

Research Article

Analysis of a Model Arising from Invasion by Precursor and Differentiated Cells

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We study the wave solutions for a degenerated reaction diffusion system arising from the invasion of cells. We show that there exists a family of waves for the wave speed larger than or equal a certain number and below which there are no monotonic wave solutions. We also investigate the monotonicity, uniqueness, and asymptotics of the waves.

1. Introduction

In [1], the following coupled partial differential equation system was proposed to study the invasion by precursor and differentiated cells:

$$\begin{aligned} u_t &= Du_{xx} + \alpha u \left(1 - \frac{u + \nu v}{k_1}\right) - \beta u \left(1 - \frac{\nu}{k_2}\right), \\ v_t &= \beta u \left(1 - \frac{\nu}{k_2}\right), \end{aligned} \quad (1)$$

where $u(x, t)$ denotes the population densities of the precursor cells. The constant $D > 0$ is the diffusion rate of the cell u , which has proliferation rate $\alpha > 0$, and $k_1 > 0$ is the carrying capacity of u . The parameter ν measures the relative contribution that the differentiated cell with population density $v(x, t)$ makes to the carrying capacity k_1 . The cell population density v is limited by its carrying capacity k_2 and has a maximum differentiation rate $\beta > 0$. The model assumes that the differentiated cells do not have mobility.

By letting (see [1])

$$\hat{u} = \frac{u}{k_1}, \quad \hat{v} = \frac{\nu}{k_1}, \quad \hat{t} = \alpha t, \quad \hat{x} = \sqrt{\frac{\alpha}{D}} x \quad (2)$$

and dropping the hat notation for convenience, system (1) is changed into

$$\begin{aligned} u_t &= u_{xx} + u(1 - u - \nu v) - \lambda u(1 - K\nu), \\ v_t &= \lambda u(1 - K\nu), \end{aligned} \quad (3)$$

where $\lambda = \beta/\alpha$ and $K = k_1/k_2$.

System (1) or (3) belongs to reaction diffusion systems of degenerate type, and such systems have attracted much attention in research fields such as epidemics and wound healing [2–4] as well as combustion and calcium wave problems [5–8]. However, system (3) differs from the above systems in the appearance of degenerate reaction terms. In fact, $u = 0$ coupling with any $\nu = \text{constant}$ consists of a constant solution of (3). This resembles the combustion wave equation considered in [9]; however, our method in proving the existence of the fronts of (3) differs from theirs.

If the parameters satisfy

$$0 \leq \nu < K, \quad (4)$$

then system (3) admits an additional equilibrium: $B : (1 - \nu/K, 1/K)$ representing the state that the spatial domain is successfully invaded. We also separate the equilibrium $A : (0, 0)$ from the rest of the line of equilibria, $u = 0$. The unstable equilibrium $(0, 0)$ represents the state before the invasion.

We are interested in the existence of the wave solutions connecting A with B as time and space evolve from $-\infty$ to $+\infty$. Setting $\xi = x + ct$, $x \in \mathbb{R}$, $t \in \mathbb{R}^+$, a traveling wave solution to (3) solves

$$\begin{aligned} u_{\xi\xi} - cu_{\xi} + u(1 - u - \nu v) - \lambda u(1 - K\nu) &= 0, \\ -cv_{\xi} + \lambda u(1 - K\nu) &= 0, \end{aligned} \quad (5)$$

with boundary conditions:

$$(u, v)(-\infty) = (0, 0), \quad (u, v)(+\infty) = \left(1 - \frac{\nu}{K}, \frac{1}{K}\right). \tag{6}$$

For the notational convenience, we further set

$$\bar{u} = \frac{u}{1 - \nu/K}, \tag{7}$$

and drop the bar on u to have

$$\begin{aligned} u_{\xi\xi} - cu_{\xi} + u \left[1 - \lambda - \left(1 - \frac{\nu}{K}\right)u + (\lambda K - \nu)\nu\right] &= 0, \\ -cv_{\xi} + \lambda \left(1 - \frac{\nu}{K}\right)u(1 - Kv) &= 0, \\ (u, v)(-\infty) = (0, 0), \quad (u, v)(+\infty) &= \left(1, \frac{1}{K}\right). \end{aligned} \tag{8}$$

Numerical investigations [1] strongly suggest that system (10) and (9) admit traveling wave solutions for $\nu = 0$ and $\nu = 1$. When the differentiated cell density does not affect the proliferation of the precursor cells, we have $\nu = 0$; when the total cell population contributes to the proliferation carrying capacity, we have $\nu = 1$. Numerically, however, when $\nu = 1$, (8) may have nonmonotone traveling wave solutions and requires a different treatment. Hence, in this paper we only study the wave solutions for $\nu = 0$. The system (8) in this case can be further reduced to

$$\begin{aligned} u_{\xi\xi} - cu_{\xi} + u(1 - \lambda - u + \lambda K\nu) &= 0, \\ -cv_{\xi} + \lambda u(1 - Kv) &= 0. \end{aligned} \tag{10}$$

The computations in [1] show that the wave may exist for $c \geq 2\sqrt{1 - \lambda}$, but a rigorous existence proof is still lacking. We will confirm this observation by a mathematical analysis of the model. The system is of cooperative type, and we can use the monotone iteration scheme developed in [10] for the existence proof. Such method reduces the existence of the wave solutions to that of the ordered upper and lower solution pairs for (10) and (9). The upper and lower solutions in this paper come directly from two KPP type equations, which are constructed so that they have the same decay rate at $-\infty$. Such information is also relevant to the monotonicity and uniqueness of the wave solutions. Indeed, since we have a good understanding of the decay properties of the solutions at infinities, we then can study the properties of the solutions on finite domain, in which the powerful sliding domain method (see [11]) can be used to have the desired results. We remark that the methods we used in the proofs of the monotonicity and the uniqueness have subtle difference from the ones used in [12].

For a comprehensive study and interesting applications of the traveling wave solutions arising in various degenerate or nondegenerate parabolic equations and systems, please see [13].

2. The Main Result

In this section, we will use monotone iteration method to set up the upper and lower solutions for system (10) and (9).

Definition 1. A $C^2(\mathbb{R}) \times C^1(\mathbb{R})$ function $(\bar{u}(\xi), \bar{v}(\xi))^T, \xi \in \mathbb{R}$ is an upper solution of (10) and (9) if it satisfies

$$\begin{aligned} u_{\xi\xi} - cu_{\xi} + u(1 - \lambda - u + \lambda K\nu) &\leq 0, \\ -cv_{\xi} + \lambda u(1 - Kv) &\leq 0 \end{aligned} \tag{11}$$

and the boundary conditions

$$\begin{pmatrix} u \\ v \end{pmatrix}(-\infty) \geq \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \begin{pmatrix} u \\ v \end{pmatrix}(+\infty) \geq \begin{pmatrix} 1 \\ \frac{1}{K} \end{pmatrix}. \tag{12}$$

We can similarly define the lower solution $(\underline{u}, \underline{v})(\xi), \xi \in \mathbb{R}$ by reversing the inequalities (11) and (12).

The following known result [14] is needed in the construction of the upper and lower solutions.

Consider the following form of the KPP equation:

$$\begin{aligned} \omega'' - c\omega' + f(\omega) &= 0, \\ \omega(-\infty) = 0, \quad \omega(+\infty) &= b, \end{aligned} \tag{13}$$

where $f \in C^2([0, b])$ and $f > 0$ on the open interval $(0, b)$ with $f(0) = f(b) = 0, f'(0) = \bar{a} > 0$, and $f'(b) = -b_1 < 0$.

Lemma 2. *Corresponding to every $c \geq 2\sqrt{\bar{a}}$, system (13) has a unique (up to a translation of the origin) monotonically increasing traveling wave solution $\omega(\xi)$ for $\xi \in \mathbb{R}$. The traveling wave solution ω has the following asymptotic behaviors.*

For the wave solution with noncritical speed $c > 2\sqrt{\bar{a}}$, one has

$$\begin{aligned} \omega(\xi) &= \bar{a}_{\omega} e^{((c - \sqrt{c^2 - 4\bar{a}})/2)\xi} + o\left(e^{((c - \sqrt{c^2 - 4\bar{a}})/2)\xi}\right) \quad \text{as } \xi \rightarrow -\infty, \\ \omega(\xi) &= b - \bar{b}_{\omega} e^{((c - \sqrt{c^2 + 4b_1})/2)\xi} \\ &\quad + o\left(e^{((c - \sqrt{c^2 + 4b_1})/2)\xi}\right) \quad \text{as } \xi \rightarrow +\infty, \end{aligned} \tag{14}$$

where \bar{a}_{ω} and \bar{b}_{ω} are positive constants.

For the wave with critical speed $c = 2\sqrt{\bar{a}}$, one has

$$\begin{aligned} \omega(\xi) &= \bar{d}_c \xi e^{\sqrt{\bar{a}}\xi} + o\left(\xi e^{\sqrt{\bar{a}}\xi}\right) \quad \text{as } \xi \rightarrow -\infty, \\ \omega(\xi) &= b - \bar{b}_c e^{(\sqrt{\bar{a}} - \sqrt{\bar{a} + b_1})\xi} + o\left(e^{(\sqrt{\bar{a}} - \sqrt{\bar{a} + b_1})\xi}\right) \quad \text{as } \xi \rightarrow +\infty, \end{aligned} \tag{15}$$

where the constant \bar{d}_c is negative and \bar{b}_c is positive.

We next consider the following version of the KPP system:

$$\begin{aligned} \omega'' - c\omega' + (1 - \lambda)\omega(1 - \omega) &= 0, \\ \omega(-\infty) = 0, \quad \omega(+\infty) &= 1. \end{aligned} \tag{16}$$

According to Lemma 2, for every $c \geq 2\sqrt{1-\lambda}$ system, (16) has a unique (up to a translation of the origin) monotone solution $\tilde{u}(\xi)$, $\xi \in \mathbb{R}$. Now, fix this $\tilde{u}(\xi)$ and consider the equation

$$-cv_\xi + \lambda\tilde{u}(1 - Kv) = 0. \tag{17}$$

For each fixed $c \geq 2\sqrt{1-\lambda}$ and the corresponding $\tilde{u}(\xi)$, (17) has a solution

$$\bar{v}(\xi) = \frac{1}{K} \left(1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \tilde{u}(s) ds} \right). \tag{18}$$

We next compare $\tilde{u}(\xi)$ with $\bar{v}(\xi)$ for $\xi \in \mathbb{R}$.

Lemma 3. *There exists a $\zeta_1 \geq 0$ such that if*

$$0 < \lambda \leq \frac{2}{2 + K(1 + \sqrt{2})}, \tag{19}$$

one has

$$\frac{1}{K} \tilde{u}(\xi + \zeta_1) \geq \bar{v}(\xi), \quad \xi \in \mathbb{R}. \tag{20}$$

Proof. According to Lemma 2, the wave solution $\tilde{u}(\xi)$ to (16) has the following asymptotic behaviors.

For $c > 2\sqrt{1-\lambda}$,

$$\begin{aligned} \tilde{u}(\xi) &= a_\omega e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi} \\ &+ o\left(e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi}\right) \quad \text{as } \xi \rightarrow -\infty, \end{aligned} \tag{21}$$

$$\begin{aligned} \tilde{u}(\xi) &= b - b_\omega e^{((c-\sqrt{c^2+4(1-\lambda)})/2)\xi} \\ &+ o\left(e^{((c-\sqrt{c^2+4(1-\lambda)})/2)\xi}\right) \quad \text{as } \xi \rightarrow +\infty, \end{aligned} \tag{22}$$

and a_ω, b_ω are positive constants.

For $c = 2\sqrt{1-\lambda}$, we have

$$\tilde{u}(\xi) = d_c \xi e^{\sqrt{1-\lambda}\xi} + o\left(\xi e^{\sqrt{1-\lambda}\xi}\right) \quad \text{as } \xi \rightarrow -\infty, \tag{23}$$

$$\tilde{u}(\xi) = b - b_c e^{(1-\sqrt{2})\sqrt{1-\lambda}\xi} + o\left(e^{(1-\sqrt{2})\sqrt{1-\lambda}\xi}\right) \quad \text{as } \xi \rightarrow +\infty, \tag{24}$$

where the constant d_c is negative and b_c is positive.

We now study the asymptotics of the function $\bar{v}(\xi)$. Formulas (21) and (23) imply that

$$\int_{-\infty}^{\xi} \tilde{u}(s) ds \rightarrow 0 \quad \text{as } \xi \rightarrow -\infty. \tag{25}$$

We can then expand

$$\begin{aligned} e^{-(\lambda/c)K \int_{-\infty}^{\xi} \tilde{u}(s) ds} &= 1 - \frac{\lambda}{c} K \int_{-\infty}^{\xi} \tilde{u}(s) ds \\ &+ o\left(\left(\int_{-\infty}^{\xi} \tilde{u}(s) ds\right)^2\right). \end{aligned} \tag{26}$$

A further expanding of (26) for $\xi \rightarrow -\infty$ and for $c > 2\sqrt{1-\lambda}$ yields

$$\begin{aligned} 1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \tilde{u}(s) ds} &= \frac{2\lambda a_\omega}{(c - \sqrt{c^2 - 4(1-\lambda)})c} e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi} \\ &+ o\left(e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi}\right), \end{aligned} \tag{27}$$

and for $c = 2\sqrt{1-\lambda}$,

$$\begin{aligned} 1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \tilde{u}(s) ds} &= \frac{\lambda}{2\sqrt{1-\lambda}} \left(d_c \xi - \frac{d_c}{1-\lambda} \right) e^{\sqrt{1-\lambda}\xi} + o\left(\xi e^{\sqrt{1-\lambda}\xi}\right). \end{aligned} \tag{28}$$

As for $\xi > 0$ sufficiently large, we have

$$\lim_{\xi \rightarrow +\infty} \frac{\int_{-\infty}^{\xi} \tilde{u}(s) ds}{\xi} = \lim_{\xi \rightarrow +\infty} \tilde{u}(\xi) = 1; \tag{29}$$

therefore,

$$\bar{v}(\xi) = K \left(1 - e^{-(\lambda/c)K\xi} \right) + o\left(e^{-(\lambda/c)K\xi}\right) \quad \text{as } \xi \rightarrow +\infty. \tag{30}$$

We next show

$$-\frac{\lambda}{c} K \geq \frac{c - \sqrt{c^2 + 4(1-\lambda)}}{2}, \tag{31}$$

or equivalently

$$\frac{2c(1-\lambda)}{c + \sqrt{c^2 + 4(1-\lambda)}} \geq \lambda K. \tag{32}$$

Setting $g(c) = 2(1-\lambda)/1 + \sqrt{1+4(1-\lambda)/c^2}$, then it is easy to see that $g(c)$ increases as c does. Hence,

$$g(c) \geq g(2\sqrt{1-\lambda}) = \frac{2(1-\lambda)}{1 + \sqrt{2}}. \tag{33}$$

We therefore require $0 < \lambda \leq 2/(2 + K(1 + \sqrt{2}))$ to have (31).

We now shift $\tilde{u}(\xi)$. Since (16) is shifting invariant, $\tilde{u}(\xi + \zeta)$, $\xi \in \mathbb{R}$ is also a solution for any $\zeta \in \mathbb{R}$. It then follows from (21) for $c > \sqrt{1-\lambda}$,

$$\begin{aligned} \tilde{u}(\xi + \zeta) &= a_\omega e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\zeta} e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi} \\ &+ o\left(e^{((c-\sqrt{c^2-4(1-\lambda)})/2)\xi}\right) \quad \text{as } \xi \rightarrow -\infty, \end{aligned} \tag{34}$$

and for $c = \sqrt{1-\lambda}$,

$$\begin{aligned} \tilde{u}(\xi + \zeta) &= d_c (\xi + \zeta) e^{\sqrt{1-\lambda}\zeta} e^{\sqrt{1-\lambda}\xi} \\ &+ o\left(\xi e^{\sqrt{1-\lambda}\xi}\right) \quad \text{as } \xi \rightarrow -\infty. \end{aligned} \tag{35}$$

If we choose $\zeta > 0$ sufficiently large, the positiveness of $((c - \sqrt{c^2 - 4(1 - \lambda)})/2)\zeta$ and $\sqrt{1 - \lambda}\zeta$ implies that if $c > 2\sqrt{1 - \lambda}$,

$$d_c(\xi + \zeta)e^{\sqrt{1 - \lambda}\zeta} > \frac{\lambda}{2\sqrt{1 - \lambda}} \left(d_c \xi - \frac{d_c}{1 - \lambda} \right) \quad (36)$$

and if $c > 2\sqrt{1 - \lambda}$,

$$a_\omega e^{((c - \sqrt{c^2 - 4(1 - \lambda)})/2)\zeta} > \frac{2\lambda a_\omega}{(c - \sqrt{c^2 - 4(1 - \lambda)})c}. \quad (37)$$

It then follows from (31), (34), and (35) that there exists a $\bar{N} > 0$ sufficiently large,

$$\frac{1}{K} \bar{u}(\xi + \zeta) \geq \bar{v}(\xi) \quad \text{for } \xi \in (-\infty, -N] \cup [N, +\infty), \quad (38)$$

and for $\xi \in [-N, N]$, since \bar{u} and \bar{v} are both monotonically increasing on \mathbb{R} we can further shift $\bar{u}(\xi + \zeta)$ to the left at most $2N$ units to have $(1/K)\bar{u}(\xi + \zeta) \geq \bar{v}(\xi)$, $\xi \in \mathbb{R}$. Hence there exists a finite $\zeta_1 \geq 0$ such that the conclusion of the Lemma holds. \square

Now, we write $\bar{u}(\xi) = \bar{u}(\xi + \zeta_0)$, $\xi \in \mathbb{R}$ and let $\bar{v}(\xi)$ be defined in (18). We remark here that the computation of $\bar{v}(\xi)$ still uses $\bar{u}(\xi)$.

Lemma 4. Assume the conditions in Lemma 3, then $(\bar{u}, \bar{v})(\xi)$, $\xi \in \mathbb{R}$ defines an upper solution for (10) and (9).

Proof. We can easily verify that $(\bar{u}, \bar{v})(\xi)$ satisfies the boundary conditions (12).

For the u component, we have

$$\begin{aligned} & \bar{u}'' - c\bar{u}' + \bar{u}(1 - \lambda - \bar{u} + \lambda K\bar{v}) \\ &= \bar{u}[1 - \lambda - \bar{u} + \lambda K\bar{v} - (1 - \lambda)(1 - \bar{u})] \\ &= -\lambda K\bar{u} \left(\frac{1}{K}\bar{u} - \bar{v} \right) \leq 0. \end{aligned} \quad (39)$$

The last inequality follows from the previous lemma.

As for the v component, for each \bar{u} , we have

$$-c\bar{v}' + \lambda\bar{u}(1 - K\bar{v}) = 0. \quad (40)$$

\square

We next set up the lower solution for (10) and (9).

For a fixed $l > 0$, we consider another version of the KPP system:

$$\begin{aligned} & w'' - cw' + (1 - \lambda)w \left(1 - \frac{1 - \lambda + l}{1 - \lambda} w \right) = 0, \\ & w(-\infty) = 0, \quad w(+\infty) = \frac{1 - \lambda}{1 - \lambda + l} < 1. \end{aligned} \quad (41)$$

Then, for any $c \geq 2\sqrt{1 - \lambda}$, (41) has correspondingly a unique wave solution $\check{u}(\xi)$, $\xi \in \mathbb{R}$.

We define

$$\underline{v}(\xi) = \frac{1}{K} \left(1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \check{u}(s)ds} \right). \quad (42)$$

The next lemma gives the relation between $\check{u}(\xi)$ and $\underline{v}(\xi)$, $\xi \in \mathbb{R}$.

Lemma 5. There exists a $\zeta_1 \geq 0$ such that

$$\frac{1}{K} \check{u}(\xi - \zeta_1) \leq \underline{v}(\xi), \quad \xi \in \mathbb{R}. \quad (43)$$

Proof. The proof is similar to that of Lemma 3. Noting as $\xi \rightarrow +\infty$, $\check{u}(\xi) \rightarrow (1/K)((1 - \lambda)/(1 - \lambda + l)) < 1/K$. Hence, we do not need condition (19) here. \square

We denote $\underline{u}(\xi) = \check{u}(\xi - \zeta_1)$, $\xi \in \mathbb{R}$. Then, we have the following.

Lemma 6. Such defined $(\underline{u}, \underline{v})(\xi)$, $\xi \in \mathbb{R}$ consists of a lower solution for (10) and (9).

Proof. One the boundary, we have

$$\begin{aligned} & (\underline{u}, \underline{v})(-\infty) = (0, 0), \\ & (\underline{u}, \underline{v})(+\infty) = \left(\frac{1 - \lambda}{1 - \lambda + l}, \frac{1}{K} \right) \leq \left(1, \frac{1}{K} \right) \end{aligned} \quad (44)$$

and for the u component,

$$\begin{aligned} & \underline{u}'' - c\underline{u}' + \underline{u}(1 - \lambda - \underline{u} + \lambda K\underline{v}) \\ &= \underline{u}'' - c\underline{u}' + (1 - \lambda)\underline{u} \left(1 - \frac{1 - \lambda + l}{1 - \lambda} \underline{u} \right) \\ & \quad - (1 - \lambda)\underline{u} \left(1 - \frac{1 - \lambda + l}{1 - \lambda} \underline{u} \right) \\ & \quad + \underline{u}(1 - \lambda - \underline{u} + \lambda K\underline{v}) \\ &= \underline{u}[1 - \lambda - \underline{u} + \lambda K\underline{v} - (1 - \lambda) + (1 - \lambda + l)\underline{u}] \geq 0 \end{aligned} \quad (45)$$

due to Lemma 5.

Noting that $\underline{v}(\xi)$ solves the equation

$$-c\underline{v}' + \lambda\check{u}(1 - K\underline{v}) = 0, \quad (46)$$

it satisfies the inequality trivially. \square

Lemma 7. The upper and lower solutions are ordered

$$(\bar{u}, \bar{v})(\xi) \geq (\underline{u}, \underline{v})(\xi), \quad \xi \in \mathbb{R}. \quad (47)$$

Proof. For each fixed $c \geq 2\sqrt{1 - \lambda}$, if $\check{u}(\xi)$ solves the system (41), then the function $\bar{u}(\xi) = ((1 - \lambda + l)/(1 - \lambda))\check{u}(\xi)$ solves (16). Hence, it follows that $\bar{u}(\xi) > \check{u}(\xi)$, and then $\bar{u}(\xi) > \underline{u}(\xi)$ for all $\xi \in \mathbb{R}$.

By definition of $\bar{v}(\xi)$ and $\underline{v}(\xi)$, we have

$$\begin{aligned} & \bar{v}(\xi) = \frac{1}{K} \left(1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \bar{u}(s)ds} \right) \\ &= \frac{1}{K} \left(1 - e^{-(\lambda/c)K((1 - \lambda + l)/(1 - \lambda)) \int_{-\infty}^{\xi} \check{u}(s)ds} \right) \\ &> \frac{1}{K} \left(1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} \check{u}(s)ds} \right) = \underline{v}(\xi). \end{aligned} \quad (48)$$

Hence, the conclusion of the lemma holds. \square

Theorem 8. Let the parameters satisfy (19), then for each $c \geq 2\sqrt{1-\lambda}$, system (10) and (9) have a unique (up to a translation of the origin) strictly monotonically increasing traveling wave solution, while for $0 < c < 2\sqrt{1-\lambda}$, there is no monotonic traveling wave. The traveling wave solution has the following asymptotic behaviors.

For $c = 2\sqrt{1-\lambda}$,

$$\begin{pmatrix} u \\ v \end{pmatrix}(\xi) = \begin{pmatrix} c_{11}\xi \\ c_{12}\xi \end{pmatrix} e^{\sqrt{1-\lambda}\xi} + o\left(e^{\sqrt{1-\lambda}\xi}\right), \quad \text{as } \xi \rightarrow -\infty, \tag{49}$$

$$\begin{pmatrix} u \\ v \end{pmatrix}(\xi) = \begin{pmatrix} 1 \\ \frac{1}{K} \end{pmatrix} - \begin{pmatrix} c_{21}e^{-(\lambda K/2\sqrt{1-\lambda})\xi} \\ c_{22}e^{-(\lambda K/2\sqrt{1-\lambda})\xi} \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda K/2\sqrt{1-\lambda})\xi}\right) \\ o\left(e^{-(\lambda K/2\sqrt{1-\lambda})\xi}\right) \end{pmatrix}, \quad \text{as } \xi \rightarrow +\infty, \tag{50}$$

and for $c > 2\sqrt{1-\lambda}$,

$$\begin{pmatrix} u \\ v \end{pmatrix}(\xi) = \begin{pmatrix} d_{11}\xi \\ d_{12}\xi \end{pmatrix} e^{((c-\sqrt{c^2+4(1-\lambda)})/2)\xi} + o\left(e^{((c-\sqrt{c^2+4(1-\lambda)})/2)\xi}\right), \quad \text{as } \xi \rightarrow -\infty, \tag{51}$$

$$\begin{pmatrix} u \\ v \end{pmatrix}(\xi) = \begin{pmatrix} 1 \\ \frac{1}{K} \end{pmatrix} - \begin{pmatrix} d_{21}e^{-(\lambda K/c)\xi} \\ d_{22}e^{-(\lambda K/c)\xi} \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda K/c)\xi}\right) \\ o\left(e^{-(\lambda K/c)\xi}\right) \end{pmatrix} \quad \text{as } \xi \rightarrow +\infty, \tag{52}$$

where $c_{11}, c_{12}, c_{21}, c_{22}, d_{21}$, and $d_{22} > 0$ and $d_{11}, d_{12} < 0$.

Proof. Noting that between the upper and lower solutions, there is no equilibrium other than (0,0) and (1, 1/K) of system (10) and (9). Hence, the monotone iteration scheme developed in [10] is still applicable. Such monotone iteration scheme reduces the existence of the traveling wave solutions to that of the ordered upper and lower solution pairs, and the existence of the traveling waves then follows by Lemmas 6, 4, and 7, and by [10], so the obtained traveling wave solutions are nondecreasing, while for $c < 2\sqrt{1-\lambda}$, it is easy to verify, by analyzing the equilibrium (0, 0), that the nontrivial bounded solutions of (10) are oscillatory.

We next show that the wave solutions are strictly monotonically increasing on \mathbb{R} .

For any fixed $c \geq \sqrt{1-\lambda}$, let $(u_c, v_c)(\xi)$ be the corresponding traveling wave solution and $(w_1(\xi), w_2(\xi))$ be

its derivative. Then, $(w_1(\xi), w_2(\xi)) \geq 0$ for $\xi \in \mathbb{R}$, and $(w_1(\xi), w_2(\xi))$ satisfies the following systems:

$$\begin{aligned} w_{1,\xi\xi} - cw_{1,\xi} + (1 - \lambda - 2u_c + \lambda K v_c) w_1 + \lambda K u_c w_2 &= 0, \\ -cw_{2,\xi} + \lambda(1 - K v_c) w_1 - \lambda K u_c w_2 &= 0, \\ (w_1, w_2)(\pm\infty) &= 0. \end{aligned} \tag{53}$$

It then follows that

$$\begin{aligned} w_{1,\xi\xi} - cw_{1,\xi} + (1 - \lambda - 2u_c + \lambda K v_c) w_1 &\leq 0, \\ -cw_{2,\xi} + \lambda(1 - K v_c) w_1 - \lambda K u_c w_2 &= 0, \\ (w_1, w_2)(\pm\infty) &= 0. \end{aligned} \tag{54}$$

Applying the maximum principle to the first inequality of (54), we immediately conclude that $w_1(\xi) > 0$ for $\xi \in \mathbb{R}$. Thus, $u_c(\xi)$ is strictly monotonically increasing.

The strict monotonicity of $v_c(\xi)$ comes from (10). Since $u_c(\xi) > 0$ for all $\xi \in \mathbb{R}$, and for such $u_c(\xi)$, we have

$$v_c(\xi) = \frac{1}{K} \left(1 - e^{-(\lambda/c)K \int_{-\infty}^{\xi} u_c(s) ds} \right), \tag{55}$$

then it follows that $w_2(\xi) = v_c'(\xi) > 0$, $\xi \in \mathbb{R}$. This shows that the wave solution (u_c, v_c) is strictly monotonically increasing.

We then derive the asymptotics of the wave solutions at $\pm\infty$. Noting that the upper and lower solutions have the same exponential decay rate at $-\infty$, (49) and (51) come directly from comparison.

We next study the asymptotics of the function $(w_1, w_2)(\xi)$ at $+\infty$, recalling that $(w_1, w_2)(\xi) = (u_c, v_c)'(\xi)$ and that it satisfies the system (53). Since this system is hyperbolic at $+\infty$, (w_1, w_2) approaches (0, 0) exponentially. We will derive the exact exponential rate.

The limit equation at $+\infty$ of system (53) is

$$\begin{aligned} w_{1,\xi\xi}^+ - cw_{1,\xi}^+ - w_1^+ + \lambda K w_2^+ &= 0, \\ -cw_{2,\xi}^+ - \lambda K u_c w_2^+ &= 0. \end{aligned} \tag{56}$$

Since the second equation is decoupled from the system, we immediately have

$$w_2^+(\xi) = \underline{A} e^{-(\lambda K/c)\xi}. \tag{57}$$

Plugging the above into the first equation yields a bounded solution (up to the first order approximation) of the form

$$w_1^+(\xi) = \overline{A}_1 e^{-(\lambda K/c)\xi} + \overline{A}_2 e^{((c-\sqrt{c+4})/2)\xi}. \tag{58}$$

By roughness of exponential dichotomy [15], we have

$$\begin{pmatrix} w_1(\xi) \\ w_2(\xi) \end{pmatrix} = \begin{pmatrix} \frac{A_1 e^{-(\lambda K/c)\xi}}{\overline{A}_2 e^{\mu\xi}} \\ o\left(e^{\mu\xi}\right) \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda K/c)\xi}\right) \\ o\left(e^{\mu\xi}\right) \end{pmatrix}, \tag{59}$$

where μ is either $-\lambda K/c$ or $(c - \sqrt{c+4})/2$.

Integrating the above from ξ_0 to $+\infty$ and comparing the decay rates of $(u_c, v_c)(\xi)$ with that of the upper solution $(\bar{u}, \bar{v})(\xi)$, we have (50) and (52).

On the uniqueness of the traveling wave solution for every $c \geq 2\sqrt{1-\lambda}$, we only prove the conclusion for traveling wave solutions with asymptotic rates given in (51) and (52) since the other case can be proved similarly. Let $U_1(\xi) = (u_1, v_1)(\xi)$ and $U_2(\xi) = (u_2, v_2)(\xi)$ be two traveling wave solutions of system (10) and (9) with the same speed $c > 2\sqrt{1-\lambda}$. There exist positive constants $A_{ij}, B_{ij}, i, j = 1, 2$ and a large number $N > 0$ such that for $\xi < -N$,

$$U_1(\xi) = \begin{pmatrix} A_{11} \\ A_{12} \end{pmatrix} e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi} + o\left(e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi}\right) \tag{60}$$

$$U_2(\xi) = \begin{pmatrix} A_{21} \\ A_{22} \end{pmatrix} e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi} + o\left(e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi}\right) \tag{61}$$

and for $\xi > N$,

$$U_1(\xi) = \begin{pmatrix} 1 - B_{11}e^{-(\lambda/c)K\xi} \\ \frac{1}{K} - B_{12}e^{-(\lambda/c)K\xi} \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda/c)K\xi}\right) \\ e^{-(\lambda/c)K\xi} \end{pmatrix}, \tag{62}$$

$$U_2(\xi) = \begin{pmatrix} 1 - B_{21}e^{-(\lambda/c)K\xi} \\ \frac{1}{K} - B_{22}e^{-(\lambda/c)K\xi} \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda/c)K\xi}\right) \\ e^{-(\lambda/c)K\xi} \end{pmatrix}. \tag{63}$$

The traveling wave solutions of system (10)-(9) are translation invariant; thus, for any $\theta > 0$, $U_1^\theta(\xi) := U_1(\xi + \theta)$ is also a traveling wave solution of (10)-(9). By (60) and (62), the solution $U_1(\xi + \theta)$ has the asymptotics

$$U_1^\theta(\xi) = \begin{pmatrix} A_{11}e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\theta} \\ A_{12}e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\theta} \end{pmatrix} e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi} + o\left(e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\xi}\right) \tag{64}$$

for $\xi \leq -N$ and

$$U_1^\theta(\xi) = \begin{pmatrix} 1 - B_{11}e^{-(\lambda/c)K\theta}e^{-(\lambda/c)K\xi} \\ \frac{1}{K} - B_{12}e^{-(\lambda/c)K\theta}e^{-(\lambda/c)K\xi} \end{pmatrix} + \begin{pmatrix} o\left(e^{-(\lambda/c)K\xi}\right) \\ e^{-(\lambda/c)K\xi} \end{pmatrix} \tag{65}$$

for $\xi \geq N$.

Choosing $\theta > 0$ large enough such that

$$\begin{aligned} A_{11}e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\theta} &> A_{21}, \\ A_{12}e^{((c+\sqrt{c^2-4(1-\lambda)})/2)\theta} &> A_{22}, \\ B_{11}e^{-(\lambda/c)K\theta} &< B_{21}, \\ B_{12}e^{-(\lambda/c)K\theta} &< B_{22}, \end{aligned} \tag{66}$$

then one has for $\xi \in (-\infty, -N] \cup [N, +\infty)$,

$$U_1^\theta(\xi) > U_2(\xi). \tag{67}$$

We now consider system (10) on $[-N, +N]$. There are two possibilities.

Case 1. Suppose that we already have $U_1^\theta(\xi) \geq U_2(\xi)$ on $[-N, +N]$, then the function $W(\xi) = (w_1(\xi), w_2(\xi))^T := U_1^\theta(\xi) - U_2(\xi) \geq 0$ and it satisfies for some $\zeta_i \in (0, 1), i = 1, 2$,

$$\begin{pmatrix} w_1'' \\ 0 \end{pmatrix} - c \begin{pmatrix} w_1' \\ w_2' \end{pmatrix} + M \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = 0, \tag{68}$$

$$W(-N) > 0, \quad W(+N) > 0. \quad \xi \in (-N, N),$$

where the matrix M is given by

$$\begin{aligned} M(w_1, w_2) &= \begin{pmatrix} 1 - \lambda - 2(u_2 + \zeta_1 w_1) + \lambda K(v_2 + \zeta_2 w_2), & \lambda K(u_2 + \zeta_1 w_1) \\ \lambda(1 - K(v_2 + \zeta_2 w_2)), & -\lambda K(u_2 + \zeta_2 w_1) \end{pmatrix}. \end{aligned} \tag{69}$$

Since $w_1(\xi) \geq 0, \xi \in [-N, N]$ and $\lambda K(u_2 + \zeta_1 w_1) \geq 0$, then we have on $\xi \in [-N, N]$,

$$\begin{aligned} w_1'' - cw_1' + [1 - \lambda - 2(u_2 + \zeta_1 w_1) + \lambda K(v_2 + \zeta_2 w_2)]w_1 \\ + \lambda K(u_2 + \zeta_2 w_1)w_2 &= 0, \\ w_1(-N) > 0, \quad w_1(N) > 0. \end{aligned} \tag{70}$$

The maximum principle then implies that $w_1(\xi) > 0$ on $[-N, N]$. We then move to the second equation of (68). We have

$$\begin{aligned} -cw_2' - \lambda K(u_2 + \zeta_2 w_1)w_2 \\ = -\lambda(1 - K(v_2 + \zeta_2 w_2))w_1 < 0, \quad \xi \in [-N, N], \\ w_2(-N) > 0, \quad w_2(N) > 0. \end{aligned} \tag{71}$$

The strict inequality comes from the fact that $v_2(\xi) \leq v_2(\xi) + \zeta_2 w_2(\xi) \leq v_1^\theta < 1/K$ for $\xi \in [-N, N]$. It then follows that $w_2(\xi) > 0$ for $\xi \in [-N, N]$. For if there is a $\bar{\xi} \in (-N, N)$ such that $w_2(\bar{\xi}) = 0$, then w_2 takes local minimum at $\bar{\xi}$ and the left hand side of the first inequality of (71) is zero at $\bar{\xi}$. We then have a contradiction.

Case 2. We may suppose that there is some point in $(-N, N)$ such that one of the components, say the j th component, satisfies $(U_1^\theta(\xi))_j < (U_2(\xi))_j$ at that point, $j = 1$ or 2 . We then increase θ , that is, shift $U_1^\theta(\xi)$ further left, so that $U_1^\theta(-N) > U_2(-N), U_1^\theta(N) > U_2(N)$. By the monotonicity of U_1^θ and U_2 , we can find a $\bar{\theta} \in (0, 2N)$ such that in the interval $(-N, N)$ we have $U_1^{\bar{\theta}}(\xi + \theta) > U_2(\xi)$. Shifting $U_1^{\bar{\theta}}(\xi + \theta)$ back until one

component of $U_1^\theta(\xi + \bar{\theta})$ first touches its counterpart of $U_2(\xi)$ at some point $\bar{\xi} \in [-N, N]$, we then return back to Case 1 again, where it has been shown that this is impossible. Therefore, we must have

$$U_1^\theta(\xi) > U_2(\xi) \quad (72)$$

for all $\xi \in \mathbb{R}$, where θ is the one chosen by means of (66) as described above.

Now, decrease θ until one of the following situations happens.

- (1) There exists a $\bar{\theta} \geq 0$, such that $U_1^{\bar{\theta}}(\xi) \equiv U_2(\xi)$. In this case, we have finished the proof.
- (2) There exists a $\bar{\theta} \geq 0$ and $\xi_1 \in \mathbb{R}$, such that one of the components of $U_1^{\bar{\theta}}$ and U_2 are equal there; for all $\xi \in \mathbb{R}$, we have $U_1^{\bar{\theta}}(\xi) \geq U_2(\xi)$. On applying the maximum principle on \mathbb{R} and using the same argument as we did for Case 1, we see that this is impossible.

Consequently, in either situation, there exists a $\bar{\theta} \geq 0$, such that

$$U_1^{\bar{\theta}}(\xi) \equiv U_2(\xi) \quad (73)$$

for all $\xi \in \mathbb{R}$. □

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