Co-invasion waves in a reaction diffusion model for competing pioneer and climax species

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ABSTRACT

In this paper, we consider a reaction diffusion model for competing pioneer and climax species. A previous work has established the existence of traveling wave fronts connecting two competition-exclusion equilibria in certain range of the parameters, while in this paper, we explore the possibility of traveling wave fronts connecting the pioneer-invasion-only equilibrium and the co-invasion equilibrium. By combining the Schauder's fixed point theorem with a pair of the so called desired functions, we show that the model does support such co-invasion waves in some other ranges of parameters. We also determine the minimal speed for such co-invasion waves in terms of the parameters, and discuss some biological implications and significance of the results.

1. Introduction

In ecology and evolution, interactions among species could be very complicated but play a crucial role in the process of evolution and in maintaining the biological diversity of nature. Animal or plant populations may in some occasions *compete*, while in other situations *cooperate* with one another in order to obtain sufficient natural resources such as food, shelter, light, space, carbon dioxide, and soil nutrients to sustain growth and survival. As a result, the population growth rates of the involving species may depend more on the total density of all populations in an ecosystem than on any individual species. Such observations have led to the development of population models where a species' per capita growth rate (i.e., fitness) is a function of a weighted average of the populations of all interacting species. The most classic example of such a model is the Lotka-Volterra system, in which the per capita growth rate is a linear combination of the densities of the interacting populations. Other pioneering work along this line include those of Buchanan [2,3], Comins and Hassell [4], Cushing [5,6], Franke and Yakubu [7,8], Hofbauer et al. [11], May [16], Selgrade and Namkoong [18,19], Selgrade [20–22], and Summer[23,24].

The interaction between a pioneer species and a climax species provides a more specific example. As is known, some species thrive best at lower densities and thus are good candidates for pioneering. For example, certain varieties of pine and poplar have a fitness which decreases with total population density, mainly due to the effects of crowding on reproduction and survival. Such species are often referred to as "pioneer" species. In contrast, some other species have higher survival and reproduction rates at higher densities, due to group defense for prey, increased gene pools, enhanced soil nutrients and photosynthetic adaption to shade etc. Such species are referred to as "climax" species. The differential equations describing the interaction between a pioneer species and a climax species offer a class of important population models where the fitness functions are described as pioneer and climax fitness respectively. By the features of the interaction, a pioneer fitness function should be a decreasing function of a weighted total population density. Ricker [17] has hypothesized that some fish

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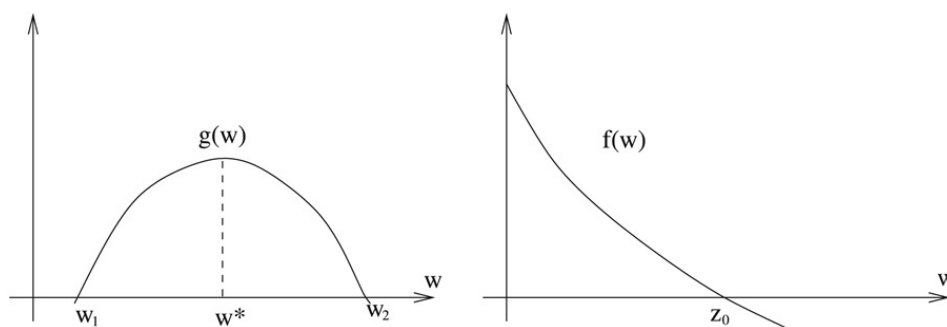 *E-mail address:* xzou@uwo.ca (X. Zou).

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

populations have pioneer fitness of exponential decay type. Hassell and Comins [10] analyzed some discrete time Lotka-Volterra models containing rational pioneer fitness functions. Climax species express a different response to environmental crowding. The fitness of a climax species increases at lower total densities to a maximum before decreasing at higher densities. Such a "one-humped" fitness functions reflects the beneficial effects of increasing density between certain lower range and the disadvantageous effects of extreme overcrowding on reproduction and survival. For more details on such responses, interested readers are referred to Cushing [6], Freedman and Wolkowicz [9], and Wolkowicz [26].

Ignoring spatial variances and considering continuous time, a typical model for the interaction of a pioneering species and a climax species is given by the following system of ordinary differential equations:

$$\begin{cases} \dfrac{du}{dt} = uf(c_{11}u + c_{12}v), \\ \dfrac{dv}{dt} = vg(c_{21}u + c_{22}v), \end{cases} \tag{1.1}$$

where the variables u and v represent densities of the pioneer and the climax species respectively, f and g are continuous functions and denote pioneer fitness function and climax fitness function respectively. The matrix

$$\begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}$$

with $c_{ij} > 0 \, (i, j = 1, 2)$ gives the weight distribution among species, and is called the interaction matrix. A rescaling $c_{21}u \to u$, $c_{12}v \to v$ transforms (1.1) to

$$\begin{cases} \dfrac{du}{dt} = uf(c_{11}u + v), \\ \dfrac{dv}{dt} = vg(u + c_{22}v). \end{cases} \tag{1.2}$$

The pioneer fitness function $f \in C^1(-\infty, \infty)$ and satisfies:

$$f'(y) < 0, \qquad f(z_0) = 0 \quad \text{for } y \in R, \text{ some } z_0 > 0. \tag{1.3}$$

The climax fitness $g \in C^1(-\infty, \infty)$ is a lumped function which attains its maximum at the intermediate density w^* while negative below a low density w_1 and above a high density w_2, that is,

$$\begin{cases} g(w_1) = g(w_2) = 0, & \text{for } 0 < w_1 < w_2 \\ (w^* - w)g'(w) > 0, & \text{for } w > 0 \text{ and } w \neq w^* \in (w_1, w_2). \end{cases} \tag{1.4}$$

Fig. 1 depicts typical fitness functions for climax species and pioneer species.

It turns out that depending on the locations of the three nullclines:

$$c_{11}u + v = z_0,$$
$$u + c_{22} = w_1,$$
$$u + c_{22} = w_2,$$

the long term behavior of solutions to (1.2) can be qualitatively different. Selgrade and Namkoong [18,19], Selgrade and Roberds [22] and Sumner [23] analyzed the Hopf bifurcation of (1.2). Selgrade and Namkoong [18,19] presented examples where the pioneer and the climax populations may coexist in the sense that there is a stable coexistence equilibrium. Buchanan [2] has given a good classification for (1.2).

In reality, spatial variance may be significant and species may disperse. For simplicity, we only consider one-dimensional space R. Assuming a random dispersal mechanism and by incorporating a spatial variable x into (1.2), we are given the following reaction-diffusion system

$$\begin{cases} u_t = uf(c_{11}u + v) + d_1 u_{xx}, \\ v_t = vg(u + c_{22}v) + d_2 v_{xx}. \end{cases} \tag{1.5}$$

Here, $u \equiv u(x, t)$ and $v \equiv v(x, t)$ represent densities of the pioneer and the climax species respectively at location x at time t, and $d_i > 0$, $i = 1, 2$, account for the species dispersion in the spatially continuous space R. An immediate problem for (1.5) is the impact of the diffusion on the dynamics of solutions. Indeed, Buchanan [3] already investigated the Turing instability for (1.5), the instability caused by diffusion. Another important topic for (1.5) is traveling wave solutions, because such solutions explain spatial spread or invasion of the species. A traveling wave solution of (1.5) is a solution of the form $u(t, x) = \phi(x + ct)$ and $v(t, x) = \psi(x + ct)$ with $\phi, \psi \in C^2(R, R)$ being called the profile of the traveling wave and $c > 0$ being the wave speed. When d_2 is small relative to d_1, using the singular perturbation method, Brown et al. [1] studied the existence of traveling wave solution of (1.5) connecting two boundary equilibria. These traveling waves gives a pattern of switching: spatial domain initially occupied by pioneering specie will be eventually taken over fully by the climax species with certain speed. Thus, no co-existence is observed in such a situation. On the other hand, co-existence is common in the real world. As we mentioned above, Selgrade and Namkoong [18,19] obtained stable co-existence equilibrium for (1.2). One may naturally ask: does system (1.5) allow traveling wave solutions connecting a boundary equilibrium (the pioneer-invasive equilibrium) and a co-existence equilibrium? This question constitutes the purpose of this paper. In this paper, we combine the techniques developed in recent work [27,31] with the Schauder's fixed point theorem to show that in some parameter ranges, system (1.5) does support traveling waves connecting the pioneer-invasion-only equilibrium and a co-existence equilibrium. We point out that this approach has also been applied recently by [12–15,28] to various reaction-diffusion systems with delays. The main results are summarized in the following theorem:

Theorem 1. *Assume that* (1.3) *and* (1.4) *and* $d_2 \geq d_1/2$ *hold. Then,*

(i) *for any* $c \geq 2\sqrt{d_2 g(z_0/c_{11})}$, *system* (1.5) *has a co-invasion traveling wave front connecting the pioneer-invasion-only equilibrium* $(z_0/c_{11}, 0)$ *and a coexistence equilibrium* (u^*, v^*), *with speed* c.

(ii) $c^* := 2\sqrt{d_2 g(z_0/c_{11})}$ *is the minimal wave speed in the sense for any* $c \in (0, c^*)$ *there will be no traveling front with speed* c, *connecting these two equilibria.*

The rest of this paper is organized as follows: Section 2 contains some preliminary results about the approach. In Section 3, by constructing a pair of appropriated upper and lower solutions, we obtain a subset. Applying the Schauder's fixed point theorem to the corresponding operator in this subset, we prove the existence of monotone traveling wave fronts connecting a boundary equilibrium and a co-existence equilibrium. We also indentify the minimal wave speed for such monotone traveling wave fronts in this section. Section 4 concludes the paper with a brief discussion.

2. Preliminaries

A traveling wave solution of (1.5) is a solution of the form $u(t, x) = \phi(x + ct)$ and $v(t, x) = \psi(x + ct)$, where $\phi, \psi \in C^2(R, R)$ and $c > 0$ is a constant corresponding to the wave speed. Substituting $u(t, x) = \phi(x + ct)$ and $v(t, x) = \psi(x + ct)$ into (1.5) and letting $s = x + ct$, one finds that the profile functions $\phi(s)$ and $\psi(s)$ satisfy the following system of ordinary differential equations

$$\begin{cases} d_1\phi''(s) - c\phi'(s) + \phi(s)f(c_{11}\phi(s) + \psi(s)) = 0, \\ d_2\psi''(s) - c\psi'(s) + \psi(s)g(\phi(s) + c_{22}\psi(s)) = 0. \end{cases} \tag{2.1}$$

If $\lim_{s\to\pm\infty} \phi(s) = u_\pm$ and $\lim_{s\to\pm\infty} \psi(s) = v_\pm$ exist, the traveling wave solution is referred to as a traveling wave front which explains the transition from the state (u_-, v_-) to the other state (u_+, v_+). It is known that these two states must be equilibria of (1.5) (as well as (1.2)), meaning that

$$u_+ f(c_{11}u_+ + v_+) = 0, \qquad v_+ g(u_+ + c_{22}v_+) = 0,$$
$$u_- f(c_{11}u_- + v_-) = 0, \qquad v_- g(u_- + c_{22}v_-) = 0.$$

As mentioned in the introduction, we are interested in traveling wave fronts accounting for co-invasion of the two species, and hence it is natural to pose conditions that guarantee existence of a co-existence equilibrium. By the properties of f and g, a co-existence equilibrium is obtained by solving either

$$\begin{cases} c_{11}u + v = z_0 \\ u + c_{22}v = w_1 \end{cases} \tag{2.2}$$

or

$$\begin{cases} c_{11}u + v = z_0 \\ u + c_{22}v = w_2 \end{cases} \tag{2.3}$$
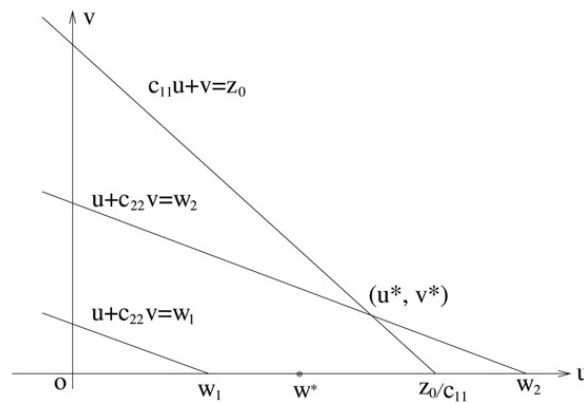
Fig. 2. Typical fitness functions for climax species and pioneer species.

for positive solution. Here we consider the following range of parameters:

$$z_0 > \frac{w_2}{c_{22}}, \qquad w_1 < \frac{z_0}{c_{11}} < w_2, \quad \text{and} \quad c_{11}c_{22} > 1. \tag{2.4}$$

Under the above assumption, it is easy to see that in addition to the trivial equilibrium $(0, 0)$, (1.5) has the following four non-trivial equilibria: $(\frac{z_0}{c_{11}}, 0)$, $(0, \frac{w_2}{c_{22}})$, $(0, \frac{w_1}{c_{22}})$ and the co-existence equilibrium (u^*, v^*) where

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

It is obvious that $u^* < z_0/c_{11}$. For a detailed discussion of all equilibria of (1.1), we refer to Buchanan [2]. For convenience of discussion, we further assume, in the remainder of the paper, the following technical condition

$$w^* \leq u^*. \tag{2.5}$$

See Fig. 2 the positions of the involving points corresponding to our assumptions.

With the above conditions, our aim becomes to seek traveling wave fronts of (1.5) connecting the two equilibria $(\frac{z_0}{c_{11}}, 0)$ and (u^*, v^*). Thus, we need assign to (2.1) the following asymptotic boundary conditions:

$$\begin{cases} \lim_{s \to -\infty} \phi(s) = \frac{z_0}{c_{11}}, & \lim_{s \to \infty} \phi(s) = u^*, \\ \lim_{s \to -\infty} \psi(s) = 0, & \lim_{s \to \infty} \psi(s) = v^*. \end{cases} \tag{2.6}$$

In the sequel, we need to investigate positive solutions of (2.1)–(2.6). To this end, we need some preparation.

Let

$$D = \{(\phi, \psi) \in C(R, R^2) : u^* \leq \phi(s) \leq z_0/c_{11}, 0 \leq \psi(s) \leq v^*, s \in R\}.$$

For constants β_1 and β_2, define the operator $H = (H_1, H_2) : D \to C(R, R^2)$ by

$$\begin{cases} H_1(\phi, \psi)(t) = \phi(t)f(c_{11}\phi(t) + \psi(t)) + \beta_1\phi(t), \\ H_2(\phi, \psi)(t) = \psi(t)g(\phi(t) + c_{22}\psi(t)) + \beta_2\psi(t). \end{cases} \tag{2.7}$$

Then (2.1) can be rewritten as

$$\begin{cases} d_1\phi''(t) - c\phi'(t) - \beta_1\phi(t) + H_1(\phi(t), \psi(t)) = 0, \\ d_2\psi''(t) - c\psi'(t) - \beta_2\psi(t) + H_2(\phi(t), \psi(t)) = 0. \end{cases} \tag{2.8}$$

Let

$$\lambda_1 = \frac{c - \sqrt{c^2 + 4d_1\beta_1}}{2d_1}, \qquad \lambda_2 = \frac{c + \sqrt{c^2 + 4d_1\beta_1}}{2d_1},$$

$$\lambda_3 = \frac{c - \sqrt{c^2 + 4d_2\beta_2}}{2d_2}, \qquad \lambda_4 = \frac{c + \sqrt{c^2 + 4d_2\beta_2}}{2d_2}.$$

Then it is easy to verify that

$$\lambda_1 < 0 < \lambda_2, \qquad \lambda_3 < 0 < \lambda_4,$$
$$d_1\lambda_i^2 - c\lambda_i - \beta_1 = 0, \quad i = 1, 2,$$
$$d_2\lambda_i^2 - c\lambda_i - \beta_2 = 0, \quad i = 3, 4.$$

Define the operator $F = (F_1, F_2) : D \to C(R, R^2)$ by

$$
\begin{cases}
F_1(\phi, \psi)(t) = \dfrac{1}{d_1(\lambda_2 - \lambda_1)} \left[\displaystyle\int_{-\infty}^{t} e^{\lambda_1(t-s)} H_1(\phi, \psi)(s)\mathrm{d}s + \int_{t}^{\infty} e^{\lambda_2(t-s)} H_1(\phi, \psi)(s)\mathrm{d}s \right], \\
F_2(\phi, \psi)(t) = \dfrac{1}{d_2(\lambda_4 - \lambda_3)} \left[\displaystyle\int_{-\infty}^{t} e^{\lambda_3(t-s)} H_2(\phi, \psi)(s)\mathrm{d}s + \int_{t}^{\infty} e^{\lambda_4(t-s)} H_2(\phi, \psi)(s)\mathrm{d}s \right].
\end{cases}
\tag{2.9}
$$

It is obvious that $(F_1(\phi, \psi), F_2(\phi, \psi)) \in C^2(R, R^2)$ if ϕ, ψ are continuous and bounded in R (see, [15,28,30]).

One can verify that the operator F is well defined and for any $(\phi, \psi) \in D$,

$$
\begin{cases}
d_1(F_1(\phi, \psi))''(t) - c(F_1(\phi, \psi))'(t) - \beta_1(F_1(\phi, \psi))(t) + H_1(\phi(t), \psi(t)) = 0, \\
d_2(F_2(\phi, \psi))''(t) - c(F_2(\phi, \psi))'(t) - \beta_2(F_2(\phi, \psi))(t) + H_2(\phi(t), \psi(t)) = 0.
\end{cases}
\tag{2.10}
$$

Thus, a fixed point of F is a solution of (2.1).

Next, we introduce the exponential decay norm in $C(R, R^2)$. For $\mu > 0$, define

$$
B_\mu(R, R^2) = \{\Phi \in C(R, R^2) : \sup_{t \in R} |\Phi(t)| e^{-\mu|t|} < \infty\}
$$

and

$$
|\Phi|_\mu = \sup_{t \in R} |\Phi(t)| e^{-\mu|t|}.
$$

Then it is easy to check that $(B_\mu(R, R^2), |\cdot|_\mu)$ is a Banach space. For our purpose, we will take $\mu > 0$ such that

$$
\mu < \min\{-\lambda_1, \lambda_2, -\lambda_3, \lambda_4\}.
\tag{2.11}
$$

Now we explore some basic properties of H.

Lemma 1. *For sufficiently large $\beta_1, \beta_2 > 0$ and for $(\phi_i, \psi_i) \in D$, $i = 1, 2$ with $\phi_1(s) \leq \phi_2(s)$ and $\psi_1(s) \leq \psi_2(s)$, $s \in R, i = 1, 2$, we have*

$$
\begin{cases}
H_1(\phi_2, \psi_1)(t) \geq H_1(\phi_1, \psi_1)(t), \\
H_1(\phi_1, \psi_2)(t) \leq H_1(\phi_1, \psi_1)(t), \\
H_2(\phi_1, \psi_2)(t) \geq H_2(\phi_1, \psi_1)(t), \\
H_2(\phi_2, \psi_1)(t) \leq H_2(\phi_1, \psi_1)(t)
\end{cases}
\tag{2.12}
$$

for all $t \in R$.

Proof. Let $f_1(x, y) = xf(c_{11}x + y) + \beta_1 x$ and $f_2(x, y) = yg(x + c_{22}y) + \beta_2 y$. For $u^* \leq x \leq z_0/c_{11}$ and $0 \leq y \leq v^*$ and sufficiently large numbers $\beta_1 > 0$ and $\beta_2 > 0$, it follow that

$$
\frac{\partial}{\partial x} f_1(x, y) = f(c_{11}x + y) + c_{11}xf'(c_{11}x + y) + \beta_1 \geq 0
$$

and

$$
\frac{\partial}{\partial y} f_2(x, y) = g(x + c_{22}y) + c_{22}yg'(x + c_{22}y) + \beta_2 \geq 0.
$$

Thus, the first and the third inequalities hold.

From (1.3) it follows that

$$
H_1(\phi_1, \psi_2)(t) - H_1(\phi_1, \psi_1)(t) = \phi_1(t) \left[f(c_{11}\phi_1(t) + \psi_2(t)) - f(c_{11}\phi_1(t) + \psi_1(t)) \right] \leq 0
$$

for all $t \in R$. On the other hand, since $\phi + c_{22}\psi \geq u^* \geq w^*$ for $u^* \leq \phi \leq z_0/c_{11}$ and $0 \leq \psi \leq v^*$, it follows that

$$
H_2(\phi_2, \psi_1)(t) - H_2(\phi_1, \psi_1)(t) = \psi_1(t) \left[g(\phi_2(t) + c_{22}\psi_1(t)) - g(\phi_1(t) + c_{22}\psi_1(t)) \right] \leq 0
$$

for all $t \in R$, competing the proof. $\square$

Lemma 2. *Assume $\beta_1 > 0$ and $\beta_2 > 0$ are sufficiently large. For $(\phi, \psi) \in D$ with $\phi(t)$ nonincreasing and $\psi(s)$ nondecreasing in R, $H_1(\phi, \psi)(t)$ is nonincreasing and $H_2(\phi, \psi)(t)$ is nondecreasing in R.*

Proof. For any $s > 0, \phi(t + s) \leq \phi(t)$ and $\psi(t + s) \geq \psi(t)$. It follows from Lemman 1 that

$$
\begin{aligned}
H_1(\phi, \psi)(t + s) - H_1(\phi, \psi)(t) &= [H_1(\phi(t + s), \psi(t + s)) - H_1(\phi(t), \psi(t + s))] \\
&\quad + [H_1(\phi(t), \psi(t + s)) - H_1(\phi(t), \psi(t))] \\
&\leq 0, \quad \text{for } s \geq 0.
\end{aligned}
$$

Similarly, we can prove that $H_2(\phi, \psi)(t)$ is nondecreasing, completing the proof. $\square$

By Lemmas 1 and 2 and (2.9), we can easily see that $F = (F_1, F_2)$ also enjoys the same properties as those for $H = (H_1, H_2)$ stated in Lemmas 1 and 2.

Lemma 3. *For sufficiently large $\beta_1, \beta_2 > 0$ and for $(\phi_i, \psi_i) \in D$, $i = 1, 2$ with $\phi_1(s) \leq \phi_2(s)$ and $\psi_1(s) \leq \psi_2(s)$, $s \in R$, $i = 1, 2$, we have*

$$\begin{cases} F_1(\phi_2, \psi_1)(t) \geq F_1(\phi_1, \psi_1)(t), \\ F_1(\phi_1, \psi_2)(t) \leq F_1(\phi_1, \psi_1)(t), \\ F_2(\phi_1, \psi_2)(t) \geq F_2(\phi_1, \psi_1)(t), \\ F_2(\phi_2, \psi_1)(t) \leq F_2(\phi_1, \psi_1)(t) \end{cases} \tag{2.13}$$

for all $t \in R$.

Lemma 4. *Assume $\beta_1 > 0$ and $\beta_2 > 0$ are sufficiently large. For $(\phi, \psi) \in D$ with $\phi(t)$ nonincreasing and $\psi(s)$ nondecreasing in R, $F_1(\phi, \psi)(t)$ is nonincreasing and $F_2(\phi, \psi)(t)$ is nondecreasing in R.*

Denote

$$\Lambda^+ = \left\{ (\phi, \psi) \in D \cap C^2(R, R^2) \left| \begin{array}{l} d_1 \phi''(t) - c\phi'(t) - \beta_1 \phi(t) + H_1(\phi(t), \psi(t)) \geq 0; \\ d_2 \psi''(t) - c\psi'(t) - \beta_2 \psi(t) + H_2(\phi(t), \psi(t)) \leq 0, \end{array} \right. \text{for } t \in R, \right\},$$

and

$$\Lambda^- = \left\{ (\phi, \psi) \in D \cap C^2(R, R^2) \left| \begin{array}{l} d_1 \phi''(t) - c\phi'(t) - \beta_1 \phi(t) + H_1(\phi(t), \psi(t)) \leq 0; \\ d_2 \psi''(t) - c\psi'(t) - \beta_2 \psi(t) + H_2(\phi(t), \psi(t)) \geq 0, \end{array} \right. \text{for } t \in R, \right\}.$$

In what follows, we assume that there exist $\overline{\Phi} = (\overline{\phi}, \overline{\psi}) \in \Lambda^+$ and $\underline{\Phi} = (\underline{\phi}, \underline{\psi}) \in \Lambda^-$ satisfying

(P1) $u^* \leq \overline{\phi} \leq \underline{\phi} \leq z_0/c_{11}$, $0 \leq \underline{\psi} \leq \overline{\psi} \leq v^*$;

(P2) $\overline{\phi}(t) \leq \inf_{s \leq t} \underline{\phi}(s)$ and $\sup_{s \leq t} \underline{\psi}(s) \leq \overline{\psi}(t)$ for $t \in R$;

(P3) $(uf(c_{11}u + v), vg(u + c_{22}v)) \neq (0, 0)$ for $u \in [\sup_{t \in R} \overline{\phi}(t), z_0/c_{11}) \cup (u^*, \inf_{t \in R} \underline{\phi}(t)]$ and $v \in (0, \inf_{t \in R} \overline{\psi}(t)] \cup [\sup_{t \in R} \underline{\psi}(t), v^*)$.

Using this pair of desirable functions, we define the following profile set:

$$\Gamma(\underline{\Phi}, \overline{\Phi}) = \left\{ (\phi, \psi) \in D, \begin{array}{ll} \text{(i)} & \overline{\phi}(t) \leq \phi(t) \leq \underline{\phi}(t), \ \underline{\psi}(t) \leq \psi(t) \leq \overline{\psi}(t) \\ \text{(ii)} & \phi(t) \text{ is non-increasing in } R \\ \text{(iii)} & \psi(t) \text{ is nondecreasing in } R \end{array} \right\}.$$

Obviously, $\Gamma(\underline{\Phi}, \overline{\Phi})$ is non-empty since $(\varphi_1(t), \varphi_2(t)) \in \Gamma(\underline{\Phi}, \overline{\Phi})$ with $\varphi_1(t) = \inf_{s \leq t} \underline{\phi}(s)$ and $\varphi_2(t) = \sup_{s \leq t} \underline{\psi}(s)$.

In the rest of this section, we will apply Schauder's fixed point theorem to F on the set $\Gamma(\underline{\Phi}, \overline{\Phi})$ to establish the existence of solution to (2.1). The following lemmas verify the conditions for this fixed point theorem. The proofs are similar to those in [12–14], but for the sake of completeness and for readers' convenience, we will give their proofs here.

Lemma 5. *The map $F = (F_1, F_2) : D \to C(R, R^2)$ is continuous with respect to the norm $|\cdot|_\mu$ in $B_\mu(R, R^2)$.*

Proof. We first prove that $H_1 : D \to C(R, R^2)$ is continuous with respect to the norm $|\cdot|_\mu$. For $\Phi = (\phi_1, \psi_1)$, $\Psi = (\phi_2, \psi_2) \in D$, since the functions $f, g \in C^1(-\infty, \infty)$, it follows that there exist constants $L_1 > 0$, $L_2 > 0$ such that

$$|f(c_{11}\phi_1(t) + \psi_1(t))| \leq L_1$$

and

$$|f(c_{11}\phi_1(t) + \psi_1(t)) - f(c_{11}\phi_2(t) + \psi_2(t))| \leq L_2(c_{11}|\phi_1(t) - \phi_2(t)| + |\psi_1(t) - \psi_2(t)|).$$

Thus,

$$\begin{aligned} &|H_1(\phi_1, \psi_1)(t) - H_1(\phi_2, \psi_2)(t)|e^{-\mu|t|} \\ &= |\phi_1(t)f(c_{11}\phi_1(t) + \psi_1(t)) - \phi_2(t)f(c_{11}\phi_2(t) + \psi_2(t)) + \beta_1(\phi_1(t) - \phi_2(t))|e^{-\mu|t|} \\ &= |(\phi_1(t) - \phi_2(t))f(c_{11}\phi_1(t) + \psi_1(t)) + \phi_2(t)(f(c_{11}\phi_1(t) + \psi_1(t)) - f(c_{11}\phi_2(t) + \psi_2(t))) \\ &\quad + \beta_1(\phi_1(t) - \phi_2(t))|e^{-\mu|t|} \\ &\leq [L_1|\phi_1(t) - \phi_2(t)| + z_0 c_{11}^{-1} L_2(c_{11}|\phi_1(t) - \phi_2(t)| + |\psi_1(t) - \psi_2(t)|) + \beta_1|\phi_1(t) - \phi_2(t)|]e^{-\mu|t|} \\ &\leq (L_1 + z_0 L_2 + z_0 L_2 c_{11}^{-1} + \beta_1) \sup_{t \in R} |\Phi(t) - \Psi(t)|e^{-\mu|t|} \\ &= (L_1 + z_0 L_2 + z_0 L_2 c_{11}^{-1} + \beta_1)|\Phi - \Psi|_\mu. \end{aligned}$$

Now for any fixed $\epsilon > 0$, let $\delta < \epsilon(L_1 + z_0L_2 + z_0L_2c_{11}^{-1} + \beta_1)^{-1}$. If $\Phi = (\phi_1, \psi_1)$, $\Psi = (\phi_2, \psi_2) \in D$ satisfy $|\Phi - \Psi|_\mu < \delta$, then

$$
\begin{aligned}
|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu &= |H_1(\phi_1, \psi_1)(t) - H_1(\phi_2, \psi_2)(t)|e^{-\mu|t|} \\
&\leq (L_1 + z_0L_2 + z_0L_2c_{11}^{-1} + \beta_1)|\Phi - \Psi|_\mu < \epsilon.
\end{aligned}
$$

That is, $H_1 : D \to C(R, R^2)$ is continuous with respect to the norm $|\cdot|_\mu$.

Now, we show that $F_1 : D \to C(R, R^2)$ is also continuous with respect to the norm $|\cdot|_\mu$. For $t \geq 0$, we find

$$
\begin{aligned}
|F_1(\phi_1, \psi_1)(t) - F_1(\phi_2, \psi_2)(t)| &\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_{-\infty}^t e^{\lambda_1(t-s)}|H_1(\phi_1, \psi_1)(s) - H_1(\phi_2, \psi_2)(s)|ds \right. \\
&\quad \left. + \int_t^\infty e^{\lambda_2(t-s)}|H_1(\phi_1, \psi_1)(s) - H_1(\phi_2, \psi_2)(s)|ds\right] \\
&= \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_{-\infty}^t e^{\lambda_1(t-s)+\mu|s|}|H_1(\phi_1, \psi_1)(s) - H_1(\phi_2, \psi_2)(s)|e^{-\mu|s|}ds \right. \\
&\quad \left. + \int_t^\infty e^{\lambda_2(t-s)+\mu|s|}|H_1(\phi_1, \psi_1)(s) - H_1(\phi_2, \psi_2)(s)|e^{-\mu|s|}ds\right] \\
&\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_0^t e^{\lambda_1(t-s)+\mu s}ds + \int_{-\infty}^0 e^{\lambda_1(t-s)-\mu s}ds \right. \\
&\quad \left. + \int_t^\infty e^{\lambda_2(t-s)+\mu s}ds\right]|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu \\
&= \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\frac{\lambda_2 - \lambda_1}{(\mu - \lambda_1)(\lambda_2 - \mu)}e^{\mu t} + \frac{2\mu}{\lambda_1^2 - \mu^2}e^{\lambda_1 t}\right]|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu.
\end{aligned}
$$

Hence, for $t \geq 0$ we have

$$
\begin{aligned}
&|F_1(\phi_1, \psi_1)(t) - F_1(\phi_2, \psi_2)|e^{-\mu|t|} \\
&\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\frac{\lambda_2 - \lambda_1}{(\mu - \lambda_1)(\lambda_2 - \mu)} + \frac{2\mu}{\lambda_1^2 - \mu^2}e^{(\lambda_1 - \mu)t}\right]|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu \\
&\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\frac{\lambda_2 - \lambda_1}{(\mu - \lambda_1)(\lambda_2 - \mu)} + \frac{2\mu}{\lambda_1^2 - \mu^2}\right]|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu.
\end{aligned}
$$

Similarly, for $t \leq 0$, we have

$$
\begin{aligned}
&|F_1(\phi_1, \psi_1)(t) - F_1(\phi_2, \psi_2)|e^{-\lambda|t|} \\
&\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\frac{\lambda_2 - \lambda_1}{-(\mu + \lambda_1)(\lambda_2 + \mu)} + \frac{2\mu}{\lambda_1^2 - \mu^2}\right]|H_1(\phi_1, \psi_1) - H_1(\phi_2, \psi_2)|_\mu.
\end{aligned}
$$

The above two inequalities together with the continuity of H_1 establish the continuity of F_1. By a similar argument, we can obtain the continuity of F_2. Therefore the map $F = (F_1, F_2) : D \to C(R, R^2)$ is continuous with respect to the norm $|\cdot|_\mu$ in $B_\mu(R, R^2)$. This completes the proof. $\square$

Lemma 6. *For sufficiently large $\beta_1 > 0$ and $\beta_2 > 0$, we have $F(\Gamma(\underline{\Phi}, \overline{\Phi})) \subset \Gamma(\underline{\Phi}, \overline{\Phi})$.*

Proof. For any $(\phi, \psi) \in \Gamma(\underline{\Phi}, \overline{\Phi})$, by Lemma 3, it is easy to see that

$$
\begin{aligned}
F_1(\overline{\phi}, \overline{\psi}) &\leq F_1(\phi, \psi) \leq F_1(\underline{\phi}, \underline{\psi}), \\
F_2(\underline{\phi}, \underline{\psi}) &\leq F_2(\phi, \psi) \leq F_2(\overline{\phi}, \overline{\psi}).
\end{aligned}
$$

Now, in order to verify the condition (i) in the set $\Gamma(\underline{\Phi}, \overline{\Phi})$ for $F(\phi, \psi) = (F_1(\phi, \psi), F_2(\phi, \psi))$, we need to prove

$$
\begin{aligned}
\overline{\phi} &\leq F_1(\overline{\phi}, \overline{\psi}) \leq F_1(\underline{\phi}, \underline{\psi}) \leq \underline{\phi}, \\
\underline{\psi} &\leq F_2(\underline{\phi}, \underline{\psi}) \leq F_2(\overline{\phi}, \overline{\psi}) \leq \overline{\psi}.
\end{aligned}
$$

Employing the integration by parts and by the definitions of λ_1 and λ_2, we obtain

$$
F_1(\overline{\phi}, \overline{\psi})(t) = \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_{-\infty}^t e^{\lambda_1(t-s)} + \int_t^\infty e^{\lambda_2(t-s)}\right]H_1(\overline{\phi}, \overline{\psi})(s)ds
$$

$$\geq \frac{1}{d_1(\lambda_2 - \lambda_1)} \left[\int_{-\infty}^{t} e^{\lambda_1(t-s)} + \int_{t}^{\infty} e^{\lambda_2(t-s)} \right] (\beta_1 \overline{\phi}(s) + c\overline{\phi}'(s) - d_1\overline{\phi}''(s)) ds$$

$$= \overline{\phi}(t), \quad t \in R.$$

In a similar way, we can prove that $F_1(\underline{\phi}, \underline{\psi}) \leq \underline{\phi}, \underline{\psi} \leq F_2(\underline{\phi}, \underline{\psi})$, and $F_2(\overline{\phi}, \overline{\psi}) \leq \overline{\psi}$. On the other hand, Lemma 4 implies that $\overline{F_1}(\underline{\phi}, \underline{\psi})(t)$ is nonincreasing and $\overline{F_2}(\overline{\phi}, \underline{\psi})(t)$ is nondecreasing in R verifying conditions (ii) and (iii) for $F(\phi, \psi)$. The proof is complete. $\square$

Lemma 7. *For sufficiently large $\beta_1 > 0$ and $\beta_2 > 0$, $F : \Gamma(\underline{\Phi}, \overline{\Phi}) \to \Gamma(\underline{\Phi}, \overline{\Phi})$ is compact.*

Proof. We first establish an estimate for F. For any $(\phi, \psi) \in \Gamma(\underline{\Phi}, \overline{\Phi})$,

$$(F_1(\phi, \psi))'(t) = \frac{\lambda_1 e^{\lambda_1 t}}{d_1(\lambda_2 - \lambda_1)} \int_{-\infty}^{t} e^{-\lambda_1 s} H_1(\phi, \psi)(s) ds + \frac{\lambda_2 e^{\lambda_2 t}}{d_1(\lambda_2 - \lambda_1)} \int_{t}^{\infty} e^{-\lambda_2 s} H_1(\phi, \psi)(s) ds.$$

Thus,

$$|(F_1(\phi, \psi))'|_\mu \leq \sup_{t \in R} \left[e^{-\mu|t|} \frac{|\lambda_1| e^{\lambda_1 t}}{d_1(\lambda_2 - \lambda_1)} \int_{-\infty}^{t} e^{-\lambda_1 s} H_1(\phi, \psi)(s) ds + e^{-\mu|t|} \frac{\lambda_2 e^{\lambda_2 t}}{d_1(\lambda_2 - \lambda_1)} \int_{t}^{\infty} e^{-\lambda_2 s} H_1(\phi, \psi)(s) ds \right]$$

$$\leq \frac{|\lambda_1|}{d_1(\lambda_2 - \lambda_1)} \sup_{t \in R} e^{\lambda_1 t - \mu|t|} \int_{-\infty}^{t} e^{-\lambda_1 s} e^{\mu|s|} e^{-\mu|s|} H_1(\phi, \psi)(s) ds$$

$$+ \frac{\lambda_2}{d_1(\lambda_2 - \lambda_1)} \sup_{t \in R} e^{\lambda_2 t - \mu|t|} \int_{t}^{\infty} e^{-\lambda_2 s} e^{\mu|s|} e^{-\mu|s|} H_1(\phi, \psi)(s) ds$$

$$\leq \frac{|\lambda_1|}{d_1(\lambda_2 - \lambda_1)} |H_1(\phi, \psi)|_\mu \sup_{t \in R} e^{\lambda_1 t - \mu|t|} \int_{-\infty}^{t} e^{-\lambda_1 s + \mu|s|} ds$$

$$+ \frac{\lambda_2}{d_1(\lambda_2 - \lambda_1)} |H_1(\phi, \psi)|_\mu \sup_{t \in R} e^{\lambda_2 t - \mu|t|} \int_{t}^{\infty} e^{-\lambda_2 s + \mu|s|} ds.$$

Therefore, for $t > 0$, we have

$$|(F_1(\phi, \psi))'|_\mu \leq \frac{|\lambda_1|}{d_1(\lambda_2 - \lambda_1)(-\lambda_1 - \mu)} |H_1(\phi, \psi)|_\mu + \frac{\lambda_2}{d_1(\lambda_2 - \lambda_1)(\lambda_2 - \mu)} |H_1(\phi, \psi)|_\mu$$

$$= \frac{1}{d_1(\lambda_2 - \lambda_1)} \left[\frac{\lambda_1}{\lambda_1 + \mu} + \frac{\lambda_2}{\lambda_2 - \mu} \right] |H_1(\phi, \psi)|_\mu.$$

Similarly, for $t \leq 0$, we have

$$|(F_1(\phi, \psi))'|_\mu \leq \frac{|\lambda_1|}{d_1(\lambda_2 - \lambda_1)(-\lambda_1 - \mu)} |H_1(\phi, \psi)|_\mu$$

$$+ \frac{\lambda_2}{d_1(\lambda_2 - \lambda_1)(\lambda_2 - \mu)} \left[\left| \frac{1}{\lambda_2 - \mu} - \frac{1}{\lambda_2 + \mu} \right| + \frac{1}{\lambda_2 + \mu} \right] |H_1(\phi, \psi)|_\mu$$

$$= \frac{1}{d_1(\lambda_2 - \lambda_1)} \left[\frac{\lambda_1}{\lambda_1 + \mu} + \frac{\lambda_2}{\lambda_2 - \mu} \right] |H_1(\phi, \psi)|_\mu.$$

Since $H : D \to C(R, R^2)$ is continuous with respect to the norm $|\cdot|_\mu$ and the set $\Gamma(\underline{\Phi}, \overline{\Phi})$ is uniformly bounded, there exists a constant M_1 such that $|(F_1(\phi, \psi))'|_\mu \leq M_1$. Similarly, there exists a constant M_2 such that $|(F_2(\phi, \psi))'|_\mu \leq M_2$. Hence F is equicontinuous on $\Gamma(\underline{\Phi}, \overline{\Phi})$ and $F\Gamma(\underline{\Phi}, \overline{\Phi})$ is uniformly bounded.

Define $F^n(\phi, \psi)$ by

$$F^n(\phi, \psi)(t) = \begin{cases} F(\phi, \psi)(t), & t \in [-n, n]; \\ F(\phi, \psi)(n), & t \in (n, \infty); \\ F(\phi, \psi)(-n), & t \in (-\infty, -n). \end{cases}$$

Then, for any $n \geq 1$, F^n is also equicontinuous and uniformly bounded. Ascoli–Arzela lemma implies that F^n is compact. The following estimate is obvious:

$$\sup_{t \in R} |F^n(\phi, \psi)(t) - F(\phi, \psi)(t)| e^{-\mu|t|} = \sup_{t \in (-\infty, -n) \cup (n, \infty)} |F^n(\phi, \psi)(t) - F(\phi, \psi)(t)| e^{-\mu|t|}$$

$$\leq 2M_0 e^{-\mu n} \to 0 \text{ as } n \to \infty.$$

where M_0 is a positive constant such that

$$|(\phi, \psi)| \leq M_0 \quad \text{for any } (\phi, \psi) \in \Gamma(\underline{\Phi}, \overline{\Phi}),$$

Thus, the sequence of compact operators $\{F^n\}_0^\infty$ converges to F in $\Gamma(\underline{\Phi}, \overline{\Phi})$ with respect to the norm $|\cdot|_\mu$. By Proposition 2.1 in [29], we conclude that F is also compact. $\quad\square$

Lemma 8. *Assume that $\overline{\phi}, \overline{\psi}, \underline{\phi}$ and $\underline{\psi}$ satisfy properties (P1)–(P3), then (2.1) has a monotone solution (ϕ, ψ) in $\Gamma(\underline{\Phi}, \overline{\Phi})$ satisfying (2.6).*

Proof. By Lemmas 5–7 and the obvious fact that the set $\Gamma(\underline{\Phi}, \overline{\Phi})$ is closed, bounded and convex in the space $B_\mu(R, R^2)$, Schauder's fixed point is applicable to the map F, implying that F has a fixed point $\Phi = (\phi, \psi)$ in $\Gamma(\underline{\Phi}, \overline{\Phi})$. That is, (2.1) has a solution (ϕ, ψ) in $\Gamma(\underline{\Phi}, \overline{\Phi})$.

Also, we have

$$\sup_{t \in R} \overline{\phi}(t) \le \phi_- =: \lim_{t \to -\infty} \phi(t) \le z_0/c_{11}, \qquad u^* \le \phi_+ =: \lim_{t \to \infty} \phi(t) \le \inf_{t \in R} \underline{\phi}(t) \tag{2.14}$$

and

$$0 \le \psi_- =: \lim_{t \to -\infty} \psi(t) \le \inf_{t \in R} \overline{\psi}(t), \qquad \sup_{t \in R} \underline{\psi}(t) \le \psi_+ =: \lim_{t \to \infty} \psi(t) \le v^*. \tag{2.15}$$

Then by a similar argument as in [15,27], we have

$$\phi_+ f(c_{11}\phi_+ + \psi_+) = 0, \qquad \psi_+ g(\phi_+ + c_{22}\psi_+) = 0,$$
$$\phi_- f(c_{11}\phi_- + \psi_-) = 0, \qquad \psi_- g(\phi_- + c_{22}\psi_-) = 0.$$

Therefore, it follows follows from (2.14), (2.15), and Property (P3) that

$$\phi_- = \lim_{t \to -\infty} \phi(t) = z_0/c_{11}, \qquad \phi_+ = \lim_{t \to \infty} \phi(t) = u^*,$$
$$\psi_- = \lim_{t \to -\infty} \psi(t) = 0, \qquad \psi_+ = \lim_{t \to \infty} \psi(t) = v^*.$$

Thus (ϕ, ψ) is a monotone solution of (2.1) satisfying (2.6) in $\Gamma(\underline{\Phi}, \overline{\Phi})$, giving a the profile of a co-invasion wave front of (1.5). This completes the proof. $\quad\square$

3. The existence of wave fronts

From the results in Section 2, we see that if we can find a pair of desirable functions $\underline{\Phi} \in \Lambda^-$ and $\overline{\Phi} \in \Lambda^+$ satisfying (P1)–(P3), then we can claim that there exists a traveling wave front for (1.5) connecting pioneer-invasion-only equilibrium $(z_0/c_{11}, 0)$ and the co-invasion equilibrium (u^*, v^*). In this section, we construct such a pair of functions within certain range of parameters, via the following lemmas.

Lemma 9. *Suppose $d_2 \ge d_1/2$ and $c \ge 2\sqrt{d_2 g(z_0/c_{11})}$. Define*

$$\overline{\rho}_1(t) = \max\left\{\frac{z_0}{c_{11}} - e^{\lambda_0 t}, u^*\right\}, \qquad \overline{\rho}_2(t) = \min\{c_{11} e^{\lambda_0 t}, v^*\}, \tag{3.1}$$

where

$$\lambda_0 =: \frac{c - \sqrt{c^2 - 4d_2 g(z_0/c_{11})}}{2d_2}. \tag{3.2}$$

Then

$$(\overline{\phi}(t), \overline{\psi}(t)) \triangleq F(\overline{\rho}_1(t), \overline{\rho}_2(t)) \in \Lambda^+.$$

Proof. Let t_{11} and t_{12} be such that

$$\frac{z_0}{c_{11}} - e^{\lambda_0 t_{11}} = u^*, \qquad c_{11} e^{\lambda_0 t_{12}} = v^*.$$

Notice that $c_{11}u^* + v^* = z_0$, we solve that $t_{11} = t_{12} \triangleq \frac{1}{\lambda_0} \ln \frac{v^*}{c_{11}}$. Using $d_2 \ge d_1/2$, we have

$$d_1 \overline{\rho}_1''(t) - c\overline{\rho}_1'(t) + \overline{\rho}_1(t)f(c_{11}\overline{\rho}_1(t) + \overline{\rho}_2(t)) = e^{\lambda_0 t}(-d_1\lambda_0^2 + c\lambda_0) + \left(\frac{z_0}{c_{11}} - e^{\lambda_0 t}\right)f(z_0)$$
$$= \lambda_0 e^{\lambda_0 t}(-d_1\lambda_0 + c) \ge 0, \quad t < t_0;$$
$$d_1 \overline{\rho}_1''(t) - c\overline{\rho}_1'(t) + \overline{\rho}_1(t)f(c_{11}\overline{\rho}_1(t) + \overline{\rho}_2(t)) = 0, \quad t > t_0,$$

and

$$d_2\overline{\rho}_2''(t) - c\overline{\rho}_2'(t) + \overline{\rho}_2(t)g\left(\overline{\rho}_1(t) + c_{22}\overline{\rho}_2(t)\right) = c_{11}e^{\lambda_0 t}(d_2\lambda_0^2 - c\lambda_0) + c_{11}e^{\lambda_0 t}g\left(\frac{z_0}{c_{11}} - e^{\lambda_0 t} + c_{11}c_{22}e^{\lambda_0 t}\right)$$

$$\le c_{11}e^{\lambda_0 t}[d_2\lambda_0^2 - c\lambda_0 + g(z_0/c_{11})] = 0, \quad t < t_0,$$

and

$$d_2\overline{\rho}_2''(t) - c\overline{\rho}_2'(t) + \overline{\rho}_2(t)g(\overline{\rho}_1(t) + c_{22}\overline{\rho}_2(t)) = v^*g(u^* + c_{22}v^*) = v^*g(w_2) = 0, \quad t > t_0.$$

By integration by parts (see [15,28,30]) and the fact that $\overline{\rho}_2'(t_0+) < \overline{\rho}_2'(t_0-)$ (see e.g., [15,28,30]), we have

$$
\begin{aligned}
\overline{\psi}(t) &= F_2(\overline{\rho}_1, \overline{\rho}_2) \\
&\le \frac{1}{d_2(\lambda_4 - \lambda_3)}\left[\int_{-\infty}^{t} e^{\lambda_3(t-s)}(-d_2\overline{\rho}_2''(s) + c\overline{\rho}_2'(s) + \beta_2\overline{\rho}_2(s))\right. \\
&\quad \left. + \int_t^{\infty} e^{\lambda_4(t-s)}(-d_2\overline{\rho}_2''(s) + c\overline{\rho}_2'(s) + \beta_2\overline{\rho}_2(s))\right] \\
&= \overline{\rho}_2(t) + \frac{1}{d_2(\lambda_4 - \lambda_3)}e^{\lambda(t-t_0)}[\overline{\rho}_2'(t_0+) - \overline{\rho}_2'(t_0-)] \quad (\lambda = \lambda_3 \text{ or } \lambda_4) \\
&\le \overline{\rho}_2(t), \quad t \in R.
\end{aligned}
$$

By a similar argument, we have

$$
\begin{aligned}
\overline{\phi}(t) &= F_1(\overline{\rho}_1, \overline{\rho}_2) \\
&\ge \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_{-\infty}^{t} e^{\lambda_1(t-s)}(-d_1\overline{\rho}_1''(s) + c\overline{\rho}_1'(s) + \beta_1\overline{\rho}_1(s))\right. \\
&\quad \left. + \int_t^{\infty} e^{\lambda_2(t-s)}(-d_1\overline{\rho}_1''(s) + c\overline{\rho}_1'(s) + \beta_1\overline{\rho}_1(s))\right] \\
&= \overline{\rho}_1(t) + \frac{1}{d_2(\lambda_2 - \lambda_1)}e^{\lambda(t-t_0)}[\overline{\rho}_1'(t_0+) - \overline{\rho}_1'(t_0-)] \quad (\lambda = \lambda_1 \text{ or } \lambda_2) \\
&\ge \overline{\rho}_1(t), \quad t \in R.
\end{aligned}
$$

Now, $(\overline{\phi}, \overline{\psi}) \in C^2(R, R^2)$ and Lemma 1 leads to

$$
\begin{aligned}
d_1\overline{\phi}''(t) - c\overline{\phi}'(t) + \overline{\phi}(t)f(c_{11}\overline{\phi}(t) + \overline{\psi}(t)) &= d_1\overline{\phi}''(t) - c\overline{\phi}'(t) - \beta_1\overline{\phi}(t) + H_1(\overline{\phi}(t), \overline{\psi}(t)) \\
&\ge d_1\overline{\phi}''(t) - c\overline{\phi}'(t) - \beta_1\overline{\phi}(t) + H_1(\overline{\rho}_1(t), \overline{\rho}_2(t)) = 0
\end{aligned}
$$

and

$$
\begin{aligned}
d_2\overline{\psi}''(t) - c\overline{\psi}'(t) + \overline{\phi}(t)g(\overline{\phi}(t) + c_{22}\overline{\psi}(t)) &= d_2\overline{\psi}''(t) - c\overline{\psi}'(t) - \beta_2\overline{\psi}(t) + H_2(\overline{\phi}, \overline{\psi})(t) \\
&\le d_2\overline{\psi}''(t) - c\overline{\psi}'(t) - \beta_2\overline{\psi}(t) + H_2(\overline{\rho}_1, \overline{\rho}_2)(t) = 0.
\end{aligned}
$$

Noticing that $F(\overline{\rho}_1, \overline{\rho}_2) \in D \cap C^2(R, R^2)$, we conclude that $(\overline{\phi}, \overline{\psi}) \in \Lambda^+$. This completes the proof. $\quad\square$

Lemma 10. *If* $c \ge 2\sqrt{d_2 g(z_0/c_{11})}$, *then*

$$(\underline{\phi}(t), \underline{\psi}(t)) \triangleq F(\underline{\rho}_1(t), \underline{\rho}_2(t))$$

satisfies $(\underline{\phi}, \underline{\psi}) \in \Lambda^-$ *with*

$$\underline{\rho}_1(t) = z_0/c_{11}, \qquad \underline{\rho}_2(t) = \max\{c_{11}(1 - Le^{\epsilon t})e^{\lambda_0 t}, 0\}, \tag{3.3}$$

where λ_0 *is given by* (3.2), $L > 0$ *is sufficiently large and* $\epsilon > 0$ *is sufficiently small.*

Proof. Notice that

$$d_2\lambda_0^2 - c\lambda_0 + g(z_0/c_{11}) = 0$$

has exactly two positive real zeros $0 \le \lambda_0 < \lambda^*$, so we choose $\epsilon > 0$ sufficiently small such that

$$0 < \epsilon < \lambda_0, \qquad d_2(\lambda_0 + \epsilon)^2 - c(\lambda_0 + \epsilon) + g(z_0/c_{11}) < 0. \tag{3.4}$$

Let $L > 1$ be sufficiently large so that

$$-L[d_2(\lambda_0 + \epsilon)^2 - c(\lambda_0 + \epsilon) + g(z_0/c_{11})] - mc_{11}c_{22} \geq 0, \tag{3.5}$$

where

$$m = - \min_{s \in [z_0/c_{11}, z_0/c_{11} + c_{22}v^*]} g'(s) > 0.$$

By simple calculation, we know that

$$\max_{t \in R}\{\underline{\rho}_2(t)\} = \frac{c_{11}\epsilon}{\lambda_0 + \epsilon}\left(\frac{\lambda_0}{L(\lambda_0 + \epsilon)}\right)^{\frac{\lambda_0}{\epsilon}} \leq v^*,$$

for L sufficiently large. Thus $(\underline{\rho}_1, \underline{\rho}_2) \in D$ if L is sufficiently large.

Let $t_1 = \frac{1}{\epsilon}\ln\frac{1}{L}$. Then, for $t < t_1$,

$$
\begin{aligned}
(1 - Le^{\epsilon t})g(z_0/c_{11} + c_{11}c_{22}(1 - Le^{\epsilon t})e^{\lambda_0 t}) &= (1 - Le^{\epsilon t})\{[g(z_0/c_{11} + c_{11}c_{22}(1 - Le^{\epsilon t})e^{\lambda_0 t}) - g(z_0/c_{11})] + g(z_0/c_{11})\} \\
&\geq (1 - Le^{\epsilon t})[-mc_{11}c_{22}(1 - Le^{\epsilon t})e^{\lambda_0 t} + g(z_0/c_{11})] \\
&\geq g(z_0/c_{11}) - Lg(z_0/c_{11})e^{\epsilon t} - mc_{11}c_{22}e^{\lambda_0 t}.
\end{aligned}
$$

Hence, for $t < t_1$,

$$
\begin{aligned}
d_2\underline{\rho}_2''(t) - c\underline{\rho}_2'(t) + \underline{\rho}_2(t)g(\underline{\rho}_1(t) + c_{22}\underline{\rho}_2(t)) &= c_{11}(d_2\lambda_0^2 - c\lambda_0)e^{\lambda_0 t} - Lc_{11}[d_2(\lambda_0 + \epsilon)^2 - c(\lambda_0 + \epsilon)]e^{(\lambda_0 + \epsilon)t} \\
&\quad + c_{11}(1 - Le^{\epsilon t})e^{\lambda_0 t}g(z_0/c_{11} + c_{11}c_{22}(1 - Le^{\epsilon t})e^{\lambda_0 t}) \\
&\geq c_{11}[d_2\lambda_0^2 - c\lambda_0 + g(z_0/c_{11})]e^{\lambda_0 t} - c_{11}\{L[d_2(\lambda_0 + \epsilon)^2 - c(\lambda_0 + \epsilon) + g(z_0/c_{11})] + mc_{11}c_{22}e^{(\lambda_0 - \epsilon)t}\}e^{(\lambda_0 + \epsilon)t} \\
&\geq -c_{11}\{L[d_2(\lambda_0 + \epsilon)^2 - c(\lambda_0 + \epsilon) + g(z_0/c_{11})] + mc_{11}c_{22}\}e^{(\lambda_0 + \epsilon)t} \geq 0.
\end{aligned}
$$

When $t \geq t_1$ it is obvious that

$$d_2\underline{\rho}_2''(t) - c\underline{\rho}_2'(t) + \underline{\rho}_2(t)g(\underline{\rho}_1(t) + c_{22}\underline{\rho}_2(t)) = 0.$$

Noting that $\underline{\rho}_2'(t_1+) > \underline{\rho}_2'(t_1-)$, we obtain

$$
\begin{aligned}
\underline{\psi}(t) &= F_2(\underline{\rho}_1, \underline{\rho}_2) \\
&\geq \frac{1}{d_2(\lambda_4 - \lambda_3)}\left[\int_{-\infty}^{t} e^{\lambda_3(t-s)}(-d_2\underline{\rho}_2''(s) + c\underline{\rho}_2'(s) + \beta_2\underline{\rho}_2(s)) + \int_{t}^{\infty} e^{\lambda_4(t-s)}(-d_2\underline{\rho}_2''(s) + c\underline{\rho}_2'(s) + \beta_2\underline{\rho}_2(s))\right] \\
&= \underline{\rho}_2(t) + \frac{1}{d_2(\lambda_4 - \lambda_3)}e^{\lambda(t-t_1)}[\underline{\rho}_2'(t_1+) - \underline{\rho}_2'(t_1-)] \quad (\lambda = \lambda_3 \text{ or } \lambda_4) \\
&\geq \underline{\rho}_2(t), \quad t \in R.
\end{aligned}
$$

By a similar argument, we obtain

$$
\begin{aligned}
\underline{\phi}(t) &= F_1(\underline{\rho}_1, \underline{\rho}_2) \\
&\leq \frac{1}{d_1(\lambda_2 - \lambda_1)}\left[\int_{-\infty}^{t} e^{\lambda_1(t-s)}(-d_1\underline{\rho}_1''(s) + c\underline{\rho}_1'(s) + \beta_1\underline{\rho}_1(s))\right. \\
&\quad \left. + \int_{t}^{\infty} e^{\lambda_2(t-s)}(-d_1\overline{\rho}_1''(s) + c\underline{\rho}_1'(s) + \beta_1\underline{\rho}_1(s))\right] = \underline{\rho}_1(t), \quad t \in R.
\end{aligned}
$$

Now, $(\underline{\phi}, \underline{\psi}) \in C^2(R, R^2)$ and Lemma 1 leads to

$$
\begin{aligned}
d_1\underline{\phi}''(t) - c\underline{\phi}'(t) + \underline{\phi}(t)f(c_{11}\underline{\phi}(t) + \underline{\psi}(t)) &= d_1\underline{\phi}''(t) - c\underline{\phi}'(t) - \beta_1\underline{\phi}(t) + H_1(\underline{\phi}(t), \underline{\psi}(t)) \\
&\leq d_1\underline{\phi}''(t) - c\underline{\phi}'(t) - \beta_1\underline{\phi}(t) + H_1(\underline{\rho}_1(t), \underline{\rho}_2(t)) = 0
\end{aligned}
$$

and

$$
\begin{aligned}
d_2\underline{\psi}''(t) - c\underline{\psi}'(t) + \underline{\phi}(t)g(\underline{\phi}(t) + c_{22}\underline{\psi}(t)) &= d_2\underline{\psi}''(t) - c\underline{\psi}'(t) - \beta_2\underline{\psi}(t) + H_2(\underline{\phi}, \underline{\psi})(t) \\
&\geq d_2\overline{\underline{\psi}}''(t) - c\overline{\underline{\psi}}'(t) - \beta_2\underline{\psi}(t) + H_2(\underline{\rho}_1, \underline{\rho}_2)(t) = 0.
\end{aligned}
$$

Noting that $F(\underline{\rho}_1, \underline{\rho}_2) \in D \cap C^2(R, R^2)$, we conclude that $(\underline{\phi}, \underline{\psi}) \in \Lambda^-$. This completes the proof. $\quad\square$

Lemma 11. *If $d_2 \geq d_1/2$ and*

$$c \geq 2\sqrt{d_2 g(z_0/c_{11})} \tag{3.6}$$

then functions $(\overline{\phi}(t), \overline{\psi}(t))$ and $(\underline{\phi}(t), \underline{\psi}(t))$ defined in Lemmas 9 and 10 satisfy (P1)–(P3).

Proof. Obviously $\overline{\rho}_1(t) \leq \underline{\rho}_1(t)$ and $\overline{\rho}_2(t) \geq \underline{\rho}_2(t)$. It follows from Lemma 3 that $(\overline{\phi}, \overline{\psi})$ and $(\underline{\phi}, \underline{\psi})$ satisfy the property (P1).

In order to complete the proof of (P2) and (P3) for $(\overline{\phi}, \overline{\psi})$ and $(\underline{\phi}, \underline{\psi})$, we first prove $(\overline{\rho}_1, \overline{\rho}_2)$ and $(\underline{\rho}_1, \underline{\rho}_2)$ satisfy (P2) and (P3). Noting that $\overline{\rho}_1(t) \leq z_0/c_{11} = \inf_{s \leq t} \underline{\rho}_1(t)$ and the above argument, we have

$$\sup_{s \leq t} \underline{\rho}_2(s) = \underline{\rho}_2(t) \leq \overline{\rho}_2(t), \quad t \leq t_2 \triangleq \frac{1}{\epsilon} \ln \frac{\lambda_0}{L(\lambda_0 + \epsilon)},$$

and

$$\sup_{s \leq t} \underline{\rho}_2(s) = \underline{\rho}_2(t_2) \leq \overline{\rho}_2(t_2) \leq \overline{\rho}_2(t), \quad t > t_2,$$

which imply that

$$\sup_{s \leq t} \underline{\rho}_2(s) \leq \overline{\rho}_2(t), \quad t \in R. \tag{3.7}$$

Hence, $(\overline{\rho}_1, \overline{\rho}_2)$ and $(\underline{\rho}_1, \underline{\rho}_2)$ satisfy (P2). Noting that in the first quadrant (1.5) has exactly two non-trivial steady states

$$P_0 = (z_0/c_{11}, 0), \qquad P_1 = (u^*, v^*).$$

Thus, there are exactly two zeros of equations

$$uf(c_{11}u + v) = 0, \qquad vg(u + c_{22}v) = 0$$

for $u \in [u^*, z_0/c_{11}]$ and $v \in [0, v^*]$ and thus,

$$(uf(c_{11}u + v), vg(u + c_{22}v)) \neq (0, 0),$$
$$\forall u \in [\sup_{t \in R} \overline{\rho}_1(t), z_0/c_{11}) \cup (u^*, \inf_{t \in R} \underline{\rho}_1(t)] \quad \text{and} \quad v \in (0, \inf_{t \in R} \overline{\rho}_2(t)] \cup [\sup_{t \in R} \underline{\rho}_2(t), v^*).$$

Therefore, $(\overline{\rho}_1, \overline{\rho}_2)$ and $(\underline{\rho}_1, \underline{\rho}_2)$ satisfy (P1)–(P3) as well.

Finally, we will prove $(\overline{\phi}, \overline{\psi}) = (F_1(\overline{\rho}_1, \overline{\rho}_2), F_2(\overline{\rho}_1, \overline{\rho}_2))$ and $(\underline{\phi}, \underline{\psi}) = (F_1(\underline{\rho}_1, \underline{\rho}_2), F_2(\underline{\rho}_1, \underline{\rho}_2))$ also satisfy (P2) and (P3). Denote

$$\hat{\phi}(t) \triangleq \inf_{s \leq t} \underline{\rho}_1(s) = z_0/c_{11}, \qquad \hat{\psi}(t) \triangleq \sup_{s \leq t} \underline{\rho}_2(s).$$

Obviously, $\hat{\psi}(t)$ is nondecreasing in $t \in R$. Since $(\overline{\rho}_1, \overline{\rho}_2)$ and $(\underline{\rho}_1, \underline{\rho}_2)$ satisfy (P1), it follows from Lemmas 3 and 4 that $F_1(\hat{\phi}(t), \hat{\psi}(t))$ is nonincreasing and $F_2(\hat{\phi}(t), \hat{\psi}(t))$ is nondecreasing in $t \in R$. In view of $\hat{\phi}(t) \geq \overline{\rho}_1(t)$ and $\hat{\psi}(t) \leq \overline{\rho}_2(t)$, it is easy to see from (3.7) that

$$\overline{\phi}(t) = F_1(\overline{\rho}_1, \overline{\rho}_2)(t) \leq F_1(\hat{\phi}, \hat{\psi})(t) = \inf_{s \leq t} F_1(\hat{\phi}, \hat{\psi})(s) \leq \inf_{s \leq t} F_1(\underline{\rho}_1, \underline{\rho}_2)(s) = \inf_{s \leq t} \underline{\phi}(s),$$

$$\sup_{s \leq t} \underline{\psi}(s) = \sup_{s \leq t} F_2(\underline{\rho}_1, \underline{\rho}_2)(s) \leq \sup_{s \leq t} F_2(\hat{\phi}, \hat{\psi})(s) = F_2(\hat{\phi}, \hat{\psi})(t) \leq F_2(\overline{\rho}_1, \overline{\rho}_2)(t) = \overline{\psi}(t),$$

implying that $(\overline{\phi}, \overline{\psi})$ and $(\underline{\phi}, \underline{\psi})$ also satisfy (P2).

On the other hand, from the proof of Lemmas 8 and 9, we have

$$\overline{\phi}(t) \geq \overline{\rho}_1(t), \qquad \overline{\psi}(t) \leq \overline{\rho}_2(t), \qquad \underline{\phi}(t) \leq \underline{\rho}_1(t), \qquad \underline{\psi}(t) \geq \underline{\rho}_2(t), \quad t \in R, \tag{3.8}$$

which, together with the fact $(\overline{\rho}_1, \overline{\rho}_2)$ and $(\underline{\rho}_1, \underline{\rho}_2)$ satisfy (P3), implies that $(\overline{\phi}, \overline{\psi})$ and $(\underline{\phi}, \underline{\psi})$ satisfy the property (P3). This completes the proof. □

Proof of Theorem 1. Combining the results in Section 2 with Lemmas 9–11, we have proved part (i) of Theorem 1. Part (ii) can be proved in a similar way to that in [25], by showing that $c \geq 2\sqrt{d_2 g(z_0/c_{11})}$ is actually a necessary condition for the wave speed c. Indeed, if we linearize the second equation in (2.1) at $(z_0/c_{11}, 0)$, we obtain

$$d_2 \psi''(s) - c\psi'(s) + \psi g(z_0/c_{11}) = 0,$$

which has the eigenvalues

$$\mu_1 = \frac{c - \sqrt{c^2 - 4d_2 g(z_0/c_{11})}}{2d_2}, \qquad \mu_2 = \frac{c + \sqrt{c^2 - 4d_2 g(z_0/c_{11})}}{2d_2}.$$

Thus, if $c < 2\sqrt{d_2 g(z_0/c_{11})}$, then μ_1 and μ_2 are complex, implying that solutions of (2.1) near $(z_0/c_{11}, 0)$ oscillate about $(z_0/c_{11}, 0)$ as $s \to -\infty$. Hence, the $\psi(s)$ component of solutions would take negative values. Therefore, biologically meaningful traveling wave front can not exist in such a case. The proof of the theorem is completed. □

4. Conclusion and discussion

We have considered a reaction diffusion model for competing pioneer and climax species. Recent work [1] showed that the model supports traveling wave fronts connecting two boundary equilibria (two competition-exclusion equilibria) in certain range of parameters, while our results here have shown that in some other parameter ranges, the model allows traveling wave fronts connecting the pioneer-invasion-only equilibrium to the co-invasion equilibrium. The existence of such co-invasion waves may account for a "friendly competition", explaining the situation where the pioneer species first invades spatially, followed by a climax species competing *mildly* with the pioneer species, resulting in co-existence of both species in the long term.

In addition to the conditions (1.3) and (1.4) determining the distribution of the equilibria, there are other two conditions for the existence of co-invasion waves. Although we do not have a good explanation for the inequality $d_1 \leq 2d_2$, the whole condition set seemingly suggests that appropriate diffusion rates for the two species also play a role in determining the co-invasion waves, and this may partially confirm the argument that spatial diffusion/dispersal is one of the important factors that lead to biological diversity.

The nature of interaction of pioneer-climax species allows complicated equilibrium structure, as was shown in [2]. The work [1] and our work here only considered two possible cases. Traveling wave fronts connecting other pair of equilibria are also possible for some other parameter ranges, among which, the one connecting the trivial equilibrium $(0, 0)$ with another equilibrium would be of great interest since it corresponds to the concerns of co-extinction.

Acknowledgments

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