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TRAVELING WAVES OF A MUTUALISTIC MODEL OF MISTLETOES AND BIRDS

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Abstract. The existences of an asymptotic spreading speed and traveling wave solutions for a diffusive model which describes the interaction of mistletoe and bird populations with nonlocal diffusion and delay effect are proved by using monotone semiflow theory. The effects of different dispersal kernels on the asymptotic spreading speeds are investigated through concrete examples and simulations.

1. **Introduction.** Most mistletoes are vector-borne parasites whose vectors are their avian seed-dispersers [3]. In most vector-borne parasites and diseases, the vector maintains a parasitic, or, at best, a commensal relationship with the parasite. Mistletoes are unique among vector-borne parasites because they maintain a mutualistic interaction with their vectors [2, 3, 7]. Birds obtain nutrients, energy, and, in the desert, water from mistletoes. In turn, mistletoes receive directed movement of their propagules into safe germination sites [3].

Because of the apparently specialized nature of the interaction between mistletoes and birds, the dispersal of mistletoes has received considerable attention [2, 3, 7, 15]. A model describing the dynamics of mistletoes in an isolated patch assuming the birds are constant was considered in [14]. In order to better understand the interaction between mistletoes and the avian seed dispersers, a mathematical model which incorporated the spatial dispersal and interaction of mistletoes and birds was derived and studied in [17] to gain insights of the spatial heterogeneity in abundance of mistletoes. Fickian diffusion and chemotaxis were used to model

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the random movement of birds and the aggregation of birds due to the attraction of mistletoes, respectively. The spread of mistletoes by birds is expressed by a convolution integral with a dispersal kernel. A Holling type II functional response was used to model the process that fruits were removed by birds. And a time delay was introduced to model the maturation time of mistletoes. The model in [17] is a reaction-diffusion equation of bird population with chemotactic effect and nonlocal growth rate, coupled with a nonlocal delayed differential equation for the mistletoe population. With appropriate initial and boundary conditions, it takes the following form:

$$\begin{cases} \dfrac{\partial m}{\partial t} = \alpha e^{-d_i \tau} \displaystyle\int_{\Omega} k(x,y) \dfrac{m(t-\tau,y)b(t-\tau,y)}{m(t-\tau,y)+w} dy - d_m m, & x \in \overline{\Omega},\ t>0, \\ \dfrac{\partial b}{\partial t} = D\Delta b - \beta \nabla (b \nabla m) + b(1-b) + c \displaystyle\int_{\Omega} k(x,y) \dfrac{m(t,y)b(t,y)}{m(t,y)+w} dy, & x \in \Omega,\ t>0, \\ m(t,x) = m_0(t,x),\ b(t,x) = b_0(t,x), \quad x \in \Omega, & -\tau \le t \le 0, \\ (D\nabla b(t,x) - \beta b(t,x) \nabla m(t,x)) \cdot n(x) = 0, & x \in \partial\Omega. \end{cases} \tag{1}$$

Here, Ω is the spatial habitat for both the mistletoes and birds, $m(t,x)$ and $b(t,x)$ are the densities of mistletoes and birds at time t and location $x \in \Omega$, 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, c is the conversion rate from mistletoe fruits into bird population, and w is used to reflect the fact that birds may stop in other trees and structures irrelevant to the dynamic process of mistletoes. Apart from assuming logistic growth for birds population which measures the bird population growth due to other food resources besides mistletoes in the habitat, we assume that the birds make directed dispersal from lower to higher concentration of mistletoes, since the birds are attracted by the trees with more mistletoes. Hence a chemotactic term with $\beta > 0$ is included in the equation. The kernel function $k(x,y)$ describes the dispersal of mistletoe fruits by birds from location y to location x. Different types of kernel functions are used to investigate (1), showing that the spatial heterogenous patterns of the mistletoes are related to the specific dispersal pattern of birds which carry mistletoe seeds. A no-flux boundary condition is imposed for the bird population so that the birds are confined to the known habitat.

Besides the spatial pattern formation studies in [17], the spatial invasive spreading speeds of the mistletoes into new territories is of particular interest to the conservation biologists. In this article, we consider the traveling wave dynamics of (1) without the chemotactic effect ($\beta = 0$) in a linear habitat $\Omega = \mathbb{R}$, then system (1) turns into

$$\begin{cases} \dfrac{\partial m}{\partial t} = \alpha e^{-d_i \tau} \displaystyle\int_{\mathbb{R}} k(x,y) \dfrac{m(t-\tau,y)b(t-\tau,y)}{m(t-\tau,y)+w} dy - d_m m, & x \in \mathbb{R},\ t>0, \\ \dfrac{\partial b}{\partial t} = D b_{xx} + b(1-b) + c \displaystyle\int_{\mathbb{R}} k(x,y) \dfrac{m(t,y)b(t,y)}{m(t,y)+w} dy, & x \in \mathbb{R},\ t>0, \\ m(t,x) = m_0(t,x),\ b(t,x) = b_0(t,x), & x \in \mathbb{R},\ -\tau \le t \le 0. \end{cases} \tag{2}$$

The parameters $\alpha, d_i, d_m, D, c, w$ are assumed to be positive, and the time delay τ is assumed to be nonnegative. Throughout this paper, we also make the following assumptions.

$(H1)$ $d_m < \widetilde{d}_m := \dfrac{\alpha e^{-d_i \tau}}{w}$,

$(H2)$ $k(x,y) = k(x-y)$, $k : \mathbb{R} \to \mathbb{R}^+$ is piecewise continuous, $k(z) > 0$, $k(z) = k(-z)$ for any $z \in \mathbb{R}$, $\int_{\mathbb{R}} k(z)dz = 1$ and $\int_{\mathbb{R}} k(z)e^{\nu|z|}dz < \infty$ for any $\nu > 0$.

Under the assumption $(H1)$, it is known that (see [17]) (2) has a unique positive constant equilibrium (m_+, b_+), in addition to trivial constant equilibria $(0,0)$ and $(0,1)$. The kernel function $k(x,y)$ satisfying $(H2)$ is positive and symmetric, and the dispersal only depends on the distance between two points in the habitat. We also assume that the kernel function decays faster than an exponential function. Note that our theoretical results for the existence of asymptotical spreading speed and traveling wave are proved under the assumption that $k(z)$ is positive in $(H2)$, but these results may still hold if $k(z)$ is non-negative with a compact support set or finite dispersal range. In Section 5, an example of non-negative and compact support $k(z)$ is shown in numerical simulation along with a positive kernel example.

Our purpose in the current paper is to investigate the asymptotic spreading speed and traveling wave solutions of (2) under the assumptions $(H1)$ and $(H2)$, by using the theory of traveling waves for monotone semiflows developed in [6, 11] and related work. More precisely, we first prove the existence of the asymptotic spreading speed ρ^* of (2), which is later shown to be the minimal wave speed of traveling wave solution. The main results are summarized in the following theorem (the precise meaning of the asymptotic spreading speed is given in Section 3):

Theorem 1.1. *Assume that the parameters $\alpha, d_i, d_m, D, c, w$ are positive, the time delay τ is nonnegative, and the assumptions $(H1)$ and $(H2)$ hold. Then,*

(1) *there exists $\rho^* > 0$ which is the asymptotic spreading speed of (2).*
(2) *for any $\rho \geq \rho^*$, system (2) has a traveling wave $\phi(x+\rho t)$ connecting $(0,1)$ and the unique positive equilibrium (m_+, b_+) such that $\phi(s)$ is smooth and nondecreasing in s.*
(3) *there is no monotone traveling wave $\phi(x+\rho t)$ connecting $(0,1)$ and (m_+, b_+) of (2) for $0 < \rho < \rho^*$.*

We also create some constructive ways to estimate the lower and upper bounds of the asymptotic spreading speed ρ^* by using some auxiliary systems whose asymptotic spreading speeds can be more explicitly calculated (see Section 3). These lower and upper bounds can be numerically calculated by using the formulas derived in this paper (see Section 5 for more details).

There have been many recent work in asymptotic spreading speed and traveling wave solutions for cooperative reaction-diffusion systems. In [5, 8, 21, 22], traveling waves of partially degenerate reaction-diffusion systems were considered. The asymptotic spreading speed for cooperative systems was studied in [1, 9, 11, 12, 20], and the traveling waves of delayed cooperative systems were considered in [10, 13, 18, 19].

The remaining part of this paper is organized as follows. Section 2 is devoted to present the basic results on the equilibria of model (2) from [17] and to introduce some notations and assumptions for the traveling waves from [11]. In Section 3, we show the existence of the asymptotic spreading speed of (2) and provide some lower and upper bound estimates of the asymptotic spreading speed. In Section 4, the existence of traveling wave solutions is shown by using recently developed theory in [6], and the minimal wave speed coincides with the asymptotic spreading speed proved in Section 3. Some examples and numerical simulations are shown in Section 5 to illustrate the spreading dynamics of mistletoes and birds.

2. **Preliminaries.** First we recall the basic kinetic dynamics of (2) shown in [17]. Define $\widetilde{d}_m = \dfrac{\alpha e^{-d_i\tau}}{w}$ and $d_m^* = \dfrac{(1+c)^2\alpha}{4cwe^{d_i\tau}}$. It has been shown in [17] that the following results on the existence of equilibria hold.

Lemma 2.1. *Model (2) always has a trivial equilibrium $E_0 = (0,0)$ and a boundary equilibrium $E_1 = (0,1)$, and for the constant interior equilibria, there are two cases:*

1. *If $c > 1$, then for $d_m > d_m^*$, there is no positive equilibrium; for $d_m \in (\widetilde{d}_m, d_m^*)$, there are two positive equilibria $E_\pm$ of (2); for $d_m \in (0, \widetilde{d}_m]$, there is a unique positive equilibrium E_+.*
2. *If $0 < c \leq 1$, then for $d_m > \widetilde{d}_m$, there is no positive equilibrium; for $d_m \in (0, \widetilde{d}_m]$, there is a positive equilibrium E_+.*

It follows from Lemma 2.1 that under the assumption $(H1)$, (2) admits three equilibria

$$E_0 = (0,0), \quad E_1 = (0,1), \quad E_+ = (m_+, b_+),$$

where m_+ and b_+ are uniquely determined by

$$b = 1 + \frac{cm}{m+w}, \qquad \frac{d_m}{\alpha e^{-d_i\tau}}(m+w) = b. \tag{3}$$

Furthermore, E_0 and E_1 are unstable with respect to the corresponding kinetic model, while E_+ is locally asymptotically stable. Let $M = m$ and $B = b - 1$. Then (2) becomes:

$$\begin{cases} \dfrac{\partial M}{\partial t} = & \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(y) \frac{M(t-\tau, x-y)}{M(t-\tau, x-y) + w} \\ & (B(t-\tau, x-y) + 1)dy - d_m M, \quad x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial B}{\partial t} = & DB_{xx} - B(1+B) \\ & +c \displaystyle\int_{\mathbb{R}} k(y) \frac{M(t, x-y)}{M(t, x-y) + w} (B(t, x-y) + 1)dy, \quad x \in \mathbb{R},\ t > 0, \\ M(t,x) = & m_0(t,x) := \phi_1(t,x), \quad x \in \mathbb{R},\ -\tau \leq t \leq 0, \\ B(t,x) = & b_0(t,x) - 1 := \phi_2(t,x), \quad x \in \mathbb{R},\ -\tau \leq t \leq 0, \end{cases} \tag{4}$$

which has exactly two nonnegative equilibria under the assumption $(H1)$:

$$\mathbf{0} := (0,0), \qquad \mathbf{K} := (m_+, b_+ - 1).$$

The spatially homogeneous system associated with (4) is

$$\begin{cases} M' = \dfrac{\alpha e^{-d_i\tau} M(t-\tau)(B(t-\tau)+1)}{M(t-\tau) + w} - d_m M, \\ B' = -B(1+B) + \dfrac{cM(B+1)}{M+w}. \end{cases} \tag{5}$$

In order to prove the existence of traveling wave solutions of (2) connecting E_1 and E_+, it suffices to consider the traveling waves of (4) connecting $\mathbf{0}$ and $\mathbf{K}$, which belongs to the monostable case.

The proper phase space for (4) 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 $\overline{\mathcal{C}} := C([-\tau, 0], \mathbb{R}^2)$ (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 $u_i(\theta, x) \geq v_i(\theta, x)$

for $i = 1, 2$, $\theta \in [-\tau, 0]$ and $x \in \mathbb{R}$; $u > v$ if $u \geq v$ and $u \neq v$; and $u \gg v$ if $u_i(\theta, x) > v_i(\theta, x)$. For any $\mathbf{r} \in \mathbb{R}^2$ and $\mathbf{r} \geq 0$, define $\mathcal{C}_{\mathbf{r}} := \{\phi \in \mathcal{C} : \mathbf{r} \geq \phi \geq \mathbf{0}\}$ and $\overline{\mathcal{C}}_{\mathbf{r}} := \{\phi \in \overline{\mathcal{C}} : \mathbf{r} \geq \phi \geq \mathbf{0}\}$. The solution operator of (4) is defined by

$$\begin{aligned} Q_t(\phi)(\theta, x) &= (Q_t^1(\phi)(\theta, x), Q_t^2(\phi)(\theta, x)) \\ &= (M_t(\theta, x, \phi), B_t(\theta, x, \phi)), \quad \theta \in [-\tau, 0], x \in \mathbb{R}, \phi \in \mathcal{C}. \end{aligned} \tag{6}$$

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 $y \in \mathbb{R}$. In order to apply the theory in [11] to address the existence of an asymptotic spreading speed for (4), we need to verify that the solution operator Q_t defined in (6) at time $t = 1$ satisfies the following conditions.

$(A1)$ $Q_1[\mathcal{R}[u]] = \mathcal{R}[Q_1[u]]$ and $T_y[Q_1[u]] = Q_1[T_y[u]]$, for any $y \in \mathbb{R}$.

$(A2)$ $Q_1 : \mathcal{C}_{\mathbf{K}} \to \mathcal{C}_{\mathbf{K}}$ is continuous with respect to the compact open topology.

$(A3)$ One of the following two properties holds:

  (a) $\{Q_1[u](\cdot, x) : u \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is precompact in $\overline{\mathcal{C}}_{\mathbf{K}}$, or

  (b) Let X be the set of all bounded continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$. $Q_1[\mathcal{C}_{\mathbf{K}}](0, \cdot)$ is precompact in X, and there is a positive number $\varsigma \leq \tau$ such that $Q_1[u](\theta, x) = u(\theta + \varsigma, x)$ for $-\tau \leq \theta \leq -\varsigma$, and the operator

$$S[u](\theta, x) = \begin{cases} u(0, x), & -\tau \leq \theta \leq -\varsigma, \\ Q_1[u](\theta, x), & -\varsigma \leq \theta \leq 0, \end{cases} \tag{7}$$

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

$(A4)$ $Q_1 : \mathcal{C}_{\mathbf{K}} \to \mathcal{C}_{\mathbf{K}}$ is monotone in the sense that $Q_1[u] \leq Q_1[v]$ whenever $u \geq v$ in $\mathcal{C}_{\mathbf{K}}$.

$(A5)$ $Q_1 : \overline{\mathcal{C}}_{\mathbf{K}} \to \overline{\mathcal{C}}_{\mathbf{K}}$ admits exactly two fixed points $\mathbf{0}$ and $\mathbf{K}$, and for any positive number ϵ, there is $\zeta \in \overline{\mathcal{C}}_{\mathbf{K}}$ with $\|\zeta\| < \epsilon$ such that $Q_1[\zeta] \gg \zeta$, where $\|\cdot\|$ is the maximum norm in $\overline{\mathcal{C}}$.

3. **Asymptotic spreading speed.**

In this section, we show that the solution of (4) possesses an asymptotic spreading speed as defined in [11]. To apply the abstract theory in [11], we verify that Q_1 defined in (6) satisfies properties $(A1) - (A5)$ defined in Section 2. It is straightforward to verify that $(A1)$ holds, since $(M(t, -x), B(t, -x))$ and $(M(t, x - y), B(t, x - y))$ are also solutions of (4) provided that $(M(t, x), B(t, x))$ is a solution of (4) and $y \in \mathbb{R}$. To prove $(A2)$, we first prove the following existence, uniqueness and continuous dependence of solutions of (4) on the initial values.

Lemma 3.1. *For any* $\phi(\theta, x) = (\phi_1(\theta, x), \phi_2(\theta, x)) \in \mathcal{C}_{\mathbf{K}}$, *system* (4) *has a unique nonnegative solution* $(M(t, x, \phi), B(t, x, \phi))$ *with initial value* ϕ, *satisfying* $\mathbf{0} \leq (M(t, x, \phi), B(t, x, \phi)) \leq \mathbf{K}$ *for* $t \geq 0$.

Proof. Let δ be a fixed positive constant, and define the operator $F=(F_1,F_2)$ on $C([-\tau,\infty)\times\mathbb{R},\Theta)$, where $\Theta=[0,m_+]\times[0,b_+-1]$, by

$$F[M,B](t,x) = \begin{pmatrix} \delta M + \alpha e^{-d_i\tau}\int_{\mathbb{R}} k(y)\dfrac{M(t-\tau,x-y)}{M(t-\tau,x-y)+w}(B(t-\tau,x-y)+1)dy \\ \delta B - B^2 + c\int_{\mathbb{R}} k(y)\dfrac{M(t,x-y)}{M(t,x-y)+w}(B(t,x-y)+1)dy \end{pmatrix},$$

for $t\in(0,\infty)$ and $F[M(t,x),B(t,x)]=\phi(t,x)$ for $t\in[-\tau,0]$. So F is a nondecreasing map on $C([-\tau,\infty)\times\mathbb{R},\Theta)$ for a sufficiently large δ. In the following, we fix $\delta>0$ so that F is a nondecreasing map. Let $T(t)$, $t\geq 0$, be the solution operator generated by the Cauchy problem

$$\begin{cases} \dfrac{\partial B}{\partial t} = DB_{xx}-(\delta+1)B, & x\in\mathbb{R},\ t>0,\\ B(0,x)=\psi(x), & x\in\mathbb{R}, \end{cases}$$

in the space of bounded continuous functions on $\mathbb{R}$. In particular, we have

$$|T(t)\psi(x)| \leq \max_{x\in\mathbb{R}}|\psi(x)|e^{-(\delta+1)t},\quad x\in\mathbb{R}. \tag{8}$$

Then system (4) is equivalent to the following integral equations:

$$\begin{cases} M(t,x)=e^{-(\delta+d_m)t}\phi_1(0,x)+\displaystyle\int_0^t e^{-(\delta+d_m)(t-s)}F_1[M,B](s,x)ds := G_1[M,B](t,x),\\ B(t,x)=T(t)\phi_2(0,x)+\displaystyle\int_0^t T(t-s)F_2[M,B](s,x)ds := G_2[M,B](t,x), \end{cases} \tag{9}$$

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

$$\Gamma := \{(M,B)\in C([-\tau,\infty)\times\mathbb{R},\Theta) : M(\theta,x)=\phi_1(\theta,x),\ B(\theta,x)=\phi_2(\theta,x),\theta\in[-\tau,0]\}.$$

with the metric of Γ induced by the norm defined on $C([-\tau,\infty)\times\mathbb{R},\mathbb{R})$:

$$\|(M,B)\|_\lambda = \sup_{t\in[-\tau,0],x\in\mathbb{R}}(|M(t,x)|+|B(t,x)|) + \sup_{t\in\mathbb{R}_+,x\in\mathbb{R}}(|M(t,x)|+|B(t,x)|)e^{-\lambda t},\ \text{for } \lambda>0.$$

Suppose that $(M,B)\in\Gamma$. We observe that

$$\frac{F_1(m_+,b_+-1)}{\delta+d_m}=m_+,\quad\text{and}\quad \frac{F_2(m_+,b_+-1)}{\delta+1}=b_+-1. \tag{10}$$

By using (10) and the monotonicity of F, we obtain

$$\begin{aligned} 0\leq G_1[M,B](t,x) &\leq e^{-(\delta+d_m)t}\left[\phi_1(0,x)+F_1(m_+,b_+-1)\int_0^t e^{(\delta+d_m)s}ds\right]\\ &\leq e^{-(\delta+d_m)t}\left[\phi_1(0,x)-\frac{F_1(m_+,b_+-1)}{\delta+d_m}\right]+\frac{F_1(m_+,b_+-1)}{\delta+d_m}\\ &= e^{-(\delta+d_m)t}[\phi_1(0,x)-m_+]+m_+\leq m_+, \end{aligned}$$

and similarly, also by using (8),

$$0 \le G_2[M,B](t,x) \le e^{-(\delta+1)t}(b_+ - 1) + F_2(m_+, b_+ - 1)\int_0^t e^{-(\delta+1)(t-s)}ds$$
$$= \frac{F_2(m_+, b_+ - 1)}{\delta + 1} = b_+ - 1.$$

Hence $G(\Gamma) \subseteq \Gamma$. Moreover, for any $(M,B), (\bar{M},\bar{B}) \in \Gamma$,

$$\begin{aligned}
&|G_1[M,B] - G_1[\bar{M},\bar{B}]| \\
&\le \int_0^t \delta e^{-(\delta+d_m)(t-s)}|M-\bar{M}|(s,x)ds \\
&\quad + \int_0^t e^{-(\delta+d_m)(t-s)}\alpha e^{-d_i\tau}\int_{\mathbb{R}} k(y)\left|\frac{M(s-\tau,x-y)}{M(s-\tau,x-y)+w}(B(s-\tau,x-y)+1)\right. \\
&\quad \left.-\frac{\bar{M}(s-\tau,x-y)}{\bar{M}(s-\tau,x-y)+w}(\bar{B}(s-\tau,x-y)+1)\right| dyds \\
&\le \int_0^t \delta e^{-(\delta+d_m)(t-s)}|M-\bar{M}|(s,x)ds + \alpha e^{-d_i\tau}\int_0^t\int_{\mathbb{R}} e^{-(\delta+d_m)(t-s)}k(y) \\
&\quad \times \left[\frac{b_+}{w}|M-\bar{M}|(s-\tau,x-y) + |B-\bar{B}|(s-\tau,x-y)\right] dyds.
\end{aligned}$$

Therefore,

$$\begin{aligned}
&|G_1[M,B] - G_1[\bar{M},\bar{B}]|e^{-\lambda t} \\
&\le \int_0^t \delta e^{-(\delta+d_m+\lambda)(t-s)}e^{-\lambda s}|M-\bar{M}|(s,x)ds + \alpha e^{-d_i\tau}\int_0^t\int_{\mathbb{R}} e^{-(\delta+d_m+\lambda)(t-s)}k(y) \\
&\quad \times \left[\frac{b_+}{w}e^{-\lambda s}|M-\bar{M}|(s-\tau,x-y) + e^{-\lambda s}|B-\bar{B}|(s-\tau,x-y)\right] dyds.
\end{aligned} \tag{11}$$

Similarly we also have

$$\begin{aligned}
&|G_2[M,B] - G_2[\bar{M},\bar{B}]|e^{-\lambda t} \\
&\le \int_0^t (\delta + 2(b_+ - 1))e^{-(\delta+1+\lambda)(t-s)}e^{-\lambda s}|B-\bar{B}|(s,x)ds + c\int_0^t\int_{\mathbb{R}} e^{-(\delta+1+\lambda)(t-s)}k(y) \\
&\quad \times \left[\frac{b_+}{w}e^{-\lambda s}|M-\bar{M}|(s,x-y) + e^{-\lambda s}|B-\bar{B}|(s,x-y)\right] dyds.
\end{aligned} \tag{12}$$

Letting $A = \delta + 2(b_+ - 1) + (b_+ w^{-1} + 1)(\alpha e^{-d_i\tau} + c)$ and $\delta^0 = \delta + \min\{d_m, 1\}$, we get

$$\|G(M,B) - G(\bar{M},\bar{B})\|_\lambda \le 2A\int_0^t e^{-(\delta_0+\lambda)(t-s)}\|(M,B) - (\bar{M},\bar{B})\|_\lambda ds$$

$$\leq \frac{2A}{\delta_0+\lambda}\|(M,B)-(\bar{M},\bar{B})\|_\lambda.$$

We choose $\lambda > 0$ large enough so that G is a contraction in Γ. This implies the existence and uniqueness of solution to (4) from the contraction mapping principle. □

Now by using Lemma 3.1, we prove that the solution operator Q_t generates a semiflow on $\mathcal{C}_{\mathbf{K}}$ which implies $(A2)$.

Lemma 3.2. *Let Q_t be the solution operator of* (4) *defined in* (6)*. Then $\{Q_t\}_{t\geq 0}$ is a semiflow on $\mathcal{C}_{\mathbf{K}}$.*

Proof. We prove that Q_t is continuous in ϕ with respect to the compact open topology uniformly for $t\in[0,t_0]$ with $t_0>0$. Let $\tilde{T}(t)$ be the solution operator of the heat equation

$$\frac{\partial u}{\partial t}=D\triangle u,\ \ t>0,\ x\in\mathbb{R},\ \ u(0,x)=\psi(x),\ \ x\in\mathbb{R},$$

that is,

$$\tilde{T}(t)\psi(x)=\int_{\mathbb{R}}\frac{e^{\frac{-(x-y)^2}{4Dt}}}{\sqrt{4\pi Dt}}\psi(y)dy,\quad t>0,\ x\in\mathbb{R},$$

for any ψ in the set of all bounded continuous functions from $\mathbb{R}$ to $\mathbb{R}$. Then, system (4) can be rewritten into the following system of integral equations:

$$\begin{cases} M(t,x,\phi)=e^{-d_m t}\phi_1(0,x)+\int_0^t e^{-d_m(t-s)}\tilde{F}_1[M,B](s,x)ds:=\tilde{G}_1[M,B](t,x), \\ B(t,x,\phi)=\tilde{T}(t)\phi_2(0,x)+\int_0^t \tilde{T}(t-s)\tilde{F}_2[M,B](s,x)ds:=\tilde{G}_2[M,B](t,x), \end{cases} \tag{13}$$

where

$$\tilde{F}[M,B](t,x)=\begin{pmatrix} \alpha e^{-d_i\tau}\int_{\mathbb{R}}k(y)\frac{M(t-\tau,x-y)}{M(t-\tau,x-y)+w}(B(t-\tau,x-y)+1)dy \\ -B-B^2+c\int_{\mathbb{R}}k(y)\frac{M(t,x-y)}{M(t,x-y)+w}(B(t,x-y)+1)dy \end{pmatrix}.$$

Suppose that for $\phi^1=(\phi_1^1,\phi_2^1),\phi^2=(\phi_1^2,\phi_2^2)\in\mathcal{C}_{\mathbf{K}}$. Define

$$\begin{aligned} &\nu(t,x)=(\nu^1(t,x),\nu^2(t,x)),\\ &\nu^1(t,x)=|M(t,x,\phi^1)-M(t,x,\phi^2)|,\ \nu^2(t,x)=|B(t,x,\phi^1)-B(t,x,\phi^2)|,\\ &\Omega_N(z)=[-\tau,0]\times[z-N,z+N],\quad N>0,\ z\in\mathbb{R},\\ &|\phi|_{\Omega_N(z)}=\sup_{(\theta,x)\in\Omega_N(z)}|\phi_1(\theta,x)|+\sup_{(\theta,x)\in\Omega_N(z)}|\phi_2(\theta,x)|,\quad \text{for}\quad \phi=(\phi_1,\phi_2). \end{aligned}$$

Fix $t_0>0$ and $\varepsilon>0$. Let $k_0=(k_0^1,k_0^2)=\sup_{s\in[-\tau,t],x\in\mathbb{R}}(\nu^1(s,x),\nu^2(s,x))$. Set $\chi=\frac{(\alpha e^{-d_i\tau}+c)(b_++w)}{w}+(2b_+-1)$ and $\varepsilon_0=\frac{\varepsilon}{2\chi t_0e^{\chi t_0}}$. Then, there exists

(t^*, x^*) such that $\nu_s(\theta, x) \le k_0 \le \nu(t^*, x^*) + (\varepsilon_0, \varepsilon_0)$ for $(s, \theta, x) \in [0, t] \times [-\tau, 0] \times \mathbb{R}$. Choose $\eta = \dfrac{\varepsilon}{4e^{\chi t_0}}$ and $N = N(t_0, \varepsilon)$ such that for $0 \le s \le t$,

$$\int_{\mathbb{R}} k(y) \left[\frac{b_+}{w} \nu^1(s, x^* - y) + \nu^2(s, x^* - y) \right] dy \le \frac{b_+ + w}{w} |\nu_s|_{\Omega_N(x^*)} + \varepsilon_0.$$

With these choices, together with (11), (12) and (13), if $|\phi^1 - \phi^2|_{\Omega_N(x^*)} < \eta$, then

$$\begin{aligned}
&|\nu_t(\theta, x)|_{\Omega_N(x^*)} \\
\le& \nu^1(t^*, x^*) + \nu^2(t^*, x^*) + \varepsilon \\
\le& e^{-d_m t^*} \nu^1(0, x^*) + \nu^2(0, x^*) \\
&+ \alpha e^{-d_i \tau} \int_0^{t^*} \int_{\mathbb{R}} e^{-d_m (t^* - s)} k(y) \left[\frac{b_+}{w} \nu^1(s - \tau, x^* - y) + \nu^2(s - \tau, x^* - y) \right] dy ds \\
&+ \int_0^{t^*} (2b_+ - 1) \nu^2(s, x^*) ds + c \int_0^{t^*} \int_{\mathbb{R}} k(y) \left[\frac{b_+}{w} \nu^1(s, x^* - y) + \nu^2(s, x^* - y) \right] dy ds \\
\le& 2|\phi^1 - \phi^2|_{\Omega_N(x^*)} + (2b_+ - 1) \int_0^t (|\nu_s|_{\Omega_N(x^*)} + \varepsilon_0]) ds \\
&+ \frac{(\alpha e^{-d_i \tau} + c)(b_+ + w)}{w} \int_0^t (|\nu_s|_{\Omega_N(x^*)} + \varepsilon_0) ds \\
\le& 2\eta + \varepsilon_0 t \chi + \chi \int_0^t |\nu_s|_{\Omega_N(x^*)} ds.
\end{aligned}$$

Now the Gronwall's inequality implies that

$$|\nu_t(\theta, x)|_{\Omega_N(x^*)} \le (2\eta + \varepsilon_0 t \chi) e^{\chi t} \le (2\eta + \varepsilon_0 t_0 \chi) e^{\chi t_0} = \varepsilon,$$

for $t \in [0, t_0]$ when $|\phi^1 - \phi^2|_{\Omega_N(x^*)} < \eta$. This shows that Q_t is continuous in ϕ with respect to compact open topology uniformly for $t \in [0, t_0]$. By the continuity of Q_t in t from Lemma 3.1, it then follows that Q_t is continuous in (t, ϕ). □

In the next three lemmas, we prove that the solution map Q_1 satisfies the assumptions $(A3)$, $(A4)$ and $(A5)$. First we recall the following definition of upper and lower solutions (see for example [21]).

Definition 3.3. A function $(\overline{M}, \overline{B}) \in C^1([-\tau, \infty) \times \mathbb{R}, [0, m_+]) \times C^2([-\tau, \infty) \times \mathbb{R}, [0, b_+ - 1])$ is called an upper solution of (4) if it satisfies

$$\begin{cases}
\dfrac{\partial \overline{M}}{\partial t} \ge \alpha e^{-d_i \tau} \displaystyle\int_{\mathbb{R}} k(y) \frac{\overline{M}(t - \tau, x - y)}{\overline{M}(t - \tau, x - y) + w} (\overline{B}(t - \tau, x - y) + 1) dy - d_m \overline{M}(t, x), \\
\dfrac{\partial \overline{B}}{\partial t} \ge D \overline{B}_{xx} - \overline{B}(t, x)(1 + \overline{B}(t, x)) + c \displaystyle\int_{\mathbb{R}} k(y) \frac{\overline{M}(t, x - y)}{\overline{M}(t, x - y) + w} (\overline{B}(t, x - y) + 1) dy.
\end{cases} \tag{14}$$

for all $(t, x) \in [-\tau, \infty) \times \mathbb{R}$. A lower solution of (4) is defined in a similar way by reversing the inequalities in (14).

For a pair of upper and lower solutions of (4), the following comparison principle holds:

Lemma 3.4. *Let* $(\overline{M}, \overline{B})$ *and* $(\underline{M}, \underline{B})$ *be a pair of upper and lower solutions of* (4) *with* $\overline{M}(\theta, x) \geq \underline{M}(\theta, x)$ *and* $\overline{B}(\theta, x) \geq \underline{B}(\theta, x)$ *for* $\theta \in [-\tau, 0]$, $x \in \mathbb{R}$. *Then* $\overline{M}(t, x) \geq \underline{M}(t, x)$ *and* $\overline{B}(t, x) \geq \underline{B}(t, x)$ *for all* $t \geq 0$ *and* $x \in \mathbb{R}$.

Proof. Denote $v_1(t, x) = \overline{M}(t, x) - \underline{M}(t, x)$, $v_2(t, x) = \overline{B}(t, x) - \underline{B}(t, x)$ and

$$v(t) = \min_{i=1,2} \inf_{x \in \mathbb{R}} v_i(t, x), \ t \geq 0.$$

We now show that $v(t) \geq 0$ for all $t \geq 0$. If there exists a $t_0 > 0$ such that $v(t_0) < 0$, then there is a t_0 such that

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

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

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

Moreover, $\{x_k\}_{k=1}^{\infty}$ can be chosen properly as local minimums of $v_i(x, t_k)$, that is, $\frac{\partial v_i^2(t_k, x_k)}{\partial x^2} \geq 0$ if the second order partial derivative of v_i with respect to x exists. Then, a similar argument as in [21] gives

$$\frac{\partial v_i(t_k, x_k)}{\partial t} \leq \delta v_i(t_k, x_k).$$

If $i = 1$, we have

$$\begin{aligned}
0 \leq &\frac{\partial v_1(t_k, x_k)}{\partial t} + d_m v_1(t_k, x_k) \\
&- \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{\overline{M}(t_k - \tau, x_k - y)}{\overline{M}(t_k - \tau, x_k - y) + w} (\overline{B}(t_k - \tau, x_k - y) + 1) dy \\
&+ \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{\underline{M}(t_k - \tau, x_k - y)}{\underline{M}(t_k - \tau, x_k - y) + w} (\underline{B}(t_k - \tau, x_k - y) + 1) dy \\
\leq &(\delta + d_m) v_1(t_k, x_k) - \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{\overline{M}}{\overline{M} + w} v_2(t_k - \tau, x_k - y) dy \\
&- \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \frac{w(\underline{B} + 1)}{(\overline{M} + w)(\underline{M} + w)} v_1(t_k - \tau, x_k - y) dy \\
\leq &(\delta + d_m) v_1(t_k, x_k) - \alpha e^{-d_i \tau} \int_{\mathbb{R}} k(y) \left[\frac{m_+}{m_+ + w} + \frac{b_+}{w} \right] v(t_k) dy \\
\leq &(\delta + d_m) v_1(t_k, x_k) - \frac{\alpha e^{-d_i \tau} b_+}{w} v(t_k) < 0,
\end{aligned}$$

and if $i = 2$, we have

$$0 \leq \frac{\partial v_2(t_k, x_k)}{\partial t} - D \frac{\partial v_2^2(t_k, x_k)}{\partial x^2} + (1 + \overline{B} + \underline{B}) v_2(t_k, x_k)$$

$$
\begin{aligned}
&- c\int_{\mathbb{R}} k(y)\frac{\overline{M}(t_k,x_k-y)}{\overline{M}(t_k,x_k-y)+w}(\overline{B}(t_k,x_k-y)+1)dy\\
&+ c\int_{\mathbb{R}} k(y)\frac{\underline{M}(t_k,x_k-y)}{\underline{M}(t_k,x_k-y)+w}(\underline{B}(t_k,x_k-y)+1)dy\\
\le&(\delta+1+\overline{B}+\underline{B})v_2(t_k,x_k)\\
&- c\int_{\mathbb{R}} k(y)\left[\frac{\overline{M}}{\overline{M}+w}v_2(t_k,x_k-y)+\frac{w(\underline{B}+1)}{(\overline{M}+w)(\underline{M}+w)}v_1(t_k,x_k-y)\right]dy\\
\le&(\delta+1+\overline{B}+\underline{B})v_2(t_k,x_k)-c\int_{\mathbb{R}} k(y)\left[\frac{m_+}{m_++w}+\frac{b_+}{w}\right]v(t_k)dy\\
\le&(\delta+1+\overline{B}+\underline{B})v_2(t_k,x_k)-\frac{cb_+}{w}v(t_k)<0,
\end{aligned}
$$

for sufficient large k and δ, which is a contradiction. □

We observe that the property $(A4)$ can be guaranteed by Lemma 3.4. Also the comparison principle in Lemma 3.4 implies the following positivity result for the solution of (4).

Corollary 3.5. *For any $\phi \in \mathcal{C}_{\mathbf{K}}$ with $\phi \not\equiv 0$, let $(M(t,x,\phi), B(t,x,\phi))$ be the solution of (4) with initial condition ϕ. Then there exists $t = t(\phi) > 0$ such that $M(t,x,\phi) > 0$ and $B(t,x,\phi) > 0$ for any $t > t(\phi)$, $x \in \mathbb{R}$.*

Proof. Comparing the second equation of (4) with

$$
\begin{cases}
\dfrac{\partial U}{\partial t} = \triangle U - U(1+U), & x\in\mathbb{R},\ t>0,\\
U(0,x)=\phi_2(0,x), & x\in\mathbb{R},
\end{cases}
\tag{15}
$$

from Lemma 3.4, we know that $B(t,x) \ge U(t,x) > 0$ for $t > 0$ and $x \in \mathbb{R}$, since each solution of (15) is positive provided the initial condition is nonnegative. Now we claim that there exists a $t_0 \in [0,\tau]$ such that $M(t_0,x) \not\equiv 0$ for all $x \in \mathbb{R}$. Assume, by contradiction, that $M(t,x) \equiv 0$ for all t and x. From the first equation in (9), we have $\phi_1(t,x) \equiv 0$ for $t \in [-\tau, 0]$ and $x \in \mathbb{R}$, which is a contradiction. Then, for $t \in [t_0, t_0+\tau]$, $M(t,x) \not\equiv 0$ for all $x \in \mathbb{R}$, since $\frac{\partial M}{\partial t} \ge -d_m M$. From M's equation in (4), we know that

$$
\begin{aligned}
&M(t,x)\\
\ge&\int_0^t e^{-d_m(t-s)}\left[\alpha e^{-d_i\tau}\int_{\mathbb{R}} k(y)\frac{M(s-\tau,x-y)}{M(s-\tau,x-y)+w}(B(s-\tau,x-y)+1)dy\right]ds,
\end{aligned}
$$

Let $t(\phi) = t_0 + \tau$. It follows from the inequality above that $M(t,x) > 0$ for $t > t(\phi)$, $x \in \mathbb{R}$. □

Now we are ready to prove the property $(A3)$ and $(A5)$ in the next two lemmas.

Lemma 3.6. *Q_1 satisfies $(A3)(a)$ if $\tau \le 1$, and satisfies $(A3)(b)$ if $\tau > 1$.*

Proof. By Lemma 3.1, it follows that all solutions of (4) are bounded with initial value $\phi \in \mathcal{C}_{\mathbf{K}}$. Since there is no diffusion term in M's equation of (4), it is immediate that $\frac{\partial M}{\partial t}$ is bounded for $t \ge 0$. By the Arzela-Ascoli Theorem, we obtain that $\{Q_t^1[u](\cdot,x) : u \in \mathcal{C}_{\mathbf{K}}, x \in \mathbb{R}\}$ is precompact in $C([-\tau,0],\mathbb{R})$ if $t \ge \tau$. Therefore, Q_t^1

satisfies $(A3)(a)$ for $t \geq \tau$. 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 (7). It is obvious that $\{S^1[\Pi](\theta, 0) : \theta \in [-\tau, -\varsigma]\}$ is an infinite set of constant functions in $C([-\tau, -\varsigma], \mathbb{R})$, hence it is precompact in $C([-\tau, -\varsigma], \mathbb{R})$. Thus, Q_t^1 satisfies $(A3)(b)$ for $t < \tau$.

For Q_t^2, similar arguments in Lemma 2.3 in [4] imply that $Q_t^2[\mathcal{C}_{\mathbf{K}}]$ is precompact in $C([-\tau, 0] \times \mathbb{R}, \mathbb{R})$ if $t \geq \tau$, and if $t < \tau$, $S^2[\Pi]$ is precompact in $C([-\tau, 0] \times \mathbb{R}, \mathbb{R})$ for any T-invariant set $\Pi \subset \mathcal{C}_{\mathbf{K}}$ with $\Pi(0, \cdot)$ precompact in X. This proves that Q_t^2 satisfies $(A3)(a)$ if $t \geq \tau$ and $(A3)(b)$ if $t < \tau$, which completes the proof of the lemma. □

Lemma 3.7. *For each $t > 0$, Q_t satisfies $(A5)$.*

Proof. Let $\hat{Q}_t$ be the restriction of Q_t on $\bar{\mathcal{C}}$. Then $\hat{Q}_t$ is the semiflow generated by (5). Since (5) is a cooperative and irreducible system, it follows from Corollary 5.3.5 in [16] that $\mathbf{K}$ is a globally asymptotically stable equilibrium in $\bar{\mathcal{C}} \backslash \{\mathbf{0}\}$, and $\hat{Q}_t$ is a strongly monotone semiflow on $\bar{\mathcal{C}}$. By the Dancer-Hess connecting orbit lemma (see [23]), it follows that $\hat{Q}_t$ admits a strongly monotone full orbit connecting $\mathbf{0}$ and $\mathbf{K}$. For any positive number ϵ, there exists $\zeta \in \overline{\mathcal{C}}_{\mathbf{K}}$ with $\|\zeta\| < \epsilon$ such that $Q_1[\zeta] = \hat{Q}_t[\zeta] \gg \zeta$, and hence, Q_t satisfies $(A5)$. □

Now with all properties $(A1)$-$(A5)$ proved, we are ready to apply the general theory in [11, Theorem 2.17] to show that the map Q_1 has an asymptotic spreading speed ρ^*, which is also the asymptotic spreading speed of solutions to (2) in the following sense.

Theorem 3.8. *Assume that $(H1)$ and $(H2)$ hold, then there exists an asymptotic spreading speed ρ^* of Q_t, in the following sense:*

(1) For any $\rho > \rho^*$, 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

$$\lim_{t\to\infty, |x|\geq t\rho} M(t, x, \phi) = \lim_{t\to\infty, |x|\geq t\rho} B(t, x, \phi) = 0.$$

(2) For any $\rho < \rho^*$ and any $\sigma \in \bar{\mathcal{C}}_{\mathbf{K}}$ with $\sigma \gg 0$, there is 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

$$\lim_{t\to\infty, |x|\leq t\rho} M(t, x, \phi) = m_+, \quad \text{and} \quad \lim_{t\to\infty, |x|\leq t\rho} B(t, x, \phi) = b_+ - 1.$$

Next we give an estimate of the upper bound of the asymptotic spreading speed ρ^* by computing the spreading speed of a linear reaction diffusion system, which will be used later on to show the existence of traveling wave solutions with upper and lower solution method. First we consider the following linear system:

$$\begin{cases} \dfrac{\partial M}{\partial t} = & \alpha e^{-d_i\tau} \int\limits_{\mathbb{R}} k(y) \left[\dfrac{1}{w} M(t-\tau, x-y) + \dfrac{m_+}{m_+ + w} B(t-\tau, x-y) \right] dy \\ & -d_m M, \qquad x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial B}{\partial t} = & DB_{xx} - B \\ & +c \displaystyle\int_{\mathbb{R}} k(y) \left[\dfrac{1}{w} M(t, x-y) + \dfrac{m_+}{m_+ + w} B(t, x-y) \right] dy, \qquad x \in \mathbb{R},\ t > 0. \end{cases} \tag{16}$$

For any $\mu \in \mathbb{R}_+$, define $M(t,x) = e^{-\mu x}\eta_1(t)$, $B(t,x) = e^{-\mu x}\eta_2(t)$. Then $\eta = (\eta_1, \eta_2)$ satisfies

$$\eta'(t) = U\eta(t) + V\eta(t-\tau), \tag{17}$$

where

$$U = \begin{pmatrix} -d_m & 0 \\ \dfrac{cA(\mu)}{w} & D\mu^2 - 1 + \dfrac{cm_+ A(\mu)}{m_+ + w} \end{pmatrix}, \tag{18}$$

and

$$V = \begin{pmatrix} \dfrac{\alpha e^{-d_i\tau}A(\mu)}{w} & \dfrac{m_+\alpha e^{-d_i\tau}A(\mu)}{m_+ + w} \\ 0 & 0 \end{pmatrix}. \tag{19}$$

where $A(\mu) = \int_{\mathbb{R}} k(y)e^{\mu y}dy < \infty$ for any $\mu > 0$. If $\eta(t)$ is a solution of (17), then $e^{-\mu x}\eta(t)$ is a solution of (16). Define

$$\mathcal{B}_\mu^t(\eta^0) := N_t(\eta^0 e^{-\mu x})(0) = \eta(t, \eta^0), \tag{20}$$

where N_t is the solution operator of (16), and $\eta(t,\eta^0)$ is the solution of (17) with $\eta^0 = \eta(\theta)$ for $\theta \in [-\tau, 0]$. Since system (17) is cooperative and irreducible, we know from [16, Theorem 5.1] that its characteristic equation

$$\Delta(\lambda) = \det(\lambda I - U - Ve^{-\lambda\tau}) = 0 \tag{21}$$

have a real root $\lambda(\mu) > 0$, and the real parts of all other roots are less than $\lambda(\mu)$. Let $q = (q_1(\theta), q_2(\theta))$ be the eigenfunction of the infinitesimal generator corresponding to $\lambda(\mu)$. In fact, u can take the form $(q_1(\theta), q_2(\theta)) = (q_{10}e^{\lambda(\mu)\theta}, q_{20}e^{\lambda(\mu)\theta})$ with $q_{10}, q_{20} > 0$, $\theta \in [-\tau, 0]$. Then $e^{\lambda(\mu)t}$ is the principal eigenvalue of $\mathcal{B}_\mu^t$ with eigenfunction q. In particular, $\gamma(\mu) := e^{\lambda(\mu)}$ is the eigenvalue of $\mathcal{B}_\mu^1$. Define

$$\Phi(\mu) := \frac{1}{\mu}\ln\gamma(\mu) = \frac{\lambda(\mu)}{\mu}, \text{ for } \mu \in \mathbb{R}_+. \tag{22}$$

By using [11, Lemma 3.8], we have the following properties of $\Phi(\mu)$.

Lemma 3.9. *Let U and V be defined as in (18) and (19), and let $\lambda(\mu)$, $\gamma(\mu)$ and $\Phi(\mu)$ be defined as above. Then we have the following characteristics of $\Phi(\mu)$:*

(1) $\Phi(\mu) \to \infty$ as $\mu \to 0^+$;
(2) $\Phi(\mu)$ is strictly decreasing for μ near 0;
(3) $\Phi'(\mu)$ changes sign at most once on $(0, \infty)$;
(4) $\lim_{\mu\to\infty} \Phi(\mu)$ exists, where the limit may be infinite.

Now the following proposition provides an estimate of an upper bound of the asymptotic speed of spread ρ^*.

Proposition 3.10. *Let ρ^* be the asymptotic spreading speed of Q_t defined as in Theorem 3.8, and let $\lambda(\mu)$, $\gamma(\mu)$ and $\Phi(\mu)$ be defined as above. Then*

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

Proof. Suppose that $(M(t,x), B(t,x))$ is the solution of (4) with initial condition $\phi \in C_{\mathbf{K}}$. It is easy to verify that it is a lower solution of (16), which implies $Q_1(\phi) \leq N_1(\phi)$ for any $\phi \in C_{\mathbf{K}}$. Also note that N_1 and $\mathcal{B}_\mu^1$ satisfies $(C1)$-$(C6)$ in [11]. By Theorem 3.10 in [11], it suffices to show that the principal eigenvalue $\gamma(0)$

is greater than 1, and the infimum of $\Phi(\mu)$ is attained at some positive $\mu^* > 0$. For $\mu = 0$, (21) becomes

$$\begin{aligned}\Delta(\lambda) &= (\lambda + d_m - \frac{\alpha e^{-d_i\tau}}{w} e^{-\lambda\tau})(\lambda + 1 - \frac{cm_+}{m_+ + w}) - \frac{cm_+\alpha e^{-d_i\tau}}{w(m_+ + w)} e^{-\lambda\tau} \\ &= \lambda^2 + (d_m + 1 - \frac{cm_+}{m_+ + w})\lambda + (1 - \frac{cm_+}{m_+ + w})d_m - \frac{\alpha e^{-d_i\tau}}{w}(\lambda + 1)e^{-\lambda\tau} = 0.\end{aligned}$$

Let

$$\begin{aligned}h_1(\lambda) &= \lambda^2 + (d_m + 1 - \frac{cm_+}{m_+ + w})\lambda + (1 - \frac{cm_+}{m_+ + w})d_m, \\ h_2(\lambda, \tau) &= \frac{\alpha e^{-d_i\tau}}{w}(\lambda + 1)e^{-\lambda\tau}.\end{aligned}$$

Then we have $h_1(0) = (1 - \frac{cm_+}{m_+ + w})d_m < h_2(0, \tau) = \frac{\alpha e^{-d_i\tau}}{w}$, since $d_m < \tilde{d}_m := \frac{\alpha e^{-d_i\tau}}{w}$. If $\tau \geq 1$, we have $\frac{\partial h_2}{\partial \lambda} \leq 0$ for $\lambda \geq 0$. If $\tau < 1$, then $h_2(\lambda, \tau)$ reaches its unique local (thus global) maximum at $\lambda = \frac{1}{\tau} - 1$ and tends to 0 as $\lambda \to +\infty$. Moreover $h_1(\lambda)$ is convex for $\lambda > 0$, while for any fixed $\tau > 0$, $h_2(\lambda, \tau)$ has at most one reflection point for $\lambda > 0$. Accordingly, there is a unique $\lambda^* > 0$ such that $h_1(\lambda^*) = h_2(\lambda^*, \tau)$ no matter what value τ takes. This implies that $\lambda(0) = \lambda^* > 0$, and hence $\gamma(0) > 1$, *i.e.* the condition (C7) in [11] is satisfied.

It remains to show that $\Phi(\mu)$ attains its infimum at some $\mu^* > 0$. This is accomplished by proving that $\lim_{\mu\to\infty} \Phi(\mu) = \infty$. From (21),

$$\begin{aligned}\Delta(\lambda) &= \lambda^2 + (d_m - D\mu^2 + 1 - \frac{cm_+}{m_+ + w}A(\mu))\lambda + (-D\mu^2 + 1 - \frac{cm_+}{m_+ + w}A(\mu))d_m \\ &\quad - \frac{\alpha e^{-d_i\tau}}{w}A(\mu)(\lambda - D\mu^2 + 1)e^{-\lambda\tau} = 0,\end{aligned} \tag{23}$$

Similar as above, we define

$$\begin{aligned}h_3(\lambda) &= \lambda^2 + (-D\mu^2 + d_m + 1 - \frac{cm_+}{m_+ + w}A(\mu))\lambda + (-D\mu^2 + 1 - \frac{cm_+}{m_+ + w}A(\mu))d_m, \\ h_4(\lambda, \tau) &= \frac{\alpha e^{-d_i\tau}}{w}A(\mu)(\lambda - D\mu^2 + 1)e^{-\lambda\tau}.\end{aligned}$$

For any large μ, we have $h_3(D\mu^2 - 1 + \tau^{-1}) < 0$, $h_3'(\lambda) > 0$ for $\lambda > D\mu^2 - 1 + \tau^{-1}$ and $\lim_{\lambda\to\infty} h_3(\lambda) = \infty$. Also, $h_4(D\mu^2 - 1 + \tau^{-1}, \tau) > 0$, $\frac{\partial h_4(\lambda, \tau)}{\partial \lambda} < 0$ for $\lambda > D\mu^2 - 1 + \tau^{-1}$, and $\lim_{\lambda\to+\infty} h_4(\lambda, \tau) = 0$. So (23) admits a unique positive root $\lambda(\mu) > D\mu^2 - 1 + \tau^{-1}$. Therefore, $\lim_{\mu\to\infty} \Phi(\mu) = \lim_{\mu\to\infty} \frac{\lambda(\mu)}{\mu} = \infty$. ☐

Finally we provide an estimate of the lower bound of the asymptotic spreading speed ρ^* of (2). Choose any small $\varepsilon > 0$. Let P_t^ε, $t \geq 0$, be the solution operator of the following linear system:

$$\begin{cases}\dfrac{\partial M}{\partial t} = \alpha e^{-d_i\tau} \displaystyle\int_{\mathbb{R}} k(y)\frac{1}{w + \varepsilon}M(t - \tau, x - y)dy - d_m M, & x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial B}{\partial t} = DB_{xx} - (1 + \varepsilon)B + c\displaystyle\int_{\mathbb{R}} k(y)\frac{1}{w + \varepsilon}M(t, x - y)dy. & x \in \mathbb{R},\ t > 0.\end{cases} \tag{24}$$

Similar arguments as in the proof of Proposition 3.10 show that P_t^ε also satisfies $(C1)$-$(C7)$ in [11]. Moreover, for given $\varepsilon \in (0,1)$, there exists $\epsilon = (\epsilon_1, \epsilon_2)$ such that the solution (M, B) of (24) satisfying

$$0 < M(t,x,u) < \varepsilon,\ 0 < B(t,x,u) < \varepsilon,\ t \in [0,1],$$

for any initial $u = (u_1, u_2)$ with $0 \le u_1 \le \epsilon_1$, $0 \le u_2 \le \epsilon_2$. Thus $(M(t,x,u), B(t,x,u))$ satisfies

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

and

$$\begin{aligned}\frac{\partial B}{\partial t} &= DB_{xx} - B(1+B) + c\int_{\mathbb{R}} k(y)\frac{M(t,x-y)}{M(t,x-y)+w}(B(t,x-y)+1)dy \\ &\ge DB_{xx} - (1+\varepsilon)B + c\int_{\mathbb{R}} k(y)\frac{1}{w+\varepsilon}M(t,x-y)dy,\ t\in[0,1].\end{aligned}$$

The comparison principle implies that $P_t^\varepsilon[u] \le Q_t[u]$ for $t \in [0,1]$. In particular, $P_1^\varepsilon[u] \le Q_1[u]$ for $0 \le u_1 \le \epsilon_1$, $0 \le u_2 \le \epsilon_2$. By using Theorem 3.10 in [11] again, we know that the asymptotic spreading speed of P_t^ε is attained by the infimum of $\Psi^\varepsilon(\mu) := \dfrac{\Lambda^\varepsilon(\mu)}{\mu}$, and $\Lambda^\varepsilon(\mu)$ is the principal eigenvalue of

$$\left(\Lambda + d_m - \frac{\alpha e^{-d_i\tau}A(\mu)}{w+\varepsilon}e^{-\Lambda\tau}\right)(\Lambda - D\mu^2 + 1 + \varepsilon) = 0, \tag{25}$$

which is the characteristic equation for the equation of η corresponding to (24). One can show that results in Lemma 3.9 also hold for $\Psi^\varepsilon(\mu)$. Moreover from the comparison argument above, we have

$$\rho^* \ge \inf_{\mu>0} \Psi^\varepsilon(\mu), \tag{26}$$

which provides a lower bound of the asymptotic spreading speed of (2). Since $\varepsilon > 0$ can be chosen arbitrarily, then indeed we have

$$\rho^* \ge \inf_{\mu>0} \Psi(\mu) = \inf_{\mu>0} \frac{\Lambda(\mu)}{\mu}, \tag{27}$$

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

$$\left(\Lambda + d_m - \frac{\alpha e^{-d_i\tau}A(\mu)}{w}e^{-\Lambda\tau}\right)(\Lambda - D\mu^2 + 1) = 0. \tag{28}$$

In summary we obtain the following result for the lower bound of the asymptotic spreading speed ρ^*:

Proposition 3.11. *Let ρ^* be the asymptotic spreading speed of Q_t defined as in Theorem 3.8, and let $\Lambda(\mu)$ and $\Psi(\mu)$ be defined as above. Then*

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

In particular, $\Lambda(\mu) = \max\{D\mu^2 - 1, \Lambda_2(\mu)\}$ *where* $\Lambda_2(\mu)$ *is the unique positive number satisfying* $f(\Lambda, \mu) := \Lambda + d_m - \dfrac{\alpha e^{-d_i\tau} A(\mu)}{w} e^{-\Lambda\tau} = 0.$

For a fixed $\mu > 0$, the existence and uniqueness of $\Lambda_2(\mu)$ follows easily from the monotonicity of the function $f(\Lambda, \mu)$ in Λ, the assumption $(H1)$ that $d_m - \dfrac{\alpha e^{-d_i\tau}}{w} = d_m - \tilde{d}_m < 0$ and the assumption $(H2)$ that $A(\mu) > 1$ for $\mu > 0$.

The results in Propositions 3.10 and 3.11 imply that $\rho^*(c) \geq \rho^*(0)$ for $c > 0$, since $\rho^*(0)$ is a lower bound of $\rho^*(c)$ for positive c. This suggests that the additional birth of the birds due to mistletoes will speed up the spreading of the mistletoe and bird into new territory.

4. Traveling wave.

In this section we prove the existence of traveling wave solutions with speed $\rho \geq \rho^*$, where ρ^* is the asymptotic spreading speed defined in Section 3. A traveling wave front of (4) is a solution with the special from

$$M(t, x) = \phi_1(x + \rho t) := \phi_1(s),\ B(t, x) = \phi_2(x + \rho t) := \phi_2(s), \tag{29}$$

where $\rho > 0$ is the wave speed. Substituting (29) into (4) gives

$$\begin{aligned} \rho\phi_1' &= \alpha e^{-d_i\tau} \int_{\mathbb{R}} k(y) \frac{\phi_1(s - y - \rho\tau)}{\phi_1(s - y - \rho\tau) + w} (\phi_2(s - y - \rho\tau) + 1) dy - d_m\phi_1, \\ \rho\phi_2' &= D\phi_2'' - \phi_2(1 + \phi_2) + c \int_{\mathbb{R}} k(y) \frac{\phi_1(s - y)}{\phi_1(s - y) + w} (\phi_2(s - y) + 1) dy, \end{aligned} \tag{30}$$

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

The existence of traveling wave solution is proved using the newly developed theory in [6], even though the system is not linearly determined. Note that the solution operator Q_t fails to be compact for any $t > 0$ due to time delay and the absence of diffusion term for the mistletoe's equation. We have the following result regarding the existence of traveling wave solutions for any $\rho \geq \rho^*$, the asymptotic spreading speed.

Theorem 4.1. *Assume that* $(H1)$ *and* $(H2)$ *hold, and let* ρ^* *be the asymptotic spreading speed of* Q_t *defined as in Theorem 3.8. Then for any* $\rho \geq \rho_*$*, system* (4) *has a monotone traveling wave solution connecting* $\mathbf{0}$ *and* $\mathbf{K}$ *with wave speed* ρ*, and for* $0 < \rho < \rho^*$*, system* (4) *has no monotone traveling wave solution connecting* $\mathbf{0}$ *and* $\mathbf{K}$*. That is, the asymptotic spreading speed* ρ^* *is also the minimal wave speed for the monotone traveling waves. Furthermore, these traveling waves are also classical solutions to* (4).

Proof. We apply the abstract theory in [6]. In Section 3, we have proved the existence of an asymptotic spreading speed ρ^* following the theory in [11] by showing that assumptions $(A1)$-$(A5)$ in Section 2 are satisfied. Note that Theorem 4.1 in [6] requires conditions $(A1)$, $(A2')$ and $(A3)$-$(A5)$ of paper [6], which are not exactly the same ones in Section 2 here. Comparing the conditions, we can see that $(A1)$, $(A4)$ and $(A5)$ in Section 2 (or [11]) and the ones in [6] are exactly same. The condition $(A2')$ in [6] can be proved for our situation by using arguments in the proof of Lemmas 3.1 and 3.2. Hence we only need to verify the assumption $(A3)$ in [6]. It is sufficient to show that the solution operator Q_t satisfies a certain compactness property (point-α-contraction), that is, there exits $k \in [0, 1)$ such that for any $u \in \mathcal{M}$, $\alpha(Q_t[u](0)) \leq k\alpha(u(0))$, for $t > 0$, where $\mathcal{M}$ is the set of all non-decreasing and bounded functions from $\mathbb{R}$ to $\overline{\mathcal{C}}$, and $\alpha(\cdot)$ is the Kuratowski measure for a bounded set in $C([-\tau, 0], \mathbb{R}^2)$.

Indeed we can follow the same idea of the proof of Theorem 5.2 in [6] to write $Q_t = L_t + S_t$, where L_t is the solution map of a delay differential equation, and S_t is compact. Then we obtain that

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

for some positive $\gamma > 0$. Therefore, by Theorem 4.1 in [6], it follows that ρ^* is the minimal wave speed for monotone traveling waves connecting $\mathbf{0}$ and $\mathbf{K}$.

It remains to show the smoothness of wave profile $(M(x+\rho t), B(x+\rho t))$ for any $\rho \geq \rho^*$. Note that

$$B(x+\rho t) = \tilde{T}(t)[B](x) + \int_0^t \tilde{T}(t-s)\tilde{F}_2[M,B](x-\rho s)ds.$$

By the expression of $\tilde{T}$, it follows that B is twice differentiable. For $M(x+\rho t)$, we have

$$M(x+\rho t) = M(x) + \int_0^t (\tilde{F}_1[M,B](x-\rho s) - d_m M(x-\rho s))ds,$$

which implies M' exists for any $x \in \mathbb{R}$. □

5. **Examples and simulations.** It is important to have more information about the asymptotic spreading speed ρ^*. From the comparison arguments used in Section 3, we have that

$$\rho_L^* \equiv \inf_{\mu>0} \frac{\Lambda(\mu)}{\mu} \leq \rho^* \leq \inf_{\mu>0} \frac{\lambda(\mu)}{\mu} \equiv \rho_U^*, \tag{31}$$

where $\lambda(\mu)$ and $\Lambda(\mu)$ are defined through auxiliary systems (16) and (24). We can have a more precise estimate of the spreading speed ρ^* with further assumptions. Indeed from (23), $\lambda(\mu)$ is the principal eigenvalue of the eigenvalue problem

$$(\lambda - D\mu^2 + 1)(\lambda + d_m - \tilde{d}_m A(\mu)e^{-\lambda\tau}) - \frac{cm_+}{m_+ + w}A(\mu)(\lambda + d_m) = 0, \tag{32}$$

hence ρ_U^* depends on $D, d_m, \tilde{d}_m, A(\mu), \tau$ and c. On the other hand, $\Lambda(\mu)$ is the principal eigenvalue of the eigenvalue problem

$$(\Lambda - D\mu^2 + 1)(\Lambda + d_m - \tilde{d}_m A(\mu)e^{-\Lambda\tau}) = 0, \tag{33}$$

which is same as (32) with $c = 0$. Hence when $D, d_m, \tilde{d}_m, A(\mu), \tau$ and c are known, then the upper and lower bounds of ρ^* can always be numerically calculated. We use two examples to illustrate the effect of the kernel function $k(z)$ which determines $A(\mu)$.

Example 5.1. Suppose that the kernel function is a Dirac delta function $k(z) = \delta(z)$, that is, the birds drop mistletoe seeds only locally. Note that in this case, the assumption $(H2)$ is not satisfied, but the proof given in this paper can be modified to cover this case as well. In this example we have $A(\mu) \equiv 1$. If in addition we assume that the delay $\tau = 0$, then we obtain that

$$\rho_L^* = \sqrt{\frac{D}{\tilde{d}_m - d_m + 1}(\tilde{d}_m - d_m)}, \quad \text{where} \quad \tilde{d}_m = \frac{\alpha}{w}. \tag{34}$$

For delay $\tau > 0$, there exists a unique $\Lambda_\tau > 0$ such that $\Lambda_\tau + d_m - \tilde{d}_m A(\mu) e^{-\Lambda_\tau \tau} = 0$ where $\tilde{d}_m = \dfrac{\alpha e^{-d_i \tau}}{w}$ and Λ_τ is strictly decreasing in τ. Then $\rho_L^* = \sqrt{\dfrac{D}{\Lambda_\tau + 1}} \Lambda_\tau$. For small $\tau > 0$, it is easy to see that $\Lambda_\tau \approx \dfrac{\tilde{d}_m - d_m}{1 + \tilde{d}_m \tau}$. Hence in this case, the asymptotic spreading speed is smaller when τ is larger.

On the other hand, the upper bound ρ_U^* is determined by the eigenvalue problem

$$(\lambda - D\mu^2 + 1)(\lambda + d_m - \tilde{d}_m e^{-\lambda\tau}) - \frac{cm_+}{m_+ + w}(\lambda + d_m) = 0. \tag{35}$$

In general we can obtain that $\rho_U^* = \rho_L^* + O(c)$, and when $\tau = 0$ and $c > 0$ is small we obtain that

$$\rho_U^* \approx \sqrt{\frac{D}{\tilde{d}_m - d_m + 1}} \left[(\tilde{d}_m - d_m) + \frac{cm_+}{m_+ + w}(\tilde{d}_m + 1/2) \right].$$

Example 5.2. Consider that the kernel function is a square wave with a finite influence region. Given $K > 0$, and let

$$k(z) = \begin{cases} K^{-1}, & |z| < K/2, \\ 0, & \textit{otherwise}. \end{cases} \tag{36}$$

Note that here again $(H2)$ is not satisfied as $k(z)$ is not strictly positive. But numerical simulation shows that a spreading speed and travel waves exist. The upper and lower bounds given above can still be explicitly calculated. Indeed $A(\mu) = \int_{-K/2}^{K/2} K^{-1} e^{\mu|y|} dy = \dfrac{2}{K\mu}(e^{\frac{K\mu}{2}} - 1)$. Then the principal eigenvalue $\lambda(\mu)$ (as well as $\Phi(\mu) = \lambda(\mu)/\mu$) of (32) and the principal eigenvalue $\Lambda(\mu)$ (as well as $\Psi(\mu) = \Lambda(\mu)/\mu$)(33) can be calculated numerically. Here we use the following set of parameters:

Parameter	w	α	c	d_i	d_m	τ	D
Value	1	1	0.5	0.1	0.1	1	1

Table 1. Parameter values used in Example 5.2

In Fig. 1, the graphs of $\Phi(\mu)$ and $\Psi(\mu)$ with $K = 4, 6, 8$ and 10 are plotted, from which the upper and lower bounds of the asymptotic spreading speed ρ^* can be estimated. For example, if $K = 4$, then $0.91 \le \rho^* \le 1.83$, and if $K = 10$, then $2.27 \le \rho^* \le 3.99$. It appears that ρ^* is increasing in K, which means that the spreading is faster when the bird flying range is wider. A numerical simulation of the traveling wave with square wave kernel and parameters given in Table 1 with $K = 4$ is given in Fig. 2. The wave profile of the corresponding traveling waves with $K = 4$ and $K = 10$ are given in Fig. 3 and 4.

Example 5.3. Let the kernel $k(z)$ be a normal distribution function with mean zero and variance σ^2, that is,

$$k(z) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{z^2}{2\sigma^2}\right), \tag{37}$$

Then $\Phi(\mu)$ and $\Psi(\mu)$ for this kernel can also be calculated numerically, and are plotted in Fig. 5 with same parameters as in Table 1 and standard deviation

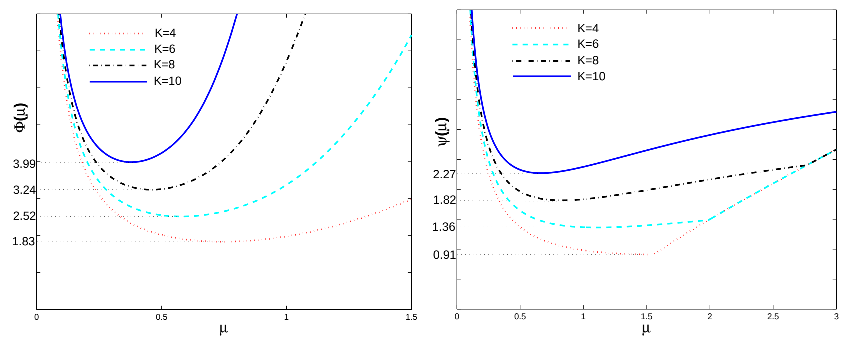

FIGURE 1. The graph of $\Phi(\mu)$ (left) and $\Psi(\mu)$ (right) for the kernel given by (36) with different parameter K. The graphs of $\Psi(\mu)$ for different K overlap since the principal eigenvalues of (33) are $D\mu^2 - 1$ for large μ, which is independent of K.

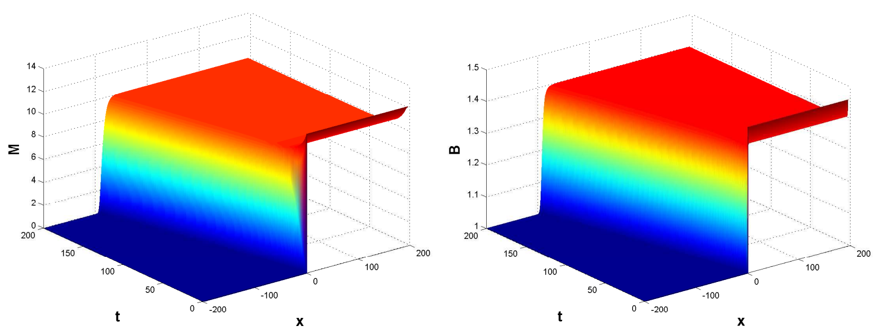

FIGURE 2. A solution of (2) for the kernel defined by (36) with parameters given in Table 1 and $K = 4$, which tends to a traveling wave solution.

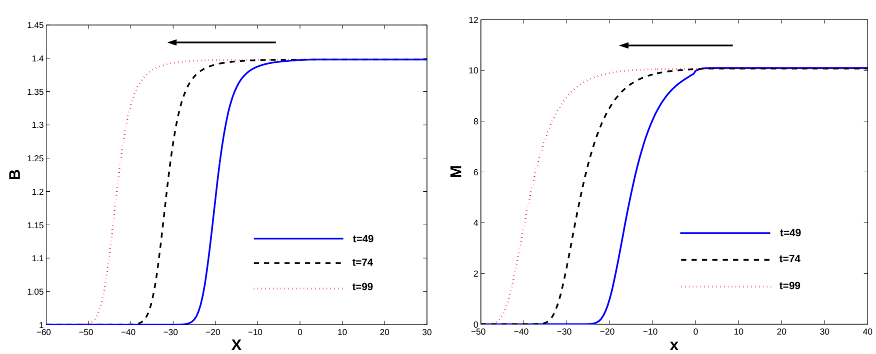

FIGURE 3. Wave profiles for mistletoes (left) and birds (right) of the traveling wave solution of (2) for the kernel defined by (36) with $K = 4$ and other parameters given in Table 1.

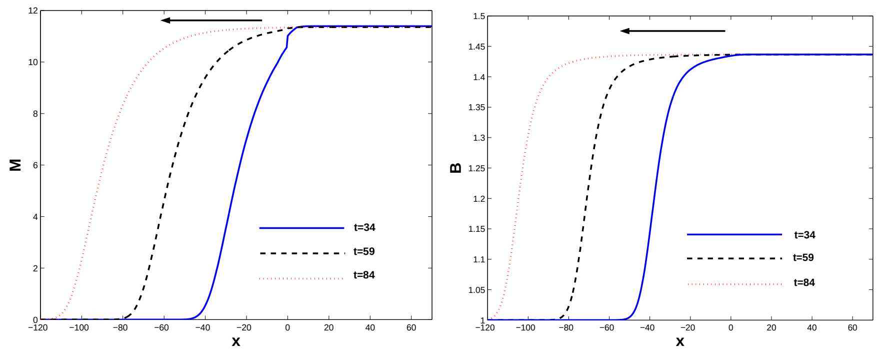

FIGURE 4. Wave profiles for mistletoes (left) and birds (right) of the traveling wave solution of (2) for the kernel defined by (36) with $K = 10$ and other parameters given in Table 1. The wave speed with $K = 10$ is faster than the one with $K = 4$.

$\sigma = 1, 2, 3, 4$. For example, if $\sigma = 1$, then $0.63 \leq \rho^* \leq 1.13$, and if $\sigma = 4$, then $2.54 \leq \rho^* \leq 3.62$. Apparently the asymptotic spreading speed ρ^* is increasing as the variance σ^2 increases. A numerical simulation of the traveling wave with normal distribution kernel and parameters given in Table 1 with $\sigma = 2$ is given in Fig. 6. The wave profile of the corresponding traveling waves with $\sigma = 2$ and $\sigma = 4$ are given in Fig. 7 and 8.

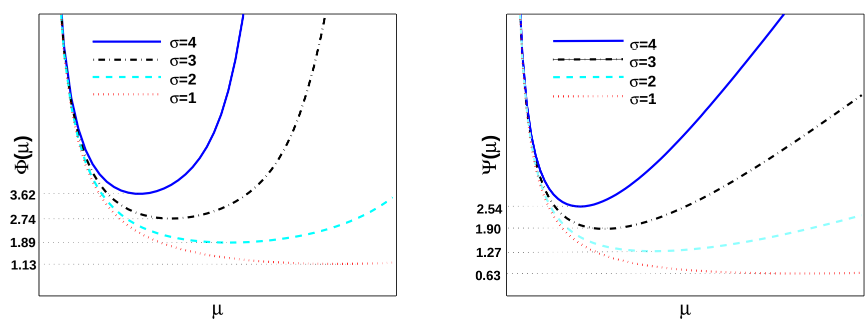

FIGURE 5. The graph of $\Phi(\mu)$ (left) and $\Psi(\mu)$ (right) for the kernel given by (37) with different variances.

It is well known that the Fisher-KPP equation $B_t = DB_{xx} + B(1 - B)$ has a family of traveling wave solutions with wave speed $\rho \geq \rho_0 = \sqrt{4D}$. In particular the asymptotic spreading speed for the Fisher-KPP equation is $\rho_0 = \sqrt{4D}$ (see [1]). Apparently this family of traveling wave solutions can also be regarded as traveling wave solutions of (2) connecting the equilibria $(0, 0)$ and $(0, 1)$ with mistletoe population always being zero. For parameters given in Table 1, we have $\rho_0 = 2$. From Example 5.2, one can see that when $\rho^* < 1.83 < 2 = \rho_0$ when $K = 4$, while $\rho^* > 2.27 > 2 = \rho_0$ when $K = 10$. Similar phenomenon occurs in Example 5.3 with normal distribution kernel. This suggests two different invasion scenarios: (i) when

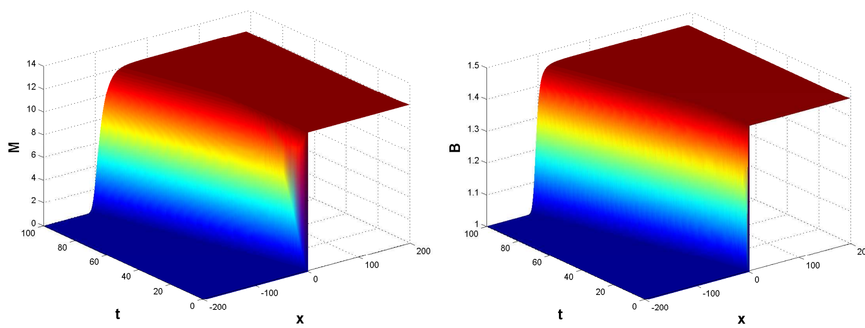

FIGURE 6. A solution of (2) for the kernel defined by (37) with $\sigma = 2$ and other parameters given in Table 1.

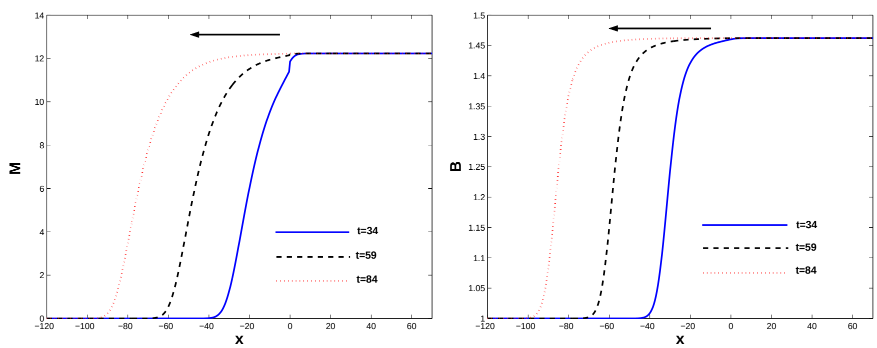

FIGURE 7. Wave profiles for mistletoes (left) and birds (right) of the traveling wave solution of (2) for the kernel defined by (37) with $\sigma = 2$ and other parameters given in Table 1.

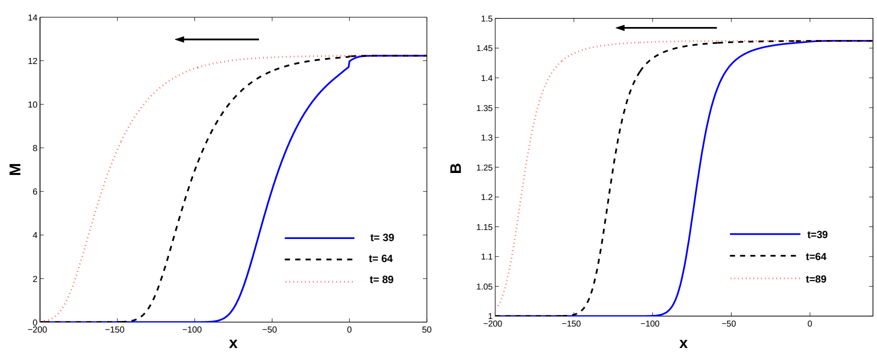

FIGURE 8. Wave profiles for mistletoes (left) and birds (right) of the traveling wave solution of (2) for the kernel defined by (37) with $\sigma = 4$ and other parameters given in Table 1. The wave speed with $\sigma = 4$ is faster than the one with $\sigma = 2$.

$\rho_* < \rho_0$, the birds will invade the new territory with a speed ρ_0 without the existence of mistletoes, and a second (and slower) wave of mistletoes and birds will follow with a speed ρ_* which will increase the bird population to a higher value $b_+ > 1$; and (ii) when $\rho_* > \rho_0$, the wave of mistletoes and birds is faster than the bird-only wave, hence when the two wave propagations both exist, the mistletoe-bird wave will catch up with and supersede the bird-only wave.

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