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Spatial propagation in nonlocal dispersal Fisher-KPP equations

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A B S T R A C T

In this paper we focus on three problems about the spreading speeds of nonlocal dispersal Fisher-KPP equations. First, we study the signs of spreading speeds and find that they are determined by the asymmetry level of the nonlocal dispersal and $f'(0)$, where f is the reaction function. This indicates that asymmetric dispersal can influence the spatial dynamics in three aspects: it can determine the spatial propagation directions of solutions, influence the stability of equilibrium states, and affect the monotone property of solutions. Second, we give an improved proof of the spreading speed result by constructing new lower solutions and using the new "forward-backward spreading" method. Third, we investigate the relationship between spreading speed and exponentially decaying initial data. Our result demonstrates that when dispersal is symmetric, spreading speed decreases along with the increase of the exponential decay rate. In addition, the results on the signs of spreading speeds are applied to two special cases where we present more details on the influence of asymmetric dispersal.

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1. Introduction

In this paper, we study spatial propagation of the following nonlocal dispersal Fisher-KPP equation

$$\begin{cases} u_t(t,x) = k * u(t,x) - u(t,x) + f(u(t,x)), & t > 0,\ x \in \mathbb{R}, \\ u(0,x) = u_0(x),\ x \in \mathbb{R}, \end{cases} \tag{1.1}$$

where $u_0 \in C(\mathbb{R})$, $f \in C^1([0,1])$ and satisfies the Fisher-KPP type condition:

(H) f is monostable; namely, $f(0) = f(1) = 0$ and $f(u) > 0$ for $u \in (0,1)$, $f'(0) > 0$ and $f(u) \leqslant f'(0)u$ for $u \in (0,1)$.

The nonlocal dispersal, represented by the following convolution integral operator

$$k * u(t,x) - u(t,x) = \int_{\mathbb{R}} k(x-y)u(t,y)dy - u(t,x),$$

describes the movements of organisms between not only adjacent but also nonadjacent spatial locations (see, e.g. Berestycki et al. [6], Kao et al. [22], Murray [31] and Wang [38]). Here the kernel $k(\cdot)$ is a continuous and nonnegative function with $\int_{\mathbb{R}} k(x)dx = 1$. Moreover, we assume that

(K1) there is a constant $\lambda > 0$ such that $\int_{\mathbb{R}} k(x)e^{\lambda|x|}dx < +\infty$;
(K2) $k(x_1) > 0$ and $k(x_2) > 0$ for some constants $x_1 \in \mathbb{R}^+$ and $x_2 \in \mathbb{R}^-$.

Assumption (K1) is called the *Mollison condition*. For classical results on traveling wave solutions of equation (1.1), we refer to Schumacher [34], Bates et al. [5], Chen [9], Chen and Guo [11], Carr and Chmaj [8], Coville, Dávila and Martínez [12], Yagisita [44], and Sun et al. [36]. Entire solutions of equation (1.1) were studied by Li et al. [24] and Sun et al. [37].

The spreading speed is an important concept that describes the phenomenon of spatial propagation in many biological and ecological problems, such as the spatial spread of infectious diseases and the invasion of species. In 1975, Aronson and Weinberger [4] studied spreading speed of the following reaction-diffusion equation

$$\begin{cases} u_t = u_{xx} + f(u), & t > 0,\ x \in \mathbb{R}, \\ u(0,x) = u_0(x),\ x \in \mathbb{R}. \end{cases} \tag{1.2}$$

When f is monostable and $f'(0) > 0$, they showed that if $u_0(\cdot) \not\equiv 0$ and $0 \leqslant u_0(x) \leqslant 1$ for $x \in \mathbb{R}$, then $u(t,x)$ satisfies

$$\lim_{t\to+\infty} u(t,x) = 1 \ \text{ for any } x \in \mathbb{R}. \tag{1.3}$$

Moreover, if $u_0(x)$ is compactly supported on $\mathbb{R}$, then there is a constant $c^* > 0$ such that

$$\lim_{t\to+\infty} u(t,x+ct) = \begin{cases} 1, & |c| < c^*, \\ 0, & |c| > c^* \end{cases} \quad \text{for any } x \in \mathbb{R}.$$

The constant c^* is called the asymptotic speed on spreading (for short, *spreading speed*) of equation (1.2). For more results on spreading speed theory, we refer to Kolmogorov et al. [23], Aronson and Weinberger [3,4], Liang and Zhao [25,26], Lui [28], Weinberger [39], Weinberger et al. [40], Yi and Zou [45], and the references cited therein.

For the nonlocal dispersal equation (1.1), Lutscher et al. [29] considered the spreading speed and proved that there are two constants c_r^* and c_l^* such that

$$\lim_{t\to+\infty} u(t,x+ct) = \begin{cases} 1, & c_l^* < c < c_r^*, \\ 0, & c < c_l^* \text{ or } c > c_r^* \end{cases} \quad \text{for any} \ \ x \in \mathbb{R}, \tag{1.4}$$

where

$$c_l^* \triangleq \sup_{\lambda\in\mathbb{R}^-} \Big\{\lambda^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\Big]\Big\}, \tag{1.5}$$

$$c_r^* \triangleq \inf_{\lambda\in\mathbb{R}^+} \Big\{\lambda^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\Big]\Big\}. \tag{1.6}$$

The constants c_l^* and c_r^* are called *spreading speeds to the left* and *to the right* of the nonlocal dispersal equation, respectively. Note that c_r^* may not be equal to $-c_l^*$ because of the asymmetry of k. Here the asymmetry of k means that the probability that organisms move from point x to point $x + y$ is not equal to that from x to $x - y$. In addition, Finkelshtein et al. [14,16] extended this conclusion to high dimensional spaces $\mathbb{R}^d$, which is more complex because of the radial asymmetry of kernels. For more results about spreading speeds of nonlocal dispersal equations, we refer to Liang and Zhou [27], Rawal et al. [32], Shen and Zhang [35] and Zhang et al. [46].

The aim of this paper is to study some new problems on spreading speeds of nonlocal dispersal equations. The three main topics we cover are: identifying the signs of spreading speeds, improving the proof of the spreading speed result and studying the relationship between spreading speed and exponentially decaying initial data, which we describe in turn next.

(a) Identifying the signs of spreading speeds. In reaction-diffusion equation, the spreading speed to the right c^* is always positive and that to the left $-c^*$ is always negative. We wonder whether this remains true in nonlocal dispersal equations. It is significant

to identify the signs of spreading speeds, since they have important influences on spatial properties of solutions and the stability of equilibrium states (see the influences on spatial dynamics below). In a related work, Coville et al. [12] showed that asymmetric kernels may induce nonpositive minimal wave speed which always coincides with spreading speed in the Fisher-KPP case. However, they did not point out when the minimal wave speed is nonpositive.

We find that the spreading speed to the left c_l^* has the same sign as that of $E(k)-f'(0)$ and the spreading speed to the right c_r^* has the same sign as that of $E(k)+f'(0)$. Here $E(k)$ stands for the asymmetry level of k and is defined by

$$E(k) \triangleq \operatorname{sign}(J(k)) \left[1 - \inf_{\lambda\in\mathbb{R}} \left\{ \int_{\mathbb{R}} k(x)e^{\lambda x}dx \right\} \right],$$

where $J(k) \triangleq \int_{\mathbb{R}} k(x)xdx$ is the first moment and k belongs to the set that consists of all nonnegative and continuous functions satisfying (K1) and $\int_{\mathbb{R}} k(x)dx = 1$. From this result, we show that asymmetric dispersal influences the signs of spreading speeds, and further influences the spatial dynamics in three aspects: it can determine the spatial propagation directions of solutions, influence the stability of equilibrium states, and affect the monotone property of solutions. More details are given in Section 2.

The results are applied to two special cases where k is a normal distribution and a uniform distribution, respectively. We present more details of the calculation of $E(k)$ and show how the asymmetric dispersal influences spatial dynamics in Section 5.

(b) Giving an improved proof of the spreading speed result. In [29], Lutscher et al. proved the spreading speed result by constructing an innovative lower solution of nonlocal dispersal equation (1.1), which can spread at any speed c in (c_l^*, c_r^*), as follows

$$\underline{u}(t,x) = \begin{cases} \varepsilon e^{-s(x-ct)} \sin(\gamma(x-ct)), & x-ct \in [0, \pi/\gamma], \\ 0, & x-ct > \pi/\gamma. \end{cases} \tag{1.7}$$

In the construction of this lower solution, they needed to make some technical requirements on k. For example, they assumed that $\operatorname{supp}(k) = \mathbb{R}$ and the function $x \mapsto \exp(sx)k(x)$ is decreasing for large enough x. They also made some requirements on the monotone property of the function $A(s) = (\int_{\mathbb{R}} k(x)e^{sx}dx - 1 + f'(0))/s$, $s \neq 0$.

In this paper, without any additional assumptions, we construct two new lower solutions which spread at speeds c_1 and c_2, respectively, as follows

$$\underline{u}_i(t,x) = \max\{0, H_i(e^{\rho_i(-x+c_it+\xi_i)})\}, \quad i = 1, 2, \tag{1.8}$$

with

$$H_i(z) = A_iz - B_iz^{1+\delta_i} - D_iz^{1-\delta_i}, \quad z > 0,$$

where $c_1 \in (c_r^* - \epsilon, c_r^*)$ and $c_2 \in (c_l^*, c_l^* + \epsilon)$ for small $\epsilon > 0$.

However, (1.8) is not as good as (1.7), because the speed of (1.8) is limited to $(c_l^*, c_l^* + \epsilon)$ or $(c_r^* - \epsilon, c_r^*)$. Therefore, we give a new method to study the whole situation of (c_l^*, c_r^*), which is called the "**forward-backward spreading**" method. In this method, for any $\tau > 0$ we divide the time period of $[0, \tau]$ into two parts $[0, \kappa\tau]$ and $[\kappa\tau, \tau]$, where κ is any number in $[0, 1]$. In $[0, \kappa\tau]$ we construct a lower solution $u_1(t, x)$ spreading at a speed of $c_1 \in (c_r^* - \epsilon, c_r^*)$. In $[\kappa\tau, \tau]$ we construct another lower solution $u_2(t, x)$ which spreads at a speed of $c_2 \in (c_l^*, c_l^* + \epsilon)$ and satisfies that $u_2(\kappa\tau, x) \leqslant u_1(\kappa\tau, x)$. Then these two lower solutions can be regarded as a lower solution defined in $[0, \tau]$ whose speed is $\bar{c} = \kappa c_1 + (1 - \kappa)c_2$. Moreover, the arbitrariness of κ ensures that $\bar{c}$ can be equal to any number in $[c_1, c_2]$. We remark that the term "forward-backward spreading" comes from the special case $c_l^* < 0 < c_r^*$, which means $u_1(t, x)$ spreads forward and $u_2(t, x)$ spreads backward.

By constructing the new lower solutions and applying the "forward-backward spreading" method, we improve the proof of spreading speed result and further obtain a property about the spatial propagation of solutions (see Corollary 3.4).

Remark 1.1. In the study of traveling wave solutions, we usually construct the lower solution $\underline{v}(t, x) = \max\{0, e^{\rho(-x+ct)} - Le^{\rho(1+\delta)(-x+ct)}\}$, where L is large enough. Note that $\underline{v}(t, x) > 0$ for x large enough. Different from $\underline{v}(t, x)$, the lower solutions defined by (1.8) have no tails on both sides, which means that the function $\underline{u}_i(t, \cdot)$ is compactly supported. Therefore, the lower solutions defined by (1.8) can be used to study the spreading speed for compactly supported initial data.

(c) Studying the relationship between spreading speed and exponentially decaying initial data. In a reaction-diffusion equation, it is well-known that the decay behavior to zero as $x \to \pm\infty$ of the initial data influences the spreading speed, see e.g. Booty et al. [7], Hamel and Nadin [20], McKean [30], and Sattinger [33]. Moreover, when the initial datum decays slower than any exponentially decaying function or the kernel is "fat-tailed", the propagation accelerates (namely, its spreading speed approaches infinity as $t \to +\infty$). This is studied by Alfaro [1], Alfaro and Coville [2], Finkelshtein et al. [15], Finkelshtein and Tkachov [18], Garnier [19], Hamel and Roques [21], and Xu et al. [41,42]. Therefore, we consider the influence of initial data on the spreading speed of equation (1.1).

Here we focus on the exponentially decaying initial function which satisfies that

$$u_0(x) \sim Ce^{-\lambda|x|} \quad \text{as } |x| \to +\infty.$$

When k is symmetric, for $\lambda \in [\lambda^*, +\infty)$ the spreading speed of equation (1.1) is $c^* \triangleq c_r^* = -c_l^*$, and for $\lambda \in (0, \lambda^*)$ the spreading speed is equal to

$$c(\lambda) = \lambda^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\Big].$$

Moreover, $c(\lambda)$ decreases strictly along with the increase of $\lambda \in (0, \lambda^*)$ and we have $c^* = c(\lambda^*)$.

The rest of this paper is organized as follows. In Section 2, we study the signs of spreading speeds and the influences of asymmetric dispersal on spatial dynamics. Section 3 presents the new lower solutions and the new "forward-backward spreading" method. By using them, we give an improved proof of the spreading speed result. Section 4 deals with the relationship between spreading speed and exponentially decaying initial data. In Section 5, two examples are provided to explain the results on the signs of spreading speeds.

2. The signs of spreading speeds

In this section we present the main results about the signs of spreading speeds and the influences of asymmetric dispersal on the spatial dynamics.

First we introduce some notations. By (K1), we denote

$$\lambda^+ = \sup \left\{ \lambda > 0 \mid \int_{\mathbb{R}} k(x)e^{\lambda x}dx < +\infty \right\} \in \mathbb{R}^+ \cup \{+\infty\}, \tag{2.1}$$

$$\lambda^- = \inf \left\{ \lambda < 0 \mid \int_{\mathbb{R}} k(x)e^{\lambda x}dx < +\infty \right\} \in \mathbb{R}^- \cup \{-\infty\}. \tag{2.2}$$

When $\lambda^+ < +\infty$, we have $\int_{\mathbb{R}} k(x)e^{\lambda x}dx \to +\infty$ as $\lambda \to \lambda^+$; otherwise, $\int_{\mathbb{R}} k(x)e^{\lambda^+ x}dx < +\infty$ and then by the continuity of $\lambda \mapsto \int_{\mathbb{R}} k(x)e^{\lambda x}dx$, there is a constant λ_0 (close to and larger than λ^+) such that $\int_{\mathbb{R}} k(x)e^{\lambda_0 x}dx < +\infty$, which contradicts (2.1). When $\lambda^+ = +\infty$, by (K2) and the continuity of k, there exist $a \in (0, x_1]$ and $b > 0$ such that

$$k(x) \geqslant b \quad \text{for } x \in [x_1 - a, x_1 + a]. \tag{2.3}$$

From the nonnegativity of k, it follows that

$$\lim_{\lambda \to +\infty} \int_{\mathbb{R}} k(x)e^{\lambda x}dx \geqslant \lim_{\lambda \to +\infty} b \int_{x_1 - a}^{x_1 + a} e^{\lambda x}dx = +\infty.$$

Then we obtain

$$\lim_{\lambda \to \lambda^+} \int_{\mathbb{R}} k(x)e^{\lambda x}dx = +\infty. \tag{2.4}$$

Similarly, we have that

$$\lim_{\lambda \to \lambda^-} \int_{\mathbb{R}} k(x)e^{\lambda x}dx = +\infty.$$

By $\frac{\partial^2}{\partial\lambda^2}\int_{\mathbb{R}} k(x)e^{\lambda x}dx > 0$, under (K1) and (K2), we can find a unique constant $\lambda(k) \in (\lambda^-, \lambda^+)$ such that

$$\int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx = \min_{\lambda\in\mathbb{R}} \int_{\mathbb{R}} k(x)e^{\lambda x}dx, \text{ namely } \int_{\mathbb{R}} k(x)e^{\lambda(k)x}xdx = 0. \tag{2.5}$$

Since the function $\lambda \mapsto \int_{\mathbb{R}} k(x)e^{\lambda x}xdx$ is strictly increasing, we know that

$$\int_{\mathbb{R}} k(x)e^{\lambda x}xdx > 0 \text{ for } \lambda \in (\lambda(k), \lambda^+) \text{ and } \int_{\mathbb{R}} k(x)e^{\lambda x}xdx < 0 \text{ for } \lambda \in (\lambda^-, \lambda(k)). \tag{2.6}$$

It follows from $J(k) = \int_{\mathbb{R}} k(x)e^{\lambda x}xdx\big|_{\lambda=0}$ that $\operatorname{sign}(J(k)) = -\operatorname{sign}(\lambda(k))$. Then we have

$$E(k) = -\operatorname{sign}(\lambda(k)) \left[1 - \int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx\right]. \tag{2.7}$$

Note that $0 \leqslant \int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx \leqslant \int_{\mathbb{R}} k(x)e^{0x}dx = 1$ by the optimality of $\lambda(k)$, so that $\operatorname{sign}(E(k)) = -\operatorname{sign}(\lambda(k))$ and $-1 \leqslant E(k) \leqslant 1$. Next, we state two properties of $E(k)$.

Proposition 2.1. *The function $E(k)$ satisfies that*

(i) *$E(k) = -E(\check{k})$, where $\check{k}(x) = k(-x)$ for $x \in \mathbb{R}$;*
(ii) *If k_1 is more skewed to the right than k_2, then $E(k_1) \geqslant E(k_2)$. Here the concept that k_1 is more skewed to the right than k_2 means that $k_1(x) \geqslant k_2(x)$ for $x \in \mathbb{R}^+$ and $k_1(x) \leqslant k_2(x)$ for $x \in \mathbb{R}^-$.*

Proof. Since $J(k) = -J(\check{k})$ and

$$\inf_{\lambda\in\mathbb{R}} \int_{\mathbb{R}} k(x)e^{\lambda x}dx = \inf_{\lambda\in\mathbb{R}} \int_{\mathbb{R}} \check{k}(x)e^{\lambda x}dx,$$

we have that $E(k) = -E(\check{k})$.

Now suppose that $k_1(x) \geqslant k_2(x)$ for $x \in \mathbb{R}^+$ and $k_1(x) \leqslant k_2(x)$ for $x \in \mathbb{R}^-$. Denote $\lambda_1 \triangleq \lambda(k_1)$ and $\lambda_2 \triangleq \lambda(k_2)$. By $\int_{\mathbb{R}}(k_1(x) - k_2(x))e^{\lambda_2 x}xdx \geqslant 0$, we get from $\int_{\mathbb{R}} k_i(x)e^{\lambda_i x}xdx = 0$ that

$$\int_{\mathbb{R}} k_1(x)e^{\lambda_2 x}xdx \geqslant 0 = \int_{\mathbb{R}} k_1(x)e^{\lambda_1 x}xdx.$$

Note that the function $\lambda \mapsto \int_{\mathbb{R}} k_1(x)e^{\lambda x}xdx$ is increasing, then $\lambda_1 \leqslant \lambda_2$. Now we consider three cases. First, when $\lambda_1 \leqslant 0 \leqslant \lambda_2$, we easily check that $E(k_1) \geqslant 0 \geqslant E(k_2)$ by

$\text{sign}(E(k)) = -\text{sign}(\lambda(k))$. Next, consider the case $\lambda_1 \leqslant \lambda_2 \leqslant 0$. Some calculations imply that

$$E(k_1) = 1 - \int_{\mathbb{R}} k_1(x)e^{\lambda_1 x}dx = \int_{\lambda_1}^{0} \left[\int_{\mathbb{R}} k_1(x)e^{\lambda x}xdx\right] d\lambda,$$

$$E(k_2) = 1 - \int_{\mathbb{R}} k_2(x)e^{\lambda_2 x}dx = \int_{\lambda_2}^{0} \left[\int_{\mathbb{R}} k_2(x)e^{\lambda x}xdx\right] d\lambda.$$

We have that

$$E(k_1) - E(k_2) = \int_{\lambda_1}^{\lambda_2} \left[\int_{\mathbb{R}} k_1(x)e^{\lambda x}xdx\right] d\lambda + \int_{\lambda_2}^{0} \left[\int_{\mathbb{R}} (k_1(x) - k_2(x))e^{\lambda x}xdx\right] d\lambda.$$

It follows from (2.6) that $\int_{\mathbb{R}} k_1(x)e^{\lambda x}xdx > 0$ for $\lambda > \lambda_1$. Then we obtain $E(k_1) \geqslant E(k_2)$ by $\int_{\mathbb{R}}(k_1(x) - k_2(x))e^{\lambda x}xdx \geqslant 0$. Finally, in the case $0 \leqslant \lambda_1 \leqslant \lambda_2$, we can prove $E(k_1) \geqslant E(k_2)$ by a similar method. □

From Proposition 2.1, we can use $E(k)$ to describe the asymmetry level of k. Note that $E(k) \in [-1, 1]$ for any nonnegative and continuous k satisfying (K1). In particular, if $k(\cdot)$ is symmetric, then $E(k) = 0$; and if $k(x) = 0$ for all $x \in \mathbb{R}^+$, then $E(k) = -1$. Similarly, if $k(x) = 0$ for all $x \in \mathbb{R}^-$, then $E(k) = 1$. Moreover, when $E(k) > 0$, k can be regarded as a function skewed to the right and when $E(k) < 0$, it is a function skewed to the left.

Remark 2.2. The properties (i) and (ii) in Proposition 2.1 are two fundamental requirements for the function describing the asymmetry level of k. For example, consider $E_g(k) \triangleq \int_{\mathbb{R}} k(x)g(x)dx$, where g is an odd function and is positive in $\mathbb{R}^+$. Then we can use E_g to describe the asymmetry level of k too. It is easy to check that $E_g(k)$ satisfies (i) and (ii). A special form of $E_g(k)$ is given by the moment function $\int_{\mathbb{R}} k(x)x^N dx$, where N is an odd number.

Let $c(\cdot)$ be the function defined by

$$c(\lambda) = \lambda^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\Big] \quad \text{for } \lambda \in (\lambda^-, 0) \cup (0, \lambda^+). \tag{2.8}$$

The following lemma will be used several times in the remainder of the paper.

Lemma 2.3. *For any $k(\cdot)$ satisfying (K1) and (K2), there are unique $\lambda_r^* \in (0, \lambda^+)$ and $\lambda_l^* \in (\lambda^-, 0)$ such that*

$$c_r^* = \min_{\lambda\in(0,\lambda^+)}\{c(\lambda)\} = c(\lambda_r^*) = \int_{\mathbb{R}} k(x)e^{\lambda_r^* x}xdx \tag{2.9}$$

and

$$c_l^* = \max_{\lambda\in(\lambda^-,0)}\{c(\lambda)\} = c(\lambda_l^*) = \int_{\mathbb{R}} k(x)e^{\lambda_l^* x}xdx. \tag{2.10}$$

Proof. For $\lambda \in (\lambda^-, 0) \cup (0, \lambda^+)$, a simple calculation implies that

$$c'(\lambda) = \lambda^{-1}\int_{\mathbb{R}} k(x)e^{\lambda x}xdx - \lambda^{-2}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\Big].$$

We obtain that $\lim_{\lambda\to 0^+} c'(\lambda) = -\infty$. Next, we show that

$$c'(\lambda) > 0 \ \text{ for any } \lambda \text{ close to } \lambda^+. \tag{2.11}$$

In the case $\lambda^+ < +\infty$, let M be a positive constant satisfying that $M\lambda^+ > 1$. Then there are two constants C_1 and C_2 such that for any $\lambda \in (0, \lambda^+)$,

$$\int_{\mathbb{R}} k(x)e^{\lambda x}xdx \geqslant M\int_M^{+\infty} k(x)e^{\lambda x}dx + C_1, \quad \int_{\mathbb{R}} k(x)e^{\lambda x}dx \leqslant \int_M^{+\infty} k(x)e^{\lambda x}dx + C_2.$$

Then we can obtain (2.11) by using $\int_M^{+\infty} k(x)e^{\lambda x}dx \to +\infty$ as $\lambda \to \lambda^+$. In the case $\lambda^+ = +\infty$, we need to rewrite $c'(\lambda)$ as

$$c'(\lambda) = \lambda^{-2}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}(\lambda x - 1)dx + 1 - f'(0)\Big].$$

Then we get (2.11) by the fact that $e^{\lambda x} \geqslant \lambda x + 1$, $x \in \mathbb{R}$. On the other hand, when $c'(\lambda) = 0$, it follows that $c''(\lambda) > 0$ for $\lambda \in (0, \lambda^+)$. Therefore, there is a unique constant $\lambda_r^* \in (0, \lambda^+)$ such that

$$c'(\lambda_r^*) = 0 \text{ and } c(\lambda_r^*) = \min_{\lambda\in(0,\lambda^+)}\{c(\lambda)\} = \int_{\mathbb{R}} k(x)e^{\lambda_r^* x}xdx.$$

Moreover, we have that

$$c'(\lambda) < 0 \text{ for } \lambda \in (0, \lambda_r^*) \ \text{ and } c'(\lambda) > 0 \text{ for } \lambda \in (\lambda_r^*, \lambda^+).$$

Similarly, the existence and uniqueness of λ_l^* can be obtained. □

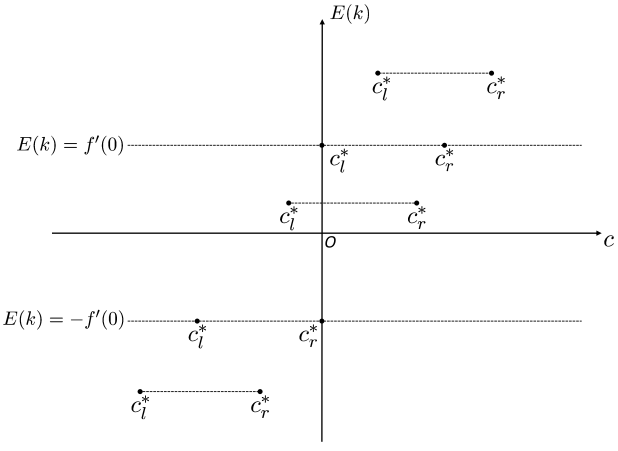

Fig. 1. An illustrative diagram showing the changes of locations and signs of c_l^* and c_r^* under different conditions given in Theorem 2.4.

Now we show that the spreading speed to the left c_l^* has the same sign as that of $E(k) - f'(0)$ and the spreading speed to the right c_r^* has the same sign as that of $E(k) + f'(0)$.

Theorem 2.4. *Suppose that* (H), (K1) *and* (K2) *hold. Then we have the following statements:*

(i) $0 < c_l^* < c_r^*$ *iff* $E(k) > f'(0)$;
(ii) $0 = c_l^* < c_r^*$ *iff* $E(k) = f'(0)$;
(iii) $c_l^* < 0 < c_r^*$ *iff* $-f'(0) < E(k) < f'(0)$;
(iv) $c_l^* < c_r^* = 0$ *iff* $E(k) = -f'(0)$;
(v) $c_l^* < c_r^* < 0$ *iff* $E(k) < -f'(0)$.

(See Fig. 1.)

Proof. By (2.9) and (2.10), it is easy to check that $c_l^* < c_r^*$, since the function $\lambda \mapsto \int_{\mathbb{R}} k(x)e^{\lambda x}xdx$ is strictly increasing. When $E(k) > f'(0)$, by (2.7) we get that $\lambda(k) < 0$ and

$$E(k) = 1 - \int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx > f'(0).$$

From (1.5) it follows that

$$c_l^* \geqslant \lambda(k)^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx - 1 + f'(0)\Big] > 0.$$

Then $0 < c_l^* < c_r^*$. When $E(k) = f'(0)$, we have $\lambda(k) < 0$ by $\operatorname{sign}(E(k)) = -\operatorname{sign}(\lambda(k))$. Then

$$\min_{\lambda\in\mathbb{R}}\left(\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)\right) = \int_{\mathbb{R}} k(x)e^{\lambda(k)x}dx - 1 + f'(0) = f'(0) - E(k) = 0.$$

This implies that $\lambda^{-1}(\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0)) \leqslant 0$ for all $\lambda < 0$, with equality at $\lambda = \lambda(k)$. Therefore, $0 = c_l^* < c_r^*$ by (1.5). When $-f'(0) < E(k) < f'(0)$, we have

$$|E(k)| = 1 - \inf_{\lambda\in\mathbb{R}}\left\{\int_{\mathbb{R}} k(x)e^{\lambda x}dx\right\} < f'(0).$$

From (1.5), (1.6) and Lemma 2.3, it follows that $c_l^* < 0 < c_r^*$. Finally, the proofs for cases (iv) and (v) are similar to those of cases (ii) and (i), respectively.

We can check that the sufficient conditions in cases (i)-(v) are necessary. For example, for case (i), if $0 < c_l^* < c_r^*$, then $E(k) > f'(0)$; otherwise, one of the conditions in cases (ii)-(v) must hold, and c_l^* and c_r^* satisfy the corresponding relationship, which contradicts $0 < c_l^* < c_r^*$. □

Combining Theorem 2.4 with (1.4), we see that $E(k)$ and $f'(0)$ determine the signs of spreading speeds. Moreover, they have three important cases about their influences on the spatial dynamics of nonlocal dispersal equation (1.1).

(a) The signs of c_r^* and c_l^* determine the spatial propagation directions of solutions. Define a level set function by

$$\Sigma_\omega(t) \triangleq \{x \in \mathbb{R} \mid u(t,x) \geqslant \omega\} \quad \text{for any } \omega \in (0,1),\ t > 0.$$

Then when t is large enough, $\Sigma_\omega(t)$ spreads to both the left and right sides of the x-axis in case (iii), spreads only to the right in case (i), and spreads only to the left in case (v). However, in case (ii), if the set $\Sigma_\omega(t)$ is connected, the movement of the left boundary of $\Sigma_\omega(t)$ is slower than linearity and we cannot identify its propagating direction. Similarly, we cannot identify the propagating direction of the right boundary of $\Sigma_\omega(t)$ in case (iv) either.

(b) The signs of c_r^* and c_l^* influence the stability of equilibrium states. In case (iii), the equilibrium state $u \equiv 1$ is globally stable and $u \equiv 0$ is globally unstable in any bounded spatial region. More precisely, if $u_0(\cdot) \not\equiv 0$ and u_0 is continuous and nonnegative, then

$$\text{for any } x \in \mathbb{R},\quad \lim_{t\to\infty} u(t,x) = 1;$$

namely, case (iii) has the same stability property as (1.3) in reaction-diffusion equations. However, in case (i) or (v), the equilibrium state $u \equiv 0$ becomes stable in any bounded spatial region for compactly supported initial data, which means that

$$\text{for any } x \in \mathbb{R}, \quad \lim_{t\to\infty} u(t,x) = 0.$$

The fundamental reason of this change is that the asymmetric dispersal plays a more important role than the reaction term, and the spatial region $\Sigma_\omega(t)$ travels in the dominating direction of dispersal (namely, the direction of $\text{sign}(J(k))$). In addition, it is worth pointing out that the equilibrium state $u \equiv 0$ remains unstable for initial data satisfying $u_0(x) \geqslant \epsilon$ with $\epsilon > 0$ (see Finkelshtein et al. [13,14]).

(c) The asymmetry of k affects the monotone property of solutions. In the reaction-diffusion equation (1.2), there is a well-known result stating that the solution preserves the symmetry and the monotonicity of initial data; that is, if $u_0(\cdot)$ is symmetric and decreasing on $\mathbb{R}^+$, so is the solution $u(t,\cdot)$ of equation (1.2) at any time $t > 0$. The following theorem shows that this result also holds in the nonlocal dispersal equation.

Theorem 2.5. *If $k(\cdot)$ and $u_0(\cdot + x_1)$ are symmetric and decreasing on $\mathbb{R}^+$ with $x_1 \in \mathbb{R}$, so is the solution $u(t, \cdot + x_1)$ of equation (1.1) at any time $t > 0$.*

Proof. By translating the x-axis, we suppose that $x_1 = 0$. The symmetry property of $u(t,\cdot)$ can be obtained easily. Indeed, if we consider the following equation

$$\begin{cases} v_t(t,x) = k * v(t,x) - v(t,x) + f(v(t,x)), & t > 0,\ x \in \mathbb{R}, \\ v(0,x) = u_0(-x),\ x \in \mathbb{R}, \end{cases}$$

then $u(t,x) = v(t,x) = u(t,-x)$ for $t \geqslant 0$ and $x \in \mathbb{R}$ by the uniqueness of the solution. For a fixed number $y \in \mathbb{R}^+$, we define

$$w(t,x) = u(t,x+2y) - u(t,x) \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}.$$

The symmetry property of $u(t,\cdot)$ implies that $w(t,-y) = 0$ for $t \geqslant 0$ and

$$w(t,x) = -w(t,-x-2y) \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}. \tag{2.12}$$

Since $u_0(\cdot)$ is symmetric and decreasing on $\mathbb{R}^+$, we have

$$w(0,x) \leqslant 0 \text{ for } x > -y, \quad w(0,x) \geqslant 0 \text{ for } x < -y.$$

In order to prove that $u(t,\cdot)$ is decreasing on $\mathbb{R}^+$ for any $t > 0$, we try to prove the following conclusion

$$w(t,x) \leqslant 0 \text{ for } t > 0,\ x > -y. \tag{2.13}$$

Indeed, if (2.13) holds, then we have that $u(t,x+2y) \leqslant u(t,x)$ for $x > -y$ and $y \in \mathbb{R}^+$ at any time $t > 0$, which means that $u(t,\cdot)$ is decreasing on $\mathbb{R}^+$.

Now we begin to prove (2.13). Since $f(u) \in C^1([0,1])$, there is a constant $M > 0$ such that

$$\begin{aligned} w_t(t,x) &= k * w(t,x) - w(t,x) + f(u(t,x+2y)) - f(u(t,x)) \\ &\leqslant k * w(t,x) - w(t,x) + M|w(t,x)| \quad \text{for } t > 0,\ x \in \mathbb{R}. \end{aligned} \tag{2.14}$$

Suppose by contradiction that (2.13) does not hold and there exist two constants $T_0 > 0$ and $\varepsilon > 0$ such that

$$\sup_{x>-y} \{w(T_0,x)\} = \varepsilon e^{KT_0} \ \text{ and } w(t,x) < \varepsilon e^{Kt} \text{ for } t \in (0,T_0),\ x > -y, \tag{2.15}$$

where $K > \max\{M+1,\ \frac{8}{3}M + \frac{4}{3}\}$. Under (2.15) we give an estimate for the nonlocal dispersal term $k*w(t,x)-w(t,x)$. From (2.12), it follows that for $t \in (0,T_0]$ and $x > -y$,

$$\begin{aligned} & k * w(t,x) - w(t,x) \\ &= \int_{-y}^{+\infty} [w(t,z) - w(t,x)]k(x-z)dz + \int_{-\infty}^{-y} [w(t,z) - w(t,x)]k(x-z)dz \\ &= \int_{-y}^{+\infty} Q(t,x,z,y)dz \\ &= \int_{\Sigma_1(t)} Q(t,x,z,y)dz + \int_{\Sigma_2(t)} Q(t,x,z,y)dz, \end{aligned}$$

where

$$Q(t,x,z,y) = [w(t,z) - w(t,x)]k(x-z) - [w(t,z) + w(t,x)]k(x+z+2y)$$

and

$$\Sigma_1(t) = \big\{z \mid w(t,z) > 0,\ z > -y\big\}, \quad \Sigma_2(t) = \big\{z \mid w(t,z) \leqslant 0,\ z > -y\big\}.$$

We also suppose that $w(t,x) \geqslant 0$ in the following estimation. When $z \in \Sigma_1(t)$, we can get from (2.15) that $w(t,z) - w(t,x) \leqslant \varepsilon e^{Kt}$. Then it follows that

$$\int_{\Sigma_1(t)} Q(t,x,z,y)dz \leqslant \int_{\Sigma_1(t)} \varepsilon e^{Kt} k(x-z)dz \leqslant \varepsilon e^{Kt} \ \text{ for } t \in (0,T_0],\ x > -y.$$

When $z \in \Sigma_2(t)$, we rewrite $Q(t,x,z,y)$ as

$$Q(t,x,z,y) = w(t,z)[k(x-z) - k(x+z+2y)] - w(t,x)[k(x-z) + k(x+z+2y)].$$

Since $k(\cdot)$ is symmetric and decreasing on $\mathbb{R}^+$, we have that $k(x-z)-k(x+z+2y)\geqslant 0$ when $x>-y$ and $z>-y$. Then it follows that

$$\int\limits_{\Sigma_2(t)} Q(t,x,z,y)dz \leqslant 0 \quad \text{for } t\in(0,T_0],\ x>-y.$$

Therefore, when $w(t,x)\geqslant 0$, we have that

$$k*w(t,x)-w(t,x)\leqslant \varepsilon e^{Kt} \quad \text{for } t\in(0,T_0],\ x>-y. \tag{2.16}$$

Next we return to the proof of (2.13). From (2.15), the continuity property of $w(T_0,\cdot)$ implies that one or both of the following two cases must happen.

Case 1: There exists $x_0\in(-y,+\infty)$ such that $w(T_0,x_0)=\max\limits_{x>-y}\{w(T_0,x)\}=\varepsilon e^{KT_0}$.
Case 2: It holds that $\limsup\limits_{x\to+\infty}\{w(T_0,x)\}=\varepsilon e^{KT_0}$.

If case 1 holds, from (2.15) we have

$$\frac{\partial}{\partial t}\left(w(t,x_0)-\varepsilon e^{Kt}\right)\Big|_{t=T_0}\geqslant 0,$$

which implies

$$w_t(T_0,x_0)\geqslant \varepsilon K e^{KT_0}. \tag{2.17}$$

From (2.16) and (2.17), it follows that

$$w_t(T_0,x_0)-k*w(T_0,x_0)+w(T_0,x_0)-M|w(T_0,x_0)|\geqslant (K-1-M)\varepsilon e^{KT_0}>0,$$

which contradicts (2.14).

If case 2 holds, then there exists a constant number $x_1>-y$ (far away from $-y$) such that $w(T_0,x_1)>\frac{3}{4}\varepsilon e^{KT_0}$. Let $p_0(x)$ be a smooth and increasing function satisfying that

$$p_0(x)=\begin{cases}1 & \text{for } x\leqslant x_1,\\ 3 & \text{for } x\geqslant x_1+1.\end{cases}$$

For $\sigma>0$, we define

$$\rho_\sigma(t,x)=\left[\frac{1}{2}+\sigma p_0(x)\right]\varepsilon e^{Kt} \text{ for } t\in[0,T_0],\ x\in\mathbb{R}$$

and

$$\sigma^* = \inf\Big\{\sigma > 0 \mid w(t,x) - \rho_\sigma(t,x) \leqslant 0 \ \text{ for } t \in [0,T_0],\ x > -y\Big\}.$$

From (2.15), some simple calculations yield that $\rho_{\frac{1}{2}}(t,x) \geqslant \varepsilon e^{Kt} \geqslant w(t,x)$ for $t \in [0,T_0]$ and $x > -y$ and $\rho_{\frac{1}{4}}(T_0,x_1) = \frac{3}{4}\varepsilon e^{KT_0} < w(T_0,x_1)$. Then, by monotonicity of $\sigma \mapsto \rho_\sigma$, we have that $\frac{1}{4} \leqslant \sigma^* \leqslant \frac{1}{2}$ and

$$\rho_{\sigma^*}(t,x) \geqslant \frac{5}{4}\varepsilon e^{Kt} > w(t,x) \ \text{ for } t \in [0,T_0],\ x \geqslant x_1 + 1.$$

From the definition of σ^*, there must exist $T_1 \in (0,T_0]$ and $x_2 \in (-y, x_1+1)$ such that

$$w(T_1,x_2) - \rho_{\sigma^*}(T_1,x_2) = \max_{t\in[0,T_0],\ x>-y}\big\{w(t,x) - \rho_{\sigma^*}(t,x)\big\} = 0,$$

which implies that

$$\frac{\partial}{\partial t}\Big(w(t,x_2) - \rho_{\sigma^*}(t,x_2)\Big)\Big|_{t=T_1} \geqslant 0.$$

Since $\frac{1}{4} \leqslant \sigma^* \leqslant \frac{1}{2}$, we have

$$w(T_1,x_2) = \rho_{\sigma^*}(T_1,x_2) \leqslant \rho_{\frac{1}{2}}(T_1,x_2) \leqslant 2\varepsilon e^{KT_1} \tag{2.18}$$

and

$$w_t(T_1,x_2) \geqslant \frac{\partial}{\partial t}\rho_{\sigma^*}(T_1,x_2) = K\rho_{\sigma^*}(T_1,x_2) \geqslant K\rho_{\frac{1}{4}}(T_1,x_2) \geqslant \frac{3}{4}K\varepsilon e^{KT_1}. \tag{2.19}$$

From (2.16), (2.18) and (2.19), we can get that

$$w_t(T_1,x_2) - k * w(T_1,x_2) + w(T_1,x_2) - M|w(T_1,x_2)| \geqslant (\frac{3}{4}K - 1 - 2M)\varepsilon e^{KT_1} > 0,$$

which contradicts (2.14).

Finally, we get (2.13) and the proof of Theorem 2.5 is finished. □

However, when k is asymmetric, Theorem 2.5 does not hold even if k has an adequate monotone property. For example, in case (i) or (v), the spatial point where the solution attains its maximum value keeps moving at a speed between c_l^* and c_r^*. We also point out that Theorem 2.5 is useful in Remark 3.5 and the proof of Theorem 4.2.

Recently, we [43] further studied the relationship between the signs of spreading speeds and the asymmetric dispersals of infectious agents and infectious humans in an epidemic model, where the infectious agents are carried by migratory birds. We found it is possible that the epidemic spreads only along the fly route of migratory birds and the spatial propagation in the opposite direction fails, as long as the infectious humans are kept from moving frequently.

Remark 2.6. In reaction-diffusion equation (1.2), the proof of the same conclusion as Theorem 2.5 is easier than that in a nonlocal dispersal equation. Indeed, we can prove (2.13) by the maximum principle of equation $w_t(t,x) = \Delta w(t,x) + Mw(t,x)$ with $(t,x) \in [0,+\infty) \times [-y,+\infty)$.

3. Improved proof of spreading speeds

In this section, we give an improved proof of the spreading speed result for equation (1.1) by constructing new lower solutions and applying the "forward-backward spreading" method. First, we state the comparison principle (see e.g. [10,12]).

Lemma 3.1 *(Comparison principle). Suppose that the bounded continuous functions $\bar{u}(t,x)$ and $\underline{u}(t,x)$ are upper and lower solutions of equation (1.1) for $t \in (0,T]$, in the sense that*

$$\bar{u}_t - k * \bar{u} + u - f(\bar{u}) \geqslant 0 \geqslant \underline{u}_t - k * \underline{u} + \underline{u} - f(\underline{u}) \quad \text{for } t \in (0,T],\ x \in \mathbb{R}.$$

If $\bar{u}(0,x) \geqslant \underline{u}(0,x)$ for $x \in \mathbb{R}$, then $\bar{u}(t,x) \geqslant \underline{u}(t,x)$ for $t \in [0,T]$ and $x \in \mathbb{R}$.

In the construction of the new lower solutions, we need an auxiliary function and some of its properties as stated in the following lemma.

Lemma 3.2. *For any $\delta \in (0,1)$, define*

$$H(z) = Az - Bz^{1+\delta} - Dz^{1-\delta} \quad \text{for } z > 0.$$

For any given $A > 0$ and $D > 0$, we have the following conclusions

$$\begin{aligned} &H^{\max} > 0 \quad \text{for } B \in \left(0, A^2/(4D)\right), \\ &H^{\max} \to 0^+,\ \nu - \mu \to 0^+ \quad \text{as } B - A^2/(4D) \to 0^-, \end{aligned}$$

where

$$\begin{aligned} H^{\max} &\triangleq \sup_{z>0} \left\{H(z)\right\} = H(z_0) \quad \text{for some } z_0 \in (\mu,\nu), \\ (\mu,\nu) &\triangleq \left\{z > 0 \mid H(z) > 0\right\} \quad \text{for } B \in \left(0, A^2/(4D)\right). \end{aligned}$$

Moreover, for any $p > 0$, there exists $B(p) \in \left(0, A^2/(4D)\right)$ such that

$$H^{\max} = p \text{ and } B(p) \to A^2/(4D) \text{ as } p \to 0^+.$$

Proof. For any given $A > 0$, $D > 0$ and $\delta \in (0,1)$, define

$$h(z,B) = Az - Bz^{1+\delta} - Dz^{1-\delta} \quad \text{for } z > 0,\ 0 < B \leqslant \frac{A^2}{4D(1-\delta^2)}.$$

Let z_0 and z_1 be two positive numbers given by

$$z_0^\delta = \frac{A + \sqrt{A^2 - 4BD(1-\delta^2)}}{2B(1+\delta)} \quad \text{and} \quad z_1^\delta = \frac{A - \sqrt{A^2 - 4BD(1-\delta^2)}}{2B(1+\delta)}.$$

A simple calculation implies that

$$\frac{\partial}{\partial z} h(z,B) \begin{cases} = 0 & \text{for } z = z_1 \text{ and } z = z_0, \\ < 0 & \text{for } z \in (0, z_1) \cup (z_0, +\infty), \\ > 0 & \text{for } z \in (z_1, z_0). \end{cases}$$

Therefore, we have $H^{\max} = \max\{0, h(z_0, B)\}$. Define

$$g(B) = h(z_0, B) = Az_0 - Bz_0^{1+\delta} - Dz_0^{1-\delta} \quad \text{for } 0 < B \leqslant \frac{A^2}{4D(1-\delta^2)}.$$

Then it follows that $g'(B) = -z_0^{1+\delta} < 0$. Notice that

$$g(B) = 0 \text{ when } B = A^2/(4D). \tag{3.1}$$

The continuity and monotone property of $g(\cdot)$ show that

$$H^{\max} = g(B) > 0 \;\; \text{for } 0 < B < A^2/(4D) \;\; \text{and} \;\; g(B) \to 0^+ \;\; \text{as } B - A^2/(4D) \to 0^-.$$

When $0 < B < A^2/(4D)$, by $(\mu,\nu) = \big\{z > 0 \mid H(z) > 0\big\}$ we get

$$\mu = \Big[\frac{A - \sqrt{A^2 - 4BD}}{2B}\Big]^{\frac{1}{\delta}} \quad \text{and} \quad \nu = \Big[\frac{A + \sqrt{A^2 - 4BD}}{2B}\Big]^{\frac{1}{\delta}}$$

and

$$\nu - \mu \to 0^+ \text{ as } B - A^2/(4D) \to 0^-.$$

Moreover, a simple calculation shows that

$$g(B) = h(z_0, B) \geqslant h\big(B^{-\frac{1}{1+\delta}}, B\big) = B^{-\frac{1}{1+\delta}}\big[A - DB^{\frac{\delta}{1+\delta}}\big] - 1,$$

which implies that $g(B) \to +\infty$ as $B \to 0$. By (3.1) and the continuity of $g(\cdot)$, for any $p > 0$ there exists $B(p) \in (0, A^2/(4D))$ such that $H^{\max} = g(B(p)) = p$ and $B(p) \to A^2/(4D)$ as $p \to 0^+$. □

Now for small $\eta > 0$, define

$$c_\eta(\lambda) = \lambda^{-1}\Big[\int_{\mathbb{R}} k(x)e^{\lambda x}dx - 1 + f'(0) - \eta\Big] \quad \text{for } \lambda \in (\lambda^-, 0) \cup (0, \lambda^+)$$

and

$$c_r^*(\eta) = \inf_{\lambda\in(0,\lambda^+)}\{c_\eta(\lambda)\} \text{ and } c_l^*(\eta) = \sup_{\lambda\in(\lambda^-,0)}\{c_\eta(\lambda)\} \quad \text{for } \eta\in(0,f'(0)).$$

It follows that $c_l^* < c_l^*(\eta) < c_r^*(\eta) < c_r^*$ and $c_l^*(\eta)\to c_l^*$, $c_r^*(\eta)\to c_r^*$ as $\eta\to 0$. Then for any small $\epsilon>0$, we can choose two constants η_1 and η_2 in $(0,f'(0))$ such that

$$c_r^*(\eta_1) = c_r^* - \epsilon, \quad c_l^*(\eta_2) = c_l^* + \epsilon. \tag{3.2}$$

For any $\eta\in(0,f'(0))$, define

$$G_\eta(c,\lambda) = c\lambda - \int_{\mathbb{R}} k(x)e^{\lambda x}dx + 1 - f'(0) + \eta \quad \text{for } \ c\in(c_l^*,c_r^*) \text{ and } \lambda\in(\lambda^-,\lambda^+). \tag{3.3}$$

We can check that

$$G_\eta(c,0) < 0 \text{ and } \frac{\partial^2}{\partial\lambda^2}G_\eta(c,\lambda) < 0. \tag{3.4}$$

When $\lambda^+ < +\infty$, by (2.4) we have that

$$\lim_{\lambda\to\lambda^+} G_\eta(c,\lambda) = -\infty.$$

When $\lambda^+ = +\infty$, it follows from (2.3) that

$$\lim_{\lambda\to+\infty}\frac{1}{\lambda}\int_{\mathbb{R}} k(x)e^{\lambda x}dx \geqslant \lim_{\lambda\to+\infty}\frac{b}{\lambda}\int_{x_1-a}^{x_1+a} e^{\lambda x}dx = +\infty,$$

which implies that

$$\lim_{\lambda\to+\infty} G_\eta(c,\lambda) = \lim_{\lambda\to+\infty}\lambda\left(c - \frac{1}{\lambda}\int_{\mathbb{R}} k(x)e^{\lambda x}dx + \frac{1-f'(0)+\eta}{\lambda}\right) = -\infty \ \text{ for } c\in(c_l^*,c_r^*).$$

Therefore, by some similar calculations for the case $\lambda\to\lambda^-$, we can get that

$$\lim_{\lambda\to\lambda^\pm} G_\eta(c,\lambda) = -\infty. \tag{3.5}$$

Consider the case $\eta=\eta_1$. For $\lambda\in(0,\lambda^+)$ and $c_1\in(c_r^*-\epsilon,c_r^*)$, we have

$$G_{\eta_1}(c_1,\lambda) = [c_1 - c_{\eta_1}(\lambda)]\lambda = [c_1 - c_r^*(\eta_1)]\lambda + [c_r^*(\eta_1) - c_{\eta_1}(\lambda)]\lambda.$$

Using the same argument as in the proof of Lemma 2.3, we can find some constant $\lambda\in(0,\lambda^+)$ such that $c_r^*(\eta_1) = c_{\eta_1}(\lambda)$, which implies $G_{\eta_1}(c_1,\lambda)>0$ for any $c_1\in(c_r^*-\epsilon,c_r^*)$.

By (3.4) and (3.5), for any $c_1 \in (c_r^* - \epsilon, c_r^*)$, there are three constants $\alpha^+(c_1)$, $\beta^+(c_1)$ and $\gamma^+(c_1)$ in $(0, \lambda^+)$ such that $\alpha^+(c_1) < \gamma^+(c_1) < \beta^+(c_1)$ and

$$G_{\eta_1}(c_1, \alpha^+(c_1)) = G_{\eta_1}(c_1, \beta^+(c_1)) = 0 \text{ and } G_{\eta_1}(c_1, \gamma^+(c_1)) > 0. \tag{3.6}$$

Moreover, we have that $G_{\eta_1}(c_1, \lambda) > 0$ for $\lambda \in (\alpha^+(c_1), \beta^+(c_1))$.

Similarly, when considering the case $\eta = \eta_2$, for any $c_2 \in (c_l^*, c_l^* + \epsilon)$ we can find three constants $\alpha^-(c_2)$, $\beta^-(c_2)$ and $\gamma^-(c_2)$ in $(\lambda^-, 0)$ such that $\beta^-(c_2) < \gamma^-(c_2) < \alpha^-(c_2)$ and

$$G_{\eta_2}(c_2, \alpha^-(c_2)) = G_{\eta_2}(c_2, \beta^-(c_2)) = 0 \text{ and } G_{\eta_2}(c_2, \gamma^-(c_2)) > 0 \tag{3.7}$$

Moreover, it follows that $G_{\eta_2}(c_2, \lambda) > 0$ for $\lambda \in (\beta^-(c_2), \alpha^-(c_2))$.

The following theorem and its proof are the main results of this section.

Theorem 3.3 *(Spreading speeds). Suppose that the assumptions* (H), (K1) *and* (K2) *hold. If $u_0(\cdot)$ satisfies that $0 \leqslant u_0(x) \leqslant 1$ for $x \in \mathbb{R}$, $u_0(x_1) > 0$ for some $x_1 \in \mathbb{R}$ and*

$$u_0(x) e^{\lambda_l^* x} \leqslant \Gamma \textit{ for } x \leqslant -x_0, \quad u_0(x) e^{\lambda_r^* x} \leqslant \Gamma \textit{ for } x \geqslant x_0, \tag{3.8}$$

where x_0 and Γ are two positive constants, then for any small $\epsilon > 0$, there is a constant $p \in (0,1)$ such that the solution $u(t,x)$ of equation (1.1) *has the following properties:*

$$\begin{cases} \lim\limits_{t \to +\infty} \sup\limits_{x \leqslant (c_l^* - \epsilon)t} u(t,x) = 0, \\ \min\limits_{(c_l^* + \epsilon)t \leqslant x - x_1 \leqslant (c_r^* - \epsilon)t} u(t,x) \geqslant p \quad \textit{for any} \;\; t > 0, \\ \lim\limits_{t \to +\infty} \sup\limits_{x \geqslant (c_r^* + \epsilon)t} u(t,x) = 0. \end{cases} \tag{3.9}$$

Proof. *Step 1* (*Lower solution and "forward-backward spreading" method*). From $u_0(x_1) > 0$, by translating the x-axis, we can find two positive constants p_1 and r such that

$$u_0(x) \geqslant p_1 \;\; \text{for} \;\; x \in [-r, r]. \tag{3.10}$$

For small $\epsilon > 0$, let $\eta_1 \in \mathbb{R}^+$ and $\eta_2 \in \mathbb{R}^+$ be the constants satisfying (3.2). By $f(u) \in C^1([0,1])$ and $f'(0) > 0$, there is a constant $p_2 \in (0, p_1]$ such that

$$f(u) \geqslant (f'(0) - \frac{\eta}{2})u \;\; \text{for } u \in [0, p_2],$$

where $\eta = \min\{\eta_1, \eta_2\}$. For any $\delta \in (0,1)$, by taking $M(\delta) = \eta p_2^{-\delta}/2$, we can get that

$$f(u) \geqslant (f'(0) - \eta_i)u + M(\delta)u^{1+\delta} \;\; \text{for } u \in [0, p_2]. \tag{3.11}$$

Now we prove that for any $c_1 \in (c_r^* - \epsilon, c_r^*)$ and $c_2 \in (c_l^*, c_l^* + \epsilon)$ there is a constant $p \in (0,1)$ such that

$$u(\tau, X) \geqslant p \text{ for any given } \tau > 0,\ X \in [c_2\tau, c_1\tau].$$

Let κ be a constant defined by

$$\kappa = \frac{X - c_2\tau}{c_1\tau - c_2\tau} \in [0,1].$$

In the following proof, we introduce the "*forward-backward spreading*" method and divide the time period of $[0,\tau]$ into two parts $[0,\kappa\tau]$ and $[\kappa\tau,\tau]$.

In $[0,\kappa\tau]$, for $c_1 \in (c_r^* - \epsilon, c_r^*)$ we choose the same $\alpha^+(c_1)$, $\beta^+(c_1)$ and $\gamma^+(c_1)$ as those in (3.6). Construct a set of lower solutions which spread at a speed of c_1 as follows

$$\underline{u}_1(t,x;\xi_1) = \max\left\{0,\ H_1(e^{\rho_1(-x+c_1t+\xi_1)})\right\} \text{ for } t \in [0,\kappa\tau],\ x \in \mathbb{R} \tag{3.12}$$

with

$$\xi_1 \in \left[-r + \rho_1^{-1}\ln\nu_1,\ r + \rho_1^{-1}\ln\mu_1\right], \tag{3.13}$$

where

$$\begin{aligned}
&H_1(z) = A_1 z - B_1 z^{1+\delta_1} - D_1 z^{1-\delta_1} \quad \text{for } z > 0,\\
&\rho_1 = \frac{\beta^+(c_1) + \gamma^+(c_1)}{2}, \quad \delta_1 = \frac{\beta^+(c_1) - \gamma^+(c_1)}{\beta^+(c_1) + \gamma^+(c_1)},\\
&(A_1)^{\delta_1} = \frac{G_{\eta_1}(c_1,\rho_1)}{M(\delta_1)}, \quad D_1 = \frac{A_1 G_{\eta_1}(c_1,\rho_1)}{G_{\eta_1}(c_1,\gamma^+(c_1))},\ B_1 \in \left(0,\ A_1^2/(4D_1)\right),\\
&(\mu_1,\nu_1) \triangleq \left\{z > 0 \mid H_1(z) > 0\right\}.
\end{aligned}$$

Here $G_\eta(c,\lambda)$ is defined by (3.3). By Lemma 3.2, we can choose $B_1 \in \left(0, A_1^2/(4D_1)\right)$ close to $A_1^2/(4D_1)$ such that

$$H_1^{\max} \triangleq \max_{z>0}\left\{H_1(z)\right\} \leqslant p_2 \leqslant p_1, \quad \rho_1^{-1}\left(\ln\nu_1 - \ln\mu_1\right) \leqslant r/2. \tag{3.14}$$

Let z_1 be the constant in (μ_1,ν_1) such that $H_1^{\max} = H_1(z_1)$. A simple calculation implies that

$$\underline{u}_1(0,x;\xi_1) = \begin{cases} 0 & \text{for } x \notin \Omega_1,\\ H_1(e^{\rho_1(-x+\xi_1)}) & \text{for } x \in \Omega_1, \end{cases}$$

where

$$\Omega_1 = (\xi_1 - \rho_1^{-1} \ln \nu_1, \xi_1 - \rho_1^{-1} \ln \mu_1).$$

By (3.13) we have that $\Omega_1 \subseteq (-r, r)$. From (3.10) and $H_1^{\max} \leqslant p_1$, it follows that

$$\underline{u}_1(0, x; \xi_1) \leqslant u_0(x) \quad \text{for } x \in \mathbb{R}.$$

Next we verify that $\underline{u}_1(t, x; \xi_1)$ is a lower solution of equation (1.1). When $x - c_1 t \notin \overline{\Omega}_1$, it is easy to check that $u_1(t, x; \xi_1) = 0$ and

$$\partial_t \underline{u}_1(t, x; \xi_1) - k * \underline{u}_1(t, x; \xi_1) + \underline{u}_1(t, x; \xi_1) - f(\underline{u}_1(t, x; \xi_1)) \leqslant 0.$$

When $x - c_1 t \in \Omega_1$, we have that $u_1(t, x; \xi_1) = H_1(e^{\rho_1(-x + c_1 t + \xi_1)})$. By (3.11), some calculations show that

$$\begin{aligned}
&\partial_t \underline{u}_1(t, x; \xi_1) - k * \underline{u}_1(t, x; \xi_1) + \underline{u}_1(t, x; \xi_1) - f(\underline{u}_1(t, x; \xi_1)) \\
&\quad \leqslant A_1 G_{\eta_1}(c_1, \rho_1) e^{\rho_1(-x + c_1 t + \xi_1)} - B_1 G_{\eta_1}(c_1, \rho_1(1 + \delta_1)) e^{\rho_1(1+\delta_1)(-x + c_1 t + \xi_1)} \\
&\qquad - D_1 G_{\eta_1}(c_1, \rho_1(1 - \delta_1)) e^{\rho_1(1-\delta_1)(-x + c_1 t - \xi_1)} + M(\delta_1) A_1^{1+\delta} e^{\rho_1(1+\delta_1)(-x + c_1 t + \xi_1)}.
\end{aligned}$$

Recall the definitions of ρ_1, δ_1, A_1 and D_1, then we get from (3.3) that

$$\begin{aligned}
&G_{\eta_1}(c_1, \rho_1(1 + \delta_1)) = G_{\eta_1}(c_1, \beta^+(c_1)) = 0, \\
&D_1 G_{\eta_1}(c_1, \rho_1(1 - \delta_1)) = D_1 G_{\eta_1}(c_1, \gamma^+(c_1)) = A_1 G_{\eta_1}(c_1, \rho_1), \\
&M(\delta_1)(A_1)^{1+\delta} = A_1 G_{\eta_1}(c_1, \rho_1).
\end{aligned}$$

It follows that

$$\begin{aligned}
&\partial_t \underline{u}_1(t, x; \xi_1) - k * \underline{u}_1(t, x; \xi_1) + \underline{u}_1(t, x; \xi_1) - f(\underline{u}_1(t, x; \xi_1)) \\
&\quad \leqslant \; A_1 G_{\eta_1}(c_1, \rho_1) \big[e^{\rho_1(-x + c_1 t + \xi_1)} - e^{\rho_1(1+\delta_1)(-x + c_1 t + \xi_1)} - e^{\rho_1(1-\delta_1)(-x + c_1 t + \xi_1)} \big] \leqslant 0.
\end{aligned}$$

Then $\underline{u}_1(t, x; \xi_1)$ is a lower solution of equation (1.1).

Therefore, Lemma 3.1 implies that

$$u(t, x) \geqslant \underline{u}_1(t, x; \xi_1) \quad \text{for } t \in [0, \kappa\tau], \; x \in \mathbb{R}.$$

Define $x_1(t) = c_1 t + \xi_1 - \rho_1^{-1} \ln z_1$ with $t \in [0, \kappa\tau]$ and it follows that

$$u(t, x_1(t)) \geqslant \underline{u}_1(t, x_1(t); \xi_1) = H_1^{\max} \text{ for } t \in [0, \kappa\tau].$$

The arbitrariness of the parameter ξ_1 in (3.13) shows that

$$u(t, x) \geqslant H_1^{\max} \text{ for } t \in [0, \kappa\tau], \; x \in [c_1 t - r/2, \; c_1 t + r/2].$$

Then we have

$$u(\kappa\tau, x) \geqslant H_1^{\max} \text{ for } x \in [c_1\kappa\tau - r/2,\ c_1\kappa\tau + r/2]. \tag{3.15}$$

In the second time period $[\kappa\tau, \tau]$, for $c_2 \in (c_l^*, c_l^* + \epsilon)$ we choose the same $\alpha^-(c_2)$, $\beta^-(c_2)$ and $\gamma^-(c_2)$ as those in (3.7). Construct another set of lower solutions which spread at a speed of c_2 as follows

$$\begin{aligned}\underline{u}_2(t, x; \xi_2) &= \max\left\{0,\ H_2(e^{\rho_2(-x+c_2t+\xi_2)})\right\} \text{ for } t \in [\kappa\tau, \tau],\ x \in \mathbb{R} \\ &= \begin{cases} 0 & \text{for } x - c_2t \notin \Omega_2, \\ H_2(e^{\rho_2(-x+c_2t+\xi_2)}) & \text{for } x - c_2t \in \Omega_2 \end{cases}\end{aligned} \tag{3.16}$$

with

$$\xi_2 \in \left[(c_1 - c_2)\kappa\tau + \rho_2^{-1}\ln\mu_2 - r/2,\ (c_1 - c_2)\kappa\tau + \rho_2^{-1}\ln\nu_2 + r/2\right], \tag{3.17}$$

where

$$\begin{aligned}&\Omega_2 = (\xi_2 - \rho_2^{-1}\ln\mu_2,\ \xi_2 - \rho_2^{-1}\ln\nu_2), \\ &H_2(z) = A_2z - B_2z^{1+\delta_2} - D_2z^{1-\delta_2} \quad \text{for } z > 0, \\ &\rho_2 = \frac{\beta^-(c_2) + \gamma^-(c_2)}{2}, \quad \delta_2 = \frac{\beta^-(c_2) - \gamma^-(c_2)}{\beta^-(c_2) + \gamma^-(c_2)}, \\ &(A_2)^{\delta_2} = \frac{G_{\eta_2}(c_2, \rho_2)}{M(\delta_2)}, \quad D_2 = \frac{A_2G_{\eta_2}(c_2, \rho_2)}{G_{\eta_2}(c_2, \gamma^-(c_2))},\ B_2 \in \left(0, A_2^2/(4D_2)\right), \\ &(\mu_2, \nu_2) \triangleq \{z > 0 \mid H_2(z) > 0\}.\end{aligned}$$

Here $G_\eta(c, \lambda)$ is defined by (3.3) and note that ρ_2 is a negative number. By Lemma 3.2, we can choose $B_2 \in \left(0, A_2^2/(4D_2)\right)$ close to $A_2^2/(4D_2)$ such that

$$H_2^{\max} \triangleq \max_{z>0}\left\{H_2(z)\right\} \leqslant H_1^{\max} \leqslant p_2 \leqslant p_1, \quad \rho_2^{-1}(\ln\mu_2 - \ln\nu_2) \leqslant r/2. \tag{3.18}$$

Let z_2 be the constant in (μ_2, ν_2) such that $H_2^{\max} = H_2(z_2)$. At time $t = \kappa\tau$, we have

$$\underline{u}_2(\kappa\tau, x; \xi_2) = \begin{cases} 0 & \text{for } x \notin \Omega_2 + c_2\kappa\tau, \\ H_2(e^{\rho_2(-x+c_2\kappa\tau+\xi_2)}) & \text{for } x \in \Omega_2 + c_2\kappa\tau, \end{cases}$$

where

$$\Omega_2 + c_2\kappa\tau \triangleq (\xi_2 - \rho_2^{-1}\ln\mu_2 + c_2\kappa\tau,\ \xi_2 - \rho_2^{-1}\ln\nu_2 + c_2\kappa\tau) \subseteq (c_1\kappa\tau - r/2, c_1\kappa\tau + r/2).$$

Then it follows from (3.15) that $u(\kappa\tau, x) \geqslant \underline{u}_2(\kappa\tau, x; \xi_2)$ for $x \in \mathbb{R}$ and any ξ_2 satisfying (3.17). Similar to the case of $\underline{u}_1(t, x; \xi_1)$, it can be verified that $\underline{u}_2(t, x; \xi_2)$ is a lower solution of equation (1.1) in time $[\kappa\tau, \tau]$. Then for any ξ_2 satisfying (3.17), by Lemma 3.1 we have that

$$u(t,x) \geqslant \underline{u}_2(t,x;\xi_2) \text{ for } t \in [\kappa\tau, \tau],\ x \in \mathbb{R}.$$

For $t \in [\kappa\tau, \tau]$, we define $x_2(t) = c_2 t + \xi_2 - \rho_2^{-1} \ln z_2$ and it follows that

$$u(t, x_2(t)) \geqslant \underline{u}_2(t, x_2(t); \xi_2) = H(z_2) = H_2^{\max}.$$

Since

$$\rho_2^{-1}(\ln \mu_2 - \ln z_2) \leqslant \rho_2^{-1}(\ln \mu_2 - \ln \nu_2) \leqslant r/2 \text{ and}$$
$$\rho_2^{-1}(\ln z_2 - \ln v_2) \leqslant \rho_2^{-1}(\ln \mu_2 - \ln \nu_2) \leqslant r/2,$$

we can choose ξ_2 satisfying (3.17) and

$$\xi_2 = (c_1 - c_2)\kappa\tau + \rho_2^{-1} \ln z_2.$$

It follows that $x_2(\tau) = c_1\kappa\tau + c_2(1-\kappa)\tau = X$. By taking $p = H_2^{\max}$, we have that

$$u(\tau, X) \geqslant p \quad \text{for any } \tau > 0,\ X \in [c_2\tau, c_1\tau].$$

Therefore, for any small $\epsilon > 0$ there is a constant $p \in (0,1)$ such that

$$\min_{(c_l^*+\epsilon)t \leqslant x \leqslant (c_r^*-\epsilon)t} u(t,x) \geqslant p \quad \text{for any} \quad t > 0.$$

Step 2 (*Upper solution*). Now we begin to prove that

$$\lim_{t\to+\infty} \sup_{x \leqslant (c_l^*-\epsilon)t} u(t,x) = 0 \quad \text{and} \quad \lim_{t\to+\infty} \sup_{x \geqslant (c_r^*+\epsilon)t} u(t,x) = 0. \tag{3.19}$$

Construct an upper solution as follows

$$\bar{u}(t,x) = \min\left\{1,\ \Gamma_0 e^{\lambda_r^*(-x+c_r^*t)},\ \Gamma_0 e^{\lambda_l^*(-x+c_l^*t)}\right\},$$

where the constant $\Gamma_0 \geqslant \max\{1, \Gamma\}$ is large enough such that $\bar{u}(0,x) \geqslant u_0(x)$.

Next we verify that $\bar{u}(t,x)$ is an upper solution of equation (1.1). Define

$$G(c,\lambda) = c\lambda - \int_{\mathbb{R}} k(x)e^{\lambda x}dx + 1 - f'(0) \quad \text{for } c \in \mathbb{R},\ \lambda \in (\lambda^-, \lambda^+).$$

Then it follows from (2.9) and (2.10) that $G(c_r^*, \lambda_r^*) = G(c_l^*, \lambda_l^*) = 0$. By a simple calculation, if $x \leqslant c_l^* t + (\lambda_l^*)^{-1} \ln \Gamma_0$, then $\bar{u}(t,x) = \Gamma_0 e^{\lambda_l^*(-x+c_l^*t)}$ and it follows from (H) that

$$\bar{u}_t(t,x) - k * \bar{u}(t,x) + \bar{u}(t,x) - f(\bar{u}(t,x)) \geqslant G(c_l^*, \lambda_l^*)\Gamma_0 e^{\lambda_l^*(-x+c_l^*t)} = 0.$$

If $x \geqslant c_r^* t + (\lambda_r^*)^{-1} \ln \Gamma_0$, then $\bar{u}(t,x) = \Gamma_0 e^{\lambda_r^*(-x+c_r^* t)}$ and we get from (H) that

$$\bar{u}_t(t,x) - k * \bar{u}(t,x) + \bar{u}(t,x) - f(\bar{u}(t,x)) \geqslant G(c_r^*, \lambda_r^*) \Gamma_0 e^{\lambda_r^*(-x+c_r^* t)} = 0.$$

If $c_l^* t + (\lambda_l^*)^{-1} \ln \Gamma_0 \leqslant x \leqslant c_r^* t + (\lambda_r^*)^{-1} \ln \Gamma_0$, then $\bar{u}(t,x) = 1$ and

$$\bar{u}_t(t,x) - k * \bar{u}(t,x) + \bar{u}(t,x) - f(\bar{u}(t,x)) \geqslant 0.$$

Therefore, we get that $\bar{u}(t,x)$ is an upper solution of equation (1.1). Lemma 3.1 implies that $u(t,x) \leqslant \bar{u}(t,x)$ for $t \geqslant 0$, $x \in \mathbb{R}$. It follows that

$$\sup_{x \leqslant (c_l^* - \epsilon)t} u(t,x) \leqslant \sup_{x \leqslant (c_l^* - \epsilon)t} \bar{u}(t,x) \leqslant \Gamma_0 e^{\lambda_l^* \epsilon t},$$
$$\sup_{x \geqslant (c_r^* + \epsilon)t} u(t,x) \leqslant \sup_{x \geqslant (c_r^* + \epsilon)t} \bar{u}(t,x) \leqslant \Gamma_0 e^{-\lambda_r^* \epsilon t},$$

which means that (3.19) holds. □

By Theorem 6.2 in the classic spreading speed theory [39], we can get from the second inequality of (3.9) that for any small $\epsilon > 0$,

$$\min_{(c_l^* + \epsilon)t \leqslant x \leqslant (c_r^* - \epsilon)t} u(t,x) \to 1 \quad \text{as } t \to +\infty.$$

Then combining with the other two inequalities of (3.9), we see that $u(t,x)$ satisfies the propagation property (1.4).

By using the new lower solutions and the above "forward-backward spreading" method, we obtain a corollary which shows that if $u_0(x_1) > 0$ for some $x_1 \in \mathbb{R}$, then the property $u > 0$ will spread over an expanding spatial region.

Corollary 3.4. *Suppose that* (H), (K1) *and* (K2) *hold. For any small $\epsilon > 0$ and small $p > 0$, there is a constant $r_\epsilon(p) > 0$ such that if*

$$u_0(x) \geqslant p, \ x \in [x_1 - r_\epsilon(p), x_1 + r_\epsilon(p)] \ \textit{ for some } x_1 \in \mathbb{R},$$

then the solution $u(t,x)$ of equation (1.1) *satisfies that*

$$u(t,x) \geqslant p \ \textit{ for } t > 0, \ x \in [x_1 + (c_l^* + \epsilon)t, \ x_1 + (c_r^* - \epsilon)t].$$

Moreover, for any small $\epsilon > 0$, we have that $r_\epsilon(p) \to 0$ as $p \to 0$.

Proof. We use the same notations as those in the proof of Theorem 3.3. By translating the x-axis, we suppose that $x_1 = 0$. From Lemma 3.2, for any $p \in (0, p_2]$, there are $B_1(p) \in \big(0, \ A_1^2/(4D_1)\big)$ and $B_2(p) \in \big(0, A_2^2/(4D_2)\big)$ satisfying that $H_1^{\max} = H_2^{\max} = p$.

We define $r(p) = 2(r_1(p)+r_2(p))$, where $r_i(p)$ is the length of the set $\{x \in \mathbb{R} \mid H_i(e^{-\rho_i x}) > 0\}$. We suppose that

$$u_0(x) \geqslant p \quad \text{for } x \in [-r(p), r(p)].$$

Define the lower solutions $\underline{u}_1(t,x;\xi_1)$ and $\underline{u}_2(t,x;\xi_2)$ by (3.12) and (3.16), respectively, where

$$\xi_1 \in \left[-r(p) + \rho_1^{-1} \ln \nu_1,\ r(p) + \rho_1^{-1} \ln \mu_1\right],$$
$$\xi_2 \in \left[(c_1 - c_2)\kappa\tau + \rho_2^{-1} \ln \mu_2 - r_2(p),\ (c_1 - c_2)\kappa\tau + \rho_2^{-1} \ln \nu_2 + r_2(p)\right].$$

It follows that

$$\Omega_1 \subseteq (-r(p), r(p)),\ \Omega_2 + c_2\kappa\tau \subseteq (c_1\kappa\tau - r_2(p), c_1\kappa\tau + r_2(p)).$$

Then by the same method as the proof of Theorem 3.3, we can prove Corollary 3.4. Moreover, as $p \to 0^+$, it follows from Lemma 3.2 that $B_i(p) \to A_i^2/(4D_i)$, which implies that $r_i(p) \to 0$. We can see that $r_i(p)$ is dependent on c_i, since H_i and ρ_i are dependent on c_i. Therefore, $r_i(p)$ is also dependent on ϵ. □

Remark 3.5. When considering a reaction-diffusion equation or when the kernel in equation (1.1) is symmetric, we point out that the new lower solutions (3.12) and (3.16) remain valid. However, it is not necessary to apply the "forward-backward spreading" method, since we can use Theorem 2.5 instead (more details are found in proof of Theorem 4.2). Then the conclusion in Corollary 3.4 still holds in the reaction-diffusion equation (1.2).

4. Spreading speeds for exponentially decaying initial data

In this section we study the relationship between spreading speed and exponentially decaying initial data. First we state the weak "*hair-trigger*" effect in nonlocal dispersal equations (see e.g. [1,3,17]).

Lemma 4.1 *(Weak "hair-trigger" effect). Suppose that (H) holds and $k(\cdot)$ is a symmetric kernel satisfying (K1). Let $u(t,x)$ be the solution of equation (1.1) with initial data $u_0(x)$. If there are two constants $x_0 \in \mathbb{R}$ and $\omega_0 \in (0,1)$ such that*

$$u_0(x) \geqslant \omega_0 \quad \textit{for} \quad x \in B_1(x_0),$$

then for any $\omega \in (0,1)$, there exists $T_{\omega_0}^{\omega} \geqslant 0$ (independent of x_0) such that

$$u(t,x) \geqslant \omega \quad \textit{for} \quad x \in B_1(x_0),\ t \geqslant T_{\omega_0}^{\omega},$$

where $B_1(x_0) \triangleq \{x \in \mathbb{R} \mid |x - x_0| \leqslant 1\}$.

The following theorem is the main result of this section.

Theorem 4.2. *Suppose* (H) *holds and* $k(\cdot)$ *is a symmetric kernel which is decreasing on* $\mathbb{R}^+$ *and satisfies* (K1)*. Denote* $c^* \triangleq c_r^* = -c_l^*$ *and* $\lambda^* \triangleq \lambda_r^* = -\lambda_l^*$*. If* $f \in C^{1+\delta_0}\big([0, p_0]\big)$ *for some* $p_0, \delta_0 \in (0, 1)$ *and* $u_0(\cdot)$ *satisfies*

$$0 < u_0(x) \leqslant 1 \text{ for } x \in \mathbb{R}, \;\; u_0(x) \sim Ce^{-\lambda|x|} \;\; \text{as } |x| \to +\infty \text{ with } \lambda \in (0, \lambda^*),$$

then for any $\epsilon \in (0, c(\lambda))$*, the solution* $u(t, x)$ *of equation* (1.1) *has the following properties*

$$\begin{cases} \min\limits_{|x|\leqslant(c(\lambda)-\epsilon)t} u(t,x) \to 1, \\ \sup\limits_{|x|\geqslant(c(\lambda)+\epsilon)t} u(t,x) \to 0 \end{cases} \quad \text{as } t \to +\infty,$$

where $c(\lambda)$ *is defined by* (2.8)*. Moreover, we have that* $c'(\lambda) < 0$ *for* $\lambda \in (0, \lambda^*)$.

Proof. From the proof of Lemma 2.3, we have that

$$c'(\lambda) < 0 \text{ for } \lambda \in (0, \lambda^*) \;\; \text{and } c'(\lambda) > 0 \text{ for } \lambda \in (\lambda^*, \lambda^+).$$

Since $c(\lambda) \to +\infty$ as $\lambda \to \lambda^+$, for any $\lambda \in (0, \lambda^*)$ there is a unique constant $\delta_\lambda > 0$ such that

$$c(\lambda) = c(\lambda(1 + \delta_\lambda)) \text{ and } c(s) < c(\lambda) \text{ for } s \in (\lambda, \lambda(1 + \delta_\lambda)).$$

Define

$$G(c, \lambda) = c\lambda - \int\limits_{\mathbb{R}} k(x)e^{\lambda x}dx + 1 - f'(0) \;\; \text{for } c \geqslant c^*, \;\; \lambda \in (\lambda^-, \lambda^+).$$

For any $\lambda \in (0, \lambda^*)$, it follows from (2.8) that

$$G(c(\lambda), \lambda) = G(c(\lambda), \lambda(1 + \delta_\lambda)) = 0$$

and

$$G(c(\lambda), s) > G(c(s), s) = 0 \text{ for } s \in (\lambda, \lambda(1 + \delta_\lambda)).$$

Now we prove that for any $\epsilon \in (0, c(\lambda))$,

$$\min_{|x|\leqslant(c(\lambda)-\epsilon)t} u(t, x) \to 1 \text{ as } t \to +\infty. \tag{4.1}$$

By the assumptions of u_0 in Theorem 4.2, there is a function $v_0(\cdot) \in C(\mathbb{R})$ which is symmetric and decreasing on $\mathbb{R}^+$ and satisfies that

$$u_0(x) \geqslant v_0(x) = \begin{cases} \gamma e^{-\lambda|x|}, & |x| \geqslant y_0, \\ p_1 \triangleq \gamma e^{-\lambda y_0}, & |x| \leqslant y_0, \end{cases} \tag{4.2}$$

where γ and y_0 are two positive constants. Let $v(t,x)$ be the solution of equation (1.1) with the initial condition $v(0,x) = v_0(x)$. From Lemma 3.1 it follows that

$$u(t,x) \geqslant v(t,x) \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}. \tag{4.3}$$

Theorem 2.5 shows that $v(t,\cdot)$ is also symmetric and decreasing on $\mathbb{R}^+$ for any $t > 0$. We denote $p \triangleq \min\{p_0, p_1\}$ and $\delta \triangleq \min\{\delta_0, \delta_\lambda/2\}$, then $G(c(\lambda), \lambda(1+\delta)) > 0$. By $f(\cdot) \in C^{1+\delta_0}([0,p_0])$ we can find some constant $M > 0$ such that

$$f(u) \geqslant f'(0)u - Mu^{1+\delta} \quad \text{for } u \in (0,p]. \tag{4.4}$$

Construct a lower solution as follows

$$\underline{u}(t,x) = \max\left\{0,\ g\left(\gamma e^{\lambda(-x+c(\lambda)t)}\right)\right\} \quad \text{for } t \geqslant 0,\ x \in \mathbb{R},$$

where $g(z) = z - Lz^{1+\delta}$ for $z > 0$ and

$$L \geqslant \max\left\{p^{-\delta},\ \gamma^{-\delta}e^{\lambda\delta},\ M/G(c(\lambda), \lambda(1+\delta))\right\}. \tag{4.5}$$

Let z_0 be the constant satisfying $z_0^\delta = L^{-1}(1+\delta)^{-1}$, then $\omega_0 \triangleq g(z_0) \geqslant g(z)$ for all $z > 0$ and

$$\underline{u}(t,x) \leqslant \omega_0 = L^{-\frac{1}{\delta}}\delta(1+\delta)^{-\frac{1+\delta}{\delta}} \leqslant p \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}.$$

From (4.2) it follows that $v_0(x) \geqslant \underline{u}(0,x)$ for $x \in \mathbb{R}$. Now we verify that $\underline{u}(t,x)$ is a lower solution of equation (1.1). If $x < c(\lambda)t + \lambda^{-1}(\ln\gamma + \delta^{-1}\ln L)$, we can check that $\underline{u}(t,x) = 0$ and

$$\underline{u}_t(t,x) - k * \underline{u}(t,x) + \underline{u}(t,x) - f(\underline{u}(t,x)) \leqslant 0.$$

If $x \geqslant c(\lambda)t + \lambda^{-1}(\ln\gamma + \delta^{-1}\ln L)$, then $\underline{u}(t,x) = g\left(\gamma e^{\lambda(-x+c(\lambda)t)}\right)$. From (4.4) it follows that

$$\begin{aligned} &\underline{u}_t(t,x) - k * \underline{u}(t,x) + \underline{u}(t,x) - f(\underline{u}(t,x)) \\ &\quad \leqslant G(c(\lambda),\lambda)\gamma e^{\lambda(-x+c(\lambda)t)} - \left[G(c(\lambda), \lambda(1+\delta))L - M\right]\gamma^{1+\delta}e^{\lambda(1+\delta)(-x+c(\lambda)t)}. \end{aligned}$$

By $G(c(\lambda),\lambda) = 0$ and $L \geqslant M/G(c(\lambda), \lambda(1+\delta))$, we get that $\underline{u}(t,x)$ is a lower solution.

Lemma 3.1 implies that

$$v(t,x) \geqslant \underline{u}(t,x) \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}.$$

Let $x_0(t) = c(\lambda)t + \lambda^{-1}(\ln\gamma - \ln z_0) \geqslant 1$ with $t \geqslant 0$ and we have that

$$v(t, x_0(t)) \geqslant \underline{u}(t, x_0(t)) = g(z_0) = \omega_0 \text{ for } t \geqslant 0.$$

The symmetry and monotone property of $v(t,\cdot)$ yield that

$$v(t,x) \geqslant \omega_0 \quad \text{for} \quad t \geqslant 0,\ |x| \leqslant x_0(t).$$

For any $\omega \in (0,1)$, let $T^{\omega}_{\omega_0}$ be the positive constant defined in Lemma 4.1 and we have

$$v(t + T^{\omega}_{\omega_0}, x) \geqslant \omega \quad \text{for } t \geqslant 0,\ |x| \leqslant x_0(t),$$

which implies that

$$\min_{|x| \leqslant x_0(t) - c(\lambda)T^{\omega}_{\omega_0}} v(t,x) \geqslant \omega \quad \text{for } t \geqslant T^{\omega}_{\omega_0}.$$

For $\epsilon \in (0, c(\lambda))$, there is a constant $T \geqslant T^{\omega}_{\omega_0}$ (dependent on ϵ and ω) such that

$$\epsilon T \geqslant c(\lambda)T^{\omega}_{\omega_0} - \lambda^{-1}(\ln\gamma - \ln z_0).$$

Then we have that $x_0(t) - c(\lambda)T^{\omega}_{\omega_0} \geqslant (c(\lambda) - \epsilon)t$ and

$$\min_{|x| \leqslant (c(\lambda)-\epsilon)t} u(t,x) \geqslant \min_{|x| \leqslant (c(\lambda)-\epsilon)t} v(t,x) \geqslant \omega \quad \text{for } t \geqslant T,$$

which completes the proof of (4.1).

Finally, it suffices to check that for any $\epsilon > 0$,

$$\sup_{|x| \geqslant (c(\lambda)+\epsilon)t} u(t,x) \to 0 \quad \text{as } t \to +\infty. \tag{4.6}$$

Construct an upper solution as follows

$$\bar{u}(t,x) = \min\left\{1,\ \Gamma e^{\lambda(-|x| + c(\lambda)t)}\right\} \quad \text{for } t \geqslant 0,\ x \in \mathbb{R}.$$

By the same method as the step 2 of the proof of Theorem 3.3, we can get (4.6). □

Combining Theorems 3.3 and 4.2, when k is symmetric, we obtain the relationship between spreading speed and initial data that decays exponentially or faster. If $u_0(x) \sim Ce^{-\lambda|x|}$ as $|x| \to +\infty$, then for $\lambda \in [\lambda^*, +\infty)$ the spreading speed is equal to c^* and for $\lambda \in (0, \lambda^*)$ the spreading speed $c(\lambda)$ decreases strictly along with the increase of λ. Moreover, we have that $c^* = c(\lambda^*)$. This relationship shows that the nonlocal dispersal equation with symmetric kernel shares the same property of spreading speed as the corresponding reaction-diffusion equation.

5. Case studies

In this section we show how to calculate $E(k)$ and apply Theorem 2.4 to two examples of dispersal kernels: normal distribution and uniform distribution. For more applications to complex systems, refer to our recent paper [43].

5.1. Normal distribution

Assume that the dispersal kernel k satisfies

$$k(x) = \frac{1}{\sqrt{2\pi\sigma}} \exp\left(-\frac{(x-\alpha)^2}{2\sigma}\right),$$

where $\alpha \in \mathbb{R}$ is the expectation and $\sigma > 0$ is the variance. Define a constant

$$r = \alpha/\sqrt{2\sigma}.$$

Then some calculations yield that $\mathrm{sign}(r) = \mathrm{sign}(J(k))$ and

$$\begin{aligned} E(k) &= \mathrm{sign}(r)\left[1 - \inf_{\lambda\in\mathbb{R}}\left\{\exp\left(\alpha\lambda + \frac{\sigma}{2}\lambda^2\right)\right\}\right] \\ &= \mathrm{sign}(r)\left(1 - \exp\left(-r^2\right)\right). \end{aligned}$$

The following result is a straightforward consequence of Theorem 2.4 and we omit its proof.

Corollary 5.1. *When $f'(0) \geqslant 1$, it holds that $c_l^* < 0 < c_r^*$ and when $f'(0) < 1$, there exists a constant $r^* > 0$ such that*

(i) *if $r > r^*$, then $0 < c_l^* < c_r^*$;*
(ii) *if $r = r^*$, then $0 = c_l^* < c_r^*$;*
(iii) *if $-r^* < r < r^*$, then $c_l^* < 0 < c_r^*$;*
(iv) *if $r = -r^*$, then $c_l^* < c_r^* = 0$;*
(v) *if $r < -r^*$, then $c_l^* < c_r^* < 0$.*

Remark 5.2. Since the dispersal coefficient in equation (1.1) is 1, the condition $f'(0) > 1$ implies that the reaction term plays a more important role than the dispersal term; on the other hand, the condition $f'(0) < 1$ means that the dispersal term is more important. In the latter case, we show that the asymmetry level of dispersal determines the propagation directions.

5.2. Uniform distribution

Suppose that the kernel k is given by

$$k(x) = \begin{cases} \dfrac{1}{a-b} & \text{for } x \in [b,a], \\ 0 & \text{for } x \notin [b,a], \end{cases}$$

where $a \in \mathbb{R}^+$ and $b \in \mathbb{R}^-$ stand for the farthest distances of organism movements during a unit time period along and against x-axis, respectively. The average moving speed is $\int k(x)xdx = (a+b)/2$. Some calculations yield that

$$E(k) = \operatorname{sign}(a+b)\big[1 - \inf_{\lambda \neq 0} \{h(\lambda)\}\big],$$

where $h(\lambda) = (e^{a\lambda} - e^{b\lambda})/(a\lambda - b\lambda)$ with $\lambda \neq 0$. Next, we define an auxiliary function and give its property in the following lemma.

Lemma 5.3. *Define $\omega(x) = (x-1)e^x$. Then there is a unique continuous function $z(\cdot)$ from $(0,+\infty)$ to $(-\infty,1)$ with $z(\cdot) \not\equiv 0$ such that $\omega(z(\theta)) = \omega(-\theta z(\theta))$ for any $\theta > 0$. Moreover, the function $z(\cdot)$ is increasing on $(0,+\infty)$.*

Proof. For any $\theta > 0$, define

$$\bar{\omega}(\theta,x) = \omega(x) - \omega(-\theta x) = (x-1)e^x + (\theta x + 1)e^{-\theta x} \quad \text{for } \theta \in (0,+\infty),\ x \in \mathbb{R}.$$

It follows that $\frac{\partial}{\partial x}\bar{\omega}(\theta,x) = xe^x - \theta^2 x e^{-\theta x}$ for $x \in \mathbb{R}$. Denote $x_1 = 0$ and $x_2(\theta) = 2(1+\theta)^{-1}\ln\theta$, then $\frac{\partial}{\partial x}\bar{\omega}(\theta,x_1) = \frac{\partial}{\partial x}\bar{\omega}(\theta,x_2(\theta)) = 0$. Some calculations yield that

$$\bar{\omega}(\theta,0) = 0, \quad \bar{\omega}(\theta,1) > 0, \quad \bar{\omega}(\theta,-1/\theta) < 0, \tag{5.1}$$

and

$$\bar{\omega}\,(\theta, 1-1/\theta) = e^{1-\theta}(\theta^2 - e^{\theta - 1/\theta})/\theta.$$

Notice that the function $\theta \mapsto \theta - 1/\theta - 2\ln\theta$ is strictly increasing on $(0,+\infty)$ and it equals 0 when $\theta = 1$. Then we have that

$$\bar{\omega}(\theta, 1-1/\theta) < 0 \text{ for } \theta > 1,\ \bar{\omega}(\theta,1-1/\theta) > 0 \text{ for } 0 < \theta < 1. \tag{5.2}$$

If $\theta > 1$, then $x_1 < x_2(\theta)$ and

$$\frac{\partial}{\partial x}\bar{\omega}(\theta,x) < 0 \text{ for } x \in (x_1, x_2(\theta)),\ \frac{\partial}{\partial x}\bar{\omega}(\theta,x) > 0 \text{ for } x \in \mathbb{R}\backslash[x_1,x_2(\theta)]. \tag{5.3}$$

By (5.1) and (5.2), for any $\theta > 1$ there is a unique $z(\theta) \in (1-1/\theta, 1)$ such that $\bar{\omega}(\theta, z(\theta)) = 0$. On the other hand, if $0 < \theta < 1$ then $x_1 > x_2(\theta)$ and

$$\frac{\partial}{\partial x}\bar{\omega}(\theta, x) < 0 \text{ for } x \in (x_2(\theta), x_1), \ \frac{\partial}{\partial x}\bar{\omega}(\theta, x) > 0 \text{ for } x \in \mathbb{R}\backslash[x_2(\theta), x_1].$$

For any $\theta \in (0, 1)$, we can find a unique $z(\theta) \in (-1/\theta, 1-1/\theta)$ such that $\bar{\omega}(\theta, z(\theta)) = 0$. In addition, when $\theta = 1$ we define $z(\theta) = 0$. Finally, we show that

$$z(1) = 0, \ z(\theta) \in (1-1/\theta, 1) \text{ for } \theta > 1, \ z(\theta) \in (-1/\theta, 1-1/\theta) \text{ for } 0 < \theta < 1. \tag{5.4}$$

Now we prove that $z(\cdot)$ is continuous on $(0, +\infty)$. Indeed, it suffices to show that

$$\lim_{\theta\to 1^+} z(\theta) = \lim_{\theta\to 1^-} z(\theta) = 0.$$

Notice that

$$\bar{\omega}(\theta, z(\theta)) - \bar{\omega}(\theta, 1-1/\theta) = \int_{1-1/\theta}^{z(\theta)} \frac{\partial}{\partial x}\bar{\omega}(\theta, x)dx,$$

which means that

$$-e^{1-\theta}(\theta^2 - e^{\theta-1/\theta})/\theta = \int_{1-1/\theta}^{z(\theta)} xe^x - \theta^2 xe^{-\theta x}dx.$$

Let $\theta \to 1^+$ or 1^-, then

$$\lim_{\theta\to 1^+} \int_0^{z(\theta)} xe^x - xe^{-x}dx = \lim_{\theta\to 1^-} \int_0^{z(\theta)} xe^x - xe^{-x}dx = 0.$$

It follows that $\lim_{\theta\to 1^+} z(\theta) = \lim_{\theta\to 1^-} z(\theta) = 0$. Therefore, $z(\cdot)$ is continuous on $(0, +\infty)$.

Next, we prove that $z(\cdot)$ is increasing on $(0, +\infty)$. Consider the function $\bar{\omega}(\theta, x)$ with $(\theta, x) \in (1, +\infty) \times (0, +\infty)$. For any fixed $\theta_0 > 1$, it holds that $\bar{\omega}(\theta_0, z(\theta_0)) = 0$ and $\frac{\partial}{\partial x}\bar{\omega}(\theta_0, z(\theta_0)) > 0$ by (5.3). Then implicit function theorem implies that $z(\cdot)$ has a continuous derivative at θ_0 and

$$z'(\theta) = -\frac{\partial\bar{\omega}(\theta, z(\theta))}{\partial\theta} \Bigg/ \frac{\partial\bar{\omega}(\theta, z(\theta))}{\partial x} = \frac{\theta z^2(\theta)e^{-\theta z(\theta)}}{z(\theta)e^{z(\theta)} - \theta^2 z(\theta)e^{-\theta z(\theta)}} \quad \text{for } \theta > 1.$$

From $\omega(z(\theta)) = \omega(-\theta z(\theta))$ it follows that

$$z'(\theta) = \frac{z(\theta)(z(\theta)-1)}{(\theta+1)[1-1/\theta-z(\theta)]} \quad \text{for } \theta > 1. \tag{5.5}$$

When $\theta > 1$, by $z(\theta) \in (1-1/\theta, 1)$, we have that $z'(\theta) > 0$. Similarly, we can prove that $z'(\cdot)$ is continuous on $(0,1)$ and

$$z'(\theta) = \frac{z(\theta)(z(\theta)-1)}{(\theta+1)[1-1/\theta-z(\theta)]} \quad \text{for} \quad \theta \in (0,1).$$

Then for $\theta \in (0,1)$, by $z(\theta) \in (-1/\theta, 1-1/\theta)$ we obtain that $z'(\theta) > 0$. Therefore, we have proved that $z(\cdot)$ is increasing on $(0,+\infty)$. This completes the proof. □

Define a constant

$$\theta \triangleq -a/b \in (0,+\infty).$$

From $h'(\lambda) = (\omega(a\lambda) - \omega(b\lambda))/(a\lambda^2 - b\lambda^2)$, it follows that $h'(z(\theta)/b) = 0$. Then by $\omega(z(\theta)) = \omega(-\theta z(\theta))$, we have that $h(z(\theta)/b) = e^{z(\theta)}/(1+\theta z(\theta))$ and

$$E(k) = \operatorname{sign}(\theta-1)\Big[1 - \frac{e^{z(\theta)}}{1+\theta z(\theta)}\Big].$$

Denote

$$r \triangleq (\theta-1)/(\theta+1) = (a+b)/(a-b) \in (-1,1).$$

Corollary 5.4. *All results in Corollary 5.1 hold for the uniform distribution case.*

Proof. It suffices to prove the results in the case $0 < f'(0) < 1$, since $-1 < E(k) < 1$. Now we only consider the case $r \geqslant 0$, namely $\theta \geqslant 1$ (otherwise consider the new spatial variable $y = -x$). Denote

$$q(\theta) = 1 - \frac{e^{z(\theta)}}{1+\theta z(\theta)}.$$

For $\theta > 1$, it follows that

$$q'(\theta) = \frac{e^{z(\theta)}(\theta - \theta z(\theta) - 1)}{[1+\theta z(\theta)]^2} z'(\theta) + \frac{e^{z(\theta)} z(\theta)}{[1+\theta z(\theta)]^2}.$$

From (5.5) we get that

$$q'(\theta) = \frac{e^{z(\theta)} z(\theta)[\theta z(\theta) - \theta + 1]}{[1+\theta z(\theta)]^2} \text{ for } \theta > 1.$$

Then (5.4) implies that $q'(\theta) > 0$ for $\theta > 1$, which means that $q(\cdot)$ is strictly increasing on $[1, +\infty)$. Moreover, since $z(\theta) \to 1$ as $\theta \to +\infty$, we have that

$$q(1) = 0 \text{ and } q(\theta) \to 1 \text{ as } \theta \to +\infty.$$

Therefore, when $f'(0) \in (0, 1)$, there exists a unique constant $\theta^* > 1$ such that $q(\theta^*) = f'(0)$. Denote $r^* = (\theta^* - 1)/(\theta^* + 1)$. Finally, by Theorem 2.4, the monotone property of q completes the proof. □

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