3.4}$$

The $(2, 1)$ entry in the matrix C_0 is $-(w_2/c_{22})g'(w_2)$ which is obviously positive. Thus, the hypothesis (v) in Proposition 3.1 is satisfied.

Note that

$$\Phi(\mu) := \frac{\gamma_1(\mu)}{\mu} = d_1\mu + \frac{f(\frac{w_2}{c_{22}})}{\mu} \tag{3.5}$$

is a concave up function of $\mu > 0$. Thus, there is a finite $\bar{\mu} > 0$ such that $\Phi(\bar{\mu}) = \inf_{\mu>0} \Phi(\mu)$. Indeed, simple calculations give

$$\bar{\mu} = \sqrt{\frac{f(\frac{w_2}{c_{22}})}{d_1}} \text{ and } \Phi(\bar{\mu}) = 2\sqrt{d_1 f\left(\frac{w_2}{c_{22}}\right)}.$$

Since

$$\gamma_1(\bar{\mu}) = 2f\left(\frac{w_2}{c_{22}}\right), \quad \gamma_2(\bar{\mu}) = \frac{d_2}{d_1} f\left(\frac{w_2}{c_{22}}\right) + w_2 g'(w_2),$$

the hypothesis $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$ in (vi) of Proposition 3.1 is equivalent to

$$\left(2 - \frac{d_2}{d_1}\right) f\left(\frac{w_2}{c_{22}}\right) > w_2 g'(w_2), \tag{3.6}$$

which is guaranteed by the condition (C1).

For any constant $\rho > 0$,

$$\mathbf{F}(\rho\zeta(\bar{\mu})) = \begin{pmatrix} \rho\zeta_1(\bar{\mu}) f(\frac{w_2}{c_{22}} + c_{11}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu})) \\ -\left[\frac{w_2}{c_{22}} - \rho\zeta_2(\bar{\mu})\right] g(w_2 + \rho\zeta_1(\bar{\mu}) - c_{22}\rho\zeta_2(\bar{\mu})) \end{pmatrix}$$

and

$$\rho D\mathbf{F}(\theta)\zeta(\bar{\mu}) = \begin{pmatrix} f\left(\frac{w_2}{c_{22}}\right)\rho\zeta_1(\bar{\mu}) \\ -\frac{w_2}{c_{22}} g'(w_2)\rho\zeta_1(\bar{\mu}) + w_2 g'(w_2)\rho\zeta_2(\bar{\mu}) \end{pmatrix}.$$

Making use of (3.3), we can see that condition (vii) in Proposition 3.1 is equivalent to

$$\begin{cases} f\left(\frac{w_2}{c_{22}} + c_{11}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu})\right) \le f(\frac{w_2}{c_{22}}), \\ g(w_2 + \rho\zeta_1(\bar{\mu}) - c_{22}\rho\zeta_2(\bar{\mu})) - \rho g'(w_2)[\zeta_1(\bar{\mu}) - c_{22}\zeta_2(\bar{\mu})] \\ \quad + \rho g'(w_2) g(w_2 + \rho\zeta_1(\bar{\mu}) - c_{22}\rho\zeta_2(\bar{\mu})) \ge 0. \end{cases} \tag{3.7}$$

By the formulas of $\bar{\mu}$, $\zeta_1(\bar{\mu})$ and $\zeta_2(\bar{\mu})$, and using (C1) again, we obtain

$$\begin{aligned} &c_{11}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu}) \\ &\quad = \rho c_{11}\left[\zeta_1(\bar{\mu}) - \tfrac{1}{c_{11}}\zeta_2(\bar{\mu})\right] \\ &\quad = \rho c_{11}\left[(2 - \tfrac{d_2}{d_1}) f(\tfrac{w_2}{c_{22}}) - w_2\left(1 - \tfrac{1}{c_{11}c_{22}}\right) g'(w_2)\right] \ge 0. \end{aligned}$$

Thus, the first inequality in (3.7) follows from the monotone property of the fitness function f.

For the second inequality in (3.7), first we note that $\zeta_1(\bar{\mu}) - c_{22}\zeta_2(\bar{\mu}) = (2 - d_2/d_1) f(w_2/c_{22}) \ge 0$ leading to

$$w_2 + \zeta_1(\bar{\mu}) - c_{22}\zeta_2(\bar{\mu}) \ge w_2.$$

It follows from the concave up property of g that

$$g(w_2 + \rho\zeta_1(\bar{\mu}) - c_{22}\rho\zeta_2(\bar{\mu})) - \rho g'(w_2)[\zeta_1(\bar{\mu}) - c_{22}\zeta_2(\bar{\mu})] \ge 0.$$

Finally, the properties of g also imply

$$\rho g'(w_2) g(w_2 + \rho\zeta_1(\bar{\mu}) - c_{22}\rho\zeta_2(\bar{\mu})) \ge 0.$$

Hence, the second inequality in (3.7) also holds, implying that (vii) in Proposition 3.1 is satisfied. The proof of this theorem is then completed by using Proposition 3.1. □

Remark 3.1 Assume that $0 \le p(x,0) < u^*$, $0 \le q(x,0) < \frac{w_2}{c_{22}} - v^*$, and $p(x,0)$ and $q(x,0)$ are zero outside a bounded set. By the meaning of c^*, we know that for any $\epsilon > 0$, the corresponding solution to (2.4) satisfies

$$\lim_{t\to\infty} \sup_{|x|\ge(c^*+\epsilon)t} \left[p^2(x,t)+q^2(x,t)\right] = 0;$$

and if $(p(x,0), q(x,0)) \gg 0$ on an interval, then

$$\lim_{t\to\infty} \sup_{|x|\le(c^*-\epsilon)t} \left(\left[u^* - p(x,t)\right]^2 + \left[\frac{w_2}{c_{22}} - v^* - q(x,t)\right]^2\right) = 0.$$

Next, we consider (2.5) under the assumptions (H1)–(A2). For convenience of applying Proposition 3.1, we rewrite (2.5) as

$$\begin{cases} \dfrac{\partial q}{\partial t} = d_2\dfrac{\partial^2 q}{\partial x^2} + q\, g\left(\dfrac{z_0}{c_{11}} - p + c_{22}q\right) =: d_2\dfrac{\partial^2 q}{\partial x^2} + G_1(q,p), \\ \dfrac{\partial p}{\partial t} = d_1\dfrac{\partial^2 p}{\partial x^2} - \left(\dfrac{z_0}{c_{11}} - p\right) f(z_0 - c_{11}p + q) =: d_1\dfrac{\partial^2 p}{\partial x^2} + G_2(q,p). \end{cases} \tag{3.8}$$

The linearized system of (3.8) at the equilibrium $\theta = (0,0)$ is

$$\begin{cases} \dfrac{\partial q}{\partial t} = d_2\dfrac{\partial^2 q}{\partial x^2} + g\left(\dfrac{z_0}{c_{11}}\right) q, \\ \dfrac{\partial p}{\partial t} = d_1\dfrac{\partial^2 p}{\partial x^2} - \dfrac{z_0}{c_{11}} f'(z_0)q + z_0 f'(z_0)p. \end{cases} \tag{3.9}$$

Let $\mathbf{G} = (G_1, G_2)$. The Jacobian matrix of (3.8) at $\theta = (0,0)$ is

$$D\mathbf{G}(\theta) = \begin{pmatrix} g\left(\dfrac{z_0}{c_{11}}\right) & 0 \\ -\dfrac{z_0}{c_{11}} f'(z_0) & z_0 f'(z_0) \end{pmatrix}.$$

and accordingly, the so-called coefficient matrix of (3.9) is

$$C_\mu = \begin{pmatrix} d_2\mu^2 + g\left(\dfrac{z_0}{c_{11}}\right) & 0 \\ -\dfrac{z_0}{c_{11}} f'(z_0) & d_1\mu^2 + z_0 f'(z_0) \end{pmatrix}.$$

Parallel to Theorem 3.1 for (2.4), we have the following result for (3.8).

THEOREM 3.2 *Assume that* (H1), (A2)*, and the following hold:*

(C2) $\frac{d_1}{d_2} \le 2$,

then system (3.8) *(i.e.* (2.5)*) has a single spreading speed* c^* *and it is linearly determinate. Moreover, the speed is indeed given by*

$$c^* = 2\sqrt{d_2 g\left(\frac{z_0}{c_{11}}\right)}.$$

Proof Obviously, Proposition 3.1 is also valid for (3.8) with (2.4) replaced by (3.8), **F** replaced by **G** and the order of p and q switched. Again it is easy to verify that the hypotheses (i)–(iv) in Proposition 3.1 are satisfied for system (3.8). In the rest of the proof, we just need to verify the conditions (v)–(vii).

The principal eigenvalues of the first diagonal block and the second block of C_μ are

$$\gamma_1(\mu) = d_2\mu^2 + g\left(\frac{z_0}{c_{11}}\right), \quad \gamma_2(\mu) = d_1\mu^2 + z_0 f'(z_0) \tag{3.10}$$

respectively. The eigenvector associated with $\gamma_1(\mu)$ is $\zeta(\mu) = (\zeta_1(\mu), \zeta_2(\mu))$, where

$$\begin{aligned}\zeta_1(\mu) &= \gamma_1(\mu) - \gamma_2(\mu) = (d_2 - d_1)\mu^2 + \left[g\left(\frac{z_0}{c_{11}}\right) - z_0 f'(z_0)\right],\\ \zeta_2(\mu) &= -\frac{z_0}{c_{11}} f'(z_0) > 0.\end{aligned} \tag{3.11}$$

It follows from (H1) that $\gamma_1(0) = g(z_0/c_{11}) > 0 > z_0 f'(z_0) = \gamma_2(0)$, verifying (v).

To verify condition (vi), we calculate

$$\Phi(\mu) := \frac{\gamma_1(\mu)}{\mu} = d_2\mu + \frac{g(\frac{z_0}{c_{11}})}{\mu} \tag{3.12}$$

which attains its global infimum at $\bar{\mu} > 0$ with

$$\bar{\mu} = \sqrt{\frac{g(\frac{z_0}{c_{11}})}{d_2}} > 0 \text{ and } \Phi(\bar{\mu}) = 2\sqrt{d_2 g\left(\frac{z_0}{c_{11}}\right)}.$$

Note that

$$\gamma_1(\bar{\mu}) = 2g\left(\frac{z_0}{c_{11}}\right), \quad \gamma_2(\bar{\mu}) = \frac{d_1}{d_2} g\left(\frac{z_0}{c_{11}}\right) + z_0 f'(z_0).$$

Hence, the hypothesis $\gamma_1(\bar{\mu}) > \gamma_2(\bar{\mu})$ in (vi) of Proposition 3.1 is equivalent to

$$\left(2 - \frac{d_1}{d_2}\right) g\left(\frac{z_0}{c_{11}}\right) > z_0 f'(z_0), \tag{3.13}$$

which is guaranteed by the condition (C2).

It remains to verify the condition (vii) which is expressed as $\mathbf{G}(\rho\zeta(\bar{\mu})) \le \rho D\mathbf{G}(\theta)\zeta(\bar{\mu})$ for any constant $\rho > 0$. Note that for $\rho > 0$,

$$\mathbf{G}(\rho\zeta(\bar{\mu})) = \begin{pmatrix} \rho\zeta_1(\bar{\mu}) g\left(\frac{z_0}{c_{11}} + c_{22}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu})\right) \\ -\left[\frac{z_0}{c_{11}} - \rho\zeta_2(\bar{\mu})\right] f(z_0 + \rho\zeta_1(\bar{\mu}) - c_{11}\rho\zeta_2(\bar{\mu})) \end{pmatrix}$$

and

$$\rho D\mathbf{G}(\theta)\zeta(\bar{\mu}) = \begin{pmatrix} g\left(\dfrac{z_0}{c_{11}}\right)\rho\zeta_1(\bar{\mu}) \\ -\dfrac{z_0}{c_{11}}f'(z_0)\rho\zeta_1(\bar{\mu}) + z_0 f'(z_0)\rho\zeta_2(\bar{\mu}) \end{pmatrix}.$$

Hence, (vii) in Proposition 3.1 is equivalent to

$$\begin{cases} g\left(\dfrac{z_0}{c_{11}} + c_{22}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu})\right) \le g\left(\dfrac{z_0}{c_{11}}\right), \\ f(z_0 + \rho\zeta_1(\bar{\mu}) - c_{11}\rho\zeta_2(\bar{\mu})) - \rho f'(z_0)[\zeta_1(\bar{\mu}) - c_{11}\zeta_2(\bar{\mu})] \\ \quad + \rho f'(z_0) f(z_0 + \rho\zeta_1(\bar{\mu}) - c_{11}\rho\zeta_2(\bar{\mu})) \ge 0. \end{cases} \tag{3.14}$$

By the formulas of $\bar{\mu}$, $\zeta_1(\bar{\mu})$, and $\zeta_2(\bar{\mu})$, as well as the condition (C2), we then have

$$\begin{aligned} &c_{22}\rho\zeta_1(\bar{\mu}) - \rho\zeta_2(\bar{\mu}) \\ &\quad = \rho c_{22}\left[\zeta_1(\bar{\mu}) - \tfrac{1}{c_{22}}\zeta_2(\bar{\mu})\right] \\ &\quad = \rho c_{22}\left[\left(2 - \tfrac{d_1}{d_2}\right) g\left(\tfrac{z_0}{c_{11}}\right) - z_0\left(1 - \tfrac{1}{c_{11}c_{22}}\right) f'(z_0)\right] \ge 0. \end{aligned}$$

Thus, by the monotone property of fitness function g on $[\frac{z_0}{c_{11}}, \infty)$ (noting $w^* < \frac{z_0}{c_{11}}$ under $(A2)$), the first inequality in (3.14) holds.

Note that $\zeta_1(\bar{\mu}) - c_{11}\zeta_2(\bar{\mu}) = \left(2 - \frac{d_1}{d_2}\right) g\left(\frac{z_0}{c_{11}}\right) \ge 0$ by (C2), that is,

$$z_0 + \zeta_1(\bar{\mu}) - c_{11}\zeta_2(\bar{\mu}) \ge z_0.$$

Since the fitness function f is concave up on $[z_0, \infty)$, we obtain

$$f(z_0 + \rho\zeta_1(\bar{\mu}) - c_{11}\rho\zeta_2(\bar{\mu})) - \rho f'(z_0)[\zeta_1(\bar{\mu}) - c_{11}\zeta_2(\bar{\mu})] \ge 0.$$

Furthermore, we know from the property of f that

$$\rho f'(z_0) f(z_0 + \rho\zeta_1(\bar{\mu}) - c_{11}\rho\zeta_2(\bar{\mu})) \ge 0.$$

Thus, the second inequality in (3.14) also holds, implying that (vii) in Proposition 3.1 is satisfied. The proof of this theorem is completed. □

Remark 3.2 Assume that $0 \le p(x, 0) < \frac{z_0}{c_{11}} - u^*$, $0 \le q(x, 0) < v^*$, and $p(x, 0)$ and $q(x, 0)$ are zero outside a bounded set. By the meaning of c^*, we know that for any $\epsilon > 0$, the corresponding solution to (2.5) satisfies

$$\lim_{t\to\infty} \sup_{|x|\ge(c^*+\epsilon)t} \left[p^2(x, t) + q^2(x, t)\right] = 0;$$

and if $(p(x, 0), q(x, 0)) \gg 0$ on an interval, then

$$\lim_{t\to\infty} \sup_{|x|\le(c^*-\epsilon)t} \left(\left[\frac{z_0}{c_{11}} - u^* - p(x, t)\right]^2 + [v^* - q(x, t)]^2\right) = 0.$$

Summarizing the above results, we obtain the following theorem for the original pioneer/climax system (2.1).

THEOREM 3.3 *The following conclusions hold for system* (2.1).

(i) *Suppose either* (H1)–(A1) *or* (H2)–(A1) *hold. Assume that* $\frac{d_2}{d_1} \le 2$. *Then* (2.1) *has a single spreading speed* c^* *given by* $c^* = \bar{c} = 2\sqrt{d_1 f(\frac{w_2}{c_{22}})}$ *and it is linearly determinate. Moreover, if* $0 \le u(x,0) < u^*$, $v^* < v(x,0) \le \frac{w_2}{c_{22}}$, *and* $u(x,0) = 0$ *and* $v(x,0) = \frac{w_2}{c_{22}}$ *outside a bounded set, then for any* $\epsilon > 0$,

$$\lim_{t\to\infty} \sup_{|x|\ge(c^*+\epsilon)t} \left(u^2(x,t) + \left[\frac{w_2}{c_{22}} - v(x,t)\right]^2 \right) = 0;$$

in addition, if $u(x,0) > 0$ *and* $v(x,0) < \frac{w_2}{c_{22}}$ *on an interval, then*

$$\lim_{t\to\infty} \sup_{|x|\le(c^*-\epsilon)t} \left(\left[u^* - u(x,t)\right]^2 + \left[v^* - v(x,t)\right]^2 \right) = 0.$$

(ii) *Suppose* (H1)–(A2) *hold. Assume that* $\frac{d_1}{d_2} \le 2$. *Then* (2.1) *has a single spreading speed* c^* *given by* $c^* = \bar{c} = 2\sqrt{d_2 g(\frac{z_0}{c_{11}})}$ *which is linearly determinate. Moreover, if* $u^* < u(x,0) \le \frac{z_0}{c_{11}}$, $0 \le v(x,0) < v^*$, *and* $u(x,0) = \frac{z_0}{c_{11}}$ *and* $v(x,0) = 0$ *outside a bounded set, then for any* $\epsilon > 0$,

$$\lim_{t\to\infty} \sup_{|x|\ge(c^*+\epsilon)t} \left(\left[\frac{z_0}{c_{11}} - u(x,t)\right]^2 + v^2(x,t) \right) = 0;$$

in addition, if $u(x,0) < \frac{z_0}{c_{11}}$ *and* $v(x,0) > 0$ *on an interval, then*

$$\lim_{t\to\infty} \sup_{|x|\le(c^*-\epsilon)t} \left(\left[u^* - u(x,t)\right]^2 + \left[v^* - v(x,t)\right]^2 \right) = 0.$$

4. Spreading speed as the minimal wave speed

As mentioned in the introduction, the notion of a traveling wave front is closely related to the concept of spreading speed. In this section, we shall consider a suitable family of traveling wave fronts of the model (2.1) within the same range of model parameters as identified in Section 3.

A traveling wave solution of (2.1) is a solution of (2.1) of the form $u(x,t) = \phi(x+ct)$, $v(x,t) = \psi(x+ct)$, where $\phi, \psi \in C^2(\mathbb{R}, \mathbb{R})$ are called the profiles of the traveling wave solution and $c > 0$ is a constant which accounts for the wave speed. Substituting $u(t,x) = \phi(x+ct)$ and $v(t,x) = \psi(x+ct)$ into (2.1) and letting $s = x + ct$, one finds that the profile functions $\phi(s)$ and $\psi(s)$ satisfy the following system of ordinary differential equations

$$\begin{cases} d_1\phi''(s) - c\phi'(s) + \phi(s) f(c_{11}\phi(s) + \psi(s)) = 0, \\ d_2\psi''(s) - c\psi'(s) + \psi(s) g(\phi(s) + c_{22}\psi(s)) = 0. \end{cases} \tag{4.1}$$

When the limits $\lim_{s\to\pm\infty} \phi(s)$ and $\lim_{s\to\pm\infty} \psi(s)$ exist, the traveling wave solution is referred to as a traveling wave front.

We will confine ourselves to the range of the parameters considered in Sections 2 and 3. Accordingly, we will only consider the traveling wave fronts satisfying the following asymptotic boundary conditions:

$$\text{under either (H1)–(A1) or (H2)–(A1):} \quad \begin{cases} \lim_{s\to-\infty} \phi(s) = 0, & \lim_{s\to\infty} \phi(s) = u^*, \\ \lim_{s\to-\infty} \psi(s) = \frac{w_2}{c_{22}}, & \lim_{s\to\infty} \psi(s) = v^*; \end{cases} \tag{4.2}$$

$$\text{under (H1)–(A2):} \quad \begin{cases} \lim_{s\to-\infty} \phi(s) = \frac{z_0}{c_{11}}, & \lim_{s\to\infty} \phi(s) = u^*, \\ \lim_{s\to-\infty} \psi(s) = 0, & \lim_{s\to\infty} \psi(s) = v^*. \end{cases} \tag{4.3}$$

Note that (H1)–(A2) give the exact range of parameters considered in [13] where the following result has been established:

THEOREM 4.1 *Assume that* (H1)–(A2) *hold and that* $\frac{d_1}{d_2} \le 2$. *Then* $c_* = 2\sqrt{d_2 g(\frac{z_0}{c_{11}})}$ *is the minimal wave speed of traveling wave fronts of* (2.1) *connecting* $E_3 = (z_0/c_{11}, 0)$ *and* $E^* = (u^*, v^*)$, *in the sense that for any* $c \ge c_*$, *there is a co-invasion traveling wave front with speed c connecting* E_3 *and* E^*; *and for* $c \in (0, c_*)$ *there is no such traveling wave front with speed c, connecting these two equilibria.*

From this theorem, we see that under (H1)–(A2), the single spreading speed confirmed in Section 3 is nothing but the minimal wave speed. In the sequel, we will show that under either (H1)–(A1) or (H2)–(A1), a similar conclusion holds, as is stated in the following theorem.

THEOREM 4.2 *Assume that either* (H1)–(A1) *or* (H2)–(A1) *hold and* $\frac{d_2}{d_1} \le 2$. *Then* $c_* = 2\sqrt{d_1 f(\frac{w_2}{c_{22}})}$ *is the minimal wave speed of* (2.1) *in the sense that for* $c \ge c_*$, (2.1) *has a traveling wave front with speed c connecting the climax-invasion-only equilibrium* $E_2 = (0, \frac{w_2}{c_{22}})$ *and the coexistence equilibrium* $E^* = (u^*, v^*)$; *and for* $c \in (0, c^*)$ *there is no such traveling wave front with speed c, connecting these two equilibria.*

Proof By equivalence, we only need to consider the traveling wave fronts of (2.4) connecting $\hat{E}_2 = (0, 0)$ and $\hat{E}^* = (u^*, w_{22}/c_{22} - v^*)$. Let $p(t, x) = P(s)$ and $q(t, x) = Q(s)$ with $s = x + ct$. Then the profile functions $P(s)$ and $Q(s)$ need to satisfy

$$\begin{cases} d_1 P''(s) - cP'(s) + F_1(P(s), Q(s)) = 0, \\ d_2 Q''(s) - cQ'(s) + F_2(P(s), Q(s)) = 0, \end{cases} \tag{4.4}$$

as well as the following asymptotic boundary conditions

$$\begin{cases} \lim_{s\to-\infty} P(s) = 0, & \lim_{s\to\infty} P(s) = u^*, \\ \lim_{s\to-\infty} Q(s) = 0, & \lim_{s\to\infty} Q(s) = \frac{w_2}{c_{22}} - v^*. \end{cases} \tag{4.5}$$

Let

$$D = \{(\phi, \psi) \in C(R, R^2) : 0 \le \phi(s) \le u^*, 0 \le \psi(s) \le \frac{w_2}{c_{22}} - v^*, s \in R\}.$$

We define the following wave profile set for the traveling wave fronts for (2.4):

$$\Sigma = \left\{ (\phi, \psi) \in D : \begin{array}{l} (i)\ \phi(s) \text{ is non-decreasing in } R,\ \lim_{s\to-\infty} \phi(s) = 0,\ \lim_{s\to\infty} \phi(s) = u^*, \\ (ii)\ \psi(s) \text{ is non-decreasing in } R,\ \lim_{s\to-\infty} \psi(s) = 0,\ \lim_{s\to\infty} \psi(s) = \frac{w_2}{c_{22}} - v^*. \end{array} \right\}$$

A pair of continuous functions (ϕ, ψ) is called an upper solution of (4.4) if ϕ, ψ are twice continuously differentiable on $\mathbb{R} \setminus S$ and satisfy

$$\begin{aligned} d_1\phi''(s) - c\phi'(s) + F_1(\phi(s), \psi(s)) \le 0, \\ d_2\psi''(s) - c\psi'(s) + F_2(\phi(s), \psi(s)) \le 0, \end{aligned} \tag{4.6}$$

for $s \in \mathbb{R} \setminus S$, where S consists of at most finitely many points. (ϕ, ψ) is called a lower solution of (4.4) if the inequalities in (4.6) are reversed.

Next, we proceed to construct a pair of required upper and lower solutions for (4.4). To this end, we make use of the principal eigenvalue $\gamma_1(\mu)$ and its corresponding eigenvector $\zeta_(\mu)$ given by (3.2) and (3.3). By (H1), $0 < \frac{w_2}{c_{22}} < z_0$, and thus

$$\gamma_1(\mu) = d_1\mu^2 + f\left(\frac{w_2}{c_{22}}\right) > 0 \text{ for } \mu > 0.$$

Note that as a function of μ,

$$\zeta_1(\mu) = \gamma_1(\mu) - \gamma_2(\mu) = (d_1 - d_2)\mu^2 + \left[f\left(\frac{w_2}{c_{22}}\right) - w_2 g'(w_2)\right]$$

is either increasing on $[0, \bar{\mu}]$ (if $d_1 > d_2$) or decreasing on $[0, \bar{\mu}]$ (if $d_1 < d_2$). On the other hand, we have shown in Section 3 that

$$\gamma_1(0) > \gamma_2(0), \quad \gamma_1(\bar{\mu}) = 2f\left(\frac{w_2}{c_{22}}\right) > \frac{d_2}{d_1} f\left(\frac{w_2}{c_{22}}\right) + w_2 g'(w_2) = \gamma_2(\bar{\mu}),$$

implying $\zeta(0) > 0$ and $\zeta(\bar{\mu}) > 0$. Therefore, $\zeta(\mu)$ is in fact a strictly positive eigenvector corresponding to $\gamma_1(\mu)$ for all $\mu \in [0, \bar{\mu}]$.

Note that $c_* = \inf_{\mu > 0} \Phi(\mu) = \Phi(\bar{\mu})$. It is obvious that $\Phi(\mu) = d_1\mu + f(\frac{w_2}{c_{22}})/\mu$ has the following properties: (i) $\Phi(\mu) \to \infty$ as $\mu \to 0^+$; $\Phi(\mu) \to \infty$ as $\mu \to \infty$. (ii) $\Phi(\mu)$ is decreasing for $\mu \in (0, \bar{\mu})$ and increasing for $\mu \in (\bar{\mu}, \infty)$.

Let $c > c^*$ be given. By the above properties, we know that on the interval $(0, \bar{\mu})$ the equation $\Phi(\mu) = c$ has exactly one solution, denoting it by $\mu_1 = \mu(c)$. Choose $\epsilon > 0$ sufficiently small so that $\mu_\epsilon = \mu_1 + \epsilon < \bar{\mu}$ and $\zeta_\epsilon = (\zeta_1(\mu_\epsilon), \zeta_2(\mu_\epsilon)) \gg 0$. Let

$$\gamma_\epsilon = \gamma_1(\mu_\epsilon), \quad c_\epsilon = \Phi(\mu_\epsilon).$$

Obviously, $c_* < c_\epsilon < c$.

Define

$$\begin{aligned} &\bar{P}(s) := \min\{u^*, \zeta_1(\mu_1)e^{\mu_1 s}\}, && \bar{Q}(s) := \min\left\{\tfrac{w_2}{c_{22}} - v^*, \zeta_2(\mu_1)e^{\mu_1 s}\right\}, \\ &\underline{P}(s) := \max\{0, \zeta_1(\mu_1)e^{\mu_1 s} - \delta\zeta_1(\mu_\epsilon)e^{\mu_\epsilon s}\}, && \underline{Q}(s) := 0, \end{aligned}$$

where $\delta > 0$ is sufficiently large. Then we have

$$\underline{P}(s) \le \bar{P}(s), \quad \underline{Q}(s) \le \bar{Q}(s) \quad \text{for } s \in \mathbb{R}.$$

Straightforward but tedious verifications show that $(\bar{P}(s), \bar{Q}(s))$ is an upper solution of (4.4), and $(\underline{P}(s), \underline{Q}(s))$ is a lower solution of (4.4) if $\delta > 0$ is large. Noting that the cooperative property of (2.4) means that the $\mathbf{F}(p, q) = (F_1(p, q), F_2(p, q))$ satisfies the so-called quasi-monotonicity condition. Therefore, the standard iteration approach using the upper solution $(\bar{P}(s), \bar{Q}(s))$ as the initial function lead to existence of a solution to (4.4) satisfying (4.5), implying that (2.4) has a traveling wave front with speed c connecting $\hat{E}$ and $\hat{E}^*$. For details of such iteration schemes see, e.g. [29,30].

For the critical case $c = c_*$, by an argument of perturbing c and taking a limit, similar to that in [29,31], one can also show that (2.4) has a traveling wave front with speed c_* connecting $\hat{E}$ and $\hat{E}^*$. For $c \in (0, c_*)$, the second limit in Remark 3.1 will prevent the existence of a traveling wave front with speed c connecting $\hat{E}$ and $\hat{E}^*$, see, e.g. [19, Theorem 4.3]. The proof is completed. □

Remark 4.1 In the proof of Theorem 4.2, we have made use of the positive eigenvector $\zeta(\mu)$ associated with the principal eigenvalue $\gamma_1(\mu)$ of the matrix C_μ to construct the required upper-lower solutions. For an irreducible nonnegative matrix, the existence of such a positive principal eigenvalue and the corresponding positive eigenvector is guaranteed by the Perron-Frobenius Theorem. In our case, C_μ is nonnegative but it is *reducible*. Thus, the Perron-Frobenius Theorem can not be applied. However, we have shown that C_μ *also* has a positive principal eigenvalue $\gamma_1(\mu)$ and a corresponding *positive* eigenvector $\zeta(\mu)$.

5. Conclusion and discussion

The work [13] considered the existence of traveling wave fronts connecting the pioneer-only boundary equilibrium and a coexistence equilibrium under some conditions on the model parameters. In this work, we have identified some other new ranges of model parameters in the context of traveling wave fronts. Moreover, both within the range of parameters given in [13] and the new ranges newly identified in this paper, we have also confirmed that the two species spread by *a single* spreading speed, and this speed is *linearly determinate* and it coincides with the minimal speed of traveling wave fronts connecting the two relevant equilibria. Note that among the two relevant equilibria is a coexistence equilibrium. Thus, these ranges present a scenario of mild (or friendly) competition, leading to an ultimate coexistence state.

We point out that a common feature for these identified ranges is that the model system (2.1) is quasi-monotone in the corresponding region depending on the two relevant equilibria under consideration, which makes it possible to apply the theory developed in [28]. As the structure of equilibria for this model system is rich, it is also interesting and worthwhile to investigate the same issues as addressed in this paper but for other parameter ranges allowing different equilibrium structure. A complete classification of parameters in this regard will surely help us better understand the causes of biological diversity in nature.

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