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PAPER

Propagation dynamics of a mutualistic model of mistletoes and birds with nonlocal dispersal

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Abstract

This paper is devoted to the study of the propagation dynamics of a mutualistic model of mistletoes and birds with nonlocal dispersal. By applying the theory of asymptotic speeds of spread and travelling waves for monotone semiflows, we establish the existence of the asymptotic spreading speed c^*, the existence of travelling wavefronts with the wave speed $c \geq c^*$ and the nonexistence of travelling wavefronts with $c < c^*$. It turns out that the spreading speed coincides with the minimal wave speed of travelling wavefronts. Moreover, some lower and upper bound estimates of the spreading speed c^* are provided.

1. Introduction

In ecology, mutual benefit between different populations is a common phenomenon. A special case is the relationship between mistletoes and birds. Mistletoes are typical aerial stem-parasites plants. Birds eat the fruit of mistletoes to obtain nutrients, energy and water. In turn, mistletoes receive directed movement of their propagules into safe germination sites [3]. To better understand the interaction between mistletoes and birds, Wang et al. [26] proposed a reaction-diffusion model

$$\begin{cases} u_t(t,x) = -d_m u + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(x-y)\frac{u(t-\tau,y)}{u(t-\tau,y)+\omega} v(t-\tau,y)dy,\ t\geq 0,\ x\in\bar{\Omega}, \\ v_t(t,x) = D\Delta v + v(1-v) - \gamma\nabla(v\nabla u) \\ \qquad\qquad +d\displaystyle\int_{\mathbb{R}} k(x-y)\frac{u(t,y)}{u(t,y)+\omega} v(t,y)dy,\ t\geq 0,\ x\in\bar{\Omega}, \\ (D\nabla v - \gamma v\nabla u)\cdot n(x) = 0,\ t\geq 0,\ x\in\partial\Omega, \\ u(s,x) = u_0(s,x),\ v(s,x) = v_0(s,x),\ s\in[-\tau,0],\ x\in\Omega, \end{cases} \tag{1.1}$$

where the parameters α, d_i, d_m, D, d, ω are positive constants, and the time delay τ is non-negative. In this model, $u(t,x)$ and $v(t,x)$ are the densities of mature mistletoes and birds at location $x\in\Omega$ and time t, respectively, α is the hanging rate of mistletoe fruits to trees, d_i and d_m are the mortality rates of immature and mature mistletoes, respectively, τ is the maturation time of mistletoes, D is the diffusion rate of birds, d is the conversion rate from mistletoe fruits into bird population. The term $v(1-v)$ models the logistic growth for bird population which measures the bird population growth due to other food resources besides mistletoes in the habitat, $\gamma\nabla(v\nabla u)$ is a chemotactic term that models the effect that birds are attracted by trees with more mistletoes, γ is the chemotactic coefficient, and ω is used to reflect the fact that birds may perch on other trees without mistletoes and structures irrelevant to the dynamic process of mistletoes. In [26], the authors studied the spatial pattern formation under two different types

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of kernel functions k. When $\Omega = \mathbb{R}$ and $\gamma = 0$, Wang et al. [27] further investigated the existence of an asymptotic spreading speed and travelling wave solutions.

Note that in (1.1), the Fickian diffusion $D\Delta v$ is used to model the random movement of birds. It essentially is a local behaviour and hence maybe not accurate enough to describe the long-range effects of the dispersal of birds. In order to describe the dispersal of birds reasonably, Liang, Weng and Tian [19] introduced a nonlocal operator

$$(\mathcal{D}w)(t,x) = (J*w)(t,x) - w(t,x) = \int_{\mathbb{R}} J(x-y)[w(t,y) - w(t,x)]dy$$

in (1.2) and presented the following nonlocal dispersal model of mistletoes and birds:

$$\begin{cases} u_t(t,x) = -d_m u + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(x-y) \frac{u(t-\tau,y)}{u(t-\tau,y)+\omega} v(t-\tau,y)dy, \\ v_t(t,x) = D(J*v - v) + v(1-v) + d \displaystyle\int_{\mathbb{R}} k(x-y) \frac{u(t,y)}{u(t,y)+\omega} v(t,y)dy, \end{cases} \tag{1.2}$$

where $x \in \mathbb{R}$ and $t \geq 0$. In this system, $J*v - v$ models nonlocal dispersal processes of birds; $\alpha e^{-d_i\tau} \int_{\mathbb{R}} k(x-y) \frac{u(t-\tau,y)}{u(t-\tau,y)+\omega} v(t-\tau,y)dy$ is mature mistletoes recruitment, where the integral with a kernel function $k(x-y)$ expresses the spread of mistletoes fruits by birds from location y to location x and at time $t-\tau$, the Holling type II functional response $\frac{u}{u+\omega}$ is used to model the fruits removal by birds, and $e^{-d_i\tau}$ represents the probability of the mistletoe from immature survival to maturity; the term $d \int_{\mathbb{R}} k(x-y) \frac{u(t,y)}{u(t,y)+\omega} v(t,y)dy$ represents the growth of birds caused by eating mistletoe fruits; the other terms and parameters have the same meaning as that in (1.1). We should point out that the background and applications of nonlocal dispersal $J*v - v$ are described in Bates et al. [4], Fife [11], Hutson et al. [13], Lee et al. [15], Murray [23] and Medlock and Kot [22]. In the past 20 years, nonlocal dispersal equations have been extensively studied. We refer readers to [4, 5, 7, 24, 32, 34] for travelling wave solutions, [6, 14] for asymptotic behaviours of solutions for initial boundary value problems, [8, 12, 18, 33] for spreading speeds and [17, 30] for entire solutions. The following hypotheses are imposed in [19]:

(H1) Both kernels $J(x)$ and $k(x)$ are non-negative, symmetric and normalised, i.e.

$$J(x) \geq 0, \quad J(x) = J(-x) \geq 0, \quad \int_{\mathbb{R}} J(x)dx = 1,$$

$$k(x) \geq 0, \quad k(x) = k(-x) \geq 0, \quad \int_{\mathbb{R}} k(x)dx = 1,$$

and satisfy

$$\int_{\mathbb{R}} J(x)e^{-\nu|x|}dx < +\infty \text{ and } \int_{\mathbb{R}} k(x)e^{-\nu|x|}dx < +\infty \text{ for every } \nu > 0;$$

(H2) $d_m < \tilde{d}_m := \frac{\alpha e^{-d_i\tau}}{\omega}$.

It is easy to see that system (1.2) always has a trivial equilibrium $E_0 = (0,0)$ and a boundary equilibrium $E_1 = (0,1)$. If (H2) holds, then there exists a unique positive equilibrium $E_+ := (u_+, v_+)$ with

$$\begin{cases} u_+ := \dfrac{1+d+\sqrt{(1+d)^2 - 4d\omega\sigma}}{2\sigma} - \omega > 0, \\ v_+ := 1 + \dfrac{du_+}{u_+ + \omega} \in (1, 1+d), \end{cases}$$

where $\sigma = \dfrac{d_m}{\alpha e^{-d_i\tau}}$. It was proved in [19] that E_0 and E_1 are linearly unstable with respect to the corresponding kinetic system, while E_+ is locally asymptotically stable.

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It is well known that without birds, the adult mistletoes can only spread in a small area. However, with the nonlocal movements of birds, the mistletoes can invade into new large territories. As such, it is a very interesting problem to model the spatial invasion process of the mistletoes. One way to mathematically characterise this dynamics of the process is travelling wave solution. Travelling wave solutions (in short, travelling waves) of (1.1) are bounded functions with the special form $(u(t, x), v(t, x)) = (\phi(\xi), \psi(\xi))$, $\xi = x + ct$, which connect two equilibria E_1 and E_+, where $c > 0$ is the wave speed. Clearly, each wave profile (ϕ, ψ) to (1.2) satisfies

$$\begin{cases} c\phi'(\xi) = -d_m\phi + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(y) \frac{\phi(\xi - y - c\tau)}{\phi(\xi - y - c\tau) + \omega} \psi(\xi - y - c\tau)dy, \\ c\psi'(\xi) = D(J * \psi - \psi) + \psi(1 - \psi) + d \displaystyle\int_{\mathbb{R}} k(y) \frac{\phi(\xi - y)}{\phi(\xi - y) + \omega} \psi(\xi - y)dy, \\ (\phi, \psi)(-\infty) = E_1, \quad (\phi, \psi)(+\infty) = E_+, \end{cases} \tag{1.3}$$

where $(\phi, \psi)(\pm\infty) = \lim_{\xi\to\pm\infty} (\phi, \psi)(\xi)$. In [19], Liang, Weng and Tian have proved the existence of travelling wave solutions by Schauder's fixed point theorem and upper-lower solutions technique, i.e. there exists c^* such that for every $c \geq c^*$, (1.2) admits a travelling wavefront connecting E_1 and E_+. We should remark that the nonexistence of travelling wavefronts $c < c^*$ is not addressed in [19].

Another way to characterise the spatial invasion process of the mistletoes into new territories is the spatial invasion speeds (or called asymptotic speeds of spread). The asymptotic speed of spread (in short, spreading speed) was first introduced by Aronson and Weinberger [1] for reaction-diffusion equations and has been an important ecological metric in a wide range of ecological applications, see e.g. [2, 20, 21] and references therein. Since then, there have been extensive investigations on the spreading speed for various evolution systems, see e.g. [2, 9, 10, 16, 20, 21, 28, 31] and references therein. In this paper, we are devoted to investigating the spreading speeds and travelling wavefronts of (1.2). Since system (1.2) is cooperative and its solution maps are monotone, we shall use the theory in [20] to study the existence of spreading speeds for (1.2). Note that the theory of spreading speeds was developed in [20] for monotonic systems under a very general setting. The verification of some abstract assumptions in [20] is highly nontrivial for the solution maps of (1.2) due to the emergence of nonlocal dispersal and time delay along with nonlocal interaction. In addition, we provide the upper and lower bounds of the established spreading speed.

Finally, we investigate the travelling wavefronts of (1.2). With the help of the spreading features, we derive the nonexistence of travelling wavefronts with speed $c \in (0, c^*)$. As mentioned earlier, the existence of travelling wavefronts of (1.2) with speed $c \geq c^*$ has been obtained by Liang, Weng and Tian [19] by using Schauder's fixed point theorem together with the upper-lower solutions. However, in order to construct a pair of upper-lower solutions successfully, they needed an additional condition (A) and $\omega \geq 1$. In this paper, we shall remove these assumptions and prove the existence of travelling wavefronts of (1.2) with speed $c \geq c^*$. We appeal to the monotone semiflow method which is different from that in [19]. Note that the first equation of system (1.2) has no diffusion term and the diffusion term in the second equation is nonlocal dispersal $J * v - v$. Thus, the solution maps associated with (1.2) are not compact with respect to the compact open topology. Therefore, the theory in [20] is no longer applicable to prove the existence of travelling wavefronts. Fortunately, the monotone semiflow generated by (1.2) has some weak compactness, and hence, we can use the abstract results in [8] to obtain the existence of travelling wavefronts with speed $c \geq c^*$. Our result shows that the asymptotic speed of spread coincides with the minimal wave speed c^*.

This paper is organised as follows. In Section 2, we establish the well-posedness and the comparison principle for the initial value problem. In Section 3, we show the existence of the spreading speed of (1.2) and provide some lower and upper bound estimates of the spreading speed. In Section 4, the existence and nonexistence of travelling wavefronts are investigated.

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2. Initial value problem

In this section, we shall investigate the existence and uniqueness theorem of solution to the initial value problem and the comparison theorem. By a change of variables $U = u$ and $V = v - 1$ in (1.2), we obtain

$$\begin{cases} U_t(t,x) = -d_m U + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(x-y)\frac{U(t-\tau,y)}{U(t-\tau,y)+\omega}(V(t-\tau,y)+1)dy, \\ V_t(t,x) = D(J*V-V) - V(V+1) + d\displaystyle\int_{\mathbb{R}} k(x-y)\frac{U(t,y)}{U(t,y)+\omega}(V(t,y)+1)dy. \end{cases} \tag{2.1}$$

The spatially homogeneous system associated with (2.1) is

$$\begin{cases} U' = \dfrac{\alpha e^{-d_i\tau}U(t-\tau)(V(t-\tau)+1)}{U(t-\tau)+\omega} - d_m U, \\ V' = -V(1+V) + \dfrac{dU(V+1)}{U+\omega}. \end{cases} \tag{2.2}$$

It is easy to see that the equilibria of (1.2), respectively, become

$$\mathbf{E} := (0,-1), \ \ \mathbf{0} := (0,0), \ \ \mathbf{K} := (u_+, v_+ - 1).$$

For the convenience, in what follows, we let $\tilde{u}_+ = u_+$ and $\tilde{v}_+ = v_+ - 1$. Now we consider the corresponding initial value problem of (2.1):

$$\begin{cases} U_t(t,x) = -d_m U + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(x-y)\frac{U(t-\tau,y)}{U(t-\tau,y)+\omega}(V(t-\tau,y)+1)dy, \\ V_t(t,x) = D(J*V-V) - V(V+1) + d\displaystyle\int_{\mathbb{R}} k(x-y)\frac{U(t,y)}{U(t,y)+\omega}(V(t,y)+1)dy, \\ U(s,x) = \phi_1(s,x), \quad V(s,x) = \phi_2(s,x), \quad (s,x) \in [-\tau,0]\times\mathbb{R}. \end{cases} \tag{2.3}$$

We begin with some notation. The proper phase space for (2.3) can be chosen as $\mathcal{C} := C([-\tau,0]\times\mathbb{R},\mathbb{R}^2)$. Clearly, any vector in $\mathbb{R}^2$ (which is constant in (t,x)), or any element in $\bar{\mathcal{C}} := C([-\tau,0],\mathbb{R}^2)$ (which is constant in x), can be regarded as an element in $\mathcal{C}$. A natural order "$\geq$" in $\mathcal{C}$ is defined by $u \geq v$ for $u = (u_1,u_2)$ and $v = (v_1,v_2) \in \mathcal{C}$, if $u_i(s,x) \geq v_i(s,x)$ for $i = 1,2$, $s \in [-\tau,0]$ and $x \in \mathbb{R}$; $u > v$ if $u \geq v$ and $u \neq v$; and $u \gg v$ if $u_i(s,x) > v_i(s,x)$. For any $\mathbf{r} \in \mathbb{R}^2$ and $\mathbf{r} \geq 0$, defined $\mathcal{C}_{\mathbf{r}} := \{\phi \in \mathcal{C} : \mathbf{0} \leq \phi \leq \mathbf{r}\}$ and $\bar{\mathcal{C}}_{\mathbf{r}} := \{\phi \in \bar{\mathcal{C}} : \mathbf{0} \leq \phi \leq \mathbf{r}\}$. Moreover, let $X := BC(\mathbb{R},\mathbb{R}^2)$ be the set of all bounded continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$, and $X_{\mathbf{r}} := \{\phi \in X : \mathbf{0} \leq \phi \leq \mathbf{r}\}$.

We first study the existence and uniqueness of solution to the initial value problem (2.3).

Lemma 2.1. *For any initial value* $\phi := (\phi_1,\phi_2) \in \mathcal{C}_{\mathbf{K}}$, (2.3) *admits a unique solution* $(U(t,x;\phi), V(t,x;\phi))$ *satisfying*

$$\mathbf{0} \leq (U(t,x;\phi), V(t,x;\phi)) \leq \mathbf{K}, \ \forall\, t \geq 0, \ x \in \mathbb{R}.$$

Proof. Let $\beta > 0$. Then, system (2.3) can be rewritten as

$$\begin{cases} U_t = -(\beta + d_m)U + \mathcal{F}_1[U,V](t,x), \ \ t > 0, \ x \in \mathbb{R}, \\ V_t = -(\beta+1)V + \mathcal{F}_2[U,V](t,x), \quad t > 0, \ x \in \mathbb{R}, \\ U(s,x) := \phi_1(s,x), \quad -\tau \leq s \leq 0, \ x \in \mathbb{R}, \\ V(s,x) := \phi_2(s,x), \quad -\tau \leq s \leq 0, \ x \in \mathbb{R}, \end{cases} \tag{2.4}$$

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where $(\mathcal{F}_1, \mathcal{F}_2)$ is defined on $C([-\tau, \infty] \times \mathbb{R}, I)$, with $I = [0, \tilde{u}_+] \times [0, \tilde{v}_+]$, by

$$\begin{cases} \mathcal{F}_1[U, V](t, x) := \beta U + \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(y) \frac{U(t-\tau, x-y)}{U(t-\tau, x-y) + \omega}(V(t-\tau, x-y) + 1)dy, \\ \mathcal{F}_2[U, V](t, x) := \beta V - V^2 + d \displaystyle\int_{\mathbb{R}} k(y) \frac{U(t, x-y)}{U(t, x-y) + \omega}(V(t, x-y) + 1)dy \\ \qquad\qquad + D \displaystyle\int_{\mathbb{R}} J(y)[V(t, x-y) - V(t, x)]dy \end{cases}$$

for $t \in (0, \infty)$. It is easy to verify that if we choose β large enough, then $\mathcal{F}_i$ is nondecreasing in U and V, $i = 1, 2$. Obviously, system (2.4) is equivalent to the following integral system

$$\begin{cases} U(t, x) = e^{-(\beta+d_m)t}\phi_1(0, x) + \displaystyle\int_0^t e^{-(\beta+d_m)(t-r)}\mathcal{F}_1[U, V](r, x)dr, \\ V(t, x) = e^{-(\beta+1)t}\phi_2(0, x) + \displaystyle\int_0^t e^{-(\beta+1)(t-r)}\mathcal{F}_2[U, V](r, x)dr, \end{cases} \tag{2.5}$$

for $t > 0$ and $x \in \mathbb{R}$.

Define the set

$$\Gamma := \big\{(U, V) \in C([-\tau, \infty] \times \mathbb{R}, I) : U(s, x) = \phi_1(s, x), \\ V(s, x) = \phi_2(s, x), s \in [-\tau, 0],\ x \in \mathbb{R}\big\},$$

and an operator $\mathcal{G} = (\mathcal{G}_1, \mathcal{G}_2) : \Gamma \to \Gamma$ by

$$\begin{cases} \mathcal{G}_1[U, V](t, x) := e^{-(\beta+d_m)t}\phi_1(0, x) + \displaystyle\int_0^t e^{-(\beta+d_m)(t-r)}\mathcal{F}_1[U, V](r, x)dr, \\ \mathcal{G}_2[U, V](t, x) := e^{-(\beta+1)t}\phi_2(0, x) + \displaystyle\int_0^t e^{-(\beta+1)(t-r)}\mathcal{F}_2[U, V](r, x)dr, \end{cases}$$

where $(t, x) \in \mathbb{R}_+ \times \mathbb{R}$. For any $(U, V) \in \Gamma$, by the monotonicity of $\mathcal{F}_i$, we have

$$\begin{aligned} 0 \le \mathcal{G}_1[U, V](t, x) &\le e^{-(\beta+d_m)t}\tilde{u}_+ + \mathcal{F}_1[\tilde{u}_+, \tilde{v}_+] \int_0^t e^{-(\beta+d_m)(t-r)}dr \\ &\le e^{-(\beta+d_m)t}\tilde{u}_+ + \tilde{u}_+(1 - e^{-(\beta+d_m)t}) = \tilde{u}_+ \end{aligned}$$

and

$$\begin{aligned} 0 \le \mathcal{G}_2[U, V](t, x) &\le e^{-(\beta+1)t}\tilde{v}_+ + \mathcal{F}_2[\tilde{u}_+, \tilde{v}_+] \int_0^t e^{-(\beta+1)(t-r)}dr \\ &\le e^{-(\beta+1)t}\tilde{v}_+ + \tilde{v}_+(1 - e^{-(\beta+1)t}) = \tilde{v}_+, \end{aligned}$$

and hence, $\mathcal{G}(\Gamma) \subseteq \Gamma$.

For $\mu > 0$ and $(U, V) \in \Gamma$, we define

$$\begin{aligned} \|(U, V)\|_\mu = &\sup_{t\in[-\tau,0], x\in\mathbb{R}} (|U(t, x)| + |V(t, x)|) \\ &+ \sup_{t\in[0,+\infty), x\in\mathbb{R}} (|U(t, x)| + |V(t, x)|)e^{-\mu t}, \\ d_\mu(w_1, w_2) := &\|w_1 - w_2\|_\mu, \end{aligned}$$

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where $w_1=(U_1,V_1)$ and $w_2=(U_2,V_2)$. Then, (Γ,d_μ) is a complete metric space. For any $(U,V),(\overline{U},\overline{V})\in\Gamma$, we obtain

$$
\begin{aligned}
&|\mathcal{G}_1[U,V]-\mathcal{G}_1[\overline{U},\overline{V}]|\\
&\quad\le\int_0^t\beta e^{-(\beta+d_m)(t-r)}|U-\overline{U}|(r,x)dr\\
&\qquad+\int_0^t e^{-(\beta+d_m)(t-r)}\alpha e^{-d_i\tau}\int_{\mathbb{R}}k(y)\Bigg|\frac{U(r-\tau,x-y)}{U(r-\tau,x-y)+\omega}(V(r-\tau,x-y)+1)\\
&\qquad-\frac{\overline{U}(r-\tau,x-y)}{\overline{U}(r-\tau,x-y)+\omega}(\overline{V}(r-\tau,x-y)+1)\Bigg|dydr\\
&\quad\le\int_0^t\beta e^{-(\beta+d_m)(t-r)}|U-\overline{U}|(r,x)dr+\alpha e^{-d_i\tau}\int_0^t\int_{\mathbb{R}}e^{-(\beta+d_m)(t-r)}k(y)\\
&\qquad\times\left[\frac{\tilde{v}_+}{\omega}|U-\overline{U}|(r-\tau,x-y)+|V-\overline{V}|(r-\tau,x-y)\right]dydr,
\end{aligned}
$$

and hence,

$$
\begin{aligned}
&|\mathcal{G}_1[U,V]-\mathcal{G}_1[\overline{U},\overline{V}]|e^{-\mu t}\\
&\quad\le\int_0^t\beta e^{-(\beta+d_m+\mu)(t-r)}e^{-\mu r}|U-\overline{U}|(r,x)dr+\alpha e^{-d_i\tau}\int_0^t\int_{\mathbb{R}}e^{-(\beta+d_m+\mu)(t-r)}k(y)\\
&\qquad\times\left[\frac{\tilde{v}_+}{\omega}e^{-\mu r}|U-\overline{U}|(r-\tau,x-y)+e^{-\mu r}|V-\overline{V}|(r-\tau,x-y)\right]dydr.
\end{aligned}
$$

Similarly, one has

$$
\begin{aligned}
&|\mathcal{G}_2[U,V]-\mathcal{G}_2[\overline{U},\overline{V}]|\\
&\quad\le\int_0^t e^{-(\beta+1)(t-r)}\left[\beta|V-\overline{V}|+|V^2-\overline{V}^2|\right]dr\\
&\qquad+\int_0^t e^{-(\beta+1)(t-r)}d\int_{\mathbb{R}}k(y)\Bigg|\frac{U(r,x-y)}{U(r,x-y)+\omega}(V(r,x-y)+1)\\
&\qquad-\frac{\overline{U}(r,x-y)}{\overline{U}(r,x-y)+\omega}(\overline{V}(r,x-y)+1)\Bigg|dydr\\
&\qquad+\int_0^t e^{-(\beta+1)(t-r)}D\int_{\mathbb{R}}J(y)\left[|V-\overline{V}|(r,x-y)+|V-\overline{V}|(r,x)\right]dydr\\
&\quad\le\int_0^t(\beta+D+2(\tilde{v}_+-1))e^{-(\beta+1)(t-r)}|V-\overline{V}|(r,x)dr\\
&\qquad+d\int_0^t\int_{\mathbb{R}}e^{-(\beta+1)(t-r)}k(y)\left[\frac{\tilde{v}_+}{\omega}|U-\overline{U}|(r,x-y)+|V-\overline{V}|(r,x-y)\right]dydr\\
&\qquad+D\int_0^t\int_{\mathbb{R}}e^{-(\beta+1)(t-r)}J(y)|V-\overline{V}|(r,x-y)dydr,
\end{aligned}
$$

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and hence,

$$
\begin{aligned}
&|\mathcal{G}_2[U,V]-\mathcal{G}_2[\overline{U},\overline{V}]|e^{-\mu t}\\
&\quad\le \int_0^t(\beta+D+2(\tilde{v}_+-1))e^{-(\beta+1+\mu)(t-r)}e^{-\mu r}|V-\overline{V}|(r,x)dr\\
&\qquad+d\int_0^t\int_{\mathbb{R}}e^{-(\beta+1+\mu)(t-r)}k(y)\\
&\qquad\times\left[\frac{\tilde{v}_+}{\omega}e^{-\mu r}|U-\overline{U}|(r,x-y)+e^{-\mu r}|V-\overline{V}|(r,x-y)\right]dydr\\
&\qquad+D\int_0^t\int_{\mathbb{R}}e^{-(\beta+1+\mu)(t-r)}J(y)e^{-\mu r}|V-\overline{V}|(r,x-y)dydr.
\end{aligned}
$$

Let

$$
M=\beta+D+2(\tilde{v}_+-1)+\left(\frac{\tilde{v}_+}{\omega}+1+\frac{D}{d}\right)(\alpha e^{-d_i\tau}+d),\qquad \beta_0=\beta+\min\{d_m,1\}.
$$

It then follows that

$$
\begin{aligned}
\|\mathcal{G}[U,V]-\mathcal{G}[\overline{U},\overline{V}]\|_\mu &\le 2M\int_0^t e^{-(\beta_0+\mu)}(t-r)\|(U,V)-\overline{U},\overline{V}\|_\mu dr\\
&\le\frac{2M}{\beta_0+\mu}\|(U,V)-(\overline{U},\overline{V})\|_\mu.
\end{aligned}
$$

Choose $\mu>0$ large enough such that $\frac{2M}{\beta_0+\mu}<1$. Then, $\mathcal{G}$ is a contracting mapping in Γ. By the contraction mapping theorem, we see that $\mathcal{G}$ has a unique fixed point in Γ, which is the solution of (2.3). The proof is complete. □

Next, we establish the comparison principle for upper and lower solutions of (2.3). For this purpose, we introduce the definition of upper and lower solutions.

Definition 2.2. *A function $(\overline{U},\overline{V})\in C^1([-\tau,\infty),X_{\mathbf{K}})$ is called an upper solution of (2.3) if it satisfies*

$$
\begin{cases}
\dfrac{\partial\overline{U}}{\partial t}\ge -d_m\overline{U}(t,x)+\alpha e^{-d_i\tau}\displaystyle\int_\Omega k(y)\frac{\overline{U}(t-\tau,x-y)}{\overline{U}(t-\tau,x-y)+\omega}(\overline{V}(t-\tau,x-y)+1)dy,\\
\dfrac{\partial\overline{V}}{\partial t}\ge D\displaystyle\int_{\mathbb{R}}J(y)\left[\overline{V}(t,x-y)-\overline{V}(t,x)\right]dy-\overline{V}(1+\overline{V})\\
\qquad+d\displaystyle\int_\Omega k(y)\frac{\overline{U}(t,x-y)}{\overline{U}(t,x-y)+\omega}(\overline{V}(t,x-y)+1)dy,\\
\overline{U}(s,x)\ge\phi_1(s,x),\quad \overline{V}(s,x)\ge\phi_2(s,x),\quad (s,x)\in[-\tau,0]\times\mathbb{R},
\end{cases}
\tag{2.6}
$$

for all $(t,x)\in[0,\infty)\times\mathbb{R}$. A lower solution of (2.3) is defined in a similar way by reversing the inequalities in (2.6).

Lemma 2.3. *Let $(\overline{U},\overline{V})$ and $(\underline{U},\underline{V})$ be a pair of upper and lower solutions of (2.3). Then, $\overline{U}(t,x)\ge\underline{U}(t,x)$ and $\overline{V}(t,x)\ge\underline{V}(t,x)$ for all $t\ge 0$ and $x\in\mathbb{R}$.*

Proof. Let $W_1(t,x):=\overline{U}(t,x)-\underline{U}(t,x)$, $W_2(t,x):=\overline{V}(t,x)-\underline{V}(t,x)$, $\forall(t,x)\in\mathbb{R}_+\times\mathbb{R}$, and

$$
W(t):=\min_{i=1,2}\inf_{x\in\mathbb{R}}W_i(t,x),\quad\forall t\ge 0.
$$

It then follows that $W(t)$ is a continuous function. We shall prove that $W(t)\ge 0$, $\forall t\ge 0$. Assume, by contradiction, that the assertion is not true. Then, there exists a number $t_0>0$ such that $W(t_0)<0$. Since $W(t)e^{-\delta t}$ with $\delta>0$ is continuous and $W(0)\ge 0$. By the property of continuous function, without loss of generality, for such t_0, we have

$$
W(t_0)e^{-\delta t_0}=\min_{t\in[0,t_0]}W(t)e^{-\delta t}<W(s)e^{-\delta s},\quad\forall\, s\in[0,t_0).
$$

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Thus, there exist an index $i \in \{1,2\}$ and a sequence of points $\{x_k\}_{k=1}^{\infty}$ such that $W_i(t_0, x_k) < 0$, $\forall k \geq 1$ and $\lim_{k\to\infty} W_i(t_0, x_k) = W(t_0)$. Let $\{t_k\}_{k=1}^{\infty} \subset [0, t_0]$ be a sequence such that

$$W_i(t_k, x_k)e^{-\delta t_k} = \min_{t\in[0,t_0]} W_i(t, x_k)e^{-\delta t}.$$

Moreover, $\{x_k\}_{k=1}^{\infty}$ can be chosen properly as local minimisers of $W_i(t_k, x)$. Then, we obtain that $\int_{\mathbb{R}} J(y)[W_i(t_k, x_k - y) - W_i(t_k, x_k)]dy \geq 0$. By a similar argument as that in [29, Theorem 2.2], we can obtain that $\frac{\partial W_i(t_k, x_k)}{\partial t} \leq \delta W_i(t_k, x_k)$. Hence, we further have

$$\begin{aligned}
0 \leq & \frac{\partial W_1(t_k, x_k)}{\partial t} + d_m W_1(t_k, x_k) \\
& - \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\overline{U}(t_k - \tau, x_k - y)}{\overline{U}(t_k - \tau, x_k - y) + \omega} (\overline{V}(t_k - \tau, x_k - y) + 1) dy \\
& + \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\underline{U}(t_k - \tau, x_k - y)}{\underline{U}(t_k - \tau, x_k - y) + \omega} (\underline{V}(t_k - \tau, x_k - y) + 1) dy \\
\leq & (\delta + d_m) W_1(t_k, x_k) - \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\overline{U}}{\overline{U} + \omega} W_2(t_k - \tau, x_k - y) dy \\
& - \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\omega(\underline{V} + 1)}{(\overline{U} + \omega)(\underline{U} + \omega)} W_1(t_k - \tau, x_k - y) dy \\
\leq & (\delta + d_m) W_1(t_k, x_k) - \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \left[\frac{\tilde{u}_+}{\tilde{u}_+ + \omega} + \frac{\tilde{v}_+}{\omega} \right] W(t_k) dy \\
\leq & (\delta + d_m) W_1(t_k, x_k) - \frac{\alpha e^{-d_i\tau} \tilde{v}_+}{\omega} W(t_k)
\end{aligned}$$

and

$$\begin{aligned}
0 \leq & \frac{\partial W_2(t_k, x_k)}{\partial t} - D \int_{\mathbb{R}} J(y)[W_2(t_k, x_k - y) - W_2(t_k, x_k)] dy \\
& + (1 + \overline{V} + \underline{V}) W_2(t_k, x_k) - d \int_{\mathbb{R}} k(y) \frac{\overline{U}(t_k, x_k - y)}{\overline{U}(t_k, x_k - y) + \omega} (\overline{V}(t_k, x_k - y) + 1) dy \\
& + d \int_{\mathbb{R}} k(y) \frac{\underline{U}(t_k, x_k - y)}{\underline{U}(t_k, x_k - y) + \omega} (\underline{V}(t_k, x_k - y) + 1) dy \\
\leq & (\delta + 1 + \overline{V} + \underline{V}) W_2(t_k, x_k) \\
& - d \int_{\mathbb{R}} k(y) \left[\frac{\overline{U}}{\overline{U} + \omega} W_2(t_k, x_k - y) - \frac{\omega(\underline{V} + 1)}{(\overline{U} + \omega)(\underline{U} + \omega)} W_1(t_k, x_k - y) \right] dy \\
\leq & (\delta + 1 + \overline{V} + \underline{V}) W_2(t_k, x_k) - d \int_{\mathbb{R}} k(y) \left[\frac{\tilde{u}_+}{\tilde{u}_+ + \omega} + \frac{\tilde{v}_+}{\omega} \right] W(t_k) dy \\
\leq & (\delta + 1 + \overline{V} + \underline{V}) W_2(t_k, x_k) - \frac{d\tilde{v}_+}{\omega} W(t_k).
\end{aligned}$$

Letting $k \to \infty$, we have that $\left(\delta + d_m - \frac{\alpha e^{-d_i\tau}\tilde{v}_+}{\omega}\right) W(t_0) \geq 0$ or $\left(\delta + 1 - \frac{d\tilde{v}_+}{\omega}\right) W(t_0) \geq 0$, which imply that $W(t_0) \geq 0$ by choosing $\delta > \max\{-d_m + \frac{\alpha e^{-d_i\tau}\tilde{v}_+}{\omega}, -1 + \frac{d\tilde{v}_+}{\omega}\}$. It contradicts to $W(t_0) < 0$. The proof is complete. $\square$

Proposition 2.4. *For any $\phi \in \mathcal{C}_{\mathbf{K}}$ with $\phi \not\equiv 0$, let $(U(t, x; \phi), V(t, x; \phi))$ be the solution of (2.3). Then, there exists $t_1 = t_1(\phi) > 0$ such that $U(t, x; \phi) > 0$ and $V(t, x; \phi) > 0$ for any $t > t_1(\phi)$, $x \in \mathbb{R}$.*

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Proof. In view of Lemma 2.1, when $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{\mathbf{K}}$, $(U, V)(t, x) \in [0, \tilde{u}_+] \times [0, \tilde{v}_+]$ for $(t, x) \in (0, +\infty) \times \mathbb{R}$. Then, it is easy to see that

$$\begin{cases} \dfrac{\partial V}{\partial t} = (J * V - V) - V(1 + V) + d \displaystyle\int_{\mathbb{R}} k(x-y) \frac{U(t, y)}{U(t, y) + \omega}(V(t, y) + 1) dy \\ \qquad \geq (J * V - V) - V(1 + \tilde{v}_+), \\ V(0, x) = \phi_2(0, x), \quad x \in \mathbb{R}. \end{cases} \tag{2.7}$$

By the strong maximum principle (see e.g. [17, Theorem 2.1]), we obtain that $V(t, x) > 0$ for $(t, x) \in (0, +\infty) \times \mathbb{R}$, if $\phi_2(0, x) \geq (\not\equiv) 0$ for $x \in \mathbb{R}$.

Next, we show that there exists $t_0 \in [0, \tau]$ such that $U(t_0, x) \not\equiv 0$ for all $x \in \mathbb{R}$, which means there exists some x such that $U(t_0, x) > 0$. Assume, by contradiction, that $U(t, x) \equiv 0$ for all t and x. It then follows from the first equation in (2.5) that $\phi_1(t, x) \equiv 0$ for $t \in [-\tau, 0]$ and $x \in \mathbb{R}$, which is a contradiction. Since $U_t > -d_m U$, we obtain that for $t \in [t_0, t_0 + \tau]$, $U(t, x) \not\equiv 0$ for all $x \in \mathbb{R}$. Thus, by the first equation of (2.3), we get

$$U(t, x) \geq \int_0^t e^{-d_m(t-s)} \left[\alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{U(s-\tau, x-y)}{U(s-\tau, x-y) + \omega}(V(s-\tau, x-y) + 1) dy \right] ds. \tag{2.8}$$

Let $t_1(\phi) = t_0 + \tau$. Then by (2.8), we obtain that $U(t, x) > 0$ for $t > t_1(\phi)$, $x \in \mathbb{R}$. The proof is complete. $\square$

3. Spreading speeds

3.1. Existence of spreading speed

In this subsection, we are devoted to establishing that the solution of (2.3) has a spreading speed.

Definition 3.1. *A family of mappings $\{Q_t\}_{t \geq 0}$ is said to be a semiflow on $\mathcal{C}_{\mathbf{K}}$, if the following three properties hold: (i) $Q_0 = I$, where I is the identity mapping; (ii) $Q_t \circ Q_s = Q_{t+s}$ for all $t, s > 0$; (iii) $Q_t[\phi](x)$ is continuous in $(t, \phi) \in (0, +\infty) \times \mathcal{C}_{\mathbf{K}}$.*

For any $u = (u_1(\theta, x), u_2(\theta, x)) \in \mathcal{C}$, define the reflection operator $\mathcal{R}$ by

$$\mathcal{R}[u](\theta, x) = (u_1(\theta, -x), u_2(\theta, -x)).$$

Given $y \in \mathbb{R}$, define the translation operator T_y by

$$T_y[u](\theta, x) = (u_1(\theta, x-y), u_2(\theta, x-y)).$$

A set $W \subseteq \mathcal{C}$ is said to be T-invariant if $T_y[W] = W$ for any $y \in \mathbb{R}$. For a given operator $Q : \mathcal{C}_{\mathbf{K}} \to \mathcal{C}_{\mathbf{K}}$, we make the following assumptions:

- **(A1)** $Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]]$, $T_y[Q[u]] = Q[T_y[u]]$, $\forall y \in \mathbb{R}$.
- **(A2)** $Q : \mathcal{C}_{\mathbf{K}} \to \mathcal{C}_{\mathbf{K}}$ is continuous with respect to the compact open topology.
- **(A3)** One of the following two properties holds:
  - (a) $\{Q[u](\cdot, x) : u \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is precompact in $\bar{\mathcal{C}}_{\mathbf{K}}$.
  - (b) $Q[\mathcal{C}_{\mathbf{K}}](0, \cdot)$ is precompact in X, and there is a positive number $\varsigma \leq \tau$ such that $Q[u](\theta, x) = u(\theta + \varsigma, x)$ for $-\tau \leq \theta \leq -\varsigma$, and the operator

$$S[u](\theta, x) = \begin{cases} u(0, x), & -\tau \leq \theta \leq -\varsigma, \\ Q[u](\theta, x), & -\varsigma \leq \theta \leq 0, \end{cases} \tag{3.1}$$

has the property that $S[\Pi](\cdot, 0) := \{S[u](\theta, 0) : u \in \Pi\}$ is precompact in $\bar{\mathcal{C}}_{\mathbf{K}}$ for any T-invariant set $\Pi \subset \mathcal{C}_{\mathbf{K}}$ with $\Pi(0, \cdot) := \{u(0, x) : u \in \Pi\}$ precompact in X.

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(A4) $Q:\mathcal{C}_{\mathbf{K}}\to\mathcal{C}_{\mathbf{K}}$ is monotone in the sense that $Q[u]\geq Q(v)$ whenever $u\geq v$ in $\mathcal{C}_{\mathbf{K}}$.

(A5) $Q:\bar{\mathcal{C}}_{\mathbf{K}}\to\bar{\mathcal{C}}_{\mathbf{K}}$ admits exactly two fixed points $\mathbf{0}$ and $\mathbf{K}$, and for any positive number ϵ, there is a $\zeta\in\bar{\mathcal{C}}_{\mathbf{K}}$ with $\|\zeta\|<\epsilon$ such that $Q[\zeta]\gg\zeta$, where $\|\cdot\|$ is the maximum norm in $\bar{\mathcal{C}}$.

Let Q_t be the solution map of (2.3), that is,

$$\begin{aligned}Q_t(\phi)(\theta,x)&=(Q_t^1(\phi)(\theta,x),Q_t^2(\phi)(\theta,x))\\&=(U_t(\theta,x;\phi),V_t(\theta,x;\phi)),\ \theta\in[-\tau,0],\ x\in\mathbb{R},\ \phi\in\mathcal{C}.\end{aligned}\tag{3.2}$$

In order to apply the theory in [20] to address the existence of a spreading speed for (2.3), we need to verify that the solution map Q_t defined in (3.2) satisfies the above properties (A1)–(A5). It is straightforward to verify that (A1) holds, since $(U(t,-x),V(t,-x))$ and $(U(t,x-y),V(t,x-y))$ are also solution of (2.1) provided that $(U(t,x),V(t,x))$ is a solution (2.1) and $y\in\mathbb{R}$.

Lemma 3.2. *Let Q_t be the solution map of (2.3) defined in (3.2). Then, $\{Q_t\}_{t\geq0}$ is a semiflow on $\mathcal{C}_{\mathbf{K}}$.*

Proof. We shall prove that Q_t is the continuous in ϕ with respect to the compact open topology uniformly for $t\in[0,t_0]$ with $t_0>0$. In view of [29, Lemma 3.1], the solution semigroup of the following linear nonlocal dispersal equation

$$\begin{cases}\dfrac{\partial V(t,x)}{\partial t}=D(J*V-V)(t,x),\quad t>0,\ x\in\mathbb{R}\\ V(0,x)=\psi(x),\quad x\in\mathbb{R},\end{cases}\tag{3.3}$$

is given by

$$[P(t)\psi](x)=e^{-Dt}\sum_{k=0}^{\infty}\frac{(Dt)^k}{k!}a_k(\psi)(x),\quad t>0,\ x\in\mathbb{R}\tag{3.4}$$

for any $\psi\in\mathbb{Y}$, where $\mathbb{Y}$ is the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$, and

$$a_0(\psi)(x)=\psi(x),\quad a_m(\psi)(x)=\int_{\mathbb{R}}J(x-y)a_{m-1}(\psi)(y)dy,\ \forall m\geq1.$$

For any $\psi\in\mathbb{Y}$, define $\|\cdot\|=\sup_{x\in\mathbb{R}}|\psi(x)|$. It is easy to see that $\|a_0(\psi)\|=\|\psi\|$, $\|a_1(\psi)(x)\|=\|\int_{\mathbb{R}}J(x-y)a_0(\psi)(y)dy\|\leq\|\psi\|$. By induction, we can obtain $\|a_k(\psi)(x)\|\leq\|\psi\|$ for all $k=0,1,2,\cdots$. By (3.4), we have

$$\|P(t)\psi\|\leq e^{-Dt}\sum_{k=0}^{\infty}\frac{(Dt)^k}{k!}\|a_k(\psi)\|\leq\|\psi\|.\tag{3.5}$$

It is clear that the system (2.3) can be rewritten into the following integral system

$$\begin{cases}U(t,x)=e^{-d_mt}\phi_1(0,x)+\displaystyle\int_0^t e^{-d_m(t-s)}\mathcal{H}_1[U,V](s,x)ds,\\ V(t,x)=P(t)\phi_2(0,x)+\displaystyle\int_0^t P(t-s)\mathcal{H}_2[U,V](s,x)ds,\end{cases}\tag{3.6}$$

where

$$\begin{cases}\mathcal{H}_1[U,V](t,x):=\alpha e^{-d_i\tau}\displaystyle\int_{\mathbb{R}}k(y)\frac{U(t-\tau,x-y)}{U(t-\tau,x-y)+\omega}(V(t-\tau,x-y)+1)dy,\\ \mathcal{H}_2[U,V](t,x):=-V(1+V)+d\displaystyle\int_{\mathbb{R}}k(y)\frac{U(t,x-y)}{U(t,x-y)+\omega}(V(t,x-y)+1)dy.\end{cases}\tag{3.7}$$

For $\phi^1=(\phi_1^1,\phi_2^1)$, $\phi^2=(\phi_1^2,\phi_2^2)\in\mathcal{C}_{\mathbf{K}}$, we define

$$w(t,x)=(w^1(t,x),w^2(t,x)),$$

where

$$w^1(t,x)=|U(t,x;\phi^1)-U(t,x;\phi^2)|,\quad w^2(t,x)=|V(t,x;\phi^1)-V(t,x;\phi^2)|.$$

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Choose $t_0 > 0$ and for any $\varepsilon > 0$, we let

$$\sigma = \frac{(\alpha e^{-d_i\tau} + d)(v_+ + \omega)}{\omega} + (2v_+ - 1) \text{ and } \varepsilon_1 = \frac{\varepsilon}{2\sigma t_0 e^{\sigma t_0}}.$$

It is easy to see that there exists $(t^*, x^*) \in [-\tau, t] \times \mathbb{R}$ such that

$$w_s(\theta, x) \le \sup_{s\in[-\tau,t],x\in\mathbb{R}} (w^1(s, x), w^2(s, x)) \le w(t^*, x^*) + \left(\frac{\varepsilon}{8}e^{-\sigma t_0}, \frac{\varepsilon}{8}e^{-\sigma t_0}\right)$$

for $(s, \theta, x) \in [0, t] \times [-\tau, 0] \times \mathbb{R}$ with $t \in [0, t_0]$. Set

$$\|\phi\|_{\Sigma_M(z)} = \sup_{(\theta,x)\in\Sigma_M(z)} |\phi_1(\theta, x)| + \sup_{(\theta,x)\in\Sigma_M(z)} |\phi_2(\theta, x)| \text{ for } \phi = (\phi_1, \phi_2),$$

with

$$\Sigma_M(z) = [-\tau, 0] \times [z - M, z + M], \quad M > 0, \; z \in \mathbb{R}.$$

Then, there exists $M = M(t_0, \varepsilon)$ such that

$$\int_{\mathbb{R}} k(y) \left[\frac{v_+}{\omega} w^1(s, x^* - y) + w^2(s, x^* - y)\right] dy \le \frac{v_+ + \omega}{\omega} \|w_s\|_{\Sigma_M(x^*)} + \varepsilon_1$$

for $0 \le s \le t$. Hence, for above $\varepsilon > 0$, choose $\delta = \frac{\varepsilon}{8}e^{-\sigma t_0}$ such that when $\|\phi^1 - \phi^2\|_{\Sigma_M(x^*)} < \delta$, by (3.5) and (3.6), we obtain

$$\begin{aligned}
&\|w_t(\theta, x)\|_{\Sigma_M(x^*)} \\
&\quad \le w^1(t^*, x^*) + w^2(t^*, x^*) + \frac{\varepsilon}{4}e^{-\sigma t_0} \\
&\quad \le e^{-d_m t} w^1(0, x^*) + w^2(0, x^*) + \frac{\varepsilon}{4}e^{-\sigma t_0} \\
&\qquad + \alpha e^{-d_i\tau} \int_0^{t^*} \int_{\mathbb{R}} e^{-d_m(t^*-s)} k(y) \left[\frac{v_+}{\omega} w^1(s-\tau, x^* - y) + w^2(s-\tau, x^* - y)\right] dyds \\
&\qquad + \int_0^{t^*} (2v_+ - 1) w^2(s, x^*) ds + d \int_0^{t^*} \int_{\mathbb{R}} k(y) \left[\frac{v_+}{\omega} w^1(s, x^* - y) + w^2(s, x^* - y)\right] dyds \\
&\quad \le 2\|\phi^1 - \phi^2\|_{\Sigma_M(x^*)} + \frac{\varepsilon}{4}e^{-\sigma t_0} + (2v_+ - 1) \int_0^t (\|w_s\|_{\Sigma_M(x^*)} + \varepsilon_1) ds \\
&\qquad + \frac{(\alpha e^{-d_i\tau} + d)(v_+ + \omega)}{\omega} \int_0^t (\|w_s\|_{\Sigma_M(x^*)} + \varepsilon_1) ds \\
&\quad \le 2\delta + \frac{\varepsilon}{4}e^{-\sigma t_0} + \varepsilon_1 \sigma t + \sigma \int_0^t \|w_s\|_{\Sigma_M(x^*)} ds.
\end{aligned}$$

By Gronwall's inequality, we further have

$$\|w_t(\theta, x)\|_{\Sigma_M(x^*)} \le \left(\frac{\varepsilon}{2}e^{-\sigma t_0} + \varepsilon_1 \sigma t\right) e^{\sigma t} \le \left(\frac{\varepsilon}{2}e^{-\sigma t_0} + \varepsilon_1 \sigma t_0\right) e^{\sigma t_0} = \varepsilon, \quad t \in [0, t_0].$$

This shows that Q_t is continuous in ϕ with respect to compact open topology uniformly for $t \in [0, t_0]$, which, together with the continuity of Q_t in t from Lemma 2.1, implies that Q_t is continuous in (t, ϕ) with respect to the compact open topology. The proof is complete. □

By Lemma 3.2, the property (A2) holds. The property (A4) can be guaranteed by Lemma 2.3. It is easy to verify that the property (A5) also holds, see also [27, Lemma 3.7]. We just need to prove that the solution map Q_t satisfies the property (A3).

Lemma 3.3. *Q_t satisfies* (A3)(a) *if $t \ge \tau$ and satisfies* (A3)*(b) if $t < \tau$.*

Proof. In view of Lemma 2.1, when $\phi \in \mathcal{C}_{\mathbf{K}}$, the solution $(U(t, x; \phi), V(t, x; \phi))$ of (2.3) is bounded. More precisely, $\mathbf{0} \le (U(t, x; \phi), V(t, x; \phi)) \le \mathbf{K}$, $\forall\, t \ge 0$, $x \in \mathbb{R}$. It then follows from the first equation of (2.3) that

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$$
\begin{aligned}
|U_t(t,x;\phi)| \le & d_m|U| + \alpha e^{-d_i\tau}\int_{\mathbb{R}} k(x-y)\left|\frac{U(t-\tau,y;\phi)}{U(t-\tau,y;\phi)+\omega}\right| |V(t-\tau,y;\phi)+1|dy \\
\le & d_m\tilde{u}_+ + \alpha e^{-d_i\tau}\frac{\tilde{u}_+}{\omega}(\tilde{v}_+ + 1) =: L,
\end{aligned}
$$

which means that U_t is bounded for $t \ge 0$. Let $[a,b] \subseteq \mathbb{R}$ with $a > 0$ be any bounded interval, $I \subseteq \mathbb{R}$ be a compact interval and $\tilde{K} = \min\{K \in \mathbb{N} : I \subseteq [-K,K]\}$. Then for any $t_1, t_2 \in [a,b]$ and $x \in I$, one has

$$|U(t_1,x;\phi) - U(t_2,x;\phi)| \le L|t_1 - t_2|.$$

Hence, for any $\varepsilon > 0$, there exists $\delta = \frac{\varepsilon}{L}$, such that for any $\phi \in \mathcal{C}_{\mathbf{K}}$, any $x \in I$, $s_1, s_2 \in [-\tau, 0]$ with $|s_1 - s_2| < \delta$, we obtain

$$|Q^1_{t_0}[\phi](s_1,x) - Q^1_{t_0}[\phi](s_2,x)| \le |U(t_0+s_1,x;\phi) - U(t_0+s_2,x;\phi)| < \varepsilon,$$

where $t_0 > \tau$, which implies that $\{Q^1_t[\phi](s,x) : \phi \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is a family of equicontinuous functions of $s \in [-\tau, 0]$. By the Arzela-Ascoli Theorem, we obtain that $\{Q^1_t[\phi](\cdot,x) : \phi \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is precompact in $C([-\tau,0],\mathbb{R})$ if $t \ge \tau$. Thus, Q^1_t satisfies (A3)(a) for $t \ge \tau$. On the other hand, if $t < \tau$, we set $\varsigma = 1$. Then, for the T-invariant set Π defined in (A3), the set $\{S^1[\Pi](\theta,0) : \theta \in [-\varsigma,0]\}$ is precompact in $C([-\varsigma,0],\mathbb{R})$, where S^1 is the first component of the operator S defined in (3.1). It is clear that $\{S^1[\Pi](\theta,0) : \theta \in [-\tau,-\varsigma]\}$ is an infinite set of constant functions in $C([-\tau,-\varsigma],\mathbb{R})$, and hence, it is precompact in $C([-\tau,-\varsigma],\mathbb{R})$. Therefore, Q^1_t satisfies (A3)(b) for $t < \tau$.

Now we prove that Q^2_t satisfies (A3). By the second equation of (2.3), we have

$$|V_t(t,x;\phi)| \le 2D\tilde{v}_+ + \tilde{v}_+(\tilde{v}_+ + 1) + d\frac{\tilde{u}_+}{\tilde{u}_+ + \omega}(\tilde{v}_+ + 1).$$

By a similar argument as that for Q^1_t, we obtain that $\{Q^2_t[\phi](\cdot,x) : \phi \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is precompact in $C([-\tau,0],\mathbb{R})$ if $t \ge \tau$. Thus, Q^2_t satisfies (A3)(a) for $t \ge \tau$. In the following, we verify that Q^2_t satisfies (A3)(b) when $t \in [0,\tau]$. For any $\phi \in \mathcal{C}_{\mathbf{K}}$, we fix $\tilde{t} \in (0,\tau]$ and define

$$
S^2[\phi](\theta,x) = \begin{cases} \phi_2(0,x), & -\tau \le \theta \le -\tilde{t}, \\ Q^2_{\tilde{t}}[\phi](\theta,x), & -\tilde{t} \le \theta \le 0. \end{cases}
$$

Let $\Pi \subset \mathcal{C}_{\mathbf{K}}$ be a T-invariant set with $\Pi(0,\cdot) := \{u(0,x) : u \in \Pi\}$ precompact in X. We just need to show that for any given compact interval $I \in \mathbb{R}$, $S^2(\Pi)$ is equicontinuous on $[-\tau,0] \times I$.

When $(s,x) \in [-\tau,-\tilde{t}] \times I$, one has $S^2[\phi](s,x) = \phi_2(0,x)$ for all $\phi \in \Pi$. Hence, by the precompactness of $\Pi(0,\cdot)$ in X, we obtain that $S^2(\Pi)$ is equicontinuous on $[-\tau,-\tilde{t}] \times I$.

Since $P(t)$ is uniformly continuous for t in a bounded interval in the compact open topology with respect to the initial value, one can show that

$$\{P(t-s)\mathcal{H}_2[\phi](s,x) : t \in [0,\tilde{t}],\ s \in [0,t],\ \phi \in \mathcal{C}_{\mathbf{K}}\}$$

is bounded in X_+, where $\mathcal{H}_2$ is defined in (3.7). Then there exists $M > 0$ such that

$$\|P(t-s)\mathcal{H}_2[\phi](s,\cdot)\|_X \le M \text{ for } t \in [0,\tilde{t}],\ s \in [0,t],\ \phi \in \mathcal{C}_{\mathbf{K}},$$

where the norm

$$\|\phi\|_X = \sum_{k=1}^{\infty}\frac{\max_{|x|\le k}|\phi|}{2^k}, \quad \forall \phi \in X,$$

with $|\cdot|$ is the usual norm in $\mathbb{R}$. Thus, we derive that $\sup_{|x|\le\tilde{K}}|P(t-s)\mathcal{H}_2[\phi](x)| \le 2^{\tilde{K}}M$. Hence, for any $\varepsilon > 0$, there exists $\delta_1 = \min\{\frac{\varepsilon}{2^{\tilde{K}}4M}, \tilde{t}\}$, such that for any $t \le \delta_1$, $x \in I$ and $\phi \in \Pi$, we have

$$\left|\int_0^t P(t-s)\mathcal{H}_2[\phi](s,x)ds\right| \le 2^{\tilde{K}}M\delta_1 < \frac{\varepsilon}{4}. \tag{3.8}$$

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In [14, Section 2], Ignat and Rossi showed that the solution of (3.3) can also be written as $V(t,x) = [P(t)\psi](x) = \int_{\mathbb{R}} G(t,y)\psi(x-y)dy$, where $G(t,x) = e^{-Dt}\delta_0(x) + R(t,x)$, $\delta_0(x)$ is the delta measure at zero and $R(t,x) = \frac{1}{2\pi}\int_{\mathbb{R}}(e^{D(\hat{J}(\xi)-1)t} - e^{-Dt})e^{jx\xi}d\xi$ with $j = \sqrt{-1}$ and $\hat{J}$ being the Fourier transform of J. Moreover, it is proved that $|G(t,\cdot)|_{L^1(\mathbb{R})} \le 3$ for any $t > 0$. Since $(\phi_1, \phi_2) \in \Pi(0,\cdot)$ and $\Pi(0,\cdot)$ is precompact in X, then for the above I, there exists $\delta_2 > 0$ such that for any $x_1, x_2 \in I$ satisfying $|x_1 - x_2| < \delta_2$, we have $|\phi_2(x_1) - \phi_2(x_2)] < \frac{\varepsilon}{12}$, and hence,

$$\begin{aligned}|P(t)[\phi_2](x_1) - P(t)[\phi_2](x_2)| &= \left|\int_{\mathbb{R}} G(t,y)[\phi_2(x_1-y) - \phi_2(x_2-y)]dy\right| \\ &\le \int_{\mathbb{R}} |G(t,y)||\phi_2(x_1-y) - \phi_2(x_2-y)|dy \\ &\le \|G(t,\cdot)\|_{L^1(\mathbb{R})}\frac{\varepsilon}{12} \le \frac{\varepsilon}{4}, \ \forall t \in [0,\delta_1]. \end{aligned} \tag{3.9}$$

On the other hand, for all $t > 0$, $x \in \mathbb{R}$ and $\phi \in \mathcal{C}_{\mathbf{K}}$, we have $|[P(t)\phi_2](x)| \le \tilde{v}_+$. It is easy to see that

$$\left|\frac{\partial P(t)[\phi_2](x)}{\partial t}\right| = \left|D\left(\int_{\mathbb{R}} J(x-y)P(t)[\phi_2](y)dy - P(t)[\phi_2](x)\right)\right| \le 2D\tilde{v}_+.$$

Hence, for $t_1, t_2 \in [0,\delta_1]$, $(\phi_1,\phi_2) \in \Pi(0,\cdot)$, there exists $\delta_3 := \dfrac{\varepsilon}{8D\tilde{v}_+}$ such that when $|t_1 - t_2| \le \delta_3$, we derive

$$|P(t_1)[\phi_2](x) - P(t_2)[\phi_2](x)| = 2D\tilde{v}_+|t_1 - t_2| < \frac{\varepsilon}{4}. \tag{3.10}$$

Combining (3.8)–(3.10), when $s_1, s_2 \in [-\tilde{t}, \delta_1 - \tilde{t}]$ and $x_1, x_2 \in I$ satisfying $|s_1 - s_2| < \delta_3$ and $|x_1 - x_2| < \delta_2$, for any $\phi \in \Pi(0,\cdot)$, we obtain

$$\begin{aligned}&|S^2(\phi)(s_1,x_2) - S^2(\phi)(s_2,x_2)| = |Q^2_{\tilde{t}}[\phi](s_1,x_1) - Q^2_{\tilde{t}}[\phi](s_2,x_2)| \\ &\quad = |V(\tilde{t}+s_1,x_1;\phi) - V(\tilde{t}+s_2,x_2;\phi)| \\ &\quad \le |P(\tilde{t}+s_1)[\phi_2](x_1) - P(\tilde{t}+s_2)[\phi_2](x_2)| \\ &\qquad + \left|\int_0^{\tilde{t}+s_1} P(\tilde{t}+s_1-s)\mathcal{H}_2[U,V](s,x_1)ds - \int_0^{\tilde{t}+s_2} P(\tilde{t}+s_2-s)\mathcal{H}_2[U,V](s,x_2)ds\right| \\ &\quad \le |P(\tilde{t}+s_1)[\phi_2](x_1) - P(\tilde{t}+s_1)[\phi_2](x_2)| + |P(\tilde{t}+s_1)[\phi_2](x_2) - P(\tilde{t}+s_2)[\phi_2](x_2)| \\ &\qquad + \left|\int_0^{\tilde{t}+s_1} P(\tilde{t}+s_1-s)\mathcal{H}_2[U,V](s,x_1)ds\right| + \left|\int_0^{\tilde{t}+s_2} P(\tilde{t}+s_2-s)\mathcal{H}_2[U,V](s,x_2)ds\right| \\ &\quad < \varepsilon,\end{aligned}$$

which means $S^2(\Pi)$ is equicontinuous on $[-\tilde{t}, \delta_1 - \tilde{t}] \times I$.

Finally, we need to verify that $S^2(\Pi)$ is equicontinuous on $[\delta_1 - \tilde{t}, 0] \times I$. Note that if $s \in [\delta_1 - \tilde{t}, 0]$, then $\tilde{t} + s \in [\delta_1, \tilde{t}]$. Thus, we can prove the current case similar to that for (A3)(a). Therefore, $S^2(\Pi)$ is equicontinuous on $[-\tau, 0] \times I$. The proof is complete. □

Now we are ready to apply the general theory in [20, Theorem 2.17] to show that the map Q_t admits a spreading speed c^*, which is also the spreading speed of solutions to (2.3).

Theorem 3.4. *Assume that* (H1) *and* (H2) *hold. Then, there exists a spreading speed c^* of Q_t in the following sense.*

(i) *For any $c > c^*$, if $\phi \in \mathcal{C}_{\mathbf{K}}$ with $\mathbf{0} \ll \phi \ll \mathbf{K}$ and $\phi(\cdot,x) = 0$ for x outside a bounded interval, then*

$$\lim_{t\to\infty, |x|\ge ct} U(t,x;\phi) = \lim_{t\to\infty,|x|\ge ct} V(t,x;\phi) = 0.$$

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(ii) *For any $c < c^*$ and any $\sigma \in \bar{\mathcal{C}}_{\mathbf{K}}$ with $\sigma \gg 0$, there exists a positive number r_σ such that if $\phi \in \mathcal{C}_{\mathbf{K}}$ and $\phi \gg \sigma$ for x on an interval of length $2r_\sigma$, then*

$$\lim_{t\to\infty, |x|\le ct} U(t,x;\phi) = \tilde{u}_+ \quad \text{and} \quad \lim_{t\to\infty, |x|\le ct} V(t,x;\phi) = \tilde{v}_+.$$

3.2. Estimates of spreading speed

In this subsection, we study the upper and lower bounds of the spreading speed established in Section 3.1. We first give an estimate of the upper bound of the spreading speed c^*. Consider the following linear system

$$\begin{cases} \dfrac{\partial U}{\partial t} & = -d_m U + \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \left[\frac{1}{\omega} U(t-\tau, x-y) + \frac{\tilde{u}_+}{\tilde{u}_+ + \omega} V(t-\tau, x-y) \right] dy, \\ \dfrac{\partial V}{\partial t} & = D \int_{\mathbb{R}} J(y)[V(t,x-y) - V(x,t)]dy - V \\ & \quad + d \displaystyle\int_{\mathbb{R}} k(y) \left[\frac{1}{\omega} U(t,x-y) + \frac{\tilde{u}_+}{\tilde{u}_+ + \omega} V(t,x-y) \right] dy, \end{cases} \tag{3.11}$$

where $t > 0$, $x \in \mathbb{R}$. For any $\mu \in \mathbb{R}_+$, define $U(t,x) = e^{-\mu x}\eta_1(t)$ and $V(t,x) = e^{-\mu x}\eta_2(t)$. Then, it is easy to see that $\eta = (\eta_1, \eta_2)$ satisfies

$$\eta'(t) = M\eta(t) + B\eta(t-\tau), \tag{3.12}$$

where

$$M = \begin{pmatrix} -d_m & 0 \\ \frac{d\tilde{k}(\mu)}{\omega} & D\tilde{J}(\mu) - D - 1 + \frac{d\tilde{u}_+\tilde{k}(\mu)}{\tilde{u}_+ + \omega} \end{pmatrix}$$

and

$$B = \begin{pmatrix} \frac{\alpha e^{-d_i\tau}\tilde{k}(\mu)}{\omega} & \frac{\alpha e^{-d_i\tau}\tilde{u}_+\tilde{k}(\mu)}{\tilde{u}_+ + \omega} \\ 0 & 0 \end{pmatrix},$$

where $\tilde{k}(\mu) = \int_{\mathbb{R}} k(y)e^{\mu y}dy < \infty$ and $\tilde{J}(\mu) = \int_{\mathbb{R}} J(y)e^{\mu y}dy < \infty$ for any $\mu > 0$. It is clear that if $\eta(t)$ is a solution of (3.12), then $e^{-\mu x}\eta(t)$ is a solution of (3.11). Define

$$\mathcal{B}^t_\mu(\eta^0) := N_t(\eta^0 e^{-\mu x})(0) = \eta(t, \eta^0),$$

here N_t is the solution operator of (3.11), and $\eta(t,\eta^0)$ is the solution of (3.12) with $\eta^0 = \eta(\theta)$ for $\theta \in [-\tau, 0]$. Since system (3.12) is cooperative and irreducible, by [25, Theorem 5.1], we obtain that the characteristic equation

$$\mathcal{P}(\lambda) = \det(\lambda I - M - Be^{-\lambda\tau}) = 0 \tag{3.13}$$

has a real root $\lambda(\mu) > 0$, and the real parts of all other roots are less than $\lambda(\mu)$. Let $\zeta = (\zeta_1(\theta), \zeta_2(\theta))$ be the eigenfunction of the infinitesimal generator corresponding to $\lambda(\mu)$. In fact, ζ can take the form $(\zeta_1(\theta), \zeta_2(\theta)) = (\zeta_{10}e^{\lambda(\mu)\theta}, \zeta_{20}e^{\lambda(\mu)\theta})$ with $\zeta_{10}, \zeta_{20} > 0$, $\theta \in [-\tau, 0]$. Then, $e^{\lambda(\mu)t}$ is the principle eigenvalue of $\mathcal{B}^t_\mu$ with eigenfunction ζ. In particular, $\gamma(\mu) := e^{\lambda(\mu)}$ is the eigenvalue of $\mathcal{B}^1_\mu$. Define

$$\Phi(\mu) := \frac{1}{\mu}\ln\gamma(\mu) = \frac{\lambda(\mu)}{\mu} \quad \text{for } \mu > 0.$$

By using [20, Lemma 3.8], we can easily obtain the following properties of $\Phi(\mu)$.

Lemma 3.5. *The statements are valid:*

(i) $\Phi(\mu) \to \infty$ *as* $\mu \to 0^+$*;*

(ii) $\Phi(\mu)$ *is strictly decreasing for* μ *near* 0*;*

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(iii) $\Phi'(\mu)$ *changes sign at most once on* $(0, \infty)$;

(iv) $\lim_{\mu\to\infty} \Phi(\mu)$ *exists, where the limit may be infinite.*

Then, we can get an estimate of an upper bound of the spreading speed c^*.

Proposition 3.6. *Let* c^* *be the spreading speed of* Q_t *defined as in Theorem 3.4, and let* $\lambda(\mu)$ *and* $\Phi(\mu)$ *be defined as above. Then,*

$$c^* \le \inf_{\mu>0} \Phi(\mu) = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu}.$$

Proof. Clearly, the solution $(U(t,x), V(t,x))$ of (2.1) is a lower solution of (3.11), and hence, $Q_1(\phi) \le N_1(\phi)$ for any $\phi \in \mathcal{C}_{\mathbf{K}}$. It is easy to verify that N_1 and $\mathcal{B}^1_\mu$ satisfies (C1)–(C6) in [20]. By [20, Theorem 3.10], it suffices to show that the principal eigenvalue $\gamma(0)$ is greater than 1, and the infimum of $\Phi(\mu)$ is attained at some $\mu^* > 0$.

When $\mu = 0$, it follows from (3.13) that

$$\begin{aligned}\mathcal{P}(\lambda) &= \left(\lambda + d_m - \frac{\alpha e^{-d_i\tau}}{\omega} e^{-\lambda\tau}\right)\left(\lambda + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right) - \frac{d\alpha e^{-d_i\tau}\tilde{u}_+}{\omega(\tilde{u}_+ + \omega)} e^{-\lambda\tau}\\ &= \lambda^2 + \left(d_m + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right)\lambda + \left(1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right) d_m - \frac{\alpha e^{-d_i\tau}}{\omega}(\lambda + 1)e^{-\lambda\tau} = 0.\end{aligned}$$

Let

$$\begin{aligned} f_1(\lambda) &= \lambda^2 + \left(d_m + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right)\lambda + \left(1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right) d_m,\\ f_2(\lambda, \tau) &= \frac{\alpha e^{-d_i\tau}}{\omega}(\lambda + 1)e^{-\lambda\tau}.\end{aligned}$$

Since $d_m < \tilde{d}_m := \frac{\alpha e^{-d_i\tau}}{\omega}$ by (H2), we obtain

$$f_1(0) = \left(1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\right) d_m < f_2(0, \tau) = \frac{\alpha e^{-d_i\tau}}{\omega}.$$

It is easy to see that $\frac{\partial f_2(\lambda,\tau)}{\partial\lambda} = \frac{\alpha e^{-d_i\tau}}{\omega} e^{-\lambda\tau}(1 - \tau(\lambda + 1))$. Hence, if $\tau \ge 1$, then $\frac{\partial f_2(\lambda,\tau)}{\partial\lambda} \le 0$ for $\lambda \ge 0$. If $\tau < 1$, then $f_2(\lambda, \tau)$ reaches its unique local (thus global) maximum at $\lambda = \frac{1}{\tau} - 1$ and tends to 0 as $\lambda \to +\infty$. Moreover, $f_1(\lambda)$ is convex for $\lambda > 0$, while for any fixed $\tau > 0$, $f_2(\lambda, \tau)$ has at most one reflection point for $\lambda > 0$. Hence, there is a unique $\lambda^* > 0$ such that $f_1(\lambda^*) = f_2(\lambda^*, \tau)$ no matter what value τ takes. This implies that $\lambda(0) = \lambda^* > 0$, and hence, $\gamma(0) = e^{\lambda(0)} > 1$, i.e. the condition (C7) in [20] is satisfied.

We now prove that $\Phi(\mu)$ attains its infimum at some $\mu^* > 0$, which can be obtained by proving that $\lim_{\mu\to+\infty} \Phi(\mu) = +\infty$. By (3.13), we have

$$\begin{aligned}\mathcal{P}(\lambda) =& \lambda^2 + \left(d_m - D\tilde{J}(\mu) + D + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\tilde{k}(\mu)\right)\lambda\\ &+ \left(-D\tilde{J}(\mu) + D + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\tilde{k}(\mu)\right) d_m\\ &- \frac{\alpha e^{-d_i\tau}}{\omega}\tilde{k}(\mu)(\lambda - D\tilde{J}(\mu) + D + 1)e^{-\lambda\tau} = 0. \end{aligned} \tag{3.14}$$

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Let

$$f_3(\lambda) = \lambda^2 + \left(d_m - D\tilde{J}(\mu) + D + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\tilde{k}(\mu)\right)\lambda$$
$$+ \left(-D\tilde{J}(\mu) + D + 1 - \frac{d\tilde{u}_+}{\tilde{u}_+ + \omega}\tilde{k}(\mu)\right)d_m,$$
$$f_4(\lambda, \tau) = \frac{\alpha e^{-d_i\tau}}{\omega}\tilde{k}(\mu)(\lambda - D\tilde{J}(\mu) + D + 1)e^{-\lambda\tau}.$$

It is easy to compute that $\tilde{J}'(\mu) > 0$ for $\mu > 0$ and $\lim_{\mu\to+\infty}\tilde{J}(\mu) = +\infty$. Hence, for any large μ, we have

$$f_3\left(D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau}\right) < 0,$$
$$f_3'(\lambda) > 0, \quad \forall\lambda > D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau},$$
$$\lim_{\lambda\to+\infty} f_3(\lambda) = +\infty,$$

and

$$f_4\left(D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau}, \tau\right) > 0,$$
$$\frac{\partial f_4(\lambda, \tau)}{\partial\lambda} < 0, \quad \forall\lambda > D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau},$$
$$\lim_{\lambda\to+\infty} f_4(\lambda, \tau) = 0.$$

Thus, (3.14) has a unique positive root $\lambda(\mu) > D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau}$. Hence,

$$\lim_{\mu\to+\infty}\Phi(\mu) = \lim_{\mu\to+\infty}\frac{\lambda(\mu)}{\mu} \geq \lim_{\mu\to+\infty}\frac{D\tilde{J}(\mu) - D - 1 + \frac{1}{\tau}}{\mu} = +\infty.$$

The proof is complete. □

Next, we provide an estimate of the lower bound of the spreading speed c^*.

Proposition 3.7. *Let c^* be the spreading speed of Q_t defined as in Theorem 3.4. Then,*

$$c^* \geq \inf_{\mu>0}\Psi(\mu) = \inf_{\mu>0}\frac{\Lambda(\mu)}{\mu}.$$

Here, $\Lambda(\mu) = \max\{D\tilde{J}(\mu) - D - 1, \Lambda_2(\mu)\}$, where $\Lambda_2(\mu)$ is the unique positive root of $\mathcal{L}(\Lambda, \mu) := \Lambda + d_m - \frac{\alpha e^{-d_i\tau}\tilde{k}(\mu)}{\omega}e^{-\Lambda\tau} = 0$.

Proof. Choose any small $\varepsilon > 0$. Let P_t^ε be the solution operator of the following linear system:

$$\begin{cases} \dfrac{\partial U}{\partial t} = -d_m U + \alpha e^{-d_i\tau}\displaystyle\int_{\mathbb{R}} k(y)\frac{1}{\omega+\varepsilon}U(t-\tau, x-y)dy, \\ \dfrac{\partial V}{\partial t} = D\displaystyle\int_{\mathbb{R}} J(y)[V(t, x-y) - V(x, t)]dy - (1+\varepsilon)V \\ \qquad +d\displaystyle\int_{\mathbb{R}} k(y)\frac{1}{\omega+\varepsilon}U(t, x-y)dy, \end{cases} \tag{3.15}$$

where $t > 0$, $x \in \mathbb{R}$. By a similar argument as that in the proof of Proposition 3.6, we can obtain that P_t^ε satisfies (C1)–(C7) in [20]. Moreover, for any given $\varepsilon \in (0, 1)$, there exists $\delta = (\delta_1, \delta_2)$ such that the solution (U, V) of (3.15) satisfying

$$0 < U(t, x; \phi) < \varepsilon, \quad 0 < V(t, x; \phi) < \varepsilon, \quad t \in [0, 1],$$

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for any initial $\phi = (\phi_1, \phi_2)$ with $0 \le \phi_1 \le \delta_1$, $0 \le \phi_2 \le \delta_2$. Hence, $(U(t, x; \phi), V(t, x; \phi))$ satisfies

$$\begin{aligned}\frac{\partial U}{\partial t} &= -d_m U + \alpha e^{-d_i \tau} \int_{\Omega} k(y) \frac{U(t-\tau, x-y)}{U(t-\tau, x-y) + \omega}(V(t-\tau, x-y) + 1) dy \\ &\ge -d_m U + \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{1}{\omega + \varepsilon} U(t-\tau, x-y) dy, \quad t \in [0, 1],\end{aligned}$$

and

$$\begin{aligned}\frac{\partial V}{\partial t} &= D \int_{\mathbb{R}} J(y)[V(t, x-y) - V(t, x)]dy - V(1+V) \\ &\quad + d \int_{\Omega} k(y) \frac{U(t, x-y)}{U(t, x-y) + \omega}(V(t, x-y) + 1) dy \\ &\ge D \int_{\mathbb{R}} J(y)[V(t, x-y) - V(t, x)]dy - (1+\varepsilon)V \\ &\quad + d \int_{\mathbb{R}} k(y) \frac{1}{\omega + \varepsilon} U(t, x-y) dy, \quad t \in [0, 1].\end{aligned}$$

By the comparison principle, we obtain that $P_t^\varepsilon[\phi] \le Q_t[\phi]$ for $t \in [0, 1]$. In particular, $P_1^\varepsilon[\phi] \le Q_1[\phi]$ for $0 \le \phi_1 \le \delta_1$ and $0 \le \phi_2 \le \delta_2$. It then follows from [20, Theorem 3.10] that the spreading speed of P_t^ε can be attained by the infimum of $\Psi^\varepsilon(\mu) := \frac{\Lambda^\varepsilon(\mu)}{\mu}$, where $\Lambda^\varepsilon(\mu)$ is the principle eigenvalue of

$$\left(\Lambda + d_m - \frac{\alpha e^{-d_i \tau} \tilde{k}(\mu)}{\omega + \varepsilon} e^{-\Lambda \tau}\right)\left(\Lambda - D\tilde{J}(\mu) + D + 1 + \varepsilon\right) = 0,$$

which is the characteristic equation for the equation of η corresponding to (3.15). It is easy to verify that the statements in Lemma 3.5 also hold for $\Psi^\varepsilon(\mu)$. Then we obtain

$$c^* \ge \inf_{\mu > 0} \Psi^\varepsilon(\mu).$$

Since $\varepsilon > 0$ can be chosen arbitrarily, one further has

$$c^* \ge \inf_{\mu > 0} \Psi(\mu) = \inf_{\mu > 0} \frac{\Lambda(\mu)}{\mu},$$

where $\Lambda(\mu)$ is the principal eigenvalue of

$$\left(\Lambda + d_m - \frac{\alpha e^{-d_i \tau} \tilde{k}(\mu)}{\omega} e^{-\Lambda \tau}\right)\left(\Lambda - D\tilde{J}(\mu) + D + 1\right) = 0.$$

The proof is complete. □

Remark 3.8. For a fixed $\mu > 0$, we can compute that $\frac{\partial \mathcal{L}(\Lambda, \mu)}{\partial \Lambda} = 1 + \tau \frac{\alpha e^{-d_i \tau} \tilde{k}(\mu)}{\omega} e^{-\Lambda \tau} > 0$ and $\mathcal{L}(0, \mu) = d_m - \frac{\alpha e^{-d_i \tau} \tilde{k}(\mu)}{\omega}$. Since $d_m - \frac{\alpha e^{-d_i \tau}}{\omega} < 0$ by (H2) and $\tilde{k}(\mu) > 1$ for $\mu > 0$ by (H1), we have that $\mathcal{L}(0, \mu) < 0$. Hence, the existence and uniqueness of $\Lambda_2(\mu)$ can be easily obtained.

4. Travelling wavefronts

In this section, we shall prove the existence of travelling wavefronts with speed $c \ge c^*$, and nonexistence of travelling wavefronts with speed $c < c^*$, where c^* is the spreading speed defined in Section 3. A travelling wavefront of (2.1) is a monotone solution with the special form

$$U(t, x) = \varphi_1(\xi), \qquad V(t, x) = \varphi_2(\xi), \tag{4.1}$$

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where $\xi = x + ct$, $c > 0$ is the wave speed. Substituting (4.1) into (2.1) gives

$$\begin{cases} c\varphi_1' = -d_m\varphi_1 + \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\varphi_1(\xi-y-c\tau)}{\varphi_1(\xi-y-c\tau)+\omega} (\varphi_2(\xi - y - c\tau) + 1)dy, \\ c\varphi_2' = D \int_{\mathbb{R}} J(y)[\varphi_2(\xi - y) - \varphi_2(\xi)]dy - \varphi_2(1 + \varphi_2) \\ \qquad + d \int_{\mathbb{R}} k(y) \frac{\varphi_1(\xi-y)}{\varphi_1(\xi-y)+\omega} (\varphi_2(\xi - y) + 1)dy, \end{cases}$$

where $'$ denotes $\frac{d}{d\xi}$.

In Section 3, we have verified that the map Q_t satisfies (A1)–(A5). Then, the nonexistence of travelling wavefronts of (2.1) follows from [20, Theorem 4.3].

Theorem 4.1. *Assume that* (H1) *and hold. Then, for any* $0 < c < c^*$, *system* (2.1) *has no travelling wavefronts connecting* $\mathbf{0}$ *and* $\mathbf{K}$.

Since the solution map of (2.3) is not compact, we need to use the theory of travelling wavefronts developed in [8] for monotone semiflows with weak compactness to establish the existence of travelling wavefronts of (2.1). Let (X, X^+) be a Banach lattice with the norm $\|\cdot\|$ and the positive cone X^+. We use $\mathcal{M}$ to denote the set of all bounded and nondecreasing functions from $\mathbb{R}$ to X and equip $\mathcal{M}$ with the compact open topology. We use the Kuratowski measure of noncompactness in X (see e.g. [5]), which is defined by

$$\alpha(B) := \inf\{r : B \text{ has a finite cover of diameter } < r\}$$

for any bounded set B. It is easy to see that B is precompact (i.e. the closure of B is compact) if and only if $\alpha(B) = 0$. Let $\beta \in IntX^+ \neq \emptyset$. We define $X_\beta := \{u \in X : 0 \le u \le \beta\}$ and $\mathcal{M}_\beta := \{u \in \mathcal{M} : 0 \le u \le \beta\}$.

By employing arguments similar to those in Lemma 2.1, we can easily prove the following well-posedness result.

Lemma 4.2. *For any initial value* $\phi := (\phi_1, \phi_2) \in \mathcal{M}_{\mathbf{K}}$, *system* (2.3) *has a unique non-negative solution* $(U(t, x; \phi), V(t, x; \phi))$ *which exists globally in time* $t \ge -\tau$, *satisfying*

$$\mathbf{0} \le (U(t, x; \phi), V(t, x; \phi)) \le \mathbf{K}, \ \forall t \ge 0.$$

Definition 4.3. *A family of mappings* $\{Q_t\}_{t\ge 0}$ *is said to be a semiflow on* $\mathcal{M}_\beta$, *if the following three properties hold: (i)* $Q_0 = I$, *where* I *is the identity mapping; (ii)* $Q_t \circ Q_s = Q_{t+s}$ *for all* $t, s > 0$; *(iii)* $t_n \to t$ *and* $\phi_n \to \phi$ *in* $\mathcal{M}_\beta$, *then both* $Q_{t_n}[\phi](x) \to Q_t[\phi](x)$ *and* $Q_t[\phi_n](x) \to Q_t[\phi](x)$ *in* $\mathcal{M}_\beta$ *almost everywhere.*

Choose $X = \mathbb{R}^2$ and let Q_t be the solution mapping of system (2.3), i.e.

$$Q_t = (Q_t^{(1)}, Q_t^{(2)}) : \mathcal{M}_{\mathbf{K}} \to \mathcal{M}_{\mathbf{K}},$$

where

$$(Q_t^{(1)}, Q_t^{(2)})[\phi](\theta, x) = (U_t(\theta, x; \phi), V_t(\theta, x; \phi)), \ (\theta, x) \in [-\tau, 0] \times \mathbb{R}, \ t \ge 0,$$

where $\phi = (\phi_1, \phi_2) \in \mathcal{M}_{\mathbf{K}}$ and $(U(t, x; \phi), V(t, x; \phi))$ is the mild solution of system (2.3).

Clearly, the solution mapping $\{Q_t\}_{t\ge 0}$ is a semiflow on $\mathcal{M}_{\mathbf{K}}$. We need to verify that the solution semiflow Q_t satisfies the assumptions in [8] for each $t > 0$, which are listed as follows.

- **(B1)** $Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]]$, $T_y[Q[u]] = Q[T_y[u]]$, $\forall y \in \mathbb{R}$.
- **(B2)** $Q : \mathcal{M}_{\mathbf{K}} \to \mathcal{M}_{\mathbf{K}}$ is continuous with respect to the compact open topology.
- **(B3)** (Point-α-contraction) There exists $k \in [0, 1)$ such that for any $\mathcal{U} \subseteq \mathcal{M}_\beta$, $\alpha(Q[\mathcal{U}](0)) \le k\alpha(\mathcal{U}(0))$.
- **(B4)** Q:$\mathcal{M}_{\mathbf{K}} \to \mathcal{M}_{\mathbf{K}}$ is monotone in the sense that $Q[u] \ge Q(v)$ whenever $u \ge v$ in $\mathcal{M}_{\mathbf{K}}$.
- **(B5)** Q:$\bar{\mathcal{C}}_{\mathbf{K}} \to \bar{\mathcal{C}}_{\mathbf{K}}$ admits exactly two fixed points $\mathbf{0}$ and $\mathbf{K}$, and for any positive number ϵ, there is a $\zeta \in \bar{\mathcal{C}}_{\mathbf{K}}$ with $\|\zeta\| < \epsilon$ such that $Q[\zeta] \gg \zeta$, where $\|\cdot\|$ is the maximum norm in $\bar{\mathcal{C}}$.

Now we are in a position to prove the main result of this subsection.

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Theorem 4.4. *Assume that* (H1) *and* (H2) *hold, let c^* be the asymptotic spreading speed of Q_t defined as in Theorem 3.4. Then, for any $c \geq c^*$, system (2.1) admits a travelling wavefront $(\varphi_1(x+ct), \varphi_2(x+ct))$ connecting $\mathbf{0}$ and $\mathbf{K}$. Furthermore, $(\varphi_1(x+ct), \varphi_2(x+ct))$ is also a classical solution to* (2.1).

Proof. It is easy to see that each time-t map Q_t with $t > 0$ satisfies (B1), (B2), (B4) and (B5) with $Q = Q_t$. Thus, it remains to show that Q_t satisfies the weak compactness assumption (B3). We write $Q_t = L_t + S_t$, where

$$L_t[\phi](\theta, x) = \begin{cases} \phi(t+\theta, x) - \phi(0, x), & t+\theta < 0, \\ 0, & t+\theta \geq 0, \end{cases}$$

and

$$S_t[\phi](\theta, x) = \begin{cases} \phi(0, x), & t+\theta < 0, \\ Q_t[\phi](\theta, x), & t+\theta \geq 0. \end{cases}$$

For any bounded set $\mathcal{U}$ in $\mathcal{M}_{\mathbf{K}}$, the set $S_t[\mathcal{U}](\cdot, 0)$ is compact due to the uniform boundedness of the derivatives $(\partial_t U(t, 0; \phi), \partial_t V(t, 0; \phi))$ for $t > 0$ and $\phi \in \mathcal{U}$. On the other hand, by the α-contraction property of the solution map of delay differential equations (see e.g. [21]), there exists some constant $\gamma > 0$ such that $\alpha(L_t[\mathcal{U}](0)) \leq e^{-\gamma t}\alpha(\mathcal{U}(0))$. Then we obtain that

$$\alpha(Q_t[\mathcal{U}](0)) \leq \alpha(L_t[\mathcal{U}](0)) + \alpha(S_t[\mathcal{U}](0)) \leq e^{-\gamma t}\alpha(\mathcal{U}(0)),$$

for some positive $\gamma > 0$, which implies that Q_t satisfies $(B3)$ with $k = e^{-\gamma t}$. By [8, Theorem 3.8], it follows that Q_t admits a left-continuous travelling wavefront connecting $\mathbf{0}$ and $\mathbf{K}$.

Finally, we show that the obtained travelling wavefront $(\varphi_1(x+ct), \varphi_2(x+ct))$ for any $c \geq c^*$ is also a classical solution of (2.1). Note that

$$\varphi_2(x+ct) = P(t)[\varphi_2](x) + \int_0^t P(t-s)\tilde{\mathcal{F}}_2[\varphi_1, \varphi_2](x-cs)ds. \tag{4.2}$$

By the expression of $P(t)$, it is easy to calculate that

$$\frac{\partial[P(t)\phi](x)}{\partial t} = -D[P(t)\phi](x) + D\int_{\mathbb{R}} J(y)[P(t)\phi](x-y)dy,$$

which indicates that the right side of (4.2) is differential with respect to t. Hence, φ_2 is differentiable. On the other hand,

$$\varphi_1(x+ct) = \varphi_1(x) + \int_0^t (\tilde{\mathcal{F}}_1[\varphi_1, \varphi_2](x-cs) - d_m\varphi_1(x-cs))ds,$$

which implies φ_1' exists for any $x \in \mathbb{R}$. Hence, $(\varphi_1(x+ct), \varphi_2(x+ct))$ is also a classical solution to (2.1). The proof is complete. □

5. Conclusions

In this paper, we have studied the propagation dynamics of a mutualistic model of mistletoes and birds with nonlocal dispersal. We proved the well-posedness and the comparison principle for the initial value problem. We have also established the existence of the spreading speed and provided the upper and lower bound estimates of the spreading speed. In addition, the travelling wavefronts are considered again. Our result shows that the spreading speed coincides with the minimal wave speed of travelling wavefronts for this model. Our main methods are based on the comparison argument and the theory of asymptotic speeds of spread for the monotone semiflow developed in [8, 20].

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Competing interest. We declare that we have no Competing interest.

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