SPATIAL DYNAMICS OF A NONLOCAL AND DELAYED POPULATION MODEL IN A PERIODIC HABITAT

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Abstract. We derived an age-structured population model with nonlocal effects and time delay in a periodic habitat. The spatial dynamics of the model including the comparison principle, the global attractivity of spatially periodic equilibrium, spreading speeds, and spatially periodic traveling wavefronts is investigated. It turns out that the spreading speed coincides with the minimal wave speed for spatially periodic travel waves.

1. Introduction. In the last thirty years, there have been extensive investigations on the spatial dynamics including traveling wave fronts and spreading speeds for reaction-diffusion equations, recursion equations, integral or integro-differential equations, lattice systems, epidemic or biological models and monotone semiflows, see, e.g., [25, 28, 32, 19, 20, 33, 3, 29, 30, 37, 24, 35, 38, 17] and the references therein. Although most of the studies have been devoted to the evolution equations with spatially homogeneous environment, there are also quite a few important works on front propagation in heterogeneous media (see, e.g., [39]). In particular, Gärtner and Friedlin [5, 7] used probabilistic methods to study the spreading speed for an equation of Fisher type in which the mobility and the growth function vary periodically in space. In the ecological context, Shigesada et al. [26] first introduced a reaction-diffusion model for the spread of a single species in a patchy habitat with periodic variations in diffusivity and growth rate.

Recently, traveling wave fronts and spreading speeds have been addressed under the framework of spatially heterogeneous habitat. Berestycki, Hamel and Roques [1, 2] investigated the following reaction-diffusion model with periodic coefficients on $x$:

$$u_t - \nabla \cdot (A(x)\nabla u) = f(x, u), \quad x \in \mathbb{R}^N,$$

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where $A(x)$ and $f(x,u)$ depend on $x = (x_1, \cdots, x_N)$ in a periodic fashion. If $f(x,u) = u(\mu(x) - \nu(x)u)$, then it is the model proposed in [26]. Berestycki et al. obtained the existence, uniqueness and stability results for the stationary problem associated with (1), and these results provide a necessary and sufficient condition for the species to survive. They also analyzed the biological invasion problem for system (1), and connected the necessary and sufficient condition for the survival of species to that for the propagation of pulsating front invading the uniform steady state. They further gave a variational formula for the minimal speed of propagation of such traveling waves, and studied the influence of the heterogeneity on this speed.

Another important work in this aspect is due to Weinberger [34]. He generalized the earlier works on the monotone and translation-invariant system $u_{n+1} = Q(u_n)$ in [19, 20, 33] to the spatially periodic habitat. Let $x \in \mathbb{R}^d$. A set of vectors in $\mathbb{R}^d$ is a lattice if $a + b$ is in $\mathcal{L}$ whenever $a$ and $b$ are in $\mathcal{L}$. Define a translation operator $T_a[u](x) := u(x - a)$. We say that $u$ is periodic with respect to $\mathcal{L}$ if $T_a[u] = u$ for all $a \in \mathcal{L}$. We say the operator $Q$ is periodic with respect to $\mathcal{L}$ if $Q[T_a[u]] = T_a[Q[u]]$ for all $a \in \mathcal{L}$.

Under the assumptions that $Q$ is $\mathcal{L}$-periodic and order preserving, the spreading speeds and the existence of spatially periodic traveling wavefronts were obtained in [34]. Furthermore, a method of estimating spreading speeds was also presented there.

More works on traveling wave solutions and spreading speeds in periodic habitat can be found in Guo and Hamel [8], Kinezaki et al. [15], and Weinberger et al. [36]. More recently, Jin and Zhao [13] studied a general discrete-time population model in a periodic lattice habitat by using the theory in [34], comparison arguments and the Schauder fixed point theorem. As mentioned in [13], although a vast number of mathematical studies assume that the environment is spatially homogeneous, the real environment is generally heterogeneous due to natural phenomena or exposure to artificial distributions. It is very important to understand how the heterogeneous environment influences the asymptotic pattern of the species when $t$ is large. Clearly, a simple form of heterogeneous environment is the periodic habitat.

Assume that a species lives in a periodic habitat, by which we mean that the recruitment function (or the growth function) and dispersal properties vary periodically in the habitat. By considering the age structure of the population, we will derive a model of a mature population in a periodic habitat with nonlocal effects and time delays, and further investigate its spatial dynamics including a threshold type stability result, spreading speeds, and spatially periodic wavefronts. We also show that the spreading speed coincides with the minimal wave speed, and give a computational formula for this speed. It seems that this is the first study of time-delayed population model with nonlocal effect in a periodic habitat. To establish the threshold dynamics for the model system with spatially periodic initial data, and the spreading speeds and traveling waves for the model system with general initial data, we will appeal to the theory of monotone and subhomogeneous semiflows developed in [40, Section 2.3] and [34, 18], respectively. Associated with our nonlocal and time-delayed model system, there is a nonlocal and periodic eigenvalue problem of delay type. With the help of the abstract result in [14, Section 4], we are able to obtain the existence of the principal eigenvalue and determine its sign from the principal eigenvalue of a nonlocal periodic eigenvalue problem without time delay (see Lemma 3.3). In order to employ the linear operators approach to estimate
spreading speeds as in [19, 34, 17], we need to know the convexity of the principal eigenvalue with respect to a parameter \( \mu \). Since no variational formula is available for the principal eigenvalue of our nonlocal and periodic eigenvalue problem of delay type, we will develop a new method to prove the convexity (see Proposition 4.1). This method is also of its own interest.

We should point out that the theory in [34] cannot be applied directly to solution maps of our time-delayed and nonlocal reaction-diffusion model. This is because these maps are defined on the space of continuous functions on the domain \([-\tau, 0] \times \mathbb{R} \), which is different from the standard habitat \( \mathbb{R} \). Further, for each \( t \in (0, \tau) \), the solution map \( Q_t \) is not compact with respect to the compact open topology; that is, \( Q_t \) does not satisfy the compactness assumption [34, Hypothesis 2.1 (vi)]. Thus, we need to use the theory recently developed in [18], together with some ideas in [34], to study spreading speeds and periodic traveling waves for the model system.

The rest of this paper is organized as follows. Section 2 is devoted to the model derivation. In section 3, we establish a threshold type result on the global dynamics for the periodic initial value problem. We consider spreading speeds, spatially periodic traveling wavefronts and minimal wave speeds in section 4. Two examples are also given at the end of this section to illustrate the applicability of our main results. For the sake of convenience, we present in the Appendix some results of [18] for abstract monostable evolution systems in a periodic habitat.

### 2. Model derivation.

Let \( u(t, a, x) \) be the density of individuals with age \( a \) at point \( x \) and time \( t \), and \( \tau > 0 \) the length of the juvenile period. Assume that \( u_m(t, x) \) denotes the density of mature (or adult) individuals at point \( x \) and time \( t \). As argued in [27, 9] and [30, Section 4.1], it then follows that \( u(t, a, x) \) and \( u_m(t, x) \) satisfy

\[
\begin{aligned}
\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} & = D_j(a, x) \frac{\partial^2 u}{\partial x^2} - \mu_j(a, x) u, \quad a \in (0, \tau], t > 0, x \in \mathbb{R}, \\
\frac{\partial u_m}{\partial t} & = D_m(x) \frac{\partial^2 u_m}{\partial x^2} - d(x, u_m) + u(t, \tau, x), \quad t > 0, x \in \mathbb{R},
\end{aligned}
\]

where \( b(x, u) \) and \( d(x, u) \) are the birth and mortality rates of mature individuals, respectively, and \( \mu_j(a, x) \geq 0 \) denotes the per capita mortality rate of juveniles at age \( a \) and point \( x \). For simplicity, we have assumed that the length of the juvenile period is the same for all juvenile individuals.

In order to obtain a closed system for \( u_m(t, x) \), we need to evaluate \( u(t, \tau, x) \). We first make the following assumptions:

(A1) There is a positive constant \( \omega > 0 \) such that \( D_j(a, x) \geq \omega \) for all \( a \in (0, \tau], x \in \mathbb{R} \), that is, the linear operator \( Lu := D_j(a, x) \frac{\partial^2 u}{\partial x^2} - \mu_j(a, x) u - \frac{\partial u}{\partial a} \) is uniformly parabolic.

(A2) \( D_j(a, x) \) and \( \mu_j(a, x) \) are bounded and continuous functions. Furthermore, there are two constants \( \nu \in (0, 1) \) and \( A > 0 \), such that for any \( a, a' \in (0, \tau], x, x' \in \mathbb{R} \), the coefficients \( D_j(a, x) \) and \( \mu_j(a, x) \) satisfy

\[
\begin{aligned}
|D_j(a, x) - D_j(a', x')| & \leq A|a - a'|^{\nu/2} + |x - x'|^{\nu}, \\
|\mu_j(a, x) - \mu_j(a, x')| & \leq A|x - x'|^{\nu}.
\end{aligned}
\]
For fixed $s \geq 0$, let $v(s, a, x) = u(a + s, a, x)$. From (2), we obtain
\[
\frac{d}{ds}v(s, a, x) = \frac{\partial}{\partial t}u(t, a, x)|_{t=s} + \frac{\partial}{\partial a}u(t, a, x)|_{t=s} = D_j(a, x)\frac{\partial^2 u}{\partial x^2}(a + s, a, x) - \mu_j(a, x)u(a + s, a, x)
\]
\[
= D_j(a, x)\frac{\partial^2 u}{\partial x^2}(s, a, x) - \mu_j(a, x)v(s, a, x),
\]
\[
v(s, 0, x) = u(s, 0, x) = b(x, u_m(s, x)).
\]
Taking $s$ as a parameter, we have from (3), (A1), (A2) and the conclusions for parabolic partial differential equations (see, e.g., [6]) that
\[
v(s, a, x) = \int_\mathbb{R} \Gamma(a, x, 0, y)b(y, u_m(s, y))dy = \int_\mathbb{R} \Gamma(a, x, y)b(y, u_m(s, y))dy,
\]
where $\Gamma(a, x, \xi, y)$ is the fundamental solution associated with the equation $Lu = 0$, and $\Gamma(a, x, y) := \Gamma(a, x, 0, y)$. Since
\[
u(t, a, x) = v(t - a, a, x) = \int_\mathbb{R} \Gamma(a, x, y)b(y, u_m(t - a, y))dy
\]
it follows that
\[
u(t, \tau, x) = v(t - \tau, \tau, x) = \int_\mathbb{R} \Gamma(\tau, x, y)b(y, u_m(t - \tau, y))dy
\]
for $t \geq a$.

Substituting (4) into (2), we obtain the equation for the mature population
\[
\frac{\partial u_m}{\partial t} = D_m(x)\frac{\partial^2 u_m}{\partial x^2} - d(x, u_m) + \int_\mathbb{R} \Gamma(\tau, x, y)b(y, u_m(t - \tau, y))dy,
\]
t $\geq \tau, x \in \mathbb{R}$. Since the above system is autonomous, without loss of generality, we consider the following model
\[
\frac{\partial u_m}{\partial t} = D_m(x)\frac{\partial^2 u_m}{\partial x^2} - d(x, u_m) + \int_\mathbb{R} \Gamma(\tau, x, y)b(y, u_m(t - \tau, y))dy,
\]
t $\geq 0, x \in \mathbb{R},$
\[
(5)
\]
with initial data $u(t, x) = \phi(t, x)$ for $t \in [-\tau, 0], x \in \mathbb{R}$.

**Lemma 2.1.** The function $\Gamma(a, x, y)$ has the following properties:

(i) If $D_j(a, x) = D_j(a, x + L), \mu_j(a, x) = \mu_j(a, x + L)$, then one has
\[
\Gamma(a, x + L, y + L) = \Gamma(a, x, y) \quad \text{for } a > 0, x \in \mathbb{R}, y \in \mathbb{R}.
\]

(ii) $\Gamma(a, x, y) > 0$ for $a > 0, x \in \mathbb{R}, y \in \mathbb{R}$.

(iii) $0 < \int_\mathbb{R} \Gamma(a, x, y)dy \leq 1$ for any $a > 0, x \in \mathbb{R}$.

**Proof.** The statement (i) is from the formula of fundamental solution (2.8) on page 4 in [6]. The details of the construction of fundamental solution are given on pages 4-24 in [6]. On the other hand, the conclusion (ii) comes from Theorem 11 in [6, Chapter 2]. Now we prove the statement (iii). Consider the initial value problem
\[
\frac{\partial u}{\partial t} = D_j(a, x)\frac{\partial^2 u}{\partial x^2} - \mu_j(a, x)u, \quad a > 0, x \in \mathbb{R},
\]
\[
u(0, x) = \phi(x) = \phi(x + L), \quad x \in \mathbb{R}.
\]

Let $v(a, x) \equiv 1$ for $x \in \mathbb{R}, a \in \mathbb{R}$. Then $v(a, x)$ satisfies
\[
\frac{\partial}{\partial a} v(a, x) \geq D_j(a, x)\frac{\partial^2 v}{\partial x^2} - \mu_j(a, x)v.
\]
This shows that \( v(a, x) \equiv 1 \) is an upper solution of (6) with the initial condition \( u(0, x) = 1, x \in \mathbb{R} \). On the other hand, we define \( \gamma(a, x) \) by

\[
\gamma(a, x) := \int_{\mathbb{R}} \Gamma(a, x, y)dy \quad \text{for } x \in \mathbb{R}, a \in \mathbb{R}.
\]

Then \( \gamma(a, x) \) is a solution of (6) with the same initial condition \( u(0, x) = 1, x \in \mathbb{R} \). Note that \( u(a, x) \equiv 0 \) is a lower solution of (6). Therefore, we have \( 0 < \int_{\mathbb{R}} \Gamma(a, x, y)dy \leq 1, \forall a \in \mathbb{R} \), and hence, the statement (iii) follows.

3. The threshold dynamics. Let \( \mathbb{R}_+ := [0, \infty) \), and \( L > 0 \) be a constant. Assume that \( D_m(x), b(x, u) \) and \( d(x, u) \) satisfy the following assumptions:

(P1) \( D_m \in C^\nu(\mathbb{R}) \), where \( C^\nu(\mathbb{R}) \) is a Hölder continuous space with the Hölder exponent \( \nu \in (0, 1) \); there exists a positive constant \( \alpha_0 \), such that \( D_m(x) \geq \alpha_0 \) for \( x \in \mathbb{R} \), i.e., the operator \( D_m(x)\frac{\partial}{\partial x} \) is uniformly elliptic; \( D_m(x + L) = D_m(x) \) for \( x \in \mathbb{R}, u \in \mathbb{R}_+ \).

(P2) There exists a constant \( M > 0 \) such that

\[
d(x, M) \geq \int_{\mathbb{R}} \Gamma(\tau, x, y)b(y, M)dy, \quad \forall x \in [0, L].
\]

(P3) \( b \in C^1(\mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+), b(x, 0) = 0, \frac{\partial}{\partial u}b(x, 0) = -b_u(x, 0) > 0; b(x, u) = b(x + L, u) \) for \( x \in \mathbb{R}, u \in \mathbb{R}_+ \): for every \( x \in \mathbb{R} \), \( b(x, u) \) is nondecreasing in \( u \in [0, M] \); and \( b(x, u) \) is strictly subhomogeneous in \( u \in [0, M] \), i.e., \( b(x, \gamma u) > \gamma b(x, u) \) for any \( \gamma \in (0, 1) \) and \( x \in \mathbb{R}, u \in (0, M] \).

(P4) \( d \in C^{1+\nu}(\mathbb{R} \times \mathbb{R}_+, \mathbb{R}_+), d(x, 0) = 0; d(x + L, u) = d(x, u) \) for \( x \in \mathbb{R}, u \in \mathbb{R}_+ \); \( \frac{\partial}{\partial u}d(x, u) \geq \frac{\partial}{\partial u}d(x, 0) = -d_u(x, 0) \geq 0 \), and \( -d(x, u) \) is subhomogeneous in \( u \in [0, M] \).

Throughout this paper, we always assume that the kernel function \( \Gamma(\tau, x, y) \) satisfies

\[
\Gamma(\tau, x, y) > 0, \quad 0 < \int_{\mathbb{R}} \Gamma(\tau, x, y)dy \leq 1, \quad \forall x, y \in \mathbb{R},
\]

\[
\Gamma(\tau, x + L, y + L) = \Gamma(\tau, x, y), \quad \forall x, y \in \mathbb{R}.
\]

In this section, we mainly concern about the existence and uniqueness of positive equilibrium and the threshold dynamics of system (5) with spatially periodic initial data. Let \( \mathbb{P} = PC(\mathbb{R}, \mathbb{R}) \) be the set of all continuous and \( L \)-periodic functions from \( \mathbb{R} \) to \( \mathbb{R} \), and \( \mathbb{P}_+ = \{ \varphi \in \mathbb{P} : \varphi(x) \geq 0, \forall x \in \mathbb{R} \} \). Define \( [0, \zeta[p] = \{ \varphi \in \mathbb{P}_+ : 0 \leq \varphi(x) \leq \zeta(x), \forall x \in \mathbb{R} \} \). Thus, \( \mathbb{P}_+ \) is a closed cone of \( \mathbb{P} \) and induces a partial ordering on \( \mathbb{P} \). Moreover, we define a norm \( \| \varphi \|_p \) by

\[
\| \varphi \|_p = \max_{x \in \mathbb{R}} |\varphi(x)|.
\]

It then follows that \( (\mathbb{P}, \| \varphi \|_p) \) is a Banach lattice.

Assume that \( p, q \in C^\nu(\mathbb{R}) \) \( (\nu \in (0, 1)) \) and \( p(x + L) = p(x), q(x + L) = q(x) \). We consider the linear parabolic problem

\[
\frac{\partial u(x, t)}{\partial t} = D_m(x)\frac{\partial^2 u(x, t)}{\partial x^2} + p(x)\frac{\partial u(t, x)}{\partial x} + q(x)u, \quad t > 0, x \in \mathbb{R},
\]

\[
\begin{align*}
\text{u(0,x) = } & \varphi(x) = \varphi(x + L), \\
\text{for } & x \in \mathbb{R}.
\end{align*}
\]  

(7)

Let \( u(t, x) \) be a bounded solution of (7). It is then easy to see that \( u(t, x) \) is \( L \)-periodic in \( x \) for any \( t \geq 0 \). Let \( K(t, x, s, y) \) be the fundamental solution of

\[
\frac{\partial u(x, t)}{\partial t} = D_m(x)\frac{\partial^2 u(x, t)}{\partial x^2} + p(x)\frac{\partial u(t, x)}{\partial x} + q(x)u, \quad t > 0, x \in \mathbb{R}
\]
with \( u(t, x) = u(t, x + L), t > 0, x \in \mathbb{R} \). According to the property of autonomous systems, we can derive that \( K(t, x, s, y) = K(t - s, x, 0, y) \). Let \( \hat{G}(t - s, x, y) := K(t - s, x, 0, y) \). We have from [6] that there is a linear semigroup \( \hat{T}(t) : \mathbb{P}_+ \to \mathbb{P}_+ \) for \( t \geq 0 \) such that

\[
\hat{T}(t)\varphi(x) = \int_\mathbb{R} \hat{G}(t, x, y)\varphi(y)dy, \quad x \in \mathbb{R}
\]

with function \( \varphi \) satisfying

\[
|\varphi(x)| \leq C_1 \exp\{hx^2\} \text{ for some positive constant } h < \frac{\lambda_0}{4T_1}, \quad t \in [0, T_1],
\]

where \( T_1, C_1, \lambda_0 \) are positive constants, \( T_1 \) is arbitrary, and \( \lambda_0 \) can be determined from the uniformly parabolic property of equations (6.5) and (2.2) on pages 23 and 4 of [6]. Furthermore, we have from (6.13) on page 24 of [6] that

\[
\left| \frac{\partial \hat{G}(t, x, y)}{\partial x} \right| \leq C_2 t^{-1} \exp \left\{ -\frac{\lambda_0^2}{4t} (x - y)^2 \right\}
\]

for any \( \lambda_0^2 < \lambda_0 \) and some \( C_2 > 0 \).

We will show that for any \( t > 0, \hat{T}(t) \) is compact on \( \mathbb{P} \). Let \( t \in (0, T_1] \) be given. Suppose that \( \{\varphi_n(x)\} \) is a bounded sequence in \( \mathbb{P} \) and \( |\varphi_n(x)| \leq C_1 \) for \( x \in \mathbb{R}, n \geq 1 \). Then the sequence of functions \( \{\hat{T}(t)\varphi_n(x)\} \) is uniformly bounded. Let

\[
\psi_n(t, x) := [\hat{T}(t)\varphi_n](x) = \int_\mathbb{R} \hat{G}(t, x, y)\varphi_n(y)dy.
\]

Because \( D_{m, p, q} \) are Hölder continuous, they satisfy \( (A_1)' \) and \( (A_2)' \) on page 22 of [6]. On the other hand, we know that every \( \varphi_n \) is continuous and satisfies (9). Now, we have from (11) and (10) that

\[
\left| \frac{\partial \psi_n(t, x)}{\partial x} \right| \leq C_1 \int_\mathbb{R} \left| \frac{\partial \hat{G}(t, x, y)}{\partial x} \right| dy \\
\leq C_3 C_4 \int_\mathbb{R} \exp \left\{ -\frac{\lambda_0^2}{4t} (x - y)^2 \right\} dy = C_3 \int_\mathbb{R} \exp \left\{ -\frac{\lambda_0^2}{4t} z^2 \right\} dz
\]

for any \( n \geq 1 \), where \( C_3 = C_1 C_2 \). Thus, \( \{\psi_n(t, x)\} \) is equi-continuous. Therefore, in view of the Arzela-Ascoli theorem, noting that \( T_1 > 0 \) is arbitrary, we know that \( \hat{T}(t) \) is compact for each \( t > 0 \). In the following, if \( p(x) = 0, q(x) = 0, x \in \mathbb{R} \), we denote \( \hat{T}(t) \) and \( \hat{G} \) as \( T(t) \) and \( G \), respectively.

Let \( \mathcal{C} = C([-\tau, 0], \mathbb{P}) \) be the Banach space of continuous functions from \([-\tau, 0]\) to \( \mathbb{P} \). For any \( \zeta \in \mathbb{P}_+ \), let \( [0, \zeta]_\mathcal{C} = \{ \varphi \in \mathcal{C} : \varphi(\theta) \in [0, \zeta]_\mathbb{P}, \forall \theta \in [-\tau, 0]\} \). Then \( \mathcal{C}_+ := C([-\tau, 0], \mathbb{P}_+) \) is a closed cone of \( \mathcal{C} \). As usual, we identify an element \( \varphi \in \mathcal{C} \) with a function from \([0, \zeta]_\mathcal{C} \times \mathbb{R} \) into \( \mathbb{R} \) defined by \( \varphi(\theta, x) = \varphi(\theta)(x) \).

For any function \( u : [-\tau, a) \to \mathbb{P}, a > 0 \), we define \( u_\theta \in \mathcal{C} \) with \( t \in [0, a) \) by \( u_\theta(\theta) = u(t + \theta) \) for \( \theta \in [-\tau, 0] \).

We consider the periodic initial value problem

\[
\frac{\partial u(t, x)}{\partial t} = D_m(x) \frac{\partial^2 u(t, x)}{\partial x^2} - d(x, u) + \int_\mathbb{R} \Gamma(\tau, x, y)b(y, u(t - \tau, y))dy, \quad t > 0, x \in \mathbb{R},
\]

\[
u(\theta, x) = \varphi(\theta, x) = \varphi(\theta + L), \quad \theta \in [-\tau, 0], x \in \mathbb{R}.
\]  

(12)

From now on, we drop the subscript \( m \) of \( u_m \) in (5) for the sake of convenience. The solution of (12) will be denoted by \( u(t, x; \varphi) \). For any \( \varphi \in \mathcal{C}_+ \), define \( F : \mathcal{C}_+ \to \mathbb{P} \) by

\[
F(\varphi)(x) = -d(x, \varphi(0, x)) + \int_\mathbb{R} \Gamma(\tau, x, y)b(y, \varphi(-\tau, y))dy, \quad x \in \mathbb{R}.
\]  

(13)
Then $F$ is Lipschitz continuous in any bounded subset of $C_+$. Further, letting $A = D_m(\cdot)\frac{\partial^2}{\partial x^2}$ and $u(t)(\cdot) = u(t, \cdot)$, we then have the abstract setting for (12):

$$\frac{du}{dt} = Au + F(u_t), \quad t > 0, u_t \in C, \quad u_0 = \varphi \in C_+.$$  \hspace{1cm} (14)

Let $T(t)$ be the linear semigroup associated with $A$. Then we consider the integral form of (12):

$$u(t) = T(t)\varphi(0) + \int_0^t T(t - s) F(u_s) ds, \quad t > 0, \quad u_0 = \varphi \in C_+.$$  \hspace{1cm} (15)

**Definition 3.1.** An upper solution (lower solution) of (12) is a function $v : [-\tau, a) \to \mathbb{R}$ with $a > 0$ satisfying

$$v(t) \geq (\leq) T(t)v(0) + \int_0^t T(t - s) F(v_s) ds, \quad t \in [0, a).$$  \hspace{1cm} (16)

If $v$ is both an upper solution and lower solution on $[0, a)$, then $v$ is called a mild solution of (12).

**Remark 3.1.** Assume that there is a continuous $v : \mathbb{R} \times [-\tau, a) \to \mathbb{R}$ with $a > 0$ such that $v$ is in $C^2$ and $L$-periodic for $x \in \mathbb{R}$, $C^1$ for $t \in [0, a)$ and satisfies

$$\frac{\partial v(t,x)}{\partial t} \geq (\leq) \frac{\partial^2 v(t,x)}{\partial x^2} - d(x,v(t,x)) + \int_0^a \Gamma(t,x,y)b(y,v(t - \tau, y))dy,$$

$$t \in [0, a), \quad x \in \mathbb{R}.$$  \hspace{1cm} (17)

Since $T(t)P_+ \subset P_+$ for all $t \geq 0$, it follows that (16) holds, and hence, $v$ is an upper solution (lower solution) of (12) on $[0, a)$.

**Theorem 3.1.** Assume that (P1)-(P4) hold. Then for any given initial function $\varphi \in [0, M]_{C}$, there exists a unique nonnegative solution $u(t, x; \varphi)$ of (12) defined on $[0, \infty)$, and $u_t \in [0, M]_{C}$ for $t \geq 0$.

**Proof.** Let $M > 0$ be defined as in (P2). We have from (P4) that there is $\gamma > 0$ and $\alpha_d > 0$ such that

$$d_u(x, 0)u \leq d(x, u) \leq d_u(x, 0)u + \gamma u, \quad \forall u \in [0, M],$$

$$|d(x, u_1) - d(x, u_2)| \leq \alpha_d |u_1 - u_2|, \quad \forall u_1, u_2 \in [0, M].$$  \hspace{1cm} (18)

For any $\varphi \in [0, M]_{C}$, we have

$$\varphi(0, x) + hF(\varphi, x) = \varphi(0, x) + h[-d(x, \varphi(0, x)) + \int_0^a \Gamma(t, x, y)b(y, \varphi(-\tau, y))dy]$$

$$\geq \varphi(0, x)[1 - h(d_u(x, 0) + \gamma)] \geq 0,$$

when $h > 0$ is so small that $1 - h(d_u(x, 0) + \gamma) > 0, \forall x \in \mathbb{R}$. On the other hand, for any $\varphi \in [0, M]_{C}$, we have from (P2) that

$$\varphi(0, x) + hF(\varphi, x)$$

$$\leq \varphi(0, x) + h[-d(x, \varphi(0, x)) + \int_0^a \Gamma(t, x, y)b(y, \varphi(-\tau, y))dy]$$

$$\leq \varphi(0, x) + h[-d(x, \varphi(0, x)) + d(x, M) - d(x, M) + \int_0^a \Gamma(t, x, y)b(y, M)dy]$$

$$\leq \varphi(0, x) + h[d(x, M) - d(x, \varphi(0, x))].$$

Therefore, we have $\varphi(0) + hF(\varphi) \in [0, M]_{\bar{P}}$. Consequently, we obtain

$$\lim_{h \to 0^+} \frac{1}{h} \text{dist}(\varphi(0) + hF(\varphi); [0, M]_{\bar{P}}) = 0, \quad \forall \varphi \in [0, M]_{C}.$$
By [21, Corollary 4] with $K = [0, M]_\mathbb{C}, S(t,s) = T(t-s), B(t, \varphi) = F(\varphi)$, we conclude that (12) admits a unique mild solution $u(t, \varphi)$ with $u(t, \varphi) \in [0, M]_\mathbb{C}$ for $t \in [0, \infty)$. Moreover, by the same argument as in [22, Proposition 1.1], we see that $u(t, \varphi)$ is a classical solution of (12) for $t \geq \tau$.

We now establish the following comparison principle.

**Lemma 3.1.** Assume that (P1)-(P4) hold, and let $\tilde{u}(t,x), \underline{u}(t,x)$ be the upper solution and lower solution of (12) with $\tilde{u}(t,x), \underline{u}(t,x) \in [0, M]$, respectively. If $\tilde{u}(\theta, x) \geq \underline{u}(\theta, x)$ for $\theta \in [-\tau, 0]$, then $\tilde{u}(t,x) \geq \underline{u}(t,x)$ for all $t \geq 0$. Moreover, if $\tilde{u}_0 := \tilde{u}(0, x) \geq \underline{u}_0 := \underline{u}(0, x)$ for $\theta \in [-\tau, 0]$ with $\tilde{u}(0, x) \neq \underline{u}(0, x)$, then $\tilde{u}(t,x) \geq \underline{u}(t,x)$, $\forall (t,x) \in (0, \infty) \times \mathbb{R}$.

**Proof.** Note that $F$ is globally Lipschitz continuous in $[0, M]_\mathbb{C}$ and $F$ is quasimonotone on $[0, M]_\mathbb{C}$ in the sense that

$$\lim_{h \to 0^+} \frac{1}{h} \text{dist} ([\varphi_1(0) - \varphi_2(0)] + h[F(\varphi_1) - F(\varphi_2)]; \mathbb{P}_+^\tau) = 0 \quad (19)$$

for all $\varphi_1, \varphi_2 \in [0, M]_\mathbb{C}$ with $\varphi_1 \geq \varphi_2$. In fact, it follows from the monotonicity of $b(x, u)$ on $u$ that

$$F(\varphi_1)(x) - F(\varphi_2)(x) = -d(x, \varphi_1(0, x)) + d(x, \varphi_2(0, x)) + \int_0^1 F(\tau, x, y)[b(y, \varphi_1(\tau, y)) - b(y, \varphi_2(\tau, y))]dy \geq -\alpha_d(\varphi_1(0, x) - \varphi_2(0, x)),$$

and hence, for any $h > 0$ with $1 > h\alpha_d$, we have

$$\varphi_1(0, x) - \varphi_2(0, x) + h[F(\varphi_1)(x) - F(\varphi_2)(x)] \geq [1 - h\alpha_d][\varphi_1(0, x) - \varphi_2(0, x)] \geq 0, \forall x \in \mathbb{R},$$

from which (19) follows.

Assume that $\tilde{u}, \underline{u}$ are a pair of upper solution and lower solution of (12) with $\tilde{u}(t, x), \underline{u}(t, x) \in [0, M]$ for $t \in [-\tau, \infty)$ and $x \in \mathbb{R}$, respectively. We have from [21, Corollary 5] and the fact $\tilde{u}(\theta, x) \geq \underline{u}(\theta, x)$ for $(\theta, x) \in [-\tau, 0] \times \mathbb{R}$, that the solutions of (12) satisfy

$$0 \leq \underline{u}(t, \cdot) \leq u(t, \cdot; \underline{u}_0) \leq u(t, \cdot; \tilde{u}_0) \leq \tilde{u}(t, \cdot) \leq M, \quad t \geq 0.$$

Thus, we have $\underline{u}(t, x) \leq \tilde{u}(t, x)$ for all $(t, x) \in (0, \infty) \times \mathbb{R}$.

Let $v = \tilde{u} - \underline{u}$. Then we have already known that $v(t, x) \geq 0$ for all $(t, x) \in (0, \infty) \times \mathbb{R}$. By the definition of upper solution and lower solution, the monotonicity of $b$ on $[0, M]$, and the fact $T\mathbb{P}_+ \subset \mathbb{P}_+$, it follows that

$$v(t) \geq T(t)v(0) + \int_0^t T(t-s)[F(\tilde{u}_s) - F(\underline{u}_s)]ds \geq T(t)v(0) + \int_0^t T(t-s)[b(\cdot, \tilde{u}(s)) - b(\cdot, \underline{u}(s))]ds \geq T(t)v(0) + \int_0^t T(t-s)\alpha_d v(s)ds, \quad t \geq 0.$$

Consider the solution $z(t)$ of the linear equation

$$z(t) = T(t)v(0) - \int_0^t T(t-s)\alpha_d z(s)ds, \quad t \geq 0.$$

By the comparison principle of abstract functional differential equations (see, e.g., [21, Proposition 3]), we get $v(t) \geq z(t)$ for $t \geq 0$. Let $p(x) = 0, q(x) = -\alpha_d$ in (7). Then $z(t, x) := z(t)(x)$ satisfies

$$\frac{\partial z(t, x)}{\partial t} = D_m(x)\frac{\partial^2 z(t, x)}{\partial x^2} - \alpha_d z(t, x), \quad t > 0, x \in \mathbb{R},$$

$$z(0, x) = \tilde{u}(0, x) - \underline{u}(0, x) = v(0, x), \quad x \in \mathbb{R},$$
and can be expressed as
\[ z(t, x) = e^{-\alpha t} \int_{\mathbb{R}} G(t, x, y) z(0, y) dy \text{ for } x \in \mathbb{R}, \]
where \( G(t, x, y) \) is defined in (8) with \( p(x) \equiv 0 \) and \( q(x) \equiv 0 \). Thus, we have
\[ v(t) \geq e^{-\alpha t} \int_{\mathbb{R}} G(t, \cdot, y) v(0, y) dy > 0, \quad \forall t > 0, \]
provided that \( v(0, x) \neq 0 \) on \( \mathbb{R} \).

Our focus here is on the dynamics of (12), and it is essential to describe the structure of equilibria. We see from (P3) and (P4) that (12) has a trivial equilibrium \( u = 0 \). Other equilibria for (12) are independent of \( t \), and hence, are nonnegative solutions of the following equation:
\[ D_m(x) \frac{d^2 u}{dx^2} - d(x, u) + \int_{\mathbb{R}} \Gamma(\tau, x, y)b(y, u(y))dy = 0, \quad x \in \mathbb{R}, \tag{20} \]
with the periodic condition \( u(x) = u(x + L), \quad x \in \mathbb{R} \). Linearizing (12) at zero solution, we obtain
\[ \frac{dv(t,x)}{dt} = D_m(x) \frac{d^2 v(t,x)}{dx^2} - d_u(x,0)v + \int_{\mathbb{R}} \Gamma(\tau, x, y)b_u(y,0)v(t - \tau, y)dy, \quad t > 0, \quad x \in \mathbb{R}, \]
\[ v(\theta, x) = \varphi(\theta, x) = \varphi(\theta, x + L), \quad \theta \in [-\tau, 0], \quad x \in \mathbb{R}, \]
\[ \varphi(0, x) = \varphi(x, x), \quad x \in \mathbb{R}. \tag{21} \]
Substituting \( v(t, x) = e^{\lambda t} \xi(x) \) into (21), we have the following nonlocal and periodic eigenvalue problem of delay type:
\[ \lambda \xi(x) = D_m(x) \frac{d^2 \xi(x)}{dx^2} - d_u(x,0)\xi + e^{-\lambda \tau} \int_{\mathbb{R}} \Gamma(\tau, x, y)b_u(y,0)\xi(y)dy, \quad x \in \mathbb{R}, \tag{22} \]
We also consider another nonlocal and periodic eigenvalue problem
\[ \lambda \xi(x) = D_m(x) \frac{d^2 \xi(x)}{dx^2} - d_u(x,0)\xi + \int_{\mathbb{R}} \Gamma(\tau, x, y)b_u(x,0)\xi(y)dy, \quad x \in \mathbb{R}, \xi(x + L) = \xi(x), \quad x \in \mathbb{R}. \tag{23} \]
Define operators \( B := D_m(\cdot) \frac{d^2}{dx^2} - d_u(\cdot,0)I \), \( I \) being the identity operator, \( \mathcal{L} : \mathbb{C} \to \mathbb{P} \) by
\[ [\mathcal{L} \varphi](x) = \int_{\mathbb{R}} \Gamma(\tau, x, y)b_u(y,0)\varphi(-\tau, y)dy, \quad x \in \mathbb{R}, \varphi \in \mathbb{C}. \]
It is obvious that \( \mathcal{L} \) is a positive operator, that is, \( \mathcal{L}(\mathbb{C}_+) \subset \mathbb{P}_+ \). Then the abstract form of (21) is
\[ \frac{dv}{dt} = Bv(t) + \mathcal{L}v_1, \quad t \geq 0, \tag{24} \]
We can define upper solution and lower solution of (21) in a similar way to Definition 3.1.

The following lemma gives the eventual strong positivity of solutions of (21).

**Lemma 3.2.** Assume that (P1)-(P4) hold, and let \( \bar{u}(t, x) \), \( \underline{u}(t, x) \) be the upper solution and lower solution of (21) with \( \bar{u}(t, x), \underline{u}(t, x) \in [0, M] \), respectively. If \( \bar{u}(\theta, x) \geq \underline{u}(\theta, x) \) and \( \bar{u}(\theta, x) \neq \underline{u}(\theta, x) \) for \( \theta \in [-\tau, 0], \quad x \in \mathbb{R}, \) then \( \bar{u}(t, x) > \underline{u}(t, x), \quad \forall (t, x) \in (\tau, \infty) \times \mathbb{R}. \)
Proof. Let \( v = \bar{u} - \underline{u} \). Then \( v \) satisfies (21) with \( \varphi(\theta, x) \geq 0, \varphi(\theta, x) = \bar{u}(\theta, x) - \underline{u}(\theta, x) \neq 0, \theta \in [-\tau, 0), x \in \mathbb{R} \). By similar arguments as in Lemma 3.1, we have \( v(t, x) \geq 0, \forall t > 0, x \in \mathbb{R} \). Further, if \( \varphi(0, x) \neq 0 \), then \( v(t, x) > 0, \forall t > 0, x \in \mathbb{R} \).

Now, assume that \( \tau > 0 \) and there is \( \theta_0 \in (-\tau, 0) \) such that \( \varphi(\theta_0, x) \neq 0 \). We want to show that \( v(\tau + \theta_0, x) \neq 0 \) by a way of contradiction. If \( v(\tau + \theta_0, x) \equiv 0 \), then we have from (21) and the definitions of upper and lower solutions that

\[
\frac{\partial v(x, t)}{\partial t} \big|_{t=\tau+\theta_0} = \int_{\mathbb{R}} \Gamma(\tau, x, y)b_u(y, 0)\varphi(\theta_0, y)dy > 0 \text{ for } x \in \mathbb{R}.
\]

On the other hand, since \( v(t, x) \geq 0 \) for \( t > 0, x \in \mathbb{R} \) and \( v(\tau + \theta_0, x) \equiv 0 \) for \( x \in \mathbb{R} \), we obtain \( \frac{\partial v(x, t)}{\partial t} \big|_{t=\tau+\theta_0} \leq 0 \), a contradiction. Thus, we have \( v(t, x) > 0 \) for all \( t > \tau + \theta_0, x \in \mathbb{R} \).

By the same argument as in [31, Theorem 2.2], together with Lemma 3.2 and a result about the sign of \( s(A) \) on page 303 of [14, Section 4], we have the following observation.

Lemma 3.3. Assume that (P1)-(P4) hold. Then there exists a principal eigenvalue \( \lambda^* \) of (22) associated with a strictly positive eigenfunction, and for any \( \tau > 0 \), \( \lambda^* \) has the same sign as \( \lambda^* \), where \( \lambda^* \) is the principal eigenvalue of (23).

Now we are in a position to describe the global dynamics of (12) in term of \( \lambda^* \).

Theorem 3.2. Assume that (P1)-(P4) hold, and let \( u(t, x; \varphi) \) be the solution of (12). Then the following statements are valid:

(i) If \( \lambda^* > 0 \), then there exists a unique periodic equilibrium \( u^*(x) \) of (5) such that \( u^* \in [0, M] \) and for any \( \varphi \in [0, M] \setminus \{0\} \), \( \lim_{t \to \infty} u(t, x; \varphi) = u^*(x) \) uniformly for \( x \in \mathbb{R} \).

(ii) If \( \lambda^* \leq 0 \), then for any \( \varphi \in [0, M] \), \( \lim_{t \to \infty} u(t, x; \varphi) = 0 \) uniformly for \( x \in \mathbb{R} \).

Proof. Let \( \Phi_t(\varphi) = u_t(\cdot, \cdot; \varphi) \) be the solution map generated by (12). Then it is easy to see that \( [0, M] \) is an invariant set of \( \Phi_t \) by (P2). We see from Lemma 3.1 that \( \Phi_t \) is monotone. On the other hand, we shall show that \( \Phi_t \) is strongly subhomogeneous in the sense that \( \Phi_t[\gamma \varphi] \geq \gamma \Phi_t \varphi \) if \( \gamma \in (0, 1) \) and \( \varphi \neq 0 \). In fact, let \( \bar{u} = u(t, x; \gamma \varphi), \underline{u} = \gamma u(t, x; \varphi) \). Then \( \bar{u}, \underline{u} \in [0, M] \), and (P3) and (P4) imply that

\[
\frac{\partial \bar{u}}{\partial t} = D_m(x)\frac{\partial^2 \bar{u}}{\partial x^2} - d(x, \bar{u}) + \int_{\mathbb{R}} \Gamma(\tau, x, y)b(\bar{u}(t - \tau, y))dy, \quad t > 0, x \in \mathbb{R}, \tag{25}
\]

and

\[
\frac{\partial \underline{u}}{\partial t} = D_m(x)\frac{\partial^2 \underline{u}}{\partial x^2} - \gamma d(x, \underline{u}) + \int_{\mathbb{R}} \Gamma(\tau, x, y)b(\underline{u}(t - \tau, y))dy
\]

\[
- D_m(x)\frac{\partial^2 \underline{u}}{\partial x^2} - d(x, \underline{u}) + \int_{\mathbb{R}} \Gamma(\tau, x, y)b(\underline{u}(t - \tau, y))dy, \quad t > 0, x \in \mathbb{R}, \tag{26}
\]

Therefore, \( \bar{u} \) and \( \underline{u} \) are upper and lower solutions of (12), respectively, with \( \bar{u}(\theta, x) = \underline{u}(\theta, x) \) for \( \theta \in [-\tau, 0], \in \mathbb{R} \). Again, Lemma 3.1 yields the \( \bar{u}(t, x) \geq \underline{u}(t, x), \forall t > 0, x \in \mathbb{R} \). That is, \( \Phi_t \) is subhomogeneous in \( [0, M] \) for any \( t > 0 \). We now need to show the strongly subhomogeneous property of \( \Phi_t \) in \( [0, M] \) for any \( t > 2\tau \). Because of the strict inequality in (26), we see that \( \bar{u}(t, x) \neq \underline{u}(t, x) \) for \( t \in (0, \tau), x \in \mathbb{R} \). Since \( b(x, u) \) is strictly subhomogeneous in \( \bar{u} \in [0, M] \), a similar argument as in the
proof of Lemma 3.2 shows that \( \bar{u}(t,x) > \underline{u}(t,x) \), \( \forall t > 2\tau, x \in \mathbb{R} \). Therefore, \( \Phi_t \) is strongly subhomogeneous in \([0, M] \) for any \( t > 2\tau \).

Note that the linear equation (21) generates a semiflow \( U(t) \), and \( U(t) \) is compact and strongly positive for any \( t > 2\tau \). Let \( t_0 > 2\tau \) be fixed. Then \( \Phi_{t_0} \) is monotone and strongly subhomogeneous in \([0, M] \), and \( \Phi_{t_0}(0) = 0 \). By the Krein-Rutman theorem (see, e.g., [11, Theorem 7.2]) and the point spectral mapping theorem (see, e.g., [23, Theorem 2.2.4]), it follows that the spectral radius \( r = r(D[\Phi_{t_0}(0)]) \) is a positive eigenvalue of \( D[\Phi_{t_0}(0)] \), and hence, \( r = e^{\lambda^* - t_0} \). Note that \( \phi_{t} : [0, M] \rightarrow [0, M] \) is compact for \( t > 2\tau \). Let \( V := [0, M] \). By [40, Theorem 2.3.4], we then obtain the threshold property for \( \Phi_{t_0} \):

(a) If \( r(D[\Phi_{t_0}(0)]) > 1 \), then there exists a unique fixed point \( u^* \gg 0 \) of \( \Phi_{t_0} \) in \( V \) such that every positive orbit for \( \Phi_{t_0} \) in \( V \) converges to \( u^* \).
(b) If \( r(D[\Phi_{t_0}(0)]) \leq 1 \), then every positive orbit for \( \Phi_{t_0} \) in \( V \) converges to 0.

Since (12) is an autonomous system, we can regard it as a time \( t_0 \)-periodic system.

For any \( t \geq 0 \), we have

\[
\Phi_t(u^*) = \Phi_t(\Phi_{t_0}(u^*)) = \Phi_{t_0}(\Phi_t(u^*)),
\]

and hence, \( \Phi_t(u^*) \) is a fixed point of \( \Phi_{t_0} \). Since the fixed point of \( \Phi_{t_0} \) is unique, we obtain \( \Phi_t(u^*) = u^* \) for all \( t \geq 0 \). Thus, \( u^* \) is an equilibrium of (12) in the space \( \mathbb{P} \).

If \( \lambda^* > 0 \), then \( r(D[\Phi_{t_0}(0)]) > 1 \). By the property of periodic semiflows, we have

\[
\lim_{t \to \infty} \|\Phi_t(\varphi) - \Phi_t(u^*)\| = \lim_{t \to \infty} \|\Phi_t(\varphi) - u^*\| = 0, \quad \forall \varphi \in V \setminus \{0\}.
\]

This implies that the statement (i) holds. We have already know that 0 is an equilibrium of (12) in \( \mathbb{P} \). A similar argument as above shows that the statement (ii) holds.

4. Spreading speeds and traveling wavefronts. Consider the following general initial value problem

\[
\frac{\partial u}{\partial t} = D_m(x) \frac{\partial^2 u}{\partial x^2} - d(x,u) + \int_{\mathbb{R}} \Gamma(t,x,y) b(y,u(t - \tau, y)) dy, \quad t > 0, x \in \mathbb{R},
\]

\[
u(0, x) = \phi(0, x), \quad \theta \in [-\tau, 0], x \in \mathbb{R}.
\]

(27)

To study the dynamics of invasion for (27), we assume that \( \lambda^* > 0 \) throughout this section. Without any confusion, we still denote the solution of (27) as \( u(t, x; \phi) \).

Let \( \mathbb{B} = BC(\mathbb{R}, \mathbb{B}) \) be the set of all continuous and bounded functions from \( \mathbb{R} \) to \( \mathbb{R} \). Let \( \mathbb{B}_+ = \{ \psi \in \mathbb{B} : \psi(x) \geq 0, \forall x \in \mathbb{R} \} \), and \( [0, u^*]_B = \{ \psi \in \mathbb{B} : 0 \leq \psi(x) \leq u^*(x), \forall x \in \mathbb{R} \} \). \( \mathbb{B}_+ \) is a closed cone of \( \mathbb{B} \) and induces a partial ordering on \( \mathbb{B} \). We equip \( \mathbb{B} \) with the compact open topology. Moreover, we define a norm \( \|\psi\|_B \) by

\[
\|\psi\|_B = \sum_{k=1}^{\infty} \frac{\max_{|x| \leq k} |\psi(x)|}{2^k}.
\]

It follows that \((\mathbb{B}, \|\psi\|_B)\) is a normed space, and the topology induced by \( \|\psi\|_B \) on \([0, u^*]_B \) is equivalent to the compact open topology on \([0, u^*] \). Furthermore, \( \mathbb{B} \) has a lattice structure and \([0, u^*]_B \) is a complete metric space.

Let \( C = C([-\tau, 0], \mathbb{B}) \) be the space of continuous functions from \([-\tau, 0] \) to \( \mathbb{B} \). Let \( G(t - s, x, y) \) be the fundamental solution of the following linear equation

\[
\frac{\partial u(x,t)}{\partial t} = D_m(x) \frac{\partial^2 u(x,t)}{\partial x^2}, \quad t > 0, x \in \mathbb{R},
\]

\[
u(0, \cdot) = \psi \in \mathbb{B}.
\]

(28)
Define a family of linear operators \( T(t) : \mathbb{B} \to \mathbb{B}, t \geq 0 \), by \( T(0) = I \) and
\[
[T(t)\psi](x) = \int_{\mathbb{R}} G(t, x, y)\psi(y)dy, \quad \forall t > 0, x \in \mathbb{R}, \psi \in \mathbb{B}.
\]
By the properties of \( G(t, x, y) \) (see [6]), it then follows that \( T(t + s) = T(t)T(s) \) for all \( t, s \in [0, \infty) \), and \( T(t)\psi \) is continuous in \((t, \psi) \in [0, \infty) \times \mathbb{B}\). Clearly, \( T(t) \) satisfies \( T(t)\mathbb{B}_+ \subset \mathbb{B}_+ \) for all \( t \geq 0 \). It is easy to verify that for any given \( t > 0 \) and uniformly bounded subset \( \mathbb{M} \) of \( \mathbb{B} \), \( T(t)(\mathbb{M}) \) is precompact with respect to the compact open topology.

We write (27) as the following integral equation:
\[
\begin{align*}
\hat{u}(t) &= T(t)\phi(0) + \int_{0}^{t} T(t - s)F(\hat{u}_s)ds, \quad t > 0, \\
\hat{u}_0 &= \phi \in C^+, \quad (29)
\end{align*}
\]
where \( \hat{u}_t(\theta) = u(t + \theta), \forall \theta \in [-\tau, 0] \), and \( F \) is defined as in (13). As usual, we define a solution of (29) to be the (mild) solution of (27). Now we use \( \mathbb{B}, \mathbb{C} \) and \( \varphi \) to replace \( \mathbb{P}, \mathbb{C} \) and \( \phi \) from (13) to (19), respectively, and define upper solution and lower solution of (27) in a similar way as in Definition 3.3. By similar arguments as in Theorem 3.1 and Lemma 3.1, we have the following two results.

**Theorem 4.1.** Assume that (P1)-(P4) hold. Then for any given initial condition \( \phi \in [0, u^*]_C \), system (27) admits a unique nonnegative solution \( u(t, x; \phi) \) on \( t \in [0, \infty) \), and \( u_t \in [0, u^*]_C \) for all \( t \geq 0 \).

**Lemma 4.1.** Assume (P1)-(P4) hold, and let \( \hat{u}(t, x), \ u(t, x) \in [0, u^*]_C \) be the upper and lower solutions of (27), respectively. If \( \bar{u}(\theta, x) \geq \underline{u}(\theta, x) \) for \( \theta \in [-\tau, 0] \), then \( \hat{u}(t) \geq \underline{u}(t) \) for all \( t \geq 0 \). Moreover, if \( \bar{u}_0 := \bar{u}(0, x) \geq \underline{u}_0 := \underline{u}(0, x) \) for \( \theta \in [-\tau, 0] \) with \( \bar{u}(0, x) \neq \underline{u}(0, x) \), then \( \bar{u}(t, x) > \underline{u}(t, x), \forall t, x \in (0, \infty) \times \mathbb{R} \).

In what follows, the theory for traveling waves and spreading speeds for abstract monostable evolution systems developed in [18] will be used to study the spatial dynamics of (27). The notations and the abstract results in the case of a periodic habitat can be found in the Appendix. Define \( X := C([-\tau, 0], \mathbb{R}) \) with the maximum norm. Then \( X \) is a Banach lattice. Let
\[
\mathcal{C} := \{ \phi : \phi : \mathbb{R} \to X \text{ is bounded and continuous} \},
\]
and \( \mathcal{C}_{u^*} := \{ u \in \mathcal{C} : u^*(x) \geq u \geq 0 \} \). For the sake of convenience, we also identify an element \( \phi \in \mathcal{C} \) as a function from \([-\tau, 0] \times \mathbb{R} \) into \( \mathbb{R} \) defined by \( \phi(\theta, x) = \phi(x)(\theta) \).

We equip \( \mathcal{C} \) with the compact open topology, and define
\[
|\phi|_C = \sum_{k=1}^{\infty} \max_{x \in \mathbb{R}, |x| \leq k} |\phi(x)|_X = \frac{\max_{x \in \mathbb{R}, |x| \leq k} |\phi(x)|_X}{2^k}. \quad (30)
\]
It then follows that \( (\mathcal{C}, | \cdot |_C) \) is a normed space. Moreover, the topology induced by \( | \cdot |_C \) on \( \mathcal{C}_{u^*} \) is equivalent to the compact open topology on \( \mathcal{C}_{u^*} \), and \( \mathcal{C}_{u^*} \) is a complete metric space. Note that \( \mathcal{C} \) has a lattice structure.

Recall that a family of operators \( \{ \Psi_t \}_{t \geq 0} \) is said to be a semiflow on a metric space \((X, \rho)\) with metric \( \rho \) provided it has the following properties:
\begin{enumerate}
\item \( \Psi_0(v) = v, \forall v \in X \).
\item \( \Psi_{t_1}[[\Psi_{t_2}[v]] = \Psi_{t_1+t_2}[v], \forall t_1, t_2 \geq 0, v \in X \).
\item \( \Psi(t, v) := \Psi_t(v) \) is continuous in \((t, v)\) on \([0, \infty) \times X \).
\end{enumerate}
It is easy to see that the property (iii) holds if \( \Psi(\cdot, v) \) is continuous on \([0, +\infty)\) for each \( v \in \mathcal{X} \), and \( \Psi(t, \cdot) \) is uniformly continuous for \( t \) in any bounded intervals in the sense that for any \( v_0 \in \mathcal{X} \), bounded interval \( I \) and \( \epsilon > 0 \), there exists \( \delta = \delta(v_0, I, \epsilon) > 0 \) such that if \( \rho(v, v_0) < \delta \), then \( \rho(\Psi(t)[v], \Psi(t)[v_0]) < \epsilon \) for all \( t \in I \).

Define a family of operators \( \{Q_t\}_{t \geq 0} \) on \( C_u^* \) by
\[
[Q_t(\phi)](\theta, x) = u_t(\theta, x; \phi), \quad \forall \phi \in C_u^*, \theta \in [-\tau, 0], x \in \mathbb{R},
\]
where \( u(t, x; \phi) \) is the solution of (27) with an initial function \( \phi \in C_u^* \). Here \( u_t(\theta, x; \phi) = u(t + \theta, x; \phi), \theta \in [-\tau, 0] \). Then we have the following observation.

**Theorem 4.2.** Assume that (P1)-(P4) hold. Then \( \{Q_t\}_{t \geq 0} \) is a monotone and subhomogeneous semiflow on \( C_u^* \).

**Proof.** Clearly, \( Q_t \) satisfies the property (i) of semiflows. Since (27) is autonomous, the uniqueness of solutions implies the semiflow property (ii). It remains to prove that \( Q_t(\phi) \) is continuous in \( (t, \phi) \in \mathbb{R}_+ \times C_u^* \). By Theorem 4.1, for any given \( \phi \in C_u^* \), \( Q_t(\phi) \) is continuous in \( t \in \mathbb{R}_+ \) with respect to the compact open topology. We first prove the following claim.

**Claim.** \( Q_t(\phi) \) is continuous in \( \phi \in C_u^* \) uniformly for \( t \in [0, \tau] \).

For any \( \phi, \bar{\phi} \in C_u^* \), we define \( \hat{\phi} = \max\{\phi, \bar{\phi}\} \) and \( \bar{\phi} = \min\{\phi, \bar{\phi}\} \). Then Lemma 4.1 implies that
\[
u(t, x; \hat{\phi}) \leq u(t, x; \phi), \quad u(t, x; \bar{\phi}) \leq u(t, x; \phi), \quad \forall (t, x) \in \mathbb{R}_+ \times \mathbb{R},
\]
and hence,
\[
u(t, x; \phi) - u(t, x; \phi) \leq u(t, x; \hat{\phi}) - u(t, x; \bar{\phi}), \quad \forall (t, x) \in \mathbb{R}_+ \times \mathbb{R}.
\]

Thus, without loss of generality, we assume that \( \phi \geq \bar{\phi} \). Then \( u(t, x; \phi) \geq u(t, x; \bar{\phi}) \) for all \( (t, x) \in \mathbb{R}_+ \times \mathbb{R} \). For the sake of convenience, we let \( u(t, x) = u(t, x; \phi) \), \( \bar{u}(t, x) = u(t, x; \bar{\phi}) \), and \( v(t, x) = u(t, x) - \bar{u}(t, x) \). Let
\[
d_0 := \min_{(x, u) \in [0, L] \times [0, M]} \frac{\partial d}{\partial u}(x, u), \quad b_0 := \max_{(x, u) \in [0, L] \times [0, M]} \left| \frac{\partial b}{\partial u}(x, u) \right|.
\]

Clearly, \( b_0 \geq 0 \), and the assumption (P4) implies \( d_0 \geq 0 \). It then follows that \( v(t, x) \) satisfies
\[
\frac{\partial v(t, x)}{\partial t} \leq D_m(x) \frac{\partial^2 v(t, x)}{\partial x^2} - d_0 v(t, x) + b_0 \int_{\mathbb{R}} \Gamma(\tau, x, y)v(t - \tau, y)dy, \quad t > 0, x \in \mathbb{R},
\]
(31)

Define a linear operator \( T_0 : \mathbb{B} \to \mathbb{B} \) by
\[
[T_0 \psi](x) = b_0 \int_{\mathbb{R}} \Gamma(\tau, x, y)\psi(y)dy, \quad \forall x \in \mathbb{R}, \psi \in \mathbb{B}.
\]
(32)

It is easy to verify that \( T_0 \) is continuous on \( \mathbb{B} \) with respect to the compact open topology. By (31) and (32), we then have
\[
v(t, \cdot) \leq e^{-dt}T(t)v(0, \cdot) + \int_0^t e^{-d(t-s)}T(t-s)T_0(v(s - \tau, \cdot))ds, \quad t \geq 0.
\]

Since \( v(\theta, x) = \phi(\theta, x) - \bar{\phi}(\theta, x), \forall \theta \in [-\tau, 0], x \in \mathbb{R} \), it follows that
\[
v(t, \cdot) \leq e^{-dt}T(t)(\phi(0, \cdot) - \bar{\phi}(0, \cdot)) + \int_0^t e^{-d(t-s)}[T(t-s)T_0(\phi(s - \tau, \cdot) - \bar{\phi}(s - \tau, \cdot))]ds, \quad t \in [0, \tau].
\]

This, together with the continuity of \( T(t) \) and \( T_0 \), implies the above claim.
Since for any \( t, t_0 \geq 0 \) and \( \phi, \phi_0 \in C_{u^*} \), there holds
\[
|Q_t(\phi) - Q_{t_0}(\phi_0)| \leq |Q_t(\phi) - Q_t(\phi_0)| + |Q_t(\phi_0) - Q_{t_0}(\phi_0)|,
\]
it follows that \( Q_t(\phi) \) is continuous in \( (t, \phi) \in [0, \tau] \times C_{u^*} \). Note that for any \( t \in \mathbb{R}_+ \), we have \( t = mt + t' \) for some \( m \in \mathbb{Z}_+ \) and \( t' \in [0, \tau) \), and hence, \( Q_t(\phi) = (Q_{t'})^m((Q_{\tau'})(\phi)) \). Thus, \( Q_t(\phi) \) is continuous in \( (t, \phi) \in \mathbb{R}_+ \times C_{u^*} \). Consequently, \( \{Q_t\}_{t \geq 0} \) is a continuous semiflow on \( C_{u^*} \).

Clearly, Lemma 4.1 implies that \( Q_t \) is monotone on \( C_{u^*} \). Similar arguments as in Theorem 3.2 show that \( Q_t \) is subhomogeneous in \( C_{u^*} \) in the sense that \( Q_t[\gamma \phi] \geq \gamma Q_t[\phi] \) for all \( \gamma \in [0, 1] \) and \( \phi \in C_{u^*} \).

Lemma 4.2. For any \( \phi \in C_{u^*} \) with \( \phi \neq 0 \), we have \( u(t, x; \phi) > 0 \) for all \( t > \tau, x \in \mathbb{R} \).

Proof. Let \( \phi \in C_{u^*} \) with \( \phi \neq 0 \). By Lemma 4.1, \( u(t, x; \phi) \geq 0 \) for all \( t \geq 0, x \in \mathbb{R} \). We claim that there is \( t_0 \in [0, \tau] \) such that \( u(t_0, \cdot; \phi) \neq 0 \). Assume, by contradiction, that \( u(t, \cdot; \phi) \equiv 0 \) for all \( t \in [0, \tau] \). Choose \( \theta_0 \in [\tau, 0] \) and \( x_0 \in \mathbb{R} \) such that \( \phi(\theta_0, x_0) > 0 \). Letting \( t = \theta_0 + \tau \) in (27), we then obtain
\[
0 = -0 + \int_{\mathbb{R}} \Gamma_{t}(\tau, x, y)b(y, u(t - \tau, y; \phi))dy = \int_{\mathbb{R}} \Gamma_{t}(\tau, x, y)b(y, \phi(\theta_0, \phi))dy > 0,
\]
a contradiction. Thus, we have \( u(t_0, \cdot; \phi) \neq 0 \) for some \( t_0 \in [0, \tau] \). By Lemma 4.1, we conclude that \( u(t, x; u(t_0)) > 0 \) for all \( t > 0, x \in \mathbb{R} \). This implies that \( u(t, x; \phi) > 0 \) for all \( t > \tau, x \in \mathbb{R} \).

Let \( \mathcal{H} = \mathbb{R}, \mathcal{X} = \mathcal{Y} = C([-\tau, 0], \mathbb{R}), \beta = u^*, \mathcal{M} = C_{u^*}, \mathcal{D} = \mathcal{C} \) and \( \mathcal{H} = \{n \mathcal{L} : n \in \mathbb{Z}\} \) in the Appendix. Then \( \beta \) is \( L \)-periodic.

Lemma 4.3. Assume that (P1)-(P4) hold, and the principal eigenvalue of (22) satisfies \( \lambda^* > 0 \). Then for any \( t > 0 \), \( Q_t \) satisfies (E1), (E2), (E3'), (E4) and (E5) in the Appendix.

Proof. Note that if \( u(t, x; \phi) \) is a solution of (27), then \( u(t, x - a; \phi) \), \( a \in \mathcal{H} \), is also a solution of (27). This implies that (E1) is true. (E2) and (E4) are obvious by using the definition and properties of \( Q_t \). We obtain (E5) from Theorem 3.2 (i). Therefore, we only need to verify (E3)'.

Following [10], we define a family of linear operators \( \{\tilde{L}(t)\}_{t > 0} \) on \( \mathcal{X} \) by
\[
\tilde{L}(t)[\psi](\theta) := \begin{cases} \psi(t + \theta) - \psi(0) & \text{for } t + \theta < 0, \\ 0 & \text{for } t + \theta \geq 0. \end{cases}
\]
It then follows from [18, Section 4] that for any given \( \gamma > 0 \), there is an equivalent norm \( |\cdot|^\gamma \) in \( \mathcal{X} \) such that \( |\tilde{L}(t)||^\gamma \leq e^{-\gamma t}, \forall t \geq 0 \). In what follows, we show that for each \( t \geq 0 \), the map \( Q_t \) satisfies (E3)' with \( (\mathcal{X}, |\cdot|^\gamma) \) replaced by \( (\mathcal{X}, |\cdot|^\gamma') \).

Let \( Q_t \) be the solution semiflow of (27) on \( C_{u^*} \), that is, \( Q_t[\phi](\theta, x) = u_t(\phi)(\theta, x), \forall t \geq 0, \phi \in C_{u^*} \), where \( u(t, x; \phi) \) is the solution of (27). To verify hypotheses (E3)', we use the same argument as in [18, Remark 4.1]. Define
\[
L(t)[\phi](\theta, x) := \begin{cases} \phi(t + \theta, x) - \phi(0, x) & \text{for } t + \theta < 0, \\ 0 & \text{for } t + \theta \geq 0, \end{cases}
\]
and
\[
S(t)[\phi](\theta, x) := \begin{cases} \phi(0, x) & \text{for } t + \theta < 0, \\ u(t + \theta, x; \phi) & \text{for } t + \theta \geq 0. \end{cases}
\]
Then \( Q_t[\phi] = L(t)[\phi] + S(t)[\phi], \forall t \geq 0, \phi \in C_{u^*} \). Since
\[
Q_t[\phi](0, \cdot) = u(t, \cdot; \phi) = T(t)\phi(0) + \int_0^t T(t - s)F(u_s)ds,
\]

where $T(t)$ is the semigroup generated by the linear equation (28), and $T(t)(C_{u^\star})$ is precompact for each $t > 0$, we see that $Q_t[C_{u^\star}](0, \cdot) = u(t, \cdot; C_{u^\star})$ is precompact in $C(\mathbb{R}, \mathbb{R})$. Given $U \subset C_{u^\star}$ with $U(0, \cdot)$ precompact in $C(\mathbb{R}, \mathbb{R})$, it then follows that $S(t)[U]$ is precompact in $C_{u^\star}$. Thus, for any interval $I = [a, b]$ of the length $r$, we have

$$
\alpha((Q_t[U])_I) \leq \alpha((L(t)[U])_I) + \alpha((S(t)[U])_I) \leq e^{-\gamma t}\alpha(U_I),
$$

where $\alpha$ is the Kuratowski measure of noncompactness on $C_I$ with $(X, |\cdot|)$ replaced by $(X, |\cdot|^*)$. This implies that for each $t > 0$, $Q_t$ satisfies (E3)' with $k = e^{-\gamma t}$. □

The subsequent result is the consequence of Lemmas 4.2-4.3, Theorem 4.2, and Theorem 5.2 in the Appendix. Note that Theorem 5.2 (ii) needs the condition $c^*_- > -c^*_+$. In Theorem 4.5, we will show that this condition is satisfied under the assumptions of Theorem 4.3.

**Theorem 4.3.** Assume that (P1)-(P4) hold, and the principal eigenvalue of (22) satisfies $\lambda^* > 0$. Then there exist $c^*_+$ and $c^*_-$, being the rightward and leftward spreading speeds of $Q_1$, respectively, such that the following statements are valid:

(i) For each $c > c^*_+$ and $c' > c^*_-$, if $\phi \in C_{u^\star}$ with $0 \leq \phi \leq \varpi$ for some L-periodic $\varpi \in X$ and $\varpi \ll u^*$, and $\phi(\cdot, x) = 0$ for $x$ outside a bounded interval, then

$$
\lim_{t \to \infty, x \geq ct} u(t, x; \phi) = 0 \quad \text{and} \quad \lim_{t \to \infty, x \leq -c't} u(t, x; \phi) = 0.
$$

(ii) For any $c < c^*_+, c' < c^*_-$, if $\phi \in C_{u^\star}$ with $\phi \neq 0$, then

$$
\lim_{t \to \infty, -c't \leq x \leq ct} [u(t, x; \phi) - u^*(x)] = 0.
$$

**Proof.** The statement (i) follows from Theorem 5.2(i). Since $Q_1$ is subhomogeneous, the positive number $r_\sigma$ in Theorem 5.2 (ii) can be chosen to be independent of $\sigma \gg 0$. Let $r_\sigma = r$. For each $c > c^*_+$ and $c' > c^*_-$, if $\phi \in C_{u^\star}$ with $\phi(\theta, x) > 0$ for all $\theta \in [-\tau, 0]$ and $x$ on an interval $I$ of length $2r$, then there exists a vector $\sigma \gg 0$ such that $\varphi(\theta, x) \gg \sigma$, $\forall \theta \in [-\tau, 0], x \in I$, and hence, Theorem 5.2(ii) implies that

$$
\lim_{t \to \infty, -c't \leq z \leq ct} [u(t, x; \phi) - u^*(x)] = 0.
$$

For any $\phi \in C_{u^\star}$ with $\phi \neq 0$, it follows from Lemma 4.2 that $u(t, x; \phi) > 0$, $\forall t > \tau, x \in \mathbb{R}$. Fix a $t_0 > 2\tau$. Then $u_{t_0}(\phi) \gg 0$. By taking $u_{t_0}$ as a new initial data, we see that statement (ii) holds. □

By Lemmas 4.2-4.3, Theorem 4.2, and Theorem 5.3 in the Appendix, we have the following result.

**Theorem 4.4.** Assume that (P1)-(P4) hold, and the principal eigenvalue of (22) satisfies $\lambda^* > 0$. Let $c^*_+$ and $c^*_-$ be the rightward and leftward spreading speeds of $Q_1$, respectively. Then the following statements are valid:

(i) Equation (27) has a L-periodic rightward traveling wave $V(x-ct, x)$ connecting $u^*$ to 0 with $V(\xi, x)$ being continuous and nonincreasing in $\xi \in \mathbb{R}$ if and only if $c \geq c^*_+$. 

(ii) Equation (27) has a L-periodic leftward traveling wave $V(x+ct, x)$ connecting 0 to $u^*$ with $V(\xi, x)$ being continuous and increasing in $\xi \in \mathbb{R}$ if and only if $c \geq c^*_-$.

Consider the linearized equation of (27) at its zero solution:

$$
\frac{\partial u}{\partial t} = D_m(x)\frac{\partial^2 u}{\partial x^2} - d(x, 0)u + \int_{\mathbb{R}} \Gamma(\tau, x, y)b(u(y, 0))u(t - \tau, y)dy, \quad t > 0, x \in \mathbb{R},
$$

$$
u_0 = \phi \in C.
$$

(33)
Let \( \{L(t)\}_0^\infty \) be the linear solution maps associated with (33), that is, \( L(t)\phi = u_t(\phi) \). Letting \( u(x, t) = e^{-\mu x}v(t, x) \) in (33), we see that \( v(t, x) \) satisfies

\[
\frac{\partial v}{\partial t} = D_m(x)\frac{\partial^2 v}{\partial x^2} + p(x, \mu)\frac{\partial v}{\partial x} + q(x, \mu)v + \int_\mathbb{R} \Gamma_1(\tau, x, y, \mu)v(t - \tau, y)dy, \quad t > 0, x \in \mathbb{R},
\]

(34)

where \( p(x, \mu) := -2\mu D_m(x) \), \( q(x, \mu) := D_m(x)\mu^2 - d_u(x, 0) \), and

\[
M_1(\tau, x, y, \mu) := \Gamma(\tau, x, y)e^{\mu(x-y)}b_u(y, 0),
\]

\[
M_2(\tau, x, y, \mu) = \Gamma(\tau, x, y, \mu), \forall x, y \in \mathbb{R}.
\]

Furthermore, letting \( v(t, x) = e^{\lambda t}w(x) \), \( w(x) = w(x + L) > 0 \) for \( x \in \mathbb{R} \), we obtain the following nonlocal and periodic eigenvalue problem of delay type:

\[
\lambda w(x) = D_m(x)\frac{d^2 w(x)}{dx^2} + p(x, \mu)\frac{d w(x)}{dx} + q(x, \mu)w(x) + e^{-\lambda \tau} \int_\mathbb{R} M_1(\tau, x, y, \mu)w(y)dy, \quad w(x + L) = w(x), \quad x \in \mathbb{R}.
\]

(35)

For any given \( \mu \in \mathbb{R} \), let \( L_\mu(t) \) be the linear solution maps associated with (34), that is, \( L_\mu(t)\varphi = v_t(\varphi) \) with \( v(x, \theta) = \varphi(x + L, \theta) \). As argued in Lemmas 3.2 and 3.3, it follows that (35) has a principal eigenvalue \( \lambda(\mu) \) with a strictly positive eigenfunction. Note that \( \lambda(0) = \lambda^* \), which is discussed in Lemma 3.3. On the other hand, \( L_\mu(t) \) is strongly positive and compact for every \( t > \tau \). By the Krein-Rutman theorem, it follows that for each \( t > \tau \), the spectral radius \( r(L_\mu(t)) > 0 \) and is the principal eigenvalue of \( L_\mu(t) \), and hence, \( r(L_\mu(t)) = e^{\lambda(\mu)t} \).

**Proposition 4.1.** \( \lambda(\mu) \) is a convex function of \( \mu \) on \( \mathbb{R} \).

**Proof.** For any given two real numbers \( \mu_1 \) and \( \mu_2 \), let \( w_i(x) = w_i(x + L) \) be the eigenfunctions corresponding to the principal eigenvalue \( \lambda_i = \lambda(\mu_i) \), \( i = 1, 2 \), respectively. Define \( w_i^*(x) = e^{-\mu_i x}w_i(x) \). Then for any \( x \in \mathbb{R} \), we have \( w_i^*(x) > 0 \) and

\[
\lambda_i w_i^*(x) = D_m(x)\frac{d^2 w_i^*(x)}{dx^2} - d_u(x, 0)w_i^*(x) + e^{-\lambda_i \tau} \int_\mathbb{R} M_1(\tau, x, y, \mu)w_i(y)dy,
\]

(36)

for \( i = 1, 2 \). We further have the following observation.

**Claim.** The function \( \tilde{w}(x) := (w_1^*(x)w_2^*(x))^\frac{1}{2} = e^{-\frac{\mu_1 + \mu_2}{2} x} (w_1(x)w_2(x))^{\frac{1}{2}} \) satisfies

\[
\frac{\lambda_1 + \lambda_2}{2} \tilde{w}(x) \geq D_m(x)\frac{d^2 \tilde{w}(x)}{dx^2} - d_u(x, 0)\tilde{w}(x) + e^{-\frac{\lambda_1 + \lambda_2}{2} \tau} \int_\mathbb{R} M_1(\tau, x, y, \mu)\tilde{w}(y)dy
\]

for all \( x \in \mathbb{R} \).

Indeed, a direct computation shows that

\[
\frac{d\tilde{w}(x)}{dx} = \frac{1}{2} \left( \frac{w_2^*}{w_1^*} \frac{dw_1^*}{dx} + \frac{w_1^*}{w_2^*} \frac{dw_2^*}{dx} \right),
\]

\[
\frac{d^2 \tilde{w}(x)}{dx^2} = \frac{1}{4} \left[ \frac{2}{\tilde{w}} \frac{dw_1^*}{dx} \frac{dw_2^*}{dx} - \left( \frac{\tilde{w}}{w_1^*} \right)^2 \left( \frac{dw_1^*}{dx} \right)^2 - \left( \frac{\tilde{w}}{w_2^*} \right)^2 \left( \frac{dw_2^*}{dx} \right)^2 \right]
\]

\[
\quad + \frac{1}{2} \left( \frac{w_2^*}{w_1^*} \frac{d^2 w_1^*}{dx^2} + \frac{w_1^*}{w_2^*} \frac{d^2 w_2^*}{dx^2} \right),
\]
and

\[ D_m(x) \frac{d^2 \bar{w}(x)}{dx^2} - d_u(x, 0) \bar{w}(x) + e^{-\frac{1}{2}(\lambda_1 + \lambda_2)\tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w(y)dy = \]

\[ = \frac{D_m(x)}{4} \left[ 2 \frac{d u_1^*}{dx} \frac{d w_1^*}{dx} - \frac{\bar{w}}{(w_1^*)^2} \frac{d w_1^*}{dx} \left( \frac{d w_1^*}{dx} \right)^2 - \frac{\bar{w}}{(w_2^*)^2} \right] \]

\[ + \frac{D_m(x)}{2} \left[ \left( \frac{w_1^*}{w_2^*} \right)^2 \frac{d^2 w_1^*}{dx^2} + \left( \frac{w_1^*}{w_2^*} \right)^2 \frac{d^2 w_2^*}{dx^2} \right] - d_u(x, 0)(w_1^* w_2^*)^{\frac{1}{2}} \]

\[ + e^{-\frac{1}{2}(\lambda_1 + \lambda_2)\tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)\{w_1^*(y)w_2^*(y)\}^{\frac{1}{2}} dy. \]

(37)

By the inequality \( a^2 + b^2 \geq 2ab \) and Schwarz’s inequality, we have

\[ \frac{2}{\bar{w}} \frac{d u_1^*}{dx} \frac{d w_1^*}{dx} - \frac{\bar{w}}{(w_1^*)^2} \left( \frac{d w_1^*}{dx} \right)^2 - \frac{\bar{w}}{(w_2^*)^2} \leq 0, \]

(38)

and

\[ e^{-\frac{1}{2}(\lambda_1 + \lambda_2)\tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)[w_1^*(y)w_2^*(y)]^{\frac{1}{2}} dy \]

\[ \leq \left[ e^{-\lambda_1 \tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_1^*(y)dy \right]^{\frac{1}{2}} \left[ e^{-\lambda_2 \tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_2^*(y)dy \right]^{\frac{1}{2}}. \]

(39)

It then follows that

\[ D_m(x) \frac{d^2 \bar{w}(x)}{dx^2} - d_u(x, 0)\bar{w}(x) + e^{-\frac{1}{2}(\lambda_1 + \lambda_2)\tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)\bar{w}(y)dy \]

\[ \leq \frac{D_m(x)}{2} \left[ \left( \frac{w_1^*}{w_2^*} \right)^2 \frac{d^2 w_1^*}{dx^2} + \left( \frac{w_1^*}{w_2^*} \right)^2 \frac{d^2 w_2^*}{dx^2} \right] - \frac{d_u(x, 0)}{2} \left[ (w_1^* w_2^*)^{\frac{1}{2}} + (w_1^* w_2^*)^{\frac{1}{2}} \right] \]

\[ + \left[ e^{-\lambda_1 \tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_1^*(y)dy \right]^{\frac{1}{2}} \left[ e^{-\lambda_2 \tau} \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_2^*(y)dy \right]^{\frac{1}{2}} \]

\[ = \frac{1}{2} \lambda_1 \bar{w} - \frac{1}{2} \left[ e^{-\lambda_1 \tau} \left( \frac{w_1^*}{w_2^*} \right)^2 \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_1^*(y)dy \right] \]

\[ + \frac{1}{2} \lambda_2 \bar{w} - \frac{1}{2} \left[ e^{-\lambda_2 \tau} \left( \frac{w_1^*}{w_2^*} \right)^2 \int_\mathbb{R} \Gamma(\tau, x, y)b_u(y, 0)w_2^*(y)dy \right] \]

\[ \leq \frac{\lambda_1 + \lambda_2}{2} \bar{w}(x). \]

By the claim above, we see that \( \bar{u}(t, x) := e^{\frac{\lambda_1 + \lambda_2}{2}t} \bar{w}(x) \) satisfies

\[ \frac{\partial \bar{u}}{\partial t} \geq D_m(x) \frac{d^2 \bar{u}}{dx^2} - d_u(x, 0)\bar{u} + \int_\mathbb{R} \Gamma(t, x, y)b_u(y, 0)\bar{u}(t - \tau, y)dy, \quad t > 0, x \in \mathbb{R}. \]

(40)

Define \( \phi(\theta, x) := e^{\frac{\lambda_1 + \lambda_2}{2}x} \bar{w}(x), \forall \theta \in [-\tau, 0], x \in \mathbb{R}. \) By the comparison theorem for the linear equation (33), it then follows that

\[ e^{\frac{(\lambda_1 + \lambda_2)x}{2}} \bar{w}(x) = \bar{u}(t, x) \geq u(t, x; \phi), \quad \forall t \geq 0, x \in \mathbb{R}, \]

where \( u(t, x; \phi) \) is the solution of (33) with the initial condition \( u_0 = \phi. \) By (40), we further have

\[ e^{\frac{(\lambda_1 + \lambda_2)x}{2}} \phi(\theta, x) \geq e^{\frac{(\lambda_1 + \lambda_2)x}{2}} (L(t)\phi)(\theta, x), \quad \forall \theta \in [-\tau, 0], x \in \mathbb{R}. \]

Let \( \varphi(\theta, x) := e^{\frac{(\lambda_1 + \lambda_2)x}{2}} \phi(\theta, x) = e^{\frac{(\lambda_1 + \lambda_2)x}{2}} w(x) \) and \( w(x) := \{w_1(x)w_2(x)\}^{\frac{1}{2}}. \) Then we obtain

\[ e^{\frac{(\lambda_1 + \lambda_2)x}{2}} \varphi(\theta, x) \geq (L_{\mu_1 + \mu_2} - t)(\varphi)(\theta, x), \quad \forall \theta \in [-\tau, 0], x \in \mathbb{R}, \]

that is,

\[ \left( e^{\frac{(\lambda_1 + \lambda_2)x}{2}} I - L_{\mu_1 + \mu_2} \right)(\varphi)(\theta, x) \geq 0, \quad \forall t \geq 0, \]

where \( I \) is the identity operator. Note that

\[ \varphi(\theta, x + L) = e^{\frac{(\lambda_1 + \lambda_2)x}{2}} w(x + L) = e^{\frac{(\lambda_1 + \lambda_2)x}{2}} w(x) = \varphi(\theta, x) > 0, \quad \forall \theta \in [-\tau, 0], x \in \mathbb{R}, \]
that is, $\varphi \gg 0$, and that $L_\mu(t)$ is a compact and strongly positive linear operator for each $t > \tau$. By the Krein-Rutman theorem (see [11, Theorem 7.3]), we have
\[ e^{(\lambda_1+\lambda_2)t} \geq r \left( L_{\frac{\lambda_1+\lambda_2}{2}}(t) \right) = e^{\lambda(t_{\frac{\lambda_1+\lambda_2}{2}})}, \quad \forall t > \tau, \]
where $r \left( L_{\frac{\lambda_1+\lambda_2}{2}}(t) \right)$ is the spectral radius of the operator $L_{\frac{\lambda_1+\lambda_2}{2}}(t)$. This implies that $\frac{\lambda_1+\lambda_2}{2} \geq \lambda(\frac{\mu_1+\mu_2}{2})$, that is,
\[ \lambda \left( \frac{\mu_1+\mu_2}{2} \right) \leq \frac{1}{2} \lambda(\mu_1) + \frac{1}{2} \lambda(\mu_2). \]
It then follows that $\lambda(\mu)$ is a convex function on $\mathbb{R}$.

Now we are ready to give a computational formula for spreading speeds.

**Theorem 4.5.** Let $c^*_+$ and $c^-_-$ be the rightward and leftward asymptotic speeds of spread of $Q_1$, respectively. Then
\[ c^*_+ = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu}, \quad c^-_- = \inf_{\mu > 0} \frac{\lambda(-\mu)}{\mu}. \]
Furthermore, $c^*_+ + c^-_- > 0$.

**Proof.** Since both $b(x, u)$ and $-d(x, u)$ are subhomogeneous in $u$, we have
\[ b(x, u) \leq b_u(x, 0)u, \quad -d(x, u) \leq -d_u(x, 0)u, \quad \forall x \in \mathbb{R}, u \in \mathbb{R}. \] (41)
It then follows that the solution of (27) satisfies
\[ \frac{\partial u}{\partial t} \leq D_m(x) \frac{\partial^2 u}{\partial x^2} - d_u(x, 0)u + \int_{\mathbb{R}} \Gamma(t, x, y)b_u(y, 0)u(t - \tau, y)dy, \quad t > 0, y \in \mathbb{R}, \]
\[ u(0, x, y) = \phi \in C. \quad (42) \]
Thus, the comparison principle implies that $Q_1(\phi) \leq L(t)\phi, \quad \forall t > 0, \phi \in [0, u^*]_C$. Letting $t = 1$, we have $Q_1(\phi) \leq L(1)\phi, \quad \forall \phi \in [0, u^*]_C$.

For any given $\mu \in \mathbb{R}$, we define a linear operator $L_\mu$ on $C = C([-\tau, 0], \mathbb{R})$ associated with $L(1)$ by
\[ L_\mu(\psi)(\theta, x) = e^{\mu x} \cdot L(1)(e^{-\mu x} \psi)(\theta, x) = e^{\mu x} \cdot e^{-\mu x} L_\mu(1)(\psi)(\theta, x) = L_\mu(1)(\psi)(\theta, x), \quad \forall \theta \in [-\tau, 0], \ x \in \mathbb{R}, \ \psi \in \mathbb{C}, \]
that is, $L_\mu = L(1)$. Thus, $e^{\lambda(\mu)}$ is the principal eigenvalue of $L_\mu$. By Proposition 4.1, we see that $\ln \left( e^{\lambda(\mu)} \right) = \lambda(\mu)$ is a convex function of $\mu \in \mathbb{R}$. With this convexity, we can use the similar arguments as in [34, Theorem 2.5] and [17, Theorem 3.10(i)] to obtain
\[ c^*_+ \leq \inf_{\mu > 0} \frac{\ln e^{\lambda(\mu)}}{\mu} = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu}. \] (43)
Since $\lim_{u \to 0} \frac{d(x,u)-d(x,0)}{u} = \lim_{u \to 0} \frac{d(x,u)}{u} = d_u(x, 0)$ for any $x \in \mathbb{R}$, it then follows that for any $\epsilon \in (0, 1)$, there is a $\delta > 0$ such that for any $\phi \in C_\delta$, we have
\[ d(x, u(t, x; \phi)) \leq (1 + \epsilon)d_u(x, 0)u(t, x; \phi), \quad \forall x \in \mathbb{R}, \ t \in [0, 1]. \]
Similarly, we have
\[ b(x, u(t - \tau, x; \phi)) \geq (1 - \epsilon)b_u(x, 0)u(t - \tau, x; \phi), \quad \forall x \in \mathbb{R}, \ t \in [0, 1]. \]
Thus, \( u(t, x) = u(t, x; \phi) \) satisfies
\[
\frac{\partial u}{\partial t} \geq D_m(x) \frac{\partial^2 u}{\partial x^2} - (1 + \epsilon) a_u(x, 0) u + (1 - \epsilon) \int_\mathbb{R} \Gamma(\tau, x, y) b_u(y, 0) u(t - \tau, y) dy
\]
for all \( t \in [0, 1], x \in \mathbb{R} \). Consider the linear system
\[
\frac{\partial u}{\partial t} = D_m(x) \frac{\partial^2 u}{\partial x^2} - (1 + \epsilon) a_u(x, 0) u + (1 - \epsilon) \int_\mathbb{R} \Gamma(\tau, x, y) b_u(y, 0) u(t - \tau, y) dy,
\]
\( t > 0, x \in \mathbb{R} \).

Let \( \{L'(t)\}_0^\infty \) be the solution semigroup generated by the above linear system. Then the comparison principle implies that \( L'(t)(\phi) \leq Q_t(\phi), \forall \phi \in C_0, t \in [0, 1] \).

In particular, \( L'(1)(\phi) \leq Q_1(\phi), \forall \phi \in C_0 \).

Let \( \lambda'(\mu) \) be the principal eigenvalue of the eigenvalue problem associated with the linear system (44). As argued above, the convexity of \( \lambda'(\mu) \) and the similar arguments as in [34, Theorem 2.4] and [17, Theorem 3.10(ii)] give rise to
\[
c^*_+ \geq \inf_{\mu > 0} \frac{\ln e^{\lambda'(\mu)}}{\mu} = \inf_{\mu > 0} \frac{\lambda'(\mu)}{\mu}, \quad \forall \epsilon \in (0, 1).
\]

Combining (43) and (45), we obtain
\[
\inf_{\mu > 0} \frac{\lambda'(\mu)}{\mu} \leq c^*_+ \leq \inf_{\mu > 0} \frac{\lambda'(\mu)}{\mu}, \quad \forall \epsilon \in (0, 1).
\]

Letting \( \epsilon \to 0 \) in the above, we then have \( c^*_+ = \inf_{\mu > 0} \frac{\lambda'(\mu)}{\mu} \). By the change of variable \( v(t, x) = u(t, -x) \), it follows that \( c^*_+ \) is the rightward spreading speed of the resulting equation for \( v \). This implies that \( c^*_+ = \inf_{\mu > 0} \frac{\lambda(-\mu)}{\mu} \).

Let \( \mu_1 > 0, \mu_2 > 0 \) be such that
\[
c^*_+ = \frac{\lambda(\mu_1)}{\mu_1} = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu}, \quad c^-_+ = \frac{\lambda(\mu_2)}{\mu_2} = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu}.
\]

Choose \( \eta = \frac{\mu_2}{\mu_1 + \mu_2} \). Then \( \eta \mu_1 - (1 - \eta) \mu_2 = 0 \), and \( \eta \in (0, 1) \). Since \( \lambda(\mu) \) is convex in \( \mu \), we have
\[
c^*_+ + c^-_+ = \frac{\lambda(\mu_1)}{\mu_1} + \frac{\lambda(-\mu_2)}{\mu_2} = \frac{\mu_1 + \mu_2}{\mu_1 + \mu_2} [\eta \lambda(\mu_1) + (1 - \eta) \lambda(-\mu_2)]
\]
\[
\geq \frac{\mu_1 + \mu_2}{\mu_1 + \mu_2} [\eta \lambda(\mu_1 - (1 - \eta) \mu_2)] = \frac{\lambda(\mu_1)}{\mu_1 + \mu_2} \lambda(0) = \frac{\mu_1 + \mu_2}{\mu_1 + \mu_2} \lambda^* > 0.
\]

This completes the proof.

\[ \square \]

We note that in the case where \( D_j(a, x), \mu_j(a, x), D_m(x), d(x, u) \) and \( b(x, u) \) are all even functions in \( x \in \mathbb{R} \), it is easy to see that \( \lambda(\mu) = \lambda(-\mu), \forall \mu \in \mathbb{R} \), and hence, \( c^*_+ = c^*_- \).

**Remark 4.1.** In the hypothesis (P3), we assume that \( b(x, u) \) is nondecreasing in \( u \in [0, M] \). In the case where \( b(x, u) \) is only nondecreasing in \( u \in [0, \delta] \) for a small positive number \( \delta \), we can show that the spreading speeds are also linearly determinate for the nonmonotone system (27) by sandwiching it in between two monotone systems in a similar way as in [12, 36, 13].
Example 4.1  Consider the Nicholson blowflies model
\[
\frac{\partial u(t, x)}{\partial t} = D_m(x) \frac{\partial^2 u(t, x)}{\partial x^2} - d_m(x) u(t, x) + \int_{-\infty}^{\infty} \Gamma(\tau, x, y) u(t - \tau, y) p(y) e^{-\beta(y) u(t - \tau, y)} dy \tag{46}
\]
for \(t \geq 0, x \in \mathbb{R}\). If all coefficients in the model are independent of \(x\), then
\[
\Gamma(\tau, x, y) = \varepsilon \frac{1}{\sqrt{4\pi \alpha}} \exp \left( - \frac{(x - y)^2}{4\alpha} \right),
\]
where \(\alpha = \int_0^1 D_j(a) da > 0, \varepsilon = \exp \left\{ - \int_0^1 \mu_j(a) da \right\}, D_j(a)\) and \(\mu_j(a)\) are coefficients in (2). We note that the existence of traveling wavefronts connecting two equilibria for (46) with constant coefficients was obtained in [27], and that the spreading speed, the nonexistence and uniqueness of traveling wavefronts were established in [30, Theorems 4.1-4.3]. Now, let \(d(x, u) = d_m(x) u, b(x, u) = p(x) u e^{-\beta(x) u}\), where \(D_m, d_m, p, \beta\) are smooth \(L\)-periodic positive functions. Define \(\mathcal{B} := \max_{x \in [0, L]} \{\beta(x)\}\), and choose \(M = \frac{1}{\mathcal{B}}\). Then it is easy to see that (P1), (P3) and (P4) are satisfied, and the inequality in (P2) reduces to
\[
d_m(x) \geq \int_\mathbb{R} \Gamma(\tau, x, y) p(y) e^{-\beta(y) u(t - \tau, y)} dy, \quad \forall x \in [0, L]. \tag{47}
\]
Further, Lemma 3.3 implies that the sign of \(\lambda^*\) in Theorems 4.3-4.4 is the same as the sign of principal eigenvalue \(\bar{\lambda}\) of the nonlocal eigenvalue problem
\[
\lambda w(x) = D_m(x) \frac{d^2 w(x)}{dx^2} - d_m(x) w(x) + \int_\mathbb{R} \Gamma(\tau, x, y) p(y) w(y) dy, \quad x \in \mathbb{R}, \tag{48}
\]
Example 4.2  Consider the following population model
\[
\frac{\partial u(t, x)}{\partial t} = D_m(x) \frac{\partial^2 u(t, x)}{\partial x^2} - d_m(x) u^2(t, x) + \int_{-\infty}^{\infty} \Gamma(\tau, x, y) p(y) u(t - \tau, y) dy \tag{49}
\]
for \(t \geq 0, x \in \mathbb{R}\). If the coefficients in the model are independent of \(x\), then
\[
\Gamma(\tau, x, y) = \frac{e^{-\mu_j \tau}}{\sqrt{4\pi D_j \tau}} \exp \left\{ - \frac{(x - y)^2}{4D_j \tau} \right\},
\]
where \(D_j(a) \equiv D_j, \mu_j(a) \equiv \mu_j\). In the case where \(p, D_m\) and \(d_m\) are constants, the linear stability, global convergence and the existence of traveling wavefronts were established in [9]; and the spreading speed, the minimal wave speed and the uniqueness of traveling wavefronts were established in [30, Theorems 4.1-4.3]. Now, let \(d(x, u) = d_m(x) u^2, b(x, u) = p(x) u\), where \(D_m, d_m, p\) are smooth \(L\)-periodic positive functions. Then (P1)-(P4) are satisfied. Indeed, the inequality in (P2) is equivalent to
\[
M \geq \frac{1}{d_m(x)} \int_\mathbb{R} \Gamma(\tau, x, y) p(y) dy, \quad \forall x \in [0, L], \tag{50}
\]
which holds for all sufficiently large \(M > 0\). Moreover, the principal eigenvalue \(\bar{\lambda}\) satisfies
\[
\lambda w(x) = D_m(x) \frac{d^2 w(x)}{dx^2} + \int_\mathbb{R} \Gamma(\tau, x, y) p(y) w(y) dy, \quad x \in \mathbb{R}, \tag{51}
\]
\(w(x + L) = w(x), \quad x \in \mathbb{R}\).
5. **Appendix.** In this Appendix, we present some results of [18] on spreading speeds and traveling waves for abstract monostable evolution systems in a periodic habitat. As mentioned in [18], this theory is a generalization of that in [34] to continuous-time semiflows under a weaker compactness assumption.

Assume that $\mathbb{X}$ is a Banach lattice with the norm $|\cdot|$ and the cone $\mathbb{X}_+$, and $\mathbb{Y}$ is a subspace of $\mathbb{X}$ with the norm $\|\cdot\|$. Let the spatial habitat $\mathcal{H}$ be the real line $\mathbb{R}$ or the lattice

$$r\mathbb{Z} = \{\cdots, -2r, -r, 0, r, 2r, \cdots\}$$

for some positive number $r$. We say a function $\phi : \mathcal{H} \to \mathbb{X}$ (or $\mathbb{Y}$) is bounded if \{$|\phi(x)| : x \in \mathcal{H}\$} is bounded. Let $\mathcal{C}(\mathcal{D})$ be the set of all bounded and continuous functions from $\mathcal{H}$ to $\mathbb{X}$ (or $\mathbb{Y}$). We say a subset $\mathcal{S}$ of $\mathcal{C}(\mathcal{D})$ is uniformly bounded if \{$|\phi(x)| : \phi \in \mathcal{S}, x \in \mathcal{H}\$} is bounded. For simplicity, let $r = 1$. Moreover, any element in $\mathbb{X}$ (or $\mathbb{Y}$) can be regarded as a constant function in $\mathcal{C}(\mathcal{D})$.

For $u, v \in \mathcal{C}$, we write $u \geq v$ provided $u(x) \geq v(x), \forall x \in \mathcal{H}$; and $u > v$ provided $u \geq v$ but $u \neq v$. For $u, v \in \mathcal{C}$, we define $\max(u, v)$ by $\max(u, v)(s) := \max(u(s), v(s))$. By the property of Banach lattice, it it known that $\max(u, v) \in \mathcal{C}$. For $u, v \in \mathcal{D}$, we write $u \gg v$ provided $u(x) \gg v(x), \forall x \in \mathcal{H}$. For any $\gamma \in \mathbb{X}$ with $\gamma > 0$, we define $\mathcal{C}_\gamma := \{u \in \mathcal{C} : \gamma \geq u \geq 0\}$ ($\mathcal{D}_\gamma := \{u \in \mathcal{D} : \gamma \geq u \geq 0\}$). By the definition of Banach lattice, we know that $\text{sup}\{|\phi(x)| : \phi \in \mathcal{C}_\gamma, x \in \mathcal{H}\} = |\gamma|$.

But $\text{sup}\{|\phi(x)| : \phi \in \mathcal{D}_\gamma, x \in \mathcal{H}\}$ is not necessarily equal to $|\gamma|$. We equip $\mathcal{C}$ with the norm $|\cdot|_c$ by

$$|\phi|_c = \sum_{k=1}^{\infty} \max_{x \in \mathcal{H}, |x| \leq k} \frac{|\phi(x)|}{2^k}, \quad \forall \phi \in \mathcal{C}.$$ 

We also equip $\mathcal{D}$ with a norm given by

$$\|\phi\|_d = \sum_{k=1}^{\infty} \max_{x \in \mathcal{H}, |x| \leq k} \frac{\|\phi(x)\|}{2^k}, \quad \forall \phi \in \mathcal{D}.$$ 

The compact open topology on $\mathcal{C}$ and $\mathcal{D}$ can also be given in the following sense: $v_n \to v$ in $\mathcal{C}(\mathcal{D})$ means that the sequence of functions $v_n(x)$ converges to $v(x)$ in $\mathbb{X}$ (or $\mathbb{Y}$) uniformly for $x$ in every compact interval. The topology generated by the norm $|\cdot|_c$ ($\|\cdot\|_d$) and the compact open topology on $\mathcal{C}(\mathcal{D})$ are equivalent on any uniformly bounded subset of $\mathcal{C}(\mathcal{D})$.

Let $[a, b]_H$ denote a closed subset of $\mathcal{H}$ in the sense that if $\mathcal{H} = \mathbb{R}$, then $[a, b]_H = [a, b]$ with $a, b \in \mathbb{R}$ and $a \leq b$; and if $\mathcal{H} = \mathbb{Z}$, then $[a, b]_H = \{a, a+1, \cdots, b-1\}$ with $a, b \in \mathbb{Z}$ and $a < b$. The length of $[a, b]_H$ is $b - a$. Let $I = [a, b]_H$ be a bounded and closed interval. For a function $\phi \in \mathcal{C}$, we define the function $\phi_I : I \to \mathbb{X}$ by $\phi_I(x) = \phi(x)$. Given a subset $\mathcal{U}$ of $\mathcal{C}$, we define $\mathcal{U}_I := \{\phi_I : \phi \in \mathcal{U}\}$ and the norm $|\cdot|$ in $\mathcal{U}_I$ by $|u_I| = \max_{x \in I} |u_I(x)|$.

Given $y \in \mathcal{H}$, define a translation operator $T_y$ by $T_y[u](x) := u(x - y)$. Let $\beta \in \mathbb{Y}$ with $\beta \gg 0$. Assume that $Q$ is an operator which takes a set $\mathcal{M}$ into itself. Let $\tilde{\mathcal{H}}$ be a (discrete) sub-lattice of $\mathcal{H}$, that is, $\tilde{\mathcal{H}}$ is a lattice and there is some $L \in \mathcal{H}$ with $L > 0$ such that $\mathcal{H} = \{a + b : a \in \tilde{\mathcal{H}}, b \in [0, L]_\mathcal{H}\}$.

Suppose that every translation $T_a$ with $a \in \tilde{\mathcal{H}}$ takes the habitat $\mathcal{H}$ into itself. We say that $u \in \mathcal{C}$ is periodic with respect to $\tilde{\mathcal{H}}$ (or, more briefly, $L$–periodic) if
Theorem 5.2. \[ \text{Theorem 5.1.} \]

Theorem 5.1. \[ \text{the following hypotheses on } Q \]

(T) \[ \text{spread of } T(E3) \]

E3 \[ \text{There is an equivalent norm } | \cdot | \]

(E2) \[ \text{Q(M) } \subset \text{D is uniformly bounded and } Q : M \to D \text{ is continuous}. \]

(E3) \[ \text{There is an equivalent norm } | \cdot | \text{ on } X \text{ such that for any interval } I = [0, p]\]

with \( p \in H \), there is some positive number \( k(p) < 1 \) such that \( \alpha((Q(U))_I \leq k(p)\alpha(U_I) \) for any \( U \subset M \), where \( \alpha \) denotes the Kuratowski measure of non-compactness on \( C_I \) with \( (X, | \cdot |) \) replaced by \( (X, | \cdot |) \).

(E4) \[ \text{Q : M } \to \text{M is monotone (order-preserving) in the sense that } Q[u] \geq Q[v] \]

whenever \( u \geq v \) in \( M \).

(E5) \[ \text{Q admits exactly two } L \text{-periodic fixed points } 0 \text{ and } \beta \text{ in } M, \]

and for any \( L \text{-periodic function } u \in D \text{ with } 0 \ll u \ll \beta \), we have \( \lim_{n \to \infty} |Q^n[u]|(x) = \beta(x) = 0 \) uniformly for \( x \in H \).

In order to discuss time-delayed reaction-diffusion equations, we can choose \( X = Y = C([-\tau, 0], \mathbb{R}^m) \), and replace (E3) with the following assumption (see \[ 18, \text{Sections 4-5}) \):

(E3) \[ \text{The set } Q[M](0, \cdot) \text{ is precompact in the space } C(\mathbb{R}, \mathbb{R}^m) \text{ equipped with the}

compact open topology, and there is an equivalent norm } | \cdot | \text{ on } X \text{ such that for any number } r \geq 0 \text{, there exists } k = k(r) \in [0, 1] \text{ such that for any interval } I = [a, b] \text{ of the length } r \text{ and any } U \subset M \text{ with } U(0, \cdot) \text{ precompact in } C(\mathbb{R}, \mathbb{R}^m), \text{we have } \alpha((Q(U))_I) \leq k\alpha(U_I), \text{where } \alpha \text{ is the Kuratowski measure of non-compactness on } C_I \text{ with } (X, | \cdot |) \text{ replaced by } (X, | \cdot |)\).

Theorem 5.1. \[ 18, \text{Theorem 5.1} \]

Assume that \( Q \) satisfies all hypotheses (E1)-(E5). Then there exist \( c^*_+ \) and \( c^*_+ \), called the rightward and leftward asymptotic speeds of spread, such that the following two statements are valid:

(i) \[ \text{If } u_0 \in M \text{ be such that } 0 \leq u_0 \leq \omega \ll \beta \text{ where } \omega \in M \text{ is } L \text{-periodic and}

\( u_0(x) = 0 \) for } x \text{ outside a bounded interval, then for any } c > c^*_+ \text{ and } c' > c^*_+ \text{,}

\[ \lim_{n \to \infty, x \geq nc} |Q^n[u_0](x)| = 0 \text{ and } \lim_{n \to \infty, x \leq -nc'} |Q^n[u_0](x)| = 0. \]

(ii) \[ \text{Suppose } c^*_+ > -c^*_+ \text{. For any } c < c^*_+, c' < c^*_+ \text{ and any } \sigma \in Y \text{ with } \sigma \gg 0, \text{there is a positive number } r_{\sigma} \text{ such that if } u_0 \in M \text{ and } u_0(x) \geq \sigma \text{ for } x \text{ on an interval of length } 2r_{\sigma}, \text{then}

\[ \lim_{n \to \infty, -r_{\sigma} \leq x \leq r_{\sigma}} |Q^n[u_0](x) - \beta(x)| = 0. \]

If in addition, \( Q \) is subhomogeneous, then \( r_{\sigma} \) can be chosen to be independent of \( \sigma \gg 0 \).

Theorem 5.2. \[ 18, \text{Theorem 5.2} \]

Let \( \{Q_t\}_{t=0}^{\infty} \) be a semiflow on \( M \) with \( Q_t[0] = 0, Q_t[\beta] = \beta \) for all \( t \geq 0 \). Suppose that \( Q_t \) satisfies all hypotheses (E1)-(E5) for each \( t > 0 \), and let \( c^*_+ \) and \( c^*_+ \) be the rightward and leftward asymptotic speeds of spread of \( Q_1 \). Then \( c^*_+ \) and \( c^*_+ \) are the rightward and leftward asymptotic speeds of spread of \( \{Q_t\}_{t=0}^{\infty} \) in the following sense:

(i) \[ \text{For each } c > c^*_+ \text{ and } c' > c^*_+, \text{if } v \in M \text{ with } 0 \leq v \leq \omega \text{ for some}

\( \omega \in Y \text{ and } \omega \ll \beta \text{, and } v(x) = 0 \text{ for } x \text{ outside a bounded interval, then}

\[ \lim_{t \to \infty, x \geq tc} |Q_t[v](x)| = 0 \text{ and } \lim_{t \to \infty, x \leq -tc'} |Q_t[v](x)| = 0 \text{ in } X. \]

(ii) \[ \text{Suppose } c^*_+ > -c^*_+. \text{ For any } c < c^*_+, c' < c^*_+ \text{ and } \sigma \in Y \text{ with } \sigma \gg 0, \text{there is a positive number } r_{\sigma} \text{ such that if } v \in M \text{ with } v(x) \geq \sigma \text{ for } x \text{ on an interval of length } 2r_{\sigma}, \text{then}

\[ \lim_{t \to \infty, -r_{\sigma} \leq x \leq r_{\sigma}} |Q_t[v](x) - \beta(x)| = 0 \text{ in } X. \]

If in addition, \( Q_1 \) is subhomogeneous, \( r_{\sigma} \) can be chosen to be independent of \( \sigma \gg 0 \).
A function $V(x - ct, x)$ is said to be a $L$-periodic rightward traveling wave of $\{Q_t\}_{t \geq 0}$ if $V(\cdot + a, \cdot) \in M, \forall a \in \mathbb{R}, Q_t[U](x) = V(x - ct, x)$, $\forall t \geq 0$, and $V(\xi, x)$ is a $L$-periodic function in $x$ for any given $\xi \in \mathbb{R}$, where $U(x) := V(x, x)$. Moreover, we say that $V(x - ct, x)$ connects $\beta$ to 0 if
\[
\lim_{x \to -\infty} |V(x, x) - \beta(x)| = 0, \quad \lim_{x \to \infty} |V(x, x)| = 0.
\]
Similarly, we say $V(x + ct, x)$ is a $L$-periodic leftward traveling wave of $\{Q_t\}_{t \geq 0}$ if $V(\cdot + a, \cdot) \in M, \forall a \in \mathbb{R}, Q_t[U](x) = V(x + ct, x)$, $\forall t \geq 0$, and $V(\xi, x)$ is a $L$-periodic function in $x$ for any given $\xi \in \mathbb{R}$, where $U(x) := V(x, x)$. Moreover, we say that $V(x - ct, x)$ connects 0 to $\beta$ if
\[
\lim_{x \to -\infty} |V(x, x) - \beta(x)| = 0, \quad \lim_{x \to \infty} |V(x, x)| = 0.
\]

**Theorem 5.3.** [18, Theorem 5.3] Suppose that for each $t > 0$, $Q_t$ satisfies (E1)-(E3), and let $c^*_+$ and $c^*_-$ be the rightward and leftward asymptotic speeds of spread of $Q_1$. Then $Q_t$ has an $L$-periodic rightward traveling wave $V(x - ct, x)$ connecting $\beta$ to 0 with $V(\xi, x)$ being continuous and nonincreasing in $\xi \in \mathbb{R}$ if and only if $c \geq c^*_+$. Further, $\{Q_t\}_{t \geq 0}$ has a $L$-periodic leftward traveling wave $V(x + ct, x)$ connecting 0 to $\beta$ with $V(\xi, x)$ being continuous and increasing in $\xi \in \mathbb{R}$ if and only if $c \geq c^*_-$.  

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