CAN PATHOGEN SPREAD KEEP PACE WITH ITS HOST INVASION?[*]

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Abstract. We consider the Fisher-KPP equation in a wavelike shifting environment for which the wave profile of the environment is given by a monotonically decreasing function changing signs (shifting from favorable to unfavorable environment). This type of equation arises naturally from the consideration of pathogen spread in a classical susceptible-infected-susceptible epidemiological model of a host population where the disease impact on host mobility and mortality is negligible. We conclude that there are three different ranges of the disease transmission rate where the disease spread has distinguished spatiotemporal patterns: extinction; spread in pace with the host invasion; spread not in a wave format and slower than the host invasion. We calculate the disease propagation speed when disease does spread. Our analysis for a related elliptic operator provides closed form expressions for two generalized eigenvalues in an unbounded domain. The obtained closed forms yield unsolvability of the related elliptic equation in the critical case, which relates to the open problem 4.6 in [H. Berestycki and L. Rossi, *J. Eur. Math. Soc. (JEMS)*, 8 (2006), pp. 195–215].

Key words. disease spread, wavelike environment, Fisher-KPP wave, pulse wave, generalized eigenvalues

AMS subject classifications. 35C07, 35K57, 37N25, 92D25

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1. Introduction. Pathogen spread due to host range expansion or species invasion has substantial impact on environment, economics, and human health. Specific examples that motivate our modeling and analysis here include the spread of Lyme disease due to the range expansion of its tick hosts [13, 14, 15, 35], and the spread of avian influenza due to bird migration [10, 42].

In a series of modeling studies [9, 10, 21], using a satellite tracking data for the migratory routes of a group of bar-headed geese in Southeast Asia conducted by the UN-FAO and WHO avian influenza team, we parameterized the migratory routes using an elongated closed curve and demonstrated that it is possible to characterize essential features of bird migration dynamics by using a one-dimensional hyperbolic (parabolic) partial differential equation (PDE) (for the density of the bird population along the migratory closed curve) involving diffusion and convection, natural birth,

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and death [10]. We then, using the classical technique of integration along characteristics, reduced such a PDE system to a large scale metapopulation (patchy) model using delay differential equations so that we were able to validate the model using available bird observation data in major stopovers of the migration including the winter refuge and summer breeding sites [21]. The model analysis, using the monotone dynamical systems theory, shows that the migratory bird population converges to a spatiotemporal periodic solution, the discrete analogue of a *rotating wave*. Incorporating the avian influenza transmission among migratory birds and between migratory and domestic birds, we then extended this bird migration ecological system to an avian influenza spread model and concluded that disease transmission can be persistent (in the sense that the number of infectious birds, either migratory or domestic, will remain strictly above a positive level) [9]. However, we also noted that the avian influenza does not necessarily spread in pace with the bird migration and, more importantly, the avian influenza spread pattern is no longer a rotating wave (i.e., not periodic in time and in space) with disease peak time seeming irregular.

Here, we consider complex spatiotemporal patterns of pathogen spread facilitated by range expansion of the pathogen's host, through a simple looking susceptible-infectious-susceptible (SIS) model with spatial diffusion:

$$
\begin{aligned}
(1.1) \qquad & S_t = DS_{xx} + B(N)N - \omega SI - \mu(N)S + \gamma I, \\
& I_t = DI_{xx} + \omega SI - \mu(N)I - \gamma I
\end{aligned}
$$

with $N = S + I$, the total population. In the model, the mass action ωSI is used for disease transmission with $\omega > 0$ being the transmission rate, and the recovery period of the infectious hosts is $1/\gamma$. $B(N)$ and $\mu(N)$ are the population per capita birth rate and death rate. For the sake of illustration, we focus in this introduction on the classical logistic growth, so that $B(N) = b$ and $\mu(N) = d + \frac{N}{K}$. This leads to the Fisher-KPP equation for the total population density N,

$$
(1.2) \qquad N_t = DN_{xx} + (b-d)N\big[1 - N/N^*\big]
$$

with $N^* := (b-d)K$. We assume $b > d$ so that the species can successfully invade into and establish in new habitats. It is well known that (1.2) has the so-called traveling wavefront with the minimal wave speed $c_N^* = 2\sqrt{D(b-d)}$ that coincides with the invasion (propagation) speed, and this waveform and the minimal wave speed play a key role in determining the long-term spatiotemporal pattern of host invasion.

Replacing $N(t,x)$ by a wave solution $n(x - c_N t)$ with an appropriate wave speed c_N, and then replacing $S(t,x)$ by $n(x - c_N t) - I$ in the I-equation of system (1.1) leads to

$$
I_t = DI_{xx} + I[\omega n(x - c_N t) - d - n(x - c_N t)/K - \gamma - \omega I].
$$

Rescaling the time and space variable appropriately, we are led to the following scalar reaction-diffusion equation

$$
(1.3) \qquad v_t = v_{xx} + v(a(x - ct) - v).
$$

This equation was considered in [5] in a wave environment with a bounded length of spatial region habitable for a single species, so the function a there is positive in this region and then negative outside. In comparison, here the *intrinsic growth rate* function a motivated by the disease spread in the host has some special property to render the arguments in the work [5] inapplicable.

This special property of the monotone C^1 function a is relevant to the disease epidemiology. Namely, if the transmission rate ω is less than ω_1 (the formula will be defined later in section 2), the threshold value for the disease outbreak to take place when the total population follows the intrinsic growth rate, the function a is negative everywhere in the entire environment. However, when $\omega > \omega_1$, we have

$$(1.4) \qquad \alpha := a(-\infty) > 0 > a(+\infty) =: \beta,$$

so the environment shifts from favorable to unfavorable for the disease spread. Disease extinction in the case where $\omega < \omega_1$ is naturally expected, but whether disease outbreak is possible and how disease spreads (patterns and speed) is less intuitive when $\omega > \omega_1$. Indeed, as we shall see in the next section, (1.3) has a traveling wave of the same speed as the host invasion if and only if the disease transmission rate ω is larger than $\omega_2 > \omega_1$, with ω_2 being the next threshold of the transmission rate which will be given in an explicit form in section 2. A major contribution of our work here from the disease control point of view is to describe qualitatively the spatiotemporal patterns of disease spread when the transmission rate is in the moderate range (ω_1, ω_2). Our findings show that how fast the disease spreads is determined not only by the invasion speed of the host (that is determined by the ecological features of the biological invasion) but also determined by the disease transmission between susceptible and infectious hosts. When the transmission rate is in the moderate range (ω_1, ω_2), we conclude that the total population moves faster than the infected subpopulation. In this case, we anticipate that the infected subpopulation is approximately governed by a diffusive SIS model when the demographic dynamics (reproduction and natural death) is balanced, so we observe a typical epidemic curve of disease outbreak (where the infectious population grows exponentially initially, and then the infection dies out quickly) propagation in space. This leads naturally to the consideration of pulse waves–disease outbreak curves moving in space; see the next section in details.

In model (1.1), we consider the case where disease carried by the pathogen can be transmitted within the host, but for the host the infection is often subclinical, and hence asymptomatic and nonlethal. We also restrict ourselves to the case where the infection does not alter the host's mobility, hence infected or susceptible hosts may follow the same or similar movement patterns. Therefore, disease transmission normally follows with the biological invasion or range expansion of the host, so the invasion of the host is the first indicator of the disease risk. Our focus here is on whether the disease spreads at the same speed of species invasion, and if not then how much delay is there between the host invasion and the pathogen spread and how does this delay impact on the complexity of disease spread patterns. In the final discussion section, we further relate our modeling and analysis to the issue of biological invasion due to climate change.

2. Main results. We start with the *limiting* system (1.3) for which the moving environment a satisfies (1.4). We first consider positive traveling wave solutions with the same speed as the environment shifting, that is, $v(t, x) = u(x - ct)$. These solutions satisfy

$$(2.1) \qquad u'' + cu' + u(a(x) - u) = 0, \quad x \in \mathbb{R},$$

where the symbol prime stands for the derivative. Applications of the elliptic strong maximum principle yield that any bounded nonnegative solution $u \not\equiv 0$ of (2.1) satisfies $0 < u < \alpha$ and it is either a *KPP wave* in the sense that

$$u(+\infty) = 0, \ u(-\infty) = \alpha, \quad \text{and} \quad u' < 0$$

or a *pulse wave* in the sense that

$$u(\pm\infty) = 0 \quad \text{and} \quad \{x : u' = 0\} \text{ is a singleton.}$$

Our first general result, stated below, shows how the environment shifting speed and the convergence rate of the environment to the maximum capacity (at $-\infty$) impact on the existence and shape of traveling wave solutions (for the infected hosts).

THEOREM 2.1. *Define* $c^* := 2\sqrt{\alpha}$. *The following statements on traveling wave solutions of* (1.3) *are valid:*
  (i) *A KPP wave exists if and only if* $c < c^*$.
  (ii) *If* $c > -c^*$, *then no pulse wave exists.*
  (iii) *If* $c < -c^*$ *and* $\alpha - a \in L^1(-\infty, 0)$, *then there are infinitely many different pulse waves.*

To obtain the above results on the existence of pulse waves, we need to have an a priori estimate on the behaviors of wave profiles at $-\infty$, in particular, the exponential decay rate given in Lemma 5.2 (in section 5.1). This estimate allows us to construct appropriate lower solutions. As for KPP waves, since $u \equiv \alpha$ is an upper solution, to prove the existence when $c < c^*$ we need to construct a lower solution $u_- < \alpha$ with $\limsup_{x \to -\infty} u_-(x) > 0$. This lower solution is constructed by considering a piecewise constant *lower environment* a_- (in the sense that a_- is piecewise constant and $a_- \leq a$) and by constructing solutions of the system with the piecewise constant environment a_-. Using a similar argument based on a piecewise constant environment a_+, for the nonexistence when $c \geq c^*$, we construct an *upper environment* a_+ for which no bounded wave exists: since the wave in environment a serves as a lower solution to the equation in environment a_+, we then can argue by contradiction to rule out the existence. In short, since the shifting environment is favorable at one side and unfavorable at the other side, we need to sandwich this environment in-between two piecewise constant ones to construct various upper and lower solutions to establish the critical value of shifting speed for the existence of waves. The proof of Theorem 2.1 can be found in sections 5.2 and 5.3.

To state a nontrivial byproduct result on two generalized eigenvalues of elliptic operators that were introduced in [6] and [7], respectively, we define the elliptic operator $L_{c,a}u = u'' + cu' + a(x)u, x \in \mathbb{R}$. Using the notations from [8], we define the eigenvalues for the operator $-L_{c,a}$ in the unbounded domain $\mathbb{R}$ as follows:

$$\lambda_{1,c,a} := \sup\{\lambda | \exists \phi \in C^2(\mathbb{R}), \phi > 0, (L_{c,a} + \lambda)\phi \leq 0\}$$

and

(2.2) $$\lambda'_{1,c,a} := \inf\{\lambda | \exists \phi \in C^2(\mathbb{R}) \cap W^{2,\infty}(\mathbb{R}), (L_{c,a} + \lambda)\phi \geq 0\}.$$

Recall that $a(-\infty) = \alpha > 0$ and $a(+\infty) = \beta < 0$ as assumed.

THEOREM 2.2. *Eigenvalues* $\lambda_{1,c,a}$ *and* $\lambda'_{1,c,a}$ *can be explicitly expressed, respectively, as*

$$\lambda_{1,c,a} = -\alpha + \frac{c^2}{4} \quad \text{and} \quad \lambda'_{1,c,a} = \begin{cases} -\alpha, & c \leq 0, \\ \lambda_{1,c,a}, & c \in (0, 2\sqrt{\alpha - \beta}), \\ -\beta, & c \geq 2\sqrt{\alpha - \beta}. \end{cases}$$

The proof of this theorem can be found in section 5.4. Based on this result, we observe that $\lambda_{1,c,a}$ is independent of the negative value $a(+\infty)$ but $\lambda'_{1,c,a}$ is dependent

on this value. The sign of $\lambda_{1,c,a}$ cannot completely determine the solvability solutions of (2.1) but $\lambda'_{1,c,a}$ can. In the critical case where $\lambda'_{1,c,a} = 0$ (that is, $c = c^*$), (2.1) has no positive bounded solutions. This then gives a negative answer to the open problem 4.6 in [8] on the existence of solutions for a general elliptic equation with $\lambda'_{1,c,a} = 0$. Besides, we note that as a function of c, $\lambda'_{1,c,a}$ is continuously nondecreasing in c but not differentiable at $c = 2\sqrt{\alpha - \beta}$.

We also remark that applications of the comparison arguments enable us to show that Theorem 2.2 holds if the monotonicity of a is replaced by a weaker condition: there are two monotone functions $a_\pm$ having the same limit at $\pm\infty$ and such that $a_- \leq a \leq a_+$.

To demonstrate the general results, we consider the diffusive SIS model (1.1) with logistic growth (we will discuss the case for the Allee effect in the appendix). Recall that the *limiting* equation for the total population has traveling waves with wave speeds $c \geq c_N^* = 2\sqrt{D(b-d)}$. Define

$$(2.3) \qquad \omega_1 = \frac{1}{N^*}[\mu(N^*) + \gamma], \quad \omega_2 = \omega_1 + \frac{1}{K},$$

and

$$(2.4) \qquad c_\omega = 2\sqrt{DN^*(\omega - \omega_1)} \quad \forall \omega > \omega_1$$

with N^* being the carrying capacity in (1.2). Clearly, $c_\omega < c_N^*$ when $\omega \in (\omega_1, \omega_2)$ and $c_\omega > c_N^*$ when $\omega > \omega_2$. Therefore, we have the following corollary.

COROLLARY 2.3. *Whether the model (1.1) has a positive wave is completely determined by the threshold value ω_2.*
  (i) *If $\omega > \omega_2$, then for any $c \in [c_N^*, c_\omega)$, model (1.1) admits a positive wave solution $(S(x - ct), I(x - ct))$, where S is connecting $\frac{\omega_1}{\omega}N^*$ to 0 and I is decreasingly connecting $\frac{\omega - \omega_1}{\omega}N^*$ to 0.*
  (ii) *If $\omega \leq \omega_2$, then model (1.1) admits no positive bounded waves.*

The first part of the result is what most existing studies focused on, and it confirms that the epidemic system has a family of traveling waves where the total and infectious populations move at the same speed, the disease spreads at in the same speed of the host invasion or range expansion. We illustrate this result in Figure 1. This conclusion however is true only when the transmission rate is sufficient large so that $\omega > \omega_2$. The critical value ω_1 is where the basic reproduction number R_0 is equal to 1 when the population reaches its equilibrium state (N). As the disease induced mortality (for the host) is ignored, the total population will eventually stabilize at the positive equilibrium state at which the disease will spread in the population as long as

$$R_0 := \frac{\omega N^*}{\gamma + d + \frac{N^*}{K}} > 1.$$

The corollary above also concludes that the model for the infected population does not have any positive bounded solution when $\omega \in [\omega_1, \omega_2]$. So a natural question arises, in this case, in what format and speed does the disease spread? The next question is, what is the epidemiological significance of two thresholds of the transmission rate? These questions are addressed in the following theorem on disease propagation.

THEOREM 2.4. *Assume that S_0, $I_0 \in C(\mathbb{R}, \mathbb{R}^+)$ with $I_0 \not\equiv 0$ having compact supports. Let $(S(t,x), I(t,x))$ be the solution of (1.1) with $S(0,x) = S_0(x)$ and $I(0,x) = I_0(x)$. Then the following statements are valid:*
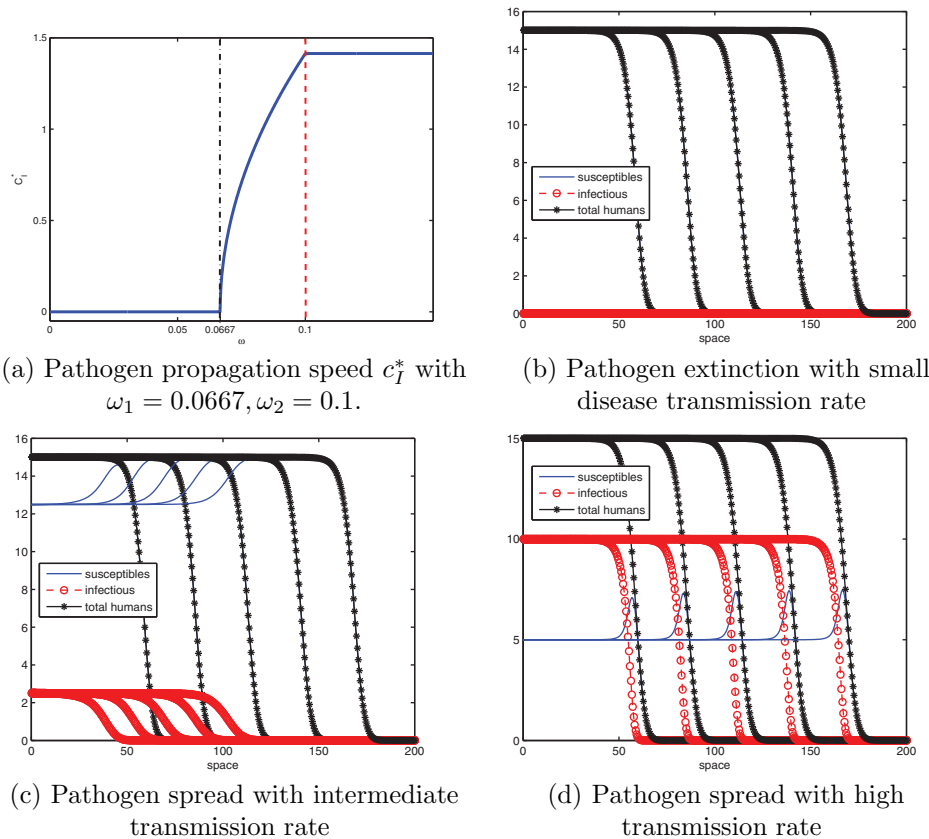
(a) Pathogen propagation speed c_I^* with $\omega_1 = 0.0667, \omega_2 = 0.1$.

(b) Pathogen extinction with small disease transmission rate

(c) Pathogen spread with intermediate transmission rate

(d) Pathogen spread with high transmission rate

FIG. 1. *Existence* $(\omega > \omega_1)$ *and nonexistence of traveling waves* $(\omega \leq \omega_1)$. *Parameters are illustratively set as* $D = 1, b = 1, d = 0.5, K = 30, \omega$ *(* $\omega = 0.05, 0.08$ *and* 0.2 *for* (b), (c), *and* (d), *respectively),* $\gamma = 0$. *In this setting,* $\omega_1 = 0.0667$ *and* $\omega_2 = 0.1$. *In* (b), (c), *and* (d), *the spatial patterns are plotted at times* 20, 40, 60, 80, *and* 100. *The plots in* (d) *show that the infectious subpopulation propagates in pace with the whole population with transit delay that converges to a positive number, the delay between susceptible and infectious populations invasion.*

(i) *If* $\omega \in (0, \omega_1]$, *then* $\lim_{t \to \infty} I(t, x) = 0$ *uniformly in* $x \in \mathbb{R}$.

(ii) *If* $\omega \in (\omega_1, \omega_2)$, *then for any* $c \in (0, c_\omega)$ *there exist* $t_0 > 0$ *and* $\underline{U}, \overline{U} \in C(\mathbb{R}, \mathbb{R}^+)$ *with* $\underline{U} \not\equiv 0$ *such that*

$$\underline{U}(x - ct) \leq I(t, x) \leq \overline{U}(x - c_\omega t) \quad \forall t \geq t_0, \ x \in \mathbb{R}.$$

(iii) *If* $\omega \in [\omega_2, \infty)$, *then for any* $c \in (0, c_N^*)$ *there exist* $t_0 > 0$ *and* $\underline{U}, \overline{U} \in C(\mathbb{R}, \mathbb{R}^+)$ *with* $\underline{U} \not\equiv 0$ *such that*

$$\underline{U}(x - ct) \leq I(t, x) \leq \overline{U}(x - c_N^* t) \quad \forall t \geq t_0, \ x \in \mathbb{R}.$$

The constructions of $\overline{U}$ and $\underline{U}$ will be given in the proof in section 3.1. So, in summary, we obtain that the rightward invasion speed c_I^* of the disease has the following expression,

$$c_I^* = \begin{cases} 0, & \omega \in (0, \omega_1], \\ c_\omega, & \omega \in (\omega_1, \omega_2), \\ c_N^*, & \omega \in [\omega_2, \infty), \end{cases}$$

from which we conclude that (i) when the transmission rate $\omega < \omega_1$, the basic reproduction number $R_0 < 1$ and the infection will die out; (ii) when $\omega > \omega_1$, the disease can invade into new habitats but cannot follow the pace of the susceptible population unless $\omega \geq \omega_2$; (iii) when $\omega \in (\omega_1, \omega_2)$, susceptible and infectious population have different invasion speeds and the disease propagates slower than the host invasion. The second threshold ω_2 is the critical value of the transmission rate when the disease and host propagate at the same speed. As a function of the transmission rate $\omega \in (0, +\infty)$, the invasion speed c_I^* of disease is nondecreasing but not differentiable at two critical values (see Figure 1(a)).

3. Application. In this section, we apply the developed result to investigate the disease spread in a diffusive SIS model with logistic growth or Allee effect. We are interested in whether the infectious population can invade into new habitats, and if yes, whether the infectious population shares the same invasion speed as the susceptible population. To address these two questions, we are going to study the traveling waves and invasion speed for model system (1.1). In what follows, we consider two scenarios with different birth and death rates for the population.

3.1. Logistic growth. When $B(N) = b$ and $\mu(N) = d + \frac{N}{K}$, we obtain the Fisher-KPP equation (1.2). We remark that system (1.2) with logistic growth was studied in [1] to investigate the Hantavirus transmission in mice. We assume $b > d$ so that the species successfully invades into new habitats. It is then well known that (1.2) admits the invasion speed $c_N^* = 2\sqrt{D(b-d)}$ that coincides with the minimal wave speed. Recall that ω_1, ω_2, and c_ω were defined in (2.3) and (2.4). We now prove the corollary regarding traveling waves. For any $c_1 \geq c_N^*$, (1.2) of total population admits a decreasing traveling wave $n(x - c_1 t)$ connecting N^* to 0. Replacing $N(t, x)$ and S by $n(x - c_1 t)$ and $n(x - c_1 t) - I$ in the I-equation of system (1.1), we obtain

$$(3.1) \qquad I_t = DI_{xx} + I\left[\omega n(x - c_1 t) - d - \frac{n(x - c_1 t)}{K} - \gamma - \omega I\right].$$

Introducing new variables $\hat{t} = \omega t$ and $\hat{x} = \sqrt{\frac{\omega}{D}} x$ and dropping all the hats, (3.1) can be rescaled into the following form:

$$(3.2) \qquad I_t = I_{xx} + I(a(x) - I),$$

where

$$a(x) := \frac{1}{\omega}\left[\omega N\left(\frac{x}{\sqrt{\omega/D}}\right) - d - N\left(\frac{x}{\sqrt{\omega/D}}\right)/K - \gamma\right].$$

Then $a(x) \leq 0$ if $\omega \leq \omega_1$, and in such a case, (3.2) admits no positive bounded waves. If $\omega > \omega_1$, $a(x)$ is decreasing $\forall x \in \mathbb{R}$ due to $\omega_1 > \frac{1}{K}$ and

$$a(-\infty) = \frac{c_\omega^2}{4D\omega} > 0, \quad a(+\infty) = -\frac{d + \gamma}{\omega} < 0.$$

Define $c := \frac{c_1}{\sqrt{D\omega}}$. Substituting $I(t, x) = i(x - ct)$ into (3.2) we obtain $i'' + ci' + i(a - i) = 0$, for which we know from Theorem 2.1 that it admits a positive solution if and only if $c < 2\sqrt{a(-\infty)} = \frac{c_\omega}{\sqrt{\omega D}}$. Note that c can be any number that is not less than $\frac{c_N^*}{\sqrt{D\omega}}$. Thus, $c < c_\omega$ is equivalent to $c_\omega > c_N^*$, which then is equivalent to $\omega > \omega_2$.

We now provide a proof for Theorem 2.4 regarding the rightward invasion if the initial function has compact support. Let $N(t, x)$ be the solution of (1.2) with

$N(0, x) = S_0(x) + I_0(x)$. Then we have

$$\lim_{t \to \infty, |x| \leq ct} N(t, x) = N^* \quad \forall c \in (0, c_N^*).$$

Replacing S by $N(t, x) - I$ in the second equation of (1.1), we have the following initial value problem

$$I_t = DI_{xx} + I\left[\omega N(t, x) - d - \frac{N(t, x)}{K} - \gamma - \omega I\right],$$
$$I(0, x) = I_0(x),$$

where I_0 has compact support.

(i) If $\omega \leq \omega_1$, then $\omega N(t, x) - d - \frac{N(t,x)}{K} - \gamma \leq \omega N^* - d - \frac{N^*}{K} - \gamma \leq 0$, and hence, $I_t \leq DI_{xx}$, which implies the conclusion.

(ii) Given $c \in (0, c_\omega)$, there exists $\epsilon_1 > 0$ such that $c < c_\omega - \epsilon_1$. For such an ϵ_1, there exists $B > 0$ such that the principle eigenvalue λ of

$$\begin{cases} D\phi_B'' + c\phi_B' + \frac{(c_\omega - \epsilon_1)^2}{4D}\phi_B = \lambda\phi_B, \ x \in (-B, B), \\ \phi_B(\pm B) = 0, \end{cases}$$

is positive. Define the continuous function ρ by

$$\rho(\xi) := \begin{cases} N^* - \epsilon_2, & |\xi| \leq B, \\ 0, & |\xi| \geq B + 1, \end{cases}$$

where ϵ_2 is small enough so that

$$c_\omega - \epsilon_1 < 2\sqrt{D\left[\omega(N^* - \epsilon_2) - \left(\gamma + d + \frac{N^* - \epsilon_2}{K}\right)\right]}.$$

For such ρ and ϵ_2, there exists $t_0 > 0$ such that

$$N(t, x) \geq \rho(x - ct), \quad t \geq t_0, \ x \in \mathbb{R}.$$

For such $t_0 > 0$, we have $I(t_0, x) > 0 \ \forall x \in \mathbb{R}$ thanks to the maximum principle. Define

$$\underline{U}(x) := \begin{cases} \delta\phi_B(x), & |x| \leq B, \\ 0, & |x| > B, \end{cases}$$

where δ is small enough such that

$$I(t_0, x) \geq \underline{U}(x - ct_0) \ \forall x \in \mathbb{R} \quad \text{and} \quad \lambda > \omega\delta\phi_B(x) \ \forall |x| \leq B.$$

Define $\underline{u}(s, x) = \underline{U}(x - cs - ct_0)$. Let $u(t, x)$ be the solution of the initial value problem

$$u_s = Du_{xx} + u\left[\left(\omega - \frac{1}{K}\right)N(s + t_0, x) - d - \gamma - \omega u\right], s > 0,$$
$$u(0, x) = I(t_0, x).$$

Next we show that $\underline{u}(s,x) \leq u(s,x)$. Indeed, define $\xi = x - cs - ct_0$. When $|\xi| > B$, $\underline{u}(s,x) = 0 \leq u(s,x)$. When $|\xi| < B$, we have

$$-\underline{u}_s + D\underline{u}_{xx} + \underline{u}\left[\left(\omega - \frac{1}{K}\right)N(s+t_0,x) - d - \gamma - \omega\underline{u}\right]$$

$$\geq c\underline{U}'(\xi) + D\underline{U}''(\xi) + \underline{U}(\xi)\left[\omega\rho(\xi) - d - \frac{\rho(\xi)}{K} - \gamma - \omega\underline{U}(\xi)\right]$$

$$= \delta\left\{c\phi_B'(\xi) + D\phi_B''(\xi) + \phi_B(\xi)\left[\omega(N^* - \epsilon_2) - d - \frac{N^* - \epsilon_2}{K} - \gamma - \omega\delta\phi_B(\xi)\right]\right\}$$

$$\geq \delta\left[c\phi_B'(\xi) + D\phi_B''(\xi) + \frac{(c_\omega - \epsilon_1)^2}{4D}\phi_B(\xi)\right] - \omega\delta^2\phi_B^2(\xi)$$

$$= \delta\phi_B(\xi)[\lambda - \omega\delta\phi_B\phi_B'(\xi)]$$

$$\geq 0.$$

It then follows that $\underline{u}(s,x) \leq u(s,x)$ due to $\underline{u}(0,x) = \underline{U}(x - ct_0) \leq I(t_0,x) = u(0,x)$. Note that $I(s+t_0,x) = u(s,x) \, \forall s \geq 0, x \in \mathbb{R}$. It then follows that $I(t,x) \geq \underline{U}(x - ct)$ $\forall x \in \mathbb{R}, t \geq t_0$.

Let $\overline{U}(x - c_\omega t)$ be the traveling wave of

$$u_t = Du_{xx} + u\left(\omega N^* - d - \gamma - \frac{N^*}{K} - \omega u\right).$$

Since $\overline{U}$ is connecting $\omega N^* - d - \gamma - \frac{N^*}{K}$ to 0, any translation of $\overline{U}$ is still a traveling wave and $I_0(x)$ has compact support; we may assume, without loss of generality, that $\overline{U} \geq I_0$. It then follows that $I(t,x) \leq \overline{U}(x - c_\omega t) \, \forall x, t$.

(iii) $\underline{U}$ can be constructed in a similar way to the above. Next we construct $\overline{U}$. Since $\omega > \omega_2$, we know from Corollary 2.3 that (1.1) admits a positive traveling wave $(S(x - c_N^* t), I(x - c_N^* t))$. Without loss of generality, we may assume that $N(t,x) \leq S(x - c_N^* t) + I(x - c_N^* t)$. Then $\overline{U}$ can be chosen to be $I(x - c_N^* t)$.

3.2. Population growth with Allee effect. When $B(N) =$

$$\begin{cases} \theta(-N^2 + [K_+ + K_- + e]N + d), & 0 \leq N \leq K_+ + K_-, \\ \text{nonnegative and nonincreasing}, & \text{otherwise}, \end{cases}$$

and $\mu(N) = \theta(eN + K_+K_- + d)$ with $K_+ > K_- > 0$, the dynamics of the total population density satisfies the following growth model with Allee effect:

$$(3.3) \qquad N_t = DN_{xx} + \theta(K_+ - N)(N - K_-)N.$$

Note that a similar model to system (2.4) was studied in [24, 25] with the standard transmission term and disease-induced death.

It is well known that (3.3) admits a unique wave solution $N(x - \bar{c}t)$ connecting K_+ to 0 with $\bar{c} = \frac{2}{3}(K_+ - 2K_-)\sqrt{\theta D}$. To ensure the successful invasion of the total population of the species (i.e., $\bar{c} > 0$) we need the necessary and sufficient condition $K_+ > 2K_-$. With this result for the total population, we can now study the invasive wave of infectious population. For this purpose, we first define two numbers

$$(3.4) \qquad \omega_3 = \frac{1}{K_+}[\mu(K_+) + \gamma], \quad \omega_4 = \omega_3 + \frac{\bar{c}^2}{4DK_+}.$$
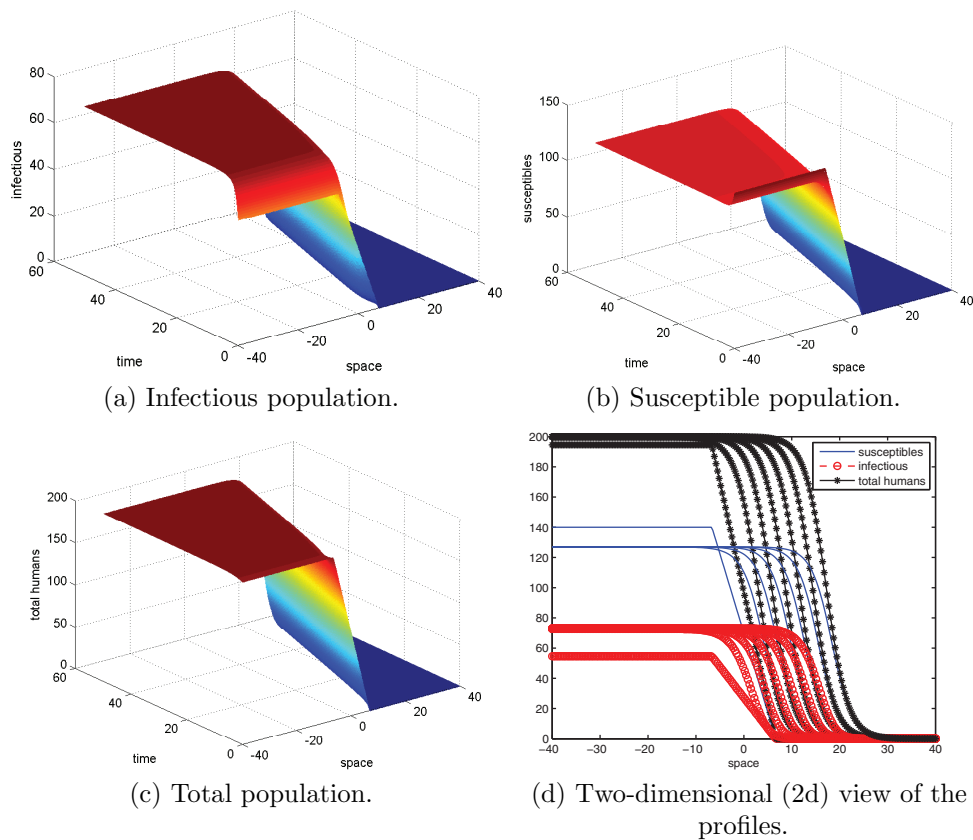
(a) Infectious population.

(b) Susceptible population.

(c) Total population.

(d) Two-dimensional (2d) view of the profiles.

FIG. 2. *Existence of traveling waves when $\omega > \omega_4$. Parameters are illustratively set as $D = 1$, $\omega = 0.05$, $\gamma = 0$, $\theta = 10^{-5}$, $b = 2.4$, $K_+ = 200$, $K_- = 50$, $e = 10^3$, and $d = 5 \times 10^4$. Then $\omega > \omega_4 = 0.0131$. Note that some parameters (θ, b, K_+, e, and d) are taken from the previous work* [24].

THEOREM 3.1 (traveling wave). *Any wave solution $(S(x-ct), I(x-ct))$ of model (2.4) with Allee effect has the property that $c = \bar{c}$ and $S + I$ is decreasingly connecting K_+ to 0. Moreover, for the I component, the KPP wave exists if and only if either $\omega > \omega_3, K_+ \leq 2K_-$ or $\omega > \omega_4, K_+ > 2K_-$; the pulse wave does not exist if $K_+ > 2K_-$ or $\omega \notin [\omega_3, \omega_4]$; and there are infinitely many pulses if $\omega \in (\omega_3, \omega_4)$ and $K_+ < 2K_-$.*

In the model, the number K_- quantifies the strength of the Allee effect and the rate ω quantifies the strength of disease transmission. Note that ω_4 defined in (3.4) is decreasing in $K_- \in [0, \frac{K_+}{2}]$. The above theorem suggests that the Allee effect helps the disease spreads among the species. It would be interesting to investigate the impact of the Alee effect on extinction of the species if the disease is fatal, which has been recently addressed for a nondispersive SI model in [19] and a patchy model in [20].

Assume that $K_+ > 2K_-$ and $N(0, x)$ has compact support. Recent studies [16, 47] have shown that there are certain critical sizes for $N(0, x)$ such that the total population invades successfully. In such a case, for the infectious population, as ω increases from 0 to $+\infty$ we may see phenomena similar to the logistic case. The critical transmission rates now are ω_3 and ω_4 defined in (3.4). The choice of $N(0, x)$ is independent of ω. Figure 2 shows the propagation of each compartment.

4. Discussions. We used a simple diffusive SIS model to illustrate the complexity of disease spread patterns when the pathogen host invades a habitat as a traveling wave. We were able to completely classify, in term of the disease transmission rate, the speed and patterns of disease spread in an environment that is divided into favorable and unfavorable regions due to the host invasion.

An important example that we considered here is the global avian influenza spread facilitated by bird migration [10]; another example of interest is the Lyme disease spread due to tick range expansion [35]. How fast the tick range expands due to the environment shifting is itself an interesting issue that our modeling and analysis approach can be used to address.

We derived a limiting system (1.3) as our staring point to investigate the pathogen dispersal in the SIS model. This limiting system can arise very naturally in other contexts. For example, if the north pole is labeled as $+\infty$ while the equator is labeled as $-\infty$ ideally, and the patch zone of a population is idealized as a one-dimensional unbounded domain, then the environmentally relevant coefficient $a(x-ct)$ considered in our study can be regarded as the per capita growth rate of a population in the spatial domain that is separated into favorable ($a(x-ct) > 0$) and unfavorable ($a(x-ct) < 0$) habitats. In this context, the sign of the parameter c determines the shifting direction of the favorable habitat, expanding poleward ($c > 0$) or retracting equatorward ($c < 0$). Therefore, our results can be used to examine the species invasion pattern in a moving environment, where the favorable and lethal habitats are moving spatially due to biotic or abiotic factors, such as climate change.

Many ecological studies observed species migration at average rates of hundreds of meters per year or more for thousands of years [11, 34], and changes in the distributions of many plants and animals, leading to severe range contractions and/or extinction of some species [32]. It is generally agreed that climatic warming plays an important role in driving the species migration and redistributing these plants and animals, often through species-specific physiological thresholds of temperature and precipitation tolerance [26, 27, 43]. By relating the environment shifting speed to such quantities as the velocity of temperature increase (km yr^{-1}) derived in [32], our model equation (1.3) can be used to address a key question in species invasion, can species populations, especially plants and other species that disperse slowly, keep pace with the climate-change-induced spatial habitat shifts [12]? Species survival may depend as much on keeping pace with moving climates as the climate's ultimate persistence [32, 34]. Those species which are unable to disperse fast enough to keep pace with changing climates share increased extinction risk [26, 39], and as a result, the loss of biodiversity. Furthermore, the decision framework with assisted colonization [26] may be carried out with careful risk analysis against those of extinction and ecosystem loss. As the first step, the estimation of the species invasion potential is of pivotal importanance.

Various theoretical frameworks have been developed by explicitly describing the ecological processes that contribute to changes of species range via biologically meaningful parameters such as dispersal, reproduction, and climate envelope [29]. In most of these frameworks, the window of favorable habitat suitable for a focal species (the climate envelope [38]) is moving. The length of the window is normally assumed to be constant [5, 36, 38, 46] except the work [30] where the persistence and spread were discussed and [4] which investigated the existence of gaps of the dominance between two competing species. By using the constant length window, the northern edge of the range is assumed to be expanding while the southern edge is retracting at the same rates. However, field studies observed the increase or decrease in the suitable

habitat size for various species. *Ixodes scapularis*, the tick vector mainly responsible for the Lyme disease transmission in North America [28], has expanded its range northward from the United States to colonize new regions in southern Canada. It would be biologically meaningful to assume the length of the window is expanding ($c > 0$) in this case. On the contrary, climate change may also decrease habitat for some species, such as those cold, cool, and even some warmwater fish species in North America reported in [17]. It is therefore also reasonable to allow the length of the suitable window to be retracting southward ($c < 0$). Our model (1.3) and analysis apply exactly to these scenarios.

It should be mentioned that starting from the early attempts of using a reaction-diffusion system framework to investigate the influence of climate change on interspecies competition [36], there is a growing body of literature on mechanistic models in terms of diffusion equations or integrodifference equations to predict the spatial spread of species under climate change [29]. Most applications have focused on determining criteria for species persistence such as the critical range-shift speed [46] or critical length of the favorable size [5]. Our study in comparison provides both new techniques and insights into the wave profiles of species invasion patterns under climate change that induces a favorable habitat in an unbounded half of an environment moving at a constant speed, an issue of current interest in the biological community [23, 29]. To illustrate this point, we start from a generalized version of the classical Fisher-KPP model [2, 18, 22], which has been widely used and extended to investigate species invasion [37, 40]:

$$u_t = Du_{xx} + u(A(x - ct) - Bu).$$

In this system, $A(x - ct)$ represents the moving per capita growth rate while B represents the density-dependent intraspecific competition. The population grows logistically with positive or negative per capita growth rate. By using changes of variables

$$\hat{t} = Bt, \ \hat{x} = \sqrt{\frac{B}{D}}x, \ \hat{c} = \frac{c}{\sqrt{BD}}, \ \hat{a}(\xi) = A\left(\sqrt{\frac{D}{B}}\xi\right)/B,$$

and dropping the hats for notational simplification, this system can be transformed into the limiting system (1.3). So we can reformulate our results as follows: define $c^* := 2\sqrt{DA(-\infty)}$. Then we conclude that (i) the KPP wave exists if and only if $c < c^*$; (ii) if $c > -c^*$, then no pulse wave exists; (iii) if $c < -c^*$ and $\int_-^0 (A(-\infty) - A(\sqrt{\frac{D}{B}}x))dx < +\infty$, then there are infinitely many different pulse waves. Consequently, we confirm that the species can keep pace with the habitat boundary expansion if the diffusion coefficient is greater than a critical value, determined by the speed of the habitat shifting and the species intrinsic maximum rate of population growth. To keep pace with the moving environment in a KPP wave profile, the minimum diffusion coefficient should be greater than $c^2/4A(-\infty)$ (see Figure 3). Note that $A(-\infty)$ represents the maximum per capita growth rate in the climate envelope, so the larger this growth rate is the easier it is for a species to keep pace with the moving environment. Note also that this minimum diffusion coefficient is independent of the intraspecific competition coefficient B. It is well known that the smallest speed of KPP waves for the Fisher-KPP equation is $2\sqrt{DA(-\infty)}$ if the whole real line is a favorable habitat (when $A(\cdot) \equiv A(-\infty)$) in the classical Fisher-KPP equation. Therefore, we conclude that if the moving speed of the climate envelope is smaller than the spreading speed for the Fisher equation, then the species
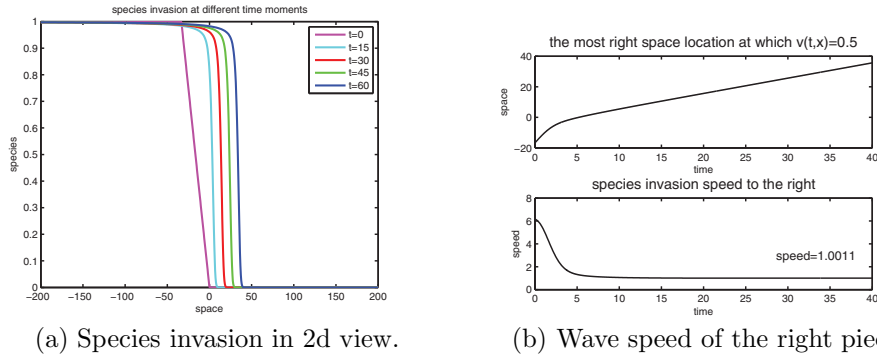
(a) Species invasion in 2d view.

(b) Wave speed of the right piece.

FIG. 3. *The KPP wave and its speed. The wavelike environment is set as* $a(x - ct) = \frac{-2\arctan(x-ct)}{\pi}$ *with* $c = 1$. *In this case,* $c < c^* = 2\sqrt{\alpha} = 2$.
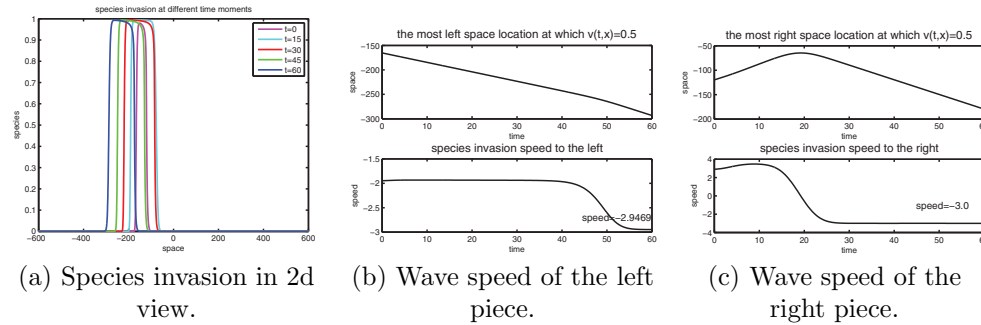

(a) Species invasion in 2d view.

(b) Wave speed of the left piece.

(c) Wave speed of the right piece.

FIG. 4. *The pulse wave. The wavelike environment is set as* $a(x - ct) = \frac{-2\arctan(x-ct)}{\pi}$ *with* $c = -3$. *In this case,* $c < -c^* = -2\sqrt{\alpha} = -2$.

can keep pace with the moving environment and species invasions in the form of a monotone traveling wave. This conclusion applies to the case when the favorable habitat expands poleward.

It is interesting to note that we have also rigorously shown the existence of traveling wave solutions even when the suitable habitat is retracting southward. These waves are in the format of pulses, and pulse waves can only be observed when the favorable habitat is retracting southward enough faster than the critical speed $2\sqrt{DA(-\infty)}$ (see Figure 3). In this situation, the environment habitat shifts faster than the intrinsic movement of the species so that the environment pushes the species to move southward in order to occupy the favorable habitat, leading to pulse waves rather than monotone KPP waves.

Pulse *wavelike* profiles can also be observed when $-c^* < c < 0$ or $c > c^*$ (Figures 4 and 5). However, these profiles are no longer traveling waves as they have different speeds for the left and right pieces. When $-c^* < c = -1 < 0$ (Figure 4), the speed of the right piece is -1 while that for the left piece is -3 and, therefore, the dominant domain of the species is expanding. Moreover, the right piece moves with speed -1, equal to that of the environment, which is driven by the environment shift. At the same time, the shifting environment also increases the speed of the left piece to a level greater than its intrinsic speed. A similar result holds when $c > c^*$ (Figure 5).

The developed results also apply when the host population follows other types of growth rates. One example is the population subject to the Allee effect where the low
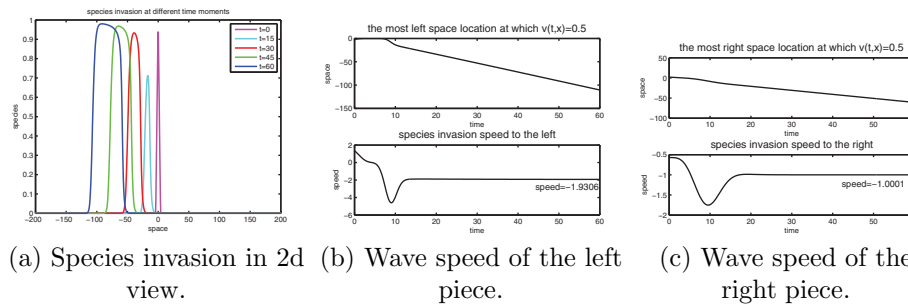
(a) Species invasion in 2d view. (b) Wave speed of the left piece. (c) Wave speed of the right piece.

FIG. 5. *A pulse-like profile when* $-c^* < c < 0$. *The wavelike environment is set as* $a(x - ct) = \frac{-2 \arctan(x-ct)}{\pi}$ *with* $c = -1$. *In this case,* $-c^* = -2\sqrt{\alpha} = -2 < c < 0$.

density population has a decreased per capita growth rate due to various mechanisms [3]. Previous studies show that populations with Allee effect and random movements admit monotone waves [25] and our main results can be extended to this scenario (see the appendix) with shifting environment. In both cases of logistic and Allee effect growth rates, the susceptibles (resources) should always move forward faster than the pathogen (Figures 1 and 2). If no resources are available for the pathogen, the colonization stage of the pathogen fails [23] in the process of species invasion. However, we also noticed differences between two different growth rates. Namely, in the case of logistic growth, there is always a pulse of the susceptibles in the moving head (Figure 1(d)). In contrast, when the host population growth is depicted by the Allee effect, the susceptible population may move forward in the format of a KPP wave (Figure 2(d)).

Finally, we would also like to raise readers' attention to the recent investigation performed by Li et al. [30, 31], where the same model $u_t = u_{xx} + u(r(x - ct) - u)$ was proposed and analyzed. However, the biological motivations and mathematical focuses are different. In [30, 31], the model was proposed with the consideration of climate change and the authors focused on the spreading speed when favorable environment is shrinking in the sense that $c > 0$ and r is nondecreasingly connecting a negative number to a positive number. In the current work, we propose the model to investigate the issue of whether the pathogen can spread as fast as its host. More precisely, we derive the model from the classical SIS transmission model. Here we first study the forced traveling waves $\forall c \in \mathbb{R}$ from which we then obtain some spreading properties for the case where $c < 0$ and r is nondecreasingly connecting a negative number to a positive number. The choice of negative c values makes it possible to describe the scenario where the total host population is expanding on the spatial habitat.

5. Appendix: Proofs of main results.

5.1. A priori estimates. We begin with the description of possible shapes of wave profiles that are solutions of (2.1).

LEMMA 5.1. *Let* $u \not\equiv 0$ *be a bounded nonnegative solution of* (2.1). *Then* $0 < u < \alpha$, $u(+\infty) = 0$, *and* $u(-\infty)$ *exists. Moreover, either*

$$u(-\infty) = \alpha \quad and \quad u' < 0$$

or

$$u(-\infty) = 0 \quad and \quad \{x : u' = 0\} \text{ is a singleton.}$$

Proof. We first rewrite (2.1) as a 2d asymptotic autonomous ODE, and then apply [41, Theorem 1.5] to obtain $u(+\infty) = 0$, $u(-\infty) \in \{0, \alpha\}$. By the elliptic strong maximum principle and assumption (1.4), we obtain $0 < u < \alpha$. Next we study the possible shape of function u. Since $a(+\infty) = \beta < 0$ and $u > 0$, we have $(u'e^{cx})' = -u(a - u)e^{cx} > 0 \ \forall x \gg 1$, which, together with $u(+\infty) = 0$, implies that $u'(x) < 0 \ \forall x \gg 1$. We proceed to distinguish between $u(-\infty) = 0$ and $u(-\infty) = \alpha$. When $u(-\infty) = \alpha$, we use the assumption $a' \leq 0$ and the strong maximum principle again to obtain $u' < 0$ if $u' \leq 0$. To show $u' \leq 0$, we assume for the sake of contradiction that $u' > 0$ somewhere. It then follows that there exist $x_1 < x_2$ such that u attains a local minimum at x_1 and a local maximum at x_2 with $u(x_1) < u(x_2)$. Hence, $a(x_1) \leq u(x_1) < u(x_2) \leq a(x_2)$, which contradicts $a' \leq 0$. When $u(-\infty) = 0$, we can similarly prove that $u'(x) > 0 \ \forall x \ll -1$. Next, we show that u does not oscillate. Otherwise, there exist $y_1 < y_2 < y_3$ such that u attains local maximums at y_1, y_3 and a local minimum at y_2 with $u(y_1) > u(y_2)$ and $u(y_3) > u(y_2)$. This leads to a contradiction with $a' \leq 0$. Finally, we show that the set $\{x : u'(x) = 0\}$ is a singleton. Otherwise, there is an interval $[z_1, z_2]$ such that $u(x) = a(x) = \gamma_2, x \in [z_1, z_2]$, where γ_2 is the global maximum of u. Since $a' \leq 0$, $w_2 := u - \gamma_2$ satisfies $w_2 \leq 0$ and $w_2'' + cw_2' + (a - 2\gamma_2 - w)w_2 = \gamma_2(\gamma_2 - a) \ \forall x \geq z_1$. Then $w_2(z_1) = 0 = w_2'(z_1)$ contradicts the Hopf lemma. This completes the proof. $\qquad \square$

We now describe the behaviors of the pulse wave profile at $-\infty$.

LEMMA 5.2. *Let u be a pulse wave. Then $c \leq -c^*$. Moreover, $U(\lambda) := \int_{\mathbb{R}} u(x)e^{-\lambda x}dx$ is finite for $\lambda \in (0, \lambda^*)$ and diverges for $\lambda > \lambda^*$, where $\lambda^* = \lambda^*(c) = \frac{-c-\sqrt{c^2-4\alpha}}{2}$.*

Proof. We first show that $c < 0$ and there exists $\lambda_0 \in (0, +\infty]$ such that $U(\lambda)$ is analytic for $\lambda \in (0, \lambda_0)$. Indeed, since $u(-\infty) = 0$ and $a(-\infty) = \alpha$, there exists $\epsilon_1 \in (0, \alpha)$ and $x_1 < 0$ such that $u(a - u) \geq (\alpha - \epsilon_1)u \ \forall x \leq x_1$. According to the proof of [45, Proposition 2.1], we have $u'(-\infty) = 0$. Hence, we may integrate both sides of (2.1) from $-\infty$ to x with $x \leq x_1$ to obtain

$$(5.1) \qquad u'(x) + cu(x) \leq -(\alpha - \epsilon) \int_{-\infty}^{x} u(y)dy.$$

Define the increasing function $w(x) := \int_{-\infty}^{x} u(y)dy$. Integrating both sides of (5.1) yields $(\alpha - \epsilon) \int_{-\infty}^{x} w(y)dy \leq -[u(x) + cw(x)] < -cw(x)$, from which we conclude that $c < 0$. Choose r_1 such that $r_2 := \frac{-c}{r_1(\alpha - \epsilon)} < 1$. Then we obtain

$$(5.2) \qquad \begin{aligned} w(x - r_1) &\leq \frac{1}{r_1} \int_{x-r_1}^{x} w(y)dy \\ &\leq \frac{1}{r_1} \int_{-\infty}^{x} w(y)dy \\ &\leq r_2 w(x) \quad \forall x \leq x_1. \end{aligned}$$

Define $\gamma_1 := \frac{1}{r_1} \ln \frac{1}{r_2} > 0$ and $f(x) := w(x)e^{-\gamma_1 x}$. Then we have

$$\begin{aligned} f(x - r_1) &= w(x - r_1)e^{-\gamma_1(x-r_1)} \\ &\leq r_2 w(x)e^{-\gamma_1(x-r_1)} = f(x) \quad \forall x \leq x_1, \end{aligned}$$

which implies that $f(x)$ is bounded for $x \leq 0$. Hence, $w(x) \leq pe^{\gamma_1 x} \ \forall x \leq 0$ for some $p > 0$. Define the iteration scheme $u^{(1)} = w$, $u^{(m)}(x) = \int_{-\infty}^{x} u^{(m-1)}(y)dy$, $m > 1$. It

then follows that $u^{(m)}(x) \le \frac{p}{\gamma_1^{m-1}} e^{\gamma_1 x}$ $\forall m \ge 1$, $x \le 0$, and, hence,

$$\int_{-\infty}^{x} e^{\lambda(x-y)} u(y) dy = \sum_{m=0}^{\infty} \lambda^m \int_{-\infty}^{x} \frac{(x-y)^m}{m!} u(y) dy$$
$$= \sum_{m=0}^{\infty} \lambda^m u^{(m+1)}(x)$$
$$\le p e^{\gamma_1 x} \sum_{m=0}^{\infty} \frac{\lambda^m}{\gamma_1^m} < +\infty \quad \forall \lambda \in (0, \gamma_1).$$

In particular, $\int_{-\infty}^{0} u(x) e^{-\lambda x} dx < +\infty$ $\forall \lambda \in (0, \gamma_1)$. This implies

$$U(\lambda) := \int_{\mathbb{R}} u(x) e^{-\lambda x} dx = \int_{-\infty}^{0} u(x) e^{-\lambda x} dx + \int_{0}^{+\infty} u(x) e^{-\lambda x} dx < +\infty \quad \forall \lambda \in (0, \gamma_1).$$

Since $u > 0$, by [44, Theorem 5b] we know that the expected λ_0 exists.

Next we show that $u(x)$, $u'(x)$, $u''(x) = o(e^{\lambda x})$ $\forall \lambda \in (0, \lambda_0)$. Choose γ_3 large enough so that $\mu^2 + c\mu - \gamma_3 = 0$ admits two solutions $\mu_1 < 0 < \mu_2$. Then we can rewrite (2.1) as the following integral equation

(5.3) $$u(x) = \int_{\mathbb{R}} k(y)[\gamma_3 + a(x-y) - u(x-y)] u(x-y) dy$$

with

(5.4) $$k(y) = \begin{cases} \frac{1}{\mu_2 - \mu_1} e^{\mu_2 y}, & y \le 0, \\ \frac{1}{\mu_2 - \mu_1} e^{\mu_1 y}, & y > 0. \end{cases}$$

Multiplying $e^{-\lambda x}$ on both sides of (5.3) we obtain the following estimate when $\lambda \in (0, \min\{\lambda_0, \mu_2\})$:

$$e^{-\lambda x} u(x) \le e^{-\lambda x} \int_{\mathbb{R}} k(y)(\gamma_3 + \alpha) u(x-y) dy$$
$$= \int_{\mathbb{R}} k(y) e^{-\lambda y}(\gamma_3 + \alpha) u(x-y) e^{-\lambda(x-y)} dy$$
$$\le (\gamma_3 + \alpha) U(\lambda) < +\infty.$$

Note that μ_2 is increasing to infinity in γ_3. It then follows that $u(x) = o(e^{\lambda x})$ $\forall \lambda \in (0, \lambda_0)$, so do u' and u'' using (5.1) and (2.1).

Finally we show that $c \le -c^*$ and $\lambda_0 = \lambda^*$, i.e., λ_0 is the smallest positive solution of $\lambda^2 + c\lambda + \alpha = 0$. It then suffices to prove the following statements: (i) $\lambda_0 < +\infty$, (ii) $\lambda^2 + c\lambda + \alpha > 0$ $\forall \lambda \in (0, \lambda_0)$, (iii) $\lambda_0^2 + c\lambda_0 + \alpha = 0$. Indeed, as $u(x)$, $u'(x)$, $u''(x) = o(e^{\lambda x})$ $\forall \lambda \in (0, \lambda_0)$, we can integrate both sides of (2.1) (after multiplying by the factor $e^{-\lambda x}$) to obtain

$$\int_{\mathbb{R}} [\lambda^2 + c\lambda + a(x) - u(x)] u(x) e^{-\lambda x} dx = 0 \quad \forall \lambda \in (0, \lambda_0).$$

This implies that for any possible λ and c the function $\lambda^2 + c\lambda + a(x) - u(x)$ must change sign in $x \in \mathbb{R}$. Thus, the first two statements hold. To prove the third one, we

argue by contradiction, assuming that $\inf_{\lambda \in (0,\lambda_0)}(\lambda^2 + c\lambda + \alpha) \neq 0$. Then by (ii) we immediately have $\inf_{\lambda \in (0,\lambda_0)}(\lambda^2 + c\lambda + \alpha) > 0$. Without loss of generality, we assume $\lambda_0 < \mu_2$. Note that

$$(\gamma_3 + \alpha) \int_{\mathbb{R}} k(y)e^{-\lambda y}dy = -\frac{\gamma_3 + \alpha}{\lambda^2 + c\lambda - \gamma_3} > 1 \quad \forall \lambda \in (0, \lambda_0).$$

Then there exist $M > 0$ and $\epsilon > 0$ such that

$$\delta := \inf_{\lambda \in (0,\lambda_0)} (\gamma_3 + \alpha - \epsilon) \int_{|y| \leq M} k(y)e^{-\lambda y}dy > 1.$$

Define $l_\lambda(\xi) = \int_{-\infty}^{\xi} u(x)e^{-\lambda x}dx$. Then by (5.3), we have

$$l_\lambda(\xi) = \int_{-\infty}^{\xi} e^{-\lambda x} \int_{\mathbb{R}} k(y)[\gamma_3 + a(x-y) - u(x-y)]u(x-y)dydx$$

$$\geq \int_{-\infty}^{\xi} \int_{|y| \leq M} k(y)e^{-\lambda y}[\gamma_3 + a(x-y) - u(x-y)]u(x-y)e^{-\lambda(x-y)}dydx.$$

Since $a(-\infty) = \alpha$ and $u(-\infty) = 0$, for the above M and ϵ there exists $N > M$ such that for any $\xi < -N$ and $\lambda \in (0, \lambda_0)$,

$$l_\lambda(\xi) \geq (\gamma_3 + \alpha - \epsilon) \int_{-\infty}^{\xi} \int_{|y| \leq M} k(y)e^{-\lambda y}u(x-y)e^{-\lambda(x-y)}dydx$$

$$\geq (\gamma_3 + \alpha - \epsilon) \int_{|y| \leq M} k(y)e^{-\lambda y}dy \int_{-\infty}^{\xi-M} u(x)e^{-\lambda x}dx$$

$$\geq \delta l_\lambda(\xi - M).$$

Next we repeat the arguments below (5.2) to obtain $\int_{\mathbb{R}} u(x)e^{-(\lambda + \frac{\gamma_4}{2})x}dx < +\infty$ with $\gamma_4 = \frac{1}{M}\ln\delta > 0$ for any $\lambda \in (0, \lambda_0)$. It contradicts the definition of λ_0 since γ_4 is independent of λ. □

5.2. KPP waves. We now consider various piecewise constant environments in order to construct appropriate upper and lower solutions to establish or rule out KPP waves. We first consider (1.3) in a piecewise constant shifting environment. Let $x_0 \in \mathbb{R}$ and b be a step function defined by

$$b(x) = \begin{cases} \theta_1, & x \leq x_0, \\ \theta_2, & x > x_0 \end{cases}$$

with

$$\theta_1 > 0 > \theta_2.$$

Consider the following wave profile equation

(5.5) $$u'' + cu' + u(b - u) = 0, \quad x \in \mathbb{R} \setminus \{x_0\},$$

for which we have the following threshold-type results.

PROPOSITION 5.3. *Equation* (5.5) *admits a positive solution* $u \in C^1(\mathbb{R})$ *with* $u(-\infty) = \theta_1$ *and* $u(+\infty) = 0$ *if and only if* $c < 2\sqrt{\theta_1}$.

Proof. Since b is a step function, it suffices to find the sufficient and necessary condition under which the unstable manifold W_u of equilibrium $(\theta_1, 0)$ of system

$$(5.6) \qquad \begin{cases} u_1' = v_1, \\ v_1' = -cv_1 - u_1(\theta_1 - u_1) \end{cases}$$

intersects with the stable manifold W_s of equilibrium $(0, 0)$ of system

$$(5.7) \qquad \begin{cases} u_2' = v_2, \\ v_2' = -cv_2 - u_2(\theta_2 - u_2). \end{cases}$$

From the proof of Lemma 5.1, we can see that $u' < 0$ and $u > 0$. So for both manifolds we may only focus on the branches in the fourth quadrant.

By analyzing the linearization around these two equilibria, we see that both manifolds of interest have dimension one. Moreover, the unstable manifold W_u will eventually connect $(0,0)$ tangentally to the vector $(1, \frac{-c+\sqrt{c^2-4\theta_1}}{2})$ when $c \geq 2\sqrt{\theta_1}$ and will eventually cross the v-axis when $c < 2\sqrt{\theta_1}$. The stable manifold W_s lies in the fourth quadrant, originates from infinity, and is tangent to the vector $(1, \frac{-c-\sqrt{c^2-4\theta_2}}{2})$ at the origin. Clearly, W_u and W_s have an intersection away from the origin when $c < 2\sqrt{\theta_1}$. Next we prove W_u and W_s have no intersection except the origin if $c \geq 2\sqrt{\theta_1}$. Indeed, near the origin there is no intersection and W_u is above W_s due to

$$\frac{-c+\sqrt{c^2-4\theta_1}}{2} > \frac{-c-\sqrt{c^2-4\theta_2}}{2}.$$

Suppose the contrary: P is an intersection away from but closest to the origin. Then at P, we must have $u_1 = u_2, v_1 = v_2, v_1' \geq v_2'$ and, hence, $\theta_1 < \theta_2$, a contradiction. $\quad\square$

Now we are ready to establish the critical value of the speed for the KPP wave.

Proof of Theorem 2.1(i). For any $c < c^* := 2\sqrt{\alpha}$, since $a(-\infty) = \alpha$, we may find $\epsilon > 0$ and x_ϵ such that $c < 2\sqrt{\alpha - \epsilon}$ and

$$a(x) \geq b_-(x) := \begin{cases} \alpha - \epsilon, & x \leq x_\epsilon, \\ 2\beta, & x > x_\epsilon. \end{cases}$$

We consider (5.5) with $b = b_-$, that is,

$$u'' + cu' + u(b_- - u) = 0, \quad x \in \mathbb{R} \setminus \{x_\epsilon\}.$$

According to Proposition 5.3, this equation admits a positive solution $u_- \in C^1$ connecting $\alpha - \epsilon$ to 0 since $c < 2\sqrt{\alpha - \epsilon}$. Thus, u_- is a satisfactory lower solution.

For the nonexistence proof, we argue by contradiction. Suppose the contrary: (2.1) admits a solution ϕ connecting α to 0 for some $c \geq c^*$. By Lemma 5.1 we know $0 < \phi < \alpha$. Choose $x_2 \in \mathbb{R}$ such that

$$a(x) \leq b_+(x) := \begin{cases} \alpha, & x \leq x_2, \\ \beta/2, & x > x_2. \end{cases}$$

We claim that equation

$$(5.8) \qquad u'' + cu' + u(b_+ - u) = 0, \quad x \in \mathbb{R} \setminus \{x_2\},$$

admits a C^1 solution connecting α to 0. Indeed, choose γ large enough such that $H(x,u) := u[\gamma + b_+(x) - u]$ is increasing in $u \in [0,\alpha]$. Let $\mu_2 > 0 > \mu_1$ be the two solutions of the equation $\mu^2 + c\mu - \gamma = 0$. Define the monotone map F on the space $BC(\mathbb{R})$ consisting of all bounded continuous functions by

$$F[u](x) = \int_{\mathbb{R}} k(y) H(x - y, u(x - y)) dy,$$

where k is defined as in (5.4). Then we have

$$F[\alpha](x) = \int_{\mathbb{R}} k(y)[\gamma + b_+(x - y) - \alpha]\alpha dy \leq \int_{\mathbb{R}} k(y)\gamma\alpha dy = \alpha$$

and

$$F[\phi](x) \geq \int_{\mathbb{R}} k(y)[\gamma + a(x - y) - \phi(x - y)]\phi(x - y) dy = \phi(x).$$

This implies that $\alpha \geq F[\alpha] \geq F[\phi] \geq \phi$. Thus, $F^n[\alpha](x)$ is nonincreasing in $n \geq 1$. Hence, $\psi(x) := \lim_{n \to +\infty} F^n[\alpha](x) \geq \phi(x)$ exists and satisfies $\psi = F[\psi]$. Since $b_+ \in C(\mathbb{R} \setminus \{x_2\})$, we may check that $\psi \in C^1(\mathbb{R}) \cap C^2(\mathbb{R} \setminus \{x_2\})$ and it is a solution to (5.8). This contradicts Proposition 5.3. The proof is complete. $\quad\square$

5.3. Pulse wave. In Lemma 5.2, the nonexistence of pulse waves when $c > -c^*$ has been proved and a rude tail behavior at $-\infty$ of a possible pulse wave has been obtained. In this part, we construct upper and lower solutions to prove the existence when $c < -c^*$. The critical case $c = -c^*$ remains unclear.

Let $c < -c^*$ be fixed. Recall that $\lambda^* = \lambda^*(c)$ defined in Lemma 5.2 is the smallest solution of the equation $\lambda^2 + c\lambda + \alpha = 0$. An upper solution that vanishes at $-\infty$ can be easily constructed. Define

$$\phi_+(x) = \min\{\gamma_+ e^{\lambda^* x}, \alpha\},$$

where γ_+ is an adjustable positive number.

LEMMA 5.4. *For any $\gamma_+ > 0$, ϕ_+ is an upper solution of* (2.1).

To prove this, let x_1 be the point at which ϕ_+ is not differentiable. Then one can quickly check that

$$\phi_+'' + c\phi_+' + a\phi_+ - \phi_+^2 \leq \phi_+'' + c\phi_+' + \alpha\phi_+ = 0 \quad \forall x \in \mathbb{R} \setminus \{x_1\}$$

and $\phi_+'(x_1^-) \geq \phi_+'(x_1^+)$.

To construct an appropriate lower solution, it is natural to extend the idea used in the previous section on the KPP wave, that is, the wave in a lower and piecewise constant environment serves as a lower solution. But it does not work since the pulse wave in a lower environment has a bigger tail than that in environment a at $-\infty$.

PROPOSITION 5.5. *For any $c \leq -2\sqrt{\theta_1}$ and $\rho \in (0, \theta_1)$,* (5.5) *admits a positive solution $u \in C^1$ with $u(\pm\infty) = 0$ and $\max_{x \in \mathbb{R}} u(x) = \rho$. Moreover, u is increasing first and then decreasing and*

$$u(x) = o(e^{\lambda x}) \quad as \ x \to -\infty \quad \forall \lambda < \frac{-c - \sqrt{c^2 - 4\theta_1}}{2}.$$

To prove this proposition, we continue to use the phase plane arguments as in Proposition 5.3. It is easy to see that for any $\rho \in (0, \theta_1)$, ODE system (5.6) admits an entire solution $\Phi_1 := (u_1, v_1)$ with $\Phi(0) = (\rho, 0)$. Any translation of Φ is still a solution of (5.6) and it connects the origin at $-\infty$ and eventually crosses the v-axis. Thus, the phase portrait of the solution Φ has an intersection with the stable manifold W_s of equilibrium $(0, 0)$ of ODE system (5.7).

As shown in Lemma 5.2, any possible pulse wave of (1.3) decays to zero faster than $e^{(\lambda^* - \epsilon)x}$ for any $\epsilon > 0$ when $x \to -\infty$. This fact, together with Proposition 5.5, implies that the pulse solution of (5.5) with $\theta_1 < \alpha$ is not an appropriate lower solution, but it is another appropriate lower solution of (2.1) for KPP waves.

To construct a lower solution appropriately, we have to think in another way, by taking the information of exponential decay for possible wave profiles at $-\infty$ into account. For this purpose, we need to assume that the environment converges to α at $-\infty$ quickly enough.

LEMMA 5.6. *Assume that* $\alpha - a \in L^1(-\infty, 0)$. *Then for any* $\gamma_- > 0$ *and* $x_- \ll -1$, *there exists an increasing function* $p \in C^2$ *with* $p(-\infty) = 0$ *and* $p(x_-) = 1$ *such that*

$$
\phi_-(x) := \begin{cases} \gamma_- e^{\lambda^* x}(1 - p(x)), & x < x_-, \\ 0, & x \geq x_- \end{cases}
$$

is a lower solution.

Proof. Define

$$
f(x) = \min\{\alpha - a_{\inf} + \gamma e^{\lambda^* x}, 2\} \quad \text{and} \quad \delta = -(2\lambda^* + c).
$$

Since $c < -c^*$, $\delta = \sqrt{c^2 - 4\alpha} > 0$. Since a is nondecreasing, we can find x_0 such that

$$
f(x) = \begin{cases} \alpha - a_{\inf} + \gamma_- e^{\lambda^* x}, & x < x_0, \\ 2, & x \geq x_0. \end{cases}
$$

Let $k(y)$ be defined as in (5.4) with $\mu_1 = 0$ and $\mu_2 = \delta$. Since $\alpha - a \in L^1(-\infty, 0)$, we can define $p_1(x) = \int_{\mathbb{R}} k(y) f(x - y) dy$, which clearly is increasingly connecting 0 to $+\infty$. Assume $p(x_1) = 1$. Choose $\xi > 0$ so that $x_- := x_1 - \xi < x_0$. Define $p(x) = p_1(x + \xi)$. Then $p(x) = \int_{\mathbb{R}} k(y) f(x + \xi - y) dy$ and $p'' - \delta p' + f(x + \xi) = 0$. Next we verify such a ϕ_- is a lower solution. Indeed, for any $x < x_-$, we have $0 \leq p(x) \leq 1$ and $\alpha - a(x) + \gamma_- e^{\lambda^* x} \leq f(x) \leq f(x + \xi)$ and, hence,

$$
\begin{aligned}
&-\gamma_-^{-1} e^{-\lambda^* x}(\phi_-'' + c\phi_-' + a\phi_- - \phi_-^2) \\
&= p'' - \delta p + (\alpha - a)(1 - p) + \gamma_- e^{\lambda^* x}(1 - p)^2 \\
&\leq p'' - \delta p + f(x + \xi) \\
&= 0.
\end{aligned}
$$

Moreover, by direct computations we have $\phi_-'(x_-^-) \leq \phi_-'(x_-^+)$. The proof is complete. $\square$

Proof of Theorems 2.1(ii) *and* 2.1(iii). The nonexistence when $c > -c^*$ has been shown in Lemma 5.2. The existence when $c < -c^*$ follows from the construction of upper and lower solutions. Indeed, we employ an iteration argument for which we refer to [33, 45] for more details. By the variation of constant formulas for second order ODEs (see (5.3)), we know that a uniformly bounded function u is a solution

of (2.1) if and only if it is a fixed point of the map $\Lambda : BC(\mathbb{R}, \mathbb{R}) \to BC(\mathbb{R}, \mathbb{R})$ defined by

$$(5.9) \qquad \Lambda[\phi](x) = \int_{\mathbb{R}} k(y)[\gamma_3 + a(x - y) - \phi(x - y)]\phi(x - y)dy,$$

where we recall that k is defined in (5.4) and $\gamma_3 > \alpha$ could be as large as we want. We proceed as in [33, Lemmas 2.5 and 2.6] (see also [45]). Set $\Omega = \mathbb{R} \setminus \{x - x_1, 0\}$ and use $\partial\Omega$ to denote the boundary. By Lemma 5.4 we obtain

$$\Lambda[\phi_+](x) = \int_{\Omega} k(y)[\gamma_3\phi_+(x - y) - \phi_+''(x - y) - c\phi_(x - y)]dy$$

$$(5.10) \qquad \leq \int_{\Omega} k(y)[\gamma_3\phi_+(x - y) - \phi_+''(x - y) - c\phi_(x - y)]dy.$$

Direction calculations give rise to

$$\int_{\Omega} k(y)\phi_+''(x - y)dy$$

$$(5.11) \qquad = -[\phi_+'(x - y)k(y) + \phi_+(x - y)k'(y)]|_{y \in \partial\Omega} + \int_{\Omega} k''(y)\phi_+(x - y)dy$$

and

$$(5.12) \qquad \int_{\Omega} k(y)\phi_+'(x - y)dy = -\phi_+(x - y)k(y)|_{y \in \partial\Omega} + \int_{\Omega} k'(y)\phi_+(x - y)dy.$$

Note that $k''(y) + ck'(y) - \gamma_3 k(y) = 0$, $y \neq 0$. Combining (5.10)–(5.12), we arrive at

$$\Lambda[\phi_+](x) \leq [\phi_+'(x - y)k(y) + \phi_+(x - y)k'(y) + c\phi_+(x - y)k(y)]|_{y \in \partial\Omega}$$

$$(5.13) \qquad = k(x - x_1)[\phi_+'(x_1^+) - \phi_+(x_1^-)] + \phi_+(x)[k'(0^-) - k'(0^+)].$$

Since $k'(0^-) - k'(0^+) = 1$ and $\phi_+'(x_1^+) - \phi_+(x_1^-) \leq 0$, we conclude $\Lambda[\phi_+] \leq \phi_+$. Similarly, $\Lambda[\phi_-] \geq \phi_-$ thanks to $\phi_-'(x_-^+) \geq \phi_-'(x_-^-)$. Since $\gamma_3 > \alpha$, we see that $\Lambda : C(\mathbb{R}, [0, \alpha]) \to C(\mathbb{R}, [0, \alpha])$ is nondecreasing. Choose γ sufficiently large such that $\phi_+ > \phi_-$. Then we arrive at

$$\phi_- \leq \Lambda[\phi_-] \leq \Lambda[\phi_+] \leq \phi_+.$$

Therefore, the nonincreasing sequence of continuous functions $\{\Lambda^n[\phi_+]\}_{n \geq 1}$ converges pointwisely to a function ϕ with $\phi_- \leq \phi \leq \phi_+$. Passing n to infinity in the equality $\Lambda^n[\phi_+] = \Lambda[\Lambda^{n-1}[\phi_+]]$ yields that $\phi = \Lambda[\phi]$ thanks to Lebesgue's dominated convergence theorem and, hence, $\phi \in C^2(\mathbb{R}, \mathbb{R})$ is a classical solution of (2.1). Moreover, the fact that $\phi_- \leq \phi \leq \phi_+$ and Lemma 5.1 imply that $\phi(\pm\infty) = 0$.

Next we show that multiple pulse waves exist for each $c < -c^*$. Now that we have a pair of upper and lower solutions $\phi_\pm$ as well as a pulse wave in-between, to obtain a different pulse wave, we can translate ϕ_+ to the right by decreasing γ_+ so that it is not bigger than ϕ_- and then decrease γ_- so that the new ϕ_- is less than the new ϕ_+. Then another pair of upper and lower solutions is constructed and, hence, a different pulse wave exists. $\quad\square$

5.4. Proof of Theorem 2.2. To figure out the explicit expressions of $\lambda_{1,c,a}$ and $\lambda'_{1,c,a}$, we recall some results from recent publications by Berestycki and his collaborators, especially for the case where domain $\Omega = \mathbb{R}$.

THEOREM 5.7.
  (i) $\lambda_{1,c,a} = \lambda_{1,0,a} + \frac{c^2}{4}$.
  (ii) $\lambda'_{1,c,a} \leq \lambda_{1,c,a}$.
  (iii) $-\|a\|_\infty \leq \lambda'_{1,c,a} \leq \|a\|_\infty$.

The first conclusion is from [5, Proposition 2], the second is from [8, Theorem 4.5], and the third is from [8, Remark 5.3].

Applying [8, Theorem 2.1] to (2.1), we obtain the following.

THEOREM 5.8.
  (i) *If either* $\lambda'_{1,c,a} < 0$ *or* $\lambda_{1,c,a} < 0$, *then* (2.1) *admits at least one positive bounded solution.*
  (ii) *If* $\lambda'_{1,c,a} > 0$, *then* (2.1) *admits no nonnegative bounded solution other than the trivial state* $u \equiv 0$.

With the aid of the above two theorems as well as our Theorem 2.1, we can calculate the two eigenvalues.

Explicit form of $\lambda_{1,c,a}$. Combining Theorems 2.1 and 5.8(i), we immediately obtain $\lambda_{1,c^*,a} \geq 0$, which then implies that $\lambda_{1,0,a} \geq -\alpha$ according to Theorem 5.7(i). Now it remains to show that $\lambda_{1,0,a} \leq -\alpha$. Indeed, let $|c| < c^* = 2\sqrt{\alpha}$ be fixed and choose $x_0 < 0, \epsilon > 0$, and $R > 0$ such that

$$a(x) > \alpha - \epsilon \quad \forall x \in [x_0 - 2R, x_0] \quad \text{and} \quad \alpha > 2\epsilon + \frac{c^2}{4} + \left(\frac{\pi}{2R}\right)^2.$$

We use $L_{c,a,R}$ to denote the operator $L_{c,a}$ on the domain $[x_0, x_0 + 2R]$ with the Dirichlet boundary condition. Let $\lambda_{1,c,a,R}$ be the eigenvalue of $L_{c,a,R}$ and $\lambda'_{1,c,a,R}$ be defined as in (2.2) with $\Omega = [x_0, x_0 + 2R]$. It then follows that $\lambda_{1,c,a,R} = \lambda'_{1,c,a,R}$. Note that there exists a positive function ϕ_R such that

$$L_{c,\alpha-\epsilon,R}\phi_R = \left(\alpha - \epsilon - \frac{c^2}{4} - \left(\frac{\pi}{2R}\right)^2\right)\phi_R > \epsilon\phi_R.$$

Consequently, $(L_{c,a,R}-\epsilon)\phi_R \geq (L_{c,\alpha-\epsilon,R}-\epsilon)\phi_R \geq 0$, which implies that $\lambda'_{1,c,a,R} \leq -\epsilon$. Since $\lambda_{1,c,a} \leq \lambda_{1,c,a,R}$, we have

$$\lambda_{1,c,a} \leq \lambda_{1,c,a,R} = \lambda'_{1,c,a,R} \leq -\epsilon < 0.$$

Thus, $\lambda_{1,0,a} < -\frac{c^2}{4} \ \forall |c| < c^*$ and, hence, $\lambda_{1,0,a} \leq -\alpha$.

Recall that $a(-\infty) = \alpha > 0$ and $a(+\infty) = \beta < 0$ as assumed. Then we have the following observation.

LEMMA 5.9. $-\alpha \leq \lambda'_{1,c,a} \leq -\beta$.

Proof. Taking $\phi \equiv 1$ as a test function in the definition (2.2) of $\lambda'_{1,c,a}$, we see that $\lambda'_{1,c,a} \leq -\beta$. For the other inequality, we argue by contradiction, assuming that $\lambda'_{1,c,a} = -\alpha - 2\epsilon$ for some c and $\epsilon > 0$. Then there exists $\phi \in C^2(\mathbb{R}) \cap W^{2,\infty}(\mathbb{R})$ with $\phi > 0$ such that $L_{c,-\epsilon}\phi \geq L_{c,a-\alpha-\epsilon}\phi \geq 0$, which is impossible due to the boundedness of ϕ. $\square$

The next result shows the monotonicity and continuity of $\lambda'_{1,c_0,a}$ in c.

LEMMA 5.10. $\lambda'_{1,c,a}$ *is continuously nondecreasing in* $c \in \mathbb{R}$.

Proof. Let $c_0 \in \mathbb{R}$ be fixed. We claim that if $\lambda'_{1,c_0,a} < -\beta$, then $\lambda'_{1,c_0-\delta,a} \le \lambda'_{1,c_0,a}$ for any $\delta > 0$. Indeed, choose $\epsilon > 0$ sufficiently small such that $\lambda'_{1,c_0,a} + \epsilon < -\beta$. Then we see from Theorem 5.8(i) that

(5.14) $$(L_{c_0,a} + \lambda'_{1,c_0,a} + \epsilon)u = u^2$$

admits at least one solution. Further, by Theorem 2.1 we see that (5.14) admits a decreasing solution ϕ connecting $\alpha + \lambda'_{1,c_0,a} + \epsilon$ to 0 as long as $\lambda'_{1,c_0,a} + \epsilon < -\beta$. Hence,

$$
\begin{aligned}
0 &\le (L_{c_0,a} + \lambda'_{1,c_0,a} + \epsilon)\phi \\
&= (L_{c_0-\delta,a} + \lambda'_{1,c_0,a} + \epsilon)\phi + \delta\phi' \\
&\le (L_{c_0-\delta,a} + \lambda'_{1,c_0,a} + \epsilon)\phi.
\end{aligned}
$$

Therefore, $\lambda'_{1,c_0-\delta,a} \le \lambda'_{1,c_0,a}$ since ϵ is arbitrarily small. The monotonicity of $\lambda'_{1,c,a}$ in c then follows directly from the fact $\lambda'_{1,c,a} \le -\beta \ \forall c \in \mathbb{R}$ that was obtained in Lemma 5.9.

For the continuity proof, we argue by contradiction, assuming that $\lambda'_{1,c,a}$ has a jump at $c = c_1 \le c_0$. As such, the left and right limits $\lambda_{1,c_1^\pm,a}$ exist and

$$\lambda'_{1,c_1^-,a} < \lambda'_{1,c_1^+,a} \le -\beta.$$

Let $\mu \in (\lambda'_{1,c_1^-,a}, \lambda_{1,c_1^+,a})$ be arbitrary. Then by the monotonicity shown above, we have

$$\lambda'_{1,c,a+\mu} < 0 \quad \forall c < c_1 \quad \text{and} \quad \lambda'_{1,c,a+\mu} > 0 \quad \forall c > c_1.$$

Combining Theorems 2.1 and 5.8 we see that $c_1 = 2\sqrt{\alpha + \mu}$, which leads to a contradiction since μ is arbitrary and c_1 is fixed. The proof is complete. □

With the above preliminary results, we are now ready to calculate $\lambda'_{1,c,a}$.

Explicit form of $\lambda'_{1,c,a}$. By Theorem 5.7 and Lemma 5.10 as well as the explicit form of $\lambda_{1,c,a}$, we immediately obtain $\lambda'_{1,c,a} \le -\alpha \ \forall c \le 0$, which, together with the lower bound obtained in Lemma 5.9, implies that $\lambda'_{1,c,a} = -\alpha \ \forall c \le 0$. For $c \in (0, \bar{c})$ with $\bar{c} = 2\sqrt{\alpha - \beta} > c^*$, we already know from Theorem 5.7 that $\lambda'_{1,c,a} \le \lambda_{1,c,a} = -\alpha + \frac{c^2}{4} < -\beta$. It then suffices to exclude the possibility $\lambda'_{1,c,a} < \lambda_{1,c,a}$ at some $c \in (0, \bar{c})$. Indeed, if this possibility happens at $c = c_2$, then we choose $\mu \in (\lambda'_{1,c_2,a}, \lambda_{1,c_2,a})$ and, consequently,

$$\lambda'_{1,c,a+\mu} < 0 \quad \forall c < c_2 \quad \text{and} \quad \lambda'_{1,c,a+\mu} > 0 \quad \forall c > c_2.$$

Combining Theorems 2.1 and 5.8 we see that $c_2 = 2\sqrt{\alpha + \mu}$. However, it contradicts

$$2\sqrt{\alpha + \mu} < 2\sqrt{\alpha + \lambda_{1,c_2,a}} = c_2.$$

Finally, for $c \ge \bar{c}$ we know from Lemma 5.9 that $\lambda'_{1,c,a} \le -\beta$. It then suffices to exclude the possibility that $\lambda'_{1,c,a} < -\beta$ at some $c \ge \bar{c}$. Otherwise if such a possibility happens at $c = c_3$, then we have the following inequality

$$\lim_{c\uparrow\bar{c}} \lambda'_{1,c,a} = \lim_{c\uparrow\bar{c}} -\alpha + \frac{c^2}{4} = -\beta > \lambda'_{1,c_3,a}.$$

It contradicts the monotonicity of $\lambda'_{1,c,a}$ in c that was obtained in Lemma 5.10. Thus, the explicit form is obtained.

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