Stationary Solutions and Spreading Speeds of Nonlocal
Monostable Equations in Space Periodic Habitats*

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Abstract. This paper deals with positive stationary solutions and spreading speeds of monostable
equations with nonlocal dispersal in spatially periodic habitats. The existence and uniqueness of positive
stationary solutions and the existence and characterization of spreading speeds of such equations with
symmetric convolution kernels are established in the authors’ earlier work [41] for following cases: the
nonlocal dispersal is nearly local; the periodic habitat is nearly globally homogeneous or it is nearly
homogeneous in a region where it is most conducive to population growth. The above conditions guarantee
the existence of principal eigenvalues of nonlocal dispersal operators associated to linearized equations
at the trivial solution. In general, a nonlocal dispersal operator may not have a principal eigenvalue.
In this paper, we extend the results in [41] to general spatially periodic nonlocal monostable equations.
As a consequence, it is seen that the spatial spreading feature is generic for monostable equations with
nonlocal dispersal.

Key words. Monostable equation; nonlocal dispersal; random dispersal; periodic habitat; spreading
speed; principal eigenvalue; principal eigenfunction; variational principle.

Mathematics subject classification. 45C05, 45G10, 45M20, 47G10, 92D25.

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1 Introduction

The current paper is an extension of the work [41] on spatial spreading dynamics of the following monostable equation with nonlocal dispersal,

\[ \frac{\partial u}{\partial t} = \int_{\mathbb{R}^N} k(y-x)u(t,y)dy - u(t,x) + u(t,x)f(x,u(t,x)), \quad x \in \mathbb{R}^N, \quad (1.1) \]

where \( k(\cdot) \) is a \( C^1 \) convolution kernel supported on a ball centered at 0 (i.e. \( k(z) > 0 \) if \( \|z\| < \delta \) and \( k(z) = 0 \) if \( \|z\| \geq \delta \) for some \( \delta > 0 \), where \( \| \cdot \| \) denotes the norm in \( \mathbb{R}^N \), and \( \int_{\mathbb{R}^N} k(z)dz = 1. \) The function \( f(x,u) \) is \( C^1 \) in \( (x,u) \in \mathbb{R}^N \times \mathbb{R} \), periodic in \( x \) with period \( p_i \) (\( p_i > 0, i = 1, 2, \cdots, N \)) (i.e. \( f(\cdot + p_i e_i, \cdot) = f(\cdot, \cdot), e_i = (\delta_{i1}, \delta_{i2}, \cdots, \delta_{iN}), \delta_{ij} = 1 \) if \( i = j \) and 0 if \( i \neq j, i,j = 1, 2, \cdots, N \)), and satisfies proper monostability assumptions. More precisely, let

\[ X_p = \{ u \in C(\mathbb{R}^N, \mathbb{R})| u(\cdot + p_i e_i) = u(\cdot), \quad i = 1, \cdots, N \} \quad (1.2) \]

with norm \( \|u\|_{X_p} = \sup_{x \in \mathbb{R}^N} |u(x)| \), and

\[ X_p^+ = \{ u \in X_p | u(x) \geq 0 \quad \forall x \in \mathbb{R}^N \}. \quad (1.3) \]

Let \( I \) be the identity map on \( X_p \), and \( K, a_0(\cdot)I : X_p \rightarrow X_p \) be defined by

\[ (Ku)(x) = \int_{\mathbb{R}^N} k(y-x)u(y)dy, \quad (Ku)(x) = \int_{\mathbb{R}^N} k(y-x)u(y)dy, \quad (1.4) \]

\[ (a_0(\cdot)I)u(x) = a_0(x)u(x), \quad (1.5) \]

where \( a_0(x) = f(x,0) \). The monostability assumptions are then stated as follows:

(H1) \( \frac{\partial f(x,u)}{\partial a} < 0 \) for \( x \in \mathbb{R}^N \) and \( u \in \mathbb{R} \) and \( f(x,u) < 0 \) for \( x \in \mathbb{R}^N \) and \( u \gg 1 \).

(H2) \( u \equiv 0 \) is linearly unstable in \( X_p \), that is, \( \lambda_0 := \sup\{ \text{Re} \lambda | \lambda \in \sigma(K-I+a_0(\cdot)I) \} \) is positive, where \( \sigma(K-I+a_0(\cdot)I) \) is the spectrum of the operator \( K-I+a_0(\cdot)I \) on \( X_p \).

It is proved in [41] that if \( k(\cdot) \) is symmetric (i.e. \( k(-x) = k(x) \) for \( x \in \mathbb{R}^N \)) and \( \lambda_0 \) in (H2) is an isolated algebraically simple eigenvalue of \( K-I+a_0(\cdot)I \) with an eigenfunction in \( X_p^+ \), then (H1) and (H2) imply that (1.1) has exactly two equilibrium solutions in \( X_p^+ \), \( u = 0 \) and \( u = u^+ \), and \( u = 0 \) is linearly unstable and \( u = u^+ \) is asymptotically stable in \( X_p \) (see [41, Proposition 2.4]). These results will be extended to the general case in this paper, i.e., the case that only (H1) and (H2) are satisfied, which reflects the monostable feature of the assumptions (H1) and (H2).

Equation (1.1) is a nonlocal dispersal counterpart of the following local or random dispersal equation

\[ \frac{\partial u}{\partial t} = \Delta u + uf(x,u), \quad x \in \mathbb{R}^N. \quad (1.6) \]

Random dispersal is essentially a local behavior which describes the movement of species between adjacent spatial locations and has been widely used to model the population spreading dynamics of species (see [1], [3], [4], [5], [13], [14], [27], [32], [44], [45], and references therein). In contrast, nonlocal dispersal characterizes the movements and interactions of species between non-adjacent spatial locations. As the movements and interactions of many species in biology and ecology can occur between non-adjacent spatial locations, nonlocal dispersal has also been used to model the population spreading dynamics of species by many people (see [2], [7], [8], [9], [11], [12], [16], [22], [23], [26], and references therein).

One of the central problems for (1.1) and (1.6) is to understand how fast the population spreads as time evolves. E.g., letting \( \xi \in S^{N-1} := \{ \xi \in \mathbb{R}^N | \|\xi\| = 1 \} \) and a given initial population \( u_0(x) \) satisfy for some \( \delta_0 > 0 \) that \( u_0(x) \geq \delta_0 \) for \( x \in \mathbb{R}^N \) with \( x \cdot \xi \ll -1 \) and \( u_0(x) = 0 \) for \( x \in \mathbb{R}^N \) with \( x \cdot \xi \gg 1 \) (\( x \cdot \xi \) is the inner product of \( x \) and \( \xi \)), how fast does the population invade into the region with no population initially?
The spatial spreading dynamics of (1.6) has been extensively studied since the pioneering works of Fisher [14] and Kolmogorov, Petrowsky, Piscunov [27] on the following special case of (1.6)

\[ \frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + u(1-u), \quad x \in \mathbb{R}, \]  
(1.7)

which models the evolutionary take-over of a habitat by a fitter genotype. See, for example, [1], [3], [4], [5], [13], [17], [20], [21], [25], [28], [29], [30], [32], [34], [35], [38], [39], [43], [44], [45], and references therein, for the study of the spatial spreading dynamics of (1.6). It is well known that, if (H1) holds and \( u \equiv 0 \) is a linearly unstable solution of (1.6), then (1.6) has a unique positive equilibrium \( u^+ \) which is asymptotically stable with respect to perturbations in \( X_p \) and for every \( \xi \in S^{N-1} \), there is a \( c^*(\xi) \in \mathbb{R} \) such that for every \( c \geq c^*(\xi) \), there is a traveling wave solution connecting \( u^+ \) and \( u^- \equiv 0 \) and propagating in the direction of \( \xi \) with speed \( c \), and there is no such traveling wave solution of slower speed in the direction of \( \xi \). Moreover, the minimal wave speed \( c^*(\xi) \) is of some important spreading properties (hence is also called spreading speed) and has the following variational characterization. Let \( \lambda(\xi, \mu) \) be the eigenvalue of

\[
\begin{aligned}

\begin{cases}

\Delta u - 2\mu \sum_{i=1}^{N} \xi \xi_i \frac{\partial u}{\partial x_i} + (a_0(x) + \mu^2)u = \lambda u, & x \in \mathbb{R}^N \\
u(x + p_i e_i) = u(x), & i = 1, 2, \cdots, N \quad x \in \mathbb{R}^N
\end{cases}
\end{aligned}
\]  
(1.8)

with largest real part, where \( a_0(x) = f(x,0) \) (it is well known that \( \lambda(\xi, \mu) \) is real and algebraically simple. \( \lambda(\xi, \mu) \) is called the principal eigenvalue of (1.8) in literature). Then

\[ c^*(\xi) = \inf_{\mu > 0} \frac{\lambda(\xi, \mu)}{\mu}. \]  
(1.9)

(See [3], [4], [5], [28], [34], [35], [45] and references therein for the above mentioned properties).

Recently, the nonlocal dispersal equation of form (1.1) has also been studied by many authors. See, for example, [2], [7], [8], [10], [12], [15], [16], [19], [22], [23], [24], [26], [40], [41], for the study of spectral theory for nonlocal dispersal operators and the existence, uniqueness, and stability of nontrivial positive stationary solutions. See, for example, [9], [11], [44], [45] for the study of the existence of spreading speeds and traveling wave solutions connecting the trivial solution \( u = 0 \) and a nontrivial positive stationary solution for some special cases of (1.1). See also [31], [33], [36] and reference therein for the study of entire solutions and traveling wave solutions of certain (delayed) nonlocal monostable systems.

In the very recent paper [41], the authors of the current paper explored the spatial spreading dynamics of (1.6) in the case that \( k(\cdot) \) is symmetric and the nonlocal counterpart of the eigenvalue problem (1.8) possesses a principal eigenvalue. In such case, the existing results on spreading speed of (1.6) have been well extended to (1.1). Note that a nonlocal dispersal operator may not have a principal eigenvalue (see an example in [41]), which reveals some essential difference between nonlocal dispersal operators and random dispersal operators.

To be more precise, consider the following eigenvalue problem, which is a nonlocal counterpart of (1.8),

\[
(K_{\xi, \mu} - I + a(\cdot)I)v = \lambda v, \quad v \in X_p,
\]  
(1.10)

where \( \xi \in S^{N-1}, \mu \in \mathbb{R}, a(x) \) is a smooth function periodic in \( x \), with period \( p_i > 0 \) (i.e. \( a(x + p_i e_i) = a(x) \)) for \( i = 1, 2, \cdots, N \). The operator \( a(\cdot)I \) has the same meaning as in (1.5) with \( a_0(\cdot) \) being replaced by \( a(\cdot) \), and \( K_{\xi, \mu} : X_p \to X_p \) is defined by

\[
(K_{\xi, \mu}v)(x) = \int_{\mathbb{R}^N} e^{-\mu(y-x) \cdot \xi} k(y-x)v(y)dy.
\]  
(1.11)

We point out the following relation between (1.1) and (1.10): if \( u(t, x) = e^{-\mu(x-x_0) \cdot \xi} \phi(x) \) with \( \phi \in X_p \setminus \{0\} \) is a solution of the linearization of (1.1) at \( u = 0 \),

\[
\frac{\partial u}{\partial t} = \int_{\mathbb{R}^N} k(y-x)u(t,y)dy - u(t,x) + a_0(x)u(t,x), \quad x \in \mathbb{R}^N,
\]  
(1.12)
Definition 1.1. Let $\sigma(K_{\xi,\mu} - I + a(\cdot)I)$ be the spectrum of $K_{\xi,\mu} - I + a(\cdot)I$ on $X_p$.

1. $\lambda_0(\xi, \mu, a) := \sup\{\text{Re}\lambda | \lambda \in \sigma(K_{\xi,\mu} - I + a(\cdot)I)\}$ is called the principal spectrum point of $K_{\xi,\mu} - I + a(\cdot)I$.

2. A number $\lambda(\xi, \mu, a) \in \mathbb{R}$ is called the principal eigenvalue of (1.10) or $K_{\xi,\mu} - I + a(\cdot)I$ if it is an algebraically simple eigenvalue of $K_{\xi,\mu} - I + a(\cdot)I$ with an eigenfunction $v \in X^+_p$, and for every $\lambda \in \sigma(K_{\xi,\mu} - I + a(\cdot)I) \setminus \{\lambda(\xi, \mu, a)\}$, $\text{Re}\lambda < \lambda(\xi, \mu, a)$.

Observe that if the principal eigenvalue $\lambda(\xi, \mu, a)$ of $K_{\xi,\mu} - I + a(\cdot)I$ exists, then $\lambda(\xi, \mu, a) = \lambda_0(\xi, \mu, a)$. If $\mu = 0$, (1.10) is independent of $\xi$ and hence we put

$$\lambda_0(a) := \lambda_0(\xi, 0, a) \quad \forall \xi \in S^{N-1}. \quad (1.13)$$

In terms of the principal eigenvalue, we make the following assumption:

(H3) The principal eigenvalue $\lambda(\xi, \mu, a_0)$ of (1.10) with $a(\cdot) = a_0(\cdot)$ exists for every $\xi \in S^{N-1}$ and $\mu \geq 0$, where $a_0(x) = f(x, 0)$.

Let

$$X = \{u \in C(\mathbb{R}^N, \mathbb{R}) | u \text{ is uniformly continuous on } \mathbb{R}^N \text{ and } \sup_{x \in \mathbb{R}^N} |u(x)| < \infty\} \quad (1.14)$$

with norm $\|u\|_X = \sup_{x \in \mathbb{R}^N} |u(x)|$, and

$$X^+ = \{u \in X | u(x) \geq 0 \quad \forall x \in \mathbb{R}^N\}. \quad (1.15)$$

For any $u_0 \in X$, let $u(t, x; u_0)$ be the solution of (1.1) with $u(0, x; u_0) = u_0(x)$ (see section 2 for the discussions on local existence of $u(t, x; u_0)$). If $u_0 \in X^+$, then $u(t, x; u_0)$ exists for all $t \geq 0$ (see Proposition 2.1).

Note that assuming (H1), (1.1) has at most one positive stationary solution in $X^+_p$ (see Theorem C). If (1.1) has a positive stationary solution $u^+(\cdot) \in X^+_p$, let

$$u^+_\inf = \inf_{x \in \mathbb{R}^N} u^+(x). \quad (1.16)$$

For a given $\xi \in S^{N-1}$, let

$$X^+(\xi) = \{u \in X^+ | \sup_{x \in \mathbb{R}^N} u(x) < u^+_\inf \liminf_{r \to -\infty} \inf_{x \cdot \xi \leq r} u(x) > 0, \quad u(x) = 0 \quad \text{for} \quad x \in \mathbb{R}^N \text{ with } x \cdot \xi \gg 1\}. \quad (1.17)$$

Definition 1.2. Assume that (1.1) has a positive stationary solution $u^+(x)$ which is stable with respect to perturbations in $X_p$ and that $\xi \in S^{N-1}$. We call a number $c^+(\xi) \in \mathbb{R}$ the spreading speed of (1.1) in the direction of $\xi$ if the following properties are satisfied:

$$\liminf_{t \to -\infty} \inf_{x \cdot \xi \leq ct} (u(t, x; u_0) - u^+(x)) = 0 \quad \forall c < c^+(\xi)$$

and

$$\limsup_{t \to -\infty} \sup_{x \cdot \xi \geq ct} u(t, x; u_0) = 0 \quad \forall c > c^+(\xi)$$

for every $u_0 \in X^+(\xi)$.

Among those, the following theorem is proved in [41].

Theorem A. Assume (H1)-(H3). Assume also that $k(\cdot)$ is symmetric. Then
dispersal operators. In practice, the convolution kernel \( k \) stated above. As is seen in [41], in general, (H3) may not be satisfied, which does not occur for random dispersal operator for following cases: the nonlocal dispersal is nearly local; the periodic habitat is nearly globally homogeneous or it is nearly homogeneous in a region.

Principal eigenvalue theory provides an important tool to prove Theorem A stated above. As is seen in [41], in general, (H3) may not be satisfied, which does not occur for random dispersal operators. In practice, the convolution kernel \( k(\cdot) \) may be not symmetric either. It is important to see whether the spatial spreading feature is generic for monostable nonlocal KPP equations in the sense that assuming (H1) and (H2), (1.1) possesses a positive stable stationary solution \( u^+ \in X_p^+ \) and a spreading speed \( c^*(\xi) \) in every direction of \( \xi \in S^{N-1} \) no matter \( k(\cdot) \) is symmetric or not and no matter (H3) is satisfied or not. In this paper, we show the spatial spreading feature is generic for general nonlocal monostable equations in the above sense. More precisely, we prove

**Theorem C.** (Existence, uniqueness, and stability of positive stationary solutions)

1. Assume (H1). (1.1) has at most one positive stationary solution \( u^+ (\cdot) \in X_p^+ \). If there is a positive stationary solution \( u^+ (\cdot) \in X_p^+ \), it is globally asymptotically stable with respect to perturbations in \( X_p^+ \).
Theorem D. (Existence and variational principle of spreading speeds) Assume (H1) and (H2). Then the following hold:

(1) for any \( \xi \in S^{N-1} \), (1.1) has a spreading speed \( c^*(\xi) \) in the direction of \( \xi \) and

\[
c^*(\xi) = \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu};
\]

(2) \( c^*(\xi) \geq \bar{c}^*(\xi) \) for every \( \xi \in S^{N-1} \), where \( \bar{c}^*(\xi) = \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu} \).

Theorem E. (Spreading features of spreading speeds) Assume (H1) and (H2).

(1) If \( u_0 \in X^+ \) satisfies that \( \sup_{x \in \mathbb{R}^N} u_0(x) < u^+_\text{inf} \) and \( u_0(x) = 0 \) for \( x \in \mathbb{R}^N \) with \( |x| \gg 1 \), then for each \( c > \max\{c^*(\xi), c^*(-\xi)\} \), \( \limsup_{t \to \infty} \sup_{|x| \geq ct} u(t, x; u_0) = 0 \).

(2) Assume that \( \xi \in S^{N-1} \) and \( 0 < c < \min\{c^*(\xi), c^*(-\xi)\} \). Then for each \( \sigma > 0 \), there is \( r_\sigma > 0 \) such that \( \liminf_{t \to \infty} \inf_{|x| \leq ct} (u(t, x; u_0) - u^+(x)) = 0 \) for every \( u_0 \in X^+ \) satisfying \( u_0(x) \geq \sigma \) for all \( x \in \mathbb{R}^N \) with \( |x \cdot \xi| \leq r_\sigma \).

(3) If \( u_0 \in X^+ \) satisfies that \( \sup_{x \in \mathbb{R}^N} u_0(x) < u^-\text{inf} \) and \( u_0(x) = 0 \) for \( x \in \mathbb{R}^N \) with \( \|x\| \gg 1 \), then \( \limsup_{t \to \infty} \sup_{\|x\| \geq ct} u(t, x; u_0) = 0 \) for all \( c > \sup_{\xi \in S^{N-1}} c^*(\xi) \).

(4) Assume that \( 0 < c < \inf_{\xi \in S^{N-1}} \{c^*(\xi)\} \). Then for any \( \sigma > 0 \), there is \( r_\sigma > 0 \) such that for every \( u_0 \in X^+ \) satisfying \( u_0(x) \geq \sigma \) for \( x \in \mathbb{R}^N \) with \( \|x\| \leq r_\sigma \), \( \liminf_{t \to \infty} \inf_{\|x\| \leq ct} (u(t, x; u_0) - u^+(x)) = 0 \).

Theorems C-E generalize most of the results in [41] to general nonlocal monostable equations. As pointed out in [41], the theories established in [28], [29], [44], [45] for spatial spreading speeds of general monostable systems cannot be applied to (1.1) due to the lack of the compactness of the solution operators of (1.1) and (1.12). The main techniques to be used in proving Theorems C-E are the principal eigenvalue theory and spatial spreading speed theory established in [41]. It should be pointed out that similar statements to Theorem C(2) are proved in [10] for time independent nonlocal KPP equations. We learned the work [10] while the current paper is almost finished. For completeness, we provide a proof of Theorem C(2) in the paper, which is different from the proof in [10].

Observe that Theorem D(2) indicates that the spatial variation cannot slow down the spatial spreading and is proved in [19] when \( k(\cdot) \) is symmetric. We will study the existence of traveling wave solutions of (1.1) connecting \( u^+ \) and \( u^- \) in [42].

The rest of the paper is organized as follows. In section 2, we present some preliminary propositions to be used in later sections. We study the positive stationary solutions of (1.1) and prove Theorem C in section 3. In section 4, we investigate the spreading speeds of (1.1) and prove Theorems D and E.

2 Preliminary

In this section, we collect some basic properties of solutions of equation (1.1) and some related nonlocal linear evolution equations to be used in later sections.
Let $X_p$ and $X$ be as in (1.2) and (1.14), respectively. Consider equation (1.1) and the following nonlocal linear evolution equation,

$$\frac{\partial u}{\partial t} = \int_{\mathbb{R}^N} e^{-\mu(y-x)} \xi k(y-x)u(t,y)dy - u(t,x) + a(x)u(t,x), \quad x \in \mathbb{R}^N$$ (2.1)

where $\mu \in \mathbb{R}$, $\xi \in S^{N-1}$, and $a \in X_p$. Note that if $\mu = 0$ and $a(x) = a_0(x)(= f(x,0))$, (2.1) reduces to (1.12), i.e., the linearization of (1.1) at $u \equiv 0$.

It follows from the general linear semigroup theory (see [18] or [37]) that for every $u_0 \in X$, (2.1) has a unique solution $u(t,\cdot; u_0, \xi, \mu, a) = u_0(x)$. Put

$$\Phi(t; \xi, \mu, a)u_0 = u(t,\cdot; u_0, \xi, \mu, a).$$ (2.2)

Note that if $u_0 \in X_p$, then $\Phi(t; \xi, \mu, a)u_0 \in X_p$ for $t \geq 0$.

By general nonlinear semigroup theory (see [18] or [37]), (1.1) has a unique (local) solution $u(t,x; u_0)$ with $u(0,x; u_0) = u_0(x)$ for every $u_0 \in X$. Also if $u_0 \in X_p$, then $u(t,x; u_0) \in X_p$ for $t$ in the existence interval of the solution $u(t,x; u_0)$.

Throughout this section, we assume that $\xi \in S^{N-1}$ and $\mu \in \mathbb{R}$ are fixed, unless otherwise specified.

### 2.1 Comparison principle and monotonicity

Let $X_p^+$ and $X^+$ be as in (1.3) and (1.15), respectively. Let

$$\text{Int}(X_p^+) = \{v \in X_p \mid v(x) > 0, x \in \mathbb{R}^N\}.$$ (2.3)

For $v_1, v_2 \in X_p$, we define

$$v_1 \leq v_2 \quad (v_1 \geq v_2) \quad \text{if} \quad v_2 - v_1 \in X_p^+(v_1 - v_2 \in X_p^+),$$

and

$$v_1 \ll v_2 \quad (v_1 \gg v_2) \quad \text{if} \quad v_2 - v_1 \in \text{Int}(X_p^+(v_1 - v_2 \in \text{Int}(X_p^+)).$$

For $u_1, u_2 \in X$, we define

$$u_1 \leq u_2 \quad (u_1 \geq u_2) \quad \text{if} \quad u_2 - u_1 \in X^+(u_1 - u_2 \in X_+).$$

A continuous function $u(t,x)$ on $[0,T) \times \mathbb{R}^N$ is called a super-solution or sub-solution of (2.1) if $\frac{\partial u}{\partial t}$ exists and is continuous on $[0,T) \times \mathbb{R}^N$ and satisfies

$$\frac{\partial u}{\partial t} \geq \int_{\mathbb{R}^N} e^{-\mu(y-x)} \xi k(y-x)u(t,y)dy - u(t,x) + a(x)u(t,x), \quad x \in \mathbb{R}^N$$

or

$$\frac{\partial u}{\partial t} \leq \int_{\mathbb{R}^N} e^{-\mu(y-x)} \xi k(y-x)u(t,y)dy - u(t,x) + a(x)u(t,x), \quad x \in \mathbb{R}^N$$

for $t \in (0,T)$. Super-solutions and sub-solutions of (1.1) are defined in an analogous way.

**Proposition 2.1** (Comparison principle).

1. If $u_1(t,x)$ and $u_2(t,x)$ are sub-solution and super-solution of (2.1) on $[0,T)$, respectively, $u_1(0,\cdot) \leq u_2(0,\cdot)$, and $u_2(t,x) - u_1(t,x) \geq -\beta_0$ for $(t,x) \in [0,T) \times \mathbb{R}^N$ and some $\beta_0 > 0$, then $u_1(t,\cdot) \leq u_2(t,\cdot)$ for $t \in [0,T)$.

2. If $u_1(t,x)$ and $u_2(t,x)$ are bounded sub- and super-solutions of (1.1) on $[0,T)$, respectively, and $u_1(0,\cdot) \leq u_2(0,\cdot)$, then $u_1(t,\cdot) \leq u_2(t,\cdot)$ for $t \in [0,T)$.

3. For every $u_0 \in X^+$, $u(t,x; u_0)$ exists for all $t \geq 0$. 

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Remark 2.1. It follows from the arguments in [41, Proposition 2.2].

Proposition 2.2 (Strong monotonicity). Suppose that $u_1, u_2 \in X$ and $u_1 \leq u_2$, $u_1 \neq u_2$.

1. $\Phi(t; \xi, \mu, a)u_1 \leq \Phi(t; \xi, \mu, a)u_2$ for all $t > 0$.

2. $u(t, \cdot; u_1) \ll u(t, \cdot; u_2)$ for every $t > 0$ at which both $u(t, \cdot; u_1)$ and $u(t, \cdot; u_2)$ exist.

Proof. It follows from the arguments in [41, Proposition 2.2].

For every $u_0 \in X(\rho)$ ($\rho \geq 0$), (2.1) has a unique solution $u(t, \cdot; u_0, \xi, \mu) \in X(\rho)$ with $u(0, x; u_0, \xi, \mu) = u_0(x)$. Also for every $u_0 \in X(\rho)$ with $u_0(x) \geq 0$ for $x \in \mathbb{R}^N$, (1.1) has a unique solution $u(t, \cdot; u_0) = u_0(\cdot)$. Moreover, Proposition 2.1 holds for such solutions of (1.1) and (2.1).

2.2 Principal Eigenvalue

Throughout this subsection, $X$ is as in (1.2), $a \in X$, and $a_{\max} = \max_{x \in X} a(x)$, $a_{\min} = \min_{x \in X} a(x)$. $a(\cdot)I : X \to X$ has the same meaning as in (1.5) with $a_0(\cdot)$ being replaced by $a(\cdot)$ and $K_{\xi, \mu} : X \to X$ is understood as in (1.11), $\xi \in S^{N-1}$, and $\mu \in \mathbb{R}$.

For given $\alpha > -1 + a_{\max}$, let $U_{\xi, \mu, a, \alpha} : X \to X$, be defined as follows

$$(U_{\xi, \mu, a, \alpha} u)(x) = \int_{\mathbb{R}^N} \frac{e^{-\mu y \cdot x} k(y - x)u(y)}{\alpha + 1 - a(y)} \, dy.$$  

(2.5)

Observe that $U_{\xi, \mu, a, \alpha}$ is a compact and positive operator on $X$. Let $r(U_{\xi, \mu, a, \alpha})$ be the spectral radius of $U_{\xi, \mu, a, \alpha}$.

Proposition 2.3. (1) $\alpha > -1 + a_{\max}$ is an eigenvalue of $K_{\xi, \mu} - I + a(\cdot)I$ (1.10) iff 1 is an eigenvalue of the eigenvalue problem

$$U_{\xi, \mu, a, \alpha} v = \lambda v.$$  

(2) For $\alpha > -1 + a_{\max}$, 1 is an eigenvalue of $U_{\xi, \mu, a, \alpha}$ with a positive eigenfunction iff $r(U_{\xi, \mu, a, \alpha}) = 1$.

(3) $r(U_{\xi, \mu, a, \alpha})$ is strictly decreasing in $\alpha > -1 + a_{\max}$. If there is $\alpha > -1 + a_{\max}$ with $r(U_{\xi, \mu, a, \alpha}) > 1$, then there is $\alpha_0 > \alpha$ such that $r(U_{\xi, \mu, a, \alpha_0}) = 1$.

(4) If $\alpha > -1 + a_{\max}$ is an eigenvalue of $K_{\xi, \mu} - I + a(\cdot)I$ (1.10), then it is the principal eigenvalue of (1.10).

Proof. (1) and (2) follow from Proposition 2.1 of [6].

(3) and (4) follow from Lemma 3 and Theorem 2.2 of [6].

Proposition 2.4. (1) If $\lambda(\xi, \mu, a)$ is the principal eigenvalue of $K_{\xi, \mu} - I + a(\cdot)I$, then $\lambda(\xi, \mu, a) > -1 + a_{\max}$.

(2) If $a(x)$ is a constant function, then $\lambda(\xi, \mu, a)$ exists and

$$\lambda(\xi, \mu, a) = \int_{\mathbb{R}^N} e^{-\mu y \cdot \xi} k(y) \, dy - 1 + a.$$  

Moreover, there is $M_0 > 0$ such that $\lambda(\mu, \xi, a) \geq M_0 \mu^2$ for $\mu \gg 1$, $\xi \in S^{N-1}$.
Proof. (1) It follows from the arguments of [41, Proposition 3.2].

(2) Note that λ = \int_{\mathbb{R}^N} e^{-\mu y \cdot x} k(y) dy - 1 + a is an eigenvalue of \( K_{\xi,\mu} - I + a(\cdot) I \) with an eigenfunction \( \phi(x) \equiv 1 \). Then by Proposition 2.3, \( \lambda(\xi,\mu,a) \) exists and \( \lambda(\mu,\xi,a) = \int_{\mathbb{R}^N} e^{-\mu y \cdot x} k(y) dy - 1 + a \).

By the fact that \( k(x) > 0 \) for \( ||x|| < \delta \), there are \( \epsilon_0,\delta_0 > 0 \) such that
\[
k(x) \geq \epsilon_0 \quad \text{for} \quad ||x|| \leq \delta_0.
\]
This implies that
\[
\lambda(\xi,\mu,a) \geq \epsilon_0 \int_{||x|| \leq \delta_0} e^{-\mu x \cdot \xi} dx - 1 + a = \epsilon_0 \int_{||x|| \leq \delta_0} \left(1 + \frac{\mu^2(x \cdot \xi)^2}{2!} + \frac{\mu^4(x \cdot \xi)^4}{4!} + \cdots\right) dx - 1 + a 
\geq M_0 \mu^2
\]
for \( \mu \gg 1 \) and \( \xi \in S^{N-1} \), where \( M_0 = \inf_{\xi \in S^{N-1}} \epsilon_0 \int_{||x|| \leq \delta_0} \frac{(x \cdot \xi)^2 dx}{2} \).

**Proposition 2.5.** If \( a \) satisfies (H4), then the principal eigenvalue \( \lambda(\xi,\mu,a) \) of (1.10) exists for all \( \xi \in S^{N-1} \) and \( \mu \in \mathbb{R} \).

**Proof.** It follows from the arguments of [41, Theorem B].

Let \( D = [0, p_1] \times [0, p_2] \times \cdots \times [0, p_N] \) and for given \( a \in X_p \), let
\[
\bar{a} = \frac{1}{p_1 p_2 \cdots p_N} \int_D a(x) dx.
\]

**Proposition 2.6.** If \( a \in X_p \) satisfies (H3), then \( \lambda(\xi,\mu,a) \geq \lambda(\xi,\mu,\bar{a}) \).

**Proof.** It follows from the arguments of [19, Theorem 2.1].

**Proposition 2.7.** Given \( a \in X_p \), \( \lambda_0(\xi,\mu,a) = \ln r(\Phi(1;\xi,\mu,a)) \) for all \( \xi \in S^{N-1} \) and \( \mu \in \mathbb{R} \).

**Proof.** It follows from the spectral theorem for bounded linear operators (see [37]).

### 3 Positive Stationary Solutions

In this section, we investigate the existence, uniqueness, and stability of positive equilibrium of (1.1) and prove Theorem C.

Suppose that \( u = u^* \) is an equilibrium solution of (1.1) in \( X^+_\mu \setminus \{0\} \). \( u = u^* \) is said to be *globally asymptotically stable in \( X^+_\mu \setminus \{0\} \) if for any \( u_0 \in X^+_\mu \setminus \{0\} \), \( u(t.;u_0) \to u^* \) in \( X_p \) as \( t \to \infty \).

As mentioned in the introduction, Theorem C(2) follows from the results and arguments in [10]. For completeness, we provide a proof. We first prove two lemmas, which will also be used to prove Theorem D in next section.

**Lemma 3.1.** Suppose that \( \{a_n\}, \{a^n\} \subset X_p \) satisfy that
\[
a_n(\cdot) \leq a(\cdot) \leq a^n(\cdot) \quad \text{for} \quad n \geq 1 \quad \text{and} \quad ||a_n - a^n||_{X_p} \to 0 \quad \text{as} \quad n \to \infty.
\]
Then for any \( \xi \in S^{N-1} \) and \( \mu \in \mathbb{R} \),
\[
\lambda_0(\xi,\mu,a_n) \leq \lambda_0(\xi,\mu,a) \leq \lambda_0(\xi,\mu,a^n) \quad \text{for} \quad n \geq 1 \tag{3.1}
\]
and
\[
\lambda_0(\xi,\mu,a_n) - \lambda_0(\xi,\mu,a^n) \to 0 \quad \text{as} \quad n \to \infty. \tag{3.2}
\]
Proof. By Propositions 2.1 and 2.2,

\[ r(\Phi(1; \xi, \mu, a_n)) \leq r(\Phi(1; \xi, \mu, a)) \leq r(\Phi(1; \xi, \mu, a^n)) \quad \forall n \geq 1, \xi \in S^{N-1}, \mu \in \mathbb{R}. \]

This together with Proposition 2.7 implies (3.1). By (3.1), for any \( \xi \in S^{N-1}, \mu \in \mathbb{R}, \) and \( \epsilon > 0, \)

\[ \lambda_0(\xi, \mu, a - \epsilon) \leq \lambda_0(\xi, \mu, a_n) \leq \lambda_0(\xi, \mu, a) \leq \lambda_0(\xi, \mu, a^n) \leq \lambda_0(\xi, \mu, a + \epsilon) \quad \forall n \gg 1. \]  

This together with \( \lambda_0(\xi, \mu, a \pm \epsilon) = \lambda_0(\xi, \mu, a) \pm \epsilon \) implies (3.2). \( \square \)

Lemma 3.2. Given \( a \in X_p, \lambda_0(\xi, \mu, a) \geq \lambda_0(\xi, \mu, \bar{a}) \) for any \( \xi \in S^{N-1} \) and \( \mu \in \mathbb{R}. \)

Proof. Take \( a_n \in C^N(\mathbb{R}^N) \cap X_p \) such that \( a_n \) satisfies (H4) and

\[ a_n(\cdot) \leq a(\cdot) \quad \text{for} \quad n \geq 1 \quad \text{and} \quad \|a_n - a\|_{X_p} \to 0 \quad \text{as} \quad n \to \infty. \]

By Proposition 2.5, \( \lambda(\xi, \mu, a_n) \) exists and \( \lambda(\xi, \mu, a_n) = \lambda_0(\xi, \mu, a_n) \) for \( n \geq 1. \) By Proposition 2.6, \( \lambda_0(\xi, \mu, a_n) \geq \lambda_0(\xi, \mu, \bar{a}_n) \) for \( n \geq 1. \) The lemma follows by letting \( n \to \infty \) and applying Lemma 3.1. \( \square \)

Proof of Theorem C. (1) It follows from the arguments in [26, Lemma 3.3].

(2) Let \( a_0(x) = f(x, 0) \) and \( 0 < \delta_0 < \epsilon_0 \) be such that

\[ \lambda_0 - 2\epsilon_0 > 0 \quad \text{and} \quad f(x, u) \geq a(x, 0) - \epsilon_0 \quad \text{for} \quad 0 < u < \delta_0. \]

Take \( a_n \in C^N(\mathbb{R}^N) \cap X_p \) such that \( a_n \) satisfies (H4) and

\[ a_n(\cdot) \leq a_0(\cdot) \quad \text{for} \quad n \geq 1 \quad \text{and} \quad \|a_n - a_0\|_{X_p} \to 0 \quad \text{as} \quad n \to \infty. \]

Then by Lemma 3.1,

\[ \lambda_0(a_n) \leq \lambda_0(a_0) \quad \forall n \geq 1 \quad \text{and} \quad \lambda_0(a_n) - \lambda_0(a_0) \to 0 \quad \text{as} \quad n \to \infty. \]

This implies that

\[ \lambda_0(a_n) - 2\epsilon_0 > 0 \quad \text{for} \quad n \gg 1. \]

Note that

\[ a_n(x) - \epsilon_0 - u \geq a_n(x) - 2\epsilon_0 \quad \text{for} \quad 0 < u < \delta_0 \]

Hence

\[ uf(x, u) \geq u(a_n(x) - 2\epsilon_0) \quad \text{for} \quad 0 < u < \delta_0. \]

Let \( \phi_n(x) \in X^+_p \) be the eigenfunction of \( K - I + a_n(\cdot)I \) associated to \( \lambda_0(a_n) \) with \( \|\phi_n\|_{X_p} = 1. \) Let \( b_0 > 0 \)

\[ b_0e^{\lambda_0(a_n) - 2\epsilon_0} < \delta_0 \quad \text{and} \quad u_0 = b_0\phi_n. \]

By Proposition 2.1,

\[ u(t, \cdot; u_0) \geq b_0e^{(\lambda_0(a_n) - 2\epsilon_0)t}\phi_n(\cdot) > u_0(\cdot) \quad \text{for} \quad 0 < t < 1. \]

It then follows that \( u(t, \cdot; u_0) \) is monotonically increasing as \( t \) increasing. Let \( u^+(x) = \lim_{t \to \infty} u(t, x; u_0). \)

By the arguments in [26, Theorem 3.2], \( u^+ \in X^+_p \setminus \{0\} \) and \( u = u^+ \) is a globally asymptotically stable stationary solutions with respect to the perturbations in \( X^+_p. \)

(3) Let \( a_n \) be as in (2). Then by (2) and Proposition 2.6,

\[ \lambda_0(a_0) \geq \lambda_0(a_n) \geq \lambda_0(\bar{a}_n) = \bar{a}_n. \]

Letting \( n \to \infty, \) we have \( \lambda_0(a_0) \geq \lambda_0(\bar{a}_0) = \bar{a}_o. \) Therefore, if \( \bar{a}_o > 0, \) then (H2) is satisfied and the conclusions in (2) hold if (H1) is also satisfied. \( \square \)
4 Spreading Speeds

In this section, we investigate the existence and characterization of the spreading speeds of (1.1) and prove Theorems D and E.

We first recall the notion of spreading speed intervals introduced in [41] and prove some lemmas.

**Definition 4.1.** For a given vector \( \xi \in S^{N-1} \), let

\[
C_{\inf}^*(\xi) = \left\{ c \mid \forall u_0 \in X^+(\xi), \liminf_{t \to \infty} \inf_{x : x \leq ct} (u(t,x) - u^+(x)) = 0 \right\}
\]

and

\[
C_{\sup}^*(\xi) = \left\{ c \mid \forall u_0 \in X^+(\xi), \limsup_{t \to \infty} \sup_{x : x \geq ct} u(t,x) = 0 \right\}.
\]

Define

\[
c_{\inf}^*(\xi) = \sup \{ c \mid c \in C_{\inf}^*(\xi) \}, \quad c_{\sup}^*(\xi) = \inf \{ c \mid c \in C_{\sup}^*(\xi) \}.
\]

We call \([c_{\inf}^*(\xi), c_{\sup}^*(\xi)]\) the spreading speed interval of (1.1) in the direction of \( \xi \).

Observe that \( c^*(\xi) \) exists if and only if \( c_{\inf}^*(\xi) = c_{\sup}^*(\xi) \).

**Lemma 4.1.** Assume (H1) and (H2). For every \( \xi \in S^{N-1} \), there is \( \mu^*(\xi) \in (0, \infty) \) such that

\[
\frac{\lambda_0(\xi, \mu^*(\xi), a_0)}{\mu^*(\xi)} = \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu}.
\]

**Proof.** First, it is not difficult to see that \( \lambda_0(\xi, \mu, a_0) \) is continuous in \( \mu \). By (H2), \( \lambda_0(\xi, 0, a_0) > 0 \) and hence \( \lim_{\mu \to 0^+} \frac{\lambda_0(\xi, \mu, a_0)}{\mu} = \infty \). By Propositions 2.4 and 2.6, \( \lim_{\mu \to \infty} \frac{\lambda_0(\xi, \mu, a_0)}{\mu} = \infty \). The lemma then follows. \( \square \)

Consider the space shifted equations of (1.1),

\[
\frac{\partial u}{\partial t} = \int_{\mathbb{R}^N} k(y-x)u(t,y)dy - u(t,x)f(x+z, u(t,x)), \quad x \in \mathbb{R}^N,
\]

where \( z \in \mathbb{R}^N \). Let \( u(t,x; u_0, z) \) be the solution of (4.1) with \( u(0, x; u_0, z) = u_0(x) \) for \( u_0 \in X \).

**Lemma 4.2.** Let \( \xi \in S^{N-1} \), \( u_0 \in X^+ \) with \( \liminf_{x : x \in \mathbb{R}^N} u_0(x) > 0 \) and \( \limsup_{x : x \in \mathbb{R}^N} u_0(x) = 0 \), and \( c \in \mathbb{R} \) be given. If there are \( \delta_0 \) and \( T_0 > 0 \) such that

\[
\liminf_{x : x \leq \delta_0, n \to \infty} u(nT_0, x; u_0, z) \geq \delta_0 \text{ uniformly in } z \in \mathbb{R}^N,
\]

then for every \( c' < c \),

\[
\liminf_{x : x \leq c't, n \to \infty} (u(t,x; u_0, z) - u^+(x + z)) = 0 \text{ uniformly in } z \in \mathbb{R}^N.
\]

**Proof.** It follows from the arguments of [41, Proposition 4.4]. \( \square \)

**Proof of Theorem D.** (1) First, we prove that \( c_{\sup}^*(\xi) \leq \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu} \).

Let \( a^n(\cdot) \in C^\infty(\mathbb{R}^N) \cap X_p \) be such that \( a^n \) satisfies (H4),

\[
a^n \geq a_0 \text{ for } n \geq 1 \text{ and } \|a^n - a\|_{X_p} \to 0 \text{ as } n \to \infty.
\]

Then by Lemma 3.1,

\[
\lambda_0(\xi, \mu, a^n) \to \lambda_0(\xi, \mu, a_0) \text{ as } n \to \infty.
\]
Let $\phi^n$ be the eigenfunction of $K_{\xi,\mu} - I + a^n(\cdot)I$ corresponding to $\lambda(\xi, \mu, a^n) = \lambda_0(\xi, \mu, a^n)$. Note that
\[ uf(x, u) \leq uf(x, 0) \leq a^n(x)u \quad \text{for} \quad x \in \mathbb{R}^N, \ u \geq 0 \]
and
\[ (\Phi(t, \xi, 0, a^n)u_{\xi,\mu})(x) = e^{-\mu(x-\frac{\lambda_0(\xi, \mu, a^n)}{\mu})} \phi^n(x), \]
where $u_{\xi,\mu}(x) = e^{-\mu x} \phi^n(x)$. Hence by Proposition 2.1 and Remark 2.1, for any $\mu > 0$,
\[ u(t, x; u_{\xi,\mu}) \leq e^{-\mu(x-\frac{\lambda_0(\xi, \mu, a^n)}{\mu})} \phi^n(x) \quad \text{for} \quad t \geq 0. \]
This implies that
\[ c^*_n(\xi) \leq \frac{\lambda_0(\xi, \mu, a^n)}{\mu} \quad \forall \mu > 0, \ n \geq 1 \]
and then
\[ c^*_n(\xi) \leq \frac{\lambda_0(\xi, \mu, a_0)}{\mu} \quad \forall \mu > 0. \]
Therefore,
\[ c^*_n(\xi) \leq \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu} \quad \text{(4.3)} \]
Next, we prove $c^*_n(\xi) \leq \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu}$. For any $\epsilon > 0$, there is $\delta_0 > 0$ such that such that
\[ f(x, u) \geq f(x, 0) - \epsilon \quad \text{for} \quad x \in \mathbb{R}^N, \ 0 < u < \delta_0. \]
Let $a_n(\cdot) \in C^N(\mathbb{R}^N) \cap X_p$ be such that $a_n$ satisfies (H4),
\[ f(\cdot, 0) - 2\epsilon \leq a_n(\cdot) \leq f(\cdot, 0) - \epsilon \quad \forall n \geq 1. \]
Let
\[ c^*_n(\xi) = \inf_{\mu > 0} \frac{\lambda(\xi, \mu, a_n)}{\mu}. \]
Applying the arguments in [41, Theorem C], there is $u_0(\cdot; z) \in X^+(\xi)$ such that
\[ \lim_{\xi \to -\infty} \inf_{z \in \mathbb{R}^N} u_0(x; z) > 0 \]
and
\[ u(1, x; u_0(\cdot; z), z) \geq u_0(x - (c^*_n(\xi) - \epsilon)\xi; (c^*_n(\xi) - \epsilon)\xi + z) \quad \forall z \in \mathbb{R}^N. \]
This implies that
\[ u(m, x; u_0(\cdot; z), z) \geq u_0(x - m(c^*_n(\xi) - \epsilon)\xi; m(c^*_n(\xi) - \epsilon)\xi + z) \quad \forall m \geq 1, \ z \in \mathbb{R}^N. \]
Then by Lemma 4.2,
\[ c^*_n(\xi) \geq c^*_n(\xi) - \epsilon. \]
By Lemma 3.1,
\[ c^*_n(\xi) \geq \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0) - 2\epsilon}{\mu} - \epsilon. \]
Letting $\epsilon \to 0$, by Lemma 4.1, we have
\[ c^*_n(\xi) \geq \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu}. \quad \text{(4.4)} \]
By (4.3) and (4.4),
\[ c_{\sup}^*(\xi) = c_{\inf}^*(\xi) = \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu}. \]
Hence \( c^*(\xi) \) exists and
\[ c^*(\xi) = \inf_{\mu > 0} \frac{\lambda_0(\xi, \mu, a_0)}{\mu}. \]

(2) It follows from (1) and Proposition 2.6. \( \square \)

**Proof of Theorem E.** If follows from the arguments of [41, Theorems D and E]. \( \square \)

**References**


