Evolution Dynamics of Some Population Models in Heterogeneous Environments

by

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Abstract

Spatial and/or temporal evolutions are very important topics in epidemiology and ecology. This thesis is devoted to the study of the global dynamics of some population models incorporating with environmental heterogeneities.

Vector-borne diseases such as West Nile virus and malaria, pose a threat to public health worldwide. Both vector life cycle and parasite development are highly sensitive to climate factors. To understand the role of seasonality on disease spread, we start with a periodic West Nile virus transmission model with time-varying incubation periods. Apart from seasonal variations, another important feature of our environment is the spatial heterogeneity. Hence, we incorporate the movement of both vectors and hosts, temperature-dependent incubation periods, seasonal fluctuations and spatial heterogeneity into a general reaction-diffusion vector-borne disease model. By using the theory of basic reproduction number, $\mathcal{R}_0$, and the theory of infinite dimensional dynamical systems, we derive $\mathcal{R}_0$ and establish a threshold-type result for the global dynamics in terms of $\mathcal{R}_0$ for each model.

As biological invasions have significant impacts on ecology and human society, how the growth and spatial spread of invasive species interact with environment becomes an important and challenging problem. We first propose an impulsive integro-differential model to describe a single invading species with a birth pulse in the reproductive stage and a nonlocal dispersal stage. Next, we study the propagation dynamics for a class of integro-difference two-species competition models in a spatially periodic habitat.

To my dearest family

Lay summary

This thesis is devoted to the study of the global dynamics of some population models incorporating with environmental heterogeneities.

Vector-borne diseases such as West Nile virus and malaria, pose a threat to public health worldwide. Both vector life cycle and parasite development are highly sensitive to climate factors. To understand the role of seasonality on disease spread, we started with a periodic West Nile virus transmission model with time-varying incubation periods. We then derived the mosquito reproduction number and basic reproduction number, and showed these two numbers serve as threshold parameters that determine whether the disease would spread. As an application, we conducted a case study for the disease transmission in Los Angeles County, CA. Apart from seasonal variations, another important feature of our environment is the spatial heterogeneity. Hence, we incorporated the movement of both vectors and hosts, temperature-dependent incubation periods, seasonal fluctuations and spatial heterogeneity into a general reaction-diffusion vector-borne disease model. We introduced the basic reproduction number and established a threshold-type result on its global dynamics. Numerically, we studied the malaria transmission in Maputo Province, Mozambique.

As biological invasions have significant impacts on ecology and human society, how growth and spatial spread of invasive species interact with environment becomes an important and challenging problem. We first proposed an impulsive integro-differential model to describe a single invading species with a birth pulse in the reproductive stage and a nonlocal dispersal stage. Next, we studied a class of integro-difference two-species competition models in a spatially periodic habitat. We mainly focused on the propagation behaviors, including the threshold dynamics, spreading speeds, and monostable traveling waves. Those are the crucial factors to characterize and predict the evolution of species in spatial ecology.

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Statement of contribution

Chapters 2–5 of this thesis consist of the following papers:

Chapter 2: Feng-Bin Wang, Ruiwen Wu and Xiao-Qiang Zhao, A West Nile virus transmission model with periodic incubation periods, SIAM J. Applied Dynamical Systems, in press, 2019.

Chapter 3: Ruiwen Wu and Xiao-Qiang Zhao, A reaction-diffusion model of vector-borne disease with periodic delays, J. Nonlinear Science, 29(2019), 29–64.

Chapter 4: Ruiwen Wu and Xiao-Qiang Zhao, Spatial invasion of a birth pulse population with nonlocal dispersal, SIAM J. Applied Mathematics, 79(2019), 1075–1097.

Chapter 5: Ruiwen Wu and Xiao-Qiang Zhao, Propagation dynamics for a spatially periodic integrodifference competition model, J. Differential Equations, 264(2018), 6507–6534.

The work of the above papers was performed by the author under the supervision of Professor Xiao-Qiang Zhao.

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Chapter 1

Preliminaries

In this chapter, we introduce some terminologies and known results which will be used in the rest of this thesis. They are involved in global attractor and chain transitivity, uniform persistence and coexistence states, monotone and subhomogeneous systems, and the theories of basic reproduction numbers, spreading speeds and traveling waves.

1.1 Global attractor and chain transitivity

Let X be a metric space with metric d and $f : X \to X$ a continuous map. A bounded set A is said to attract a bounded set B in X if $\lim_{n\to+\infty} \sup_{x\in B}\{d(f^n(x), A)\} = 0$. A subset $A \subset X$ is said to be an attractor for f if A is nonempty, compact, and invariant ($f(A) = A$), and A attracts some open neighborhood U of itself; a global attractor for f is an attractor that attracts every point in X; and a strong global attractor for f if A attracts every bounded subset of X. For a nonempty invariant set M, the set $W^s(M) := \{x \in X : \lim_{n\to+\infty} d(f^n(x), M) = 0\}$ is called the stable set of M. The omega limit set of x is defined as $\omega(x) = \{y \in X : f^{n_k}(x) \to y, \text{for some } n_k \to +\infty\}$ [145, Section 1.1].

Recall that the Kuratowski measure of noncompactness, κ, is defined by

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

for any bounded set B of X. A continuous map $f : X \to X$ is said to be compact (completely continous) is f maps any bounded set to a precompact set in X.

Definition 1.1.1. *A continuous mapping $f : X \to X$ is said to be point dissipative if there is a bounded set B_0 in X such that B_0 attracts each point in X; κ-condensing (κ-contraction of order k, $0 \le k < 1$) if f takes bounded sets to bounded sets and $\kappa(f(B)) < \kappa(B)$ ($\kappa(f(B)) < k \cdot \kappa(B)$) for any nonempty closed bounded set $B \subset X$ with $\kappa(B) > 0$; asymptotically smooth if for any nonempty closed bounded set $B \subset X$*

for which $f(B) \subset B$, there is a compact set $J \subset B$ such that J attracts B.

Theorem 1.1.1. [145, Theorem 1.1.3] *Let $f : X \to X$ be a continuous map. Assume that f is point dissipative on X, and one of the following condition holds:*

(i) f^{n_0} is compact for some integer $n_0 \geq 1$, or

(ii) f is asymptotically smooth, and for each bounded set $B \subset X$, there exists $k = k(B) \geq 0$ such that the positive orbits $\gamma^+(f^k(B))$ is bounded.

Then there is a strong global attractor A for f.

Definition 1.1.2. *Let $A \subset X$ be a nonempty invariant set (i.e., $f(A) = A$). A is said to be internally chain transitive if for any $a, b \in A$ and any $\epsilon > 0$, there is a finite sequence $x_1, \ldots, x_m$ in A with $x_1 = a$, $x_m = b$ such that $d(f(x_i), x_{i+1}) < \epsilon$, $1 \leq i \leq m-1$. The sequence $\{x_1, \ldots, x_m\}$ is called an ϵ-chain in A connecting a and b.*

Lemma 1.1.1. [145, Lemma 1.2.1] *Let $f : X \to X$ be a continuous map. Then the omega (alpha) limit set of any precompact positive (negative) orbit is internally chain transitive.*

Theorem 1.1.2. [145, Theorem 1.2.1] *Let A be an attractor and C a compact internally chain transitive set for $f : X \to X$. If $C \cap W^s(A) \neq \emptyset$, then $C \subset A$.*

Theorem 1.1.3. [145, Theorem 1.2.2] *Assume that each fixed point of f is an isolated invariant set, that there is no cyclic chain of fixed points, and that every precompact orbit converges to some fixed point of f. Then any compact internally chain transitive set is a fixed point of f.*

1.2 Uniform persistence and coexistence states

Let $f : X \to X$ be a continuous map and $X_0 \subset X$ an open set. Define $\partial X_0 := X \setminus X_0$, and $M_\partial := \{x \in \partial X_0 : f^n(x) \in \partial X_0, n \geq 0\}$, which may be empty.

Theorem 1.2.1. [145, Theorem 1.3.1 and Remark 1.3.1] *Assume that*

(C1) $f(X_0) \subset X_0$ and f has a global attractor A;

(C2) There exists a finite sequence $\mathcal{M} = \{M_1, \ldots, M_k\}$ of disjoint, compact, and isloated invariant sets in ∂X_0 such that

- *(a) $\Omega(M_\partial) := \cup_{x \in M_\partial} \omega(x) \subset \cup_{i=1}^k M_i$;*
- *(b) no subset of $\mathcal{M}$ forms a cycle in ∂X_0;*

(c) Each M_i is isolated in X;

(d) $W^s(M_i) \cap X_0 = \emptyset$ for each $1 \leq i \leq k$.

Then $f : X \to X$ is uniformly persistent with respect to $(X_0, \partial X_0)$ in the sense that there exists $\eta > 0$ such that $\liminf_{n \to +\infty} d(f^n(x), \partial X_0) \geq \eta$ for all $x \in X_0$.

Next, we assume that X is closed, and that X_0 is a convex and relatively open subset of X. Then $\partial X_0 := X \setminus X_0$ is relatively closed in X.

Theorem 1.2.2. [145, Theorem 1.3.10] *Assume that*

(1) f is point dissipative and uniformly persistent with respect to $(X_0, \partial X_0)$.

(2) One of the following two conditions holds:

(i) f^{n_0} is compact for some integer $n_0 \geq 1$, or

(ii) Positive orbits of compact subsets of X are bounded.

(3) f is κ-condensing.

Then $f : X_0 \to X_0$ admits a global attractor A_0, and f has a fixed point in A_0.

Suppose $T > 0$, a family of mappings $\Phi(t) : X \to X, t \geq 0$, is called a T-periodic semiflow on X if it possesses the following properties:

(1) $\Phi(0) = I$, where I is the identity map on X.

(2) $\Phi(t + T) = \Phi(t) \circ \Phi(T)$, $\forall t \geq 0$.

(3) $\Phi(t)x$ is continuous in $(t, x) \in [0, \infty) \times X$.

The mapping $\Phi(T)$ is called the Poincaré map associated with this periodic semiflow. In particular, if (2) holds for any $T > 0$, $\Phi(t)$ is called an autonomous semiflow.

1.3 Monotone and subhomogeneous systems

Let E be an ordered Banach space with an order cone P having nonempty interior $\mathrm{Int}(P)$. For any $x, y \in E$, we write $x \geq y$ if $x - y \in P$, $x > y$ if $x - y \in P \setminus \{0\}$, and $x \gg y$ if $x - y \in \mathrm{Int}(P)$. If $a < b$, we define $[a, b]_E := \{x \in E : a \leq x \leq b\}$.

Definition 1.3.1. *A linear operator $L : E \to E$ is said to be positive if $L(P) \subset P$; strongly positive if $L(P \setminus \{0\}) \subset \mathrm{Int}(P)$.*

Theorem 1.3.1. (KREIN-RUTMAN THEOREM) [52, THEOREMS 7.1 AND 7.2] *Assume that a compact operator $K : E \to E$ is positive and $r(K)$ be the spectral radius of K. If $r(K) > 0$, then $r(K)$ is an eigenvalue of K with an eigenfunction $x > 0$. Moreover, if K is strongly positive, then $r(K) > 0$ and it is an algebraically simple eigenvalue with an eigenfunction $x \gg 0$; there is no other eigenvalue with the associated eigenfunction $x \gg 0$; $|\lambda| < r(K)$ for all eigenvalues $\lambda \neq r(K)$.*

Definition 1.3.2. *Let U be a subset of E. Then a continuous map $f : U \to U$ is said to be monotone if $x \geq y$ implies that $f(x) \geq f(y)$; strictly monotone if $x > y$ implies that $f(x) > f(y)$; strongly monotone if $x > y$ implies that $f(x) \gg f(y)$.*

Recall that a subset K of E is said to be order convex if $[u, v]_E \in K$ whenever $u, v \in K$ satisfy $u < v$.

Definition 1.3.3. *Let $U \subset P$ be a nonempty, closed and order convex set. A continuous map $f : U \to U$ is said to be subhomogeneous if $f(\lambda x) \geq \lambda f(x)$ for any $x \in U$ and $\lambda \in [0, 1]$; strictly subhomogeneous if $f(\lambda x) > \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$; strongly subhomogeneous if $f(\lambda x) \gg \lambda f(x)$ for any $x \in U$ with $x \gg 0$ and $\lambda \in (0, 1)$.*

Lemma 1.3.1. [145, LEMMA 2.3.1] *Assume that $f : U \to U$ satisfies either*

(i) f is monotone and strongly subhomogeneous; or

(ii) f is strongly monotone and strictly subhomogeneous.

Then for any two fixed points $u,\ v \in U \cap \mathrm{Int}(P)$, there is $\sigma > 0$ such that $v = \sigma u$.

Theorem 1.3.2. [145, THEOREM 2.3.2] *Assume that $f : U \to U$ satisfies either*

(i) f is monotone and strongly subhomogeneous; or

(ii) f is strongly monotone and strictly subhomogeneous.

If $f : U \to U$ admits a nonempty compact invariant set $K \subset \mathrm{Int}(P)$, then f has a fixed point $e \gg 0$ such that every nonempty compact invariant set of f in $\mathrm{Int}(P)$ consists of e.

Denote the Fréchet derivative of f at $u = a$ by $Df(a)$ if it exists, and let $r(Df(a))$ be the spectral radius of the linear operator $Df(a) : E \to E$.

Theorem 1.3.3. (THRESHOLD DYNAMICS) [145, THEOREM 2.3.4] *Let either $V = [0, b]_E$ with $b \gg 0$ or $V = P$. Assume that*

(1) $f : V \to V$ satisfies either

(i) f is monotone and strongly subhomogeneous; or

(ii) f is strongly monotone and strictly subhomogeneous.

(2) $f : V \to V$ is asymptotically smooth, and every positive orbit of f in V is bounded.

(3) $f(0) = 0$, and $Df(0)$ is compact and strongly positive.

Then exists threshold dynamics:

(a) If $r(Df(0)) \leq 1$, then every positive orbit in V converges to 0;

(a) If $r(Df(0)) > 1$, then there exists a unique fixed point $u^* \gg 0$ in V such that every positive orbit in $V \setminus \{0\}$ converges to u^*.

1.4 Basic reproduction numbers

In epidemiology, the basic reproduction number (ratio) R_0 is the expected number of secondary cases produced, in a completely susceptible population, by a typical infective individual [123]. R_0 serves as a threshold value to measure the effort needed to control the infectious disease. Ever since the celebrated works by Diekmann et al. [30] and by van den Driessche and Watmough [123], there have been numerous papers on the analysis of R_0 for various autonomous epidemic models. Recently, there are also quite a few investigations on the theory and applications of R_0 for models in a periodic environment (see, e.g., [9–11, 58, 119, 127] and the references therein). More recently, the theory of basic reproduction number R_0 has been developed by Zhao for periodic and time-delayed population models with compartmental structure (see [144]).

In this section, we introduce the theory of the basic reproduction number for periodic and time-delayed models developed by [79, 144]. Let τ be a nonnegative real number and m be a positive integer, $C = C([-\tau, 0], \mathbb{R}^m)$, and $C^+ = C([-\tau, 0], \mathbb{R}^m_+)$. Then (C, C^+) is an ordered Banach space equipped with the maximum norm and the positive cone C^+. Let $F : \mathbb{R} \to \mathcal{L}(C, \mathbb{R}^m)$ be a map and $V(t)$ be a continuous $m \times m$ matrix function on $\mathbb{R}$. Assume that $F(t)$ and $V(t)$ are ω-periodic in t for some real number $\omega > 0$. For a continuous function $u : [-\tau, \sigma) \to \mathbb{R}^m$ with $\sigma > 0$, define $u_t \in C$ by

$$u_t(\theta) = u(t + \theta), \quad \forall \theta \in [-\tau, 0]$$

for any $t \in [0, \sigma)$.

We consider a linear and periodic functional differential system on C:

$$\frac{du(t)}{dt} = F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{1.4.1}$$

System (1.4.1) may come from the equations of infectious variables in the linearization of a given ω-periodic and time-delayed compartmental epidemic model at a disease-free ω-periodic solution. As such, m is the total number of the infectious compartments, and the newly infected individuals at time t depend linearly on the infectious individuals over the time interval $[t-\tau, t]$, which is described by $F(t)u_t$. Further, the internal evolution of individuals in the infectious compartments (e.g., natural and disease-induced deaths, and movements among compartments) is governed by the linear ordinary differential system:

$$\frac{du(t)}{dt} = -V(t)u(t). \tag{1.4.2}$$

Let $\Phi(t,s), t \geq s$, be the evolution matrices associated with system (1.4.2), that is, $\Phi(t,s)$ satisfies

$$\frac{\partial}{\partial t}\Phi(t,s) = -V(t)\Phi(t,s), \forall t \geq s, \quad \text{and} \quad \Phi(s,s) = I, \forall s \in \mathbb{R},$$

and $\omega(\Phi)$ be the exponential growth bound of $\Phi(t,s)$, that is,

$$\omega(\Phi) = \inf\left\{\tilde{\omega} : \exists M \geq 1 \text{ such that } \|\Phi(t+s,s)\| \leq Me^{\tilde{\omega}t}, \forall s \in \mathbb{R}, t \geq 0\right\}.$$

We assume that

(H1) Each operator $F(t) : C \to \mathbb{R}^m$ is positive in the sense that $F(t)C^+ \subseteq \mathbb{R}^m_+$.

(H2) Each matrix $-V(t)$ is cooperative, and $\omega(\Phi) < 0$.

We assume that the ω-periodic function $v(t)$ is the initial distribution of infectious individuals. For any given $s \geq 0$, $F(t-s)v_{t-s}$ is the distribution of newly infected individuals at time $t-s$, which is produced by the infectious individuals who were introduced over the time interval $[t-s-\tau, t-s]$. Then $\Phi(t,t-s)F(t-s)v_{t-s}$ is the distribution of those infected individuals who were newly infected at time $t-s$ and remain in the infected compartments at time t. It follows that

$$\int_0^\infty \Phi(t,t-s)F(t-s)v_{t-s}ds = \int_0^\infty \Phi(t,t-s)F(t-s)v(t-s+\cdot)ds$$

is the distribution of accumulative new infections at time t produced by all those infectious individuals introduced at all previous times to t. Note that for any given $s \geq 0$, $\Phi(t,t-s)v(t,t-s)$ is the distribution of those infectious individuals at time $t-s$ and remain in the infected compartments at time t, and hence $\int_0^{+\infty} \Phi(t,t-s)v(t-s)\mathrm{d}s$ is the distribution of accumulative infectious individuals who were introduced at all previous times to t and remain in the infected compartments at time t. Thus, the distribution of newly infected individuals at time t is $F(t)\int_0^{+\infty} \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)\mathrm{d}s$.

Let C_ω be the ordered Banach space of all continuous and ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^m$, which is equipped with the maximum norm and the positive cone $C_\omega^+ := \{v \in C_\omega : v(t) \geq 0, \forall t \in \mathbb{R}\}$. Then we define two linear operator $L : C_\omega \to C_\omega$ by

$$[Lv](t) = \int_0^{+\infty} \Phi(t, t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s, \quad \forall t \in \mathbb{R},\ v \in C_\omega,$$

and

$$[\hat{L}v](t) = F(t)\int_0^{+\infty} \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)\mathrm{d}s, \quad \forall t \in \mathbb{R},\ v \in C_\omega,$$

Let A and B be two bounded linear operator on $\mathbb{X}$ defined by

$$[Av](t) = \int_0^{+\infty} \Phi(t, t-s)v(t-s)\mathrm{d}s,\ [Bv](t) = F(t)v_t, \quad \forall t \in \mathbb{R}, v \in \mathbb{X}.$$

It then follows that $L = A \circ B$ and $\hat{L} = B \circ A$, and hence L and $\hat{L}$ have the same spectral radius. Motivated by the concept of next generation operators (see, e.g., [4,9,34,35,37,38,45]), we define the spectral radius of L and $\hat{L}$ as the basic reproduction number $\mathcal{R}_0 = r(L) = r(\hat{L})$ for periodic system (1.4.1).

Let $U(\omega, 0)$ be the Poincaré map of system (1.4.1) on C. The following result shows that R_0 is a threshold value for the stability of the zero solution for periodic system (1.4.1).

Theorem 1.4.1. [144, Theorem 2.1] *The following statements are valid:*

(i) $R_0 = 1$ *if and only if* $r(U(\omega, 0)) = 1$.

(ii) $R_0 > 1$ *if and only if* $r(U(\omega, 0)) > 1$.

(iii) $R_0 < 1$ *if and only if* $r(U(\omega, 0)) < 1$.

Thus, $R_0 - 1$ *has the same sign as* $r(U(\omega, 0)) - 1$.

Let $\{U(t, s, \lambda) : t \geq s\}$ be the evolution operators on C of the following linear periodic system with $\lambda \in (0, +\infty)$:

$$\frac{\mathrm{d}u(t)}{\mathrm{d}t} = \frac{1}{\lambda}F(t)u_t - V(t)u(t), \quad t \geq 0. \tag{1.4.3}$$

The following observation comes from [144, Theorem 2.2] (see also [145, Theorem 11.1.2]).

Theorem 1.4.2. *If* $R_0 > 0$, *then* $\lambda = R_0$ *is the unique solution of* $r(U(\omega, 0, \lambda)) = 1$.

Remark 1.4.1. *Theorem 1.4.2 can be used to compute $\mathcal{R}_0$ numerically. For any given $\lambda \in (0, +\infty)$, we choose $v_0 \in Int(C^+)$ and define*

$$a_n = \|U(\omega, 0, \lambda)v_{n-1}\|_E, \ v_n = \frac{U(\omega, 0, \lambda)v_{n-1}}{a_n}, \ \forall n \geq 1.$$

Then by [79, Lemma 2.5], it follows that if $\lim_{n\to+\infty} a_n$ exists, then $r(U(\omega, 0, \lambda)) = \lim_{n\to+\infty} a_n$. Thus, we can solve $r(U(\omega, 0, \lambda)) = 1$ for λ numerically via the bisection method, which is an approximation of $\mathcal{R}_0$.

Remark 1.4.2. [145, Remark 11.1.2] and [79, Theorem 3.8] *The theory of basic reproduction number in this subsection can be extended to abstract periodic linear systems with time delay if we replace $\mathbb{R}^m$ with an ordered Banach space E and assume that each $-V(t)$ is linear operator such that the linear equation $\frac{\mathrm{d}u}{\mathrm{d}t} = -V(t)u$ generates a positive evolution operator $\Phi(t, s)$ on E. Thus, one can apply the generalized theory to periodic and time-delayed reaction-diffusion population models. For example, letting Ω be a bounded domain with smooth boundary, $E = C(\bar{\Omega}, \mathbb{R}^m)$ and $-V(t)u = D(t)\triangle u - W(t)u$, we can consider the following periodic linear system:*

$$\frac{\partial u}{\partial t} = D(t)\triangle u + F(t)u_t - W(t)u,$$

subject to the Neumann boundary condition. Here $\triangle u = (\triangle u_1, ..., \triangle u_m)^T$, $[D(t)](x) = diag(d_1(t, x), ..., d_m(t, x))$ with $d_i(t, x) > 0$, $1 \leq i \leq m$, and for each $t \in \mathbb{R}$, $F(t) \in \mathcal{L}(C([-\tau, 0], E), E)$ and $-[W(t)](x)$ is an $m \times m$ cooperative matrix function of $x \in \bar{\Omega}$.

1.5 Traveling waves and spreading speeds

In this section, we briefly introduce the theory of monostable traveling waves and spreading speeds for monotone systems developed by [39, 139].

1.5.1 Monotone systems with weak compactness

We first introduce the results in [39] on traveling waves and spreading speeds for monotone discrete-time semiflows with weak compactness.

Let Ω be a compact metric space, $\mathbb{R}^l$ be the l-dimensional Euclidean space and $X := C(\Omega, \mathbb{R}^l)$. We endow X with the maximum norm $|\cdot|_X$ and the partial ordering induced by the positive cone $X_+ := C(\Omega, \mathbb{R}^l_+)$. Assume that $\text{Int}(X_+) \neq \emptyset$. Then for $\varphi_1, \varphi_2 \in X$, we write $\varphi_1 \geq \varphi_2$ if $\varphi_1 - \varphi_2 \in X_+$, $\varphi_1 \gg \varphi_2$ if $\varphi_1 - \varphi_2 \in \text{Int}(X_+)$, and $\varphi_1 > \varphi_2$ if $\varphi_1 \geq \varphi_2$ but $\varphi_1 \neq \varphi_2$.

Let $\mathcal{C}$ be the set of all continuous and bounded functions from $\mathbb{R}$ to X, and $\mathcal{M}$ be the set of all non-increasing and bounded functions from $\mathbb{R}$ to X. For any $u, v \in \mathcal{C}(\mathcal{M})$, we write $u \geq v (u \gg v)$ if $u(x) \geq v(x) (u(x) \gg v(x))$ for all $x \in \mathbb{R}$ and $u > v$ if $u \geq v$ but $u \neq v$. Clearly, any element in X can be regarded as a constant function in $\mathcal{C}$ or $\mathcal{M}$. We endow both $\mathcal{C}$ and $\mathcal{M}$ with the compact open topology, that is, $u_n \to u$ in $\mathcal{C}$ or $\mathcal{M}$ means that the sequence of $u_n(s)$ converges to $u(s)$ in X uniformly for s in any compact set of $\mathbb{R}$. We equip $\mathcal{C}$ and $\mathcal{M}$ with the norm $\|\cdot\|_{\mathcal{C}}$ and $\|\cdot\|_{\mathcal{M}}$, respectively, which are defined by

$$\|u\|_{\mathcal{C}} = \sum_{k=1}^{+\infty} \frac{\max_{|x|\leq k} |u(x)|_X}{2^k}, \ \forall u \in \mathcal{C}, \tag{1.5.1}$$

and

$$\|u\|_{\mathcal{M}} = \sum_{k=1}^{+\infty} \frac{\max_{|x|\leq k} |u(x)|_X}{2^k}, \ \forall u \in \mathcal{M}.$$

We say a subset S of $\mathcal{C}$ (or $\mathcal{M}$) is uniformly bounded if $\sup\{|\phi(x)|_X : \phi \in S, x \in \mathbb{R}\}$ is bounded. For any given subset A of $\mathcal{C}$ (or $\mathcal{M}$) and number $s \in \mathbb{R}$, we define $A(s) := \{u(s) : u \in A\}$. For any $r \in X$ with $r \gg 0$, define $X_r = \{u \in X : 0 \leq u \leq r\}$,

$$\mathcal{C}_r = \{\phi \in \mathcal{C} : \phi(x) \in X_r, \ \forall x \in \mathbb{R}\}, \quad \mathcal{M}_r = \{\phi \in \mathcal{M} : \phi(x) \in X_r, \ \forall x \in \mathbb{R}\}.$$

Define the translation operator $\mathcal{T}_y$ on $\mathcal{C}$ or $\mathcal{M}$ by $\mathcal{T}_y[u](x) = u(x-y)$ for any given $y \in \mathbb{R}$ and the reflection operator $\mathcal{R}$ by $\mathcal{R}[u](x) = u(-x)$.

Let $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$, where $\beta \in X$ with $\beta \gg 0$. Assume that

(A1) $\mathcal{T}_y \circ Q = Q \circ \mathcal{T}_y, \quad \forall y \in \mathbb{R}$.

(A2) If $u_k \to u$ in $\mathcal{M}$, then $Q[u_k](x) \to Q[u](x)$ in X almost everywhere.

(A3) There exists $k \in [0, 1)$ such that for any $\mathcal{U} \subset \mathcal{M}_\beta$, $\kappa(Q[\mathcal{U}](0)) \leq k \cdot \kappa(\mathcal{U}(0))$. Here κ denotes the Kuratowski measure of noncompactness in X_β.

(A4) $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ is monotone (order preserving) in the sense that $Q[u] \geq Q[w]$ whenever $u \geq w$ in $\mathcal{M}_\beta$.

(A5) $Q : X_\beta \to X_\beta$ admits two fixed points 0 and β, and $\lim_{n\to\infty} Q^n[z] = \beta$ in X for any $z \in X_+$ with $0 \ll z \leq \beta$.

In view of (A1), it follows that (A3) is equivalent to the following:

There exists $k \in [0, 1)$ such that $\kappa(Q[\mathcal{U}](x)) \leq k \cdot \kappa(\mathcal{U}(x)), \quad \forall \mathcal{U} \subset \mathcal{M}_\beta, \ x \in \mathbb{R}$. We call (A3) as the point-α-contraction assumption.

Let $\varpi \in X$ with $0 \ll \varpi \ll \beta$. Choose ϕ to be a continuous function from $\mathbb{R}$ to X with the following properties: (i) ϕ is a nonincreasing function; (ii) $\phi(x) = 0, \forall x \geq 0$;

(iii) $\phi(-\infty) = \varpi$. For any given real number c, define an operator R_c by

$$R_c[\phi](s) := \max\{\phi(s), \mathcal{T}_{-c}Q[\phi](s)\}$$

and a sequence of functions $a_n(c; s)$ by the recursion

$$a_0(c; s) = \phi(s), \quad a_{n+1}(c; s) = R_c[a_n(c; \cdot)](s).$$

Lemma 1.5.1. [39, Lemmas 3.2 and 3.3] *The following statements are valid:*

(1) For each $s \in \mathbb{R}$, $a_n(c; s)$ converges to $a(c; s)$ in X and $a(c; s)$ is nonincreasing in both s and c.

(2) $a(c; -\infty) = \beta$ and $a(c; +\infty)$ exists in X.

(3) $a(c; +\infty) \in X$ is a fixed point of Q.

According to [39, 131], we define two numbers

$$c_+^* = \sup\{c : a(c, +\infty) = \beta\}, \quad \bar{c}_+ = \sup\{c : a(c, +\infty) > 0\}. \tag{1.5.2}$$

Clearly, $c_+^* \leq \bar{c}_+$. Similarly, for the leftward traveling waves two numbers with the symbol '-' also can be defined by choosing a nondecreasing initial function ϕ in the phase space consisting of nondecreasing and bounded functions from $\mathbb{R}$ to X. In what follows, we only illustrate the theory on the rightward traveling waves for the discrete-time dynamical systems, the leftward case can be treated in a similar way.

Theorem 1.5.1. [39, Theorem 3.8] *Assume that $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ satisfies (A1)–(A5). Let c_+^* and $\bar{c}_+$ with $c_+^* \leq \bar{c}_+$ be defined as in* (1.5.2). *Then the following statements are valid:*

(1) For any $c \geq c_+^*$, there is a left-continuous traveling wave $W(x - cn)$ connecting β to some fixed point $\beta_1 \in X_\beta \setminus \{\beta\}$.

(2) If, in addition, 0 is an isolated fixed point of Q in X_β, then for any $c \geq \bar{c}_+$ either of the following holds true:

(i) There exists a left-continuous traveling wave $W(x - cn)$ connecting β to 0.

(ii) Q has two ordered fixed points α_1, α_2 in $X_\beta \setminus \{0, \beta\}$ such that there exist a left-continuous traveling wave $W_1(x - cn)$ connecting α_1 to 0 and a left-continuous traveling wave $W_2(x - cn)$ connecting β to α_2.

(3) For any $c < c_+^*$, there is no traveling wave connecting β, and for any $c < \bar{c}_+$, there is no traveling wave connecting β to 0.

Further, if Q maps left-continuous functions to left-continuous functions, then the above obtained traveling waves satisfy $Q^n[W](x) = W(x - cn)$, $\forall x \in \mathbb{R}$ and $n \geq 0$. Finally, if Q admits exactly two fixed points in X_β, then $c_+^* = \bar{c}_+$ and c_+^* is the minimal wave speed of traveling waves connecting β to 0.

Theorem 1.5.2. [39, Remark 3.7] *Assume that the map $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies assumptions (A1)–(A5) with $\mathcal{M}_\beta$ in (A3) and (A5) replaced by $\mathcal{C}_\beta$. Let $u_0 \in \mathcal{C}_\beta$ and $u_n = Q(u_{n-1})$ for $n \geq 1$. Let $c_+^* \leq \bar{c}_+$ be defined in (1.5.2) for Q. Then the following statements are valid:*

(i) If $u_0 \in \mathcal{C}_\beta$, $0 \leq u_0 \ll \beta$ and $u_0(x) = 0$ for $x \geq L$ for some $L \in \mathbb{R}$, then $\lim_{n\to\infty, x\geq cn} Q^n[u_0](x) = 0$ for any $c > \bar{c}_+$,

(ii) If $u_0 \in \mathcal{C}_\beta$ and $u_0(x) \geq \sigma$ $\forall x \leq K$ for some $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim_{n\to\infty, x\leq cn} u_n(x) = \beta$ for any $c < c_+^*$.

Moreover, if Q admits exactly two fixed points in X_β, then $c_+^* = \bar{c}_+$.

The above theorem shows that $\bar{c}_+$ and c_+^*, respectively, are the upper and lower bounds of spreading speeds for the discrete-time system $\{Q^n\}_{n\geq 0}$ on $\mathcal{C}_\beta$. In the case where $\bar{c}_+ = c_+^*$, we say that this system admits a (single) spreading speed. Moreover, Theorem 1.5.2 will help to show that the coincidence of spreading speeds and minimal wave speeds of traveling waves for monotone discrete-time semiflows with weak compactness, although we use the different phase spaces $\mathcal{C}_\beta$ and $\mathcal{M}_\beta$ to present the results.

1.5.2 Monotone systems in a periodic habitat

In this subsection, we introduce the results in [139] on traveling waves and spreading speeds for monotone discrete-time semiflows in a periodic habitat. Assume that β is a strongly positive L-periodic continuous function from $\mathbb{R}$ to $\mathbb{R}^m$. Set

$$\mathcal{C}_\beta = \{u \in \mathcal{C} : 0 \leq u(x) \leq \beta(x),\ \forall x \in \mathbb{R}\},\ \mathcal{C}_\beta^{per} = \{u \in \mathcal{C}_\beta : u(x) = u(x+L),\ \forall x \in \mathbb{R}\}.$$

Let $X = C([0,L], \mathbb{R}^m)$ equipped with the maximum norm $|\cdot|_X$, $X_+ = C([0,L], \mathbb{R}_+^m)$,

$$X_\beta = \{u \in X :\ 0 \leq u(x) \leq \beta(x),\ \forall x \in [0,L]\} \text{ and } \overline{X}_\beta = \{u \in X_\beta : u(0) = u(L)\}.$$

Let $BC(\mathbb{R}, X)$ be the set of all continuous and bounded functions from $\mathbb{R}$ to X. Then we define

$$\mathcal{X} = \{v \in BC(\mathbb{R}, X) : v(s)(L) = v(s+L)(0), \forall s \in \mathbb{R}\}, \mathcal{X}_+ = \{v \in \mathcal{X} : v(s) \in X_+, \forall s \in \mathbb{R}\}$$

and

$$\mathcal{X}_\beta = \{v \in BC(\mathbb{R}, X_\beta) : v(s)(L) = v(s+L)(0), \forall s \in \mathbb{R}\}.$$

We equip $\mathcal{C}$ and $\mathcal{X}$ with the compact open topology, that is, $u^m \to u$ in $\mathcal{C}$ or $\mathcal{X}$ means that the sequence of $u^m(s)$ converges to $u(s)$ in $\mathbb{R}^m$ or X uniformly for s in any compact set.

Define a translation operator $\mathcal{T}_a$ by $\mathcal{T}_a[u](x) = u(x-a)$ for any given $a \in L\mathbb{Z}$. Let Q be a operator on $\mathcal{C}_\beta$, where $\beta \in Int(\mathcal{C}_+)$ is L-periodic. Assume that

(B1) Q is L-periodic, that is, $\mathcal{T}_a[Q[u]] = Q[\mathcal{T}_a[u]], \quad \forall u \in \mathcal{C}_\beta,\ a \in L\mathbb{Z}$.

(B2) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is continuous with respect to the compact open topology.

(B3) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is monotone (order preserving) in the sense that $Q[u] \geq Q[w]$ whenever $u \geq w$.

(B4) Q admits two L-periodic fixed points 0 and β in $\mathcal{C}_+$, and for any $z \in \mathcal{C}_\beta^{per}$ with $0 \ll z \leq \beta$, we have $\lim_{n\to\infty} Q^n[z](x) = \beta(x)$ uniformly for $x \in \mathbb{R}$.

(B5) $Q[\mathcal{C}_\beta]$ is precompact in $\mathcal{C}_\beta$ with respect to the compact open topology.

Now we introduce a family of operators $\{\hat{Q}\}$ on $\mathcal{X}_\beta$:

$$\hat{Q}[v](s)(\theta) := Q[v_s](\theta), \quad \forall v \in \mathcal{X}_\beta,\ s \in \mathbb{R},\ \theta \in [0, L], \tag{1.5.3}$$

where $v_s \in \mathcal{C}$ is defined by

$$v_s(x) = v(s + n_x)(\theta_x), \quad \forall x = n_x + \theta_x \in \mathbb{R},\ n_x = L\left[\frac{x}{L}\right],\ \theta_x \in [0, L).$$

Let $\varpi \in \overline{X}_\beta$ with $0 \ll \varpi \ll \beta$. Choose $\phi \in \mathcal{X}_\beta$ such that the following properties hold: (i) $\phi(s)$ is nonincreasing in s; (ii) $\phi(s) \equiv 0$ for all $s \geq 0$; and (iii) $\phi(-\infty) = \varpi$.

Let c be a given real number. According to [39, 131], we define an operator R_c by

$$R_c[a](s) := \max\{\phi(s), T_{-c}\hat{Q}[a](s)\},$$

and a sequence of functions $a_n(c; s)$ by the recursion:

$$a_0(c; s) = \phi(s), \quad a_{n+1}(c; s) = R_c[a_n(c; \cdot)](s),$$

where T_{-c} is a translation operator defined by $T_{-c}[u](x) = u(x + c)$.

Lemma 1.5.2. [39, Lemmas 3.2 and 3.3] and [139, Lemma 5.4] *The following statements are valid:*

(i) For each $s \in \mathbb{R}$, $a_n(c, s)$ converges to $a(c; s)$ in X, where $a(c; s)$ is nonincreasing in both c and s, and $a(c; \cdot) \in \mathcal{X}_\beta$.

(ii) $a(c, -\infty) = \beta$, and $a(c, +\infty)$ exists in X and is a fixed point of $\hat{Q}$.

According to [39, 133, 139], we define two numbers

$$c_+^* = \sup\{c : a(c, +\infty) = \beta\}, \quad \bar{c}_+ = \sup\{c : a(c, +\infty) > 0\}. \tag{1.5.4}$$

Clearly, $c_+^* \leq \bar{c}_+$ due to the monotonicity of $a(c; \cdot)$ with respect to c.

We say that $V(x - cn, x)$ is an L-periodic rightward traveling wave of Q if $V(\cdot + a, \cdot) \in \mathcal{C}_\beta$, $\forall a \in \mathbb{R}$, $Q^n[V(\cdot, \cdot)](x) = V(x - cn, x)$, $\forall n \geq 0$, and $V(\xi, x)$ is an L-periodic function in x for any fixed $\xi \in \mathbb{R}$. Moreover, we say that $V(\xi, x)$ connects β to 0 if $\lim_{\xi \to -\infty} |V(\xi, x) - \beta(x)| = 0$ and $\lim_{\xi \to +\infty} |V(\xi, x)| = 0$ uniformly for $x \in \mathbb{R}$.

Theorem 1.5.3. [39, Theorem 3.8] and [139, Theorem 5.5] *Let Q be a map on $\mathcal{C}_\beta$ with $Q[0] = 0$, $Q[\beta] = \beta$, and $\hat{Q}$ be defined as in* (1.5.3)*. Suppose that Q satisfies (B1)–(B5). Let c_+^* and $\bar{c}_+$ be defined as in* (1.5.4)*. Then the following statements are valid:*

(1) For any $c \geq c_+^*$, there is an L-periodic rightward traveling wave $W(x - cn, x)$ connecting β to some equilibrium $\beta_1 \in C_\beta^{per} \setminus \{\beta\}$ with $W(\xi, x)$ being continuous and nonincreasing in $\xi \in \mathbb{R}$.

(2) If, in addition, 0 is an isolated equilibrium of Q in $\mathcal{C}_\beta^{per}$, then for any $c \geq \bar{c}_+$ either of the following holds true:

  (i) There exists an L-periodic rightward traveling wave $W(x - cn, x)$ connecting β to 0 with $W(\xi, x)$ being continuous and nonincreasing in $\xi \in \mathbb{R}$.

  (ii) Q has two ordered equilibria $\alpha_1, \alpha_2 \in C_\beta^{per} \setminus \{0, \beta\}$ such that there exist an L-periodic traveling wave $W_1(x - cn, x)$ connecting α_1 and 0 and an L-periodic traveling wave $W_2(x - cn, x)$ connecting β and α_2 with $W_i(\xi, x), i = 1, 2$, being continuous and nonincreasing in $\xi \in \mathbb{R}$.

(3) For any $c < c_+^*$, there is no L-periodic traveling wave connecting β, and for any $c < \bar{c}_+$, there is no L-periodic traveling wave connecting β to 0.

Theorem 1.5.4. [39, Remark 3.7] and [139, Theorem 5.4] *Let Q be a map on $\mathcal{C}_\beta$ with $Q[0] = 0, Q[\beta] = \beta$ and $\hat{Q}$ be correspondingly defined as in* (1.5.3)*. Suppose that Q satisfies (B1)–(B5). Let c_+^* and $\bar{c}_+$ be defined as in* (1.5.4)*. Then the following statements are valid:*

(i) If $\phi \in \mathcal{C}_\beta$, $0 \leq \phi \leq \omega \ll \beta$ for some $\omega \in \mathcal{C}_\beta^{per}$, and $\phi(x) = 0, \forall x \geq H$, for some $H \in \mathbb{R}$, then $\lim_{n \to \infty, x \geq cn} Q^n(\phi)(x) = 0$ for any $c > \bar{c}_+$.

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi(x) \geq \sigma$, $\forall x \leq K$, for some $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim_{n \to \infty, x \leq cn} (Q^n(\phi)(x) - \beta(x)) = 0$ for any $c < c_+^*$.

Chapter 2

A West Nile virus transmission model with periodic incubation periods

2.1 Introduction

West Nile virus (WNv), a mosquito-transmitted arbovirus, is the most prevalent *flavivirus* worldwide [48]. Since its introduction in North America in 1999, it has become endemic throughout the contiguous United States as well as all Canadian provinces [97], and caused serious public health concern. WNv is maintained in a zoonotic cycle between reservoir birds and vector mosquitoes, and *Culex* mosquitoes are one of the most effective vectors for transmitting WNv. In North America, common bird species like American crows, blue jays, and house sparrows were found to be infected with WNv [63] and serve as a reservoir for a disease outbreak [137]. In addition, the vertical transmission (from mother to offspring), observed in *Culex* populations [6, 44], which allows the virus to persist during unfavorable periods, may play an important role in the persistence of the virus in North America. Currently, humans and other mammals are believed to be 'dead-end' hosts.

Mathematical modeling of WNv started with the pioneer work of Thomas and Urena (2001) who constructed a system of discrete-time difference equations to study the changes in vector mosquitoes, reservoir birds and humans [121]. It has since been extended to a variety of different situations, including continuous-time differential models in mosquito-bird populations [136, 137], reaction-diffusion models to capture the spatial spread of the virus [76], patch models to describe bird migration [140], and more detailed analytical results can be found in [1, 15, 24]. Seasonal fluctuations in temperature have been shown to have significant impacts on vector and reservoir population dynamics, including maturation rates, per reservoir biting rate, and incubation periods [27]. To explore these impacts, more recent studies take into account the seasonality in WNv transmission [11]. Ewing *et al.* [34] proposed a stage-structured model of *Culex* mosquitoes with time-varying delays to study the effects of temperature on life stage duration. Moschini *et al.* [96] considered a WNv model where mosquitoes are assumed inactive during winters, and hence, the infection dynamics are governed by a sequence of discrete growing seasons. However, only a few papers have addressed the combined effects of the seasonality and time-varying incubation periods on the spread of WNv.

Motivated by the the vector-borne models in [114,137,148], we present and analyze a generalized WNv compartment model with vertical infection and stage-structure in vector populations in the current chapter. As a direct consequence, the equations of the model system cannot be decoupled from each other, which implies mathematically that we fail to reduce the model to a sub-system with fewer equations. And hence, this chapter can provide a general theoretical framework for the study of the long-term behaviors of a complex epidemic model where the compartments are mixed together. Moreover, we incorporate the seasonality and temperature-dependent incubation periods in both vectors and reservoirs. The time-varying delays bring new challenges not only into model derivation, for example, the total population of reservoir birds are now subject to two different time-periodic incubation periods, but also into mathematical analysis, such as the positivity of the model system. Our analysis suggests that the model admits a mosquito reproduction number $\mathcal{R}_0^V$ and a basic reproduction number $\mathcal{R}_0$, and they act as threshold parameters for disease persistence.

As an application, we employ our model to investigate WNv transmission in Los Angeles County, California. We use the relationships between changing seasonal temperatures and vector life cycles to approximate the time-periodic system parameters, including the time-varying incubation periods, and we estimate the current WNv outbreak risk. Moreover, we examine the dynamical behaviors under time-varying and time-averaged delays numerically in order to identify situations requiring the adoption of time-periodic incubation periods to provide efficient predictions. As the climate becomes more variable [60], we explore the effects of changing climate on the disease risk and find that the warming climate increases the chance of WNv outbreak.

The rest of this chapter is organized as follows. We present the model system and study its well-posedness in Section 2.2. In Section 2.3, we first introduce the mosquito reproduction number $\mathcal{R}_0^V$ and the basic reproduction number $\mathcal{R}_0$, and then establish the threshold dynamics for the model system in terms of $\mathcal{R}_0^V$ and $\mathcal{R}_0$. In Section 2.4, we conduct a case study for the WNv transmission in Los Angeles County, California. A brief discussion concludes the chapter.

2.2 The model and its well-posedness

The female mosquito population were divided into larvae and adult mosquitoes. The larvae were divided into susceptible (L_{V1}) and infective (L_{V2}) classes, respectively; the adult mosquitoes were divided into susceptible (S_V), exposed (E_V) and infective (I_V) classes, respectively; the bird population were divided into susceptible (S_R), exposed (E_R), infective (I_R) and removed (R_R) groups, respectively (see, e.g., [76,114, 136]). $b_V(t)$ represents the birth rate of larvae; $K(t)$ is the carrying capacity of larval mosquitoes; $m_V(t)$ represents maturation rate of mosquitoes; $d_L(t)$, $d_V(t)$ and $d_R(t)$ represent the (natural) death rates of larvae, adult mosquitoes and birds, respectively; $\delta_R(t)$ is the disease-induced mortality rate of birds; $\Lambda_R(t)$ is the recruitment rate of susceptible birds; $\alpha_V(t)$ and $\alpha_R(t)$ represent WNv transmission probability per bite to mosquitoes and birds, respectively; $\beta_R(t)$ is the biting rate of mosquitoes on birds; $r(t)$ represents bird recovery rate from WNv; $\eta_R(t)$ stands for the rate of immunity loss of birds; σ represents the probability of vertical transmission. Let $\mathcal{M}_V(t)$ and $\mathcal{M}_R(t)$ be the densities of newly occurred infectious mosquitoes and birds, which will be determined, respectively. Then the governing system takes the form

$$
\begin{cases}
\frac{dL_{V1}}{dt} = b_V(t)\left(S_V + E_V + (1-\sigma)I_V\right)\left(1 - \frac{L_{V1}+L_{V2}}{K(t)}\right) - (m_V(t) + d_L(t))L_{V1}, \\
\frac{dL_{V2}}{dt} = \sigma b_V(t) I_V \left(1 - \frac{L_{V1}+L_{V2}}{K(t)}\right) - (m_V(t) + d_L(t))L_{V2}, \\
\frac{dS_V}{dt} = m_V(t)L_{V1} - \alpha_V(t)\beta_R(t)\frac{I_R}{N_R}S_V - d_V(t)S_V, \\
\frac{dE_V}{dt} = \alpha_V(t)\beta_R(t)\frac{I_R}{N_R}S_V - d_V(t)E_V - \mathcal{M}_V(t) \\
\frac{dI_V}{dt} = \mathcal{M}_V(t) + m_V(t)L_{V2} - d_V(t)I_V, \\
\frac{dS_R}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t)\frac{S_R}{N_R}I_V + \eta_R(t)R_R - d_R(t)S_R, \\
\frac{dE_R}{dt} = \alpha_R(t)\beta_R(t)\frac{S_R}{N_R}I_V - d_R(t)E_R - \mathcal{M}_R(t), \\
\frac{dI_R}{dt} = \mathcal{M}_R(t) - \left(r(t) + d_R(t) + \delta_R(t)\right)I_R, \\
\frac{dR_R}{dt} = r(t)I_R - \eta_R(t)R_R - d_R(t)R_R,
\end{cases}
\tag{2.2.1}
$$

where $N_R := S_R + E_R + I_R + R_R$. We use Fig. 2.1 to illustrate the transitions of vectors and reservoirs between different compartments. The biological interpretations for parameters are listed in Table 2.1.

Next we introduce the temperature-dependent incubation periods in mosquitoes (vectors) and birds (reservoirs), which is motivated by the arguments in [100,102,129]. We start with the derivation of the expression for $\mathcal{M}_V(t)$. The temperature T is assumed to vary as a function of time t, that is, $T = T(t)$. Let q be the development level of infection such that q increases at a temperature-dependent rate $\gamma_V(T(t)) = \gamma_V(t)$, $q = q_{E_V} = 0$ at the transition from S_V to E_V, and $q = q_{I_V}$ at the transition from E_V to I_V. Let $f(q,t)$ be the density of mosquitoes with infection development level q at time t. Then, $\mathcal{M}_V(t) = \gamma_V(t) f(q_{I_V}, t)$. Let $J(q,t)$ be the flux, in the direction of increasing q, of mosquitoes with infection development level q. Then we have the

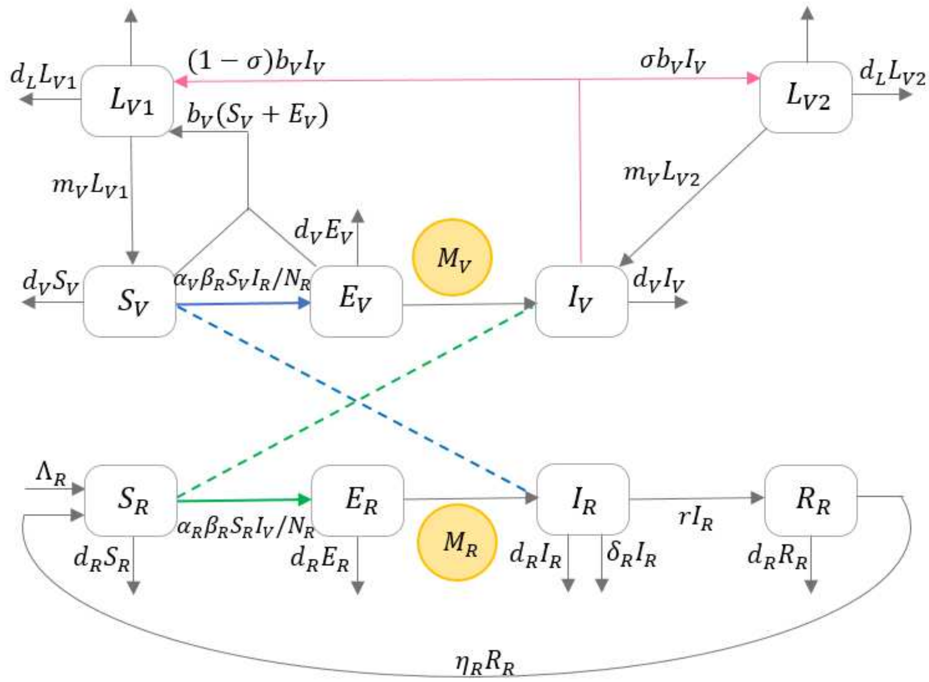


Figure 2.1: Flow diagram for the disease transmission

Table 2.1: Biological interpretations for parameters in system (2.2.15)

Parameter	Description
σ	Probability of vertical transmission
$b_V(t)$	Birth rate of larvae
$K(t)$	Carrying capacity of larval mosquitoes
$m_V(t)$	Maturation rate of mosquitoes
$d_L(t)$	Natural death rate of larvae
$d_V(t)$	Natural death rate of adult mosquitoes
$d_R(t)$	Natural death rate of birds
$\alpha_V(t)$	Transmission probability per bite to mosquitoes
$\alpha_R(t)$	Transmission probability per bite to birds
$\beta_R(t)$	Biting rate of mosquitoes on birds
$\Lambda_R(t)$	Recruitment rate of susceptible birds
$r(t)$	Bird recovery rate from WNv
$\delta_R(t)$	Disease-induced mortality rate of birds
$\eta_R(t)$	Rate of immunity loss of birds
$\tau_V(t)$	The extrinsic incubation period (EIP) in mosquitoes
$\tau_R(t)$	The incubation period in birds
$\hat{\tau}$	The maximum of $\tau_V(t)$ and $\tau_R(t)$, that is, $\max_{t\in[0,\omega]}\{\tau_V(t), \tau_R(t)\}$

following equation

$$\frac{\partial f(q,t)}{\partial t} = -\frac{\partial J}{\partial q} - d_V(t)f.$$

Substituting $J(q,t) = \gamma_V(t)f(q,t)$ into the above equatuon, we obtain

$$\frac{\partial f(q,t)}{\partial t} = -\frac{\partial}{\partial q}[\gamma_V(t)f] - d_V(t)f. \tag{2.2.2}$$

Since $J(q_{E_V},t) = \gamma_V(t)f(q_{E_V},t) = \alpha_V(t)\beta_R(t)\frac{I_R(t)}{N_R(t)}S_V(t)$, we impose the following the boundary condition on equation (2.2.2)

$$f(q_{E_V},t) = \alpha_V(t)\beta_R(t)\frac{I_R(t)}{N_R(t)\gamma_V(t)}S_V(t). \tag{2.2.3}$$

In order to solve system (2.2.2) with the boundary condition (2.2.3), we introduce a new variable

$$\eta = h(t) := q_{E_V} + \int_0^t \gamma_V(s)ds. \tag{2.2.4}$$

Let $h^{-1}(\eta)$ be the inverse function of $h(t)$, and define

$$\hat{f}(q,\eta) = f(q,h^{-1}(\eta)),\ \hat{d}_V(\eta) = d_V(h^{-1}(\eta)),\ \hat{\gamma}_V(\eta) = \gamma_V(h^{-1}(\eta)).$$

It immediately follows from system (2.2.2) that

$$\frac{\partial \hat{f}(q,\eta)}{\partial \eta} = -\frac{\partial \hat{f}(q,\eta)}{\partial q} - \frac{\hat{d}_V(\eta)}{\hat{\gamma}_V(\eta)}\hat{f}(q,\eta). \tag{2.2.5}$$

Let $V(s) = \hat{f}(s+q-\eta,s)$, and hence, system (2.2.5) becomes

$$\frac{dV(s)}{ds} = -\frac{\hat{d}_V(s)}{\hat{\gamma}_V(s)}V(s).$$

As $\eta - (q - q_{E_V}) \leq \eta$, we have

$$V(\eta) = V(\eta - (q - q_{E_V}))e^{-\int_{\eta-(q-q_{E_V})}^{\eta} \frac{\hat{d}_V(s)}{\hat{\gamma}_V(s)}ds},$$

which implies

$$\hat{f}(q,\eta) = \hat{f}(q_{E_V}, \eta - q + q_{E_V})e^{-\int_{\eta-q+q_{E_V}}^{\eta} \frac{\hat{d}_V(s)}{\hat{\gamma}_V(s)}ds}.$$

Let $\tau(q,t)$ be the time taken to grow from infection development level q_{E_V} to level q by a mosquito who arrives at infection development level q at time t. Since $\frac{dq}{dt} = \gamma_V(t)$, we have

$$q - q_{E_V} = \int_{t-\tau(q,t)}^{t} \gamma_V(s)ds. \tag{2.2.6}$$

In view of (2.2.4) and (2.2.6), we get

$$h(t-\tau(q,t))-h(t) = \int_0^{t-\tau(q,t)} \gamma_V(s)ds - \int_0^t \gamma_V(s)ds = -\int_{t-\tau(q,t)}^{t} \gamma_V(s)ds = -(q-q_{E_V}), \tag{2.2.7}$$

and hence, $h(t-\tau(q,t)) = \eta - q + q_{E_V}$. It easily follows that

$$\begin{aligned} f(q,t) &= \hat{f}(q, h(t)) \\ &= \hat{f}(q_{E_V}, \eta - q + q_{E_V}) e^{-\int_{\eta-q+q_{E_V}}^{\eta} \frac{\hat{d}_V(s)}{\hat{\gamma}_V(s)} ds} \\ &= f(q_{E_V}, t-\tau(q,t)) e^{-\int_{t-\tau(q,t)}^{t} d_V(\xi)d\xi}, \end{aligned} \tag{2.2.8}$$

where we have used the fact

$$\int_{\eta-q+q_{E_V}}^{\eta} \frac{\hat{d}_V(s)}{\hat{\gamma}_V(s)} ds = \int_{t-\tau(q,t)}^{t} d_V(\xi)d\xi$$

and

$$f(q_{E_V}, t-\tau(q,t)) = \alpha_V(t-\tau(q,t))\beta_R(t-\tau(q,t)) \frac{I_R(t-\tau(q,t))}{N_R(t-\tau(q,t))} \cdot \frac{S_V(t-\tau(q,t))}{\gamma_V(t-\tau(q,t))}.$$

Let $\tau_V(t) = \tau(q_{I_V}, t)$. Then (2.2.8) implies that

$$\begin{aligned} \mathcal{M}_V(t) &= \gamma_V(t) f(q_{I_V}, t) \\ &= \frac{\gamma_V(t)}{\gamma_V(t-\tau_V(t))} (\alpha_V \cdot \beta_R)(t-\tau_V(t)) \frac{I_R(t-\tau_V(t))}{N_R(t-\tau_V(t))} S_V(t-\tau_V(t)) e^{-\int_{t-\tau_V(t)}^{t} d_V(\xi)d\xi}, \end{aligned} \tag{2.2.9}$$

where $(\alpha_V \cdot \beta_R)(t-\tau_V(t)) = \alpha_V(t-\tau_V(t))\beta_R(t-\tau_V(t))$. Plugging $q = q_{I_V}$ into (2.2.6), we obtain

$$q_{I_V} - q_{E_V} = \int_{t-\tau_V(t)}^{t} \gamma_V(s)ds. \tag{2.2.10}$$

Taking the derivative with respect to t on both sides of (2.2.10), we obtain

$$1 - \tau_V'(t) = \frac{\gamma_V(t)}{\gamma_V(t-\tau_V(t))}, \tag{2.2.11}$$

which implies that $1-\tau_V'(t) > 0$. This condition also makes sense biologically. Recall that $\tau_V(t)$ denotes the time taken by a mosquito who arrives at the infectious stage at time t from the infected stage. For sufficiently small $s > 0$, the vector is still infectious at time $t+s$ when it was at the infectious stage at time t. Thus, $\tau_V(t+s) < \tau_V(t)+s$, and hence, $\tau_V'(t) = \lim_{s\to 0} \frac{\tau_V(t+s)-\tau_V(t)}{s} \leq 1$. From (2.2.10), we see that if $\gamma_V(t)$ is a periodic function, then $\tau_V(t)$ is also a periodic function with the same period. Indeed, equation (2.2.10) determines an implicit function $\tau_V(t)$ uniquely. If $\gamma_V(t+\omega) = \gamma_V(t)$ for some $\omega > 0$, then

$$\int_{t-\tau_V(t)}^{t} \gamma_V(s)ds = \int_{t+\omega-\tau_V(t+\omega)}^{t+\omega} \gamma_V(s)ds = \int_{t-\tau_V(t+\omega)}^{t} \gamma_V(s)ds,$$

which implies $\tau_V(t+\omega) = \tau_V(t)$. With (2.2.9) and (2.2.11), we have

$$\mathcal{M}_V(t) = (1-\tau_V'(t))(\alpha_V \cdot \beta_R)(t-\tau_V(t))\frac{I_R(t-\tau_V(t))}{N_R(t-\tau_V(t))}S_V(t-\tau_V(t))e^{-\int_{t-\tau_V(t)}^{t} d_V(\xi)d\xi}. \tag{2.2.12}$$

Similarly, we can show that

$$\mathcal{M}_R(t) = (1-\tau_R'(t))(\alpha_R \cdot \beta_R)(t-\tau_R(t))\frac{S_R(t-\tau_R(t))}{N_R(t-\tau_R(t))}I_V(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^{t} d_R(\xi)d\xi}. \tag{2.2.13}$$

Substituting (2.2.12) and (2.2.13) into system (2.2.1), we arrive at the following system:

$$\begin{cases} \frac{dL_{V1}}{dt} = b_V(t)\left(S_V + E_V + (1-\sigma)I_V\right)\left(1 - \frac{L_{V1}+L_{V2}}{K(t)}\right) - (m_V(t)+d_L(t))L_{V1}, \\ \frac{dL_{V2}}{dt} = \sigma b_V(t) I_V \left(1 - \frac{L_{V1}+L_{V2}}{K(t)}\right) - (m_V(t)+d_L(t))L_{V2}, \\ \frac{dS_V}{dt} = m_V(t)L_{V1} - \alpha_V(t)\beta_R(t)\frac{I_R}{N_R}S_V - d_V(t)S_V, \\ \frac{dE_V}{dt} = \alpha_V(t)\beta_R(t)\frac{I_R}{N_R}S_V - d_V(t)E_V \\ \qquad -(1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t))\frac{I_R(t-\tau_V(t))}{N_R(t-\tau_V(t))}S_V(t-\tau_V(t))e^{-\int_{t-\tau_V(t)}^{t} d_V(\xi)d\xi}, \\ \frac{dI_V}{dt} = (1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t))\frac{I_R(t-\tau_V(t))}{N_R(t-\tau_V(t))}S_V(t-\tau_V(t))e^{-\int_{t-\tau_V(t)}^{t} d_V(\xi)d\xi} \\ \qquad + m_V(t)L_{V2} - d_V(t)I_V, \\ \frac{dS_R}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t)\frac{S_R}{N_R}I_V + \eta_R(t)R_R - d_R(t)S_R, \\ \frac{dE_R}{dt} = \alpha_R(t)\beta_R(t)\frac{S_R}{N_R}I_V - d_R(t)E_R \\ \qquad -(1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{S_R(t-\tau_R(t))}{N_R(t-\tau_R(t))}I_V(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^{t} d_R(\xi)d\xi}, \\ \frac{dI_R}{dt} = (1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{S_R(t-\tau_R(t))}{N_R(t-\tau_R(t))}I_V(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^{t} d_R(\xi)d\xi} \\ \qquad - \left(r(t)+d_R(t)+\delta_R(t)\right)I_R, \\ \frac{dR_R}{dt} = r(t)I_R - \eta_R(t)R_R - d_R(t)R_R, \end{cases} \tag{2.2.14}$$

where $N_R := S_R+E_R+I_R+R_R$, the constant σ is positive, and other time-dependent parameters are positive, continuous and ω-periodic functions in t for some $\omega > 0$.

For convenience, we assume

$$(u_1, u_2, u_3, u_4, u_5, u_6, u_7, u_8, u_9) = (L_{V1}, L_{V2}, S_V, E_V, I_V, S_R, E_R, I_R, R_R).$$

Then system (2.2.14) becomes the following one:

$$\begin{cases} \frac{du_1}{dt} = b_V(t)\left(u_3 + u_4 + (1-\sigma)u_5\right)\left(1 - \frac{u_1+u_2}{K(t)}\right) - (m_V(t) + d_L(t))u_1, \\ \frac{du_2}{dt} = \sigma b_V(t)\left(1 - \frac{u_1+u_2}{K(t)}\right)u_5 - (m_V(t) + d_L(t))u_2, \\ \frac{du_3}{dt} = m_V(t)u_1 - \alpha_V(t)\beta_R(t)\frac{u_8}{\sum_{i=6}^9 u_i}u_3 - d_V(t)u_3, \\ \frac{du_4}{dt} = \alpha_V(t)\beta_R(t)\frac{u_8}{\sum_{i=6}^9 u_i}u_3 - d_V(t)u_4 \\ \qquad -(1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t))\frac{u_8(t-\tau_V(t))}{\sum_{i=6}^9 u_i(t-\tau_V(t))}u_3(t-\tau_V(t))e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi}, \\ \frac{du_5}{dt} = (1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t))\frac{u_8(t-\tau_V(t))}{\sum_{i=6}^9 u_i(t-\tau_V(t))}u_3(t-\tau_V(t))e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} \\ \qquad +m_V(t)u_2 - d_V(t)u_5, \\ \frac{du_6}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 + \eta_R(t)u_9 - d_R(t)u_6, \\ \frac{du_7}{dt} = \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 - d_R(t)u_7 \\ \qquad -(1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}, \\ \frac{du_8}{dt} = (1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} \\ \qquad -\left(r(t) + d_R(t) + \delta_R(t)\right)u_8, \\ \frac{du_9}{dt} = r(t)u_8 - \eta_R(t)u_9 - d_R(t)u_9. \end{cases} \tag{2.2.15}$$

In view of biological meaning of $\tau_V(t)$ and $\tau_R(t)$, we impose the following compatibility condition:

$$u_4(0) = \int_{-\tau_V(0)}^0 \alpha_V(\theta)\beta_R(\theta)\frac{u_8(\theta)}{N_R(\theta)}u_3(\theta)e^{-\int_\theta^0 d_V(\xi)d\xi}d\theta, \tag{2.2.16}$$

and

$$u_7(0) = \int_{-\tau_R(0)}^0 \alpha_R(\theta)\beta_R(\theta)\frac{u_6(\theta)}{N_R(\theta)}u_5(\theta)e^{-\int_\theta^0 d_R(\xi)d\xi}d\theta. \tag{2.2.17}$$

Moreover, in the rest of this chapter, we always impose the following condition on $K(t)$:

$$\frac{dK(t)}{dt} + (m_V(t) + d_L(t))K(t) \geq 0,\ \forall\ t \in \mathbb{R}. \tag{2.2.18}$$

Substituting

$$L(t) = u_1(t) + u_2(t),\ M(t) = u_3(t) + u_4(t) + u_5(t) \tag{2.2.19}$$

into system (2.2.15), we can see that $(L(t), M(t))$ satisfies

$$\begin{cases} \frac{dL}{dt} = b_V(t)\left(1 - \frac{L}{K(t)}\right)M - (m_V(t) + d_L(t))L, \\ \frac{dM}{dt} = m_V(t)L - d_V(t)M. \end{cases} \tag{2.2.20}$$

By the comparison argument, together with condition (2.2.18), we can easily prove the following result.

Lemma 2.2.1. *Let* $\Sigma(t) := \{(L^0, M^0) \in \mathbb{R}^2_+ : 0 \le L^0 \le K(t)\}$. *Then for any* $(L^0, M^0) \in \Sigma(0)$, *system* (2.2.20) *has a unique solution* $(L(t), M(t))$ *with* $(L(0), M(0)) = (L^0, M^0)$ *such that* $(L(t), M(t)) \in \Sigma(t)$ *for all* $t \ge 0$.

Let $\hat{\tau} = \max_{t\in[0,\omega]}\{\tau_V(t), \tau_R(t)\}$, $C := C([-\hat{\tau}, 0], \mathbb{R}^9)$, and $C^+ := C([-\hat{\tau}, 0], \mathbb{R}^9_+)$. Then (C, C^+) is an ordered Banach space equipped with the maximum norm. For any given continuous function $u : [-\hat{\tau}, \varsigma] \to \mathbb{R}^9$ with $\varsigma > 0$, define $u_t \in C$ by $u_t(\theta) = u(t + \theta)$, $\forall \theta \in [-\hat{\tau}, 0]$, for any $t \in [0, \varsigma]$. Next we define

$$X^+_\varepsilon = \left\{\phi \in C^+ : \sum_{i=6}^{9} \phi_i(s) \ge \varepsilon, \ \forall s \in [-\hat{\tau}, 0]\right\},$$

for small $\varepsilon \in \left(0, \frac{\min_{t\in[0,\omega]} \Lambda_R(t)}{\max_{t\in[0,\omega]} d_R(t) + \max_{t\in[0,\omega]} \delta_R(t)}\right)$. By standard arguments, we can show that for any $\phi \in X^+_\varepsilon$, system (2.2.15) has a unique solution, denoted by $u(t, \phi)$ on its maximal existence interval $[0, t_\phi)$ with $u_0 = \phi$, where $t_\phi \le +\infty$. For each $t \ge 0$, define

$$\begin{aligned} \mathcal{X}^+_\varepsilon(t) := \quad & \Big\{\phi \in X^+_\varepsilon : \phi_1(s) + \phi_2(s) \le K(t + s), \quad \forall s \in [-\hat{\tau}, 0], \\ & \phi_4(0) = \int_{-\tau_V(t)}^{0} \alpha_V(t + \theta)\beta_R(t + \theta)\frac{\phi_8(\theta)}{\sum_{i=6}^{9} \phi_i(\theta)}\phi_3(\theta)e^{-\int_\theta^0 d_V(t+\xi)d\xi}d\theta, \\ & \phi_7(0) = \int_{-\tau_R(t)}^{0} \alpha_R(t + \theta)\beta_R(t + \theta)\frac{\phi_6(\theta)}{\sum_{i=6}^{9} \phi_i(\theta)}\phi_5(\theta)e^{-\int_\theta^0 d_R(t+\xi)d\xi}d\theta\Big\}, \end{aligned}$$

where $K(t)$ satisfies condition (2.2.18). Then we have the following result.

Theorem 2.2.1. *For any* $\phi \in \mathcal{X}^+_\varepsilon(0)$, *system* (2.2.15) *has a unique solution* $u(t, \phi)$ *on* $[0, +\infty)$ *with* $u_0 = \phi$, *and* $u_t(\phi) \in \mathcal{X}^+_\varepsilon(t)$ *for all* $t \ge 0$. *Moreover, system* (2.2.15) *generates an* ω*-periodic semiflow* $Q(t) = u_t : \mathcal{X}^+_\varepsilon(0) \to \mathcal{X}^+_\varepsilon(t)$, $\forall t \ge 0$ *in the sense that (i)* $Q(0) = I$, *(ii)* $Q(t + \omega) = Q(t) \circ Q(\omega)$, *for all* $t \ge 0$, *and (iii)* $Q(t)\phi$ *is continuous in* $(t, \phi) \in [0, +\infty) \times \mathcal{X}^+_\varepsilon(0)$; *and* $Q(\omega)$ *has a strong global attractor.*

Proof. First we have known that for any $\phi \in \mathcal{X}^+_\varepsilon(0) \subset X^+_\varepsilon$, system (2.2.15) has a unique solution $u(t, \phi)$ on $[0, t_\phi)$ with $u_0 = \phi$, where $t_\phi \le +\infty$. By the uniqueness of solutions of system (2.2.15) and the compatibility conditions (2.2.16) and (2.2.17), it follows that

$$u_4(t) = \int_{t-\tau_V(t)}^{t} \alpha_V(\theta)\beta_R(\theta)\frac{u_8(\theta)}{\sum_{i=6}^{9} u_i(\theta)} u_3(\theta)e^{-\int_\theta^t d_V(\xi)d\xi}d\theta, \tag{2.2.21}$$

and

$$u_7(t) = \int_{t-\tau_R(t)}^{t} \alpha_R(\theta)\beta_R(\theta)\frac{u_6(\theta)}{\sum_{i=6}^{9} u_i(\theta)} u_5(\theta)e^{-\int_\theta^t d_R(\xi)d\xi}d\theta. \tag{2.2.22}$$

Hence, we have the following observation.

Claim. *If all $u_i(t) \geq 0$, $i \neq 4, 7$ are nonnegative on $[0, s) \subset [0, t_\phi)$, then so are $u_4(t) \geq 0$, $u_7(t) \geq 0$ on $[0, s)$.*

Next, for any $t \geq 0$ and $\psi \in \mathcal{X}_\varepsilon^+(t)$, define $F(t, \psi) :=$

$$\begin{pmatrix} b_V(t)\left(\psi_3(0)+\psi_4(0)+(1-\sigma)\psi_5(0)\right)\left(1-\frac{\psi_1(0)+\psi_2(0)}{K(t)}\right)-\left(m_V(t)+d_L(t)\right)\psi_1(0) \\ \sigma b_V(t)\psi_5(0)\left(1-\frac{\psi_1(0)+\psi_2(0)}{K(t)}\right)-\left(m_V(t)+d_L(t)\right)\psi_2(0) \\ m_V(t)\psi_1(0)-\alpha_V(t)\beta_R(t)\frac{\psi_8(0)\psi_3(0)}{\sum_{i=6}^{9}\psi_i(0)}-d_V(t)\psi_3(0) \\ \alpha_V(t)\beta_R(t)\frac{\psi_8(0)\psi_3(0)}{\sum_{i=6}^{9}u_i(0)}-d_V(t)\psi_4(0)-(1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t)) \\ \times\frac{\psi_8(-\tau_V(t))\psi_3(-\tau_V(t))}{\sum_{i=6}^{9}\psi_i(-\tau_V(t))}e^{-\int_{t-\tau_V(t)}^{t}d_V(\xi)d\xi} \\ m_V(t)\psi_2(0)-d_V(t)\psi_5(0)+(1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t)) \\ \times\frac{\psi_8(-\tau_V(t))\psi_3(-\tau_V(t))}{\sum_{i=6}^{9}\psi_i(-\tau_V(t))}e^{-\int_{t-\tau_V(t)}^{t}d_V(\xi)d\xi} \\ \Lambda_R(t)-\alpha_R(t)\beta_R(t)\frac{\psi_6(0)\psi_5(0)}{\sum_{i=6}^{9}\psi_i(0)}+\eta_R(t)\psi_9(0)-d_R(t)\psi_6(0) \\ \alpha_R(t)\beta_R(t)\frac{\psi_6(0)\psi_5(0)}{\sum_{i=6}^{9}\psi_i(0)}-d_R(t)\psi_7(0)-(1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t)) \\ \times\frac{\psi_6(-\tau_R(t))\psi_5(-\tau_R(t))}{\sum_{i=6}^{9}\psi_i(-\tau_R(t))}e^{-\int_{t-\tau_R(t)}^{t}d_R(\xi)d\xi} \\ (1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{\phi_6(-\tau_R(t))\psi_5(-\tau_R(t))}{\sum_{i=6}^{9}\psi_i(-\tau_R(t))}e^{-\int_{t-\tau_R(t)}^{t}d_R(\xi)d\xi} \\ -(r(t)+d_R(t)+\delta_R)\psi_8(0) \\ r(t)\psi_8(0)-\eta_R(t)\psi_9(0)-d_R(t)\psi_9(0) \end{pmatrix}.$$

Clearly, if $\psi_i(0) = 0$, then $F_i(t, \psi) \geq 0$, $i \neq 4, 7$. We can employ [116, Theorem 5.2.1] and its proof to obtain that for the above $\phi \in \mathcal{X}_\varepsilon^+(0)$, $u_i(t, \phi) \geq 0$, $i \neq 4, 7$, $\forall t \in [0, t_\phi)$. It immediately follows from the claim that $u_4(t, \phi) \geq 0$ and $u_7(t, \phi) \geq 0$, $\forall t \in [0, t_\phi)$.

The fact that $L(t) = u_1(t) + u_2(t)$ and Lemma 2.2.1, together with $u_1(t) \geq 0$ and $u_2(t) \geq 0$, imply that if $u_1(0) + u_2(0) = L(0) \leq K(0)$, then $0 \leq u_1(t) + u_2(t) = L(t) \leq K(t)$, that is, for the above $\phi \in \mathcal{X}_\varepsilon^+(0)$, $u_{1t}(\phi)(s) + u_{2t}(\phi)(s) = u_1(t + s, \phi) + u_2(t + s, \phi) \leq K(t + s)$, $\forall s \in [-\hat{\tau}, 0]$. Note that the total bird population ($N_R = u_6 + u_7 + u_8 + u_9$) satisfies

$$\frac{dN_R}{dt} = \Lambda_R(t) - d_R(t)N_R - \delta_R(t)u_8 \geq \Lambda_R(t) - (d_R(t) + \delta_R(t))N_R.$$

We can see that $\tilde{N}_R = \varepsilon$, where $\varepsilon \le \frac{\min_{t\in[0,\omega]}\Lambda_R(t)}{\max_{t\in[0,\omega]} d_R(t)+\max_{t\in[0,\omega]}\delta_R(t)}$, is a lower solution of the above equation, that is, if $N_R(0) \ge \varepsilon$, then $N_R(t) \ge \varepsilon$, for any $t \in [0, t_\phi)$. Moreover, for the above $\phi \in \mathcal{X}_\varepsilon^+(0)$, we have $\sum_{i=6}^9 u_{it}(s,\phi) = \sum_{i=6}^9 u_i(t+s,\phi) \ge \varepsilon$, $\forall t \in [0, t_\phi)$. We note that (2.2.21) can be rewritten as follows:

$$u_4(t) = \int_{-\tau_V(t)}^0 \alpha_V(t+\theta)\beta_R(t+\theta)\frac{u_8(t+\theta)}{\sum_{i=6}^9 u_i(t+\theta)} u_3(t+\theta)e^{-\int_\theta^0 d_V(t+\xi)d\xi}d\theta,$$

which is equivalent to

$$u_{4t}(0,\phi) = \int_{-\tau_V(t)}^0 \alpha_V(t+\theta)\beta_R(t+\theta)\frac{u_{8t}(\theta,\phi)}{\sum_{i=6}^9 u_{it}(\theta,\phi)} u_{3t}(\theta,\phi)e^{-\int_\theta^0 d_V(t+\xi)d\xi}d\theta.$$

Similarly, (2.2.22) is equivalent to

$$u_{7t}(0,\phi) = \int_{-\tau_R(t)}^0 \alpha_R(t+\theta)\beta_R(t+\theta)\frac{u_{6t}(\theta,\phi)}{\sum_{i=6}^9 u_{it}(\theta,\phi)} u_{5t}(\theta,\phi)e^{-\int_\theta^0 d_R(t+\xi)d\xi}d\theta.$$

Hence, we know $u_t(\phi) \in \mathcal{X}_\varepsilon^+(t)$, $\forall t \in [0, t_\phi)$.

We observe that

$$\begin{cases} \frac{dM}{dt} = m_V(t)L - d_V(t)M \le \hat{m}_v\hat{K} - \bar{d}_V M, \\ \frac{dN_R}{dt} = \Lambda_R(t) - d_R(t)N_R - \delta_R(t)I_R \le \hat{\Lambda}_R - \bar{d}_R N_R, \end{cases}$$

where $\hat{m}_V = \max_{t\in[0,\omega]} m_V(t)$, $\hat{K} = \max_{t\in[0,\omega]} K(t)$, $\hat{\Lambda}_R = \max_{t\in[0,\omega]}\Lambda_R(t)$, $\bar{d}_V = \min_{t\in[0,\omega]} d_V(t)$, and $\bar{d}_R = \min_{t\in[0,\omega]} d_R(t)$. Thus, the comparison argument implies that the solutions of system (2.2.15) with initial data in $\mathcal{X}_\varepsilon^+(0)$ exist globally on $[0, +\infty)$ and are ultimately bounded. It then follows from Theorem 1.1.1 that $Q(\omega)$ has a strong global attractor. □

2.3 Global dynamics in terms of $\mathcal{R}_0^V$ and $\mathcal{R}_0$

In this section, we first introduce the mosquito reproduction number $\mathcal{R}_0^V$ and the basic reproduction number $\mathcal{R}_0$ for the model system. Then we establish a threshold-type result on its global dynamics in terms of $\mathcal{R}_0^V$ and $\mathcal{R}_0$.

2.3.1 Reproduction numbers $\mathcal{R}_0^V$ and $\mathcal{R}_0$

We first consider the following linearized system associated with (2.2.20) at the mosquito-free solution $(0,0)$:

$$\begin{cases} \frac{dL}{dt} = b_V(t)M - (m_V(t) + d_L(t))L, \\ \frac{dM}{dt} = m_V(t)L - d_V(t)M. \end{cases} \tag{2.3.1}$$

Following [127], we define the mosquito reproduction number. To this end, we let

$$\mathbf{F}(t) = \begin{pmatrix} 0 & b_V(t) \\ 0 & 0 \end{pmatrix}, \ \mathbf{V}(t) = \begin{pmatrix} m_V(t) + d_L(t) & 0 \\ -m_V(t) & d_V(t) \end{pmatrix}.$$

Suppose $\Phi_{\mathbf{V}(\cdot)}(t)$ is the monodromy matrix of the linear ω-periodic differential system $\frac{dz(t)}{dt} = \mathbf{V}(t)z$. Assume $Y(t,s),\ t \geq s$, is the evolution operator of the linear ω-periodic system

$$\frac{dy(t)}{dt} = -\mathbf{V}(t)y, \tag{2.3.2}$$

that is, for each $s \in \mathbb{R}$, the 2×2 matrix $Y(t,s)$ satisfies

$$\frac{d}{dt}Y(t,s) = -\mathbf{V}(t)Y(t,s),\ \forall\, t \geq s,\ Y(s,s) = I,$$

where I is the 2×2 matrix. Thus, the monodromy matrix $\Phi_{-\mathbf{V}(\cdot)}(t)$ of (2.3.2) is equal to $Y(t,0),\ t \geq 0$. We assume that $\phi(s)$, ω-periodic in s, is the initial distribution of infectious individuals. Then $\mathbf{F}(s)\phi(s)$ is the rate of new infections produced by the infected individuals who were introduced at time s. Given $t \geq s$, then $Y(t,s)\mathbf{F}(s)\phi(s)$ gives the distribution of those infected individuals who were newly infected at time s and remain in the infected compartments at time t. It follows that

$$\psi(t) := \int_{-\infty}^{t} Y(t,s)\mathbf{F}(s)\phi(s)ds = \int_0^{+\infty} Y(t,t-a)\mathbf{F}(t-a)\phi(t-a)da$$

is the distribution of accumulative new infections at time t produced by all those infected individuals $\phi(s)$ introduced at time previous to t.

Let C_ω be the ordered Banach space of all ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, which is equipped with the maximum norm $\|\cdot\|$ and the positive cone $C_\omega^+ := \{\phi \in C_\omega : \phi(t) \geq 0,\ \forall\, t \in \mathbb{R}\}$. Then we define a linear operator $\mathbf{L} : C_\omega \to C_\omega$ by

$$(\mathbf{L}\phi)(t) = \int_0^{+\infty} Y(t,t-a)\mathbf{F}(t-a)\phi(t-a)da,\ \forall\, t \in \mathbb{R},\ \phi \in C_\omega.$$

Then we call $\mathbf{L}$ the next generation operator [127], and define the basic reproduction number as

$$\mathcal{R}_0^V := r(\mathbf{L}),$$

the spectral radius of $\mathbf{L}$. The following result will be used in the proof of our main result.

Lemma 2.3.1. ([127, Theorem 2.2]) *The following statements hold:*

(i) $\mathcal{R}_0^V = 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega)) = 1$;

(ii) $\mathcal{R}_0^V > 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega)) > 1$;

(iii) $\mathcal{R}_0^V < 1$ *if and only if* $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega)) < 1$.

It follows from Lemma 2.3.1 that the trivial solution $(0,0)$ is locally asymptotically stable for system (2.3.1) if $\mathcal{R}_0^V < 1$, and unstable if $\mathcal{R}_0^V > 1$.

For our subsequent discussions, we need the following result:

Lemma 2.3.2. ([141, Lemma 2.1]) *Let* $\lambda = \frac{1}{\omega}\ln r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega))$. *Then there exists a positive,* ω*-periodic function* $v^*(t)$ *such that* $e^{\lambda t}v^*(t)$ *is a solution of system* (2.3.1).

The following result is concerned with the global dynamics of system (2.2.20).

Lemma 2.3.3. *Let* $\Sigma(t)$ *be defined as in Lemma 2.2.1. Then the following statements hold:*

(i) *If* $\mathcal{R}_0^V < 1$, *then* $(0,0)$ *is globally asymptotically stable for system* (2.2.20) *in* $\Sigma(0)$;

(ii) *If* $\mathcal{R}_0^V > 1$, *then system* (2.2.20) *admits a unique positive* ω*-periodic solution* $(L_V^*(t), S_V^*(t))$, *which is globally asymptotically stable in* $\Sigma(0)\backslash\{(0,0)\}$, *that is,* $\lim_{t\to+\infty}[(L(t),M(t))-(L_V^*(t),S_V^*(t))] = (0,0)$. *Further,* $L_V^*(t) < K(t)$, $\forall\, t \in [0,\omega]$.

Proof. As a straightforward consequence of Theorem 1.3.3, we have the threshold-type result, as stated in (i) and (ii). It suffices to prove $L_V^*(t) < K(t)$, $\forall\ t \in [0,\omega]$. By Lemma 2.2.1, we already know $L_V^*(t) \le K(t)$, $\forall\ t \ge 0$. There exists $t_0 \ge 0$ such that $L_V^*(t_0) < K(t_0)$, otherwise $L_V^*(t) \equiv K(t)$, $\forall t \ge 0$, which is impossible. Without loss of generality, we can assume $t_0 = 0$. It then follows that $L_V^*(t) = L(t, L_V^*(0)) < L(t, K(0)) \le K(t)$ for all $t \ge 0$. □

Remark 2.3.1. *For each* $t \ge 0$, *define*

$$\hat{\Sigma}(t) := \{(\hat{L}^0, \hat{M}^0) \in C([-\hat{\tau}, 0], \mathbb{R}_+^2) : 0 \le \hat{L}^0(s) \le K(t+s), \quad \forall s \in [-\hat{\tau}, 0]\}.$$

By the uniqueness of solutions, we can show that Lemma 2.3.3 also holds when $\Sigma(t)$ *is replaced by* $\hat{\Sigma}(t)$.

Next we follow the results in Section 1.4 (please see also [144]) to define the disease reproduction number for system (2.2.15). It is not hard to see that the equation

$$\frac{du(t)}{dt} = \Lambda_R(t) - d_R(t)u(t), \tag{2.3.3}$$

admits a unique positive ω-periodic solution $S_R^*(t)$, which is globally attractive. This fact together with Lemma 2.3.3 imply that the disease-free solution of system (2.2.15) takes the form:

$$(u_1, u_2, u_3, u_4, u_5, u_6, u_7, u_8, u_9) = (L_V^*(t), 0, S_V^*(t), 0, 0, S_R^*(t), 0, 0, 0),$$

provided that $\mathcal{R}_0^V > 1$. Linearizing system (2.2.15) around the disease-free solution, then we get the following cooperative system for the infectious compartments:

$$\begin{cases} \frac{dw_2}{dt} = \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right) w_5 - (m_V(t) + d_L(t))w_2, \\ \frac{dw_5}{dt} = (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t))\frac{S_V^*(t-\tau_V(t))}{S_R^*(t-\tau_V(t))} e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} w_8(t - \tau_V(t)) \\ \qquad +m_V(t)w_2 - d_V(t)w_5, \\ \frac{dw_8}{dt} = (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} w_5(t - \tau_R(t)) \\ \qquad - (r(t) + d_R(t) + \delta_R(t))\, w_8. \end{cases} \tag{2.3.4}$$

Assume $C_\omega(\mathbb{R}, \mathbb{R}^3)$ is the Banach space consisting of all ω-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{R}^3$, where $\|\varphi\|_{C_\omega(\mathbb{R},\mathbb{R}^3)} = \max_{\theta\in[0,\omega]} \|\varphi(\theta)\|_{\mathbb{R}^3}$ for any $\varphi \in C_\omega(\mathbb{R}, \mathbb{R}^3)$. Recall that $\hat{\tau} = \max_{t\in[0,\omega]}\{\tau_V(t), \tau_R(t)\}$. From system (2.3.4), we define $\mathbb{F}(t) : C([-\hat{\tau}, 0], \mathbb{R}^3) \to \mathbb{R}^3$ by

$$\mathbb{F}(t)\begin{pmatrix} \varphi_2 \\ \varphi_5 \\ \varphi_8 \end{pmatrix} = \begin{pmatrix} \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right)\varphi_5(0) \\ (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t))\frac{S_V^*(t-\tau_V(t))}{S_R^*(t-\tau_V(t))} \\ \times e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi}\varphi_8(-\tau_V(t)) \\ (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}\varphi_5(-\tau_R(t)) \end{pmatrix},$$

for $t \geq 0$ and $(\varphi_2, \varphi_5, \varphi_8) \in C([-\hat{\tau}, 0], \mathbb{R}^3)$, and $-\mathbb{V}(t) : \mathbb{R}^3 \to \mathbb{R}^3$ is defined by

$$-\mathbb{V}(t)\begin{pmatrix} w_2 \\ w_5 \\ w_8 \end{pmatrix} = \begin{pmatrix} -(m_V(t) + d_L(t))w_2 \\ m_V(t)w_2 - d_V(t)w_5 \\ - (r(t) + d_R(t) + \delta_R(t))\, w_8 \end{pmatrix}, \tag{2.3.5}$$

for $t \geq 0$ and $(w_2, w_5, w_8) \in \mathbb{R}^3$. Then system (2.3.4) can be rewritten as

$$\frac{dv(t)}{dt} = \mathbb{F}(t)v_t - \mathbb{V}(t)v(t), \ \forall\ t \geq 0.$$

It is easy to see that $\mathbb{F}(t) : C([-\hat{\tau}, 0], \mathbb{R}^3) \to \mathbb{R}^3$ is positive in the sense that $\mathbb{F}(t)C([-\hat{\tau}, 0], \mathbb{R}^3_+) \subset \mathbb{R}^3_+$, and hence, the condition (H1) in Section 1.4 holds. It is easy to see that $-\mathbb{V}(t)$ is cooperative. Next, we assume $\{\mathbb{Z}(t,s),\ t \geq s\}$ is the evolution family on $\mathbb{R}^3$ associated with the following system $\frac{dv(t)}{dt} = -\mathbb{V}(t)v(t)$. Assume that $\Omega(\mathbb{Z})$ represents the exponential growth bound of the evolution family $\{\mathbb{Z}(t,s),\ t \geq s\}$, which is defined by

$$\Omega(\mathbb{Z}) := \inf\left\{\tilde{\omega} :\ \exists\ M \geq 1 \text{ such that } \parallel \mathbb{Z}(t+s,s) \parallel \leq Me^{\tilde{\omega}t},\ \forall\ s \in \mathbb{R},\ t \geq 0\right\}.$$

In the following lemma, we will show that the exponential growth bound of evolution family $\{\mathbb{Z}(t,s),\ t \geq s\}$ is negative, and hence, the condition (H2) in Section 1.4 holds.

Lemma 2.3.4. *The exponential growth bound of evolution family* $\{\mathbb{Z}(t,s),\ t \geq s\}$ *is negative, that is,* $\Omega(\mathbb{Z}) < 0$.

Proof. For any $\varphi := (\varphi_2, \varphi_5, \varphi_8)^T \in C([-\hat{\tau}, 0], \mathbb{R}^3)$, we assume that

$$\mathbb{Z}(t,s)\varphi := (\mathbb{Z}_2(t,s)\varphi, \mathbb{Z}_5(t,s)\varphi, \mathbb{Z}_8(t,s)\varphi)^T.$$

From (2.3.5), it follows that

$$\begin{cases} \mathbb{Z}_2(t,s)\varphi = e^{-\int_s^t (m_V(\theta)+d_L(\theta))d\theta}\varphi_2, \\ \mathbb{Z}_5(t,s)\varphi = e^{-\int_s^t d_V(\theta)d\theta}\varphi_5 + \int_s^t e^{-\int_\xi^t d_V(\theta)d\theta}[m_V(\xi)e^{-\int_s^\xi (m_V(\theta)+d_L(\theta))d\theta}\varphi_2]d\xi, \\ \mathbb{Z}_8(t,s)\varphi = e^{-\int_s^t (r(\theta)+d_R(\theta)+\delta_R(\theta))d\theta}\varphi_8, \end{cases}$$

Let $\hat{m}_V := \max_{t\in[0,\omega]} m_V(t)$ and

$$\bar{d} := \min_{t\in[0,\omega]}\{m_V(t) + d_L(t), d_V(t), r(t) + d_R(t) + \delta_R(t)\} > 0.$$

Then, for all $t \geq s$, it is not hard to see that

$$\begin{cases} \parallel \mathbb{Z}_2(t,s)\varphi \parallel \leq e^{-\bar{d}(t-s)} \parallel \varphi_2 \parallel, \\ \parallel \mathbb{Z}_5(t,s)\varphi \parallel \leq e^{-\bar{d}(t-s)} \parallel \varphi_5 \parallel + \hat{m}_V[(t-s)e^{-\bar{d}(t-s)}] \parallel \varphi_2 \parallel, \\ \parallel \mathbb{Z}_8(t,s)\varphi \parallel \leq e^{-\bar{d}(t-s)} \parallel \varphi_8 \parallel. \end{cases} \tag{2.3.6}$$

We may choose a $\delta_0 > 0$ such that $\bar{d} - \delta_0 > 0$. Since $\lim_{\hat{t}\to+\infty} \hat{t}e^{-\delta_0\hat{t}} = 0$, there exists a constant $M_1 > 0$ such that $\hat{t}e^{-\delta_0\hat{t}} \leq M_1,\ \forall\ \hat{t} \geq 0$. Thus,

$$(t-s)e^{-\bar{d}(t-s)} = [(t-s)e^{-\delta_0(t-s)}]e^{-(\bar{d}-\delta_0)(t-s)} \leq M_1e^{-(\bar{d}-\delta_0)(t-s)},\ \forall\ t \geq s. \tag{2.3.7}$$

In view of (2.3.6) and (2.3.7), we conclude that $\Omega(\mathbb{Z}) < 0$. □

With the above discussions, we can use the theory in Section 1.4 to define the reproduction number for system (2.2.15). We assume that $v \in C_\omega(\mathbb{R}, \mathbb{R}^3)$ and $v(t)$ is the initial distribution of infectious vectors and reservoirs (birds) at time $t \in \mathbb{R}$. For any $s \geq 0$, $\mathbb{F}(t-s)v_{t-s}$ represents the density distribution of newly infected vectors and reservoirs at time $t-s$, which is produced by the infectious vectors and reservoirs who were introduced over the time interval $[t-s-\hat{\tau}, t-s]$. Then $\mathbb{Z}(t, t-s)\mathbb{F}(t-s)v_{t-s}$ is the distribution of those infected vectors and reservoirs who were newly infected at time $t-s$ and still survive in the environment at time t for $t \geq s$. Thus, the integral

$$\int_0^{+\infty} \mathbb{Z}(t, t-s)\mathbb{F}(t-s)v_{t-s}ds = \int_0^{+\infty} \mathbb{Z}(t, t-s)\mathbb{F}(t-s)v(t-s+\cdot)ds$$

is the distribution of accumulative infective vectors and reservoirs at time t produced by all those infectious vectors and reservoirs introduced at all previous time to t. On the other hand, for any given $s \geq 0$, $\mathbb{Z}(t, t-s)v(t-s)$ is the distribution of those infectious individuals at time $t-s$ and remain in the infected compartments at time t, and hence, $\int_0^{+\infty} \mathbb{Z}(t, t-s)v(t-s)ds$ represents the distribution of accumulative infectious individuals who were introduced at all previous times to t and remain in the infected compartments at time t. Thus, $\mathbb{F}(t)\int_0^{+\infty} \mathbb{Z}(t+\cdot, t-s+\cdot)v(t-s+\cdot)ds$ represents the distribution of newly infected individuals at time t.

Define two linear operators on $C_\omega(\mathbb{R}, \mathbb{R}^3)$ by

$$[\mathbb{L}v](t) := \int_0^{+\infty} \mathbb{Z}(t, t-s)\mathbb{F}(t-s)v(t-s+\cdot)ds, \ \forall\, t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{R}^3).$$

and

$$[\mathfrak{L}v](t) := \mathbb{F}(t)\int_0^{+\infty} \mathbb{Z}(t+\cdot, t-s+\cdot)v(t-s+\cdot)ds, \ \forall\, t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{R}^3).$$

Let $\mathbb{A}$ and $\mathbb{B}$ be two bounded linear operators on $C_\omega(\mathbb{R}, \mathbb{R}^3)$ defined by

$$[\mathbb{A}v](t) := \int_0^{+\infty} \mathbb{Z}(t, t-s)v(t-s)ds, \ [\mathbb{B}v](t) := \mathbb{F}(t)v_t, \ \forall\, t \in \mathbb{R}, \ v \in C_\omega(\mathbb{R}, \mathbb{R}^3).$$

It then follows that $\mathbb{L} = \mathbb{A} \circ \mathbb{B}$ and $\mathfrak{L} = \mathbb{B} \circ \mathbb{A}$, and hence, $\mathbb{L}$ and $\mathfrak{L}$ have same spectral radius. Motivated by the concept of next generation operators (see, e.g., [11, 127]), we define the spectral radius of $\mathbb{L}$ and $\mathfrak{L}$ as the basic reproduction number for system (2.2.15), that is,

$$\mathcal{R}_0 := r(\mathbb{L}) = r(\mathfrak{L}).$$

Let $\tilde{P}(t)$ be the solution maps of system (2.3.4), that is, $\tilde{P}(t)\phi = w_t(\phi)$, $t \geq 0$, where $w(t, \phi)$ is the unique solution of system (2.3.4) with $w_0 = \phi \in C([-\hat{\tau}, 0], \mathbb{R}^3)$. Then $\tilde{P}(\omega)$ is the Poincaré map associated with linear system (2.3.4). Let $r(\tilde{P}(\omega))$ be the spectral radius of $\tilde{P}(\omega)$. By Theorem 1.4.1, we have the following observation.

Lemma 2.3.5. *$\mathcal{R}_0 - 1$ has the same sign as $r(\tilde{P}(\omega)) - 1$.*

Let

$$\mathcal{E} := \mathbb{R} \times C([-\tau_R(0), 0], \mathbb{R}) \times C([-\tau_V(0), 0], \mathbb{R}),$$

and

$$\mathcal{E}^+ := \mathbb{R}_+ \times C([-\tau_R(0), 0], \mathbb{R}_+) \times C([-\tau_V(0), 0], \mathbb{R}_+).$$

Then $(\mathcal{E}, \mathcal{E}^+)$ is an ordered Banach space. Given a function $w : [0, +\infty) \times [-\tau_R(0), +\infty) \times [-\tau_V(0), +\infty) \to \mathbb{R}^3$, we define $w_t \in \mathcal{E}$, $\forall t \geq 0$, by

$$w_t(\theta) = (w_2(t), w_5(t+\theta_5), w_8(t+\theta_8)),\ \forall\, \theta := (\theta_5, \theta_8) \in [-\tau_R(0), +\infty) \times [-\tau_V(0), +\infty).$$

By the arguments similar to those in [83, Lemma 3.3] and the method of steps, we have the following result.

Lemma 2.3.6. *For any $\varphi := (\varphi_2, \varphi_5, \varphi_8) \in \mathcal{E}^+$, system* (2.3.4) *admits a unique mild solution $w(t, \varphi)$ on $[0, +\infty)$ with $w_0 = \varphi$.*

For any given $t \geq 0$, let $P(t)$ be the solution map of system (2.3.4) on $\mathcal{E}$ defined by $P(t)\varphi = w_t(\varphi)$, $\forall\, \varphi \in \mathcal{E}$. Next, we will show that the periodic semiflow $P(t)$ is eventually strongly positive on $\mathcal{E}^+$.

Lemma 2.3.7. *For any $\varphi := (\varphi_2, \varphi_5, \varphi_8) \in \mathcal{E}^+$ with $\varphi \not\equiv 0$, the solution $w(t, \varphi)$ of system* (2.3.4) *with $w_0 = \varphi$ satisfies $w_i(t) > 0$ for all $t > 2\hat{\tau}$, $i = 2, 5, 8$. Thus, $P(t)\varphi \gg 0$, $\forall t > 3\hat{\tau}$.*

Proof. As in the proof of Lemma 2.3.6, a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$, implies that $w_i(t) \geq 0$ for all $t \geq 0$, $i = 2, 5, 8$.

Next, we choose a large $C > 0$ such that $g_2(t, w_2) := -(m_V(t) + d_L(t))w_2 + Cw_2$ is strictly increasing in w_2, $g_5(t, w_5) := -d_V(t)w_5 + Cw_5$ is strictly increasing in w_5, and $g_8(t, w_8) := -\left(r(t) + d_R(t) + \delta_R(t)\right) w_8 + Cw_8$ is strictly increasing in w_8. For convenience, we further assume that

$$\begin{cases} b_2(t) = \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right), \\ b_5(t) = (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t))\frac{S_V^*(t-\tau_V(t))}{S_R^*(t-\tau_V(t))}e^{-\int_{t-\tau_V(t)}^{t} d_V(\xi)d\xi}, \\ b_8(t) = (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^{t} d_R(\xi)d\xi}. \end{cases}$$

Then system (2.3.4) can be rewritten as follows:

$$\begin{cases} \frac{dw_2}{dt} = -Cw_2 + g_2(t, w_2) + b_2(t)w_5, \\ \frac{dw_5}{dt} = -Cw_5 + g_5(t, w_5) + m_V(t)w_2 + b_5(t)w_8(t - \tau_V(t)), \\ \frac{dw_8}{dt} = -Cw_8 + g_8(t, w_8) + b_8(t)w_5(t - \tau_R(t)). \end{cases} \tag{2.3.8}$$

It then follows that for any given $\varphi := (\varphi_2, \varphi_5, \varphi_8) \in \mathcal{E}^+$, the solution $(w_2(t, \varphi),$

$w_5(t,\varphi), w_8(t,\varphi))$ satisfies the following system of integral equations:

$$\begin{cases} w_2(t,\varphi) = e^{-Ct}\varphi_2 + \int_0^t e^{-C(t-s)} g_2(s, w_2(s))ds + \int_0^t e^{-C(t-s)} b_2(s) w_5(s)ds, \\ w_5(t,\varphi) = e^{-Ct}\varphi_5(0) + \int_0^t e^{-C(t-s)} g_5(s, w_5(s))ds + \int_0^t e^{-C(t-s)} m_V(s) w_2(s)ds \\ \qquad\qquad + \int_0^t e^{-C(t-s)} b_5(s) w_8(s-\tau_V(s))ds, \\ w_8(t,\varphi) = e^{-Ct}\varphi_8(0) + \int_0^t e^{-C(t-s)} g_8(s, w_8(s))ds + \int_0^t e^{-C(t-s)} b_8(s) w_5(s-\tau_R(s))ds, \end{cases} \tag{2.3.9}$$

for all $t \geq 0$.

Case 1. $\varphi_2 \not\equiv 0$. That is, $\varphi_2 > 0$. In view of the first equation in system (2.3.9), it follows that $w_2(t,\varphi) > 0$, for $t > 0$. This and the second equation in system (2.3.9) imply that $w_5(t,\varphi) > 0$, for $t > 0$. Note that if $s > \hat{\tau}$, then $s - \tau_R(s) > \hat{\tau} - \tau_R(\hat{\tau}) \geq \hat{\tau} - \hat{\tau} = 0$. In view of the third equations in (2.3.9), it follows that $w_8(t,\varphi) > 0,\ \forall\ t > \hat{\tau}$.

Case 2. $\varphi_5 \not\equiv 0$. Then $\varphi_5(\theta_5^0) > 0$, for some $\theta_5^0 \in [-\tau_R(0), 0]$, and hence, $w_5(\theta_5^0) > 0$. In view of third equations in system (2.3.9), it follows that $w_8(t,\varphi) > 0,\ \forall\ t > \hat{\tau}$. Note that if $s > 2\hat{\tau}$, then $s - \tau_V(s) > 2\hat{\tau} - \tau_V(2\hat{\tau}) \geq 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. Then the second equation in system (2.3.9) implies that $w_5(t,\varphi) > 0,\ \forall\ t > 2\hat{\tau}$. Thus, it follows from the first equation in system (2.3.9) that $w_2(t,\varphi) > 0,\ \forall\ t > 2\hat{\tau}$.

Case 3. $\varphi_8 \not\equiv 0$. The arguments are similar to Case 2, and we omit the details.

From the discussions in Cases 1-3, we see that $w_i(t) > 0$ for all $t > 2\hat{\tau}$, $i = 2, 5, 8$. Thus, $P(t)$ is strongly positive on $\mathcal{E}^+$, for all $t > 3\hat{\tau}$. □

Fix a n_0 such that $n_0\omega > 3\hat{\tau}$. Then it follows from Lemma 2.3.8 and the arguments in [83, Lemma 3.8] that $[P(\omega)]^{n_0} = P(n_0\omega)$ is strongly positive. Further, we have the following results:

Lemma 2.3.8. *Two Poincaré maps* $\tilde{P}(\omega) : C([-\hat{\tau}, 0], \mathbb{R}^3) \to C([-\hat{\tau}, 0], \mathbb{R}^3)$ *and* $P(\omega) : \mathcal{E} \to \mathcal{E}$ *have the same spectral radius, that is,* $r(\tilde{P}(\omega)) = r(P(\omega))$.

We further have the following observation.

Lemma 2.3.9. *Let* $\mu = \frac{\ln r(P(\omega))}{\omega}$. *Then there exists a positive* ω*-periodic function* $w^*(t)$ *such that the following statements hold:*

(i) $e^{\mu t} w^*(t)$ *is a solution of system* (2.3.4) *with the feasible domain* $\mathcal{E}^+$*, for all* $t \geq 0$*;*

(ii) $e^{\mu t} w^*(t)$ *is also a solution of system* (2.3.4) *with the feasible domain* $C([-\hat{\tau}, 0], \mathbb{R}^3)$*, for all* $t \geq 0$.

Proof. Part (i). It follows from similar arguments in [138, Proposition 1.1].

Part (ii). It follows from Part (i) that we may assume that $v^*(t) := e^{\mu t} w^*(t)$ satisfies system (2.3.4), for all $t \geq 0$, with $v_0^* = \varphi \in \mathcal{E}^+$. Since $v^*(t) := e^{\mu t} w^*(t)$

is an entire function, we can set $\varphi^*(\theta) = v^*(\theta)$, $\forall\ \theta \in [-\hat{\tau}, 0]$. Then it is easy to see that $z^*(t, \varphi^*) := e^{\mu t} w^*(t)$ satisfies system (2.3.4), for all $t \geq 0$, with $z_0^* = \varphi^* \in C([-\hat{\tau}, 0], \mathbb{R}^3)$. This implies that Part (ii) holds. □

2.3.2 Threshold dynamics

We are now in a position to prove a threshold-type result on the global dynamics of system (2.2.15) in terms of $\mathcal{R}_0^V$ and $\mathcal{R}_0$. We start with the following system

$$\begin{cases} \frac{du_2}{dt} = \sigma b_V(t) u_5 - (m_V(t) + d_L(t)) u_2, \\ \frac{du_3}{dt} = -m_V(t) u_2 - \alpha_V(t)\beta_R(t) \frac{u_8}{\sum_{i=6}^9 u_i} u_3 - d_V(t) u_3, \\ \frac{du_5}{dt} = (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t)) \frac{u_8(t-\tau_V(t))}{\sum_{i=6}^9 u_i(t-\tau_V(t))} u_3(t - \tau_V(t)) e^{-\int_{t-\tau_V(t)}^t d_V(\xi) d\xi} \\ \qquad + m_V(t) u_2 - d_V(t) u_5, \\ \frac{du_6}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t) \frac{u_6}{\sum_{i=6}^9 u_i} u_5 + \eta_R(t) u_9 - d_R(t) u_6, \\ \frac{du_7}{dt} = \alpha_R(t)\beta_R(t) \frac{u_6}{\sum_{i=6}^9 u_i} u_5 - d_R(t) u_7 \\ \qquad - (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t)) \frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))} u_5(t - \tau_R(t)) e^{-\int_{t-\tau_R(t)}^t d_R(\xi) d\xi}, \\ \frac{du_8}{dt} = (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t)) \frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))} u_5(t - \tau_R(t)) e^{-\int_{t-\tau_R(t)}^t d_R(\xi) d\xi} \\ \qquad - (r(t) + d_R(t) + \delta_R(t)) u_8, \\ \frac{du_9}{dt} = r(t) u_8 - \eta_R(t) u_9 - d_R(t) u_9, \end{cases} \tag{2.3.10}$$

with the feasible domain

$$\hat{Y}_\varepsilon^+ = \Big\{ (\varphi_2, \varphi_3, \varphi_5, \varphi_6, \varphi_7, \varphi_8, \varphi_9) \in C([-\hat{\tau}, 0], \mathbb{R}_+^7) : \sum_{i=6}^9 \varphi_i(s) \geq \varepsilon,\ \forall s \in [-\hat{\tau}, 0],$$
$$\varphi_7(0) = \int_{-\tau_R(0)}^0 \alpha_R(\theta)\beta_R(\theta) \frac{\varphi_6(\theta)}{\sum_{i=6}^9 \varphi_i(\theta)} \varphi_5(\theta) e^{-\int_\theta^0 d_R(\xi) d\xi} d\theta \Big\}.$$

Lemma 2.3.10. *Assume $\mathcal{R}_0^V < 1$. Then system (2.3.10) admits a unique ω-periodic solution $(0, 0, 0, S_R^*(t), 0, 0, 0)$, which is globally asymptotically stable in $\hat{Y}_\varepsilon^+$.*

Proof. From the second equation in system (2.3.10), it is easy to see that $u_3(t) \to 0$ as $t \to +\infty$. Thus, (u_2, u_5) in system (2.3.10) is asymptotic to the following system

$$\begin{cases} \frac{du_2}{dt} = \sigma b_V(t) u_5 - (m_V(t) + d_L(t)) u_2, \\ \frac{du_5}{dt} = m_V(t) u_2 - d_V(t) u_5. \end{cases}$$

Since $\mathcal{R}_0^V < 1$, it follows from Lemma 2.3.1 that $r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega)) < 1$, and hence, $\lambda := \frac{1}{\omega} \ln r(\Phi_{\mathbf{F}(\cdot)-\mathbf{V}(\cdot)}(\omega)) < 0$. From Lemma 2.3.2, we see that there exists a positive,

ω-periodic function $v^*(t)$ such that $e^{\lambda t}v^*(t)$ is a solution of system (2.3.1). We may choose a suitable a such that $(u_2(t), u_5(t)) \leq ae^{\lambda t}v^*(t),\ \forall t \in [-\hat{\tau}, 0]$. Since $\sigma \leq 1$ and $ae^{\lambda t}v^*(t)$ is still a solution of system (2.3.1), it follows from comparison arguments that $(u_2(t), u_5(t)) \leq ae^{\lambda t}v^*(t),\ \forall t \geq 0$. By the theories of asymptotically periodic semiflows and internally chain transitive sets (see, e.g., [145, Theorem 3.2.1, Lemma 1.2.2] and Theorem 1.1.2), it follows that $(u_2(t), u_5(t)) \to (0, 0)$ as $t \to +\infty$, due to the fact $\lambda < 0$. Thus, u_8 in system (2.3.10) is asymptotic to the following system

$$\frac{du_8}{dt} = -\left(r(t) + d_R(t) + \delta_R(t)\right) u_8,$$

and hence, $u_8(t) \to 0$ as $t \to +\infty$. Similarly, $u_7(t),\ u_9(t) \to 0$ as $t \to +\infty$. Finally, u_6 in system (2.3.10) is asymptotic to system (2.3.3), and hence, $\lim_{t\to+\infty}(u_6(t) - S_R^*(t)) = 0$. □

Next, we assume $\delta_R(t) \equiv 0$ and $\mathcal{R}_0^V > 1$. Then we consider the following system

$$\begin{cases}
\frac{du_2}{dt} = \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right) u_5 - (m_V(t) + d_L(t))u_2, \\
\frac{du_3}{dt} = m_V(t)(L_V^*(t) - u_2) - \alpha_V(t)\beta_R(t)\frac{u_8}{\sum_{i=6}^9 u_i}u_3 - d_V(t)u_3, \\
\frac{du_5}{dt} = (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t))\frac{u_8(t-\tau_V(t))}{\sum_{i=6}^9 u_i(t-\tau_V(t))}u_3(t - \tau_V(t))e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} \\
\qquad + m_V(t)u_2 - d_V(t)u_5, \\
\frac{du_6}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 + \eta_R(t)u_9 - d_R(t)u_6, \\
\frac{du_7}{dt} = \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 - d_R(t)u_7 \\
\qquad -(1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}, \\
\frac{du_8}{dt} = (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} \\
\qquad - \left(r(t) + d_R(t)\right) u_8, \\
\frac{du_9}{dt} = r(t)u_8 - \eta_R(t)u_9 - d_R(t)u_9,
\end{cases} \tag{2.3.11}$$

with the feasible domain $\hat{Y}_\varepsilon^+$.

Lemma 2.3.11. *Assume $\mathcal{R}_0^V > 1$ and $\mathcal{R}_0 < 1$. Then system* (2.3.11) *admits a unique ω-periodic solution $(0, S_V^*(t), 0, S_R^*(t), 0, 0, 0)$, which is globally asymptotically stable for* (2.3.11) *in $\hat{Y}_\varepsilon^+$.*

Proof. Since $\mathcal{R}_0 < 1$, it follows from Lemma 2.3.5 and Lemma 2.3.8 that $r(P(\omega)) < 1$. By continuity, there exists a $\rho > 0$ such that $r(P_\rho(\omega)) < 1$, where $P_\rho(\omega) : \mathcal{E} \to \mathcal{E}$ is the Poincaré map associated with the following system:

$$\begin{cases} \frac{dw_2}{dt} = \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right) w_5 - (m_V(t) + d_L(t))w_2, \\ \frac{dw_5}{dt} = (1-\tau_V'(t))(\alpha_V \cdot \beta_R)(t-\tau_V(t))\frac{S_V^*(t-\tau_V(t))}{S_R^*(t-\tau_V(t))-\rho} e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} w_8(t-\tau_V(t)) \\ \qquad +m_V(t)w_2 - d_V(t)w_5, \\ \frac{dw_8}{dt} = (1-\tau_R'(t))(\alpha_R \cdot \beta_R)(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} w_5(t-\tau_R(t)) \\ \qquad -\left(r(t) + d_R(t)\right) w_8, \end{cases} \tag{2.3.12}$$

where we have assumed that $\delta_R(t) \equiv 0$. Since $(L_V^*(t), S_V^*(t))$ is an ω-periodic solution of system (2.2.20), it follows that

$$\frac{dS_V^*(t)}{dt} = m_V(t)L_V^*(t) - d_V(t)S_V^*(t). \tag{2.3.13}$$

From the second equation in system (2.3.11), we see that

$$\frac{du_3}{dt} \le m_V(t)L_V^*(t) - d_V(t)u_3. \tag{2.3.14}$$

In view of systems (2.3.13) and (2.3.14), it follows that

$$u_3(t) \le S_V^*(t), \ \forall\ t - \hat{\tau} \ge 0. \tag{2.3.15}$$

Let $N_R = \sum_{i=6}^9 u_i$ in system (2.3.11). Then it follows that N_R satisfies system (2.3.3) with $N_R^0 \in C([-\hat{\tau}, 0], \mathbb{R}_+)$, and hence, $\lim_{t\to+\infty}(N_R(t) - S_R^*(t)) = 0$. Thus, there exists a positive integer M_1 such that

$$S_R^*(t) - \rho < N_R(t) < S_R^*(t) + \rho, \ \forall\ t - \hat{\tau} \ge M_1\omega. \tag{2.3.16}$$

From systems (2.3.11), (2.3.15), (2.3.16) and the fact $\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))} \le 1$, we see that

$$\begin{cases} \frac{du_2}{dt} = \sigma b_V(t)\left(1 - \frac{L_V^*(t)}{K(t)}\right) u_5 - (m_V(t) + d_L(t))u_2, \\ \frac{du_5}{dt} \le (1-\tau_V'(t))(\alpha_V \cdot \beta_R)(t-\tau_V(t))\frac{S_V^*(t-\tau_V(t))}{S_R^*(t-\tau_V(t))-\rho} e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} u_8(t-\tau_V(t)) \\ \qquad +m_V(t)u_2 - d_V(t)u_5, \\ \frac{du_8}{dt} \le (1-\tau_R'(t))(\alpha_R \cdot \beta_R)(t-\tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} u_5(t-\tau_R(t)) \\ \qquad -\left(r(t) + d_R(t)\right) u_8, \end{cases} \tag{2.3.17}$$

for $t - \hat{\tau} \ge M_1\omega$.

Let $\mu_\rho = \frac{\ln r(P_\rho(\omega))}{\omega}$. Then it follows from Lemma 2.3.9 that there exists a positive ω-periodic function $w_\rho^*(t)$ such that $e^{\mu_\rho t}w_\rho^*(t)$ is a solution of system (2.3.12) with the feasible domain $C([-\hat{\tau}, 0], \mathbb{R}^3)$, for all $t \ge 0$. We may choose a $K > 0$ such that $(u_2(t), u_5(t), u_8(t)) \leq Ke^{\mu_\rho t} w_\rho^*(t),\ \forall t \in [M_1\omega - \hat{\tau}, M_1\omega]$. Then the comparison theorem for delay differential equations (see, e.g., [116, Theorem 5.1.1]) imply that $(u_2(t), u_5(t), u_8(t)) \leq Ke^{\mu_\rho t} w_\rho^*(t),\ \forall t - \hat{\tau} \geq M_1\omega$. Since $\mu_\rho < 0$, it follows that $\lim_{t\to+\infty}(u_2(t), u_5(t), u_8(t)) = (0, 0, 0)$.

Thus, the equation for u_9 is asymptotic to $\frac{du_9}{dt} = -\eta_R(t)u_9 - d_R(t)u_9$. By the theories of asymptotically periodic semiflows and internally chain transitive sets (see, e.g., [145, Theorem 3.2.1, Lemma 1.2.2] and Theorem 1.1.2), it follows that $u_9(t) \to 0$ as $t \to +\infty$. Therefore, the equation for u_3 in system (2.3.11) is asymptotic to $\frac{du_3}{dt} = m_V(t)L_V^*(t) - d_V(t)u_3$, and u_6 is asymptotic to system (2.3.3), and hence, $\lim_{t\to+\infty}(u_3(t) - S_V^*(t)) = 0$ and $\lim_{t\to+\infty}(u_6(t) - S_R^*(t)) = 0$. Further, it is easy to see that $\lim_{t\to+\infty} u_7(t) = 0$. □

Theorem 2.3.1. *Assume that $u(t,\phi)$ is the unique solution of system* (2.2.15) *with $u_0 = \phi \in \mathcal{X}_\varepsilon^+(0)$. Then the following statements are vaild:*

(i) *If $\mathcal{R}_0^V < 1$, then $\lim_{t\to+\infty} (u(t,\phi) - (0,0,0,0,0,S_R^*(t),0,0,0)) = 0$;*

(ii) *Let $\delta_R(t) \equiv 0$ in system* (2.2.15)*, and $(\phi_1(0) + \phi_2(0), \phi_3(0)) \neq (0,0)$. If $\mathcal{R}_0^V > 1$ and $\mathcal{R}_0 < 1$, then $\lim_{t\to+\infty} (u(t,\phi) - (L_V^*(t), 0, S_V^*(t), 0, 0, S_R^*(t), 0, 0, 0)) = 0$.*

Proof. Assume that $L(t)$ and $M(t)$ are defined in (2.2.19), and $(L(t), M(t))$ satisfies system (2.2.20) with the feasible domain $\hat{\Sigma}(t)$, which is defined in Remark 2.3.1. We rewrite system (2.2.15) as follows

$$\begin{cases}
\frac{dL}{dt} = b_V(t)\left(1 - \frac{L}{K(t)}\right)M - (m_V(t) + d_L(t))L, \\
\frac{dM}{dt} = m_V(t)L - d_V(t)M, \\
\frac{du_2}{dt} = \sigma b_V(t)\left(1 - \frac{L}{K(t)}\right)u_5 - (m_V(t) + d_L(t))u_2, \\
\frac{du_3}{dt} = m_V(t)(L - u_2) - \alpha_V(t)\beta_R(t)\frac{u_8}{\sum_{i=6}^9 u_i}u_3 - d_V(t)u_3, \\
\frac{du_5}{dt} = (1 - \tau_V'(t))(\alpha_V \cdot \beta_R)(t - \tau_V(t))\frac{u_8(t-\tau_V(t))}{\sum_{i=6}^9 u_i(t-\tau_V(t))}u_3(t - \tau_V(t))e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi} \\
\qquad + m_V(t)u_2 - d_V(t)u_5, \\
\frac{du_6}{dt} = \Lambda_R(t) - \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 + \eta_R(t)u_9 - d_R(t)u_6, \\
\frac{du_7}{dt} = \alpha_R(t)\beta_R(t)\frac{u_6}{\sum_{i=6}^9 u_i}u_5 - d_R(t)u_7 \\
\qquad - (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}, \\
\frac{du_8}{dt} = (1 - \tau_R'(t))(\alpha_R \cdot \beta_R)(t - \tau_R(t))\frac{u_6(t-\tau_R(t))}{\sum_{i=6}^9 u_i(t-\tau_R(t))}u_5(t - \tau_R(t))e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi} \\
\qquad - (r(t) + d_R(t) + \delta_R(t))\,u_8, \\
\frac{du_9}{dt} = r(t)u_8 - \eta_R(t)u_9 - d_R(t)u_9,
\end{cases} \tag{2.3.18}$$

with the feasible domain $\hat{\Sigma}(t) \times \hat{Y}_\varepsilon^+$. Let $\hat{Q} : \hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+ \to \hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$ be the Poincaré map associated with system (2.3.18) and $\hat{\omega}(\hat{x})$ be the omega-limit set of the orbit of $\hat{Q}$ with initial values $\hat{x} \in \hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$.

Part (i). Since $\mathcal{R}_0^V < 1$, it follows from Lemma 2.3.3 and Remark 2.3.1 that $(L(t), M(t))$ in the first two equations of system (2.3.18) satisfies $\lim_{t\to+\infty}(L(t), M(t)) = (0,0)$. Then there exists a set $\hat{\mathcal{I}} \subset C([-\hat{\tau}, 0], \mathbb{R}_+^7)$ such that $\hat{\omega}(\hat{x}) = \{(0,0)\} \times \hat{\mathcal{I}}$. For any given $\hat{x}_1 \in \hat{\mathcal{I}}$, we have $(0, 0, \hat{x}_1) \in \hat{\omega}(\hat{x}) \subset \hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$, and hence, $\hat{x}_1 \in \hat{Y}_\varepsilon^+$. Thus, $\hat{\mathcal{I}} \subset \hat{Y}_\varepsilon^+$. By Lemma 1.1.1, $\hat{\omega}(\hat{x})$ is a compact, invariant and internal chain transitive set for $\hat{Q}$. Moreover, if $x^0 \in C([-\hat{\tau}, 0], \mathbb{R}_+^7)$ with $(0, 0, x^0) \in \hat{\omega}(\hat{x})$, there holds

$$\hat{Q}\mid_{\hat{\omega}(\hat{x})}(0, 0, x^0) = (0, 0, \hat{P}(x^0)),$$

where $\hat{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$ is the Poincaré map associated with system (2.3.10). It then follows that $\hat{\mathcal{I}}$ is a compact, invariant and internal chain transitive set for $\hat{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$.

By Lemma 2.3.10, it follows that system (2.3.10) admits a globally attractive ω-periodic solution $(0, 0, 0, S_R^*(t), 0, 0, 0)$ in $\hat{Y}_\varepsilon^+$. This implies that the unique fixed point $(0, 0, 0, S_R^*(0), 0, 0, 0)$ is an isolated invariant set in $\hat{Y}_\varepsilon^+$, and no cycle connecting $(0, 0, 0, S_R^*(0), 0, 0, 0)$ to itself in $\hat{Y}_\varepsilon^+$. Since $\hat{\mathcal{I}}$ is a compact, invariant and internal chain transitive set for $\hat{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$, it follows from a convergence theorem (see, e.g., Theorem 1.1.3) that $\hat{\mathcal{I}}$ is a fixed point of $\hat{P}$. That is, $\hat{\mathcal{I}} = \{(0, 0, 0, S_R^*(0), 0, 0, 0)\}$, and hence,

$$\hat{\omega}(\hat{x}) = \{(0,0)\} \times \hat{\mathcal{I}} = \{(0, 0, 0, 0, 0, S_R^*(0), 0, 0, 0)\}.$$

This implies that $(0, 0, 0, 0, 0, S_R^*(0), 0, 0, 0)$ is globally attractive for $\hat{Q}$ in $\hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$. Corresponding to the fixed point of the period map $\hat{Q}$, system (2.3.18) has a globally attractive positive ω-periodic solution $(0, 0, 0, 0, 0, S_R^*(t), 0, 0, 0)$ in $\hat{\Sigma}(t) \times \hat{Y}_\varepsilon^+$. In view of (2.2.19), we complete the proof of Part (i).

Part (ii). Since $(L(0), M(0)) \neq (0, 0)$ and $\mathcal{R}_0^V > 1$, it follows from Lemma 2.3.3 and Remark 2.3.1 that $(L(t), M(t))$ in the first two equations of system (2.3.18) satisfies

$$\lim_{t\to+\infty}[(L(t), M(t)) - (L_V^*(t), S_V^*(t))] = (0, 0).$$

Then there exists a set $\tilde{\mathcal{I}} \subset C([-\hat{\tau}, 0], \mathbb{R}_+^7)$ such that $\hat{\omega}(\hat{x}) = \{(L_V^*(0), S_V^*(0))\} \times \tilde{\mathcal{I}}$. For any given $\tilde{x}_1 \in \tilde{\mathcal{I}}$, we have $(L_V^*(0), S_V^*(0), \tilde{x}_1) \in \hat{\omega}(\hat{x}) \subset \hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$, and hence, $\tilde{x}_1 \in \hat{Y}_\varepsilon^+$. Thus, $\tilde{\mathcal{I}} \subset \hat{Y}_\varepsilon^+$. By Lemma 1.1.1, $\hat{\omega}(\hat{x})$ is a compact, invariant and internal chain transitive set for $\hat{Q}$. Moreover, if $\tilde{x}^0 \in C([-\hat{\tau}, 0], \mathbb{R}_+^7)$ with $(L_V^*(0), S_V^*(0), \tilde{x}^0) \in \hat{\omega}(\hat{x})$, there holds

$$\hat{Q}\mid_{\hat{\omega}(\hat{x})}(0, 0, \tilde{x}^0) = (L_V^*(0), S_V^*(0), \tilde{P}(\tilde{x}^0)),$$

where $\tilde{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$ is the Poincaré map associated with system (2.3.11). It then follows that $\tilde{\mathcal{I}}$ is a compact, invariant and internal chain transitive set for $\tilde{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$.

In view of Lemma 2.3.11, it follows that system (2.3.11) admits a globally attractive ω-periodic solution $(0, S_V^*(t), 0, S_R^*(t), 0, 0, 0)$ in $\hat{Y}_\varepsilon^+$. This implies that the unique fixed point $(0, S_V^*(0), 0, S_R^*(0), 0, 0, 0)$ is an isolated invariant set in $\hat{Y}_\varepsilon^+$, and no cycle connecting $(0, S_V^*(0), 0, S_R^*(0), 0, 0, 0)$ to itself in $\hat{Y}_\varepsilon^+$. Since $\tilde{\mathcal{I}}$ is a compact, invariant and internal chain transitive set for $\tilde{P} : \hat{Y}_\varepsilon^+ \to \hat{Y}_\varepsilon^+$, it follows from a convergence theorem (see, e.g., Theorem 1.1.3) that $\tilde{\mathcal{I}}$ is a fixed point of $\tilde{P}$. That is, $\tilde{\mathcal{I}} = \{(0, S_V^*(0), 0, S_R^*(0), 0, 0, 0)\}$, and hence,

$$\hat{\omega}(\hat{x}) = \{(L_V^*(0), S_V^*(0))\} \times \tilde{\mathcal{I}} = \{(L_V^*(0), S_V^*(0), 0, S_V^*(0), 0, S_R^*(0), 0, 0, 0)\}.$$

This implies that $(L_V^*(0), S_V^*(0), 0, S_V^*(0), 0, S_R^*(0), 0, 0, 0)$ is globally attractive for $\hat{Q}$ in $\hat{\Sigma}(0) \times \hat{Y}_\varepsilon^+$. Corresponding to the fixed point of the period map $\hat{Q}$, system (2.3.18) has a globally attractive positive ω-periodic solution $(L_V^*(t), S_V^*(t), 0, S_V^*(t), 0, S_R^*(t), 0, 0, 0)$ in $\hat{\Sigma}(t) \times \hat{Y}_\varepsilon^+$. In view of (2.2.19), we complete the proof of Part (ii). □

In the rest of this section, we discuss the uniform persistence of WNv.

Lemma 2.3.12. *Let $u(t, \phi)$ be the unique solution of system (2.2.15) with $u_0 = \phi \in \mathcal{X}_\varepsilon^+(0)$. Then the following statements are valid:*

(i) *If there exists some $t_0 \geq 0$ such that $u_i(t_0, \phi) \neq 0$ for some $i \in \{2, 5, 8\}$, then $u_i(t, \phi) > 0$, $\forall t > t_0$;*

(ii) *There exists a $T_0 > 0$ such that $u_1(t, \phi) + u_2(t, \phi) < K(t)$, for $t > T_0$;*

(iii) *If $\phi_i(0) \neq 0$ for all $i \in \{2, 5, 8\}$, then $u_i(t, \phi) > 0, \forall\ t > T_0,\ 1 \leq i \leq 9$, where T_0 is given in (ii);*

(iv) *Assume that $\mathcal{R}_0^V > 1$ and $\phi_i(0) \neq 0$ for all $i \in \{2, 5, 8\}$. If there exists a $\varrho^* > 0$ such that $\liminf\limits_{t \to +\infty} u_i(t, \phi) \geq \varrho^*,\ \forall\ i = 2, 5, 8$, then there exists a $\varrho \in (0, \varrho^*)$ such that $\liminf\limits_{t \to +\infty} u_i(t, \phi) \geq \varrho,\ \forall\ 1 \leq i \leq 9$.*

Proof. Part (i). By the positivity of solutions (see Theorem 2.2.1), it is easy to see that $u_2(t)$, $u_5(t)$, and $u_8(t)$ in system (2.2.15) satisfy

$$\begin{cases} \frac{du_2}{dt} \geq -(m_V(t) + d_L(t))u_2, \\ \frac{du_5}{dt} \geq -d_V(t)u_5, \\ \frac{du_8}{dt} \geq -\left(r(t) + d_R(t) + \delta_R(t)\right) u_8. \end{cases} \tag{2.3.19}$$

If there exists some $t_0 \geq 0$ such that $u_i(t_0, \phi) \neq 0$ for some $i \in \{2, 5, 8\}$, then it follows from the comparison arguments and (2.3.19) that $u_i(t, \phi) > 0$, $\forall t > t_0$.

Part (ii). Recall that $L(t) = u_1(t) + u_2(t)$ and $M(t) = u_3(t) + u_4(t) + u_5(t)$ satisfy system (2.2.20). If $\mathcal{R}_0^V < 1$, then we have $\lim_{t\to+\infty}(u_1(t, \phi) + u_2(t, \phi)) = \lim_{t\to+\infty} L(t, \phi) = 0$ by Lemma 2.3.3 (i). Therefore, for any $\varepsilon \in \left(0, \min_{t\in[0,\omega]} K(t)\right)$, there exists a $T_0^{(1)} > 0$ such that $u_1(t, \phi) + u_2(t, \phi) < \varepsilon < K(t),\ \forall t > T_0^{(1)}$. If $\mathcal{R}_0^V > 1$, then we have $\lim_{t\to+\infty}\Big[(u_1(t,\phi)+u_2(t,\phi))-L_V^*(t)\Big]=0$ by Lemma 2.3.3 (ii). Thus, for any $\epsilon\in\Big(0,\min_{t\in[0,\omega]}(K(t)-L_V^*(t))\Big)$, there exists a $T_0^{(2)}>0$ such that

$$u_1(t,\phi)+u_2(t,\phi)<L_V^*(t)+\epsilon<L_V^*(t)+K(t)-L_V^*(t)=K(t),\ \forall t>T_0^{(2)}.$$

Take $T_0=\max_{t\in[0,\omega]}\{T_0^{(1)},T_0^{(2)}\}$, and the desired result follows.

Part (iii). By (i), it is easy to see that $u_i(t,\phi)>0$ holds for $i=2,5,8$. We will show that $u_1(t,\phi)>0$, $\forall t>T_0$. Assume, by contradiction, that there exists a $t_2>T_0$ such that $u_1(t_2,\phi)=0$. Then $u_1'(t_2,\phi)=0$, and the first equation in (2.2.15) ensures that

$$b_V(t_2)\left(u_3(t_2)+u_4(t_2)+(1-\sigma)u_5(t_2)\right)\left(1-\frac{u_1(t_2)+u_2(t_2)}{K(t_2)}\right)=0.$$

By (ii) and the above equality, it follows that $u_5(t_2)=0$, which is a contradiction. And hence, $u_1(t,\phi)>0$, $\forall t>T_0$. Similarly, we can show that $u_i(t,\phi)>0$, $\forall t>T_0$, $i=3,6,9$. By (2.2.21) and (2.2.22), it is easy to see that $u_i(t,\phi)>0$, $\forall t>T_0$, $i=4,7$. We complete the proof of (iii).

Part (iv). Since $L(t)=u_1(t)+u_2(t)$ and $M(t)=u_3(t)+u_4(t)+u_5(t)$ satisfy system (2.2.20), it follows from Lemma 2.3.3 and Remark 2.3.1 that

$$\lim_{t\to+\infty}[(L(t),M(t))-(L_V^*(t),S_V^*(t))]=(0,0).$$

Then there exists a $T_1>0$ such that

$$u_1(t)+u_2(t)=L(t)<L_V^*(t)+\frac{1}{2}[K(t)-L_V^*(t)]=\frac{1}{2}[K(t)+L_V^*(t)],\ \forall\ t\geq T_1,\quad (2.3.20)$$

and

$$u_5(t)\leq M(t)\leq 2S_V^*(t),\ \forall\ t\geq T_1.\quad (2.3.21)$$

Let $N_R=\sum_{i=6}^{9}u_i$ in system (2.2.15). Then it follows that N_R satisfies

$$\frac{dN_R}{dt}=\Lambda_R(t)-d_R(t)N_R-\delta_R(t)u_8\leq\Lambda_R(t)-d_R(t)N_R,$$

and

$$\frac{dN_R}{dt}=\Lambda_R(t)-d_R(t)N_R-\delta_R(t)u_8\geq\Lambda_R(t)-(d_R(t)+\delta_R(t))N_R,$$

with $N_R^0\in C([-\hat{\tau},0],\mathbb{R}_+)$. Then it follows from the comparison principle that there exists a $T_2>T_1$ such that

$$\frac{1}{2}S_R^{**}(t)\leq N_R(t)\leq 2S_R^*(t),\ \forall\ t\geq T_2,\quad (2.3.22)$$

where $S_R^{**}(t)$ is the unique positive ω-periodic solution of the following system

$$\frac{d\hat{N}_R}{dt} = \Lambda_R(t) - (d_R(t) + \delta_R(t))\hat{N}_R,$$

with $\hat{N}_R^0 = N_R^0 \in C([-\hat{\tau}, 0], \mathbb{R}_+)$. Since there exists a $\rho* > 0$ such that $\liminf_{t\to+\infty} u_i(t,\phi) \geq \varrho^*, \ \forall\ i = 2, 5, 8$, we see that there exists a $T_3 > T_2$ such that

$$u_i(t,\phi) \geq \frac{1}{2}\varrho^*, \ \forall\ t \geq T_3, \ i = 2, 5, 8. \tag{2.3.23}$$

From the first equation of system (2.2.15), it follows that

$$\frac{du_1}{dt} \geq \frac{1}{2}(1-\sigma)\varrho^* b_V(t)\left(1 - \frac{K(t) + L_V^*(t)}{2K(t)}\right) - (m_V(t) + d_L(t))u_1, \ \forall\ t \geq T_3.$$

Since $1 - \frac{K(t)+L_V^*(t)}{2K(t)} > 0$, for all $t > 0$, it follows that there exists $\varrho_1^* > 0$ such that $\liminf_{t\to+\infty} u_1(t) \geq \varrho_1^*$. Then there exists a $T_4 > T_3$ such that

$$u_1(t,\phi) \geq \frac{1}{2}\varrho_1^*, \ \forall\ t \geq T_4. \tag{2.3.24}$$

Using $\frac{u_8}{\sum_{i=6}^{9} u_i} \leq 1$ and (2.3.24), it follows from the third equation of system (2.2.15) that

$$\frac{du_3}{dt} \geq \frac{1}{2}\varrho_1^* m_V(t) - [\alpha_V(t)\beta_R(t) + d_V(t)]u_3, \ \forall\ t \geq T_4.$$

Then there exists $\varrho_2^* > 0$ such that $\liminf_{t\to+\infty} u_3(t) \geq \varrho_2^*$, and hence, there exists a $T_5 > T_4$ such that $u_3(t,\phi) \geq \frac{1}{2}\varrho_2^*, \ \forall\ t \geq T_5$. From (2.3.23) and the ninth equation of system (2.2.15), it follows that

$$\frac{du_9}{dt} \geq \frac{1}{2}\varrho^* r(t) - [\eta_R(t) + d_R(t)]u_9, \ \forall\ t \geq T_3. \tag{2.3.25}$$

By (2.3.21), (2.3.22), and the sixth equation of system (2.2.15), it follows that

$$\frac{du_6}{dt} \geq \Lambda_R(t) - [4\alpha_R(t)\beta_R(t)\frac{S_V^*(t)}{S_R^{**}(t)} + d_R(t)]u_6, \ \forall\ t \geq T_2. \tag{2.3.26}$$

In view of (2.3.25) and (2.3.26), we see that there exists $\varrho_3^* > 0$ such that $\liminf_{t\to+\infty} u_i(t) \geq \varrho_3^*, \ i = 6, 9$. By the above discussions together with the integral forms (2.2.21) and (2.2.22), it follows that there exists $\varrho_4^* > 0$ such that $\liminf_{t\to+\infty} u_i(t) \geq \varrho_4^*, \ i = 4, 7$. Letting $\varrho = \min\{\varrho^*, \varrho_1^*, \varrho_2^*, \varrho_3^*, \varrho_4^*\} > 0$, we then obtain the desired result. □

Theorem 2.3.2. *Assume that $u(t,\phi)$ is the unique solution of system (2.2.15) with $u_0 = \phi \in \mathcal{X}_\varepsilon^+(0)$, where $\phi_2(0) \not\equiv 0$, $\phi_5(0) \not\equiv 0$, and $\phi_8(0) \not\equiv 0$. If $\mathcal{R}_0^V > 1$ and $\mathcal{R}_0 > 1$, then there exists a $\varrho > 0$ such that $\liminf_{t\to+\infty} u_i(t,\phi) \geq \varrho$, $\forall 1 \leq i \leq 9$.*

Proof. Let $\mathbb{C} = \mathcal{X}_\varepsilon^+(0)$, $\mathbb{C}_0 = \{\phi \in \mathbb{C} : \phi_2(0) \not\equiv 0,\ \phi_5(0) \not\equiv 0, \text{ and } \phi_8(0) \not\equiv 0\}$, and

$$\partial\mathbb{C}_0 := \mathbb{C}\backslash\mathbb{C}_0 = \{\phi \in \mathbb{C} : \phi_2(0) \equiv 0 \text{ or } \phi_5(0) \equiv 0 \text{ or } \phi_8(0) \equiv 0\}.$$

For any $\phi \in \mathbb{C}_0$, it follows from Lemma 2.3.12 that $u_i(t, \phi) > 0, \forall\ t > 0,\ i = 2, 5, 8$. That is to say $Q(\omega)^n\mathbb{C}_0 \subset \mathbb{C}_0$, $\forall n \in \mathbb{N}$. Further, it follows from Theorem 2.2.1 that $Q(\omega)$ admits a strong global attractor in $\mathbb{C}$.

Define

$$M_\partial := \{\phi \in \partial\mathbb{C}_0 : Q(\omega)^n\phi \in \partial\mathbb{C}_0, \forall n \in \mathbb{N}\},$$

and $\tilde{\omega}(\phi)$ be the omega limit set of the orbit $\Gamma^+ = \{Q(\omega)^n\phi : \forall n \in \mathbb{N}\}$, and set

$$\mathcal{M}_0 = \{(0, 0, 0, 0, 0, S_R^*(0), 0, 0, 0)\},$$

$$\mathcal{M}_1 = \{(L_V^*(0), 0, S_V^*(0), 0, 0, S_R^*(0), 0, 0, 0)\}.$$

Then the following claim indicates that $\mathcal{M}_0 \cup \mathcal{M}_1$ cannot form a cycle for $Q(\omega)$ in $\partial\mathbb{C}_0$.

Claim 1. *For any $\psi \in M_\partial$, the omega limit set $\tilde{\omega}(\psi) = \mathcal{M}_0 \cup \mathcal{M}_1$.*

For any given $\psi \in M_\partial$, we see that $Q(\omega)^n(\psi) \in \partial\mathbb{C}_0$, $\forall n \in \mathbb{N}$. Thus, for each $n \in \mathbb{N}$, it follows that $u_2(n\omega, \psi) = 0$ or $u_5(n\omega, \psi) = 0$ or $u_8(n\omega, \psi) = 0$. Using Lemma 2.3.12, we can further show that for each $t \geq 0$, $u_2(t, \psi) = 0$ or $u_5(t, \psi) = 0$ or $u_8(t, \psi) = 0$. If $u_5(t, \psi) = 0$ for $t \geq 0$, then it follows from the fifth equation of system (2.2.15) that $u_2(t, \psi) = 0$ for $t \geq 0$. Further, $u_7(t, \psi)$ and $u_8(t, \psi)$ in system (2.2.15) satisfy

$$\begin{cases} \frac{du_7}{dt} = -d_R(t)u_7, \\ \frac{du_8}{dt} = -\left(r(t) + d_R(t) + \delta_R(t)\right)u_8, \end{cases}$$

for $t - \hat{\tau} \geq 0$. Then it is easy to see that $\lim_{t\to+\infty}(u_7(t, \psi), u_8(t, \psi)) = (0, 0)$. Thus, u_4 is asymptotic to

$$\frac{du_4}{dt} = -d_V(t)u_4,$$

and u_9 is asymptotic to

$$\frac{du_9}{dt} = -\eta_R(t)u_9 - d_R(t)u_9.$$

By the theories of asymptotically periodic semiflows and internally chain transitive sets (see, e.g., [145, Theorem 3.2.1, Lemma 1.2.2] and Theorem 1.1.2), it follows that $(u_4(t), u_9(t)) \to (0, 0)$ as $t \to +\infty$. Similarly, u_6 is asymptotic to (2.3.3), and hence, $\lim_{t\to+\infty}(u_6(t) - S_R^*(t)) = 0$. On the hand, we see that (u_1, u_3) is asymptotic to system (2.2.20). Since $\mathcal{R}_0^V > 1$, it follows from the theory of asymptotically periodic semiflows and internally chain transitive sets (see, e.g., [145, Theorem 3.2.1, Lemma 1.2.2] and

Theorem 1.1.2), together with Lemma 2.3.3 and Remark 2.3.1 that

$$\text{either } \lim_{t\to+\infty}(u_1(t),u_3(t))=(0,0), \text{ or } \lim_{t\to+\infty}[(u_1(t),u_3(t))-(L_V^*(t),S_V^*(t))]=(0,0).$$

Thus, $\tilde{\omega}(\psi)=\mathcal{M}_0\cup\mathcal{M}_1$. In case where $u_5(t_1,\psi)\neq 0$, for some $t_1\geq 0$. By Lemma 2.3.12, we see that $u_5(t,\psi)>0$, $\forall\, t>t_1$. Thus, for each $t>t_1$, $u_2(t,\psi)=0$ or $u_8(t,\psi)=0$. We consider the case where $u_8(t,\psi)=0$, for $t>t_1$. Then it follows from the eighth equation in (2.2.15) that $u_5(t,\psi)u_6(t,\psi)=0$, for $t>t_1-\hat{\tau}$, which is a contradiction. Next, we consider the case where $u_8(t_2,\psi)\neq 0$, for some $t_2>t_1$. By Lemma 2.3.12, we see that $u_8(t,\psi)>0$, $\forall\, t>t_2$. Thus, for each $t>t_2$, $u_2(t,\psi)=0$. Again from Lemma 2.3.12, we know that there exists a large enough $T_0>0$ such that $u_1(t,\psi)+u_2(t,\psi)<K(t)$, $\forall\, t>T_0$. Then it follows from the second equation in (2.2.15) that $u_5(t,\psi)=0$, for $t>\max\{t_2,T_0\}$, which is also a contradiction. This proves Claim 1.

Since $\mathcal{R}_0>1$, it follows from Lemma 2.3.5 and Lemma 2.3.8 that $r(P(\omega))>1$. Let $P_\delta(\omega):\mathcal{E}\to\mathcal{E}$ be the Poincaré map associated with the following system:

$$\begin{cases}\frac{dw_2}{dt}=\sigma b_V(t)\left(1-\frac{L_V^*(t)+2\delta}{K(t)}\right)w_5-(m_V(t)+d_L(t))w_2,\\ \frac{dw_5}{dt}=(1-\tau_V'(t))(\alpha_V\cdot\beta_R)(t-\tau_V(t))\frac{S_V^*(t-\tau_V(t))-\delta}{S_R^*(t-\tau_V(t))+4\delta}e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi}w_8(t-\tau_V(t))\\ \qquad +m_V(t)w_2-d_V(t)w_5,\\ \frac{dw_8}{dt}=(1-\tau_R'(t))(\alpha_R\cdot\beta_R)(t-\tau_R(t))\frac{S_R^*(t-\tau_R(t))-\delta}{S_R^*(t-\tau_R(t))+4\delta}e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}w_5(t-\tau_R(t))\\ \qquad -(r(t)+d_R(t))\,w_8.\end{cases} \tag{2.3.27}$$

By continuity, we see that $\lim\limits_{\delta\to 0}r(P_\delta(\omega))=r(P(\omega))>1$. Thus, we can fix a sufficiently small number $\delta>0$ such that

$$\delta<\min\{\frac{1}{2}\min_{t\in[0,\omega]}[K(t)-L_V^*(t)],\min_{t\in[0,\omega]}S_V^*(t),\min_{t\in[0,\omega]}S_R^*(t)\} \text{ and } r(P_\delta(\omega))>1.$$

For the above fixed $\delta>0$, by the continuous dependence of solutions on the initial value, there exists $\delta^*>0$ such that for all ϕ with $\|\phi-\mathcal{M}_1\|\leq\delta^*$, then we have $\|Q(t)\phi-Q(t)\mathcal{M}_1\|<\delta$ for all $t\in[0,\omega]$. We now prove the following claim.

Claim 2. *For all* $\phi\in\mathbb{C}_0$, *there holds* $\limsup_{n\to+\infty}\|Q(\omega)^n(\phi)-\mathcal{M}_1\|\geq\delta^*$.

Suppose, by contradiction, that $\limsup_{n\to+\infty}\|Q(\omega)^n(\phi_0)-\mathcal{M}_1\|<\delta^*$ for some $\phi_0\in\mathbb{C}_0$. Then there exists $n_1\geq 1$ such that $\|Q(\omega)^n(\phi_0)-\mathcal{M}_1\|<\delta^*$ for $n\geq n_1$. For any $t\geq n_1\omega$, letting $t=n\omega+t'$ with $n=[t/\omega]$ and $t'\in[0,\omega)$, we have

$$\|Q(t)\phi_0-Q(t)\mathcal{M}_1\|=\|Q(t')(Q(\omega)^n(\phi_0))-Q(t')\mathcal{M}_1\|<\delta. \tag{2.3.28}$$

Note that

$$Q(t)\mathcal{M}_1=(L_V^*(t),0,S_V^*(t),0,0,S_R^*(t),0,0,0).$$

It then follows from (2.3.28) that for any $t \geq n_1\omega - \hat{\tau}$, we have $0 < u_j(t,\phi_0) < \delta,\ j = 2,7,8,9$, and

$$u_1(t,\phi_0) < L_V^*(t) + \delta,\ u_3(t,\phi_0) > S_V^*(t) - \delta,\ S_R^*(t) - \delta < u_6(t,\phi_0) < S_R^*(t) + \delta.$$

Thus, the equations of $u_2(t,\phi_0)$, $u_5(t,\phi_0)$ and $u_8(t,\phi_0)$ in (2.2.15) satisfy

$$\begin{cases} \frac{du_2}{dt} \geq \sigma b_V(t)\left(1 - \frac{L_V^*(t)+2\delta}{K(t)}\right)u_5 - (m_V(t) + d_L(t))u_2, \\ \frac{du_5}{dt} \geq (1-\tau_V'(t))(\alpha_V \cdot \beta_R)(t-\tau_V(t))\frac{S_V^*(t-\tau_V(t))-\delta}{S_R^*(t-\tau_V(t))+4\delta}e^{-\int_{t-\tau_V(t)}^t d_V(\xi)d\xi}u_8(t-\tau_V(t)) \\ \qquad +m_V(t)u_2 - d_V(t)u_5, \\ \frac{du_8}{dt} \geq (1-\tau_R'(t))(\alpha_R \cdot \beta_R)(t-\tau_R(t))\frac{S_R^*(t-\tau_R(t))-\delta}{S_R^*(t-\tau_R(t))+4\delta}e^{-\int_{t-\tau_R(t)}^t d_R(\xi)d\xi}u_5(t-\tau_R(t)) \\ \qquad -\left(r(t)+d_R(t)\right)u_8, \end{cases} \tag{2.3.29}$$

for $t \geq n_1\omega$.

Let $\mu_\delta = \frac{\ln r(P_\delta(\omega))}{\omega}$. Then it follows from Lemma 2.3.9 that there exists a positive ω-periodic function $w_\delta^*(t)$ such that $e^{\mu_\delta t}w_\delta^*(t)$ is a solution of system (2.3.27) with the feasible domain $C([-\hat{\tau},0],\mathbb{R}^3)$, for all $t \geq 0$. In view of Lemma 2.3.12, we see that $(u_2(t,\phi_0),u_5(t,\phi_0),u_8(t,\phi_0)) \gg (0,0,0)$. Thus, we may choose a $K_\delta > 0$ such that

$$(u_2(t,\phi_0),u_5(t,\phi_0),u_8(t,\phi_0)) \geq K_\delta e^{\mu_\delta t}w_\delta^*(t),\ \forall\ t \in [n_1\omega - \hat{\tau}, n_1\omega].$$

Then the comparison theorem for delay differential equations (see, e.g., [116, Theorem 5.1.1]) imply that

$$(u_2(t,\phi_0),u_5(t,\phi_0),u_8(t,\phi_0)) \geq K_\delta e^{\mu_\delta t}w_\delta^*(t),\ \forall t \geq n_1\omega.$$

Since $\mu_\delta > 0$, it follows that $u_i(t,\phi_0) \to +\infty$ $(i = 2,5,8)$ as $t \to +\infty$. This leads to contradiction.

By using the assumption $\mathcal{R}_0^V > 1$ and similar arguments as in Claim 2, we have the following observation.

Claim 3. *There exists a* $\delta_0^* > 0$ *such that* $\limsup_{n\to+\infty} \|Q(\omega)^n(\phi) - \mathcal{M}_0\| \geq \delta_0^*$, *for all* $\phi \in \mathbb{C}_0$.

The above s imply that, for $i = 0,1$, $\mathcal{M}_i$ is an isolated invariant set for $Q(\omega)$ in $\mathbb{C}$, and $W^s(\mathcal{M}_i)\bigcap \mathbb{C}_0 = \emptyset$, where $W^s(\mathcal{M}_i)$ is the stable set of $\mathcal{M}_i$ for $Q(\omega)$. By [90, Theorem 3.7], as applied to $Q(\omega)$, we know that $Q(\omega)$ admits a global attractor A_0 in $\mathbb{C}_0$. It then follows from Theorem 1.2.1 that $Q(\omega)$ is uniformly persistent with respect to $(\mathbb{C}_0, \partial\mathbb{C}_0)$ in the sense that there exists $\tilde{\varrho} > 0$ such that

$$\liminf_{n\to+\infty} \mathrm{d}(Q^n(\phi), \partial\mathbb{C}_0) \geq \tilde{\varrho},\ \forall\phi \in \mathbb{C}_0. \tag{2.3.30}$$

Since $A_0 = Q(\omega)A_0$, we have that $\phi_i(0) > 0$, for all $\phi \in A_0$ and $i = 2, 5, 8$. Let $B_0 := \bigcup_{t\in[0,\omega]} Q(t)A_0$. Then $B_0 \subset \mathbb{C}_0$ and $\lim_{t\to+\infty} \mathrm{d}(Q(t)\phi, B_0) = 0$, $\forall \phi \in \mathbb{C}_0$. Define a continuous function $p : \mathbb{C} \to \mathbb{R}_+$ by

$$p(\phi) = \min\{\phi_2(0), \phi_5(0), \phi_8(0)\}, \ \forall \phi \in \mathbb{C}.$$

Since B_0 is compact subset of $\mathbb{C}_0$, it follows that $\inf_{\phi\in B_0} p(\phi) = \min_{\phi\in B_0} p(\phi) > 0$. Consequently, there exists a $\varrho^* > 0$ such that

$$\liminf_{t\to+\infty} p(Q(t)\phi) = \liminf_{t\to+\infty} \min\{u_2(t,\phi), u_5(t,\phi), u_8(t,\phi)\} \geq \varrho^*, \ \forall \phi \in \mathbb{C}_0.$$

Furthermore, by Lemma 2.3.12, there exists a $\varrho \in (0, \varrho^*)$ such that

$$\liminf_{t\to+\infty} u_i(t,\phi) \geq \varrho, \ \forall \phi \in \mathbb{C}_0 \ (1 \leq i \leq 9).$$

This completes the proof. □

To finish this section, we briefly discuss the case where all the coefficients and two incubation periods of system (2.2.15) are time-independent. It then follows from [144, Corollary 2.1] that

$$\mathcal{R}_0^V = \frac{m_V b_V}{d_V(m_V + d_L)},$$

and if $\mathcal{R}_0^V > 1$, then we can further obtain

$$\mathcal{R}_0 = \sqrt{\sigma + e^{-d_R\tau_R}e^{-d_V\tau_V} \cdot \frac{\alpha_V\alpha_R\beta_R^2}{d_V(r + d_R + \delta_R)} \cdot \frac{S_V^*}{S_R^*}},$$

where $S_V^* = \dfrac{m_V b_V - (m_V + d_L)d_V}{b_V d_V} \cdot K$, and $S_R^* = \dfrac{\Lambda_R}{d_R}$. In particular, when $\mathcal{R}_0 > 1$ and $\delta_R = 0$, the unique endemic equilibrium E^* can be expressed explicitly as $E^* =$

$(u_1^*, u_2^*, u_3^*, u_4^*, u_5^*, u_6^*, u_7^*, u_8^*, u_9^*)$, where

$$u_1^* = \frac{u_3^*}{m_V}\Big(\frac{\alpha_V \beta_R d_R u_8^*}{\Lambda_R} + d_V\Big), \; u_2^* = \frac{\sigma d_V}{m_V} u_5^*,$$
$$u_3^* = \frac{(1-\sigma) d_V \Lambda_R e^{d_V \tau_V}}{\alpha_V \beta_R d_R} \cdot \frac{u_5^*}{u_8^*}, \; u_4^* = (1-\sigma)(e^{d_V \tau_V} - 1) u_5^*,$$
$$u_5^* = \frac{1}{\alpha_V \beta_R d_R e^{-d_V \tau_V}(\eta_R + d_R)[\sigma + (1-\sigma) e^{d_V \tau_V}] + (1-\sigma) d_V \times} \frac{}{[(r+d_R)(\eta_R + d_R) e^{d_R \tau_R} - r\eta_R]} \cdot \frac{d_V \Lambda_R (r + d_R)(\eta_R + d_R)(\mathcal{R}_0^2 - 1) e^{d_R \tau_R}}{\alpha_R \beta_R},$$
$$u_6^* = \frac{d_R \Lambda_R}{(1 - e^{-d_R \tau_R}) \alpha_R \beta_R d_R} \cdot \frac{u_7^*}{u_5^*}, \; u_7^* = \frac{r + d_R}{d_R}(e^{d_V \tau_V} - 1) u_8^*, \; u_9^* = \frac{r u_8^*}{\eta_R + d_R},$$
$$u_8^* = \frac{\alpha_R \beta_R \Lambda_R (\eta_R + d_R) e^{-d_R \tau_R} u_5^*}{\alpha_R \beta_R e^{-d_R \tau_R}[(r + d_R)(\eta_R + d_R) e^{d_R \tau_R} - r\eta_R] u_5^* + \Lambda_R (r + d_R)(\eta_R + d_R)}.$$

It remains an open problem whether E^* is globally asymptotically stable even in this special case.

2.4 Numerical simulations

In this section, we investigate how temperature affects the temporal dynamics of West Nile virus (WNv) transmission in Los Angeles County, California. Since WNv first appeared in Los Angeles County in 2003, it has caused infections in humans and animals, including birds, horses, cats and dogs, every year (http://publichealth.lacounty.gov/vet/WNv.htm).

Parameter estimates. Values for parameters in model (2.2.15) are listed in Table 2.2. The results in [27, 34, 45, 94, 108] show that temperature can affect the duration of development and activity of *Cluex* mosquitoes, such as larvae and adult death rates, and the biting pattern. Thus, we can use the monthly mean temperature data of Los Angeles County from 1981–2010 (Source: National Weather Service and National Climate Data Center, as shown in Table 2.3), and CFTOOL to determine the temperature-dependent parameters $b_V(t)$, $\beta_R(t)$, $m_V(t)$, $d_L(t)$, $d_V(t)$ and $\tau_V(t)$, respectively.

By appealing to the method of estimating the biting rate in [108], the temperature-dependent biting rate can be expressed as

$$\beta_R(T) = \frac{0.344}{1 + 1.231 e^{-0.184(T-20)}} \times 30.4 \text{ month}^{-1},$$

where T is the temperature in °C. The biting rate of mosquitoes in Los Angeles County

Table 2.2: Parameter values in simulation

Parameter	Value	Dimension	References
σ	0.007	dimensionless	[1]
α_V	0.16	dimensionless	[136]
α_R	0.88	dimensionless	[136]
Λ_R	800×30.4	month^{-1}	[63]
d_R	$30.4/1000$	month^{-1}	[15]
δ_R	0.0025×30.4	month^{-1}	[1]
r	0.1011×30.4	month^{-1}	[136]
τ_R	$5/30.4$	month	[117]
K	500000	dimensionless	estimated
η_R	0.00009×30.4	month^{-1}	estimated
$b_V(t)$	to be estimated	month^{-1}	see text
$\beta_R(t)$	to be estimated	month^{-1}	see text
$m_V(t)$	to be estimated	month^{-1}	see text
$d_L(t)$	to be estimated	month^{-1}	see text
$d_V(t)$	to be estimated	month^{-1}	see text
$\tau_V(t)$	to be estimated	month	see text

can then be fitted by

$$\begin{aligned}\beta_R(t) = 3.723 &- 4.018\cos(\pi t/6) - 3.225\sin(\pi t/6) - 0.01047\cos(\pi t/3)\\ &+1.685\sin(\pi t/3) + 0.07118\cos(\pi t/2) + 0.2877\sin(\pi t/2)\\ &+0.4585\cos(2\pi t/3) - 0.02509\sin(2\pi t/3) - 0.045\cos(5\pi t/6)\\ &-0.1724\sin(5\pi t/6)\ \text{month}^{-1}.\end{aligned}$$

Motivated by [108], we suppose that the birth rate of larvae is proportional to the biting rate, i.e., $b_V(t) = c\beta_R(t)$ month^{-1} , where $c = 2.325$ is the scaling factor associated with biting rate [108].

Table 2.3: Monthly mean temperature in Los Angeles County from 1981-2010 (°C)

Month	Jan	Feb	Mar	Apr	May	June
Temperature	14.4	14.9	15.9	17.3	18.8	20.7
Month	Jul	Aug	Sep	Oct	Nov	Dec
Temperature	22.9	23.5	22.8	20.3	16.9	14.2

Only adult mosquitoes can transmit WNv, and the development of *Culex tarsalis* from larval to adult stages is highly associated with temperature. In [27], the temperature-dependent maturation rate [45] can be modeled as

$$m_V(T) = \frac{0.25(T+273.15)}{298.15} \cdot \frac{e^{\frac{28094}{1.987}\left(\frac{1}{298.15}-\frac{1}{T+273.15}\right)}}{1+e^{\frac{35362}{1.987}\left(\frac{1}{298.6}-\frac{1}{T+273.15}\right)}} \times 30.4 \text{ month}^{-1},$$

and we can further obtain the following fitted function:

$$\begin{aligned} m_V(t) = {} & 2.139 - 0.9506\cos(\pi t/6) - 0.6493\sin(\pi t/6) - 0.1131 cos(\pi t/3) \\ & +0.239\sin(\pi t/3) + 0.004012\cos(\pi t/2) + 0.03228\sin(\pi t/2) \\ & +0.01943\cos(2\pi t/3) + 0.03783\sin(2\pi t/3) + 0.03785\cos(5\pi t/6) \\ & -0.03457\sin(5\pi t/6) \text{ month}^{-1}. \end{aligned}$$

The mortality rate for female larvae [45] and adult mosquitoes [34] can be evaluated as

$$d_L(T) = \left(1 - 0.85e^{-(\frac{T-17}{T_{var}})^2}\right) \times 30.4 \text{ month}^{-1},$$

where T_{var} is the variance of T, and

$$d_V(T) = \begin{cases} 2.17 \times 10^{-8}\ T^{4.48} \times 30.4 \text{ month}^{-1}, & T > 18.4°\text{C} \\ 0.01 \times 30.4 \text{ month}^{-1}, & \text{otherwise} \end{cases}$$

respectively. Thus, the mortality rates for female larvae $d_L(t)$ and adult mosquitoes $d_V(t)$ in Los Angeles County can be approximated by

$$\begin{aligned} d_L(t) = {} & 6.776 - 1.798\cos(\pi t/6) - 0.2774\sin(\pi t/6) - 1.944 cos(\pi t/3) \\ & +0.4381\sin(\pi t/3) + 1.733\cos(\pi t/2) + 0.5229\sin(\pi t/2) \\ & +0.1806\cos(2\pi t/3) - 0.1011\sin(2\pi t/3) - 0.01175\cos(5\pi t/6) \\ & -0.241\sin(5\pi t/6) \text{ month}^{-1}, \end{aligned}$$

and

$$\begin{aligned} d_V(t) = {} & 0.6258 - 0.3764\cos(\pi t/6) - 0.2862\sin(\pi t/6) + 0.008548 cos(\pi t/3) \\ & +0.1482\sin(\pi t/3) + 0.02862\cos(\pi t/2) + 0.04707\sin(\pi t/2) \\ & +0.008651\cos(2\pi t/3) - 0.00398\sin(2\pi t/3) + 0.03785\cos(5\pi t/6) \\ & -0.03457\sin(5\pi t/6) \text{ month}^{-1}, \end{aligned}$$

respectively.

According to [27], the relationship between the EIP and the temperature is given by

$$\tau_V(T) = \frac{10.45 - 0.21T}{-0.27 + 0.03T} \times \frac{1}{30.4} \text{ month},$$

which indicates that the EIP decreases with increasing temperature, thus we can obtain the following approximation for the periodic time delay $\tau_V(t)$ (see Fig. 2.2):

$$\begin{aligned}\tau_V(t) = {} & 0.8869 - 0.4873\cos(\pi t/6) + 0.2445\sin(\pi t/6) + 0.147cos(\pi t/3) \\ & +0.005816\sin(\pi t/3) + 0.06033\cos(\pi t/2) - 0.0244\sin(\pi t/2) \\ & +0.02121\cos(2\pi t/3) - 0.03937\sin(2\pi t/3) + 0.01193\cos(5\pi t/6) \\ & -0.03208\sin(5\pi t/6) \text{ month.}\end{aligned}$$

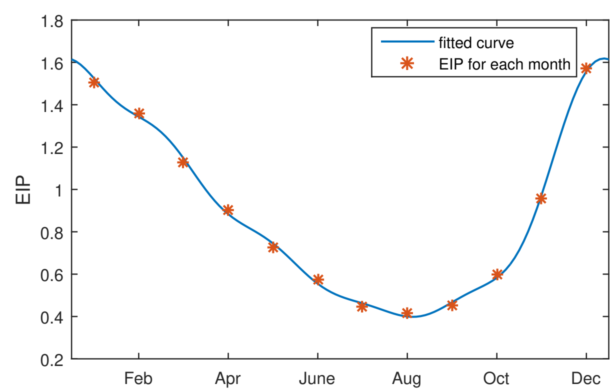


Figure 2.2: Fitted curve of extrinsic incubation period (EIP)

Model validation. Dead bird surveillance program not only helps to track where WNv is active in Los Angeles County, but also helps to identify when the transmission season begins and ends. Set initial value as $L_{V1}(\theta) = 10000$, $L_{V2}(\theta) = 10$, $S_V(\theta) = 5000$, $E_V(\theta) = 0$, $I_V(\theta) = 100$, $S_R(\theta) = 400$, $E_R(\theta) = 2$, $I_R(\theta) = 0$, $R_R(\theta) = 0$ for all $\theta \in [-\hat{\tau}, 0]$. In Fig. 2.3, we display the simulation (using the parameters listed in Table 2.2) and number of dead birds observed from January 2015 to August 2017 (source: LA Public Health, http://publichealth.lacounty.gov/vet/WNv.htm), and show the simulation result until the year 2020. We can see that the number of dead birds reported presents an obvious seasonal fluctuation, and our numerical result captures the seasonality.

$\mathcal{R}_0$ and long-term behaviors. We can use the numerical scheme recently presented in Remark 1.4.1 (please see also [79, Lemma 2.5 and Remark 3.2]) to compute $\mathcal{R}_0$. We set $\omega = 12$ months. Under the same set of parameter values as that of Fig. 2.3, we have $\mathcal{R}_0 = 1.015 > 1$. In this case, the disease will propagate and exhibit periodic fluctuation eventually. Fig. 2.4(a) shows the long-term behavior of infectious birds. By employing the mosquito control methods, such as eliminating

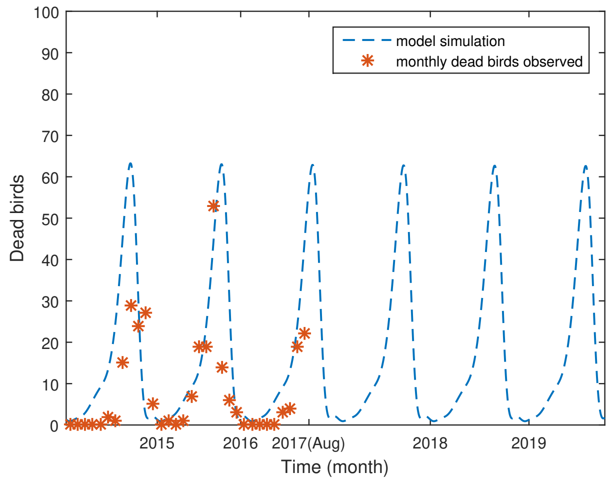


Figure 2.3: The simulation result of dead birds from 2015 to 2020, and red stars repsresent data from LA Public Health

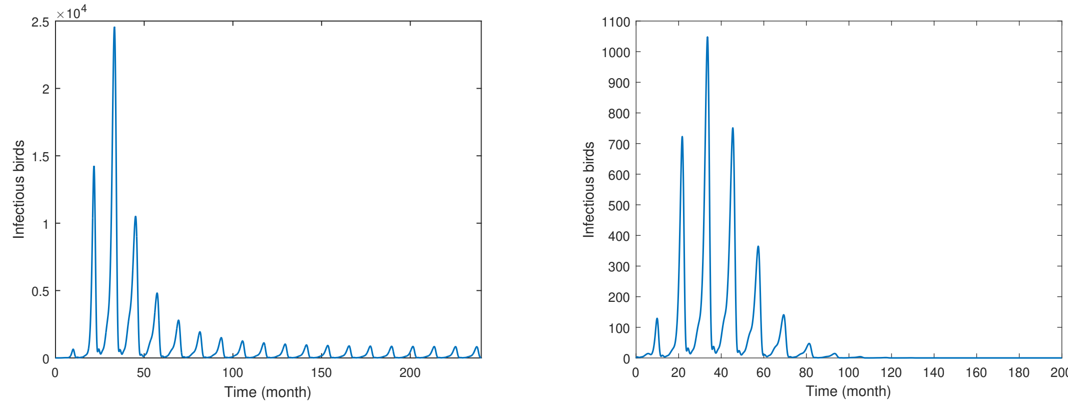
larval breeding sites, including standing water (e.g., bird baths, flower pots) and polluted water (e.g., dairy drains), or spraying insecticides from airplanes or trucks to kill adult mosquitoes, we can increase the mosquito (both larval and adult) mortality rates. On the other hand, we can use mosquito netting to cover the indoor pet birds' cages at night, and add screening for birds living outdoor in aviaries to avoid direct exposure to mosquitoes, and hence, reduce the biting rate. More specifically, suppose we can increase the mosquito death rates to $1.06d_L(t)$ and $1.1d_V(t)$, respectively, and decrease the biting rate to $0.95\beta_R(t)$ (as wild birds are still the main reservoirs for WNv), then $\mathcal{R}_0 = 0.801 < 1$, which implies the WNv epidemic cannot be sustained and will be eliminated from this area eventually. As pointed out in [93], for complex vector-borne disease models, outbreaks are still possible even for $\mathcal{R}_0 < 1$ under certain circumstances. This phenomenon is also demonstrated numerically in Fig. 2.4(b).

Sensitivity analysis of $\mathcal{R}_0$. We are interested in the sensitivity of $\mathcal{R}_0$ on different EIP durations, system parameters, and global warming, respectively.

We define the time-averaged EIP duration as

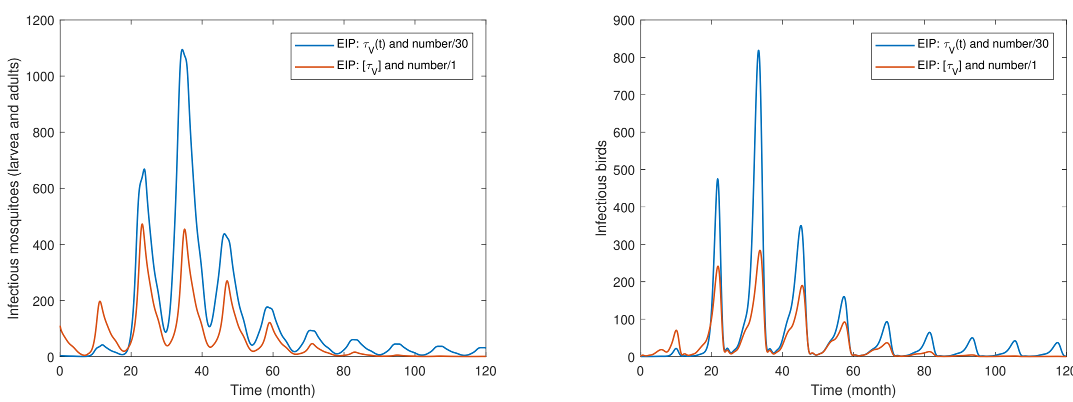
$$[\tau_V] := \frac{1}{\omega}\int_0^\omega \tau_V(t)\mathrm{d}t,$$

it follows that $[\tau_V] = 0.8869$ month. By using this time-averaged EIP duration and keeping all the other parameter values the same as those in Fig. 2.4(a), we obtain $\mathcal{R}_0 = 0.785 < 1$, which is less than 1.015 in Fig. 2.4(a). The comparison of long-term behaviors of infectious mosquitoes (adults) and birds under $\tau_V(t)$ and $[\tau_V]$ is shown in Fig. 2.5. We can see that the use of time-averaged EIP may underestimate the WNN



(a) $\mathcal{R}_0 = 1.015 > 1$ (b) $\mathcal{R}_0 = 0.801 < 1$

Figure 2.4: Long-term behaviors of the infectious birds when $\mathcal{R}_0 > 1$ and $\mathcal{R}_0 < 1$

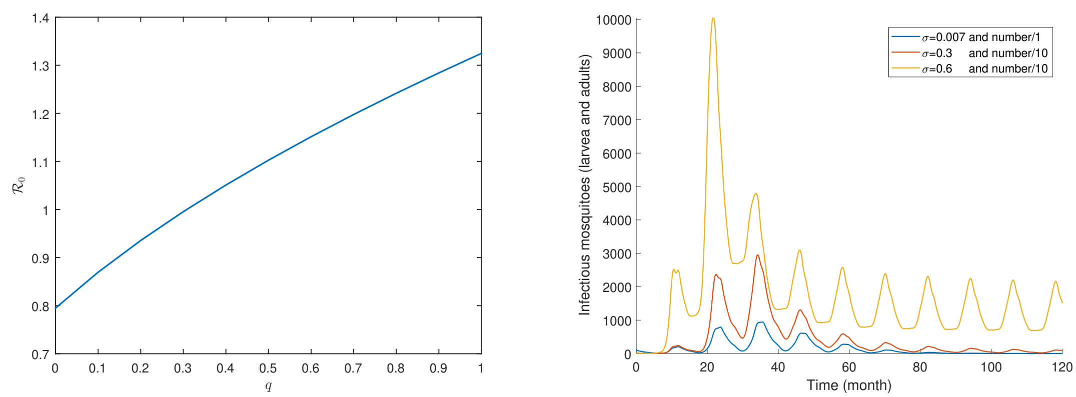


(a) Mosquitoes (b) Birds

Figure 2.5: Comparison of long-term bahaviors of infectious compartments under two different EIP durations (temperature-dependent $\tau_V(t)$: $\mathcal{R}_0 = 1.015 > 1$ and time-average $[\tau_V]$: $\mathcal{R}_0 = 0.785 < 1$)

transmission risk and the size of infectious compartments in Los Angeles County. However, note that the simulated times of WNv outbreaks are quite close under two different EIP durations, and multiple peaks are detected nearly at the same time, which suggests that if the control strategies only aim at predicting the epidemic peak to provide time for response, the use of time-average and temperature-dependent EIP can have similar outcomes.

Next, we take the vertical transmission rate σ of mosquitoes, and two bird species parameters: recovery rate r and the loss of immunity η_R as examples to explore their relative importances on WNv transmission. We set σ as varying in $(0, 1)$, other parameters as those in Fig. 2.4(b), where $\mathcal{R}_0 = 0.801 < 1$. Fig. 2.6(a) shows that $\mathcal{R}_0$ is an increasing function of σ, and grows larger than the critical value $\mathcal{R}_0 = 1$ as σ rises by $\sigma > 0.325$, which means that the WNv resurgence happens. The increasing vertical transmission rate leads to a larger number of infectious larval and adult mosquitoes (Fig. 2.6(b)), and hence, makes the WNv transmission more intense. We see that r reduces $\mathcal{R}_0$ in Fig. 2.7(a), which indicates that improving the medical treatments for birds can be an very effective strategy in controlling the disease. The main effect of η_R, as $1/\eta_R$ is the mean time of immunity, is to contribute substantially to increase in the size of susceptible birds. Though η_R does not appear in $\mathcal{R}_0$, because of its absence in the system of infectious compartments, i.e., system (2.3.4), we find that it may still affect the long-term behaviors of WNv disease, such as the (final) size of infectious birds (Fig. 2.7(b)).

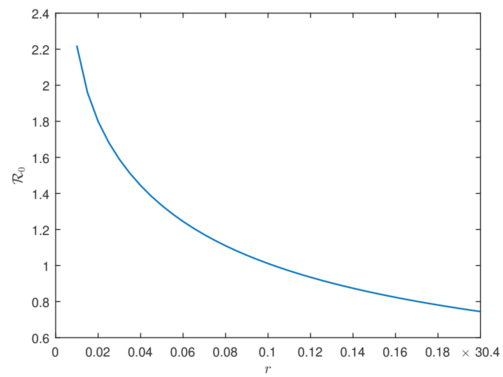


(a) $\mathcal{R}_0$ *vs* σ on the range $(0, 1)$

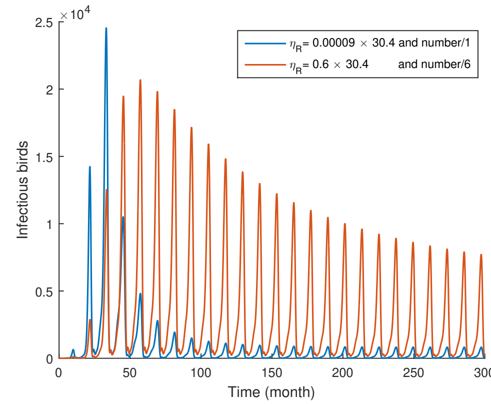
(b) Infectious mosquitoes under different σ

Figure 2.6: Effects of vertical transmission on WNv spread (other parameter values the same as those in Fig. 2.4(b))

As a consequence of climate warming, increased temperatures (Fig. 2.8(a)) and long-lasting heat waves have already been reported in Los Angeles County. As temperature is usually regarded as a primary driver of mosquito development and activity,



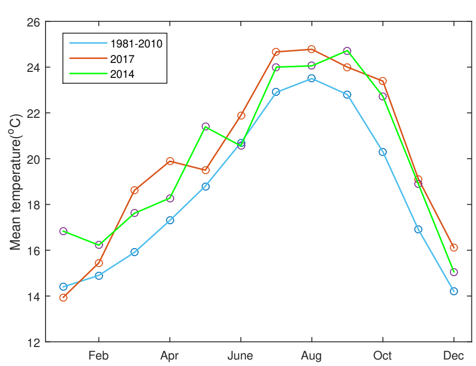
(a) $\mathcal{R}_0$ *vs* r on $(0,1) \times 30.4$ month^{-1}



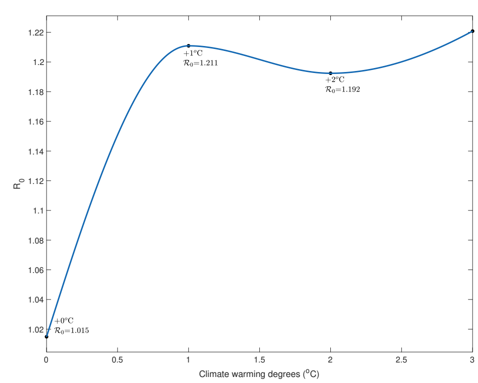
(b) Infectious birds under different η_R

Figure 2.7: Effects of recovery and immunity loss rates on WNv transmission (other parameter values the same as those in Fig. 2.4(a))

it motivates us to explore how $\mathcal{R}_0$ responses to increasing temperatures. By considering the monthly mean temperatures, as shown in Table 2.3, going up by 1°C, 2°C and 3°C, we modify the corresponding periodic temperature-dependent coefficients $b_V(t)$, $\beta_R(t)$, $m_V(t)$, $d_L(t)$, $d_V(t)$ and $\tau_V(t)$, respectively, and keep other constant parameters the same as in Fig. 2.4(a). Again, by Remark 1.4.1, we can calculate $\mathcal{R}_0$ for each increased temperature. Fig. 2.8(b) shows that $\mathcal{R}_0$ acts as a function of temperature (T), which is not monotone. Indeed, $\mathcal{R}_0(T)$ increases quickly as $T \in (0, 1°\text{C})$, but declines slowly between 1°C and 2°C.



(a) Observed monthly temperature



(b) $\mathcal{R}_0$ *vs* increasing temperature

Figure 2.8: Effects of climate warming on WNv transmission

2.5 Discussion

Mathematical models can provide important insight into vector-borne disease dynamics and control in heterogeneous environments. In this chapter, we have proposed and analyzed a WNv model that incorporates the stage-structure and vertical transmission of mosquitoes, as well as seasonal fluctuation patterns, which include temperature-dependent incubation periods. Indeed, our model structure could be further adapted to other mosquito-borne diseases, like Dengue [148].

First, the mosquito reproduction number $\mathcal{R}_0^V$ is defined. Lemma 2.3.3 implies that, if we could take control measures to reduce $\mathcal{R}_0^V$ to less than 1, then both larval and adult mosquitoes go extinct. As a consequence, WNv could be eliminated. Next, we employ the theory developed in [144] to derive an infection reproduction number $\mathcal{R}_0$. To overcome the challenges brought by time-periodic delays, we choose a suitable phase space on which the linearized system for infectious compartments generates an eventually strongly monotone periodic semiflow. By the comparison arguments and persistence theory for periodic semiflows, we show that $\mathcal{R}_0$ serves as a threshold parameter for the extinction and persistence of WNv. Moreover, WNv cannot be sustained if $\mathcal{R}_0 < 1$, and if $\mathcal{R}_0 > 1$, the disease will propagate. Biologically, Theorem 2.3.2 implies that if $\mathcal{R}_0^V$ stays above 1, in other words, if the mosquito population persists, then the pest management approach should aim to decrease $\mathcal{R}_0$.

In the simulation section, we used the model to study WNv transmission in Los Angeles County, California. We first estimated the periodic parameters by formulas related to *Culex* mosquitoes life cycle and local temperatures collected in Los Angeles. Then, the simulation of the number of dead birds caused by WNv infection was performed whereby the trend was consistent with the data published by LA Public Health (see, Fig. 2.3). We also carried out sensitivity analysis of $\mathcal{R}_0$ on system parameters.

We compared the long-term behaviors of infectious mosquitoes and birds numerically, including their size and peak time predictions, under time-varying and time-averaged extrinsic incubation periods (EIPs) (see, Fig. 2.5). Numerical value of $\mathcal{R}_0$ is 1.015 under the time-varying EIP; however, there is a notable difference with the value of $\mathcal{R}_0$ under the time-averaged EIP which is 0.8. $\mathcal{R}_0$ values and the number of infectious mosquitoes and birds were greatly underestimated when using time-averaged EIP. This conclusion might not be surprising, given that *Culex* mosquitoes are very sensitive to temperature variations. However, this finding is crucial because estimating the actual size of mosquitoes can have a significant influence on designing control programs. For example, if *Wolbachia* is introduced into mosquito populations to prevent WNv spread [5, 37], the amount that should be introduced is dependent on the number of mosquitoes, and hence, the use of time-varying EIP can provide more effective information. Nevertheless, there was little difference in predicting the timings of WNv peaks between time-varying EIP and time-averaged EIP. This observation suggests that the adoption of time-average EIP can still be reasonable when the control policy aims at issuing an early warning to the public about when WNv transmission season begins and the disease peak arrives.

According to a recent study led by UCLA, the climate variations will cause the temperatures in the Los Angeles region to rise by an average of 4°F to 5°F within this century [46]. Therefore, the relationship between $\mathcal{R}_0$ and rising temperatures was simulated in Fig. 2.8(b). This clearly shows that the increase of climate warming will increase the risk of WNv transmission. We also noticed that the positive trend was non-linear and non-monotone. To interpret this finding, it is imperative to be aware that climate warming could be accompanied by other environmental changes, such as annual precipitation, wildfires, and atmospheric moisture. Meanwhile, increasing temperatures are associated with higher probability of droughts, which may facilitate WNv transmission by concentrating available water to increase the frequency of transmission events between mosquitoes and birds [48, 111]; however, as humans take actions to mitigate the rising temperature, including rearranging urban and agricultural land use [35], and exploiting storm water management ponds [130]. This has the potential to eliminate the mosquito breeding sites and reduce the exposure to mosquitoes. Consequently, the elimination of the mosquito breeding sites during this process may result in, to some extent, a decrease of the risk of WNv spread decreases.

Chapter 3

A reaction-diffusion model of vector-borne disease with periodic delays

3.1 Introduction

The global distribution and rapid transmission of vector-borne diseases have caused serious public health concern worldwide. A vector-borne disease caused by a range of pathogens is not transmitted directly from host to host, but through a living vector. Some well-known vector-borne diseases include malaria, West Nile virus (as discussed in Chapter 2), and dengue, which can be regarded as mosquito-borne diseases, and Lyme disease, a so-called tick-borne disease.

The time pathogens spent in completing their development in the vector population is known as the extrinsic incubation period (EIP). Usually, different vector-borne diseases have different EIPs. For example, EIP for dengue virus is generally referenced as being 8-12 days [19]. If an EIP lasts longer than the vector lifetime, then the vector is unlikely to contribute the disease transmission. The other concept, the intrinsic incubation period (IIP) is the time taken by the vector-borne pathogens to complete their development in the host. The extrinsic (EIP) and intrinsic (IIP) incubation periods are important determinants of vector-borne disease transmission [16,19,83,129]. It was suggested in [109] that increasing the duration of either EIP or IIP could help to reduce the disease risk of malaria transmission. Furthermore, there is considerable evidence indicating that these incubation periods are highly sensitive to seasonally varying temperature [19, 34, 83, 103]. Hence, it is more reasonable to incorporate these seasonally forced incubation periods into both host and vector populations of a vector-borne disease model.

Climate change and environmental heterogeneity exhibit complex effects on disease transmission. The study on mosquito-borne disease shows that rising temperatures may increase mosquito populations size and per host biting rate [95], which explains why transmission rate may be higher in some warm seasons than others. As the climate change becomes more variable these years [60], the seasonal variation should be given more emphasis in the study of the vector-borne disease dynamics. Another important feature of our environment is the spatial heterogeneity, which not only refers to natural landscapes (such as mountains and rivers), but also associates with human activities, for example, the urban and rural distribution in our society. In [115], the authors proved that the landscape can generate spatial heterogeneous biting patterns on mosquito-borne diseases. Hence, a mathematical modeling is needed to understand the transmission dynamics influenced by seasonal change and spatial heterogeneity. The pioneer works on vector-borne modeling were done by Ross [107] and Macdonald [89], and have been extended by quite a few researchers, see, e.g., [2, 8, 16, 23, 33, 38, 82, 109, 129] and references therein. Our purpose is to take into account the spatial heterogeneity, the seasonality, and the temperature-dependent incubation periods of the pathogens within the host and vector populations simultaneously.

In this chapter, we employ a reaction-diffusion equation framework to explicitly model the impacts of temperature-dependent delays, the seasonal fluctuations and spatial heterogeneity on vector-borne disease transmission. To our best knowledge, it is the first time to incorporate the temperature-dependent delays in both host and vector populations of a generalized vector-borne disease model. The temperature-dependent delays bring new changes into model derivation. Our theoretical result shows the model admits a basic reproduction number and it serves as a threshold parameter, which determines whether a disease can persist in a susceptible population. In particular, in the case where all coefficients are positive constants, we prove the global attractivity of the constant steady state if $\mathcal{R}_0 > 1$. Numerically, we use the model to study the malaria transmission in Maputo Province, Mozambique. Our numerical result highlights that the time averaged delay may underestimate the disease risk.

The rest of this chapter is organized as follows. In Section 3.2, we derive a nonlocal spatial model of vector-borne disease with temperature-dependent delays, and study its well-posedness. In Section 3.3, we introduce the basic reproduction number $\mathcal{R}_0$ for this spatial model and study the solution maps of an associated linear reaction-diffusion systems with periodic delays. In Section 3.4, we establish the threshold dynamics in terms of $\mathcal{R}_0$, and in the case where all the coefficients are constants, we also prove the global attractivity of the positive constant steady state when $\mathcal{R}_0 > 1$. In Section 3.5, we present some numerical simulations to study the malaria transmission in Maputo Province, Mozambique. A brief discussion concludes this chapter.

3.2 The model

In this section, we first formulate a mathematical model with periodic delays, and then discuss its well-posedness.

3.2.1 Derivation of the model

Since the vector-borne disease is transmitted among hosts by vectors, we consider the dynamics of both host and vector populations in a bounded domain Ω with smooth boundary $\partial\Omega$. The host population is divided into susceptible, exposed, infectious and recovered compartments, and their spatial densities at time t and location x are denoted by $S_h(t,x)$, $E_h(t,x)$, $I_h(t,x)$ and $R_h(t,x)$, respectively. The vector population consists of susceptible, exposed and infectious compartments with spatial densities $S_v(t,x)$, $E_v(t,x)$ and $I_v(t,x)$, respectively. Thus, the total densities of host and vector populations are given by $N_h(t,x) = S_h(t,x) + E_h(t,x) + I_h(t,x) + R_h(t,x)$ and $N_v(t,x) = S_v(t,x) + E_v(t,x) + I_v(t,x)$. For simplicity, we assume that $N_i(t,x) \equiv \bar{N}_i(t,x)$ for some positive ω-periodic function $\bar{N}_i(t,x)$, $i \in \{h, v\}$, which may describe the situation where the total densities of host and vector populations stabilize at a positive periodic state. Let $M_h(t,x)$ and $M_v(t,x)$ be the densities of newly occurred infectious hosts and vectors, which have yet to be determined, respectively.

For model parameters, we let Λ_h and Λ_v be recruitment rates of host and vector populations, respectively. Let μ_h and α_h denote the nature death and recovery rates of host population, respectively. μ_v describes the nature death rate of the vectors. Let b be the biting rate on hosts, then $b/\bar{N}_h$ is per host biting rate. Let $\tilde{\beta}_h$ represent the disease transmission probability from infectious vectors to susceptible hosts per bite, and $\tilde{\beta}_v$ represent the transmission probability from infectious hosts to susceptible vectors per bite. Thus, $b/\bar{N}_h \cdot \tilde{\beta}_h$ and $b/\bar{N}_h \cdot \tilde{\beta}_v$ reflect the transmission probability of the disease in hosts and vectors, respectively. For notational simplicity, we let $\beta_h = \dfrac{b}{\bar{N}_h}\tilde{\beta}_h$ and $\beta_v = \dfrac{b}{\bar{N}_h}\tilde{\beta}_v$.

In order to incorporate the multiple factors of seasonal variation, environmental heterogeneity, and random diffusion in the spatial domain Ω, we assume that the coefficients $\Lambda_h(t,x)$, $\Lambda_v(t,x)$, $\mu_h(t,x)$, $\mu_v(t,x)$, $\alpha_h(t,x)$, $\beta_h(t,x)$ and $\beta_v(t,x)$ are all ω-periodic in time t for some $\omega > 0$. Furthermore, both host and vector populations are assumed to perform an unbiased random walk. Two populations remain confined to the domain Ω for all time and under no flux boundary condition. In particular, we pay our attention to the case where the disease does not have a manifest impact on the hosts and vectors' mobility. Mathematically, we then assume that S_h, E_h, I_h and R_h have the same diffusion coefficient D_h, while S_v, E_v and I_v have the same diffusion coefficient D_v. We summarize the biological meanings of parameters in Table 3.1.

We use Fig. 3.1 to illustrate the transitions of hosts and vectors between different

Table 3.1: Biological interpretations for parameters in system (3.2.6)

Parameter	Description
$\Lambda_h(t,x)$	Host recruitment rate at time t and location x
$\mu_h(t,x)$	Host death rate at time t and location x
$\alpha_h(t,x)$	Host recovery rate at time t and location x
$\Lambda_v(t,x)$	Vector recruitment rate at time t and location x
$\mu_v(t,x)$	Vector death rate at time t and location x
$\beta_h(t,x)$	Transmission probability from infectious vectors to hosts
$\beta_v(t,x)$	Transmission probability from infectious hosts to vectors
$\tau_h(t)$	The intrinsic incubation period (IIP) in hosts at time t
$\tau_v(t)$	The extrinsic incubation period (EIP) in vectors at time t
$\hat{\tau}$	The maximum of $\tau_h(t)$ and $\tau_v(t)$, that is, $\max_{t\in[0,\omega]}\{\tau_h(t),\tau_v(t)\}$
D_h	Host diffusion rate
D_v	Vector diffusion rate

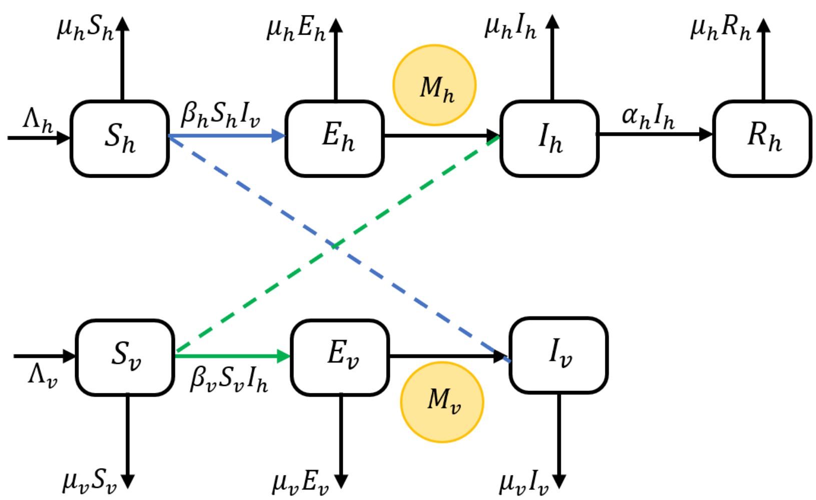


Figure 3.1: Schematic diagram for the disease transmission

compartments and their mortalities (solid arrows), the transmission of the disease from infectious vectors I_v to susceptible hosts S_h (blue dash line), and the transmission of disease from infectious hosts I_h to susceptible vectors S_v (green dash line). Accordingly, our model is governed by the following reaction-diffusion system:

$$
\begin{aligned}
&\frac{\partial S_h}{\partial t} = D_h \triangle S_h + \Lambda_h(t,x) - \beta_h(t,x) S_h I_v - \mu_h(t,x) S_h,\\
&\frac{\partial E_h}{\partial t} = D_h \triangle E_h + \beta_h(t,x) S_h I_v - M_h(t,x) - \mu_h(t,x) E_h,\\
&\frac{\partial I_h}{\partial t} = D_h \triangle I_h + M_h(t,x) - (\mu_h(t,x) + \alpha_h(t,x)) I_h,\\
&\frac{\partial R_h}{\partial t} = D_h \triangle R_h + \alpha_h(t,x) I_h - \mu_h(t,x) R_h,\\
&\frac{\partial S_v}{\partial t} = D_v \triangle S_v + \Lambda_v(t,x) - \beta_v(t,x) S_v I_h - \mu_v(t,x) S_v,\\
&\frac{\partial E_v}{\partial t} = D_v \triangle E_v + \beta_v(t,x) S_v I_h - M_v(t,x) - \mu_v(t,x) E_v,\\
&\frac{\partial I_v}{\partial t} = D_v \triangle I_v + M_v(t,x) - \mu_v(t,x) I_v,\\
&\frac{\partial S_h}{\partial \nu} = \frac{\partial E_h}{\partial \nu} = \frac{\partial I_h}{\partial \nu} = \frac{\partial R_h}{\partial \nu} = \frac{\partial S_v}{\partial \nu} = \frac{\partial E_v}{\partial \nu} = \frac{\partial I_v}{\partial \nu} = 0, \quad x \in \partial\Omega.
\end{aligned}
\tag{3.2.1}
$$

Next we introduce the temperature-dependent incubation periods, which is motivated by the arguments in [100,102,129]. We start with the derivation of the expression for $M_h(t,x)$. We assume the temperature $T = T(t)$. Let q be the development level of infection such that q increases at a temperature-dependent rate $\gamma_h(T(t)) = \gamma_h(t)$, $q = q_{E_h} = 0$ at the transition from S_h to E_h, and $q = q_{I_h}$ at the transition from E_h to I_h. Let $\rho(q,t,x)$ be the density of hosts with development level q at time t and location x. Then $M_h(t,x) = \gamma_h(t)\rho(q_I,t,x)$.

Let $J(q,t,x)$ be the flux, in the direction of increasing q, of hosts with infection development level q at time t and location x. Then we can obtain the following

$$\frac{\partial \rho(q,t,x)}{\partial t} = D_h \triangle \rho - \frac{\partial J}{\partial q} - \mu_h(t,x)\rho.$$

Since $J(q,t,x) = \gamma_h(t)\rho(q,t,x)$, we have

$$\frac{\partial \rho(q,t,x)}{\partial t} = D_h \triangle \rho - \frac{\partial [\gamma_h(t)\rho]}{\partial q} - \mu_h(t,x)\rho. \tag{3.2.2}$$

The boundary condition of system (3.2.2) is given by

$$\rho(0,t,x) = \frac{\beta_h(t,x) S_h(t,x) I_v(t,x)}{\gamma_h(t)}.$$

To solve system (3.2.2) with the above boundary condition, we introduce a new variable

$$\eta = h(t) := q_{E_h} + \int_0^t \gamma_h(s)\mathrm{d}s.$$

Let $h^{-1}(\eta)$ be the inverse function of $h(t)$, and define

$$\hat{\rho}(q,\eta,x) = \rho(q,h^{-1}(\eta),x),\ \ \hat{\mu}_h(\eta,x) = \mu_h(h^{-1}(\eta),x),\ \ \hat{\gamma}_h(\eta) = \gamma_h(h^{-1}(\eta)).$$

In view of (3.2.2), we get

$$\frac{\partial\hat{\rho}(q,\eta,x)}{\partial\eta} = \frac{D_h}{\hat{\gamma}_h(\eta)}\triangle\hat{\rho} - \frac{\partial\hat{\rho}}{\partial q} - \frac{\hat{\mu}_h(\eta,x)}{\hat{\gamma}_h(\eta)}\hat{\rho}.$$

Let $V(s,x) = \hat{\rho}(s+q-\eta,s,x)$, and then

$$\frac{\partial V(s,x)}{\partial s} = \frac{D_h}{\hat{\gamma}_h(s)}\triangle V(s,x) - \frac{\hat{\mu}_h(s,x)}{\hat{\gamma}_h(s)}V(s,x).$$

Since $\eta - (q - q_{E_h}) \le \eta$, we have

$$V(\eta,x) = \int_\Omega \Gamma_h(h^{-1}(\eta),h^{-1}(\eta-q+q_{E_h}),x,y)V(\eta-q+q_{E_h},y)\mathrm{d}y,$$

where $\Gamma_h(t,t_0,x,y)$ is the Green function associated with $\frac{\partial V}{\partial t} = D_h\triangle V - \mu_h(t,\cdot)V$ subject to the Neumann boundary condition. It then follows that

$$\hat{\rho}(q,\eta,x) = \int_\Omega \Gamma_h(h^{-1}(\eta),h^{-1}(\eta-q+q_{E_h}),x,y)\hat{\rho}(q_{E_h},\eta-q+q_{E_h},y)\mathrm{d}y.$$

Let $\tau(q,t)$ be the time taken by a host who arrives at infection development level q at time t from infection development level q_{E_h}. Since $\dfrac{\mathrm{d}q}{\mathrm{d}t} = \gamma_h(t)$, it follows that

$$q - q_{E_h} = \int_t^{t-\tau(q,t)} \gamma_h(s)\mathrm{d}s, \tag{3.2.3}$$

and hence,

$$h(t-\tau(q,t)) = q_{E_h} + \int_0^{t-\tau(q,t)} \gamma_h(s)\mathrm{d}s = h(t) - (q - q_{E_h}).$$

It follows that

$$\begin{aligned}\rho(q,t,x) &= \hat{\rho}(q,h(t),x)\\ &= \int_\Omega \Gamma_h(t,t-\tau(q,t),x,y)\rho(0,t-\tau(q,t),y)\mathrm{d}y\\ &= \int_\Omega \Gamma_h(t,t-\tau(q,t),x,y)\frac{\beta_h(t-\tau(q,t),y)S_h(t-\tau(q,t),y)I_v(t-\tau(q,t),y)}{\gamma_h(t-\tau(q,t))}\mathrm{d}y.\end{aligned}$$

Define $\tau_h(t)=\tau(q_{I_h},t)$. Then we have

$$\begin{aligned}\gamma_h(t)\rho(q_{I_h},t,x) &= \frac{\gamma_h(t)}{\gamma_h(t-\tau(q_{I_h},t))}\int_\Omega \Gamma_h(t,t-\tau(q_{I_h},t),x,y)\cdot\\ &\quad \beta_h(t-\tau(q_{I_h},t),y)S_h(t-\tau(q_{I_h},t),y)I_v(t-\tau(q_{I_h},t),y)\mathrm{d}y,\\ &= \frac{\gamma_h(t)}{\gamma_h(t-\tau_h(t))}\int_\Omega \Gamma_h(t,t-\tau_h(t),x,y)\cdot\\ &\quad \beta_h(t-\tau_h(t),y)S_h(t-\tau_h(t),y)I_v(t-\tau_h(t),y)\mathrm{d}y.\end{aligned}$$

Letting $q=q_{I_h}$ in (3.2.3), we obtain

$$q_{I_h}-q_{E_h}=\int_{t-\tau_h(t)}^{t}\gamma_h(s)\mathrm{d}s. \tag{3.2.4}$$

Taking the derivative with respective to t on both sides of the above equality yields

$$1-\tau_h'(t)=\frac{\gamma_h(t)}{\gamma_h(t-\tau_h(t))},$$

and hence, $1-\tau_h'(t)>0$. It then follows that

$$\begin{aligned}&M_h(t,x)=\gamma_h(t)\rho(q_{I_h},t,x)\\ &=(1-\tau_h'(t))\int_\Omega \Gamma_h(t,t-\tau_h(t),x,y)\beta_h(t-\tau_h(t),y)S_h(t-\tau_h(t),y)I_v(t-\tau_h(t),y)\mathrm{d}y.\end{aligned}$$

In a similar way, we can obtain $M_v(t,x)=$

$$(1-\tau_v'(t))\int_\Omega \Gamma_v(t,t-\tau_v(t),x,y)\beta_v(t-\tau_v(t),y)S_v(t-\tau_v(t),y)I_h(t-\tau_v(t),y)\mathrm{d}y,$$

where $\Gamma_v(t,t_0,x,y)$ is the Green function associated with $\dfrac{\partial u}{\partial t}=D_v\triangle u-\mu_v(t,\cdot)u$ subject to the Neumann boundary condition.

Substituting $M_h(t,x)$ and $M_v(t,x)$ into system (3.2.1), we have the following system:

$$
\begin{aligned}
\frac{\partial S_h}{\partial t} &= D_h \triangle S_h + \Lambda_h(t,x) - \beta_h(t,x) S_h I_v - \mu_h(t,x) S_h,\\
\frac{\partial E_h}{\partial t} &= D_h \triangle E_h + \beta_h(t,x) S_h I_v - \mu_h(t,x) E_h - (1-\tau_h'(t)) \cdot\\
&\qquad \int_\Omega \Gamma_h(t,t-\tau_h(t),x,y)\beta_h(t-\tau_h(t),y) S_h(t-\tau_h(t),y) I_v(t-\tau_h(t),y)\mathrm{d}y,\\
\frac{\partial I_h}{\partial t} &= D_h \triangle I_h - (\mu_h(t,x)+\alpha_h(t,x)) I_h + (1-\tau_h'(t)) \cdot\\
&\qquad \int_\Omega \Gamma_h(t,t-\tau_h(t),x,y)\beta_h(t-\tau_h(t),y) S_h(t-\tau_h(t),y) I_v(t-\tau_h(t),y)\mathrm{d}y,\\
\frac{\partial R_h}{\partial t} &= D_h \triangle R_h + \alpha_h(t,x) I_h - \mu_h(t,x) R_h, \qquad (3.2.5)\\
\frac{\partial S_v}{\partial t} &= D_v \triangle S_v + \Lambda_v(t,x) - \beta_v(t,x) S_v I_h - \mu_v(t,x) S_v,\\
\frac{\partial E_v}{\partial t} &= D_v \triangle E_v + \beta_v(t,x) S_v I_h - \mu_v(t,x) E_v - (1-\tau_v'(t)) \cdot\\
&\qquad \int_\Omega \Gamma_v(t,t-\tau_v(t),x,y)\beta_v(t-\tau_v(t),y) S_v(t-\tau_v(t),y) I_h(t-\tau_v(t),y)\mathrm{d}y\\
\frac{\partial I_v}{\partial t} &= D_v \triangle I_v - \mu_v(t,x) I_v + (1-\tau_v'(t)) \cdot\\
&\qquad \int_\Omega \Gamma_v(t,t-\tau_v(t),x,y)\beta_v(t-\tau_v(t),y) S_v(t-\tau_v(t),y) I_h(t-\tau_v(t),y)\mathrm{d}y\\
\frac{\partial S_h}{\partial \nu} &= \frac{\partial E_h}{\partial \nu} = \frac{\partial I_h}{\partial \nu} = \frac{\partial R_h}{\partial \nu} = \frac{\partial S_v}{\partial \nu} = \frac{\partial E_v}{\partial \nu} = \frac{\partial I_v}{\partial \nu} = 0, x \in \partial\Omega.
\end{aligned}
$$

Since $E_h(t,x)$, $R_h(t,x)$ and $E_v(t,x)$ of system (3.2.5) are decoupled from the other equations, it suffices to study the following system:

$$
\begin{aligned}
\frac{\partial u_1}{\partial t} &= D_h \triangle u_1 + \Lambda_h(t,x) - \beta_h(t,x)u_1u_4 - \mu_h(t,x)u_1, \\
\frac{\partial u_2}{\partial t} &= D_h \triangle u_2 - (\mu_h(t,x) + \alpha_h(t,x))u_2 + (1 - \tau_h'(t)) \cdot \\
&\qquad \int_\Omega \Gamma_h(t, t-\tau_h(t), x, y)\beta_h(t-\tau_h(t), y)u_1(t-\tau_h(t), y)u_4(t-\tau_h(t), y)\mathrm{d}y \\
\frac{\partial u_3}{\partial t} &= D_v \triangle u_3 + \Lambda_v(t,x) - \beta_v(t,x)u_3u_2 - \mu_v(t,x)u_3, \qquad (3.2.6)\\
\frac{\partial u_4}{\partial t} &= D_v \triangle u_4 - \mu_v(t,x)u_4 + (1 - \tau_v'(t)) \cdot \\
&\qquad \int_\Omega \Gamma_v(t, t-\tau_v(t), x, y)\beta_v(t-\tau_v(t), y)u_3(t-\tau_v(t), y)u_2(t-\tau_v(t), y)\mathrm{d}y \\
\frac{\partial u_1}{\partial \nu} &= \frac{\partial u_2}{\partial \nu} = \frac{\partial u_3}{\partial \nu} = \frac{\partial u_4}{\partial \nu} = 0, \quad x \in \partial\Omega,
\end{aligned}
$$

where $(u_1(t,x), u_2(t,x), u_3(t,x), u_4(t,x)) = (S_h(t,x), I_h(t,x), S_v(t,x), I_v(t,x))$. We assume that D_h and D_v in system (3.2.6) are positive constants, functions $\Lambda_h(t,x)$, $\Lambda_v(t,x)$, $\beta_h(t,x)$ and $\beta_v(t,x)$ are Hölder continuous and nonnegative nontrivial on $\mathbb{R} \times \bar{\Omega}$, and ω-periodic in t for some $\omega > 0$, functions $\mu_h(t,x)$, $\mu_v(t,x)$ and $\alpha_h(t,x)$ are Hölder continuous and positive on $\mathbb{R} \times \bar{\Omega}$, and ω-periodic in t. We also assume that the temperature $T(t)$ is ω-periodic, and hence so is $\gamma_h(t)$. In view of (3.2.4), it easily follows that $\tau_h(t)$ and $\tau_v(t)$ are ω-periodic.

3.2.2 The well-posedness

Let $\mathbb{X} := C(\bar{\Omega}, \mathbb{R}^4)$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. Let $\hat{\tau} = \max\limits_{t\in[0,\omega]} \{\tau_h(t), \tau_v(t)\}$. Define $\mathcal{X} := C([-\hat{\tau}, 0], \mathbb{X})$ with the norm $\|\phi\| = \max\limits_{\theta\in[-\hat{\tau},0]} \|\phi(\theta)\|_{\mathbb{X}}$, $\forall \phi \in \mathcal{X}$. Then $\mathcal{X}$ is a Banach space. Define $\mathbb{X}^+ := C(\bar{\Omega}, \mathbb{R}^4_+)$ and $\mathcal{X}^+ := C([-\hat{\tau}, 0], \mathbb{X}^+)$, then both $(\mathbb{X}, \mathbb{X}^+)$ and $(\mathcal{X}, \mathcal{X}^+)$ are ordered spaces. Given a function $z : [-\hat{\tau}, \sigma) \longrightarrow \mathbb{X}$ for $\sigma > 0$, we define $z_t \in \mathcal{X}$ by

$$
z_t(\theta) = (z_1(t+\theta), z_2(t+\theta), z_3(t+\theta), z_4(t+\theta)), \ \forall \theta \in [-\hat{\tau}, 0],
$$

for any $t \in [0, \sigma)$.

Let $\mathbb{Y} := C(\bar{\Omega}, \mathbb{R})$ and $\mathbb{Y}^+ := C(\bar{\Omega}, \mathbb{R}_+)$. Let $T_1(t,s),\ T_2(t,s),\ T_3(t,s) : \mathbb{Y} \longrightarrow \mathbb{Y}$ are the evolution operators associated $\frac{\partial u_1}{\partial t} = D_h \triangle u_1 - \mu_h(t,x)u_1 := A_1(t)u_1$, $\frac{\partial u_2}{\partial t} = D_h \triangle u_2 - (\mu_h(t,x) + \alpha_h(t,x))u_2 := A_2(t)u_2$, and $\frac{\partial u_3}{\partial t} = D_v \triangle u_3 - \mu_v(t,x)u_3 := A_3(t)u_3$, subject to the Neumann boundary condition, respectively. Since $\mu_h(t,\cdot)$ is ω-periodic in t, [26, Lemma 6.1] implies that $T_1(t+\omega, s+\omega) = T_1(t,s)$ for $(t,s) \in \mathbb{R}^2$ with $t \geq s$. Similar results hold for $T_2(t,s)$ and $T_3(t,s)$. Moreover, for $(t,s) \in \mathbb{R}^2$

with $t > s$, $T_i(t,s)$, $i = 1,2,3$ are compact and strongly positive. Let $T(t,s) = \operatorname{diag}\{T_1(t,s), T_2(t,s), T_3(t,s), T_3(t,s)\} : \mathbb{X} \to \mathbb{X}$, $A(t) = \operatorname{diag}\{A_1(t), A_2(t), A_3(t), A_3(t)\}$, and define $F = (F_1, F_2, F_3, F_4) : [0, +\infty) \times \mathcal{X} \longrightarrow \mathbb{X}$ by

$$
\begin{aligned}
&F_1(t,\phi) := \Lambda_h(t,\cdot) - \beta_h(t,\cdot)\phi_1(0,\cdot)\phi_4(0,\cdot),\\
&F_2(t,\phi) := (1-\tau_h'(t)) \int_\Omega \Gamma_h(t, t-\tau_h(t), \cdot, y)\beta_h(t-\tau_h(t), y)\phi_1(-\tau_h(t), y)\phi_4(-\tau_h(t), y)\mathrm{d}y,\\
&F_3(t,\phi) := \Lambda_v(t,\cdot) - \beta_v(t,\cdot)\phi_3(0,\cdot)\phi_2(0,\cdot),\\
&F_4(t,\phi) := (1-\tau_v'(t)) \int_\Omega \Gamma_v(t, t-\tau_v(t), \cdot, y)\beta_v(t-\tau_v(t), y)\phi_3(-\tau_v(t), y)\phi_2(-\tau_v(t), y)\mathrm{d}y,
\end{aligned}
$$

for $t \geq 0$, $x \in \bar{\Omega}$ and $\phi = (\phi_1, \phi_2, \phi_3, \phi_4) \in \mathcal{X}$. Then system (3.2.6) can be written as

$$
\begin{aligned}
&\frac{\mathrm{d}u}{\mathrm{d}t} = A(t)u + F(t, u_t), \ t > 0, \\
&u_0 = \phi.
\end{aligned}
\tag{3.2.7}
$$

By [92, Corollary 4 and Theorem 1], we can show that for any $\phi \in \mathcal{X}^+$, system (3.2.6) has a unique solution, denoted by $z(t,\cdot,\phi)$ on its maximal existence interval $[0, \bar{t}_\phi)$ with $z_0 = \phi$, where $\bar{t}_\phi \leq +\infty$. Before proving the global existence, we return to system (3.2.5) for more observations. In view of biological meaning of $\tau_h(t)$ and $\tau_v(t)$, we impose the following compatibility condition:

$$
E_h(0,\cdot) = \int_{-\tau_h(0)}^{0} T_1(0,s)\beta_h(s,\cdot)S_h(s,\cdot)I_v(s,\cdot)\mathrm{d}s, \tag{3.2.8}
$$

and

$$
E_v(0,\cdot) = \int_{-\tau_v(0)}^{0} T_3(0,s)\beta_v(s,\cdot)S_v(s,\cdot)I_h(s,\cdot)\mathrm{d}s. \tag{3.2.9}
$$

Now we introduce

$$
\begin{aligned}
\mathcal{D} := \Big\{\psi \in C\Big([-\hat{\tau}, 0], C(\overline{\Omega}, \mathbb{R}^7_+)\Big) : \quad &\psi_2(0,\cdot) = \textstyle\int_{-\tau_h(0)}^{0} T_1(0,s)\beta_h(s,\cdot)\psi_1(s,\cdot)\psi_7(s,\cdot)\mathrm{d}s,\\
&\psi_6(0,\cdot) = \textstyle\int_{-\tau_v(0)}^{0} T_3(0,s)\beta_v(s,\cdot)\psi_3(s,\cdot)\psi_5(s,\cdot)\mathrm{d}s\Big\}.
\end{aligned}
$$

It then follows that for any $\psi \in \mathcal{D}$, system (3.2.5) has a unique solution $U(t,\cdot,\psi) = (S_h(t,\cdot), E_h(t,\cdot), I_h(t,\cdot), R_h(t,\cdot), S_v(t,\cdot), E_v(t,\cdot), I_v(t,\cdot))$ satisfying $U_0 = \psi$. By [92, Corollary 4], we have $S_h(t,\cdot) \geq 0$, $I_h(t,\cdot) \geq 0$, $S_v(t,\cdot) \geq 0$, $I_v(t,\cdot) \geq 0$ and $R_h(t,\cdot) \geq 0$ on the maximal interval of existence. By the uniqueness of solutions of system (3.2.5) and the compatibility conditions (3.2.8) and (3.2.9), it follows that

$$
E_h(t,\cdot) = \int_{t-\tau_h(t)}^{t} T_1(t,s)\beta_h(s,\cdot)S_h(s,\cdot)I_v(s,\cdot)\mathrm{d}s, \tag{3.2.10}
$$

and

$$E_v(t,\cdot)=\int_{t-\tau_v(t)}^{t} T_3(t,s)\beta_v(s,\cdot)S_v(s,\cdot)I_h(s,\cdot)\mathrm{d}s, \tag{3.2.11}$$

and hence, $E_h(t,\cdot)\geq 0$ and $E_v(t,\cdot)\geq 0$ on the maximal interval of existence.

Since $N_h(t,\cdot)=S_h(t,\cdot)+E_h(t,\cdot)+I_h(t,\cdot)+R_h(t,\cdot)$, and $N_v(t,\cdot)=S_v(t,\cdot)+E_v(t,\cdot)+I_v(t,\cdot)$, then we obtain

$$\frac{\partial N_h}{\partial t}=D_h\triangle N_h+\Lambda_h(t,x)-\mu_h(t,x)N_h\leq D_h\triangle N_h+\hat{\Lambda}_h-\bar{\mu}_hN_h,$$

where $\hat{\Lambda}_h=\max_{t\in[0,\omega],x\in\bar{\Omega}}\Lambda_h(t,x)$, $\bar{\mu}_h=\min_{t\in[0,\omega],x\in\bar{\Omega}}\mu_h(t,x)$. Similarly for N_v, we also have $\frac{\partial N_v}{\partial t}\leq D_v\triangle N_v+\hat{\Lambda}_v-\bar{\mu}_vN_v$, where $\hat{\Lambda}_v=\max_{t\in[0,\omega],x\in\bar{\Omega}}\Lambda_v(t,x)$, $\bar{\mu}_v=\min_{t\in[0,\omega],x\in\bar{\Omega}}\mu_v(t,x)$. Thus, the comparison argument implies that the solutions of system (3.2.5) with initial data in $\mathcal{D}$, and hence those of system (3.2.6) in $\mathcal{X}^+$, exist globally on $[0,+\infty)$ and are ultimately bounded. By the arguments similar to those in [59, Lemma 2.6] and [142, Lemma 2.1], together with Theorem 1.1.1, we have the following result.

Lemma 3.2.1. *For any $\phi\in\mathcal{X}^+$, system (3.2.6) has a unique solution $u(t,\cdot,\phi)$ on $[0,+\infty)$ with $u_0=\phi$. Moreover, system (3.2.6) generates an ω-periodic semiflow $\tilde{Q}(t):=u_t(\cdot):\mathcal{X}^+\to\mathcal{X}^+$, $\forall t\geq 0$, and $\tilde{Q}(\omega)$ has a strong global attractor in $\mathcal{X}^+$.*

3.3 The basic reproduction number

In this section, we use the theory recently developed in [79, 144] (please see also Remark 1.4.2) to derive the basic reproduction number $\mathcal{R}_0$ for system (3.2.6).

Let $\mathbb{E}:=C(\bar{\Omega},\mathbb{R}^2)$, $\mathbb{E}^+:=C(\bar{\Omega},\mathbb{R}^2_+)$, and $C_\omega(\mathbb{R},\mathbb{E})$ be the Banach space consisting of all ω-periodic and continuous functions from $\mathbb{R}$ to $\mathbb{E}$, where $\|\psi\|_{C_\omega(\mathbb{R},\mathbb{E})}:=\max\limits_{\theta\in[0,\omega]}\|\psi(\theta)\|_{\mathbb{E}}$ for any $\psi\in C_\omega(\mathbb{R},\mathbb{E})$. Setting $u_2=u_4=0$, we obtain the equations for the density of susceptible species

$$\begin{aligned}\frac{\partial u_1}{\partial t}&=D_h\triangle u_1+\Lambda_h(t,x)-\mu_h(t,x)u_1,\\ \frac{\partial u_3}{\partial t}&=D_v\triangle u_3+\Lambda_v(t,x)-\mu_v(t,x)u_3,\end{aligned} \tag{3.3.1}$$

subject to Neumann boundary condition. It is easy to see that system (3.3.1) admits a globally attractive positive ω-periodic solution $(u_1^*(t,\cdot),u_3^*(t,\cdot))$ (see, e.g., [142, Lemma 2.1]). Linearizing system (3.2.6) at $(u_1^*,0,u_3^*,0)$ and considering the equations for infectious compartments, we obtain

$$\begin{aligned}
\frac{\partial v_1}{\partial t} &= D_h \triangle v_1 - (\mu_h(t,x) + \alpha_h(t,x))v_1 + (1-\tau_h'(t)) \cdot \\
&\quad \int_\Omega \Gamma_h(t, t-\tau_h(t), x, y)\beta_h(t-\tau_h(t), y)u_1^*(t-\tau_h(t), y)v_2(t-\tau_h(t), y)\mathrm{d}y \\
\frac{\partial v_2}{\partial t} &= D_v \triangle v_2 - \mu_v(t,x)v_2 + (1-\tau_v'(t)) \cdot \\
&\quad \int_\Omega \Gamma_v(t, t-\tau_v(t), x, y)\beta_v(t-\tau_v(t), y)u_3^*(t-\tau_v(t), y)v_1(t-\tau_v(t), y)\mathrm{d}y \\
\frac{\partial v_1}{\partial \nu} &= \frac{\partial v_2}{\partial \nu} = 0, \ x \in \partial\Omega,
\end{aligned} \tag{3.3.2}$$

where $(v_1(t,x), v_2(t,x)) = (u_2(t,x), u_4(t,x))$.

Let $E := C([-\hat{\tau}, 0], \mathbb{E})$ and $E^+ := C([-\hat{\tau}, 0], \mathbb{E}^+)$. Define $F(t) : E \longrightarrow \mathbb{E}$ by

$$F(t)\begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} (1-\tau_h'(t)) \int_\Omega \Gamma_h(t, t-\tau_h(t), \cdot, y) \\ \times\beta_h(t-\tau_h(t), y)\phi_1(-\tau_h(t), y)\phi_4(-\tau_h(t), y)\mathrm{d}y \\ (1-\tau_v'(t)) \int_\Omega \Gamma_v(t, t-\tau_v(t), \cdot, y) \\ \times\beta_h(t-\tau_v(t), y)\phi_3(-\tau_v(t), y)\phi_2(-\tau_v(t), y)\mathrm{d}y \end{pmatrix}$$

for any $t \in \mathbb{R}$, $(\phi_1, \phi_2) \in E$ and $-V(t)v = D\triangle v - W(t)v$, where $D = \mathrm{diag}(D_h, D_v)$ and

$$-[W(t)](x) = \begin{pmatrix} -(\mu_h(t,x) + \alpha_h(t,x)) & 0 \\ 0 & -\mu_v(t,x) \end{pmatrix}, \ x \in \bar{\Omega}.$$

Let $\Phi(t,s) = \mathrm{diag}(T_2(t,s), T_3(t,s)), \ t \geq s$, be the evolution operators, associated with the following system

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -V(t)v,$$

where $T_2(t,s)$ and $T_3(t,s)$ are defined in Section 2. Note that $\Phi(t,s)$ is a positive operator in the sense that $\Phi(t,s)\mathbb{E}^+ \subset \mathbb{E}^+$ for all $t \geq s$. Then [119, Theorem 3.12] implies that $-V(t)$ is resolvent positive. Therefore, $F(t)$ and $W(t)$ satisfy the following assumptions:

(H1) $F(t) : E \to \mathbb{E}$ is positive in the sense that $F(t)E^+ \subset \mathbb{E}^+$.

(H2) $-V(t)$ is resolvent positive.

Thus, we can follow Remark 1.4.2 (please also see [79] for more information) to introduce $\mathcal{R}_0$ for system (3.2.6). Assume that $v \in C_\omega(\mathbb{R}, \mathbb{E})$ and $v(t)$ is the initial distribution of infectious hosts and vectors at time $t \in \mathbb{R}$. For any given $s \geq 0$, $F(t-s)v_{t-s}$ represents the density distribution of newly infected hosts and vectors at time $t-s$, which is produced by the infectious hosts and vectors who were introduced over the time interval $[t-s-\hat{\tau}, t-s]$. Then $\Phi(t,t-s)F(t-s)v_{t-s}$ is the distribution of those infected hosts and vectors who were newly infected at time $t-s$ and still survive in the environment at time t for $t \geq s$. Hence, the integral

$$\int_0^{+\infty} \Phi(t,t-s)F(t-s)v_{t-s}\mathrm{d}s = \int_0^{+\infty} \Phi(t,t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s$$

is the distribution of accumulative infective hosts and vectors at time t produced by all those infectious hosts and vectors introduced at all previous time to t. Note that for any given $s \geq 0$, $\Phi(t,t-s)v(t,t-s)$ is the distribution of those infectious individuals at time $t-s$ and remain in the infected compartments at time t, and hence $\int_0^{+\infty} \Phi(t,t-s)v(t-s)\mathrm{d}s$ is the distribution of accumulative infectious individuals who were introduced at all previous times to t and remain in the infected compartments at time t. Thus, the distribution of newly infected individuals at time t is $F(t)\int_0^{+\infty} \Phi(t+\cdot, t-s+\cdot)v(t-s+\cdot)\mathrm{d}s$.

Define two linear operators on $C_\omega(\mathbb{R},\mathbb{E})$ by

$$[Lv](t) := \int_0^{+\infty} \Phi(t,t-s)F(t-s)v(t-s+\cdot)\mathrm{d}s,\ \forall t \in \mathbb{R},\ v \in C_\omega(\mathbb{R},\mathbb{E}),$$

and

$$[\mathcal{L}v](t) := F(t)\int_0^{+\infty} \Phi(t+\cdot,t-s+\cdot)v(t-s+\cdot)\mathrm{d}s,\ \forall t \in \mathbb{R},\ v \in C_\omega(\mathbb{R},\mathbb{E}).$$

Let A and B be two bounded linear operators on $C_\omega(\mathbb{R},\mathbb{E})$ defined by

$$[Av](t) = \int_0^{+\infty} \Phi(t,t-s)v(t-s)\mathrm{d}s,\ [Bv](t) = F(t)v_t,\ \forall t \in \mathbb{R},\ v \in C_\omega(\mathbb{R},\mathbb{E}).$$

It then follows that $L = A \circ B$ and $\mathcal{L} = B \circ A$, and hence L and $\mathcal{L}$ has same spectral radius. Motivated by the concept of next generation operators in [11, 119, 144], we define the spectral radius of L and $\mathcal{L}$ as the basic reproduction number for system (3.2.6), that is,

$$\mathcal{R}_0 := r(L) = r(\mathcal{L}).$$

For any given $t \geq 0$, let $\tilde{P}(t)$ be the solution map of system (3.3.2) on E given by $\tilde{P}(t)\phi = v_t(\phi)$, where $v_t(\phi)(\theta) = v(t+\theta,\phi) = (v_1(t+\theta,\phi), v_2(t+\theta,\phi))$, $\forall \theta \in [-\hat{\tau}, 0]$, and $v(t,\phi)$ is the unique solution of system (3.3.2) with $v(\theta) = \phi(\theta)$ for all $\theta \in [-\hat{\tau}, 0]$. Then $\tilde{P}(\omega)$ is the Poicaré map associated with system (3.3.2). Let $r(\tilde{P}(\omega))$ be the spectral radius of $\tilde{P}(\omega)$. By Theorem 1.4.1 and Remark 1.4.2 (see also [79, Theorem 3.7]), we have the following observation.

Lemma 3.3.1. $\mathcal{R}_0 - 1$ *has the same sign as* $r(\tilde{P}(\omega)) - 1$.

To study the global dynamics of system (3.2.6) in terms of $\mathcal{R}_0$, we show that system (3.3.2) generates an eventually strongly monotone periodic semiflow on the following phase space:

$$\mathcal{E} := C([-\tau_v(0), 0], \mathbb{Y}) \times C([-\tau_h(0), 0], \mathbb{Y}).$$

Let $\mathcal{E}^+ := C([-\tau_v(0), 0], \mathbb{Y}^+) \times C([-\tau_h(0), 0], \mathbb{Y}^+)$. Then $(\mathcal{E}, \mathcal{E}^+)$ is an ordered Banach space. Given a function $w : [-\tau_v(0), +\infty) \times [-\tau_h(0), +\infty) \to \mathbb{E}$, we define $w_t \in \mathcal{E}$ by

$$w_t(\theta) = (w_1(t + \theta_1), w_2(t + \theta_2)),\ \forall \theta := (\theta_1, \theta_2) \in [-\tau_v(0), 0] \times [-\tau_h(0), 0],\ \forall t \geq 0.$$

Lemma 3.3.2. *For any $\varphi \in \mathcal{E}^+$, system (3.3.2) admits a unique nonnegative solution $w(t, \cdot, \varphi)$ on $[0, +\infty)$ with $w_0 = \varphi$.*

Proof. Let $\bar{\tau} = \min\{\bar{\tau}_h, \bar{\tau}_v\}$, where $\bar{\tau}_h = \min_{t\in[0,\omega]} \tau_h(t)$, $\bar{\tau}_v = \min_{t\in[0,\omega]} \tau_v(t)$. For any $t \in [0, \bar{\tau}]$, since $t - \tau_h(t)$ is strictly increasing in t, we have

$$-\tau_h(0) = 0 - \tau_h(0) \leq t - \tau_h(t) \leq \bar{\tau} - \tau_h(\bar{\tau}) \leq \bar{\tau} - \bar{\tau} = 0,$$

and therefore, $w_2(t - \tau_h(t), \cdot) = \varphi_2(t - \tau_h(t), \cdot)$. Similarly, $w_1(t - \tau_v(t), \cdot) = \varphi_1(t - \tau_v(t), \cdot)$. Hence, for any $t \in [0, \bar{\tau}]$, there holds

$$\begin{aligned}
\frac{\partial w_1}{\partial t} &= D_h \triangle w_1 - (\mu_h(t,x) + \alpha_h(t,x)) w_1 + (1 - \tau_h'(t)) \cdot \\
&\quad \int_\Omega \Gamma_h(t, t - \tau_h(t), x, y) \beta_h(t - \tau_h(t), y) u_1^*(t - \tau_h(t), y) \varphi_2(t - \tau_h(t), y) \mathrm{d}y \\
\frac{\partial w_2}{\partial t} &= D_v \triangle w_2 - \mu_v(t,x) w_2 + (1 - \tau_v'(t)) \cdot \\
&\quad \int_\Omega \Gamma_v(t, t - \tau_v(t), x, y) \beta_v(t - \tau_v(t), y) u_3^*(t - \tau_v(t), y) \varphi_1(t - \tau_v(t), y) \mathrm{d}y \\
\frac{\partial w_1}{\partial \nu} &= \frac{\partial w_2}{\partial \nu} = 0,\ x \in \partial\Omega.
\end{aligned}$$

Given $\varphi \in \mathcal{E}^+$, the solution $(w_1(t, \cdot), w_2(t, \cdot))$ of the above linear system exists uniquely for $t \in [0, \bar{\tau}]$. In other words, we have obtained values of $z_1(\theta_1, \cdot) = w_1(\theta_1, \cdot)$ for $\theta_1 \in [-\tau_v(0), \bar{\tau}]$, and $z_2(\theta_2, \cdot) = w_2(\theta_2, \cdot)$ for $\theta_2 \in [-\tau_h(0), \bar{\tau}]$.

We can extend this procedure to $[n\bar{\tau}, (n+1)\bar{\tau}]$ for all $n \in \mathbb{N}$ by the method of steps. It then follows that for any initial data $\varphi \in \mathcal{E}^+$, the solution $w(t, \cdot, \varphi)$ exists uniquely for all $t \geq 0$. □

Remark 3.3.1. *By the uniqueness of solutions in Lemmas 3.2.1 and 3.3.2, it follows that for any $\varphi \in E^+$ and $\psi \in \mathcal{E}^+$ with $\varphi_1(\theta_1, \cdot) = \psi_1(\theta_1, \cdot)$, $\forall \theta_1 \in [-\tau_v(0), 0]$, and $\varphi_2(\theta_2, \cdot) = \psi_2(\theta_2, \cdot)$, $\forall \theta_2 \in [-\tau_h(0), 0]$, then $v(t, \cdot, \varphi) = w(t, \cdot, \psi)$, $t \geq 0$, where $v(t, \cdot, \varphi)$ and $w(t, \cdot, \psi)$ are solutions of system (3.3.2) satisfying $v_0 = \varphi$ and $w_0 = \psi$, respectively.*

For any given $t \geq 0$, let $P(t)$ be the solution map of system (3.3.2) on the space $\mathcal{E}$ given by $P(t)\phi = w_t(\phi)$, $\forall \phi \in \mathcal{E}$. Then $P(\omega)$ be the Poincaré map associated with system (3.3.2). The following lemma indicates that the periodic semiflow $P(t)$ is eventually strongly positive.

Lemma 3.3.3. *For any $\psi \in \mathcal{E}^+$ with $\psi \not\equiv 0$, the solution $w(t,\cdot,\psi)$ of system (3.3.2) with $w_0 = \psi$ satisfies $w_i(t,\cdot) > 0$ for all $t > 2\hat{\tau}$, $i = 1, 2$, and hence, $P(t)\psi \gg 0$ for all $t > 3\hat{\tau}$.*

Proof. As in the proof of Lemma 3.3.2, a simple comparison argument on each interval $[n\bar{\tau}, (n+1)\bar{\tau}]$, $n \in \mathbb{N}$, implies that $w_i(t) \geq 0$ for all $t \geq 0$ $(i = 1, 2)$.

Next we can choose a large number $K > \max\{\hat{\mu}_h + \hat{\alpha}_h, \hat{\mu}_v\}$, where $\hat{\mu}_h = \max_{t\in[0,\omega], x\in\bar{\Omega}} \mu_h(t,x)$, $\hat{\alpha}_h = \max_{t\in[0,\omega], x\in\bar{\Omega}} \alpha_h(t,x)$, $\hat{\mu}_v = \max_{t\in[0,\omega], x\in\bar{\Omega}} \mu_v(t,x)$, such that for each $t \in \mathbb{R}$, $g_1(t,\cdot,w_1) := -(\mu_h(t,\cdot) + \alpha_h(t,\cdot))w_1 + Kw_1$ is increasing in w_1, and $g_2(t,\cdot,w_2) := -\mu_v(t,\cdot)w_2 + Kw_2$ is increasing in w_2. It then follows that w_1 and w_2 satisfy the following system

$$\begin{aligned}
\frac{\partial w_1}{\partial t} &= D_h \triangle w_1 - Kw_1 + g_1(t,x,w_1) + (1-\tau_h'(t)) \cdot \\
&\quad \int_\Omega \Gamma_h(t, t-\tau_h(t), x, y)\beta_h(t-\tau_h(t), y)u_1^*(t-\tau_h(t), y)w_2(t-\tau_h(t), y)\mathrm{d}y \\
\frac{\partial w_2}{\partial t} &= D_v \triangle w_2 - Kw_2 + g_2(t,x,w_2) + (1-\tau_v'(t)) \cdot \\
&\quad \int_\Omega \Gamma_v(t, t-\tau_v(t), x, y)\beta_v(t-\tau_v(t), y)u_3^*(t-\tau_v(t), y)w_1(t-\tau_v(t), y)\mathrm{d}y \\
\frac{\partial w_1}{\partial \nu} &= \frac{\partial w_2}{\partial \nu} = 0, \ x \in \partial\Omega.
\end{aligned}$$

Hence, for a given $\phi \in \mathcal{E}^+$, we have

$$\begin{aligned}
w_1(t,\phi) &= \tilde{T}_1(t,0)\phi_1(0) + \int_0^t \tilde{T}_1(t,s)g_1(s,\cdot,w_1(s,\cdot))\mathrm{d}s + \int_0^t \tilde{T}_1(t,s)(1-\tau_h'(s)) \cdot \\
&\quad \int_\Omega \Gamma_h(s, s-\tau_h(s), \cdot, y)\beta_h(s-\tau_h(s), y)u_1^*(s-\tau_h(s), y)w_2(s-\tau_h(s), y)\mathrm{d}y\mathrm{d}s, \\
w_2(t,\phi) &= \tilde{T}_2(t,0)\phi_2(0) + \int_0^t \tilde{T}_2(t,s)g_2(s,\cdot,w_2(s,\cdot))\mathrm{d}s + \int_0^t \tilde{T}_2(t,s)(1-\tau_v'(s)) \cdot \\
&\quad \int_\Omega \Gamma_v(s, s-\tau_v(s), \cdot, y)\beta_v(s-\tau_v(s), y)u_3^*(s-\tau_v(s), y)w_1(s-\tau_v(s), y)\mathrm{d}y\mathrm{d}s,
\end{aligned} \tag{3.3.3}$$

where $\tilde{T}_1(t,s), \tilde{T}_2(t,s) : \mathbb{Y} \longrightarrow \mathbb{Y}$ are the evolution operators associated with $\frac{\partial w_1}{\partial t} = D_h \triangle w_1 - Kw_1$ and $\frac{\partial w_2}{\partial t} = D_v \triangle w_2 - Kw_2$ subject to the Neumann boundary condition, respectively. Since both $m_1(t) := t - \tau_h(t)$ and $m_2(t) := t - \tau_v(t)$ are increasing in $t \in \mathbb{R}$, it easily follows that $[-\tau_h(0), 0] \subset m_1([0, \hat{\tau}])$ and $[-\tau_v(0), 0] \subset m_2([0, \hat{\tau}])$. Without loss of generality, we assume that $\psi_2 > 0$. Then there exists an $(\theta_2, x_0) \in [-\tau_h(0), 0] \times \Omega$ such that $w_2(\theta_2, x_0) > 0$. In view of the first equation of (3.3.3), we have $w_1(t, \cdot, \psi) > 0$ for all $t > \hat{\tau}$. Note that if $s > 2\hat{\tau}$, then $s - \tau_h(s) > 2\hat{\tau} - \hat{\tau} = \hat{\tau}$. From the second equation of (3.3.3), it follows that $w_2(t, \cdot, \psi) > 0$ for all $t > 2\hat{\tau}$. This shows that $w_i(t, \cdot) > 0$ for all $t > 2\hat{\tau}, i = 1, 2$, and hence, the solution map $P(t)$ is strongly positive whenever $t > 3\hat{\tau}$. □

We fix an integer n_0 such that $n_0\omega > 3\hat{\tau}$. By the proof of Lemma 3.3.3, we see that $P(\omega)^{n_0} = P(n_0\omega)$ is strongly positive. Further, by the arguments similar to those in [59, Lemma 2.6], one can prove that $P(\omega)^{n_0}$ is compact. According to the Krein-Rutmann theorem, as applied to the linear operator $P(\omega)^{n_0}$, together with the fact that $r(P(\omega)^{n_0}) = (r(P(\omega)))^{n_0}$, we have $\lambda = r(P(\omega)) > 0$, where λ is a simple eigenvalue of $P(\omega)$ having a strongly positive eigenvector $\tilde{\phi} \in \mathrm{int}(\mathcal{E}^+)$. Therefore, the arguments similar to those in [83, Lemma 3.8] imply the following result.

Lemma 3.3.4. *Two Poincaré maps $\tilde{P}(\omega) : E \to E$ and $P(\omega) : \mathcal{E} \to \mathcal{E}$ have the same spectral radius, that is, $r(\tilde{P}(\omega)) = r(P(\omega))$. Moreover, $\mathcal{R}_0$ has the same sign as $r(P(\omega)) - 1$.*

By arguments similar to [12, Lemma 5] and [138, Proposition 1.1], we have the following observation.

Lemma 3.3.5. *Let $\mu = \frac{\ln r(P(\omega))}{\omega}$. Then there exists a positive ω-periodic function $w^*(t, x)$ such that $e^{\mu t} w^*(t, x)$ is a solution of system (3.3.2).*

3.4 Global dynamics

In this section, we first establish a threshold-type result on the global dynamics of system (3.2.6) in terms of $\mathcal{R}_0$, and then prove the global attractivity of the positive constant steady state in the case where all the coefficients are constants.

3.4.1 Threshold dynamics in terms of $\mathcal{R}_0$

Let

$$\mathcal{Y} = C([-\tau_h(0), 0], \mathbb{Y}) \times C([-\tau_v(0), 0], \mathbb{Y}) \times C([-\tau_v(0), 0], \mathbb{Y}) \times C([-\tau_h(0), 0], \mathbb{Y}),$$

and

$$\mathcal{Y}^+ = C([-\tau_h(0), 0], \mathbb{Y}^+) \times C([-\tau_v(0), 0], \mathbb{Y}^+) \times C([-\tau_v(0), 0], \mathbb{Y}^+) \times C([-\tau_h(0), 0], \mathbb{Y}^+).$$

By the arguments similar to those in Lemma 3.3.2, it follows that for any $\varphi \in \mathcal{X}^+$ and $\psi \in \mathcal{Y}^+$ with $\varphi_1(\eta_1,\cdot) = \psi_1(\eta_1,\cdot)$, $\forall \eta_1 \in [-\tau_h(0),0]$, $\varphi_2(\eta_2,\cdot) = \psi_2(\eta_2,\cdot)$, $\forall \eta_2 \in [-\tau_v(0),0]$, $\varphi_3(\eta_3,\cdot) = \psi_3(\eta_3,\cdot)$, $\forall \eta_3 \in [-\tau_v(0),0]$, and $\varphi_4(\eta_4,\cdot) = \psi_4(\eta_4,\cdot)$, $\forall \eta_4 \in [-\tau_h(0),0]$, where $\eta := (\eta_1,\eta_2,\eta_3,\eta_4) \in [-\tau_h(0),0] \times [-\tau_v(0),0] \times [-\tau_v(0),0] \times [-\tau_h(0),0]$, there holds $u(t,\cdot,\varphi) = z(t,\cdot,\psi)$, $t \geq 0$, where $u(t,\cdot,\varphi)$ and $z(t,\cdot,\psi)$ are solutions of system (3.2.6) satisfying $u_0 = \varphi$ and $z_0 = \psi$, respectively. It follows that solutions of system (3.2.6) on $\mathcal{Y}^+$ exist globally on $[0,+\infty)$ and ultimately bounded. Further, by the arguments similar to those in [83, Lemma 3.5] and [59], together with Theorem 1.1.1, we have the following result.

Lemma 3.4.1. *Let $Q(t)$ be the solution map of system (3.2.6) on $\mathcal{Y}^+$ given by $Q(t)\psi = u_t(\psi)$, $t \geq 0$. Then $Q(t)$ is an ω-periodic semiflow on $\mathcal{Y}^+$ in the sense that (i) $Q(0) = I$; (ii) $Q(t+\omega) = Q(t) \circ Q(\omega)$, $\forall t \geq 0$; and (iii) $Q(t)\psi$ is continuous in $(t,\psi) \in [0,+\infty) \times \mathcal{Y}^+$. Moreover, $Q(\omega)$ has a strong global attractor in $\mathcal{Y}^+$.*

As a consequence of the comparison principle and Lemma 3.4.1, we have the following observation.

Lemma 3.4.2. *Let $u(t,\cdot,\phi)$ be the solution of system (3.2.6) with $u_0 = \phi \in \mathcal{Y}^+$. If there exists some $t_0 \geq 0$ such that $u_i(t_0,\cdot,\phi) \not\equiv 0$ for some $i \in \{2,4\}$, then $u_i(t,x,\phi) > 0$, $\forall t > t_0$, $x \in \bar{\Omega}$. Moreover, for any $\phi \in \mathcal{Y}^+$, we have $u_i(t,x,\phi) > 0$, $i = 1,3$, $\forall t > 0$, $x \in \bar{\Omega}$, and $\liminf_{t\to+\infty} u_i(t,x,\phi) \geq \bar{\delta}$, $i = 1,3$ uniformly for $x \in \bar{\Omega}$, where $\bar{\delta}$ is a ϕ-independent positive constant.*

Proof. For a given $\phi \in \mathcal{Y}^+$, one can easily see that $u_2(t,x,\phi)$ and $u_4(t,x,\phi)$ satisfy

$$\begin{aligned}
\frac{\partial u_2(t,x)}{\partial t} &\geq D_h \triangle u_2(t,x) - (\hat{\mu}_h + \hat{\alpha}_h) u_2(t,x),\\
\frac{\partial u_4(t,x)}{\partial t} &\geq D_v \triangle u_4(t,x) - \hat{\mu}_v u_4(t,x),\\
\frac{\partial u_2(t,x)}{\partial \nu} &= \frac{\partial u_4(t,x)}{\partial \nu} = 0, \ \ x \in \partial\Omega,
\end{aligned}$$

where $\hat{\mu}_h = \max_{t\in[0,\omega],x\in\bar{\Omega}} \mu_h(t,x)$, $\hat{\alpha}_h = \max_{t\in[0,\omega],x\in\bar{\Omega}} \alpha_h(t,x)$, and $\hat{\mu}_v = \max_{t\in[0,\omega],x\in\bar{\Omega}}$ $\mu_v(t,x)$. If there exists $t_0 \geq 0$ such that $u_i(t_0,\cdot,\phi) \not\equiv 0$ for some $i \in \{2,4\}$, it then follows from the parabolic maximum principle that $u_i(t,x,\phi) > 0$, $\forall t > t_0$, $x \in \bar{\Omega}$.

Since system (3.2.6) is uniformly bounded, we know that for the forth equation $u_4(t,x)$, there exists a constant $B > 0$ such that $u_4(t,x,\phi) < B$, $\forall t > 0$, $x \in \bar{\Omega}$. Let $v_1(t,x,\phi_1)$ be the solution of

$$\begin{aligned}
&\frac{\partial v_1}{\partial t} = D_h \triangle v_1 + \Lambda_h(t,x) - (\beta_h(t,x)B + \mu_h(t,x))v_1,\\
&\frac{\partial v_1}{\partial \nu} = 0, \quad x \in \partial\Omega.\\
&v_1(0,x) = \phi_1(0,x).
\end{aligned} \tag{3.4.1}$$

Note that $\Lambda_h(t,x)$ is a Hölder continuous and nonnegative nontrivial on $\mathbb{R}\times\bar{\Omega}$. An application of comparison principle yields

$$u_1(t,x,\phi)\geq v_1(t,x,\phi_1)>0,\ x\in\bar{\Omega}.$$

Let $v_1^*(t,x)$ be the globally attractive positive periodic solution of system (3.4.1). Then we have

$$\liminf_{t\to+\infty}u_1(t,x,\phi)\geq\tilde{\delta}:=\min_{t\in[0,\omega],x\in\bar{\Omega}}v_1^*(t,x)$$

uniformly for $x\in\bar{\Omega}$. Similarly, we have

$$\liminf_{t\to+\infty}u_3(t,x,\phi)\geq\mathring{\delta}>0$$

uniformly for $x\in\bar{\Omega}$. Taking $\bar{\delta}=\min\{\tilde{\delta},\mathring{\delta}\}$, we then completes the proof. □

For any given $\phi\in\mathcal{Y}^+$, let $u(t,x,\phi)$ be the unique solution of system (3.2.6) with $u_0=\phi$. The following result shows that $\mathcal{R}_0$ is a threshold value for the disease invasion.

Theorem 3.4.1. *The following two statements are valid:*

- *(i) If $\mathcal{R}_0<1$, then the disease free ω-periodic solution $(u_1^*(t,x),0,u_3^*(t,x),0)$ is globally attractive.*
- *(ii) If $\mathcal{R}_0>1$, then system (3.2.6) has at least one positive ω-periodic solution $(\bar{u}_1^*(t,x),\bar{u}_2^*(t,x),\ \bar{u}_3^*(t,x),\bar{u}_4^*(t,x))$, and there exists a $\gamma>0$ such that for any $\phi\in\mathcal{Y}^+$ with $\phi_2(0,\cdot)\not\equiv0$ and $\phi_4(0,\cdot)\not\equiv0$, we have*

$$\liminf_{t\to+\infty}\min_{x\in\bar{\Omega}}u_i(t,x,\phi)\geq\gamma,\quad 1\leq i\leq4.$$

Proof. (i) In the case where $\mathcal{R}_0<1$, Lemmas 3.3.1 and 3.3.4 imply that $r(P(\omega))<1$, and hence $\mu=\frac{\ln r(P(\omega))}{\omega}<0$. Consider the following system with parameter $\varepsilon>0$:

$$\begin{aligned}
\frac{\partial v_1^\varepsilon}{\partial t}&=D_h\triangle v_1^\varepsilon-(\mu_h(t,x)+\alpha_h(t,x))v_1^\varepsilon+(1-\tau_h'(t))\cdot\\
&\qquad\int_\Omega\Gamma_h(t,t-\tau_h(t),x,y)\beta_h(t-\tau_h(t),y)(u_1^*(t-\tau_h(t),y)+\varepsilon)v_2^\varepsilon(t-\tau_h(t),y)\mathrm{d}y\\
\frac{\partial v_2^\varepsilon}{\partial t}&=D_v\triangle v_2^\varepsilon-\mu_v(t,x)v_2^\varepsilon+(1-\tau_v'(t))\cdot\\
&\qquad\int_\Omega\Gamma_v(t,t-\tau_v(t),x,y)\beta_v(t-\tau_v(t),y)(u_3^*(t-\tau_v(t),y)+\varepsilon)v_1^\varepsilon(t-\tau_v(t),y)\mathrm{d}y\\
\frac{\partial v_1^\varepsilon}{\partial\nu}&=\frac{\partial v_2^\varepsilon}{\partial\nu}=0,\ x\in\partial\Omega.
\end{aligned}\tag{3.4.2}$$

For any $\psi \in \mathcal{E}$, let $v^{\varepsilon}(t,x,\psi) = (v_1^{\varepsilon}(t,x,\psi), v_2^{\varepsilon}(t,x,\psi))$ be the unique solution of system (3.4.2) with $v_0^{\varepsilon}(\psi)(\theta,x) = (\psi(\theta_1,x), \psi(\theta_2,x))$ for all $\theta := (\theta_1,\theta_2) \in [-\tau_v(0),0] \times [-\tau_h(0),0]$, $x \in \bar{\Omega}$, where

$$v_t^{\varepsilon}(\psi)(\theta,x) = (v_1^{\varepsilon}(t+\theta_1,x,\psi), v_2^{\varepsilon}(t+\theta_2,x,\psi)),\ \theta = (\theta_1,\theta_2) \in [-\tau_v(0),0] \times [-\tau_h(0),0],$$

for any $t \geq 0$ and $x \in \bar{\Omega}$. Let $P_{\varepsilon}(\omega) : \mathcal{E} \to \mathcal{E}$ be the Poincáre map of system (3.4.2), i.e., $P_{\varepsilon}(\omega)\psi = v_{\omega}^{\varepsilon}(\psi)$, $\forall \psi \in \mathcal{E}$, and let $r(P_{\varepsilon}(\omega))$ be spectral radius of $P_{\varepsilon}(\omega)$. Since $\lim\limits_{\varepsilon \to 0} r(P_{\varepsilon}(\omega)) = r(P(\omega)) < 1$, we can fix a sufficiently small number $\varepsilon > 0$ such that $r(P_{\varepsilon}(\omega)) < 1$. According to Lemma 3.3.5, there is a positive ω-periodic function $v_{\varepsilon}^*(t,x)$ such that $v^{\varepsilon}(t,x) = e^{\mu_{\varepsilon} t} v_{\varepsilon}^*(t,x)$ is a solution of system (3.4.2), where $\mu_{\varepsilon} = \frac{\ln r(P_{\varepsilon}(\omega))}{\omega} < 0$. For the above fixed $\varepsilon > 0$, by the global attractivity of $u_i^*(t,x)$ $(i = 1,3)$ for system (3.3.1) and the comparison principle, there exists a sufficiently large integer $n_1 > 0$ such that $n_1\omega > \hat{\tau}$ and

$$u_i(t,x) \leq u_i^*(t,x) + \varepsilon,\ \forall t \geq n_1\omega - \hat{\tau}, x \in \bar{\Omega}\ (i = 1,3).$$

Then we have for $t \geq n_1\omega$

$$\begin{aligned}
\frac{\partial u_2}{\partial t} &\leq D_h \triangle u_2 - (\mu_h(t,x) + \alpha_h(t,x))u_2 + (1 - \tau_h'(t)) \cdot \\
&\qquad \int_{\Omega} \Gamma_h(t,t-\tau_h(t),x,y)\beta_h(t-\tau_h(t),y)(u_1^*(t-\tau_h(t),y)+\varepsilon)u_4(t-\tau_h(t),y)\mathrm{d}y \\
\frac{\partial u_4}{\partial t} &\leq D_v \triangle u_4 - \mu_v(t,x)u_4 + (1 - \tau_v'(t)) \cdot \\
&\qquad \int_{\Omega} \Gamma_v(t,t-\tau_v(t),x,y)\beta_v(t-\tau_v(t),y)(u_3^*(t-\tau_v(t),y)+\varepsilon)u_2(t-\tau_v(t),y)\mathrm{d}y \\
\frac{\partial u_2}{\partial \nu} &= \frac{\partial u_4}{\partial \nu} = 0,\ x \in \partial\Omega.
\end{aligned} \tag{3.4.3}$$

For any given $\phi \in \mathcal{Y}^+$, there exists some $m_1 > 0$ such that

$$(u_2(t,x,\phi), u_4(t,x,\phi)) \leq m_1 v^{\varepsilon}(t,x),\ \forall t \in [n_1\omega - \hat{\tau}, n_1\omega], x \in \bar{\Omega}.$$

By the comparison theorem for abstract functional differential equation [92, Proposition 1], it then follows that

$$(u_2(t,x,\phi), u_4(t,x,\phi)) \leq m_1 e^{\mu_{\varepsilon} t} v_{\varepsilon}^*(t,x),\ \forall t \geq n_1\omega, x \in \bar{\Omega},$$

and hence, $\lim\limits_{t \to +\infty} (u_2(t,x,\phi), u_4(t,x,\phi)) = (0,0)$ uniformly for $x \in \bar{\Omega}$.

Next we use the theory of internally chain transitive sets (see, e.g., Section 1.1 and [145]) to prove that $\lim\limits_{t \to +\infty} ((u_1(t,x,\phi), u_3(t,x,\phi)) - (u_1^*(t,x), u_3^*(t,x)) = 0$ uniformly for $x \in \bar{\Omega}$, where (u_1^*, u_3^*) is a globally attractive solution of system (3.3.1).

From the above discussion, we already know that $u_1(t,\cdot,\phi)$ and $u_3(t,\cdot,\phi)$ satisfy a nonautonomous system which is asymptotic to the periodic system (3.3.1). It is easy to check that system (3.3.1) can generate a solution semiflow $\bar{P}(t)$, $t \geq 0$ on $C([-\tau_h(0),0],\mathbb{Y}^+) \times C([-\tau_v(0),0],\mathbb{Y}^+)$. Then $\bar{P}(\omega)$ is Poincaré map associated with system (3.3.1). Clearly, $\bar{P}(\omega)$ has a global attractor in $C([-\tau_h(0),0],\mathbb{Y}^+) \times C([-\tau_v(0),0],\mathbb{Y}^+)$.

For simplicity, we treat $(u_1(t,x,\phi),u_3(t,x,\phi))$ as the susceptible compartments, and $(u_2(t,x,\phi),u_4(t,x,\phi))$ as the infectious compartment, and rearrange $Q(t)$ in Lemma 3.4.1 as $\hat{Q}(t)$ in the following way:

$$\hat{Q}(t)\phi = (u_1(t+\eta_1,\cdot,\phi),u_3(t+\eta_3,\cdot,\phi),u_2(t+\eta_2,\cdot,\phi),u_4(t+\eta_4,\cdot,\phi))),$$

for any $(\eta_1,\eta_3,\eta_2,\eta_4) \in [-\tau_h(0),0] \times [-\tau_v(0),0] \times [-\tau_v(0),0] \times [-\tau_h(0),0]$, $t \geq 0$. Let $\mathcal{J} = \omega(\phi)$ be the omega limit set of $\phi \in \mathcal{Y}^+$ for $\hat{Q}(\omega)$. Since $\lim_{t\to+\infty} u_i(t,x,\phi) = 0$, $i = 2,4$ uniformly for $x \in \bar{\Omega}$, we have $\mathcal{J} = J \times \{\hat{0}\} \times \{\tilde{0}\}$, where $\hat{0}(\theta,\cdot) = 0$, $\forall \theta \in [-\tau_v(0),0]$, and $\tilde{0}(\theta,\cdot) = 0$, $\forall \theta \in [-\tau_h(0),0]$. By Lemma 3.4.2, we know that $\hat{0} \notin J$ and $\tilde{0} \notin J$. Lemma 1.1.1 implies that $\mathcal{J}$ is an internally chain transitive set for $\hat{Q}(\omega)$, and hence, J is an internally transitive chain set for $\bar{P}(\omega)$. Define $(u_1^0,u_3^0) \in C([-\tau_h(0),0],\mathbb{Y}^+) \times C([-\tau_v(0),0],\mathbb{Y}^+)$ by $(u_1^0(\theta_1,\cdot),u_3^0(\theta_2,\cdot)) = (u_1^*(\theta_1,\cdot),u_3^*(\theta_2,\cdot))$ for $\theta_1 \in [-\tau_h(0),0]$ and $\theta_2 \in [-\tau_v(0),0]$. Since $J \neq \{\hat{0}\} \times \{\tilde{0}\}$ and (u_1^0,u_3^0) is globally attractive in $C([-\tau_h(0),0],\mathbb{Y}^+) \times C([-\tau_v(0),0],\mathbb{Y}^+) \setminus \{\hat{0}\} \times \{\tilde{0}\}$, we have $J \cap W^s((u_1^0,u_3^0)) \neq \emptyset$, where $W^s((u_1^0,u_3^0))$ is the stable set of (u_1^0,u_3^0). By Theorem 1.1.2, we get $J = \{(u_1^0,u_3^0)\}$. This proves $\mathcal{J} = \{(u_1^0,u_3^0,\hat{0},\tilde{0})\}$, and hence,

$$\lim_{t\to+\infty} \|(u_1(t,\cdot,\phi),u_2(t,\cdot,\phi),u_3(t,\cdot,\phi),u_4(t,\cdot,\phi)) - (u_1^*(t,\cdot),0,u_3^*(t,\cdot),0)\| = 0.$$

(ii) In the case where $\mathcal{R}_0 > 1$, we have $r(P(\omega)) > 1$, and hence $\mu = \frac{\ln r(P(\omega))}{\omega} > 0$. Let

$$\mathbb{C}_0 = \{\phi \in \mathcal{Y}^+ : \phi_2(0,\cdot) \not\equiv 0 \text{ and } \phi_4(0,\cdot) \not\equiv 0\},$$

and

$$\partial\mathbb{C}_0 := \mathcal{Y}^+ \backslash \mathbb{C}_0 = \{\phi \in \mathcal{Y}^+ : \phi_2(0,\cdot) \equiv 0 \text{ or } \phi_4(0,\cdot) \equiv 0\}.$$

Note that for any $\phi \in \mathbb{C}_0$, Lemma 3.4.2 implies that $u_i(t,x,\phi) > 0, \forall t > 0, x \in \bar{\Omega}$, $i = 2,4$. It follows that $Q(\omega)^n\mathbb{C}_0 \subset \mathbb{C}_0$, $\forall n \in \mathbb{N}$. From Lemma 3.4.1, we know that $Q(\omega)$ has a strong global attractor in $\mathcal{Y}^+$.

Define

$$M_\partial := \{\phi \in \partial\mathbb{C}_0 : Q(\omega)^n\phi \in \partial\mathbb{C}_0, \forall n \in \mathbb{N}\},$$

and $\omega(\phi)$ be the omega limit set of the orbit $\gamma^+ = \{Q(\omega)^n\phi : \forall n \in \mathbb{N}\}$, and set $M = (u_1^0,\hat{0},u_3^0,\tilde{0})$. Then the following claim indicates that M cannot form a cycle for $Q(\omega)$ in $\partial\mathbb{C}_0$.

Claim 1. *For any $\psi \in M_\partial$, the omega limit set $\omega(\psi) = M$.*

For any given $\psi \in M_\partial$, $Q(\omega)^n(\psi) \in \partial\mathbb{C}_0$, $\forall n \in \mathbb{N}$. Thus, for each $n \in \mathbb{N}$, either $u_2(n\omega, \cdot, \psi) \equiv 0$ or $u_4(n\omega, \cdot, \psi) \equiv 0$. It then follows that for each $t \geq 0$, $u_2(t, \cdot, \psi) \equiv 0$ or $u_4(t, \cdot, \psi) \equiv 0$. Otherwise, it contradicts Lemma 3.4.2. If $u_4(t, \cdot, \psi) \equiv 0$ for $t \geq 0$, then $\lim_{t\to+\infty}(u_1(t, x, \psi) - u_1^0(t, x)) = 0$ uniformly for $x \in \bar{\Omega}$. Note that u_2 equation in system (3.2.6) satisfies

$$\frac{\partial u_2(t, x, \psi)}{\partial t} \leq D_h \triangle u_2(t, x, \psi) - (\bar{\mu}_h + \bar{\alpha}_h) u_2(t, x, \psi),$$

where $\bar{\mu}_h = \min_{t\in[0,\omega], x\in\bar{\Omega}} \mu_h(t, x)$ and $\bar{\alpha}_h = \min_{t\in[0,\omega], x\in\bar{\Omega}} \alpha_h(t, x)$. By the comparison principle, we have $\lim_{t\to+\infty} u_2(t, x, \psi) = 0$ uniformly for $x \in \bar{\Omega}$. It then follows that u_3 satisfies an nonautonomous system which is asymptotic to the second equation of periodic system (3.3.1). Again, by the theory of internally chain transitive sets (see, e.g., Section 1.1 and [145]), we can prove $\lim_{t\to+\infty}(u_3(t, x, \psi) - u_3^0(t, x)) = 0$ uniformly for $x \in \bar{\Omega}$. If $u_4(t_0, \cdot, \psi) \not\equiv 0$ for some $t_0 \geq 0$, it follows from Lemma 3.4.2 that $u_4(t, \cdot, \psi) > 0$, $\forall t \geq t_0$. Thus we have $u_2(t, \cdot, \psi) \equiv 0$, $\forall t \geq t_0$. From the u_4 equation in system (3.2.6), we see that $\lim_{t\to+\infty} u_4(t, x, \psi) = 0$ uniformly for $x \in \bar{\Omega}$. Thus, $u_1(t, \cdot, \psi)$ and $u_3(t, \cdot, \psi)$ satisfy a nonautonomous system which is asymptotic to the periodic system (3.3.1). As argued in case (i), we have $\lim_{t\to+\infty}((u_1(t, x, \psi), u_3(t, x, \psi)) - (u_1^0(t, x), u_3^0(t, x)) = 0$ uniformly for $x \in \bar{\Omega}$. As a result, $\omega(\psi) = M$ for any $\psi \in M_\partial$.

Consider the following system with parameter $\delta > 0$:

$$\begin{aligned}
\frac{\partial v_1^\delta}{\partial t} &= D_h \triangle v_1^\delta - (\mu_h(t, x) + \alpha_h(t, x)) v_1^\delta + (1 - \tau_h'(t)) \cdot \\
&\quad \int_\Omega \Gamma_h(t, t - \tau_h(t), x, y) \beta_h(t - \tau_h(t), y)(u_1^*(t - \tau_h(t), y) - \delta) v_2^\delta(t - \tau_h(t), y) \mathrm{d}y \\
\frac{\partial v_2^\delta}{\partial t} &= D_v \triangle v_2^\delta - \mu_v(t, x) v_2^\delta + (1 - \tau_v'(t)) \cdot \\
&\quad \int_\Omega \Gamma_v(t, t - \tau_v(t), x, y) \beta_v(t - \tau_v(t), y)(u_3^*(t - \tau_v(t), y) - \delta) v_1^\delta(t - \tau_v(t), y) \mathrm{d}y \\
\frac{\partial v_1^\delta}{\partial \nu} &= \frac{\partial v_2^\delta}{\partial \nu} = 0, \ x \in \partial\Omega.
\end{aligned} \tag{3.4.4}$$

For any $\psi \in \mathcal{E}$, let $v^\delta(t, x, \psi) = (v_1^\delta(t, x, \psi), v_2^\delta(t, x, \psi))$ be the unique solution of system (3.4.4) with $v_0^\delta(\psi)(\theta, x) = (\psi_1(\theta_1, x), \psi_2(\theta_2, x))$ for all $\theta := (\theta_1, \theta_2) \in [-\tau_v(0), 0] \times [-\tau_h(0), 0]$, $x \in \bar{\Omega}$, where

$$v_t^\delta(\psi)(\theta, x) = (v_1^\delta(t + \theta_1, x, \psi), v_2^\delta(t + \theta_2, x, \psi)), \ \theta = (\theta_1, \theta_2) \in [-\tau_v(0), 0] \times [-\tau_h(0), 0],$$

for any $t \geq 0$ and $x \in \bar{\Omega}$. Let $P_\delta(\omega) : \mathcal{E} \to \mathcal{E}$ be the Poincáre map of system (3.4.4), i.e., $P_\delta(\omega)\phi = v^\delta_\omega(\phi)$, $\forall \psi \in \mathcal{E}$, and let $r(P_\delta(\omega))$ be spectral radius of $P_\delta(\omega)$. Since $\lim\limits_{\delta\to 0} r(P_\delta(\omega)) = r(P(\omega)) > 1$, we can fix a sufficiently small number $\delta > 0$ such that

$$\delta < \min\{\min_{t\in[0,\omega],x\in\bar{\Omega}} u_1^*(t,x), \min_{t\in[0,\omega],x\in\bar{\Omega}} u_3^*(t,x)\} \text{ and } r(P_\delta(\omega)) > 1.$$

For the above fixed $\delta > 0$, by the continuous dependence of solutions on the initial value, there exists $\delta^* > 0$ such that for all ϕ with $\|\phi - M\| \le \delta^*$, then we have $\|Q(t)\phi - Q(t)M\| < \delta$ for all $t \in [0,\omega]$. We now prove the following claim.

Claim 2. *For all $\phi \in \mathbb{C}_0$, there holds* $\limsup_{n\to+\infty} \|Q(\omega)^n(\phi) - M\| \ge \delta^*$.

Suppose, by contradiction, that $\limsup_{n\to+\infty} \|Q(\omega)^n(\phi_0) - M\| < \delta^*$ for some $\phi_0 \in \mathbb{C}_0$. Then there exists $n_1 \ge 1$ such that $\|Q(\omega)^n(\phi_0) - M\| < \delta^*$ for $n \ge n_1$. For any $t \ge n_1\omega$, letting $t = n\omega + t'$ with $n = [t/\omega]$ and $t' \in [0,\omega)$, we have

$$\|Q(t)\phi_0 - Q(t)M\| = \|Q(t')(Q(\omega)^n(\phi_0)) - Q(t')M\| < \delta. \tag{3.4.5}$$

It then follows from (3.4.5) and Lemma 3.4.2 that

$$u_i(t,x,\phi_0) > u_i^*(t,x) - \delta \ (i = 1,3) \text{ and } 0 < u_j(t,x,\phi_0) < \delta \ (j = 2,4),$$

for any $t \ge n_1\omega - \hat{\tau}$, and $x \in \bar{\Omega}$. Thus, when $t \ge n_1\omega$, $u_2(t,x,\phi_0)$ and $u_4(t,x,\phi_0)$ satisfy

$$\begin{aligned}
\frac{\partial u_2}{\partial t} &\ge D_h \triangle u_2 - (\mu_h(t,x) + \alpha_h(t,x))u_2 + (1 - \tau_h'(t)) \cdot \\
&\quad \int_\Omega \Gamma_h(t, t-\tau_h(t), x, y)\beta_h(t-\tau_h(t), y)(u_1^*(t-\tau_h(t), y) - \delta)u_4(t-\tau_h(t), y)\mathrm{d}y \\
\frac{\partial u_4}{\partial t} &\ge D_v \triangle u_4 - \mu_v(t,x)u_4 + (1 - \tau_v'(t)) \cdot \\
&\quad \int_\Omega \Gamma_v(t, t-\tau_v(t), x, y)\beta_v(t-\tau_v(t), y)(u_3^*(t-\tau_v(t), y) - \delta)u_2(t-\tau_v(t), y)\mathrm{d}y \\
\frac{\partial u_2}{\partial \nu} &= \frac{\partial u_4}{\partial \nu} = 0, \ x \in \partial\Omega.
\end{aligned} \tag{3.4.6}$$

Since $u(t,x,\phi_0) \gg 0$ for all $t \ge 0$ and $x \in \bar{\Omega}$, there exists an $m_2 > 0$ such that

$$(u_2(t,x,\phi_0), u_4(t,x,\phi_0)) \ge m_2 e^{\mu_\delta t} v_\delta^*(t,x), \ \forall t \in [n_1\omega - \hat{\tau}, n_1\omega], \ x \in \bar{\Omega},$$

where $v_\delta^*(t,x)$ is a positive ω-periodic function such that $e^{\mu_\delta t} v_\delta^*(t,x)$ is a solution of system (3.4.4), where $\mu_\delta = \frac{\ln r(P_\delta(\omega))}{\omega}$. By the comparison theorem, we have

$$(u_2(t,x,\phi_0), u_4(t,x,\phi_0)) \ge m_2 e^{\mu_\delta t} v_\delta^*(t,x), \ \forall t \ge n_1\omega, \ x \in \bar{\Omega}.$$

Since $\mu_\delta > 0$, it is easy to see that $u_i(t,\cdot,\phi_0) \to +\infty, \ i = 2,4$ as $t \to +\infty$. This leads to contradiction.

The above claim implies that M is an isolated invariant set for $Q(\omega)$ in $\mathcal{Y}^+$, and $W^s(M)\bigcap\mathbb{C}_0=\emptyset$, where $W^s(M)$ is the stable set of M for $Q(\omega)$. By [90, Theorem 3.7], as applied to $Q(\omega)$, we know that $Q(\omega)$ admits a global attractor A_0 in $\mathbb{C}_0$. It then follows from Theorem 1.2.1 that $Q(\omega)$ is uniformly persistent with respect to $(\mathbb{C}_0,\partial\mathbb{C}_0)$ in the sense that there exists $\tilde{\gamma}>0$ such that

$$\liminf_{n\to+\infty}\mathrm{d}(Q^n(\phi),\partial\mathbb{C}_0)\geq\tilde{\gamma},\ \forall\phi\in\mathbb{C}_0. \tag{3.4.7}$$

Since $A_0=Q(\omega)A_0$, we have that $\phi_2(0,\cdot)>0$ and $\phi_4(0,\cdot)>0$ for all $\phi\in A_0$. Let $B_0:=\bigcup\limits_{t\in[0,\omega]}Q(t)A_0$. Then $B_0\subset\mathbb{C}_0$ and $\lim\limits_{t\to+\infty}\mathrm{d}(Q(t)\phi,B_0)=0$, $\forall\phi\in\mathbb{C}_0$. Define a continuous function $p:\mathcal{Y}^+\to\mathbb{R}_+$ by

$$p(\phi)=\min\{\min_{x\in\bar{\Omega}}\phi_2(0,x),\min_{x\in\bar{\Omega}}\phi_4(0,x)\},\ \forall\phi=(\phi_1,\phi_2,\phi_3,\phi_4)\in\mathcal{Y}^+.$$

Since B_0 is compact subset of $\mathbb{C}_0$, it follows that $\inf\limits_{\phi\in B_0}p(\phi)=\min\limits_{\phi\in B_0}p(\phi)>0$. Consequently, there exists a $\gamma^*>0$ such that

$$\liminf_{t\to+\infty}p(Q(t)\phi)=\liminf_{t\to+\infty}\min(\min_{x\in\bar{\Omega}}u_2(t,x,\phi),\min_{x\in\bar{\Omega}}u_4(t,x,\phi))\geq\gamma^*,\ \forall\phi\in\mathbb{C}_0.$$

Furthermore, by Lemma 3.4.2, there exists an $\gamma\in(0,\gamma^*)$ such that

$$\liminf_{t\to+\infty}\min_{x\in\bar{\Omega}}u_i(t,x,\phi)\geq\gamma,\ \forall\phi\in\mathbb{C}_0\ (1\leq i\leq 4).$$

It remains to prove the existence of a positive periodic steady state. By [145, Theorem 3.5.1], it follows that for each $t>0$, the solution map $\tilde{Q}(t):\mathcal{X}^+\to\mathcal{X}^+$ of system (3.2.6), which is defined in Lemma 3.2.1, is an α-contraction with respect to an equivalent norm on $\mathcal{X}$. Define

$$\mathbb{W}_0=\{\phi\in\mathcal{X}^+:\phi_2(0,\cdot)\not\equiv 0\text{ and }\phi_4(0,\cdot)\not\equiv 0\},$$

and

$$\partial\mathbb{W}_0:=\mathcal{X}^+/\mathbb{W}_0=\{\phi\in\mathcal{X}^+:\phi_2(0,\cdot)=0\text{ or }\phi_4(0,\cdot)=0\}.$$

We see that $\tilde{Q}(\omega)$ is uniformly persistent with respect to $(\mathbb{W}_0,\partial\mathbb{W}_0)$. It then follows from Theorem 1.2.2, as applied to $\tilde{Q}(\omega)$, that system (3.2.6) has an ω-periodic solution $(z_1^*(t,\cdot),z_2^*(t,\cdot),z_3^*(t,\cdot),z_4^*(t,\cdot))$ with $(z_{1t}^*,z_{2t}^*,z_{3t}^*,z_{4t}^*)\in\mathbb{W}_0$. Let $\bar{u}_i^*(\eta_i,\cdot)=z_i^*(\eta_i,\cdot)$, where $(\eta_1,\eta_2,\eta_3,\ \eta_4)\in[-\tau_h(0),0]\times[-\tau_v(0),0]\times[-\tau_v(0),0]\times[-\tau_h(0),0]$. Again, by the uniqueness of solutions, we see that $(\bar{u}_1^*(t,\cdot),\bar{u}_2^*(t,\cdot),\bar{u}_3^*(t,\cdot),\ \bar{u}_4^*(t,\cdot))$ is a periodic solution of system (3.2.6) and it is also strictly positive due to Lemma 3.4.2. □

Now we derive the asymptotic behavior of $E_h(t,x),E_v(t,x)$ and $R_h(t,x)$ in system

(3.2.5). In the case where $\mathcal{R}_0 < 1$, we have

$$\lim_{t\to+\infty}\big((S_h(t,x), I_h(t,x), S_v(t,x), I_v(t,x)) - (u_1^*(t,x), 0, u_3^*(t,x), 0)\big) = 0$$

uniformly for $x \in \bar{\Omega}$. It then follows from (3.2.10) and (3.2.11) that

$$\lim_{t\to+\infty} E_h(t,x) = \lim_{t\to+\infty} E_v(t,x) = 0 \text{ uniformly for } x \in \bar{\Omega}.$$

By the theory of internally chain transitive sets (see, e.g., Section 1.1 and [145]), together with $\lim\limits_{t\to+\infty} I_h(t,x) = 0$, one can also show $\lim\limits_{t\to+\infty} R_h(t,x) = 0$.

In the case where $\mathcal{R}_0 > 1$, for any $\phi \in \mathcal{Y}^+$ with $\phi_2(0,\cdot) \not\equiv 0$ and $\phi_4(0,\cdot) \not\equiv 0$, we have

$$\liminf_{t\to+\infty} S_h(t,x,\phi) \geq \gamma, \liminf_{t\to+\infty} I_h(t,x,\phi) \geq \gamma, \liminf_{t\to+\infty} S_v(t,x,\phi) \geq \gamma, \liminf_{t\to+\infty} I_v(t,x,\phi) \geq \gamma$$

uniformly for $x \in \bar{\Omega}$. Since $\liminf\limits_{t\to+\infty} I_h(t,x,\phi) \geq \gamma$, from the R_h equation in system (3.2.5), we see that there exists $\gamma_1 > 0$ such that

$$\liminf_{t\to+\infty} R_h(t,x) \geq \gamma_1.$$

By the integral forms (3.2.10) and (3.2.11), there exists an $\gamma_2 > 0$ such that

$$\liminf_{t\to+\infty} \min_{x\in\bar{\Omega}} E_h(t,x) \geq \gamma_2 \text{ and } \liminf_{t\to+\infty} \min_{x\in\bar{\Omega}} E_v(t) \geq \gamma_2,$$

with $E_h(0,x)$ and $E_v(0,x)$ satisfying compatibility conditions (3.2.8) and (3.2.9). Moreover, if $(S_h(t,x), I_h(t,x), S_v(t,x), I_v(t,x))$ is ω-periodic, then it is easy to check $E_h(t,x)$, $E_v(t,x)$ and $R_h(t,x)$ are also ω-periodic,respectively. Consequently, we have the following result on the global dynamics of system (3.2.5).

Theorem 3.4.2. *Let $U(t,x,\phi)$ be the solution of system (3.2.5) with $U_0 = \phi$, where $(U_1, U_2, U_3, U_4, U_5, U_6, U_7) = (S_h, E_h, I_h, R_h, S_v, E_v, I_v)$. Then the following two statements are valid:*

(i) If $\mathcal{R}_0 < 1$, then the disease free ω-periodic solution $(u_1^*(t,x), 0, 0, 0, u_3^*(t,x), 0, 0)$ is globally attractive.

(ii) If $\mathcal{R}_0 > 1$, then system (3.2.5) has at least one positive ω-periodic solution $\bar{U}(t,x)$, where $\bar{U}_1(t,x) = \bar{u}_1^*(t,x)$, $\bar{U}_3(t,x) = \bar{u}_2^*(t,x)$, $\bar{U}_5(t,x) = \bar{u}_3^*(t,x)$, $\bar{U}_7(t,x) = \bar{u}_4^*(t,x)$, and there exists a $\tilde{\gamma} = \max\{\gamma, \gamma_1, \gamma_2\} > 0$ such that for any $\phi \in \mathcal{D}$ with $\phi_i \in \mathcal{Y}^+$, $i = 1,3,5,7$, $\phi_3(0,\cdot) \not\equiv 0$ and $\phi_7(0,\cdot) \not\equiv 0$, we have

$$\liminf_{t\to+\infty} \min_{x\in\Omega} \bar{U}_i(t,x,\phi) \geq \tilde{\gamma},\ 1 \leq i \leq 7.$$

3.4.2 Global attractivity in the case of constant coefficients

In the case where $\Lambda_h(t,x)$, $\Lambda_v(t,x)$, $\mu_h(t,x)$, $\mu_v(t,x)$, $\alpha_h(t,x)$, $b(t,x)$, $\beta_h(t,x)$, $\beta_v(t,x)$, $\tau_h(t)$ and $\tau_v(t)$ are positive constants, system (3.2.6) reduces to the following autonomous reaction-diffusion system:

$$
\begin{aligned}
\frac{\partial u_1}{\partial t} &= D_h\triangle u_1 + \Lambda_h - \beta_h u_1 u_4 - \mu_h u_1,\\
\frac{\partial u_2}{\partial t} &= D_h\triangle u_2 + e^{-\mu_h\tau_h}\int_\Omega \Gamma(D_h\tau_h,x,y)\beta_h u_1(t-\tau_h,y)u_4(t-\tau_h,y)\mathrm{d}y - (\mu_h+\alpha_h)u_2,\\
\frac{\partial u_3}{\partial t} &= D_v\triangle u_3 + \Lambda_v - \beta_v u_3 u_2 - \mu_v u_3,\\
\frac{\partial u_4}{\partial t} &= D_v\triangle u_4 + e^{-\mu_v\tau_v}\int_\Omega \Gamma(D_v\tau_v,x,y)\beta_v u_3(t-\tau_v,y)u_2(t-\tau_v,y)\mathrm{d}y - \mu_v u_4,\\
\frac{\partial u_1}{\partial \nu} &= \frac{\partial u_2}{\partial \nu} = \frac{\partial u_3}{\partial \nu} = \frac{\partial u_4}{\partial \nu} = 0,\ x\in\partial\Omega,
\end{aligned}
\tag{3.4.8}
$$

where $\Gamma(t,x,y)$ is the Green function associated with $\frac{\partial u}{\partial t} = \triangle u$ subject to the Neumann boundary condition. By the arguments in [144, Corollary 2.1] and [128, Theorem 3.4], it follows that the basic reproduction number $\mathcal{R}_0$ equals the spectral radius of the following 2×2 matrix

$$
\mathcal{M} = \begin{pmatrix} 0 & \dfrac{\Lambda_h\beta_h e^{-\mu_h\tau_h}}{\mu_h\mu_v} \\ \dfrac{\Lambda_v\beta_v e^{-\mu_v\tau_v}}{(\mu_h+\alpha_h)\mu_v} & 0 \end{pmatrix},
$$

and hence, the basic reproduction number for system (3.4.8) is

$$
\mathcal{R}_0 = \sqrt{\frac{\Lambda_h\Lambda_v\beta_h\beta_v e^{-\mu_h\tau_h}e^{-\mu_v\tau_v}}{\mu_h\mu_v^2(\mu_h+\alpha_h)}}.
$$

Theorem 3.4.3. *Let $u(t,\cdot,\phi)$ be the solution of system (3.2.6) with $u_0=\phi\in\mathcal{X}^+$. Then the following two statements are valid:*

(i) If $\mathcal{R}_0<1$, then the disease free ω-periodic steady state $(\frac{\Lambda_h}{\mu_h},0,\frac{\Lambda_v}{\mu_v},0)$ is globally attractive.

(ii) If $\mathcal{R}_0>1$, then system (3.4.8) has a unique constant steady state $\bar{u}^*=(\bar{u}_1^*,\bar{u}_2^*,\bar{u}_3^*,\bar{u}_4^*)$ such that for any $\phi\in\mathcal{X}^+$ with $\phi_2(0,\cdot)\not\equiv 0$ and $\phi_4(0,\cdot)\not\equiv 0$, $\lim_{t\to+\infty} u(t,x,\phi) = \bar{u}^*$ uniformly for $x\in\bar{\Omega}$.

Proof. From the discussion in Section 2.2, it is easy to see that the set

$$\mathcal{A} = \{u \in \mathcal{X}^+ : u_i(\eta, x) \leq \frac{\Lambda_h}{\mu_h} \ (i = 1, 2), \ u_j(\eta, x) \leq \frac{\Lambda_v}{\mu_v} \ (j = 3, 4), \ \eta \in [-\hat{\tau}, 0], x \in \bar{\Omega}\}$$

is positively invariant for $\tilde{Q}(t)$ and every forward orbit enters into $\mathcal{A}$ eventually. It then suffices to study the dynamics of system (3.4.8) on $\mathcal{A}$. Conclusions (i) follows directly from Theorem 3.4.1. In the case where $\mathcal{R}_0 > 1$, there is a unique constant epidemic steady state $\bar{u}^* = (\bar{u}_1^*, \bar{u}_2^*, \bar{u}_3^*, \bar{u}_4^*)$ with

$$\begin{aligned}
\bar{u}_1^* &= \frac{\Lambda_h}{\beta_h \bar{u}_4^* + \mu_h}, \bar{u}_2^* = \frac{\beta_h \Lambda_h e^{-\mu_h \tau_h} \bar{u}_4^*}{(\alpha_h + \mu_h)(\beta_h \bar{u}_4^* + \mu_h)}, \\
\bar{u}_3^* &= \frac{\Lambda_v}{\beta_v \bar{u}_2^* + \mu_v}, \bar{u}_4^* = \frac{\mu_h \mu_v^2 (\alpha_h + \mu_h)(\mathcal{R}_0^2 - 1)}{\Lambda_h \mu_v \beta_h \beta_v e^{-\mu_h \tau_h} + \beta_h \mu_v^2 (\alpha_h + \mu_h)}.
\end{aligned}$$

Next we construct a suitable Lyapunov functional to establish the global stability of the $\bar{u}^*$ for system (3.4.8). Let $f(x) = x - 1 - \ln x$ for $x > 0$. As the expressions are complicated, we define the Lyapunov functional in components and take the derivative of each component separately. Let

$$\begin{aligned}
&U_1(t, x) = f\left(\frac{u_1}{\bar{u}_1^*}\right), \ U_2(t, x) = f\left(\frac{u_2}{\bar{u}_2^*}\right), \\
&U_{+2}(t, x) = \beta_h e^{-\mu_h \tau_h} \int_{t-\tau_h}^{t} \int_{\Omega} \Gamma(D_h(t - \sigma), x, y) f(\frac{u_1(\sigma, y) u_4(\sigma, y)}{u_1^* u_4^*}) \mathrm{d}\sigma \mathrm{d}y.
\end{aligned}$$

Note that

$$\begin{aligned}
\frac{\partial}{\partial t} \int_{\Omega} U_i(t, x) dx &= \int_{\Omega} \frac{\partial U_i(t, x)}{\partial t} dx = \int_{\Omega} f'(\frac{u_i}{\bar{u}_i^*}) \frac{1}{\bar{u}_i^*} [D_h \triangle u_i + F_i(u)] \mathrm{d}x \\
&= -\int_{\Omega} f''(\frac{u_i}{\bar{u}_i^*}) \frac{|D_h \nabla u_i|^2}{\bar{u}_i^{*2}} \mathrm{d}x + \int_{\Omega} f'(\frac{u_i}{\bar{u}_i^*}) \frac{1}{\bar{u}_i^*} F_i(u) \mathrm{d}x \\
&\leq \int_{\Omega} f'(\frac{u_i}{\bar{u}_i^*}) \frac{1}{\bar{u}_i^*} F_i(u) \mathrm{d}x, \qquad (3.4.9)
\end{aligned}$$

where

$$\begin{aligned}
f'(\frac{u_1}{\bar{u}_1^*}) \frac{1}{u_1^*} F_1(u) &= \frac{1}{\bar{u}_1^*} \left(\frac{u - \bar{u}_1^*}{u_1}\right) (\Lambda_h - \beta_h u_1 u_4 - \mu_h u_1) \\
&= \frac{1}{\bar{u}_1^*} \left(\frac{u_1 - \bar{u}_1^*}{u_1}\right) [\beta_h (\bar{u}_1^* \bar{u}_4^* - u_1 u_4) - \mu_h (u_1 - \bar{u}_1^*)] \\
&= -\frac{\mu_h (u_1 - \bar{u}_1^*)^2}{u_1 \bar{u}_1^*} + \beta_h \bar{u}_4^* \left(1 - \frac{\bar{u}_1^*}{u_1} - \frac{u_1 u_4}{\bar{u}_1^* \bar{u}_4^*} + \frac{u_4}{\bar{u}_4^*}\right), \qquad (3.4.10)
\end{aligned}$$

and

$$
\begin{aligned}
& f'(\frac{u_2}{\bar{u}_2^*})\frac{1}{\bar{u}_2^*}F_2(u) \\
&= \frac{1}{\bar{u}_2^*}\left(\frac{u_2-\bar{u}_2^*}{u_2}\right)\left[e^{-\mu_h\tau_h}\int_\Omega \Gamma(D_h\tau_h,x,y)\beta_h u_1(t-\tau_h,y)u_4(t-\tau_h,y)\mathrm{d}y-(\mu_h+\alpha_h)u_2\right] \\
&= \frac{1}{\bar{u}_2^*}\left(\frac{u_2-\bar{u}_2^*}{u_2}\right)\beta_h e^{-\mu_h\tau_h}\bar{u}_4^*\bar{u}_1^*\int_\Omega \Gamma(D_h\tau_h,x,y)\left[\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}-\frac{u_2}{\bar{u}_2^*}\right]\mathrm{d}y \\
&= \frac{\beta_h e^{-\mu_h\tau_h}\bar{u}_4^*\bar{u}_1^*}{\bar{u}_2^*}\int_\Omega \Gamma(D_h\tau_h,x,y)\left[1+\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}-\frac{u_2}{\bar{u}_2^*}\right. \\
&\quad \left.-\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)\bar{u}_2^*}{\bar{u}_1^*\bar{u}_4^*u_2}\right]\mathrm{d}y. \qquad (3.4.11)
\end{aligned}
$$

Moreover, we can obtain

$$
\begin{aligned}
& \int_\Omega \frac{\partial U_{+2}(t,x)}{\partial t}\mathrm{d}x \\
&= \int_\Omega D_h\triangle U_{+2}\mathrm{d}x+\int_\Omega \beta_h e^{-\mu_h\tau_h}\times \\
&\quad \left[f\left(\frac{u_1(t,x)u_4(t,x)}{\bar{u}_1^*\bar{u}_4^*}\right)-\int_\Omega \Gamma(D_h\tau_h,x,y)f\left(\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}\right)\mathrm{d}y\right]\mathrm{d}x \\
&= \int_\Omega \beta_h e^{-\mu_h\tau_h}\int_\Omega \Gamma(D_h\tau_h,x,y)\left(\frac{u_1u_4}{\bar{u}_1^*\bar{u}_4^*}-\ln\frac{u_1u_4}{\bar{u}_1^*\bar{u}_4^*}\right. \\
&\quad \left.-\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}+\ln\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}\right)\mathrm{d}y\mathrm{d}x. \qquad (3.4.12)
\end{aligned}
$$

Set

$$
U(t,x)=\frac{e^{-\mu_h\tau_h}}{\bar{u}_4^*}U_1+\frac{\bar{u}_2^*}{\bar{u}_1^*\bar{u}_4^*}U_2+U_{+2},
$$

together with (3.4.9)–(3.4.12), it then follows that

$$
\begin{aligned}
& \frac{\partial U(t,x)}{\partial t} \\
&\le -\frac{\mu_h e^{-\mu_h\tau_h}(u_1-\bar{u}_1^*)^2}{u_1\bar{u}_1^*\bar{u}_4^*}+\beta_h e^{-\mu_h\tau_h}\left(1-\frac{\bar{u}_1^*}{u_1}-\frac{u_2}{\bar{u}_2^*}+\ln\frac{\bar{u}_1^*}{u_1}+\frac{u_4}{\bar{u}_4^*}-\ln\frac{u_4}{\bar{u}_4^*}\right)+\beta_h e^{-\mu_h\tau_h}\times \\
&\quad \int_\Omega \Gamma(D_h\tau_h,x,y)\left[1-\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)\bar{u}_2^*}{\bar{u}_1^*\bar{u}_4^*u_2}+\ln\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)}{\bar{u}_1^*\bar{u}_4^*}\right]\mathrm{d}y \\
&= -\frac{\mu_h e^{-\mu_h\tau_h}(u_1-\bar{u}_1^*)^2}{u_1\bar{u}_1^*\bar{u}_4^*}+\beta_h e^{-\mu_h\tau_h}\left(-f(\frac{\bar{u}_1^*}{u_1})-\frac{u_2}{\bar{u}_2^*}+\frac{u_4}{\bar{u}_4^*}-\ln\frac{\bar{u}_2^*u_4}{u_2\bar{u}_4^*}\right) \\
&\quad -\beta_h e^{-\mu_h\tau_h}\int_\Omega \Gamma(D_h\tau_h,x,y)f\left(\frac{u_1(t-\tau_h,y)u_4(t-\tau_h,y)\bar{u}_2^*}{\bar{u}_1^*\bar{u}_4^*u_2}\right)\mathrm{d}y,
\end{aligned}
$$

which implies

$$\int_\Omega \frac{\partial U(t,x)}{\partial t}\mathrm{d}x \le \beta_h e^{-\mu_h\tau_h}\int_\Omega\left(\frac{u_4}{\bar{u}_4^*}-\frac{u_2}{\bar{u}_2^*}+\ln\frac{\bar{u}_4^* u_2}{u_4\bar{u}_2^*}\right)\mathrm{d}x. \tag{3.4.13}$$

Similarly, let

$$\begin{aligned}
&U_3(t,x)=f(\frac{u_3}{\bar{u}_3^*}),\ U_4(t,x)=f(\frac{u_4}{\bar{u}_4^*}),\\
&U_{+4}(t,x)=\beta_v e^{-\mu_v\tau_v}\int_{t-\tau_v}^{t}\int_\Omega \Gamma(D_v(t-\sigma),x,y)f(\frac{u_2(\sigma,y)u_3(\sigma,y)}{\bar{u}_2^*\bar{u}_3^*})\mathrm{d}\sigma\mathrm{d}y,\\
&V(t,x)=\frac{e^{-\mu_v\tau_v}}{\bar{u}_2^*}U_3+\frac{\bar{u}_4^*}{\bar{u}_3^*\bar{u}_2^*}U_4+U_{+4}.
\end{aligned} \tag{3.4.14}$$

By calculating the time derivative of the functions in (3.4.14) with respect to time t along system (3.4.8), we can obtain

$$\begin{aligned}
&\int_\Omega \frac{\partial V(t,x)}{\partial t}\mathrm{d}x\\
&\le \int_\Omega\Bigg[-\frac{\mu_v e^{-\mu_v\tau_v}(u_3-\bar{u}_3^*)^2}{u_3\bar{u}_3^*\bar{u}_2^*}+\beta_v e^{-\mu_v\tau_v}\left(-f(\frac{\bar{u}_3^*}{u_3})-\frac{u_4}{\bar{u}_4^*}+\frac{u_2}{\bar{u}_2^*}-\ln\frac{\bar{u}_4^*u_2}{u_4\bar{u}_2^*}\right)\\
&\quad -\beta_v e^{-\mu_v\tau_v}\int_\Omega \Gamma(D_v\tau_v,x,y)f\left(\frac{u_3(t-\tau_v,y)u_2(t-\tau_v,y)\bar{u}_4^*}{\bar{u}_3^*\bar{u}_2^*u_4}\right)\mathrm{d}y\Bigg]\mathrm{d}x\\
&\le \beta_v e^{-\mu_v\tau_v}\int_\Omega\left(-\frac{u_4}{\bar{u}_4^*}+\frac{u_2}{\bar{u}_2^*}-\ln\frac{\bar{u}_4^*u_2}{u_4\bar{u}_2^*}\right)\mathrm{d}x.
\end{aligned} \tag{3.4.15}$$

It then follows from (3.4.13) and (3.4.15) that

$$\int_\Omega a\frac{\partial U(t,x)}{\partial t}+b\frac{\partial V(t,x)}{\partial t}\mathrm{d}x\le 0,$$

where $a=\frac{e^{\mu_h\tau_h}}{\beta_h}$ and $b=\frac{e^{\mu_v\tau_v}}{\beta_v}$. Note that

$$\int_\Omega a\frac{\partial U(t,x)}{\partial t}+b\frac{\partial V(t,x)}{\partial t}\mathrm{d}x=0.$$

if and only if $u_i(t,x)\equiv u_i(t)$, and hence, $u_i(t)=u_i^*$ and $u_i(t-\tau)=u_i^*$ $(i=1,2,3,4)$ for all $\tau\in[0,\hat{\tau}]$ for $t>0$. The largest compact invariance set in

$$\mathcal{A}_0=\{u\in\mathcal{A}:\int_\Omega a\frac{\partial U(t,x)}{\partial t}+b\frac{\partial V(t,x)}{\partial t}\mathrm{d}x=0,x\in\Omega\}$$

is $\{\bar{u}^*\}$. By LaSalle's invariance principle, we can show that $\bar{u}^*$ of system (3.4.8) is globally attractive. □

3.5 Numerical simulations

In this section, we present numerical simulations to illustrate the impacts of the spatial heterogeneity, the seasonality, and the periodic incubation periods on the basic reproduction number $\mathcal{R}_0$. More specifically, we apply the system (3.2.6) to the malaria transmission in Maputo Province, Mozambique.

Malaria transmission vectors are female *A.funestus* and *A.gambiae* mosquitoes. Mozambique is a sub-Saharan African country and the risk of malaria is present throughout the country. National Malaria Control Programme (NMCP) pointed out that malaria caused 44, 000–67, 000 deaths each year for all age groups in their 2003 report. The confirmed malaria cases keep increasing these years and it worsened substantially in 2014, according to WHO report (see http://www.who.int/malaria/publications/country-profiles/profile-moz-en.pdf): about 3,297,386 cases of malaria were already confirmed in the 1st half of 2014, and 131,936 cases in Maputo Province.

According to Mozambique Population Census in 2007 (see http://www.geohive.com/cntry/mozambique.aspx), Maputo Province had a population of 1, 205, 709, with an area of 22,693 km^2, the population density was about 53 (km^2)$^{-1}$, which can be chosen as N_h. From World Population Review, there were about 946,813 births in Mozambique in 2007 (see http://worldpopulationreview.com/countries/mozambique-population/births/), with an area of 801,590 km^2, hence we can estimate the crude human birth rate as $\Lambda_h = \frac{946{,}813}{801590\times 12} = 0.0984$ (km$^2 \cdot$ Month)$^{-1}$. In [20], the authors determined the range of important parameters in malaria dynamics. As the climate of Maputo Province is favorable for malaria transmission, the authors in [129] studied the seasonality impacts on malaria transmission, including evaluating the seasonal forced biting rate $b(t)$, and periodic mortality rate mosquitoes $\mu_v(t)$, the periodic EIP $\tau_v(t)$ and recruitment rate of mosquitoes $\Lambda_v(t)$, where

$$\begin{aligned} b(t) = {} & 6.983 - 1.993\cos(\pi t/6) - 0.4247\cos(\pi t/3) - 0.128\cos(\pi t/2) \\ & - 0.04095\cos(2\pi t/3) + 0.0005486\cos(5\pi t/6) - 1.459\sin(\pi t/6) \\ & - 0.007642\sin(\pi t/3) - 0.0709\sin(\pi t/2) + 0.05452\sin(2\pi t/3) \\ & - 0.06235\sin(5\pi t/6)\ \text{Month}^{-1}, \end{aligned} \tag{3.5.1}$$

$$\begin{aligned} \mu_v(t) = {} & 3.086 + 0.04788\cos(\pi t/6) + 0.01942\cos(\pi t/3) + 0.007133\cos(\pi t/2) \\ & + 0.0007665\cos(2\pi t/3) - 0.001459\cos(5\pi t/6) + 0.02655\sin(\pi t/6) \\ & + 0.01819\sin(\pi t/3) + 0.01135\sin(\pi t/2) + 0.005687\sin(2\pi t/3) \\ & + 0.003198\sin(5\pi t/6)\ \text{Month}^{-1}, \end{aligned} \tag{3.5.2}$$

$$\tau_v(t) = 1/30.4(17.25 + 8.369\cos(\pi t/6) + 4.806\sin(\pi t/6) + 3.27\cos(\pi t/3) + 2.857\sin(\pi t/3) + 1.197\cos(\pi t/2) + 1.963\sin(\pi t/2) + 0.03578\cos(2\pi t/3) + 1.035\sin(2\pi t/3) - 0.3505\cos(5\pi t/6) + 0.6354\sin(5\pi t/6) - 0.3257\cos(\pi t) + 0\sin(\pi t)) \text{ Month}, \tag{3.5.3}$$

$$\Lambda_v(t) = k \times b(t)\ (\text{km}^2 \cdot \text{Month})^{-1}, \text{ where } k = 5 \times 53.13. \tag{3.5.4}$$

All the variables and parameters as well as their definitions are listed in Table 3.2. We remark that in system (3.2.6), we let $\beta_h = \dfrac{b}{N_h}\tilde{\beta}_h$ and $\beta_v = \dfrac{b}{N_h}\tilde{\beta}_v$. For convenience, we take the domain to be one dimensional $\Omega = (0, \pi)$.

Table 3.2: Parameters values in simulation

Para	Definition	Value (range)	Sources
N_h	Total human population density	$53\ (\text{km}^2)^{-1}$	see text
Λ_h	Crude human birth rate	$0.0984\ (\text{km}^2 \cdot \text{month})^{-1}$	see text
μ_h	Human natural death rate	0.001574	[129]
c	Constant human recovery rate	$(0.0014 - 0.017) \times 30.4\ \text{month}^{-1}$	[20]
Λ_v	Recruitment rate at which female adult mosquitoes emerge from larvae	(3.5.4)	[129]
μ_v	Mosquito death rate	(3.5.2)	[129]
b	Mosquito biting rate	(3.5.1)	[129]
$\tilde{\beta}_h$	Transmission probability per bite from infectious mosquitoes to humans	0.010-0.27	[20]
$\tilde{\beta}_v$	Transmission probability per bite from infectious humans to mosquitoes	0.072-0.64	[20]
τ_h	Incubation period for *P.vivax* in humans (IIP)	(5-26)/30.4 month	
τ_v	Incubation period in mosquitoes (EIP)	(3.5.3)	[129]
D_h	Human diffusion rate	$0.1\ \text{km}^2 \cdot \text{month}^{-1}$	
D_v	Mosquito diffusion rate	$0.0125\ \text{km}^2 \cdot \text{month}^{-1}$	

To compute $\mathcal{R}_0$, we use the numerical scheme presented in Remark 1.4.1 (please see also [79, Lemma 2.5 and Remark 3.2]). We choose $\alpha_h = c \cdot (1.05 - \cos(2x))$ Month^{-1}, where $c = 0.0016$, to reflect the fact that people living urban area (around the center of the spatial domain) can receive better medical treatments than those in rural area, which leads to higher recovery rate around the center. We select $\tilde{\beta}_h = 0.25$, $\tilde{\beta}_v = 0.34$,

$\tau_h = 7/30.4$ Month^{-1} and keep other parameters as listed in Table 3.2. For this set of parameters, we can compute the basic reproduction number numerically and have $\mathcal{R}_0 = 2.3907 > 1$ which implies that the disease is persistent in host and vector populations. Figure 3.2 shows the corresponding long term behavior of system (3.2.6) in the case of $\mathcal{R}_0 = 2.3907$, with initial data

$$u(\theta, x) = \begin{pmatrix} 34 - 2\cos 2x \\ 5 - 2\cos 2x \\ 300 - 5\cos 2x \\ 40 - 5\cos 2x \end{pmatrix}, \ \forall \theta \in [-\hat{\tau}, 0], x \in [0, \pi].$$

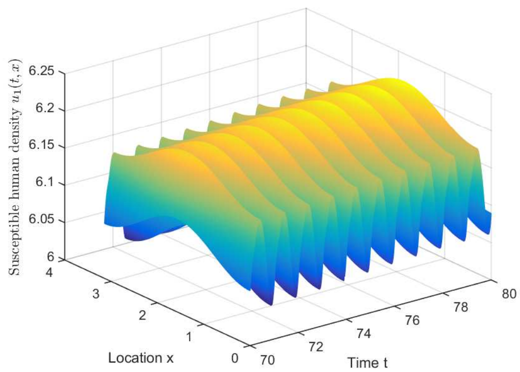
This is coincident with Theorem 3.4.1(ii). Note that we truncate the time interval by $[70, 80]$ so as to demonstrate the existence of the positive periodic solution. Decreasing the biting rate to $0.7b(t)$, and increasing the mosquito death rate to $1.5\mu_v(t)$ by using insecticide-treated nets and spraying mosquito breeding sites, then $\mathcal{R}_0 = 0.7843 < 1$. The infectious human and mosquitoes go to 0, and it describes that the disease will be eliminated (Fig. 3.3).

We are interested in the sensitivity of the disease risk $\mathcal{R}_0$ on system parameters. Take the human diffusion rate D_h and the transmission probability $\tilde{\beta}_h$ as examples. We set D_h as a parameter varying in $[0.02, 0.5]$, and $\tilde{\beta}_h$ changing from 0.010 to 0.27. Other parameters are the same as those in Fig. 3.2. This result is shown in Fig. 3.4, where $\mathcal{R}_0$ is a function of D_h and $\tilde{\beta}_h$, respectively. We plot two curves, the green one refers system (3.2.6) with a time-averaged EIP $[\tau_v]$ [129], where

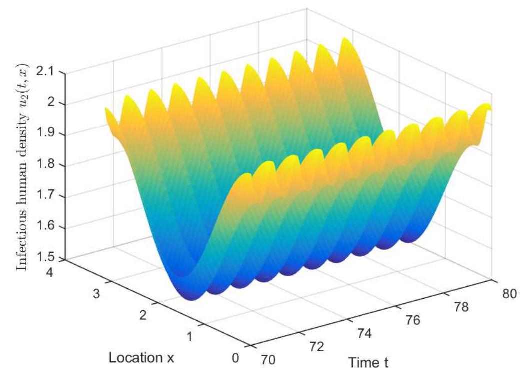
$$[\tau_v] := \frac{1}{\omega}\int_0^{\omega} \tau_v(t)\mathrm{d}t = 17.25/30.4 \text{ Month},$$

and the blue one reflects system (3.2.6) is under a time-periodic EIP. One direct observation is that, in both cases, the green curve always lie below the blue one, which reveals that the use of time-averaged EIP may underestimate the malaria disease risk. Fig. 3.4(a) shows that $\mathcal{R}_0$ is a decreasing function of D_h, there is a sharp decline when D_h is very small, and it slows down as D_h continues to increase. It seems that malaria could not be controlled by just performing a high diffusion to avoid the flying mosquitoes without doing any protection methods, such as bed nets. We notice that $\mathcal{R}_0$ increases as $\tilde{\beta}_h$ continues to increase and passes through the threshold value $\mathcal{R}_0 = 1$ (see Fig. 3.4(b)), which provide valuable insights that improving our medical treatments, such as introducing vaccine into the susceptible population, to reduce the transmission probability could be an very effective strategy in controlling the disease.

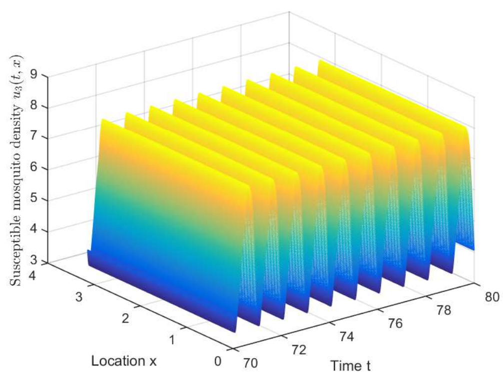
Note that the population density of infectious human at urban (central) area is less than that in rural (boundary) area in Fig. 3.2(b), which motivates us to study the effect of human recovery rate α_h on the disease risk $\mathcal{R}_0$ in a spatially heterogeneous environment. As there are more medical resources (the number of hospitals and



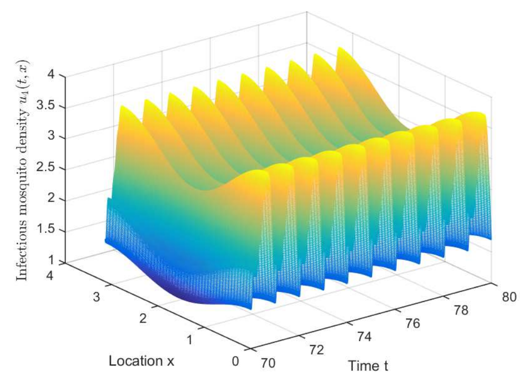
(a) The evolution of u_1.



(b) The evolution of u_2.

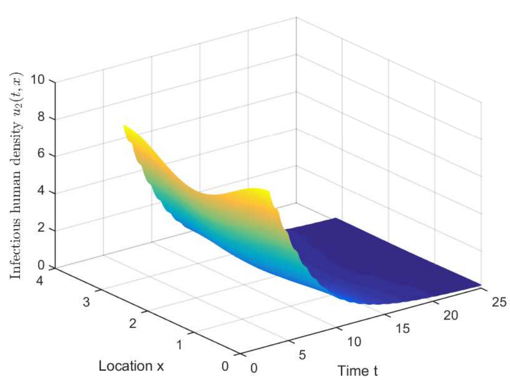


(c) The evolution of u_3.

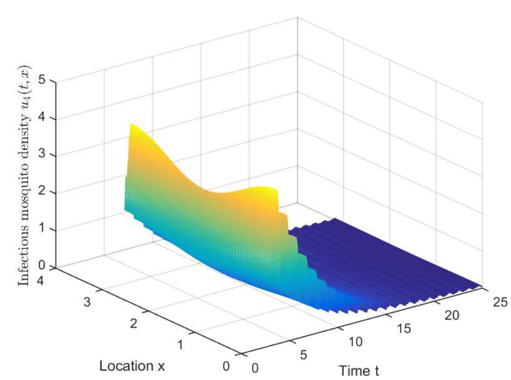


(d) The evolution of u_4.

Figure 3.2: Evolution of infectious humans and mosquitoes when $\mathcal{R}_0 = 2.3907 > 1$

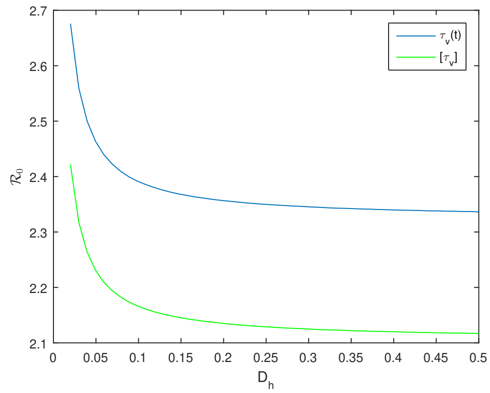


(a) The evolution of u_2 (infectious humans).

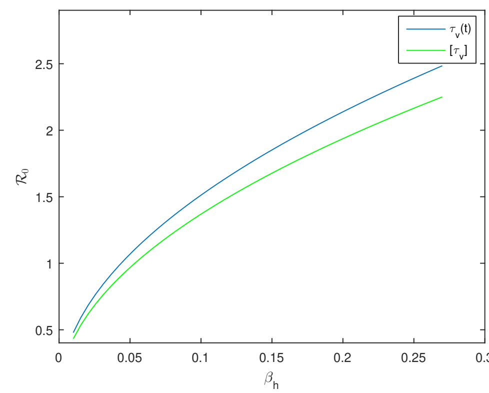


(b) The evolution of u_4 (infectious mosquitoes).

Figure 3.3: Evolution of infectious humans and mosquitoes when $\mathcal{R}_0 = 0.7843 < 1$



(a) $\mathcal{R}_0$ as a function of D_h.



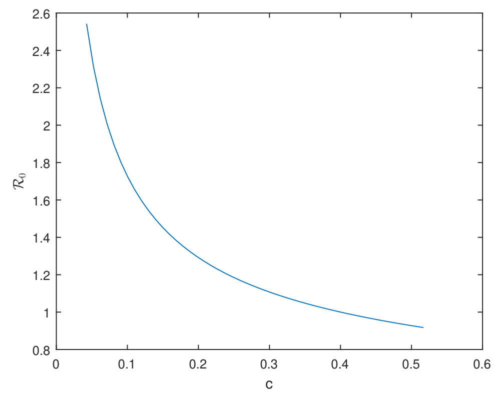
(b) $\mathcal{R}_0$ as a function of $\tilde{\beta}_h$

Figure 3.4: $\mathcal{R}_0$ *vs* D_h and $\tilde{\beta}_h$

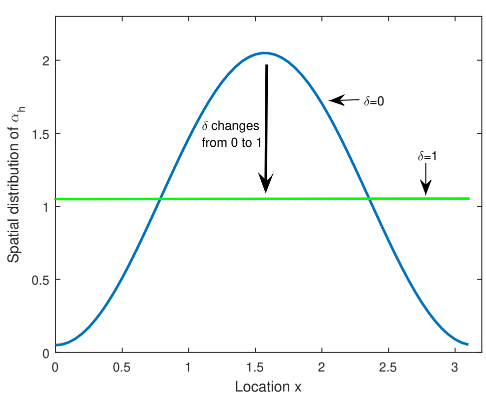
physicians, drugs supply, advanced medical equipments) in urban area than those in the rural, people can access to better medical treatments in urban area, where a higher recovery rate can be observed. In Fig. 3.5(a), we let c in α_h vary in $[0.042, 0.517]$. It describes a strategy that in the current distribution of medical resources, we make efforts to develop new drugs to improve the recovery rate. Fig. 3.5(a) demonstrates this strategy could be effective as $\mathcal{R}_0$ declines below the threshold value, hence the disease could be controlled. We test another strategy in Figs. 3.5(b) and 3.5(c). We wish to see if keeping balance of the medical resource distribution between urban and rural areas can help to control the disease for a fixed recovery level. We fix $c = 0.297$, and introduce a new parameter δ into α_h, that is, $\alpha_h(x) = 0.297 \times (1-(1-\delta)\cos(2x))$, where $\delta \in [0, 1]$. When $\delta = 0$, there is a highest recovery rate at the urban area (around the center of spatial domain, i.e., $x = \frac{\pi}{2}$). As δ changing from 0 to 1, medical resources are delivered to rural areas nearby (near $x = 0$ and $x = \pi$), and eventually distributed evenly in space (see Fig. 3.5(b)). The total medical resources remain the same since the spatial average of $\alpha_h(x)$ does not change for all $\delta \in [0, 1]$, i.e., $\int_0^\pi \alpha_h(x)\mathrm{d}x = 9.028$. $\mathcal{R}_0$ is a decreasing function of δ, drops below 1 and reaches its minimum at $\delta = 1$. This result indicates that environmental heterogeneity does play an important role in designing schemes to control the disease.

3.6 Discussion

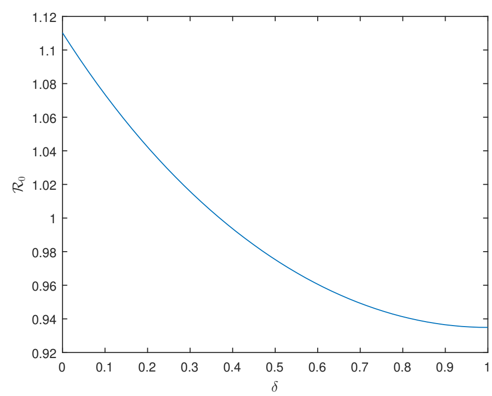
As mentioned in [16, 82, 109, 129], combined effects of varying incubation periods, spatial structure and seasonal variation are worth investigating in the study of vector-borne disease transmission. In this chapter, we formulate and analyze a nonlocal reaction-diffusion model of vector-borne disease with periodic delays.



(a) $\mathcal{R}_0$ as a function of c.



(b) Distribution of α_h.



(c) $\mathcal{R}_0$ as a function of δ.

Figure 3.5: Effect of human recovery rate α_h

With the recent theory developed in [79,144], we can derive the basic reproduction number $\mathcal{R}_0$, which describes the ability of a disease to persist [34] and measures the risk of an epidemic [51]. $\mathcal{R}_0$ is defined as the spectral radius of an next generation operator and can be computed numerically. One interesting mathematical feature of our model is the periodic delays, which reflects the impacts of seasonal fluctuation on disease dynamics. Motivated by [83], we define a suitable phase space on which the linearized system for infectious compartments generates an eventually strongly monotone periodic semiflow. By the comparison arguments and persistence theory for periodic semiflows, we show that $\mathcal{R}_0$ is a threshold parameter for the extinction and persistence of the vector-borne disease. Moreover, the disease will be eliminated if $\mathcal{R}_0 < 1$, and if $\mathcal{R}_0 > 1$, the disease persists in the susceptible populations and exhibit spatial and seasonal fluctuations. For the model with constant parameters, we obtain the explicit expression of $\mathcal{R}_0$, and further use the fluctuation method developed in [120] to prove the global attractivity of the constant positive steady state in the case of $\mathcal{R}_0 > 1$. It is worth mentioning that the method of Lyapunov functionals was employed in [50] to prove the global stability of positive constant steady state for a class of reaction-diffusion systems without nonlocal terms.

In the simulation section, we use some published data to study the malaria transmission in Maputo Province, Mozambique. Our numerical result shows that the risk of the disease, which is measured by $\mathcal{R}_0$, could be underestimated if we just consider the time-averaged extrinsic incubation period. Seasonal fluctuations may bring challenges to the control of the disease. Biologically, it is well understood that diffusion has a positive effect on reducing $\mathcal{R}_0$ to some extent, since mosquitoes could have difficulties in taking a blood meal among moving hosts. However, $\mathcal{R}_0$ declines to certain value above the critical value, which indicates that the disease could not be controlled by only performing a high diffusion to avoid the flying mosquitoes. Medical strategies (see Figs. 3.4(b) and 3.5(a)), such as improving medical treatments, developing new drugs and introducing vaccination, may be the most effective strategy to eliminate malaria from this area. Generally speaking, medical treatment, mosquito reduction and personal protections are three important disease control strategies, and the study of an optimal control among them can reveal very useful insights in control schemes [69, 70]. It has long been understood that the spatial heterogeneity has a large impact on disease transmission. Our simulation results (Figs. 3.5(b) and 3.5(c)) support the expectation that keeping balance of resources distribution could help to control the disease.

Chapter 4

A birth pulse population model with nonlocal dispersal

4.1 Introduction

How the growth and spatial spread of an invasive species interact with environment and affect the propagation process is an important and challenging problem [14,41,75], as biological invasions have significant impact on ecology and human society [75]. For many invasive species (e.g., birds, large mammals), individuals give birth only on a particular time of a year. For example, big brown bats usually reproduce only in late June in Colorado [42]. Such species is called a birth pulse population [18]. Birth pulse can generate complex dynamics that are described by matrix models [18, 98, 101] and consumer-resource models [104]. Once the individuals of a birth pulse species have established locally, they begin to spread and invade new territory. Individual dispersal serves as a driving factor. For a birth pulse species with distinct reproductive and dispersal stages, Lewis and Li [74] proposed an impulsive reaction-diffusion model to describe the within-season and between-season dynamics. The dispersal pattern is assumed to be random diffusion, that is, an individual walker performs a random walk on the real line with a fixed step [17, 122]. Recently, Fazly, Lewis and Wang [40] extended these results to a bounded domain of higher spatial dimension.

It should be pointed out that random diffusion may be regarded as a local behaviour [61], which leads to a small-scale result over a single equation model [106], and even may underestimate speeds of invasion [22]. However, some species can indeed disperse according to a non-local pattern, that is, an individual walker can choose its step randomly from some distribution [7, 72, 110]. This motivates us to consider a species with a birth pulse and a nonlocal dispersal governed by an integral operator. More precisely, we assume that the species consists of two distinct development stages: a reproductive stage that is assumed to occur at the beginning of a year, and

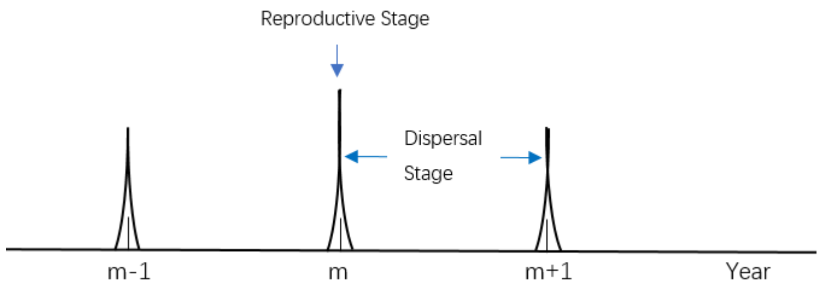


Figure 4.1: A species with distinct reproductive and dispersal stages

a dispersal stage throughout the year (Figure 4.1). Thus, we employ the following impulsive integro-differential model to study its invasion dynamics:

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = d\left\{\int_\Omega J(x,y)u_m(t,y)\mathrm{d}y - u_m\right\} + f(u_m),\ x \in \bar{\Omega},\ 0 < t \le 1, \\ &u_m(0,x) = g(N_m(x)), \\ &N_{m+1}(x) = u_m(1,x). \end{aligned} \tag{4.1.1}$$

Here $N_m(x)$ and $u_m(t,x)$ denote the population densities at location x at the beginning of year m, and within year m, respectively. For simplicity, we let $t \in [0,1]$. In the reproductive stage of year m, a birth pulse is described by a discrete-time model with a positive function g. During the dispersal stage within year m, the changes in population density are described by a density-dependent function f. Their movements in the spatial domain Ω are governed by a dispersal kernel J with a dispersal rate d. Note that the dispersal kernel $J(x,y)$ denotes the probability for the individuals to move from location y to location x. At the end of year m, $u_m(1,x)$ provides the density of the species for the start of year $m+1$, denoted by $N_{m+1}(x)$.

An interesting observation about the impulsive nonlocal dispersal model (4.1.1) is the combination of an integro-differential equation and a discrete-time iteration, which plays a key role in the following mathematical discussions. Moreover, we let Q represent the time-one solution map of the following integro-differential equation

$$\frac{\partial u}{\partial t} = d\left\{\int_\Omega J(x,y)u(t,y)\mathrm{d}y - u\right\} + f(u),\ x \in \bar{\Omega}. \tag{4.1.2}$$

Then model (4.1.1) can be reduced to a discrete-time recursion:

$$N_{m+1}(x) = Q[g(N_m(\cdot))](x) = \hat{Q}[N_m](x),\ x \in \bar{\Omega},\ \forall m \ge 0, \tag{4.1.3}$$

where $\hat{Q} = Q \circ g$.

Generally speaking, a biological invasion usually consists of four processes: introduction, establishment, spread and impact [75]. Here we focus our analysis on two questions: (i) whether a species can establish locally after some individuals are introduced to new environments, in other words, what is the asymptotic behavior for a bounded domain with a lethal exterior, and (ii) what is the propagation dynamics once they begin to spread, that is, how spreading speeds and traveling waves can be captured in an unbounded domain? To answer (i), we first derive a threshold condition, and then establish a corresponding threshold-type result. We can further prove the uniqueness and global attractivity of the positive steady state when the birth pulse is monotone. We also present an application of insect pests outbreak to briefly discuss the critical domain size. Note that if the birth pulse is monotone, then $\hat{Q}$ in system (4.1.3) is monotone. When the species spreads in an unbounded domain, by the theory developed in [39, 80], we can obtain the existence and estimation of the spreading speed and show that it coincides with the minimal wave speed for monotone traveling waves. For the propagation phenomena with a non-monotone birth pulse, the main challenge is to look for traveling waves for a non-monotone and non-compact operator, where the Schauder fixed point theorem fails to work. However, we can show that this operator is a κ-contraction under an appropriate condition, and therefore, we obtain the existence of traveling waves by applying the asymptotic fixed point theorem (see, e.g., [145, Theorem 1.1.4]). Numerically, we simulate the evolution of an invasive population in bounded and unbounded domains, respectively, and find that it could exhibit oscillations in an unbounded domain.

The rest of this paper is organized as follows. In Section 2, we discuss the threshold dynamics for system (4.1.3) in a bounded domain with a lethal exterior. We investigate the propagation dynamics in an unbounded domain in Section 3, including the existence and estimation of the spreading speed, and its coincidence with the minimal wave speed for monotone traveling waves. Simulations are presented in Section 4 and a brief discussion finishes the paper.

4.2 Threshold dynamics in a bounded domain

In this section, we assume that the spatial domain $\Omega \subset \mathbb{R}$ is a bounded and open interval containing the origin, and the environment is hostile outside $\bar{\Omega}$, which refers to the scenario when population individuals locate in $\bar{\Omega}^c$, the complement of $\bar{\Omega}$, they die immediately and hence, $u(t,x) \equiv 0$, $\forall x \in \bar{\Omega}^c$. Throughout this paper, we make the following assumptions:

(J1) $J(x,y)$ is nonnegative and continuous on $\mathbb{R} \times \mathbb{R}$ such that $J(x,x) > 0$ for any $x \in \mathbb{R}$, $\int_{\mathbb{R}} J(x,y)\mathrm{d}x \equiv 1$, and $\int_{\mathbb{R}} J(x,y)\mathrm{d}y \equiv 1$.

(H1) Two functions g and f are defined on $\mathbb{R}^+$ and admit the following properties:

(i) $g(N)$ is continuous for $N \geq 0$, $g(0) = 0$, $g'(0) > 0$, $g(N) > 0$ for $N > 0$. Moreover, $g(N)/N$ is nonincreasing for N, and there exists $\bar{N} > 0$ such that $g(\bar{N}) \leq \bar{N}$. For every bounded set $U \subset \mathbb{R}^+$, there exists $\mathcal{L}_{g,U} > 0$ such that $|g(N_1) - g(N_2)| \leq \mathcal{L}_{g,U}|N_1 - N_2|$, for any $N_1, N_2 \in U$.

(ii) $f(0) = 0$, $f'(0) \neq 0$, and there exists $\tilde{N} > 0$ such that $f(N) < 0$, $\forall N \geq \tilde{N}$. Moreover, $f(N)/N$ is strictly decreasing in N. For every bounded set $V \subset \mathbb{R}^+$, there exists $\mathcal{L}_{f,V} > 0$ such that $|f(N_1) - f(N_2)| \leq \mathcal{L}_{f,V}|N_1 - N_2|$, for any $N_1, N_2 \in V$.

The birth pulse functions commonly used in the biological literature include the Beverton-Holt function

$$g(N) = \frac{pN}{q+N}, \text{ with } p > 0 \text{ and } q > 0, \tag{4.2.1}$$

and the Ricker function

$$g(N) = Ne^{r(1-N)}, \text{ with } r > 0. \tag{4.2.2}$$

A prototypical function satisfying the assumption (H1)(ii) takes the form:

$$f(N) = -aN - bN^2, \tag{4.2.3}$$

where $a > 0$ represents the death rate during the dispersal stage, $b > 0$ denote the competition coefficient. For more general forms and biological interpretations of g and f, we refer to [40, 74] and references therein.

4.2.1 Monotone case of g

We first consider the following impulsive model without spatial dispersal

$$\begin{aligned} &\frac{\mathrm{d}u}{\mathrm{d}t} = f(u), \ 0 < t \leq 1, \\ &u(0) = g(N_m), \\ &N_{m+1} = u(1). \end{aligned} \tag{4.2.4}$$

Let A denote the time-one solution map of the ordinary differential equation in model (4.2.4). It then follows that model (4.2.4) can be reduced to a discrete-time system

$$N_{m+1} = A \circ g(N_m), \ \forall m \geq 0. \tag{4.2.5}$$

By assumption (H1)(ii), we see that A is monotone in the sense that $A(\phi) \geq A(\psi)$ if $\phi \geq \psi \geq 0$, compact, and strongly subhomogeneous in the sense that $A(\alpha\phi) \gg \alpha A(\phi)$,

$\forall \phi > 0$, $\forall \alpha \in (0,1)$. Note that (H1)(ii) implies that there exists a unique positive N^* such that $f(N^*) = 0$. Define $M_0 = \max\{\bar{N}, N^*\}$, where $\bar{N}$ is stated in (H1)(i). Let N_m be the solution of recursion (4.2.5). It is easy to see that for any $M \geq M_0$, there holds $0 \leq N_m \leq M$ whenever $0 \leq N_0 \leq M$. Clearly, $(A \circ g)'(0) = e^{f'(0)} g'(0)$. As a straightforward consequence of [145, Theorem 2.3.4], we have a threshold-type result on the global dynamics of system (4.2.5).

Proposition 4.2.1. *The following statements are valid:*

(i) If $e^{f'(0)} g'(0) \leq 1$, then $N_m = 0$ is globally asymptotically stable for system (4.2.5) in $\mathbb{R}^+$.

(ii) If $e^{f'(0)} g'(0) > 1$, then system (4.2.5) admits a unique fixed point $\beta > 0$, and it is globally asymptotically stable in $\mathbb{R}^+ \setminus \{0\}$.

Let $C(\bar{\Omega}, \mathbb{R})$ be equipped with the norm $\|\phi\| = \max_{x \in \bar{\Omega}} |\psi(x)|$. For $\phi, \psi \in C(\bar{\Omega}, \mathbb{R})$, we write $\phi \geq (\gg) \psi$ if $\phi(x) \geq (>) \psi(x)$ for all $x \in \bar{\Omega}$, and $\phi > \psi$ if $\phi \geq \psi$ but $\phi \neq \psi$. Let $C(\bar{\Omega}, \mathbb{R}^+) = \{\phi \in C(\bar{\Omega}, \mathbb{R}) : \phi(x) \geq 0, \forall x \in \bar{\Omega}\}$. For any $\phi \in C(\bar{\Omega}, \mathbb{R}^+)$, system (4.1.2) (system (4.1.3)) has a unique nonnegative solution $u(t, \phi)$ ($N_m(\phi)$) with initial condition $u(0, \phi) = \phi$ ($N_0 = \phi$). Hence, $Q(\phi) = u(1, \phi)$ and $\hat{Q}^m(\phi) = N_m(\phi)$, respectively. In order to prove the global dynamics of system (4.1.3), we make the following additional assumption on f and g.

(H2) There are real numbers $G > 0$, $F > 0$, $\sigma_g > 0$, $\sigma_f > 0$, $\nu_g > 1$ and $\nu_f > 1$ such that $g(N) \geq g'(0)N - GN^{\nu_g}$, $\forall 0 \leq N \leq \sigma_g$, and $f(N) \geq f'(0)N - FN^{\nu_f}$, $\forall 0 \leq N \leq \sigma_f$.

It is easy to verify that if g and f are twice continuous functions with $g(0) = f(0) = 0$, then (H2) is satisfied automatically. Clearly, the functions in (4.2.1), (4.2.2) and (4.2.3) satisfy (H2).

We proceed by linearizing model (4.1.1) at zero in the bounded domain:

$$
\begin{aligned}
&\frac{\partial u_m}{\partial t} = d\left\{\int_\Omega J(x,y) u_m(t,y)\mathrm{d}y - u_m\right\} + f'(0)u_m,\ x \in \bar{\Omega},\ 0 < t \leq 1,\\
&u_m(0,x) = g'(0)N_m(x),\\
&N_{m+1}(x) = u_m(1,x).
\end{aligned}
\tag{4.2.6}
$$

Let S be the time-one solution map of the linear evolution system

$$
\frac{\partial u_m}{\partial t} = d\left\{\int_\Omega J(x,y) u_m(t,y)\mathrm{d}y - u_m\right\} + f'(0)u_m,\ x \in \bar{\Omega}.
$$

Then $N_m(x)$ of model (4.2.6) satisfies the recursion system

$$
N_{m+1}(x) = S[g'(0)(N_m(\cdot))](x) = \hat{S}[N_m](x),\ x \in \bar{\Omega},\ \forall m \geq 0,
\tag{4.2.7}
$$

where $\hat{S} = S \circ g'(0)$. Define

$$S_0[\phi](x) := d \int_\Omega J(x,y)\phi(y)\mathrm{d}y, \ \forall x \in \bar{\Omega}.$$

By assumption (J1), we can verify that S_0 is compact and $S_0^k := (S_0)^k$ is strongly positive for some integer $k > 0$. In view of [80, Lemma 3.1], the spectral radius $\rho(S_0)$ is a simple eigenvalue of S_0 with a positive eigenfunction $\phi^* \in C(\bar{\Omega}, \mathbb{R}^+)$. It then follows that the following eigenvalue problem

$$\lambda\phi(x) = d \int_\Omega J(x,y)\phi(y)\mathrm{d}y, \ x \in \bar{\Omega}. \tag{4.2.8}$$

admits a principal eigenvalue $\lambda_0(\Omega) = \rho(S_0)$ associated with a positive eigenfunction ϕ^*. Thus, $\lambda(\Omega) := \lambda_0(\Omega) - d + f'(0)$ is the principal eigenvalue of the following problem

$$\lambda\phi(x) = d \int_\Omega J(x,y)\phi(y)\mathrm{d}y - d\phi(x) + f'(0)\phi(x), \ x \in \bar{\Omega},$$

and associates a positive eigenfunction ϕ^*. It easily follows that

$$N_m(x) = \Big(e^{\lambda(\Omega)} g'(0)\Big)^m \phi^*(x), \ x \in \bar{\Omega}, \ \forall m \geq 0,$$

is a solution of system (4.2.7). In the following, we will show that $e^{\lambda(\Omega)} g'(0)$ serves as a threshold value which determines whether the species can persist.

Theorem 4.2.1. *Assume (J1), (H1) and (H2) hold, and g is monotone. The following statements are valid:*

(i) If $e^{\lambda(\Omega)} g'(0) < 1$, then $\lim_{m\to+\infty} N_m(x) = 0$ uniformly for $x \in \bar{\Omega}$.

(ii) If $e^{\lambda(\Omega)} g'(0) > 1$, then system (4.1.3) has a unique positive steady state $N^* \in C(\bar{\Omega}, \mathbb{R}^+)$ with $N^* \gg 0$, which is globally attractive in the sense that for any $N_0 \in C(\bar{\Omega}, \mathbb{R}^+)$ with $N_0 > 0$, there holds $\lim_{m\to+\infty} N_m(x) = N^*(x)$ uniformly for $x \in \bar{\Omega}$.

Proof. (i) In the case where $e^{\lambda(\Omega)} g'(0) < 1$, let $W_m(x) = \delta\Big(e^{\lambda(\Omega)} g'(0)\Big)^m \phi^*(x), \forall m \geq 0$, where δ is a positive constant. We claim $W_m(x)$ satisfies the following linear problem

$$\begin{aligned}
&\frac{\partial u_m}{\partial t} = d \int_\Omega J(x,y) u_m(t,y)\mathrm{d}y - du_m + f'(0)u_m, \ x \in \bar{\Omega}, \ 0 < t \leq 1, \\
&u_m(0,x) = g'(0)W_m(x), \\
&W_{m+1}(x) = u_m(1,x).
\end{aligned} \tag{4.2.9}$$

Clearly, $u(t,x) = \delta g'(0)e^{\lambda(\Omega)t}\phi^*(x)$ is a solution of the linear equation $\frac{\partial u}{\partial t} = d\int_\Omega J(x-y)u(t,y)\mathrm{d}y - du + f'(0)u$ satisfying $u(0,x) = \delta g'(0)\phi^*(x)$. It then follows that $u(1,x) = \delta g'(0)e^{\lambda(\Omega)}\phi^*(x) = W_1(x)$, and hence, the desired result follows from the induction argument. Furthermore, one can easily see that if $e^{\lambda(\Omega)}g'(0) < 1$, then $\lim_{m\to+\infty} W_m(x) = 0$ uniformly for $x \in \bar{\Omega}$.

For any given initial value $u_0(x,0) = N_0(x)$ in system (4.1.3), we choose δ sufficiently large such that $N_0(x) \le W_0(x)$. Since

$$\frac{\partial u_m}{\partial t} = d\int_\Omega J(x,y)u_m(t,y)\mathrm{d}y - du_m + f'(0)u_m \ge d\int_\Omega J(x,y)u_m(t,y)\mathrm{d}y - du_m + f(u_m)$$

for nonnegative u_m, together with the comparison argument and induction, we have $N_m(x) \le W_m(x)$ for all $m \ge 0$ and $x \in \bar{\Omega}$. It then follows that $\lim_{m\to+\infty} N_m(x) = 0$ uniformly for $x \in \bar{\Omega}$.

(ii) In order to prove the existence and uniqueness of the positive steady state, we introduce

$$\tilde{X} = \{\psi : \bar{\Omega} \to \mathbb{R} : \psi \text{ is bounded and Lebesgue measurable in } \Omega\}$$

with norm $\|\psi\|_{\tilde{X}} = \sup_{x\in\bar{\Omega}} |\psi(x)|$. It then follows that $(\tilde{X}, \|\cdot\|_{\tilde{X}})$ is a Banach space. Define $\tilde{X}_+ = \{\psi \in \tilde{X} : \psi(x) \ge 0,\ \forall x \in \bar{\Omega}\}$. Then $\tilde{X}_+$ is a positive cone of $\tilde{X}$ and induces a partial ordering on $\tilde{X}$. It is easy to prove the interior of $\tilde{X}$, denoted by $\mathrm{int}(\tilde{X}_+)$ is nonempty, and $\mathrm{int}(\tilde{X}_+) = \{\psi \in \tilde{X}_+ : \psi(x) \ge \epsilon \text{ for some } \epsilon > 0,\ \forall x \in \bar{\Omega}\}$. Observe that for any $\psi \in \tilde{X}_+$, system (4.1.2) (system (4.1.3)) has a unique nonnegative solution $u(t,\psi)$ ($N_m(\psi)$) with initial condition $u(0,\psi) = \psi$ ($N_0 = \psi$). Put $Q(\psi) = u(1,\psi)$ and $\hat{Q}^m(\psi) = N_m(\psi)$, respectively. We can verify that Q is strongly subhomogeneous in the sense that $Q(\alpha\psi) \gg \alpha Q(\psi)$, $\forall \psi \in \mathrm{int}(\tilde{X}_+)$, $\alpha \in (0,1)$. Since $g(N)/N$ is nonincreasing, we easily see that $g(N)$ is subhomogeneous. Thus, $\hat{Q} = Q \circ g$ is strongly subhomogeneous. Moreover, $\hat{Q}$ admits at most one strongly positive fixed point in $\tilde{X}$. Indeed, let ψ_1 and ψ_2 be in $\mathrm{int}(\tilde{X}_+)$ such that $\hat{Q}(\psi_i) = \psi_i$ ($i = 1,2$). By [145, Lemma 2.3.1], it follows that $\psi_1 = \tau\psi_2$ for some $\tau \in (0,1]$. We further claim $\tau = 1$, that is, $\psi_1 = \psi_2$. Otherwise, we obtain $0 < \tau < 1$, and hence, $\psi_1 = \hat{Q}(\psi_1) = \hat{Q}(\tau\psi_2) \gg \tau\hat{Q}(\psi_2) = \tau\psi_2 = \psi_1$, which is impossible.

Notice that in the case where $e^{\lambda(\Omega)}g'(0) > 1$, that is, $e^{\lambda_0(\Omega)-d+f'(0)}g'(0) > 1$, we choose $\tilde{\lambda} < \lambda_0(\Omega)$ and $\gamma < g'(0)$ such that $e^{\tilde{\lambda}-d+f'(0)}\gamma > 1$. Let $v(t,x) = \varepsilon\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^*(x)$. It follows from (H2) that for sufficiently small $\varepsilon > 0$ and $0 < t \le 1$, we have

$$g(v(t,x)) \ge \gamma v(t,x) + v(t,x)\Big([g'(0)-\gamma] - G\varepsilon^{\nu_g-1}[\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^*(x)]^{\nu_g-1}\Big) \ge \gamma v(t,x).$$

By (H2), we have $f(v) \geq f'(0)v - Fv^{\nu_f}$, and hence

$$\begin{aligned}
&\frac{\partial v}{\partial t} - d\int_{\Omega} J(x,y)v(t,x)\mathrm{d}y + dv - f(v) \\
&\leq \varepsilon\gamma(\tilde{\lambda} - d + f'(0))e^{(\tilde{\lambda}-d+f'(0))t}\phi^* - d\int_{\Omega} J(x,y)\varepsilon\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^*(y)\mathrm{d}y \\
&\quad + d\varepsilon\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^* - \varepsilon\gamma e^{(\tilde{\lambda}-d+f'(0))t}f'(0)\phi^* + F[\varepsilon\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^*]^{\nu_f} \\
&= v\Big((\tilde{\lambda} - \lambda_0(\Omega)) + F\varepsilon^{\nu_f-1}[\gamma e^{(\tilde{\lambda}-d+f'(0))t}\phi^*]^{\nu_f-1}\Big) \leq 0,
\end{aligned}$$

which shows that $v(t,x)$ is a lower solution of system (4.1.2). Thus, there exists a sufficiently small ε_0 such that for any given $\varepsilon \in (0, \varepsilon_0]$, we have $M_0 > \varepsilon\phi^*(x)$, $\forall x \in \bar{\Omega}$, and

$$\hat{Q}(\varepsilon\phi^*)(x) = Q[g(\varepsilon\phi^*)](x) \geq Q[\gamma\varepsilon\phi^*](x) \geq v(1,x) \geq \varepsilon\phi^*(x),\ \forall x \in \bar{\Omega}.$$

This implies that

$$M_0 \geq \hat{Q}^{m+1}(\varepsilon\phi^*)(x) \geq \hat{Q}^m(\varepsilon\phi^*)(x),\ x \in \bar{\Omega},\ \forall m \geq 0.$$

It then follows that there is $N_* \in \mathrm{int}(\tilde{X}_+)$ such that

$$\lim_{m\to+\infty} \hat{Q}^m(\varepsilon\phi^*)(x) = N_*(x),\ \forall x \in \bar{\Omega}. \tag{4.2.10}$$

Moreover, N_* is lower semi-continuous, that is, for any $\tilde{x} \in \bar{\Omega}$, we have $\liminf_{x\to\tilde{x}} N_*(x) \geq N_*(\tilde{x})$. Since g is monotone, it follows that $g(\hat{Q}^m(\varepsilon\phi^*))(x) \leq g(N_*)(x) \leq g(M_0)$ for $x \in \bar{\Omega}$. Let $u_m(t,x) = u(t,x,g(\hat{Q}^m(\varepsilon\phi^*)))$, $\forall (t,x) \in [0,1] \times \bar{\Omega}$. Thus, $u_m(t,x) \leq u_{m+1}(t,x) \leq u(t,g(M_0)) \leq \max_{t\in[0,1]} u(t,g(M_0))$. Therefore, there is $u(t,x)$ such that

$$\lim_{m\to+\infty} u_m(t,x) = u(t,x) \tag{4.2.11}$$

for $(t,x) \in [0,1] \times \bar{\Omega}$. In particular, $\lim_{m\to+\infty} u_m(0,x) = \lim_{m\to+\infty} g(\hat{Q}^m(\varepsilon\phi^*))(x) = u(0,x)$ for $x \in \bar{\Omega}$. On the other hand, we have $\lim_{m\to+\infty} g(\hat{Q}^m(\varepsilon\phi^*))(x) = g(N_*)(x)$ for $x \in \bar{\Omega}$, and hence, $g(N_*)(x) = u(0,x)$ for $x \in \bar{\Omega}$. Note that

$$u_m(t,x) - u_m(0,x) = \int_0^t \Big[d\int_{\Omega} J(x,y)u_m(s,y)\mathrm{d}y - du_m(s,x)\mathrm{d}s\Big] + \int_0^t f(u_m(s,x))\mathrm{d}s.$$

By Lebesgue's dominated convergence theorem, we obtain

$$u(t,x) - u(0,x) = \int_0^t \Big[d\int_{\Omega} J(x,y)u(s,y)\mathrm{d}y - du(s,x)\mathrm{d}s\Big] + \int_0^t f(u(s,x))\mathrm{d}s,$$

that is,

$$\frac{\partial u(t,x)}{\partial t} = d\int_{\Omega} J(x,y)u(t,y)\mathrm{d}y - du(t,x) + f(u(t,x)),$$

which implies that $u(t,x)$ in (4.2.11) is indeed a solution of system (4.1.2). Since $u(0,x) = g(N_*)(x), \forall x \in \bar{\Omega}$, it follows that $u(1,\cdot) = u(1,\cdot,g(N_*))$. Note that $\lim_{m\to+\infty} u_m(1,x) = u(1,x),\ \forall x \in \bar{\Omega}$, that is,

$$\lim_{m\to+\infty} \hat{Q}^{m+1}(\varepsilon\phi^*)(x) = u(1,x),\ \forall x \in \bar{\Omega}. \tag{4.2.12}$$

Therefore, (4.2.10) and (4.2.12) yield that

$$N_*(x) = u(1,x) = u(1,x,g(N_*)) = Q \circ g(N_*)(x) = \hat{Q}(N_*)(x),$$

which implies that N_* is a fixed point of the map $\hat{Q}$.

Since M_0 is an upper solution of system (4.1.3), then for any given $\rho > 1$, we have $\hat{Q}(\rho M_0) \le \rho\hat{Q}(M_0) \le \rho M_0$, and hence, $\hat{Q}^{m+1}(\rho M_0) \le \hat{Q}^m(\rho M_0) \le \rho M_0$, $\forall m \ge 0$. Recall that for the above sufficient small ε, we have $\rho M_0 > M_0 > \varepsilon\phi^*(x)$ for $x \in \bar{\Omega}$. It then follows that $\hat{Q}^m(\rho M_0)(x) \ge \hat{Q}^m(\varepsilon\phi^*)(x) > 0$ for $x \in \bar{\Omega}$. Therefore, there exists $N^* \in \tilde{X}_+$ such that $\lim_{m\to+\infty} \hat{Q}^m(\rho M_0)(x) = N^*(x)$ for $x \in \bar{\Omega}$, and N^* is upper semi-continuous, that is, for any $\tilde{x} \in \bar{\Omega}$, we have $\limsup_{x\to\tilde{x}} N^*(x) \le N^*(\tilde{x})$, and $\hat{Q}(N^*) = N^*$.

Clearly, $0 \ll N_* \le N^*$ in $\tilde{X}$. By the aforementioned uniqueness of the strongly positive fixed point of $\hat{Q}$ in $\tilde{X}$, we obtain $N_* = N^*$. Since N_* is lower semi-continuous and N^* is upper semi-continuous, it follows that N^* is continuous and $N^* \in C(\bar{\Omega},\mathbb{R}^+)$ with $N^* \gg 0$. Further, Dini's theorem implies that $\lim_{m\to+\infty} \hat{Q}^m(\varepsilon\phi^*)(x) = N^*(x)$ and $\lim_{m\to+\infty} \hat{Q}^m(\rho M_0)(x) = N^*(x)$ uniformly for $x \in \bar{\Omega}$.

For any given $N_0 = \psi \in C(\bar{\Omega},\mathbb{R}^+)$ with $\psi > 0$, we have $g(\psi) \in C(\bar{\Omega},\mathbb{R}^+)$ with $g(\psi) > 0$. It follows that $u(1,\cdot,g(\psi)) \gg 0$ (see, e.g., [61]), and hence, $N_1 = u(1,\cdot,g(\psi)) \gg 0$. We set N_1 as an initial data and further choose a sufficiently small $\varepsilon \in (0,\varepsilon_0]$ and a sufficiently large $\rho > 1$ such that $\varepsilon\phi^* \le N_1 \le \rho M_0$. Thus, $\hat{Q}^m(\varepsilon\phi^*) \le \hat{Q}^m(N_1) \le \hat{Q}^m(\rho M_0)$, $\forall m \ge 0$. It immediately follows that $\lim_{m\to+\infty} \hat{Q}^m(\psi)(x) = N^*(x)$ uniformly for $x \in \bar{\Omega}$. □

4.2.2 Non-monotone case of g

Now we consider the threshold dynamics of system (4.1.3) in the case where the birth pulse function g is non-monotone. We make the following hypothesis:

(H3) There is $\sigma > 0$ such that $g(N)$ is nondecreasing for $0 \le N \le \sigma$.

Motivated by [56, 74, 118], we introduce two monotone functions g^+ and g^-. First we define

$$g^+(N) = \max_{0\le V\le N} g(V),\ \forall N \ge 0.$$

It then follows that g^+ is nondecreasing, locally Lipschitz continuous, and $g^{+\prime}(0) = g'(0)$. In the case where $e^{f'(0)}g'(0) > 1$, Proposition 4.2.1 (ii) implies that system (4.2.5) with g replaced by g^+ has a positive fixed point $\beta^+ \in (0, \sigma]$. In such a case, we can further define g^- as follows

$$g^-(N) = \min_{N \le V \le \beta^+} g(V), \ \forall 0 \le N \le \beta^+.$$

It is easy to see that g^- is also nondecreasing, locally Lipschitz continuous, and system (4.2.5) with g replaced by g^- admits a positive equilibrium β^-. Clearly, $0 < \beta^- \le \beta \le \beta^+$. It is easy to see $g^-(N) \le g(N) \le g^+(N)$, $g^{\pm\prime}(0) = g'(0)$, $g^{\pm}(N) \le g'(0)N$, and there exists $\sigma_0 \in (0, \sigma^*]$, where $\sigma^* = \min\{\sigma, \sigma_g\}$, such that $g^{\pm}(N) = g(N)$, $\forall N \in (0, \sigma_0]$.

With the above functions g^+ and g^-, we consider two auxiliary models:

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = d\left\{\int_\Omega J(x,y)u_m(t,y)\mathrm{d}y - u_m\right\} + f(u_m), \ x \in \bar{\Omega}, \ 0 < t \le 1, \\ &u_m(0,x) = g^+(N_m^+(x)), \\ &N_{m+1}^+(x) = u_m(1,x), \end{aligned} \tag{4.2.13}$$

and

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = d\left\{\int_\Omega J(x,y)u_m(t,y)\mathrm{d}y - u_m\right\} + f(u_m), \ x \in \bar{\Omega}, \ 0 < t \le 1, \\ &u_m(0,x) = g^-(N_m^-(x)), \\ &N_{m+1}^-(x) = u_m(1,x). \end{aligned} \tag{4.2.14}$$

Similarly, models (4.2.13) and (4.2.14) can be reduced to the following discrete-time systems

$$N_{m+1}^+(x) = Q[g^+(N_m^+(\cdot))](x) = Q \circ g^+[N_m^+](x), \ x \in \bar{\Omega}, \ \forall m \ge 0, \tag{4.2.15}$$

and

$$N_{m+1}^-(x) = Q[g^-(N_m^-(\cdot))](x) = Q \circ g^-[N_m^-](x), \ x \in \bar{\Omega}, \ \forall m \ge 0. \tag{4.2.16}$$

Let $N_m^+(x)$ and $N_m^-(x)$ be solutions of systems (4.2.15) and (4.2.16), respectively. The comparison argument shows if $0 < N_0^-(x) \le N_0(x) \le N_0^+(x) \le \beta^+$, where $N_0^-, N_0, N_0^+ \in \tilde{X}_+$, then

$$0 \le N_m^-(x) \le N_m(x) \le N_m^+(x) \le \beta^+, \ x \in \bar{\Omega}, \ \forall m \ge 0.$$

Note that models (4.2.13) and (4.2.14) have the same threshold value $e^{\lambda(\Omega)}g'(0)$ according to Theorem 4.2.1. By the arguments similar to those in the proof of Theorem

4.2.1 and the comparison argument, we have the following result.

Theorem 4.2.2. *Assume that (J1), (H1), (H2) and (H3) hold, and let* $N_m(x)$ *be the solution of system (4.1.3). Then the following two statements are valid:*

(i) If $e^{\lambda(\Omega)}g'(0) < 1$*, then* $\lim_{m\to+\infty} N_m(x) = 0$ *uniformly for* $x \in \bar{\Omega}$.

(ii) If $e^{\lambda(\Omega)}g'(0) > 1$*, then there exists a positive function* $N^* \in C(\bar{\Omega}, \mathbb{R}^+)$ *with* $N^* \gg 0$ *such that* $\liminf_{m\to+\infty} \min_{x\in\bar{\Omega}} \Big(N_m(x) - N^*(x)\Big) \geq 0$.

In the rest of this section, we present a simple scenario of insect pests outbreak to briefly discuss the critical domain size for system (4.1.3) in a bounded domain $\Omega = (l_1, l_2)$ where $l_1 \leq 0 \leq l_2$ and $|l_2 - l_1| = L$. It is well known that insect pests have a serious threat to ecology balance and a risk of spreading diseases [106]. The fact that an insect population may exhibit a long distance dispersal motivates us to apply system (4.1.3) to study the insect pest outbreaks. Inspired by [40], we choose g to be

$$g(N) = (1-s)N, \ \forall N \geq 0, \tag{4.2.17}$$

where $s \in (0,1)$ is the removal rate of pests, and hence $(1-s)$ indicates the survival fraction that contributes to the population a year later (see [40]). Clearly, $g(N)$ is increasing for $N \geq 0$, and $g'(0) = 1-s$. Following [124], we assume the pests disperse according to a Laplace kernel in one spatial dimension

$$J(x) = \frac{1}{2D}e^{-\frac{|x|}{D}}, \tag{4.2.18}$$

where D is the mean dispersal distance. The eigenvalue problem (4.2.8) can be written as

$$\lambda\phi(x) = d\int_{l_1}^{l_2} \frac{1}{2D}e^{-\frac{|x-y|}{D}}\phi(y)\mathrm{d}y, \ x \in \bar{\Omega} = [l_1, l_2], \tag{4.2.19}$$

We separate the integral of (4.2.19) into two parts

$$\lambda\phi(x) = \frac{d}{2D}e^{-\frac{x}{D}}\int_{l_1}^{x} e^{\frac{y}{D}}\phi(y)\mathrm{d}y + \frac{d}{2D}e^{\frac{x}{D}}\int_{x}^{l_2} e^{-\frac{y}{D}}\phi(y)\mathrm{d}y, \tag{4.2.20}$$

and differentiate (4.2.20) to get

$$\lambda\phi'(x) = \frac{d}{2D^2}\Big[-e^{-\frac{x}{D}}\int_{l_1}^{x} e^{\frac{y}{D}}\phi(y)\mathrm{d}y + e^{\frac{x}{D}}\int_{x}^{l_2} e^{-\frac{y}{D}}\phi(y)\mathrm{d}y\Big]. \tag{4.2.21}$$

Differentiating (4.2.21), we then obtain the following linear differential equation:

$$\lambda\phi''(x) = \frac{\lambda}{D^2}\phi(x) - \frac{d}{D^2}\phi(x), \ x \in (l_1, l_2). \tag{4.2.22}$$

With (4.2.21), we further have

$$\phi'(l_1) = \frac{\phi(l_1)}{D} \text{ and } \phi'(l_2) = -\frac{\phi(l_2)}{D}, \text{ where } |l_2 - l_1| = L. \tag{4.2.23}$$

Hence, we solve equation (4.2.22) with boundary condition (4.2.23), and find the eigenvalues of (4.2.19) satisfy the following

$$\tan \frac{L\sqrt{d/\lambda - 1}}{2D} = \frac{1}{\sqrt{d/\lambda - 1}}, \tag{4.2.24}$$

provided that $\lambda < d$, and the principal eigenvalue $\lambda_0(\Omega)$ is the largest positive root of equation (4.2.24) (we can refer to [36, 86, 124] for detail discussions of system (4.2.22) with boundary condition (4.2.23)). Further, $e^{\lambda(\Omega)}g'(0) = 1$, where $\lambda(\Omega) = \lambda_0(\Omega) - d + f'(0)$, gives rises to

$$L^* = \frac{2D}{\sqrt{\dfrac{f'(0) + \ln g'(0)}{d - f'(0) - \ln g'(0)}}} \arctan \frac{1}{\sqrt{\dfrac{f'(0) + \ln g'(0)}{d - f'(0) - \ln g'(0)}}}, \tag{4.2.25}$$

provided that $0 < f'(0) + \ln g'(0) < d$. Therefore, for a given removal rate s, as a straightforward consequence of Theorem 4.2.1, we obtain the following result on the existence of critical domain size.

Proposition 4.2.2. *Assume (J1), (H1) and (H2) hold, and* $0 < f'(0) + \ln g'(0) < d$. *Let* $g(N) = (1 - s)N$ *and define*

$$L^* := \frac{2D}{\sqrt{\dfrac{f'(0) + \ln(1 - s)}{d - f'(0) - \ln(1 - s)}}} \arctan \frac{1}{\sqrt{\dfrac{f'(0) + \ln(1 - s)}{d - f'(0) - \ln(1 - s)}}}.$$

Then the following statements hold true for system (4.1.3)*:*

(i) if $L < L^*$, *then* $\lim_{m\to+\infty} N_m(x) = 0$ *uniformly for* $x \in \bar{\Omega}$, *that is, the pests go to extinction.*

(ii) if $L > L^*$, *then* $\lim_{m\to+\infty} N_m(x) = N^*(x)$ *uniformly for* $x \in \bar{\Omega}$ *for a positive steady state* N^*, *which implies that the species persists and converges to a positive steady state.*

When the species presents a Laplace distribution, we can see that the critical domain size is proportional to the mean dispersal distance D according to (4.2.25). In the case where L is given, there exists the minimum removal rate s^* given by

$$s^* = 1 - e^{-\lambda_0(\Omega) + d - f'(0)}, \ \Omega = (l_1, l_2) \text{ with } |l_2 - l_1| = L,$$

which drives the pest population to extinction, that is, if control measures are employed, such as spraying pesticides or introducing controlling pests, to increase removal rate $s > s^*$, then the pests go to extinction, and hence, we may control the insect pest outbreaks; and if $s < s^*$, then the pests persist.

4.3 Spreading speeds and traveling waves in an unbounded domain

In this section, we aim to establish the existence of the invasion speed and its coincidence with the minimal wave speed in two cases, i.e., the birth pulse function g is monotone (Section 3.1) and non-monotone (Section 3.2), respectively.

We continue to assume (H1) holds. For simplicity, we consider a spatially homogeneous unbounded domain, and assume that the dispersal only depends on the distance between the starting point y and the destination x, that is, $J(x, y) = J(x - y)$. We further assume that

(J2) J is a nonnegative continuous function such that $\int_{\mathbb{R}} J(x)\mathrm{d}x = 1$, $J(0) > 0$, $J(x) = J(-x)$, $\forall x \in \mathbb{R}$, and $\int_{\mathbb{R}} J(x)e^{\mu x}\mathrm{d}x < +\infty, \forall \mu \in [0, \mu_+^*)$, for some positive number μ_+^*.

Under the assumption $\Omega = \mathbb{R}$ and (J2), the spatially homogeneous system associated with model (4.1.1) becomes model (4.2.4). In order to study the propagation dynamics of the discrete-time recursion (4.1.3), in view of Proposition 4.2.1, we make the following additional assumption on f and g.

(H4) $e^{f'(0)}g'(0) > 1$.

4.3.1 Monotone case of g

Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$. For $\phi, \psi \in \mathcal{C}$, we write $\phi \geq (\gg)\psi$ if $\phi(x) \geq (>)\psi(x)$ for all $x \in \mathbb{R}$, and $\phi > \psi$ if $\phi \geq \psi$ but $\phi \neq \psi$. Let $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geq 0, \forall x \in \mathbb{R}\}$. Further, we equip $\mathcal{C}$ with the compact open topology, that is, the sequence of $\phi^n(x)$ converges to $\phi(x)$ as $n \to +\infty$ uniformly in any compact set on $\mathbb{R}$. For a given number $r > 0$, we define $\mathcal{C}_r := \{\phi \in \mathcal{C} : 0 \leq \phi(x) \leq r, \forall x \in \mathbb{R}\}$. Moreover, for any $y \in \mathbb{R}$, we define a translation operator T_y by $T_y(\phi)(x) = \phi(x - y)$ for all $x \in \mathbb{R}$.

Since $\hat{Q}$ of system (4.1.3) is not compact, we will use the abstract theory shown in Section 1.5.1 (please see also [39]) for monotone discrete-time semiflows with weak compactness to study the spreading speed and traveling waves for system (4.1.3).

Theorem 4.3.1. *Assume that (J2), (H1) and (H4) hold, and g is monotone. Then system (4.1.3) with $\Omega = \mathbb{R}$ has a spreading speed c^* in the sense that*

(i) If $\phi \in \mathcal{C}_\beta$, where β is the fixed point of system (4.2.5), has a compact support, then $\lim_{m\to+\infty,|x|\geq cm} \hat{Q}^m[\phi](x) = 0$, $\forall c > c^*$.

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi \not\equiv 0$, then $\lim_{m\to+\infty,|x|\leq cm} \hat{Q}^m[\phi](x) = \beta$, $\forall c \in (0, c^*)$.

Moreover, c^* is given by

$$c^* = \inf_{\mu>0} \frac{1}{\mu}\Big[d\int_{\mathbb{R}} J(x)e^{\mu x}\mathrm{d}x - d + f'(0) + \ln g'(0)\Big].$$

Proof. First, by arguments similar to those in [135, Theorem 2.2 and Lemma 3.1], together with (H1), we see that for any $\phi \in \mathcal{C}_\beta \setminus \{0\}$, there hold $\hat{Q}(\phi) \gg 0$ and $\hat{Q}(\alpha\phi) \gg \alpha\hat{Q}(\phi)$, $\forall \alpha \in (0,1)$. Next we establish some basic properties of $\hat{Q}$.

Claim. *$\hat{Q}$ satisfies hypotheses (A1)-(A5) in Section 1.5.1 with $X_\beta = [0,\beta]$.*

Clearly, item (A1) holds. Item (A2) can be proved by the arguments similar to those in [135, Lemma 3.1]. To verify item (A3), we take $x = 0$. Since any bounded set in $\mathbb{R}$ is precompact, it follows that $\kappa(\hat{Q}[\mathcal{V}](0)) = 0$. On the other hand, we also have $\kappa(\mathcal{V}(0)) = 0$ as $\mathcal{V}(0)$ is a bounded subset of $\mathbb{R}$. And hence, $\kappa(\hat{Q}[\mathcal{V}](0)) = \kappa(\mathcal{V}(0)) = 0$. Item (A4) follows from the monotonicity of Q and g. Note that the map A in system (4.2.5) is the restriction of $\hat{Q}$ to $[0,\beta] \subset \mathbb{R}$. (H4) and Proposition 4.2.1(ii) imply item (A5) holds.

According to the above claim, we see that $\hat{Q}$ satisfies all the conditions [39, Remark 3.7]. Therefore, system (4.1.3) has a spreading speed c^* satisfying statements (i) and (ii) in Theorem 4.3.1. In order to compute c^*, we consider the linearized system at zero, which is given by

$$\begin{aligned}
&\frac{\partial u_m}{\partial t} = d\int_{\mathbb{R}} J(x-y)u_m(t,y)\mathrm{d}y - du_m + f'(0)u_m,\ 0 < t \leq 1,\\
&u(0,x) = g'(0)N_m(x),\\
&N_{m+1}(x) = u_m(1,x).
\end{aligned} \tag{4.3.1}$$

For any $\mu \in \mathbb{R}^+$, let $u(t,x) = e^{-\mu x}\eta(t)$. Then $\eta(t)$ satisfies

$$\frac{\mathrm{d}\eta(t)}{\mathrm{d}t} = \Big(d\int_{\mathbb{R}} J(y)e^{\mu y}\mathrm{d}y - d + f'(0)\Big)\eta(t). \tag{4.3.2}$$

Note that the time-one solution map of nonlocal system (4.3.2) is given by e^{C_μ}, where

$$C_\mu = d\int_{\mathbb{R}} J(x)e^{\mu x}\mathrm{d}x - d + f'(0),\ \mu \in \mathbb{R}_+.$$

Hence, model (4.3.1) can be rewritten as

$$N_{m+1}(x) = e^{-\mu x} e^{C_\mu} g'(0) N_m(x). \tag{4.3.3}$$

Since the dispersal kernel J is symmetric, by a comparison argument similar to the proof of [80, Proposition 3.9] and [135, Theorem 3.2], the spreading speed c^* can be computed as

$$c^* = \inf_{\mu>0} \frac{1}{\mu} \ln e^{C_\mu} g'(0) = \inf_{\mu>0} \frac{1}{\mu} \Big[d \int_{\mathbb{R}} J(x) e^{\mu x} \mathrm{d}x - d + f'(0) + \ln g'(0) \Big].$$

This completes the proof. □

Theorem 4.3.2. *Assume that (J2), (H1) and (H4) hold, and g is monotone. Let c^* be defined in (4.3.1). Then for any $c \geq c^*$, system (4.1.3) admits a traveling wave $U(x + cm)$ connecting 0 to β such that $U(\xi)$ is non-decreasing in ξ, and for any $c \in (0, c^*)$, system (4.1.3) has no such traveling wave connecting 0 to β.*

Proof. Let $\mathcal{M}$ denote the set of all bounded and nonincreasing functions from $\mathbb{R}$ to $\mathcal{C}$. It is not difficult to verify that the above claim still hold with $\mathcal{C}_\beta$ being replaced by $\mathcal{M}_\beta$, where $\mathcal{M}_\beta = \{\phi \in \mathcal{M} : 0 \leq \phi \leq \beta\}$. Then we can employ Theorem 1.5.1 to obtain the existence and nonexistence of monotone traveling waves. □

4.3.2 Non-monotone case of g

In this subsection, we study the spatial invading dynamics of system (4.1.3) in the case where g is non-monotone. We assume (H3) holds so that $g(N)$ is nondecreasing for small N.

As we did in Section 2.2, we introduce two auxiliary models

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = d \left\{ \int_{\mathbb{R}} J(x-y) u_m(t,y) \mathrm{d}y - u_m \right\} + f(u_m), \ x \in \mathbb{R}, \ 0 < t \leq 1, \\ &u_m(0,x) = g^+(N_m^+(x)), \\ &N_{m+1}^+(x) = u_m(1,x), \end{aligned} \tag{4.3.4}$$

and

$$\begin{aligned} &\frac{\partial u_m}{\partial t} = d \left\{ \int_{\mathbb{R}} J(x-y) u_m(t,y) \mathrm{d}y - u_m \right\} + f(u_m), \ x \in \mathbb{R}, \ 0 < t \leq 1, \\ &u_m(0,x) = g^-(N_m^-(x)), \\ &N_{m+1}^-(x) = u_m(1,x), \end{aligned} \tag{4.3.5}$$

and then reduce them to

$$N_{m+1}^{+}(x) = Q[g^{+}(N_m^{+}(\cdot))](x) = Q \circ g^{+}[N_m^{+}](x),\ x \in \mathbb{R},\ \forall m \geq 0, \tag{4.3.6}$$

and

$$N_{m+1}^{-}(x) = Q[g^{-}(N_m^{-}(\cdot))](x) = Q \circ g^{-}[N_m^{-}](x),\ x \in \mathbb{R},\ \forall m \geq 0, \tag{4.3.7}$$

where $g^{\pm}$ are defined in Section 2.2. Let $N_m^{+}(x)$ and $N_m^{-}(x)$ be solutions of discrete-time systems (4.3.6) and (4.3.7), respectively. If $0 < N_0^{-}(x) \leq N_0(x) \leq N_0^{+}(x) \leq \beta^{+}$, then the comparison argument implies that

$$0 \leq N_m^{-}(x) \leq N_m(x) \leq N_m^{+}(x),\ x \in \mathbb{R},\ \forall m \geq 0. \tag{4.3.8}$$

Recall that $c^* = \inf\limits_{\mu>0} \frac{1}{\mu} e^{C_\mu} g'(0)$ for system (4.1.3) with monotone birth pulse function. We remark that the expression of c^* only depends on the linearized system (4.3.3). Note that models (4.3.4) and (4.3.5) share the same linearized system at zero, indeed, model (4.3.1). It then follows from Theorem 4.3.1 that c^* in (4.3.1) is the spreading speed of models (4.3.4) and (4.3.5). We can obtain the following result about the spreading speed of system (4.1.3) in the case where g is non-monotone.

Theorem 4.3.3. *Let (J2), (H1), (H2), (H3) and (H4) hold. Then c^* given by (4.3.1) is the spreading speed of system (4.1.3) in the following sense:*

(i) If $\phi \in C_{\beta^+}$ has compact support, then $\lim\limits_{m\to+\infty,|x|\geq cm} \hat{Q}^m[\phi](x) = 0$, $\forall c > c^*$.

(ii) If $\phi \in C_{\beta^+} \setminus \{0\}$, then $\beta^- \leq \liminf\limits_{m\to+\infty,|x|\leq cm} \hat{Q}^m[\phi](x) \leq \limsup\limits_{m\to+\infty,|x|\leq cm} \hat{Q}^m[\phi](x) \leq \beta^+$, $\forall c \in (0, c^*)$.

Proof. A comparison argument, together with (4.3.8), shows that c^* given by (4.3.1) is also the spreading speed for system (4.1.3). Since the proof is similar to that of [56, Theorem 2.3] , we omit the details here. □

Before proving the existence of traveling waves, we return to the integro-differential system (4.1.2) for more observations. Note that $(J * u - u)(x) : \mathcal{C} \to \mathcal{C}$ is a bounded linear operator, where $(J * u - u)(x) := \int_{\mathbb{R}} J(x-y)u(t,y)\mathrm{d}y - u(x)$. It then follows from (J2) and (H1) that the linear system

$$\begin{aligned} \frac{\mathrm{d}u(t,x)}{\mathrm{d}t} &= d(J * u - u)(t,x),\ x \in \mathbb{R},\ t > 0, \\ u(0,x) &= \phi(x), \end{aligned} \tag{4.3.9}$$

generates a strongly continuous semigroup $P(t)$ on $\mathcal{C}$, which is strongly positive in the sense of $P(t)\mathcal{C}_+ \subseteq \mathcal{C}_+$ and $[P(t)\phi](x) > 0$ if $\phi(x) \geq 0$ has a nonempty support and $t > 0$. According to [135], the unique mild solution of system (4.3.9) is given by

$$[P(t)\phi](x) = e^{-dt} \sum_{k=0}^{\infty} \frac{(dt)^k}{k!} a_k(\phi)(x),$$

where $a_0(\phi)(x) = \phi(x)$ and $a_k(\phi)(x) = \int_{\mathbb{R}} J(x-y)a_{k-1}(\phi)(y)\mathrm{d}y$ for any integer $k \geq 1$. In particular, we let $P := P(1)$ be the time-one solution map associated with system (4.3.9). For any $\phi \in \mathcal{C}_+$, system (4.1.2) can be rewritten as an integral equation form:

$$u(t) = P(t)\phi + \int_0^t P(t-s)f(u(s,\phi))\mathrm{d}s, \ \forall t > 0.$$

Moreover, since Q denote the time-one solution map of system (4.1.2), then we obtain

$$Q(\phi) = u(1) = P\phi + \int_0^1 P(1-s)f(u(s,\phi))\mathrm{d}s, \ \phi \in \mathcal{C}_+.$$

For any given $c > c^*$, we choose $\rho = \rho(c) \in (0, \frac{d}{c})$. Define

$$X_\rho := \{\phi \in C(\mathbb{R}, \mathbb{R}) : \sup_{x \in \mathbb{R}} |\phi(x)| e^{-\rho|x|} < +\infty\},$$

and $\|\phi\|_\rho := \sup_{x\in\mathbb{R}} |\phi(x)|e^{-\rho|x|}$. It then follows that $(X_\rho, \|\cdot\|_\rho)$ is a Banach space. Let $Y_{\mathbb{L}+} := \{\phi \in X_\rho : 0 \leq \phi \leq \mathbb{L}_+\}$. Note that $0, \mathbb{L}_+ \in Y_{\mathbb{L}+}$. Thus, $Y_{\mathbb{L}+}$ is a nonempty, closed and convex subset of X_ρ. The following lemma shows that T_cP is a κ-contraction on $Y_{\mathbb{L}+}$.

Lemma 4.3.1. *The map T_cP is a κ-contraction on $Y_{\mathbb{L}+}$ with the contraction coefficient being $e^{\rho c - d}$.*

Proof. Note that

$$(T_cP)[\phi](x) = e^{-d} \sum_{k=0}^{+\infty} \frac{d^k}{k!} a_k(\phi)(x-c), \ \forall x \in \mathbb{R}, \ \forall \phi \in Y_{\mathbb{L}+},$$

where $a_0(\phi) = \phi$ and $a_k(\phi)(x-c) = \int_{\mathbb{R}} J(x-c-y)a_{k-1}(\phi)(y)\mathrm{d}y$ for all $k \geq 1$. For any $\phi, \psi \in Y_{\mathbb{L}+}$, we have $\|a_0(\phi) - a_0(\psi)\|_\rho = \|\phi - \psi\|_\rho$ and

$$\begin{aligned} |a_k(\phi)(x) - a_k(\psi)(x)|e^{-\rho|x|} &\leq \int_{\mathbb{R}} J(y)|a_{k-1}(\phi)(x-y) - a_{k-1}(\psi)(x-y)|\mathrm{d}y \cdot e^{-\rho|x|} \\ &\leq \|a_{k-1}(\phi) - a_{k-1}(\psi)\|_\rho \int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y, \ \forall x \in \mathbb{R}, \ k \geq 1. \end{aligned}$$

By induction, we see that

$$\|a_k(\phi) - a_k(\psi)\|_\rho \le \Big(\int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y\Big)^k \|\phi - \psi\|_\rho.$$

Further,

$$\begin{aligned}\Big|T_cP[\phi](x) - T_cP[\psi](x)\Big|e^{-\rho|x|} &\le e^{\rho c - d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\Big|a_k(\phi)(x-c) - a_k(\psi)(x-c)\Big|e^{-\rho|x-c|}\\ &\le e^{\rho c - d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\|a_k(\phi) - a_k(\psi)\|_\rho\\ &\le e^{\rho c - d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\Big(\int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y\Big)^k\|\phi - \psi\|_\rho,\ \forall x \in \mathbb{R}.\end{aligned}$$

Therefore,

$$\|T_cP[\phi] - T_cP[\psi]\|_\rho \le e^{\rho c - d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\Big(\int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y\Big)^k\|\phi - \psi\|_\rho, \tag{4.3.10}$$

which implies T_cP is continuous on $Y_{\mathbb{L}_+}$. Clearly, $T_cP = (T_cP)_1 + (T_cP)_2$ with

$$(T_cP)_1[\phi](x) = e^{-d}\phi(x-c),\ (T_cP)_2[\phi](x) = e^{-d}\sum_{k=1}^{+\infty}\frac{d^k}{k!}a_k(\phi)(x-c). \tag{4.3.11}$$

Note that $\|(T_cP)_1[\phi] - (T_cP)_1[\psi]\|_\rho \le e^{\rho c - d}\|\phi - \psi\|_\rho$, that is, $(T_cP)_1$ is κ-contraction with the contraction coefficient being $e^{\rho c - d}$. For any $\phi \in Y_{\mathbb{L}_+}$ and $x_1, x_2 \in \mathbb{R}$, a direct calculation yields that

$$\begin{aligned}|(T_cP)_2[\phi](x_1) - (T_cP)_2[\phi](x_2)| &\le e^{-d}\sum_{k=1}^{+\infty}\frac{d^k}{k!}\Big|a_k(\phi)(x_1-c) - a_k(\phi)(x_2-c)\Big|\\ &\le \mathbb{L}_+e^{-d}\sum_{k=1}^{+\infty}\frac{d^k}{k!}\int_{\mathbb{R}}\Big|J(z+x_1-x_2) - J(z)\Big|\mathrm{d}z\\ &= \mathbb{L}_+e^{-d}(e^d - 1)h(x_1 - x_2),\end{aligned}$$

where $h(x) = \int_{\mathbb{R}}|J(z+x) - J(z)|\mathrm{d}z$, $\forall x \in \mathbb{R}$. Since $\lim\limits_{x\to 0} h(x) = 0$, it follows that the family of functions $\{(T_cP)_2[\phi](x) : \phi \in Y_{\mathbb{L}_+}\}$ is equicontinuous in $x \in \mathbb{R}$. Thus, for any given sequence $\{\varphi_n := (T_cP)_2[\phi_n]\}_{n\ge 1} \subset (T_cP)_2[Y_{\mathbb{L}_+}]$, there exists $n_j \to +\infty$ and $\varphi \in C(\mathbb{R}, \mathbb{R})$ such that $\lim_{j\to+\infty}\varphi_{n_j}(x) = \varphi(x)$ uniformly for x in any compact subset of $\mathbb{R}$. Since $\varphi_{n_j} \in Y_{\mathbb{L}_+}$, it follows from (4.3.11) that $0 \le \varphi_{n_j}(x) \le \mathbb{L}_+$, and hence, $0 \le \varphi(x) \le \mathbb{L}_+$, $\forall x \in \mathbb{R}$. Obviously, $\lim_{x\to\pm\infty}(\mathbb{L}_+ - 0)e^{-\rho|x|} = 0$. Therefore, for any

$\varepsilon > 0$, there exists a $K > 0$ such that

$$0 \leq |\varphi_{n_j}(x) - \varphi(x)|e^{-\rho|x|} \leq \mathbb{L}_+ e^{-\rho|x|} < \varepsilon, \ \forall |x| \geq K.$$

Since $\lim_{j\to+\infty}(\varphi_{n_j}(x) - \varphi(x))e^{-\rho|x|} = 0$ uniformly for $x \in [-K, K]$, there exists an integer j_0 such that

$$|\varphi_{n_j}(x) - \varphi(x)|e^{-\rho|x|} < \varepsilon, \ \forall x \in [-K, K], \ j \geq j_0.$$

It then follows that

$$\|\varphi_{n_j} - \varphi\|_\rho = \sup_{x\in\mathbb{R}} |\varphi_{n_j}(x) - \varphi(x)|e^{-\rho|x|} < \varepsilon, \ j \geq j_0.$$

This implies that $\lim_{j\to\infty} \|\varphi_{n_j} - \varphi\|_\rho = 0$, and hence, $(T_cP)_2[Y_{\mathbb{L}_+}]$ is precompact in X_ρ. Therefore, T_cP is κ-contraction with the contraction coefficient being $e^{\rho c-d}$. □

Now we are ready to prove the main result of this subsection.

Theorem 4.3.4. *Let (J2), (H1), (H2), (H3) and (H4) hold. Then the following statements are valid:*

(i) For any $c \in (0, c^*)$, system (4.1.3) has no traveling wave $U(x + cm)$ with $U(-\infty) = 0$.

(ii) If, in addition, $d > \max\{\mathcal{L}_f, \mathcal{L}_f + \ln \mathcal{L}_g\}$, where $\mathcal{L}_g$ and $\mathcal{L}_f$ are the Lipschitz constants of g and f on $[0, \beta^+]$, respectively, then for any $c > c^*$, system (4.1.3) has a continuous traveling wave $U(x + cm)$ such that $U(-\infty) = 0$ and $\beta^- \leq \liminf_{\xi\to+\infty} U(\xi) \leq \limsup_{\xi\to+\infty} U(\xi) \leq \beta^+$.

Proof. (i) Assume, by contradiction, that for some $c_0 \in (0, c^*)$, system (4.1.3) has a traveling wave $N_m(x) = U(x + c_0m)$ with $U(-\infty) = 0$. By Theorem 4.3.3 (ii), there holds

$$\liminf_{m\to+\infty, |x|\leq cm} N_m(x) \geq \beta^- > 0, \ \forall c \in (0, c^*).$$

Choose $\tilde{c} \in (c_0, c^*)$ and let $x = -\tilde{c}m$. Then $\liminf_{m\to+\infty} N_m(-\tilde{c}m) = \liminf_{m\to+\infty} U((c_0 - \tilde{c})m) > 0$, but $\lim_{m\to+\infty} U((c_0 - \tilde{c})m) = U(-\infty) = 0$, a contradiction.

(ii) For any given $c > c^*$, let $\rho = \rho(c)$ be chosen as in the definition of X_ρ. By [80, Lemma 3.8], it follows that there exist $0 < \mu_1 < \mu_2 < \min\{\nu_g\mu_1, \nu_f\mu_1, \mu^*\}$, where $c^* = \frac{1}{\mu^*} \ln e^{C_{\mu^*}} g'(0)$, such that

$$c = \frac{1}{\mu_1} \ln e^{C_{\mu_1}} g'(0) := \frac{\lambda(\mu_1)}{\mu_1} \text{ and } \tilde{c} = \frac{\lambda(\mu_2)}{\mu_2} < c,$$

and hence, $e^{-c\mu_1}e^{C_{\mu_1}}g'(0) = 1$. Define

$$T_c\hat{Q}[\phi](x) = T_c(Q \circ g)[\phi](x),\ \forall x \in \mathbb{R},\ \phi \in X_\rho.$$

Let $T_c\hat{Q}^{\pm}$ be defined as above with g replaced by $g^{\pm}$. It then follows that $T_c\hat{Q}^{\pm}$ is nonincreasing on X_ρ, and that $T_c\hat{Q}^{-}[\phi] \le T_c\hat{Q}[\phi] \le T_c\hat{Q}^{+}[\phi]$, $\forall \phi \in X_\rho$.

Following [56], we define

$$\phi^+(x) = \min\{\beta^+, \beta^+ e^{\mu_1 x}\},\ \forall x \in \mathbb{R}.$$

Since $g^+(N)$ is nondecreasing in N and $\phi^+(x) \le \beta^+$, $\forall x \in \mathbb{R}$, we obtain

$$T_c\hat{Q}^+[\phi^+] = T_c(Q \circ g^+)[\phi^+](x) \le \beta^+.$$

Note that $f(N) \le f'(0)N$, and $\phi^+(x) \le \beta^+ e^{\mu_1 x}$, $\forall x \in \mathbb{R}$. It follows that

$$\begin{aligned} T_c(Q \circ g^+)[\phi^+](x) &\le \beta^+ g'(0) e^{-\mu_1 c}\Big(P[e^{\mu_1 \cdot}](x) + \int_0^1 P(1-s) f'(0) u(s, e^{\mu_1 \cdot})(x)\mathrm{d}s\Big) \\ &= \beta^+ g'(0) e^{-\mu_1 c} e^{C_{\mu_1}} e^{\mu_1 x} \\ &= \beta^+ e^{\mu_1 x},\ \forall x \in \mathbb{R}. \end{aligned}$$

Hence, $T_c\hat{Q}^+[\phi^+] \le \phi^+$.

Now we fix a $\bar{c}$ such that $\tilde{c} < \bar{c} < c$ and let $M = \max\{M_1, M_2, M_3 + 1\}$, where M_1, M_2 and M_3 are positively and sufficiently large such that

$$\begin{aligned} &\Big[1 + \frac{G\delta^{\nu_g - 1}}{M_1 g'(0)}\Big] e^{(\bar{c} - c)\mu_2} < 1, \\ &\frac{1}{M_2} e^{[-\bar{c}\mu_2 + \lambda(\mu_1)](t-1)} < 1,\ \forall t \in [0,1],\ \text{and} \\ &-\bar{c}\mu_2 + \lambda(\mu_2) + \frac{\delta^{\nu_f - 1} e^{\nu_f[\ln g'(0) - \lambda(\mu_2)](1-t)} F}{M_3 e^{[\ln g'(0) - \lambda(\mu_2)](1-t)}} < 0,\ \forall t \in [0,1], \end{aligned}$$

with $\delta = \min\{\sigma_g, \sigma_f, \beta^+\}$, respectively. Obviously, $M > 1$. Define

$$\phi^-(x) = \max\{0, \delta(e^{\mu_1 x} - M e^{\mu_2 x})\},\ \forall x \in \mathbb{R}.$$

Let $x_0 = -\frac{\ln M}{\mu_2 - \mu_1} < 0$. Then we have

$$\phi^-(x) = 0,\ \forall x \ge x_0,\ \phi^-(x) = \delta(e^{\mu_1 x} - M e^{\mu_2 x}),\ \forall x \le x_0.$$

It is easy to see that

$$0 \le \phi^-(x) \le \phi^+(x) \text{ and } (\phi^-(x))^{\nu_g} \le \delta^{\nu_g} e^{\mu_2 x},\ \forall x \in \mathbb{R}.$$

Clearly, $T_c\hat{Q}^-[\phi^-](x) \geq 0$, $\forall x \in \mathbb{R}$. Since $\phi^-(x) \geq \delta(e^{\mu_1 x} - Me^{\mu_2 x})$, $\forall x \in \mathbb{R}$, it follows that

$$\begin{aligned} g(\phi^-)(x) &\geq g'(0)\phi^-(x) - G\phi^{\nu_g}(x) \\ &\geq g'(0)\delta e^{\mu_1 x} - g'(0)\delta M e^{\mu_2 x}\Big[1 + \frac{G\delta^{\nu_g - 1}}{Mg'(0)}\Big] \\ &\geq g'(0)\delta e^{\mu_1 x} - g'(0)\delta M e^{\mu_2 x} e^{(c-\bar{c})\mu_2}, \end{aligned}$$

and hence,

$$\begin{aligned} g(\phi^-)(x-c) &\geq g'(0)\delta e^{\mu_1(x-c)} - g'(0)\delta M e^{\mu_2(x-\bar{c})} \\ &= \delta e^{\mu_1 x} g'(0) e^{-\mu_1 c} - \delta M e^{\mu_2 x} g'(0) e^{-\mu_2 \bar{c}} \\ &= \delta e^{\mu_1 x} e^{\ln g'(0) - \lambda(\mu_1)} - \delta M e^{\mu_2 x} e^{\ln g'(0) - \mu_2 \bar{c}}. \end{aligned}$$

Let $u(t,x) = \max\{0, \psi_1(t,x) - \psi_2(t,x)\}, \ \forall (t,x) \in [0,1] \times \mathbb{R}$, where

$$\psi_1(t,x) = \delta e^{\mu_1 x} e^{[\ln g'(0) - \lambda(\mu_1)](1-t)} \text{ and } \psi_2(t,x) = \delta M e^{\mu_2 x} e^{[\ln g'(0) - \bar{c}\mu_2](1-t)}.$$

Note that $\psi_1 \geq \psi_2$ provided that $x \leq \frac{\ln \frac{e^{[\lambda(\mu_1) - \bar{c}\mu_2](t-1)}}{M}}{\mu_2 - \mu_1} := x_0(t)$, $\forall t \in [0,1]$, and $x_0(t)$, $\forall t \in [0,1]$ is bounded. If $x > x_0(t)$, then $u(t,x) = 0$, and hence, $\frac{\partial u}{\partial t} - d\int_{\mathbb{R}} J(x-y)u(t,y)\mathrm{d}y + du(t,x) - f(u) = 0$. If $x < x_0(t) < 0$, then $u(t,x) = \psi_1(t,x) - \psi_2(t,x)$. Then for any $t \in [0,1]$, we have

$$\begin{aligned} &\frac{\partial u}{\partial t} - d\int_{\mathbb{R}} J(x-y)u(t,y)\mathrm{d}y + du - f(u) \\ &\leq -\psi_2[\bar{c}\mu_2 - \lambda(\mu_2)] + F(\psi_1 - \psi_2)^{\nu_f} \\ &\leq \psi_2\Big[-\bar{c}\mu_2 + \lambda(\mu_2) + F\frac{\psi_1^{\nu_f}}{\psi_2}\Big] \\ &= \psi_2\Big[-\bar{c}\mu_2 + \lambda(\mu_2) + F\frac{\delta^{\nu_f - 1} e^{(\mu_1\nu_f - \mu_2)x} e^{\nu_f[\ln g'(0) - \lambda(\mu_2)](1-t) - [\ln g'(0) - \lambda(\mu_2)](1-t)}}{M}\Big] < 0. \end{aligned}$$

Thus, $u(t,x)$ is a lower solution of system (4.1.2). Since $g(\phi^-)(x-c) \geq u(0,x)$, it follows that $u(t, g(\phi^-)(x-c)) \geq u(t,x)$, which implies $Q(g(\phi^-))(x-c) \geq u(1,x) = \max\{0, \delta(e^{\mu_1 x} - Me^{\mu_2 x})\} = \phi^-(x)$, $\forall x \in \mathbb{R}$. Hence, $T_c\hat{Q}^-[\phi^-](x) \geq \phi^-(x)$, $\forall x \in \mathbb{R}$.

It is easy to see that both ϕ^- and ϕ^+ are elements in X_ρ. Thus, the set

$$D := \{\phi \in X_\rho : \phi^- \leq \phi \leq \phi^+\}$$

is a nonempty, closed and convex subset of X_ρ. For any $\phi \in D$, we obtain

$$\phi^- \leq T_c\hat{Q}^-(\phi^-) \leq T_c\hat{Q}^-(\phi) \leq T_c\hat{Q}(\phi) \leq T_c\hat{Q}^+(\phi) \leq T_c\hat{Q}^+(\phi^+) \leq \phi^+,$$

and hence, $T_c\hat{Q}(D) \subset D$. We further have the following two claims.

Claim A. *The map $T_c\hat{Q} : D \to D$ is continuous with respect to $\|\cdot\|_\rho$.*

Indeed, for any $\phi_i \in D$ $(i = 1, 2)$, let

$$W(\phi_i) = T_c\hat{Q}[\phi_i](\cdot) = P(g\phi_i)(\cdot - c) + \int_0^1 P(1-s)f(u(s, g\phi_i))(\cdot - c)\mathrm{d}s.$$

It then follows from (4.3.10) that

$$\begin{aligned}&|W(x,\phi_1) - W(x,\phi_2)|e^{-\rho|x|}\\ &\le e^{\rho c-d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\Big(\int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y\Big)^k\mathcal{L}_g\|\phi_1-\phi_2\|_\rho + e^{\rho c}\mathcal{P}\mathcal{L}_f\|u(s,g\phi_1)-u(s,g\phi_2)\|_\rho,\end{aligned}$$

where $\mathcal{P} = \max\limits_{s\in[0,1]} \|P(s)\|$. On the other hand, we can obtain for any $t \in [0, 1]$,

$$\|u(t, g\phi_1) - u(t, g\phi_2)\|_\rho \le \mathcal{P}\mathcal{L}_g\|\phi_1 - \phi_2\|_\rho + \int_0^t \mathcal{P}\mathcal{L}_f\|u(s, g\phi_1) - u(s, g\phi_2)\|_\rho\mathrm{d}s.$$

By Gronwall's inequality, we obtain

$$\|u(t, g\phi_1) - u(t, g\phi_2)\|_\rho \le \mathcal{P}\mathcal{L}_g\|\phi_1 - \phi_2\|_\rho e^{\mathcal{P}\mathcal{L}_f t} \le \mathcal{P}\mathcal{L}_g\|\phi_1 - \phi_2\|_\rho e^{\mathcal{P}\mathcal{L}_f},\ \forall t \in [0, 1].$$

Hence,

$$e^{\rho c}\mathcal{P}\mathcal{L}_f\|u(s, g\phi_1) - u(s, g\phi_2)\|_\rho \le \mathcal{L}_g\mathcal{L}_f\mathcal{P}^2e^{\rho c+\mathcal{P}\mathcal{L}_f}\|\phi_1 - \phi_2\|_\rho.$$

It follows that

$$\|W(\phi_1)-W(\phi_2)\|_\rho \le \Big[e^{\rho c-d}\sum_{k=0}^{+\infty}\frac{d^k}{k!}\Big(\int_{\mathbb{R}} J(y)e^{\rho|y|}\mathrm{d}y\Big)^k\mathcal{L}_g + \mathcal{L}_g\mathcal{L}_f\mathcal{P}^2e^{\rho c+\mathcal{P}\mathcal{L}_f}\Big]\|\phi_1-\phi_2\|_\rho,$$

which proves the desired result.

Claim B. *The map $T_c\hat{Q} : D \to D$ is a κ-contraction with respect to $\|\cdot\|_\rho$.*

For any closed set $B \subset D$ and $t \in [0, 1]$, we have

$$\begin{aligned}\kappa(u(t, g(B))) &\le \kappa\Big(P(t)g(B)\Big) + \int_0^t \kappa\Big(P(t-s)f(u(s, g(B)))\Big)\mathrm{d}s,\\ &\le e^{-dt}\mathcal{L}_g\kappa(B) + \int_0^t e^{-d(t-s)}\mathcal{L}_f\kappa(u(s, g(B)))\mathrm{d}s,\end{aligned}$$

that is, $e^{dt}\kappa(u(t, g(B))) \le \mathcal{L}_g\kappa(B) + \int_0^t \mathcal{L}_f e^{ds}\kappa(u(s, g(B)))\mathrm{d}s$. By Gronwall's inequality, we have

$$e^{dt}\kappa(u(t, g(B))) \le \mathcal{L}_g\kappa(B)e^{\mathcal{L}_f t},$$

that is, $\kappa(u(t,g(B))) \leq \mathcal{L}_g\kappa(B)e^{(\mathcal{L}_f-d)t}$. Therefore,

$$\begin{aligned}\kappa(T_c\hat{Q}(B)) &\leq e^{\rho c-d}\mathcal{L}_g\kappa(B) + \int_0^1 e^{(\rho c-d)(1-s)}\mathcal{L}_f\mathcal{L}_g e^{(\mathcal{L}_f-d)s}\kappa(B)\mathrm{d}s \\ &\leq \left[e^{\rho c-d}\mathcal{L}_g + \mathcal{L}_g\mathcal{L}_f e^{\rho c-d}\frac{1-e^{\mathcal{L}_f-\rho c}}{\rho c-\mathcal{L}_f}\right]\kappa(B) \\ &= e^{\rho c-d}\mathcal{L}_g\frac{\rho c-\mathcal{L}_f e^{\mathcal{L}_f-\rho c}}{\rho c-\mathcal{L}_f}\kappa(B).\end{aligned}$$

Since $\mathcal{L}_g e^{\mathcal{L}_f-d} < 1$, it follows that $\lim\limits_{\rho\to 0^+} e^{\rho c-d}\mathcal{L}_g\frac{\rho c-\mathcal{L}_f e^{\mathcal{L}_f-\rho c}}{\rho c-\mathcal{L}_f} = \mathcal{L}_g e^{\mathcal{L}_f-d} < 1$, which implies that there exists $\rho \in (0,\frac{d}{c})$ small enough such that $e^{\rho c-d}\mathcal{L}_g\frac{\rho c-\mathcal{L}_f e^{\mathcal{L}_f-\rho c}}{\rho c-\mathcal{L}_f} < 1$. Hence, $T_c\hat{Q}$ is κ-contraction with the coefficient being $e^{\rho c-d}\mathcal{L}_g\frac{\rho c-\mathcal{L}_f e^{\mathcal{L}_f-\rho c}}{\rho c-\mathcal{L}_f}$.

According to Claim B, the map $T_c\hat{Q} : D \to D$ is a κ-contraction, and hence, $T_c\hat{Q}$ is κ-condensing. Note that D is bounded in X_ρ and $(T_cQ)^m(D) \subset D$ for any $m \geq 1$. It then follows that $T_c\hat{Q}$ is compact dissipative. By the asymptotic fixed point theorem (see, e.g., [145, Theorem 1.1.4]), $T_c\hat{Q}$ has a fixed point $U \in D$, that is $T_c\hat{Q}(U) = U$. Hence, $\hat{Q}(U)(x) = U(x+c)$, and $\hat{Q}^m(U)(x) = U(x+cm)$ is a traveling wave of system (4.1.3). Since $\phi^-(\xi) \leq U(\xi) \leq \phi^+(\xi)$, $\forall \xi = x+c \in \mathbb{R}$, we have $U(-\infty) = 0$.

Motivated by the proof of [56, Theorem 3.1], we let $V_m(x) := U(x+cm)$, $\forall m \geq 0$, and fix a number $\bar{c}_0 \in (0,c^*)$. By Theorem 4.3.3(ii), it follows that $0 < \beta^- \leq \liminf_{m\to+\infty,|x|\leq\bar{c}_0 m} V_m(x) \leq \limsup_{m\to+\infty,|x|\leq\bar{c}_0 m} V_m(x) \leq \beta^+$, and hence, $\beta^- \leq \liminf_{m\to+\infty} V_m(-\gamma m) \leq \limsup_{m\to+\infty} V_m(-\gamma m) \leq \beta^+$ uniformly for $\gamma \in [0,\bar{c}_0]$. This implies that $\beta^- \leq \liminf_{m\to+\infty} U(sm) \leq \limsup_{m\to+\infty} U(sm) \leq \beta^+$ uniformly for $s \in [c-\bar{c}_0, c]$. Let $a_m = m(c-\bar{c}_0)$, $b_m = mc$, $\forall m \geq 1$. Thus, there exists $j_0 > 0$ such that $a_{m+1} - b_m < 0$, $\forall m \geq j_0$, and hence, $\cup_{m\geq j}[a_m, b_m] = [a_j, +\infty)$, $\forall j \geq j_0$. It then follows that $\beta^- \leq \liminf_{\xi\to+\infty} U(\xi) \leq \limsup_{\xi\to+\infty} U(\xi) \leq \beta^+$. This completes the proof. □

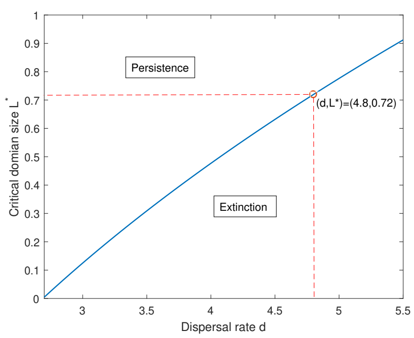
4.4 Simulations

In this section, we present the simulations to illustrate some of our results. We assume that f is of the form of (4.2.3) with $a = 1$, $b = 0.01$ [74] throughout this section.

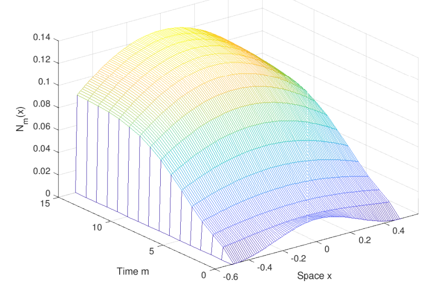
4.4.1 Persistence and spatial spread

We choose the form of g to be either Beverton-Holt function (4.2.1) or Ricker function (4.2.2) to explore the dynamics subject to a simple Laplace kernel J, which is stated in (4.2.18) with $D = 0.56$.

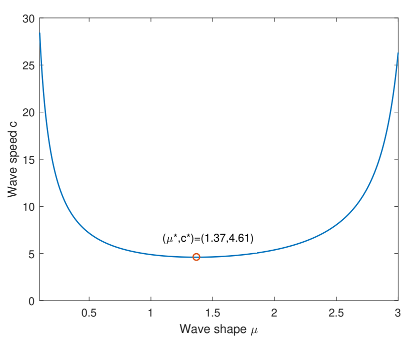
In the case where g is monotone, we consider the Beverton-Holt function (4.2.1) with $p = 8$ and $q = 0.2$ as in [74]. The simulations of invasion behaviors in a bounded domain $\Omega = (-l, l) \subset \mathbb{R}$ with $l = 0.5$ and the domain length $L = 1$, are shown in Figures 4.2(a) and 4.2(b). When the dispersal rate d is selected to be $d = 4.8$, the critical domain size (4.2.25) with $f'(0) = a$ and $g'(0) = p/q$ is $L^* = 0.72$ (the small red circle in Figure 4.2(a), where d is chosen as a varying parameter). Since $L = 1 > L^* = 0.72$, it then follows from Theorem 4.2.1(ii) that the population of model (4.1.1) approaches to a positive steady state (Figure 4.2(b)). When a population becomes established in a bounded domain, it can begin to spread and invade into new areas [75]. Figures 4.2(c) and 4.2(d) show that the population spreads in two directions from a small initial inoculation, respectively. Substitution of d, a, b, p, q, D into (4.3.1) gives the spreading speed $c^* = 4.61$ (the small red circle in Figure 4.2(c)), which is also the minimal wave speed according to Theorem 4.3.2.



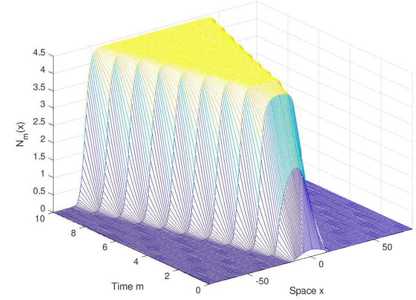
(a) Critical domain size *vs* dispersal rate.



(b) Temporal dynamics of $N_m(x)$.



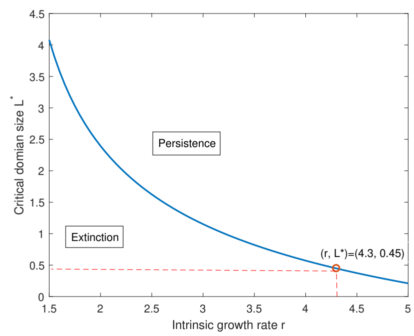
(c) Spreading speed as a function of wave shape.



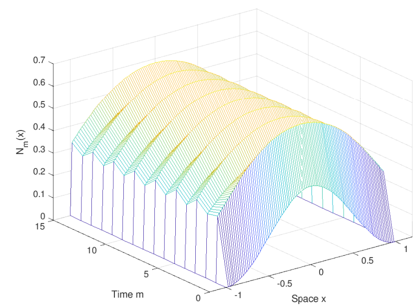
(d) $N_m(x)$ spreads in two directions.

Figure 4.2: The invasion dynamics of system (4.1.3) with g given by (4.2.1)

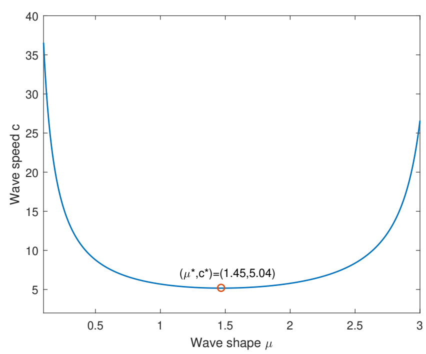
In the case where g is non-monotone, we choose $g(N)$ to be a Ricker type (4.2.2) and set $d = 4.8$. Figure 4.3(a) shows that critical domain size L^* is a decreasing function of intrinsic growth rate r (varying from 1.5 to 5), with $f'(0) = a$ and $g'(0) = e^r$ in the critical domain size formula (4.2.25). Let $r = 4.3$. Then $L^* = 0.45$ (the red circle in Figure 4.3(a)). The numerical solutions of system (4.1.3) in a bounded domain $(-l, l) = (-1, 1)$ is presented in Figure 4.3(b), which indicates that the population persists. This is coincident with Theorem 4.2.2(ii), as the domain size is $L = 2 > L^*$. Figure 4.3(c) describes the relation between the invasion speed and the wave shape with $c^* = 5.04$. For a small initial distribution with a compact support, the population spreads in two directions and oscillates in time and space (see Figure 4.3(d)).



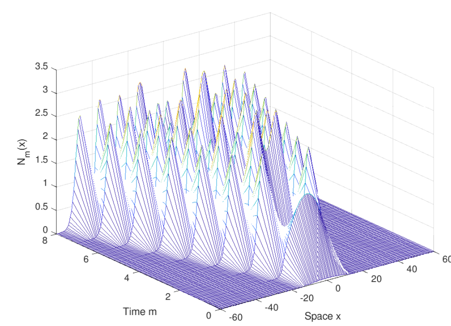
(a) Critical domain size *vs* intrinsic growth rate.



(b) Temporal dynamics of $N_m(x)$.



(c) Spreading speed as a function of wave shape.



(d) $N_m(x)$ spreads in two directions.

Figure 4.3: The invasion dynamics of system (4.1.3) with g given by (4.2.2)

4.4.2 Nonlocal dispersal *vs* random diffusion

Numerically, we estimate the spread rates for different dispersal strategies with the same variance, and find an interesting observation: regardless of the monotonicity of g (given by (4.2.1) and (4.2.2)), random diffusion gives a slowest spreading speed among four different strategies being tested. For example, in Table 4.1, all dispersal strategies have variance $\sigma^2 = 0.63$, random diffusion predicts an invasion speed of 4.02 and 4.46 in monotone and non-monotone cases, respectively, while the Laplace kernel gives fastest spreading speeds in both cases.

Table 4.1: Spread rates c^*

Dispersal strategy	Variance $\sigma^2 = 0.63$ ($\sigma = 0.79$)	g: (4.2.1) $p = 8$, $q = 0.2$	g: (4.2.2) $r = 4.3$
Laplace	$J(x) = \frac{1}{2D}e^{-\frac{\lvert x\rvert}{D}}$, with $D = 0.56$	4.61	5.04
Gaussian	$J(x) = \frac{1}{\sqrt{2\pi}\sigma}e^{-\frac{x^2}{2\sigma^2}}$, with $\sigma = 0.79$	4.45	5.01
Top-hat	$J(x) = \begin{cases} \frac{1}{2B} & x \in [-B, B] \\ 0 & \text{otherwise} \end{cases}$ with $B = 1.37$	4.29	4.98
Diffusion	diffusion constant $\tilde{d} = \frac{d\sigma^2}{2} = 1.51$	4.02	4.46

4.5 Discussion

An impulsive integro-differential model is proposed to study the invasion dynamics in a bounded and unbounded domain, respectively. We have reduced the model to an explicit map, a composition of a birth pulse discrete-time map and a time-one solution map of an integro-differential system, which is not compact. We have discussed the global dynamics for the system in a bounded domain, and shown that there exists a threshold parameter for extinction and persistence of the species. We have also used the model to study the outbreaks of the insect pests and prove the existence of a minimal removal rate to eliminate the insect pest population. When the birth pulse is monotone, the theory of monotone dynamical systems has been applied to study the spreading speed and traveling waves. In the case where birth pulse is non-monotone, we have proved the map has weak compactness under suitable technical assumptions. Then the existence of traveling waves can be obtained by the asymptotic fixed point theorem.

Analytically, we have shown that there exists a positive steady state which is globally attractive for the invasion dynamics in a bounded domain when the yearly birth pulse is monotone, which also improves the persistence result in [74, Theorem 3.2] and [40, Theorem 2.1] for the random diffusion case. From the spreading speed expression (4.3.1), we see that the spread rate for the impulsive integro-differential system depends not only on $f'(0)$, but also on the term $\ln g'(0)$. The example in Table 4.1 illustrates that among four different dispersal strategies, non-local dispersal kernels give faster spread rates than random diffusion with the same variance. Moreover, it is important to use real biological data to compare predicted and observed invasion speeds under different dispersal strategies.

Chapter 5

A spatially periodic integrodifference competition model

5.1 Introduction

Competition exists widely in the multispecies interaction. One of the crucial concepts on describing the competitive dynamics is called the competition exclusion principle, also referred to as Gause's Law [65], which states that if two species attempting to occupy the limited resources cannot coexist, then one species will drive out the other. Competition exclusion provides useful insights on ecological balance, for instance, beneficial invasion can be introduced in pest control. Among those theoretical models, a spatially-independent difference system is the following Leslie/Gower competition model:

$$\begin{aligned} p_{n+1} &= \frac{r_1 p_n}{1 + \frac{r_1 - 1}{C_1}(p_n + a_1 q_n)}, \\ q_{n+1} &= \frac{r_2 q_n}{1 + \frac{r_2 - 1}{C_2}(q_n + a_2 p_n)}, \end{aligned} \tag{5.1.1}$$

where p_n and q_n are the population densities of two competing species at time n. The competition between two species is governed by Beverton-Holt dynamics. r_i ($r_i > 1$), C_i and a_i are growth rates, carrying capacity of i-th species ($i = 1, 2$), and interspecific competition coefficients, respectively. The global dynamics of system (5.1.1) was discussed by Cushing et al. (see [25, Lemma 2]), and the competition exclusion occurs if interspecific competition is too large [25].

In nature, real species are usually spatially extended, and hence, the effects of dispersal processes are of high interest in spatial ecology. In well-known diffusion models, growth is usually assumed to occur at the same time with dispersal. However, in many situations such as annual and perennial species plants, migrating bird species, growth and dispersal are in distinct stages. Thus, integrodifference equations, which are continuous in space and discrete in time, become more realistic and popular. Kot and Schaffer [67] first applied integrodifference equations to population modeling. Since then, the study of integrodifference equations in ecology gained a lot of attention, see, e.g., [31,32,47,71,84,98,99,124]. Mathematical investigations includes the study of traveling waves [56, 64, 66, 134] and analytical approximation schemes [43]. Recently, Zhou and Kot [147] considered an integrodifference equation with shifting species ranges subject to climate changes, and Zhou and Fagan [146] investigated a single-species integrodifference model with time-varying size.

Apart from population dispersal, how species interact with space is another important topic in spatial ecology, since most landscapes are heterogeneous. Traveling waves and spreading speeds are commonly used to explore the propagation dynamics (see, e.g., [65, 112]). Shigesada et al. [113] first studied the spreading speeds for single-species continuous-time model in a periodic patchy habitat. Later, Kawasaki and Shigesada [62] extended the work to discrete-time models. A general theory of traveling waves and spreading speeds in a periodic habitat was developed by Weinberger [132], Liang and Zhao [81], and Fang and Zhao [39]. Recently, Yu and Zhao [139] studied the propagation phenomena of a two species reaction-advection-diffusion competition model in a periodic habitat by appealing to the abstract results in [39, 81].

Naturally, system (5.1.1) can be extended to the following spatial model:

$$
\begin{aligned}
p_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_1(y)p_n(y)}{1+b_1(y)(p_n(y)+a_1(y)q_n(y))} k_1(x,y)\mathrm{d}y, \\
q_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_2(y)q_n(y)}{1+b_2(y)(q_n(y)+a_2(y)p_n(y))} k_2(x,y)\mathrm{d}y, \ x \in \mathbb{R},
\end{aligned}
\tag{5.1.2}
$$

where

$$
b_i(x) = \frac{r_i(x)-1}{C_i(x)}, \ (i=1,2),
$$

$p_n(x)$ and $q_n(x)$ are the population densities of two competing species at time n and location x. $k_i(x,y)$ is the probability density function for the destination x of individuals from y of i-th species $(i=1,2)$. As mentioned in [147], both population persistence and invasion dynamics are worthy to be considered. For system (5.1.2) with distance-dependent kernel, i.e., $r_i(x)$, $C_i(x)$, $a_i(x)$ $(i=1,2)$ are constant and $k_i(x,y) = k_i(x-y)$, the propagation phenomena has been investigated by Lewis, Li and Weinberger [73] in the monostable case, and by Zhang and Zhao [143] in the bistable case. Samia and Lutscher [110] also studied the competitive coexistence for system (5.1.2) in a patchy habitat in two specific cases: competitive-ability-varying one and carrying-capacity-varying one.

Motivated by these works, we are interested in the invasion dynamics of system (5.1.2) in the case of competition exclusion. In order to consider a periodic habitat, the coefficients $r(x)$, $C(x)$, $a(x)$ and kernal $k(x,y)$ are assumed to be spatially periodic functions. Therefore, we need the following assumptions for r, C, a and $k(x,y)$:

(K1) The habitat is L-periodic for some positive number L such that $r(x) > 1$, $C(x) > 0$, $a(x) > 0$, and $r(x)$, $C(x)$, $a(x)$ are all continuous and L-periodic functions on $\mathbb{R}$.

(K2) The dispersal kernel $k(x,y)$ has the following properties:

(i) $k(x+L, y+L) = k(x,y),\ \forall x, y \in \mathbb{R}$.

(ii) For each x, $k(x,y)$ satisfies $k(x,y) \geqslant 0$ and $0 < \int_{-\infty}^{+\infty} k(x,y)\mathrm{d}y < +\infty$, and for each y,

$$\int_{-\infty}^{+\infty} k(x,y)\mathrm{d}x = 1.$$

(iii) $k(x,y)$ is lower semicontinuous in the sense that for each (x_0, y_0) and each $\varepsilon > 0$ there is a positive number $\delta(x_0, y_0, \varepsilon)$ such that $k(x,y) \geqslant k(x_0,y_0) - \varepsilon$ whenever $|x - x_0| + |y - y_0| \leqslant \delta(x_0, y_0, \varepsilon)$.

(iv) There are an integer ξ and a positive integer η with the following properties: For every α with $|\alpha| \leqslant L/2$, and for every β with $|\beta - \xi L| \leqslant L$, there is a $\eta + 1$-tuple of numbers $x_0,\ x_1,\ \cdots,\ x_\eta$ such that $x_0 = \alpha$, $x_\eta = \beta$, and $k(x_j, x_{j-1}) > 0$ for $j = 1, 2, \cdots, \eta$.

(v) $k(x,y)$ is uniformly L_1-continuous in x in the sense that

$$\lim_{h \to 0} \int_{-\infty}^{+\infty} |k(x+h, y) - k(x,y)|\mathrm{d}y = 0, \text{ uniformly in } x \in \mathbb{R}.$$

(vi) There exists $\mu^* > 0$ such that for fixed $\mu \in [0, \mu^*)$, $k(x,y)$ satisfies

$$\int_{-\infty}^{+\infty} k(x,y) e^{-\mu(y-x)}\mathrm{d}y < \infty,$$

where $\mu^* > 0$ is the abscissa of convergence and it may be infinity.

We remark that the semicontinuity assumption in (K2) is to make the model (5.1.2) contain the case in which the habitats consist of uniform patches with jumps across their boundaries [134]. Roughly, (K2(v)) is used to guarantee the equicontinuity of the integral operator Q, which is generated by system (5.1.2) [134, Hypotheses 2.1(iv)], then further to prove the compactness of Q and its Fréchet derivative $DQ(0)$ [31, Lemma 2.1]. Moreover, (K2(i)-(iv)) are needed in the proof of the strong positivity of

$DQ(0)$. Biologically, (K2(iv)) implies that the descendants in the η-th generation of an individual located in the interval $[-L/2, L/2]$ who survives to the end of the first growth period have positive population density on an interval of length $2L$ centered at an integer multiple of L [134]. We write $r_i(x),\ C_i(x),\ a_i(x)$ and $k_i(x,y)$ to denote the relevant parameters of i-th species. Throughout this chapter except for Section 5.5, we always assume that all $r_i(x),\ C_i(x),\ a_i(x)$ and $k_i(x,y)$ $(i = 1, 2)$ satisfy (K1) and (K2).

The purpose of this chapter is to study the spatially periodic traveling waves and spreading speeds for system (5.1.2). We first prove the existence of periodic steady states $(p^*(x), 0)$ and $(0, q^*(x))$, and globally attractivity of $(p^*(x), 0)$ for system (5.1.2) with periodic initial values under appropriate assumptions. Note that the steady state $(0, 0)$ is between $(p^*(x), 0)$ and $(0, q^*(x))$ with respect to the competitive ordering, which implies the possibility of multiple spreading speeds. Such a situation was also pointed out in [77]. By appealing to the theory developed in [39], which allows the existence of boundary fixed points between two ordered unstable and stable fixed points, we are able to prove the existence of the rightward spatially periodic traveling waves connecting $(p^*(x), 0)$ to $(0, q^*(x))$, and show that the system has a single spreading speed under some appropriate conditions. We also obtain a set of sufficient conditions for the rightward spreading speed to be linearly determinate.

The rest of this chapter is organized as follows. The existence of two semi-trivial periodic steady states and the global attractivity of one semi-trivial periodic steady state are investigated in Section 5.2. In Section 5.3, we present the results on spatially periodic traveling waves and the existence of single spreading speed. We obtain the linear determinacy for the spreading speed in Section 5.4. In Section 5.5, we apply the obtained results to a patchy scenario in which the carry capacity is spatially varying, and we also provide a simple example to verify the linear determinacy condition. Some numerical simulations are presented to illustrate the analytic results.

5.2 The periodic initial value problem

In this section, we study the global dynamics of the spatially periodic integrodifference competition system with the periodic initial values.

Let Y be the set of all continuous and L-period functions from $\mathbb{R}$ to $\mathbb{R}$, and $Y_+ = \{\psi \in Y :\ \psi(x) \geq 0, \forall x \in \mathbb{R}\}$. Equip Y with the maximum norm $\|\phi\|_Y$, that is, $\|\phi\|_Y = \max_{x\in\mathbb{R}} |\phi(x)|$. Then (Y, Y_+) is a strongly ordered Banach lattice. Assume that L-periodic functions $r \in C(\mathbb{R})$ satisfying $r(x) > 1,\ \forall x \in \mathbb{R}$. We can define

$$\check{L}\phi(x) = \int_{\mathbb{R}} r(y)\phi(y)k(x,y)\mathrm{d}y, \quad x \in \mathbb{R}.$$

By the arguments similar to those in [134], it is easy to verify $(\check{L})^\eta$ is strongly positive, where η is the positive integer in (K2(iv)). By [80, Lemma 3.1], we know that the spectral radius $\rho(\check{L})$ is a simple eigenvalue of $\check{L}$, with an associated strongly positive L-periodic eigenfunction $\phi(x)$. It follows that the scalar periodic eigenvalue problem

$$\begin{aligned} &\lambda\phi(x) = \int_{\mathbb{R}} r(y)\phi(y)k(x,y)\mathrm{d}y, \quad x \in \mathbb{R}, \\ &\phi(x+L) = \phi(x), \quad x \in \mathbb{R} \end{aligned} \tag{5.2.1}$$

admits a principal eigenvalue $\lambda(k,r) = \rho(\check{L})$ associated with a strongly positive L-periodic eigenfunction $\phi(x)$. As a straightforward consequence of Theorem 1.3.3, we have the following result.

Proposition 5.2.1. *Assume that the functions $r(x)$, $C(x)$, $k(x,y)$ satisfy (K1) and (K2). Let $p_n(x,\phi)$ be the unique solution of the following equation:*

$$\begin{aligned} &p_{n+1}(x) = \int_{\mathbb{R}} \frac{r(y)p_n(y)}{1+b(y)p_n(y)} k(x,y)\mathrm{d}y, \ x \in \mathbb{R}, \\ &p_0(x) = \phi(x) \in Y_+, \quad x \in \mathbb{R}, \end{aligned} \tag{5.2.2}$$

where $b(x) = \frac{r(x)-1}{C(x)}$. Then the following statements are valid:

(i) If $\lambda(k,r) \leqslant 1$, then $p_n(x) = 0$ is globally asymptotically stable with respect to initial values in Y_+;

(ii) If $\lambda(k,r) > 1$, then (5.2.2) admits a unique positive L-periodic steady state $p^*(x)$, and it is globally asymptotically stable with respect to initial values in $Y_+\backslash\{0\}$.

Let $\mathbb{P} = PC(\mathbb{R}, \mathbb{R}^2)$ be the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, and $\mathbb{P}_+ = \{\psi \in \mathbb{P} : \ \psi(x) \geq 0, \forall x \in \mathbb{R}\}$. Then $\mathbb{P}_+$ is a closed cone of $\mathbb{P}$ and induces a partial ordering on $\mathbb{P}$. Moreover, we introduce a norm $\|\phi\|_{\mathbb{P}}$ by

$$\|\phi\|_{\mathbb{P}} = \max_{x\in\mathbb{R}} |\phi(x)|.$$

It then follows that $(\mathbb{P}, \|\phi\|_{\mathbb{P}})$ is a Banach lattice. For any $\varphi \in \mathbb{P}_+$, system (5.1.2) has a unique nonnegative solution $(p_n(\cdot,\varphi), q_n(\cdot,\varphi)) \in \mathbb{P}_+$.

In view of Proposition 5.2.1, there exists two positive L-periodic functions $p^*(x)$ and $q^*(x)$ such that $E_1 := (p^*(x), 0)$, $E_2 := (0, q^*(x))$ are semi-trivial steady states of system (5.1.2) provided that $\lambda(k_i, r_i) > 1$ $(i = 1, 2)$. Since we mainly concern about the case of the competition exclusion, we impose the following conditions on system (5.1.2):

(H1) $\lambda(k_i, r_i) > 1$ $(i = 1, 2)$.

(H2) $\lambda\Big(k_1, \dfrac{r_1}{1+b_1a_1q^*}\Big) > 1.$

(H3) System (5.1.2) has no steady state in $\mathrm{Int}(\mathbb{P}_+)$.

Note that (H1) guarantees the existence of two semi-trivial steady states of system (5.1.2). (H2) implies that $(0, q^*(x))$ is unstable. Under the assumptions (H1)–(H3), there are three steady states in $\mathbb{P}_+$: $E_0 = (0,0)$, $E_1 = (p^*(x), 0)$, and $E_2 = (0, q^*(x))$. Next, we use the theory developed in [55] for abstract competitive systems (see also [53]) to prove the global attractivity of E_1.

Theorem 5.2.1. *Assume that (H1)–(H3) hold. Then $E_1 = (p^*(x), 0)$ is globally asymptotically stable for initial values $\phi = (\phi_1, \phi_2)$ in $\mathbb{P}_+$ with $\phi_1 \not\equiv 0$.*

Proof. Let $P_n(x,\phi) = (p_n(x,\phi), q_n(x,\phi))$ be the solution of system (5.1.2) with $p_0(x) = \phi(x)$. Since (H2) holds, we can fix $\varepsilon_0 \in \left(0, 1 - \dfrac{1}{\lambda(k_1, \frac{r_1}{1+b_1a_1q^*})}\right)$. By the uniform continuity of

$$F(x,P) := \frac{r_1}{1+b_1(p+a_1q)}$$

on the set $\mathbb{R}\times[0,1]\times[0,m]$, where $m = \max_{x\in\mathbb{R}} q^*(x) + 1$, it follows that there exists $\delta_0 \in (0,1)$ such that

$$|F(x,P^{(1)}) - F(x,P^{(2)})| < \varepsilon_0\cdot A, \quad \forall P^{(1)} = (p^{(1)}, q^{(1)}), P^{(2)} = (p^{(2)}, q^{(2)}) \in [0,1]\times[0,m],$$

provided that $|p^{(1)} - p^{(2)}| < \delta_0$ and $|q^{(1)} - q^{(2)}| < \delta_0$, where $A = \min_{x\in\mathbb{R}} \dfrac{r_1(x)}{1+b_1(x)a_1(x)q^*(x)}$, $A > 0$. Then we have the following claim.

Claim. *For all $\phi \in \mathbb{P}_+$ with $\phi_1 \not\equiv 0$, there holds*

$$\limsup_{n\to+\infty} \|(p_n(\cdot,\phi), q_n(\cdot,\phi)) - (0, q^*(\cdot))\|_{\mathbb{P}} \geq \delta_0.$$

Suppose, by way of contradiction, that $\limsup_{n\to+\infty} \|(p_n(\cdot,\phi), q_n(\cdot,\phi)) - (0, q^*(\cdot))\|_{\mathbb{P}} < \delta_0$ for some $\hat{\phi} \in \mathbb{P}_+$ with $\hat{\phi}_1 \not\equiv 0$. Then there exists $n_0 > 0$ such that

$$\|p_n(\cdot,\hat{\phi})\|_Y < \delta_0, \ \|q_n(\cdot,\hat{\phi}) - q^*(\cdot)\|_Y < \delta_0, \ \forall n \geq n_0.$$

Consequently, we have

$$F(x, P_n(x,\hat{\phi})) > F(x,(0,q^*(x))) - \varepsilon_0\cdot A = (1-\varepsilon_0)F(x,(0,q^*(x))), \quad \forall n \geq n_0, \ x \in \mathbb{R}.$$

Let ψ_1 be a positive eigenfunction corresponding to the principal eigenvalue

$\lambda\Big(k_1, \dfrac{r_1}{1+b_1a_1q^*}\Big)$. Then $\psi_1(x)$ satisfies

$$\lambda\Big(k_1, \frac{r_1}{1+b_1a_1q^*}\Big)\psi_1(x)=\int_{\mathbb{R}} \frac{r_1(y)}{1+b_1(y)a_1(y)q^*(y)}\psi_1(y)k_1(x,y)\mathrm{d}y, \quad x\in\mathbb{R},$$
$$\psi_1(x+L)=\psi_1(x), \quad x\in\mathbb{R}. \tag{5.2.3}$$

Since $p_0(\cdot)=\hat{\phi}_1 \geqslant\not\equiv 0$, the comparison principle, as applied to the first equation in system (5.1.2), implies that $p_{n_0}(x,\hat{\phi})>0$, $\forall x\in\mathbb{R}$. Then there exists small $\eta>0$ such that $p_{n_0}(\cdot)\geq \eta\psi_1 \gg 0$. Thus, $p_n(x,\hat{\phi})$ satisfies

$$p_{n+1}(x)\geq \int_{\mathbb{R}} \frac{r_1(y)(1-\varepsilon_0)}{1+b_1(y)a_1(y)q^*(y)}p_n(y)k_1(x,y)\mathrm{d}y, \quad \forall n>n_0,\ x\in\mathbb{R},$$
$$p_{n_0}(\cdot)\geq \eta\psi_1. \tag{5.2.4}$$

In view of (5.2.3), it easily follows that $\bar{p}_n(\cdot)=\eta[(1-\varepsilon_0)\lambda(k_1,\frac{r_1}{1+b_1a_1q^*})]^{(n-n_0)}\psi_1$ satisfies

$$\bar{p}_{n+1}(x)=\int_{\mathbb{R}} \frac{r_1(y)(1-\varepsilon_0)}{1+b_1(y)a_1(y)q^*(y)}\bar{p}_n(y)k_1(x,y)\mathrm{d}y, \quad n>n_0,\ x\in\mathbb{R},$$
$$\bar{p}_{n_0}(\cdot)=\eta\psi_1. \tag{5.2.5}$$

By (5.2.4) and (5.2.5), together with the standard comparison principle, it follows that

$$p_n(\cdot,\hat{\phi})\geq \eta\Big[(1-\varepsilon_0)\lambda\Big(k_1,\frac{r_1}{1+b_1a_1q^*}\Big)\Big]^{(n-n_0)}\psi_1, \quad \forall n\geq n_0.$$

Letting $n\to+\infty$, we see that $p_n(\cdot,\hat{\phi})$ is unbounded, a contradiction.

By the above claim and (H3), we exclude possibility (a) and (c) in [55, Theorem A]. Since E_2 is repellent in some neighborhood of itself, it follows from [55, Theorem A] that E_1 is globally asymptotically stable. □

5.3 Spreading speeds and traveling waves

In this section, we apply the results in Section 1.5.2 to study the spreading speeds and spatially periodic traveling waves for system (5.1.2). By a change of variables $u_n=p_n, v_n=q^*(x)-q_n$, we transform system (5.1.2) into the following cooperative system:

$$u_{n+1}(x)=\int_{\mathbb{R}} \frac{r_1(y)u_n(y)}{1+b_1(y)(u_n(y)+a_1(y)(q^*(y)-v_n(y))}k_1(x,y)\mathrm{d}y, \tag{5.3.1}$$
$$v_{n+1}(x)=\int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)}\cdot\frac{b_2(y)a_2(y)q^*(y)u_n(y)+v_n(y)}{1+b_2(y)(q^*(y)+a_2(y)u_n(y)-v_n(y))}k_2(x,y)\mathrm{d}y.$$

Accordingly, three steady states of (5.1.2) become

$$\hat{E}_0 = (0, q^*(x)),\ \hat{E}_1 = (p^*(x), q^*(x)),\ \hat{E}_2 = (0,0).$$

Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ and $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geqslant 0,\ \forall x \in \mathbb{R}\}$. Assume that β is a strongly positive L-periodic continuous function from $\mathbb{R}$ to $\mathbb{R}^2$. Set

$$\mathcal{C}_\beta = \{u \in \mathcal{C} :\ 0 \leqslant u(x) \leqslant \beta(x),\ \forall x \in \mathbb{R}\},\ \mathcal{C}_\beta^{per} = \{u \in \mathcal{C}_\beta :\ u(x) = u(x+L),\ \forall x \in \mathbb{R}\}.$$

Let $X = C([0,L], \mathbb{R}^2)$ equipped with the maximum norm $|\cdot|_X$, $X_+ = C([0,L], \mathbb{R}^2_+)$,

$$X_\beta = \{u \in X :\ 0 \leqslant u(x) \leqslant \beta(x),\ \forall x \in [0,L]\} \text{ and } \overline{X}_\beta = \{u \in X_\beta : u(0) = u(L)\}.$$

Let $BC(\mathbb{R}, X)$ be the set of all continuous and bounded functions from $\mathbb{R}$ to X. Define

$$\mathcal{X} = \{v \in BC(\mathbb{R}, X) : v(s)(L) = v(s+L)(0), \forall s \in \mathbb{R}\}, \mathcal{X}_+ = \{v \in \mathcal{X} : v(s) \in X_+, \forall s \in \mathbb{R}\},$$

and

$$\mathcal{X}_\beta = \{v \in BC(\mathbb{R}, X_\beta) : v(s)(L) = v(s+L)(0), \forall s \in \mathbb{R}\}.$$

We equip $\mathcal{C}$ and $\mathcal{X}$ with the compact open topology, that is, $u_m \to u$ in $\mathcal{C}$ or $\mathcal{X}$ means that the sequence of $u_m(s)$ converges to $u(s)$ in $\mathbb{R}^m$ uniformly for s in any compact set. We equip $\mathcal{C}$ with the norm $\|\cdot\|_{\mathcal{C}}$ given by

$$\|u\|_{\mathcal{C}} = \sum_{k=1}^{\infty} \frac{\max_{|x| \leqslant k} |u(x)|}{2^k},\ \forall u \in \mathcal{C},$$

where $|\cdot|$ denotes the usual norm in $\mathbb{R}^2$, and $\mathcal{X}$ with the norm $\|\cdot\|_{\mathcal{X}}$ given by

$$\|u\|_{\mathcal{X}} = \sum_{k=1}^{\infty} \frac{\max_{|x| \leqslant k} |u(x)|_X}{2^k},\ \forall u \in \mathcal{X}.$$

Let $\beta(\cdot) = (p^*(\cdot), q^*(\cdot))$, and Q be a map on $\mathcal{C}_\beta$ with $Q[0] = 0$ and $Q[\beta] = \beta$. Define an operator $Q = (Q_1, Q_2)$ on $\mathcal{C}$ by

$$Q_1[u,v](x) = \int_{\mathbb{R}} \frac{r_1(y)u(y)}{1 + b_1(y)(u(y) + a_1(y)(q^*(y) - v(y))} k_1(x,y)\mathrm{d}y,$$
$$Q_2[u,v](x) = \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)u(y) + v(y)}{1 + b_2(y)(q^*(y) + a_2(y)u(y) - v(y))} k_2(x,y)\mathrm{d}y,$$

where $U := (u,v) \in \mathcal{C}$.

Proposition 5.3.1. *Assume that (H1)–(H3) hold. Then Q satisfies the assumptions (B1)–(B5) in Section 1.5.2 with $X_\beta = \mathcal{C}_\beta^{per}$.*

Proof. According to the assumptions (K1)–(K2), it then easily follows that Q is monotone on $\mathcal{C}_\beta$. Note that if $U_n(x,\phi) = (u_n(x,\phi), v_n(x,\phi))$ is a solution of (5.3.1) with $(u_0(\cdot), v_0(\cdot)) = (\phi_1, \phi_2) := \phi$, then so is $(u_n(x-a,\phi), v_n(x-a,\phi))$, $\forall a \in L\mathbb{Z}$. This implies that (B1) holds. By Theorem 5.2.1, it follows that (B5) holds for Q. It remains to prove (B2) and (B3).

We take Q_1 as an example, since similar results hold for Q_2. First, we define

$$G_1(x) = \int_{\mathbb{R}} k_1(x,y)\mathrm{d}y,$$

and

$$H_1(U)(x) = \frac{r_1(x)u(x)}{1 + b_1(x)(u(x) + a_1(x)(q^*(x) - v(x))}.$$

By (K2(i)), (K2(ii)) and (K2(v)), it is easy to see $G_1(x)$ is a continuous and L-periodic function, hence it is bounded, denoted by $\mathcal{N}$. Note that $k(x,y)$ is nonnegative, we can use Dini's Theorem to show that $G_1(x)$ converges uniformly on any compact set of $\mathbb{R}$, that is, for any $\varepsilon > 0$, $h > 0$, there exists a $\mathcal{M} > 0$ such that

$$\int_{|y|>\mathcal{M}} k_1(x,y)\mathrm{d}y < \varepsilon,$$

for any $x \in [-h,h]$. For the above ε and h, there exists a positive $\delta_1 (< \varepsilon)$ such that $\|U_1 - U_2\|_{[-\mathcal{M},\mathcal{M}]} < \delta_1$, where $U_1 = (u^{(1)}, v^{(1)}), U_2 = (u^{(2)}, v^{(2)}) \in \mathcal{C}_\beta$. Then we have

$$\begin{aligned}
&|Q_1(U_1)(x) - Q_1(U_2)(x)| = |\int_{\mathbb{R}} (H_1(U_1)(y) - H_1(U_2)(y))k_1(x,y)\mathrm{d}y|,\\
&= |\int_{\mathbb{R}} [H_{1u}(\xi)(u^{(1)} - u^{(2)})(y) + H_{1v}(\xi)(v^{(1)} - v^{(2)})(y)]k_1(x,y)\mathrm{d}y|\\
&\leqslant \int_{\mathbb{R}} \mathcal{A}\Big[|(u^{(1)} - u^{(2)})(y)| + |(v^{(1)} - v^{(2)})(y)|\Big]k_1(x,y)\mathrm{d}y\\
&= \Big(\int_{|y|>\mathcal{M}} + \int_{|y|\leqslant\mathcal{M}}\Big)\mathcal{A}\Big[|(u^{(1)} - u^{(2)})(y)| + |(v^{(1)} - v^{(2)})(y)|\Big]k_1(x,y)\mathrm{d}y\\
&= 2\|\beta\|\mathcal{A}\int_{|y|>\mathcal{M}} k_1(x,y)\mathrm{d}y + 2\delta_1\mathcal{A}\int_{|y|\leqslant\mathcal{M}} k_1(x,y)\mathrm{d}y\\
&< 2\mathcal{A}(\|\beta\| + \mathcal{N})\varepsilon,
\end{aligned}$$

where $\mathcal{A} := \max\{\|H_{1u}\|, \|H_{1v}\|\}$, which implies that (B2) holds.

Regarding (B3), it is easy to check Q_1 is uniformly bounded. For the above $\varepsilon > 0$, there exist an $\delta_2(\varepsilon) > 0$ such that $\forall x_1,\ x_2 \in \mathbb{R}$ or any compact interval in $\mathbb{R}$ with

$|x_1 - x_2| < \delta_2$, since k_1 is L_1-contiuous, then we have

$$|Q_1(U)(x_1) - Q_1(U)(x_2))| \leqslant \max\{r_1(x)\}\|U\|\left|\int_{\mathbb{R}}\Big(k_1(x_1,y) - k_1(x_2,y)\Big)\mathrm{d}y\right| < \varepsilon,$$

which implies that Q_1 is equicontinous. By the Arzelà-Ascoli theorem, it follows that Q_1 is compact. □

Now we introduce a family of operators $\{\hat{Q}\}$ on $\mathcal{X}_\beta$:

$$\hat{Q}[v](s)(\theta) := Q[v_s](\theta), \quad \forall v \in \mathcal{X}_\beta,\ s \in \mathbb{R},\ \theta \in [0, L], \tag{5.3.2}$$

where $v_s \in \mathcal{C}$ is defined by

$$v_s(x) = v(s + n_x)(\theta_x), \quad \forall x = n_x + \theta_x \in \mathbb{R},\ n_x = L\left[\frac{x}{L}\right],\ \theta_x \in [0, L).$$

Then we can follow the procedure in Section 1.5.2 to define c_+^* and $\overline{c}_+$ as in (1.5.2). In order to show that $\overline{c}_+$ is the minimal wave speed for L-periodic traveling waves of system (5.3.1) connecting β to 0, we need the following assumption:

(H4) $c_{1+}^* + c_{2-}^* > 0$, where c_{1+}^* and c_{2-}^* are the rightward and leftward spreading speeds for (5.3.3) and (5.3.5), respectively.

Theorem 5.3.1. *Assume that (H1)–(H4) hold. Then for any $c \geq \overline{c}_+$, system* (5.3.1) *admits an L-periodic traveling wave $(U(x - cn, x), V(x - cn, x))$ connecting β to* 0*, with wave profile components $U(\xi, x)$ and $V(\xi, x)$ being continuous and non-increasing in ξ, and for any $c < \overline{c}_+$, there is no such traveling wave connecting β to* 0*.*

Proof. By Theorem 1.5.3 (2) and (3), it suffices to exclude the second case in Theorem 1.5.3 (2). Suppose, by contradiction, the statement in Theorem 1.5.3 (2(ii)) is valid for some $c \geq \overline{c}_+$. Since system (5.3.1) has exactly three L-periodic nonnegative steady states and $\hat{E}_0 = (0, q^*(x))$ is the only intermediate equilibrium between $\hat{E}_1 = \beta$ and $\hat{E}_2 = 0$, we have $\alpha_1 = \alpha_2 = \hat{E}_0$. Hence, by restricting system (5.3.1) on the order interval $[\hat{E}_0, \hat{E}_1]$ and $[\hat{E}_2, \hat{E}_0]$, respectively, we find that one scalar equation

$$u_{n+1}(x) = \int_{\mathbb{R}} \frac{r_1(y)}{1 + b_1(y)u_n(y)} u_n(y)k_1(x, y)\mathrm{d}y, \tag{5.3.3}$$

admits an L-periodic traveling wave $U(x - cn, x)$ connecting $p^*(x)$ to 0 with $U(\xi, x)$ being continuous and nonincreasing in ξ, and the other scalar equation

$$v_{n+1}(x) = \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y)q^*(y)} \cdot \frac{v_n(y)}{1 + b_2(y)(q^*(y) - v_n(y))} k_2(x, y)\mathrm{d}y, \tag{5.3.4}$$

also admits an L-periodic traveling wave $V(x-cn,x)$ connecting $q^*(x)$ to 0 with $V(\xi,x)$ being continuous and nonincreasing in ξ.

Let $W(x-cn,x) = q^*(x) - V(x-cn,x)$. Then $W(x-cn,x)$ is an L-periodic traveling wave connecting 0 to $q^*(x)$ of the following scalar equation with $W(\xi,x)$ being continuous and nondecreasing in ξ

$$w_{n+1}(x) = \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)w_n(y)} w_n(y)k_2(x,y)\mathrm{d}y. \tag{5.3.5}$$

Note that $W(x-cn,x)$ is an L-periodic leftward traveling wave connecting 0 to q^* with wave speed $-c$, and that systems (5.3.3) and (5.3.5) admit rightward spreading speed c^*_{1+} and leftward spreading speed c^*_{2-}, respectively, which are also the rightward and the leftward minimal wave speeds (see, e.g., [81, Theorems 5.2 and 5.3]). It then follows that $c \geq c^*_{1+}$ and $-c \geq c^*_{2-}$. This implies that $c^*_{1+} + c^*_{2-} \leqslant 0$, a contradiction. □

Let $\lambda_2(\mu)$ be the principal eigenvalue of the eigenvalue problem:

$$\begin{aligned}
&\lambda\psi(x) = \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)} e^{-\mu(x-y)}\psi(y)k_2(x,y)\mathrm{d}y,\\
&\psi(x+L) = \psi(x), \quad x \in \mathbb{R}.
\end{aligned} \tag{5.3.6}$$

In order to prove that system (5.3.1) admits a single rightward spreading speed, we impose the following assumption:

(H5) $\limsup_{\mu\to 0^+} \frac{\ln \lambda_2(\mu)}{\mu} < c^*_{1+}$, where c^*_{1+} is the rightward spreading speed of (5.3.3).

Theorem 5.3.2. *Assume that (H1)–(H5) hold. Then the following statements are valid for system* (5.3.1)*:*

(i) If $\phi \in \mathcal{C}_\beta$, $0 \leqslant \phi \leqslant \omega \ll \beta$ for some $\omega \in \mathcal{C}^{per}_\beta$, and $\phi(x) = 0, \forall x \geq H$, for some $H \in \mathbb{R}$, then $\lim_{n\to+\infty, x\geq cn} (u_n(x,\phi), v_n(x,\phi)) = (0,0)$ for any $c > \bar{c}_+$.

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi(x) \geq \sigma$, $\forall x \leqslant K$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim_{n\to+\infty, x\leqslant cn} ((u_n(x,\phi), v_n(x,\phi)) - \beta(x)) = 0$ for any $c < \bar{c}_+$.

Proof. By Theorem 1.5.4, it suffices to show $\bar{c}_+ = c^*_+$. If this is not valid, then the definition of $\bar{c}_+$ and c^*_+ implies that $\bar{c}_+ > c^*_+$. By Theorem 1.5.3 (1) and (3), it follows that system (5.3.1) admits an L-periodic traveling wave $(U(x-c^*_+n,x), V(x-c^*_+n,x))$ connecting $(p^*(x), q^*(x))$ to $(0, q^*(x))$ with $U(\xi,x)$ and $V(\xi,x)$ being continuous and nonincreasing in ξ. Therefore, $V \equiv q^*(x)$, and $U_1(x-c^*_+n,x)$ is an L-periodic traveling wave connecting $p^*(x)$ to 0. This implies that $c^*_+ \geq c^*_{1+}$ where c^*_{1+} is the rightward spreading of (5.3.3). By [134, (2.7)], it follows that $c_{1+}^* = \inf_{\mu>0} \frac{\ln \lambda_1(\mu)}{\mu}$, where $\lambda_1(\mu)$ is the principal eigenvalue of the following eigenvalue problem:

$$\begin{aligned} &\lambda\psi(x) = \int_{\mathbb{R}} r_1(y) e^{-\mu(y-x)} \psi(y) k_1(x,y) \mathrm{d}y, \\ &\psi(x+L) = \psi(x), \quad x \in \mathbb{R}. \end{aligned} \tag{5.3.7}$$

For any given $c_1 \in (c_+^*, \bar{c}_+)$, there exists $\mu_1 > 0$ such that $c_1 = \frac{\ln \lambda_1(\mu_1)}{\mu_1}$. Let $\phi_1^*(x)$ be the L-periodic positive eigenfunction associated with the principal eigenvalue $\lambda_1(\mu_1)$ of (5.3.7). It then easily follows that

$$u_n(x) := e^{-\mu_1(x-c_1 n)} \phi_1^*(x) = e^{-\mu_1 x} \phi_1^*(x) [\lambda_1(\mu_1)]^n, \quad n \geq 0, \ x \in \mathbb{R},$$

is a solution of the linear equation

$$u_{n+1}(x) = \int_{\mathbb{R}} r_1(y) u_n(y) k_1(x,y) \mathrm{d}y.$$

Since $c_1^* < c_1$ and (H5) holds, we can choose a small number $\mu_2 \in (0, \mu_1)$ such that $c_2 := \frac{\ln \lambda_2(\mu_2)}{\mu_2} < c_1$. Let $\phi_2^*(x)$ be the positive eigenfunction associated with the principal eigenvalue $\lambda_2(\mu_2)$ of (5.3.6). It is easy to see that

$$v_n(x) := e^{-\mu_2(x-c_2 n)} \phi_2^*(x) = e^{-\mu_2 x} \phi_2^*(x) [\lambda_2(\mu_2)]^n$$

is a solution of the linear equation

$$v_{n+1}(x) = \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y) q^*(y)} v_n(y) k_2(x,y) \mathrm{d}y. \tag{5.3.8}$$

Since $c_1 > c_2$, it follows that the function

$$\tilde{v}_n(x) := e^{-\mu_2(x-c_1 n)} \phi_2^*(x) = e^{\mu_2(c_1-c_2)n} v_n(x), \quad n \geq 0, \ x \in \mathbb{R},$$

satisfies

$$\tilde{v}_{n+1}(x) \geq \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y) q^*(y)} \tilde{v}_n(y) k_2(x,y) \mathrm{d}y. \tag{5.3.9}$$

Define the following two functions:

$$\overline{u}_n(x) := \min\{h_1 e^{-\mu_1(x-c_1 n)} \phi_1^*(x), p^*(x)\}, \quad n \geq 0, \ x \in \mathbb{R}, \tag{5.3.10}$$

and

$$\overline{v}_n(x) := \min\{h_2 e^{-\mu_2(x-c_1 n)} \phi_2^*(x), q^*(x)\}, \quad n \geq 0, \ x \in \mathbb{R}, \tag{5.3.11}$$

where

$$h_2 := \max_{x \in [0,L]} \frac{q^*(x)}{\phi_2^*(x)} > 0, \quad h_1 := \min_{x \in [0,L]} \frac{h_2 \phi_2^*(x)}{b_2(x) \phi_1^*(x)} > 0.$$

Now we want to verify that $(\overline{u}_n, \overline{v}_n)$ is an upper solution for system (5.3.1). For all $x - c_1 n > \frac{1}{\mu_1} \ln \frac{h_1\phi_1^*(x)}{p^*(x)}$, we have $\overline{u}_n(x) = h_1 e^{-\mu_1(x-c_1n)}\phi_1^*(x)$, and therefore,

$$\begin{aligned}&\overline{u}_{n+1}(x) - Q_1[\overline{u}_n, \overline{v}_n](x)\\ &= \int_{\mathbb{R}} \frac{r_1(y)b_1(y)\overline{u}_n(y)[\overline{u}_n(y) + a_1(y)(q^*(y) - \overline{v}_n(y))]}{1 + b_1(y)(\overline{u}_n(y) + a_1(y)(q^*(y) - \overline{v}_n(y))} k_1(x, y)\mathrm{d}y \geqslant 0.\end{aligned}$$

For all $x - c_1 n < \frac{1}{\mu_1} \frac{h_1\phi_1^*(x)}{p^*(x)}$, we obtain $\overline{u}_n(x) = p^*(x)$, and hence,

$$\begin{aligned}&\overline{u}_{n+1}(x) - Q_1[\overline{u}_n, \overline{v}_n](x)\\ &= \int_{\mathbb{R}} \frac{r_1(y)b_1(y)a_1(y)p^*(y)[q^*(y) - \overline{v}_n(y)]}{[1 + b_1(y)p^*(y)][1 + b_1(y)(p^*(y) + a_1(y)(q^*(y) - \overline{v}_n(y))]} k_1(x, y)\mathrm{d}y \geqslant 0.\end{aligned}$$

On the other hand, for all $x - c_1 n > \frac{1}{\mu_2} \ln \frac{h_2\phi_2^*(x)}{q^*(x)} \geqslant 0$, it follows that

$$\overline{v}_n(x) = h_2 e^{-\mu_2(x-c_1n)}\phi_2^*(x),$$

which satisfies inequality (5.3.9). Note that

$$\overline{u}_n(x) \leqslant h_1 e^{-\mu_1(x-c_1n)}\phi_1^*(x), \quad \forall t \geq 0,\ x \in \mathbb{R},$$

and $\mu_2 \in (0, \mu_1)$, we have

$$\begin{aligned}&\overline{v}_{n+1}(x) - Q_2[\overline{u}_n, \overline{v}_n](x)\\ &= \int_{\mathbb{R}} \frac{r_2(y)b_2(y)}{1 + b_2(y)q^*(y)} \cdot \frac{(q^*(y) - \overline{v}_n(y)(\overline{v}_n(y) - b_2(y)\overline{u}_n(y))}{1 + b_2(y)(q^*(y) + a_2(y)\overline{u}_n(y) - \overline{v}_n(y))} k_2(x, y)\mathrm{d}y \geqslant 0,\end{aligned}$$

where $\overline{v}_n - a_2\overline{u}_n = e^{-\mu_1(x-c_1n)}(h_2\phi_2^* - b_2h_1\phi_1^*) \geq 0$.

For all $x - c_1 n < \frac{1}{\mu_2} \ln \frac{h_2\phi_2^*(x)}{q^*(x)}$, we have $\overline{v}_n(x) = q^*(x)$. Therefore,

$$\begin{aligned}&\overline{v}_{n+1}(x) - Q_2[\overline{u}_n, \overline{v}_n](x)\\ &= \int_{\mathbb{R}} \frac{r_2(y)q^*(y)}{1 + b_2(y)q^*(y)} \big[1 - \frac{1 + b_2(y)a_2(y)\overline{u}_n(y)}{1 + b_2(y)a_2(y)\overline{u}_n(y)}\big] k_2(x, y)\mathrm{d}y = 0.\end{aligned}$$

It then follows that $\overline{U}_n := (\overline{u}_n, \overline{v}_n)$ is a continuous upper solution of system (5.3.1).

Let $\phi \in \mathcal{C}_\beta$ with $\phi(x) \geq \sigma$, $\forall x \leqslant K$ and $\phi(x) = 0$, $\forall x \geq H$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K, H \in \mathbb{R}$. By the arguments in [133, Lemma 2.2] and [139, Theorem 5.4], it follows that for any $c < \overline{c}_+$, there exists $\delta(c) > 0$ such that

$$\liminf_{n\to+\infty, x\leqslant cn} |U_n(x, \phi)| \geq \delta(c) > 0. \tag{5.3.12}$$

Moreover, there exists a sufficiently large positive constant $A \in L\mathbb{Z}$ such that

$$\phi(x) \leqslant \overline{U}_0(x-A) := \psi(x), \quad \forall x \in \mathbb{R}.$$

By the translation invariance of Q, it follows that $\overline{U}_n(x-A) = (\overline{u}_n(x-A), \overline{v}_n(x-A))$ is still an upper solution of system (5.3.1), and hence for U_n, we have

$$0 \leqslant U_n(x,\phi) \leqslant U_n(x,\psi) = \overline{U}_n(x-A), \quad \forall x \in \mathbb{R},\ n \geq 0. \tag{5.3.13}$$

Fix a number $\hat{c} \in (c_1, \overline{c}_+)$. Letting $x = \hat{c}n$ and $n \to +\infty$ in (5.3.13), together with (5.3.12), we have

$$0 < \delta(\hat{c}) \leqslant \liminf_{n\to+\infty} |U_n(\hat{c}n,\phi)| \leqslant \lim_{n\to+\infty} |\overline{U}_n(\hat{c}n - A)| = 0,$$

which is a contradiction. Thus, we have $c_+^* = \overline{c}_+$. □

To finish this section, we present some results on the principal eigenvalue problem.

Proposition 5.3.2. *Let $\lambda_m(\mu)(\mu \in [0,\mu^*))$ be the principal eigenvalue of the following eigenvalue problem:*

$$\lambda\psi = \int_{\mathbb{R}} m(y)e^{-\mu(y-x)}\psi(y)k(x,y)\mathrm{d}y, \tag{5.3.14}$$
$$\psi(x+L) = \psi(x), \quad x \in \mathbb{R}.$$

Then the following statements are valid:

(i) If $m_1(x) \geqslant m_2(x) > 0$ with $m_1(x) \not\equiv m_2(x), \forall x \in \mathbb{R}$, then $\lambda_{m_1}(\mu) > \lambda_{m_2}(\mu)$.

(ii) $\lambda_m(\mu)$ is a $\ln$-convex function of μ on $(0,\mu^*)$.

(iii) If $k(x,y) = k(y,x)$, then $\lambda_m(\mu) = \lambda_m(-\mu)$.

Proof. We use the arguments similar to those in [52, Lemma 15.5] to prove that (i) holds. First we define

$$\check{L}_m[\psi](x) = \int_{\mathbb{R}} m(y)e^{-\mu(y-x)}\psi(y)k(x,y)\mathrm{d}y.$$

Let $\lambda_{m_1}(\mu)$, $\lambda_{m_2}(\mu)$ be principal eigenvalues with $m_1(x) \geqslant m_2(x) > 0$, and $m_1(x) \not\equiv m_2(x)$. Suppose by contradiction, $\lambda_{m_1}(\mu) \leqslant \lambda_{m_2}(\mu)$. Let ψ_1, ψ_2 be associated eigenfunctions and chosen in a way that $0 < \psi_2 \ll \psi_1$. Then

$$\check{L}_{m_2}(\psi_1 - \psi_2) < \check{L}_{m_1}\psi_1 - \check{L}_{m_2}\psi_2 = \lambda_{m_1}\psi_1 - \lambda_{m_2}\psi_2 \leqslant \lambda_{m_1}(\psi_1 - \psi_2).$$

It follows that $\lambda_{m_1}(\psi_1-\psi_2)-\check{L}_{m_2}(\psi_1-\psi_2)=h>0$, and hence, $\psi_1-\psi_2$ is a positive root of $\lambda_{m_1}\psi-\check{L}_{m_2}\psi=0$, which is a contradiction to [52, Theorem 7.2], which states the above euqation has no positive solution if $\lambda_{m_1}(\mu)\leqslant\lambda_{m_2}(\mu)$.

(ii) follows from the same argument as in [80, Lemma 3.7]. (iii) can be proved by the arguments similar to those in [31, Theorem 2.3]. □

5.4 Linear determinacy of spreading speed

In this section, we establish a set of sufficient conditions for the rightward spreading speed to be determined by the linearization of system (5.3.1) at $\hat{E}_1=(0,0)$, which is

$$\begin{aligned}
u_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_1(y)u_n(y)}{1+b_1(y)a_1(y)q^*(y)}k_1(x,y)\mathrm{d}y, && (5.4.1)\\
v_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)}\cdot\frac{b_2(y)a_2(y)q^*(y)u_n(y)+v_n(y)}{1+b_2(y)q^*(y)}k_2(x,y)\mathrm{d}y, \quad n>0,\ x\in\mathbb{R}.
\end{aligned}$$

Under (H2) the following scalar equation

$$u_{n+1}(x)=\int_{\mathbb{R}}\frac{r_1(y)u_n(y)}{1+b_1(y)(u_n(y)+a_1(y)q^*(y))}k_1(x,y)\mathrm{d}y, \quad n>0, x\in\mathbb{R}, \tag{5.4.2}$$

admits a rightward spreading speed (also minimal rightward wave speed) $c_+^0=\inf\limits_{\mu>0}\frac{\ln\lambda_0(\mu)}{\mu}$ (see, e.g., [134]), where $\lambda_0(\mu)$ is the principal eigenvalue of the following eigenvalue problem:

$$\begin{aligned}
&\lambda\psi(x)=\int_{\mathbb{R}}\frac{r_1(y)}{1+b_1(y)a_1(y)q^*(y)}e^{-\mu(y-x)}\psi(y)k_1(x,y)\mathrm{d}y,\\
&\psi(x+L)=\psi(x), \quad x\in\mathbb{R}.
\end{aligned} \tag{5.4.3}$$

The subsequent result shows that c_+^0 is a lower bound of the slowest spreading c_+^* of system (5.3.1).

Proposition 5.4.1. *Let (H1)–(H3) hold. Then $c_+^*\geq c_+^0$.*

Proof. In the case that $\bar{c}_+>c_+^*$, by the same arguments as in Theorem 5.3.2, we see that $c_+^*\geq c_{1+}^*$, where c_{1+}^* is the rightward spreading speed of (5.3.3). Since $r_1(x)>\frac{r_1(x)}{1+b_1(x)a_1(x)q^*(x)}, \forall x\in\mathbb{R}$, by Proposition 5.3.2 (i), we have $\lambda_1(\mu)>\lambda_0(\mu), \forall\mu\geq 0$, where $\lambda_1(\mu)$ is the principal eigenvalue of (5.3.7). Thus, we have $c_+^*\geq c_{1+}^*>c_+^0$.

In the case that $\bar{c}_+=c_+^*$, let $(u_n(\cdot,\phi),v_n(\cdot,\phi))$ be the solution of system (5.3.1) with $\phi = (\phi_1, \phi_2) \in \mathcal{C}_\beta$. Then the positivity of the solution implies that

$$u_{n+1}(x) \geqslant \int_{\mathbb{R}} \frac{r_1(y)}{1 + b_1(y)(u_n(y) + a_1(y)q^*(y))} u_n(y) k_1(x,y)\mathrm{d}y,$$

Let $w_n(x, \phi_1)$ be the unique solution of (5.4.2) with $w_0(\cdot) = \phi_1$. Then the comparison principle yields that

$$u_n(x, \phi) \geqslant w_n(x, \phi_1), \quad \forall t \geq 0,\ x \in \mathbb{R}. \tag{5.4.4}$$

Since $\lambda(k_1, \dfrac{r_1}{1 + b_1 a_1 q^*}) > 1$, Proposition 5.2.1 implies that there exists a unique positive L-periodic steady state $w^*(x)$ of (5.4.2). Let $\phi^0 = (\phi_1^0, \phi_2^0) \in \mathcal{C}_\beta$ be chosen as in Theorem 5.3.2 (i) and (ii) such that $\phi_1^0 \leqslant w^*$. Suppose, by the contradiction, that $c_+^* < c_+^0$. We choose some $\hat{c} \in (\overline{c}_+^*, c_+^0)$. Then Theorem 5.3.2 implies $\lim_{n\to+\infty, x\geq \hat{c}n} u_n(x, \phi^0) = 0$. By Theorem 1.5.4 as applied to system (5.4.2), we have $\lim_{n\to+\infty, x\leqslant \hat{c}n}(w_n(x, \phi_1^0) - w^*(x)) = 0$. However, letting $x = \hat{c}n$ in (5.4.4), we get $\lim_{n\to+\infty, x=\hat{c}n} w_n(x, \phi_1^0) = 0$, which is a contradiction. ☐

For any given $\mu \in \mathbb{R}$, letting $U_n(x) = e^{-\mu x}\phi(x)[\lambda(\mu)]^n$ in (5.4.1), we obtain the following periodic eigenvalue problem:

$$\begin{aligned}
&\lambda\phi_1 = \int_{\mathbb{R}} \frac{r_1(y)}{1 + b_1(y)a_1(y)q^*(y)} e^{-\mu(y-x)}\phi_1(y)k_1(x,y)\mathrm{d}y,\\
&\lambda\phi_2 = \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)\phi_1(y) + \phi_2(y)}{1 + b_2(y)q^*(y)} e^{-\mu(y-x)}k_2(x,y)\mathrm{d}y,\\
&\phi_i(x) = \phi_i(x + L), \quad \forall x \in \mathbb{R},\ i = 1, 2.
\end{aligned} \tag{5.4.5}$$

Let $\overline{\lambda}(\mu)$ be the principal eigenvalue of the following periodic eigenvalue problem:

$$\begin{aligned}
&\lambda\psi = \int_{\mathbb{R}} \frac{r_2(y)}{1 + b_2(y)q^*(y)} \cdot \frac{\psi(y)}{1 + b_2(y)q^*(y)} e^{-\mu(y-x)}k_2(x,y)\mathrm{d}y,\\
&\psi(x) = \psi(x + L), \quad x \in \mathbb{R}.
\end{aligned} \tag{5.4.6}$$

Then there exists $\mu_0 > 0$ such that $c_+^0 = \frac{\ln \lambda_0(\mu_0)}{\mu_0}$. Now we make the following assumption:

(D1) $\lambda_0(\mu_0) > \overline{\lambda}(\mu_0)$.

Proposition 5.4.2. *Let (H1)–(H3) and (D1) hold. Then the periodic eigenvalue problem* (5.4.5) *with* $\mu = \mu_0$ *has a simple eigenvalue* $\lambda_0(\mu_0)$ *associated with a positive* L*-periodic eigenfunction* $\phi^* = (\phi_1^*, \phi_2^*)$.

Proof. Clearly, there exists an L-periodic eigenfunction $\phi_1^* \gg 0$ associated with the principal eigenvalue $\lambda_0(\mu_0)$ of (5.4.2), that is,

$$\lambda_0(\mu_0)\phi_1^* = \int_{\mathbb{R}} \frac{r_1(y)}{1+b_1(y)a_1(y)q^*(y)} e^{-\mu_0(y-x)}\phi_1^*(y)k_1(x,y)\mathrm{d}y.$$

Since the first equation of (5.4.5) is decoupled from the second one, it suffices to show that $\lambda_0(\mu_0)$ has a positive eigenfunction $\phi^* = (\phi_1^*, \phi_2^*)$ in (5.4.5), where ϕ_2^* is to be determined. Note that

$$\begin{aligned}
\lambda\phi_2 &= \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)\phi_1^*(y)+\phi_2(y)}{1+b_2(y)q^*(y)} e^{-\mu(y-x)}k_2(x,y)\mathrm{d}y,\\
&= \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)\phi_1^*(y)}{1+b_2(y)q^*(y)} e^{-\mu(y-x)}k_2(x,y)\mathrm{d}y\\
&\quad + \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)} \cdot \frac{\phi_2(y)}{1+b_2(y)q^*(y)} e^{-\mu(y-x)}k_2(x,y)\mathrm{d}y\\
&:= h + \tilde{L}\phi_2.
\end{aligned}$$

It follows that $\lambda_0(\mu_0)\phi_2 - \tilde{L}\phi_2 = h \gg 0$. It is easy to verify $\tilde{L}$ is a positive and compact, and hence, $s(L) = \overline{\lambda}(\mu_0)$, where $s(L)$ is the spectral radius of L. Since $\lambda_0(\mu_0) > \overline{\lambda}(\mu_0) = s(L)$, by the Krein-Rutman Theorem (see, e.g. Theorem 1.3.1 and [68]), there exists a unique $\phi_2^* \gg 0$ such that $\lambda_0(\mu_0)\phi_2^* - \tilde{L}\phi_2^* = h \gg 0$. It then follows that (ϕ_1^*, ϕ_2^*) satisfies (5.4.5) with $\mu = \mu_0$. Since $\lambda_0(\mu_0)$ is a simple eigenvalue for (5.4.2), we see that so is $\lambda_0(\mu_0)$ for (5.4.5). □

By virtue of Proposition 5.4.2, we easily see that for any given $M > 0$, the function

$$S_n(x) = Me^{-\mu_0 x}[\lambda_0(\mu_0)]^n \phi^*(x), \quad n \geq 0,\ x \in \mathbb{R}, \tag{5.4.7}$$

where $S_n(x) = (s_n(x), w_n(x))$, is a positive solution of system (5.4.1). In order to obtain an explicit formula for the spreading speeding $\overline{c}_+$, we need the following additional condition:

(D2) $\dfrac{\phi_1^*(x)}{\phi_2^*(x)} \geqslant \max\left\{a_1(x), \dfrac{1}{a_2(x)}\right\}, \quad \forall x \in \mathbb{R}.$

We are now in a position to show that system (5.3.1) admits a single rightward spreading speed $\overline{c}_+$, which is linearly determinate.

Theorem 5.4.1. *Let (H1)–(H3) and (D1)–(D2) hold. Then* $\overline{c}_+ = c_+^* = c_+^0 = \inf_{\mu>0} \frac{\ln \lambda_0(\mu)}{\mu}$.

Proof. First, we verify that $S_n(x) = (s_n, w_n)$, as defined in (5.4.7), is an upper solution of system (5.3.1). Since $\dfrac{s_n}{w_n} = \dfrac{\phi_1^*}{\phi_2^*}$ and (D2) holds , it follows that

$$\begin{aligned}
& s_{n+1}(x) - \int_{\mathbb{R}} \frac{r_1(y)s_n(y)}{1+b_1(y)(s_n(y)+a_1(y)(q^*(y)-w_n(y))}k_1(x,y)\mathrm{d}y \\
&= \int_{\mathbb{R}} \frac{r_1(y)b_1(y)s_n(y)w_n(y)k_1(x,y)}{[1+b_1(y)a_1(y)q^*(y)][1+b_1(y)(s_n(y)+a_1(y)(q^*(y)-w_n(y))]}\Big(\frac{s_n(y)}{w_n(y)} - a_1(y)\Big)\mathrm{d}y \\
&= \int_{\mathbb{R}} \frac{r_1(y)b_1(y)s_n(y)w_n(y)k_1(x,y)}{[1+b_1(y)a_1(y)q^*(y)][1+b_1(y)(s_n(y)+a_1(y)(q^*(y)-w_n(y))]}\Big(\frac{\phi_1^*(y)}{\phi_2^*(y)} - a_1(y)\Big)\mathrm{d}y \\
&\geqslant 0, \qquad (5.4.8)
\end{aligned}$$

and

$$\begin{aligned}
& w_{n+1}(x) - \int_{\mathbb{R}} \frac{r_2(y)}{1+b_2(y)q^*(y)} \cdot \frac{r_2(y)a_2(y)q^*(y)s_n(y)+w_n(y)}{1+r_2(y)(q^*(y)-w_n(y)+a_2(y)s_n(y))}k_2(x,y)\mathrm{d}y \\
&= \int_{\mathbb{R}} \frac{r_2(y)b_2(y)w_n(y)k_2(x,y)}{1+b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)s_n(y)+w_n(y)}{[1+b_2(y)q^*(y)][1+b_2(y)(q^*(y)-w_n(y)+a_2(y)s_n(y))]} \cdot \\
&\quad \Big(a_2(y)\frac{s_n(y)}{w_n(y)} - 1\Big)\mathrm{d}y \\
&= \int_{\mathbb{R}} \frac{r_2(y)b_2(y)w_n(y)k_2(x,y)}{1+b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)s_n(y)+w_n(y)}{[1+b_2(y)q^*(y)][1+b_2(y)(q^*(y)-w_n(y)+a_2(y)s_n(y))]} \cdot \\
&\quad \Big(a_2(y)\frac{\phi_1^*(y)}{\phi_2^*(y)} - 1\Big)\mathrm{d}y \\
&\geqslant 0, \qquad (5.4.9)
\end{aligned}$$

Thus, $S_n(x)$ is an upper solution of (5.3.1). As we did in the proof of Proposition 5.4.1, we can choose some $\phi^0 \in \mathcal{C}_\beta$ satisfying the conditions in Theorem 5.3.2 (i) and (ii). Then there exists a sufficiently large number $M_0 > 0$ such that

$$0 \leqslant \phi^0(x) \leqslant M_0 e^{-\mu_0 x}\phi^*(x) = S_0(x), \quad \forall x \in \mathbb{R}.$$

Let $U_n(x)$ be the unique solution of system (5.3.1) with $U_0(\cdot) = \phi_0$. Then the comparison principle, together with the fact that $c_+^0\mu_0 = \ln\lambda_0(\mu_0)$, gives rise to

$$0 \leqslant U_n(x) \leqslant S_n(x) = M_0 e^{-\mu_0 x}\lambda_0(\mu_0)^n\phi^*(x) = M_0 e^{-\mu_0(x-c_+^0 n)}\phi^*(x), \quad \forall n \geqslant 0,\ x \in \mathbb{R}.$$

It follows that for any given $\varepsilon > 0$, there holds

$$0 \leqslant U_n(x) \leqslant S_n(x) \leqslant M_0 e^{-\mu_0\varepsilon n}\phi^*(x), \quad \forall n \geqslant 0,\ x \geqslant (c_+^0 + \varepsilon)n,$$

and hence,

$$\lim_{n\to+\infty, x\geqslant(c_+^0+\varepsilon)n} U_n(x) = 0.$$

By Theorem 1.5.4 (ii), we obtain $c_+^* \leqslant c_+^0 + \varepsilon$. Letting $\varepsilon \to 0$, we have $c_+^* \geqslant c_+^0$. In the case that $\overline{c}_+ > c_+^*$, the proof of Proposition 5.4.1 shows that $c_+^* > c_+^0$, a contradiction. This shows that $\overline{c}_+ = c_+^* = c_+^0$. □

5.5 An application

In this section, we assume the $k_i(x, y)$ $(i = 1, 2)$ can be written as a function of the dispersal distance, i.e., $k_i(x, y) = k_i(x - y)$, with the following property:

(K3) $\displaystyle\int_{-\infty}^{+\infty} k_i(x)\mathrm{d}x = 1$, and $k_i(-x) = k_i(x)$.

As an application, we consider a patchy landscape in which both species have the same spatially varying carrying capacity, $C_1(x) = C_2(x) = C(x)$, that is,

$$C(x) = \begin{cases} C_M, & 0 \leqslant x < L_1, \\ C_m < C_M, & L_1 \leqslant x < L, \end{cases}$$

This indicates that Patch 1 is more suitable for both species, compared with Patch 2. The growth rates r_i of i-th species $(i = 1, 2)$ are constant, which are environmental homogeneous, and $a_i(x)$ are also piecewise constant functions. Although the piecewise constant coefficient functions are discontinuous, we may choose a sequence of continuous and L-periodic functions to approximate such a coefficient function, and then carry the analytic results over to this case by a limiting process. Thus, we are led to the following spatially periodic model with kernels k_i satisfying assumptions (K2)-(K3):

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_1 p_n(y)}{1 + b_1(y)(p_n(y) + a_1(y)q_n(y))} k_1(x - y)\mathrm{d}y, \\ q_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_2 q_n(y)}{1 + b_2(y)(q_n(y) + a_2(y)p_n(y))} k_2(x - y)\mathrm{d}y, \ x \in \mathbb{R}, \end{aligned} \tag{5.5.1}$$

where $b_i(x) = \dfrac{r_i - 1}{C(y)}$.

We also need the following assumption on system (5.5.1):

(M) $a_1^M < \dfrac{C_m}{C_M}$, and $\dfrac{C_M}{C_m} < a_2^m$, where $a_1^M = \max_{x\in[0,L]} a_1(x)$, $a_2^m = \min_{x\in[0,L]} a_2(x)$.

Lemma 5.5.1. *Assume that (M) hold and both k_1 and k_2 satisfy (K2)–(K3). Then (H1)–(H5) are valid for system* (5.5.1).

Proof. (H1) holds immediately by Proposition 5.3.2 (i) with $m_i(x) = r_i > 1$.

Now we verify (H2). Let $(0, q^*)$ be the L-periodic semi-trivial steady state of system (5.5.1), which is guaranteed by (H1), and $q_0 = \max_{x \in [0,L]} q^*(x)$. By a comparison argument, we have

$$\int_{\mathbb{R}} \frac{r_2 q_0}{1 + \frac{r_2 - 1}{C(y)} q_0} k_2(x-y) \mathrm{d}y \geqslant \int_{\mathbb{R}} \frac{r_2 q^*}{1 + \frac{r_2 - 1}{C(y)} q^*} k_2(x-y) \mathrm{d}y = q^*.$$

It then follows that

$$\int_{\mathbb{R}} \frac{r_2 q_0}{1 + \frac{r_2 - 1}{C(y)} q_0} k_2(x-y) \mathrm{d}y \geqslant q_0,$$

and hence,

$$\int_{\mathbb{R}} \frac{r_2 q_0}{1 + \frac{r_2 - 1}{C_M} q_0} k_2(x-y) \mathrm{d}y \geqslant \int_{\mathbb{R}} \frac{r_2 q_0}{1 + \frac{r_2 - 1}{C(y)} q_0} k_2(x-y) \mathrm{d}y \geqslant q_0.$$

Then we have

$$\frac{r_2}{1 + \frac{r_2 - 1}{C_M} q_0} \geqslant 1, \text{ i.e., } q^* \leqslant q_0 \leqslant C_M.$$

Taking $m_1(x) = \dfrac{r_1}{1 + b_1(x) a_1(x) q^*(x)} = \dfrac{r_1}{1 + \frac{r_1 - 1}{C(y)} a_1(x) q^*(x)}$, we obtain

$$\frac{r_1}{1 + \frac{r_1 - 1}{C(y)} a_1(x) q^*(x)} \geqslant \frac{r_1}{1 + \frac{r_1 - 1}{C_m} a_1^M q^*(x)} \geqslant \frac{r_1}{1 + \frac{r_1 - 1}{C_m} a_1^M C_M} > \frac{r_1}{1 + r_1 - 1} = 1.$$

Thus, $\lambda\Big(k_1, \dfrac{r_1}{1 + b_1 a_1 q^*}\Big) > 1$ due to Proposition 5.3.2 (i).

Next we prove (H3) by a way of contradiction. Suppose $(\tilde{p}, \tilde{q})$ is a positive L-periodic steady state. We introduce the following system

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_1 p_n(y)}{1 + \frac{r_1 - 1}{C_m}(p_n(y) + a_1^M q_n(y))} k_1(x-y) \mathrm{d}y, \\ q_{n+1}(x) &= \int_{\mathbb{R}} \frac{r_2 q_n(y)}{1 + \frac{r_2 - 1}{C_M}(q_n(y) + a_2^m p_n(y))} k_2(x-y) \mathrm{d}y, \ x \in \mathbb{R}, \end{aligned} \tag{5.5.2}$$

with $\tilde{p}_0 = \min_{x \in [0,L]} \tilde{p}(x)$, $\tilde{q}_0 = \min_{x \in [0,L]} \tilde{q}(x)$. Since $(p_n(x), q_n(x))$ satisfies system (5.5.1), we have

$$\begin{aligned} p_{n+1}(x) &\geqslant \int_{\mathbb{R}} \frac{r_1 p_n(y)}{1 + \frac{r_1 - 1}{C_m}(p_n(y) + a_1^M q_n(y))} k_1(x-y) \mathrm{d}y, \\ q_{n+1}(x) &\leqslant \int_{\mathbb{R}} \frac{r_2 q_n(y)}{1 + \frac{r_2 - 1}{C_M}(q_n(y) + a_2^m p_n(y))} k_2(x-y) \mathrm{d}y, \ x \in \mathbb{R}. \end{aligned}$$

By the comparison argument, we easily verify that

$$\int_{\mathbb{R}} \frac{r_1\tilde{p}_0}{1+\frac{r_1-1}{C_m}(\tilde{p}_0+a_1^M\tilde{q}_0)} k_1(x-y)\mathrm{d}y \leqslant \int_{\mathbb{R}} \frac{r_1\tilde{p}(y)}{1+\frac{r_1-1}{C(y)}(\tilde{p}(y)+a_1(y)\tilde{q}(y))} k_1(x-y)\mathrm{d}y = \tilde{p}(x).$$

It follows that

$$\frac{r_1\tilde{p}_0}{1+\frac{r_1-1}{C_m}(\tilde{p}_0+a_1^M\tilde{q}_0)} \int_{\mathbb{R}} k_1(x-y)\mathrm{d}y \leqslant \tilde{p}_0,$$

which implies that

$$\frac{r_1}{1+\frac{r_1-1}{C_m}(\tilde{p}_0+a_1^M\tilde{q}_0)} \leqslant 1.$$

Similarly, we have $\frac{r_2}{1+\frac{r_2-1}{C_M}(\tilde{q}_0+a_2^m\tilde{p}_0)} \geqslant 1$. A simple computation shows that

$$\frac{\tilde{q}_0+a_2^m\tilde{p}_0}{C_M} \leqslant 1 \leqslant \frac{\tilde{p}_0+a_1^M\tilde{q}_0}{C_m},$$

that is,

$$\Big(C_m - C_M a_1^M\Big)\tilde{q}_0 \leqslant \Big(C_M - C_m a_2^m\Big)\tilde{p}_0. \tag{5.5.3}$$

By assumption (M), we obtain

$$C_m - C_M a_1^M > 0,\ C_M - C_m a_2^m \leqslant 0,$$

which is a contradiction to (5.5.3).

Now we prove (H4). By Proposition 5.3.2 (ii) and (iii) with $m(x) = r_1(x)$, it is easy to see that the principal eigenvalue $\lambda_1(\mu)$ of (5.3.7) is an even function of μ on $(-\mu^*, \mu^*)$. Since $\lambda_1(\mu)$ is ln-convex on $(-\mu^*, \mu^*)$ and $\lambda_1(0) > 1$, we have $\lambda_1(\mu) > 1, \forall \mu > 0$. It follows that $c_{1+}^* = \inf\limits_{\mu>0} \frac{\ln\lambda_1(\mu)}{\mu} > 0$. Similarly, we can show that $c_{2-}^* > 0$. Thus, we have $c_{1+}^* + c_{2-}^* > 0$.

To verify (H5), it suffices to show that $\lim_{\mu\to 0^+} \frac{\ln\lambda_2(\mu)}{\mu} = 0$, where $\lambda_2(\mu)$ is the principal eigenvalue of (5.3.6). By Lemma 5.3.2(b)(c), $\ln\lambda_2(\mu)$ is an even function on $(-\mu^*, \mu^*)$, and n-ordered differentiable (see [32, 80]). Since $\lambda_2(0) = 1$, it follows that $\lim_{\mu\to 0^+} \frac{\ln\lambda_2(\mu)}{\mu} = 0 < c_{1+}^*$. □

As a consequence of Lemma 5.5.1 and Theorem 5.2.1, we have the following result.

Theorem 5.5.1. *Assume that (M) hold and both k_1 and k_2 satisfy (K2)–(K3). Then $E_1 = (p^*(x), 0)$ is globally asymptotically stable with respect to initial values in $\mathbb{P}_+\backslash\{0, E_2\}$.*

For simplicity, we transfer system (5.5.1) into the following cooperative system:

$$u_{n+1}(x) = \int_{\mathbb{R}} \frac{r_1 u_n(y)}{1 + b_1(y)(u_n(y) + a_1(y)(q^*(y) - v_n(y))} k_1(x-y)\mathrm{d}y, \tag{5.5.4}$$
$$v_{n+1}(x) = \int_{\mathbb{R}} \frac{r_2}{1 + b_2(y)q^*(y)} \cdot \frac{b_2(y)a_2(y)q^*(y)u_n(y) + v_n(y)}{1 + b_2(y)(q^*(y) + a_2(y)u_n(y) - v_n(y))} k_2(x-y)\mathrm{d}y.$$

By virtue of Propositions 5.3.2 and 5.4.1, we see that $\overline{c}_+ \geq c_+^0 > 0$. The next result about spreading speeds is implied by Theorem 5.3.2.

Theorem 5.5.2. *Assume that (M) hold and both k_1 and k_2 satisfy (K2)–(K3). Let $u(t, \cdot, \phi)$ be the solution of system* (5.5.4) *with $u(0, \cdot) = \phi \in \mathcal{C}_{u^*}$. Then the following statements are valid for system* (5.5.4)*:*

(i) If $\phi \in \mathcal{C}_\beta$, $0 \leqslant \phi \leqslant \omega \ll \beta$ for some $\omega \in \mathcal{C}_\beta^{per}$, and $\phi(x) = 0, \forall x \geq H$, for some $H \in \mathbb{R}$, then $\lim\limits_{n\to+\infty, x\geq cn} (u_n(x,\phi), v_n(x,\phi)) = (0,0)$ for any $c > \overline{c}_+$.

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi(x) \geq \sigma$, $\forall x \leqslant K$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim\limits_{n\to+\infty, x\leqslant cn} ((u_n(x,\phi), v_n(x,\phi)) - \beta(x)) = 0$ for any $c < \overline{c}_+$.

In view of Theorem 5.3.1, we have the following result on periodic traveling waves for system (5.5.1).

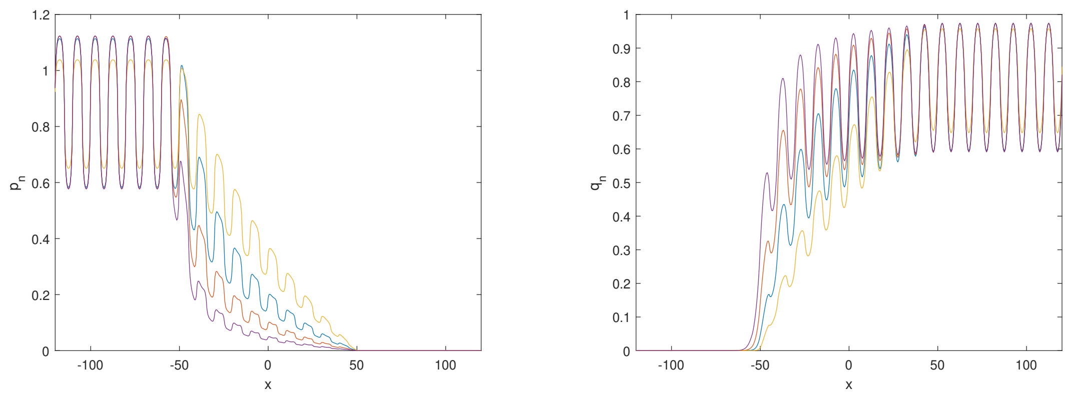
Theorem 5.5.3. *Assume that (M) hold and both k_1 and k_2 satisfy (K2)–(K3). Then for any $c \geq \overline{c}_+$, system* (5.5.1) *has an L-periodic rightward traveling wave $(U(x - cn, x), V(x-cn, x))$ connecting $(p^*(x), 0)$ to $(0, q^*(x))$ with the wave profile component $U(\xi, x)$ being continuous and non-increasing in ξ, and $V(\xi, x)$ being continuous and non-decreasing in ξ. While for any $c \in (0, \overline{c}_+)$, system* (5.5.1) *admits no L-periodic rightward traveling wave connecting $(p^*(x), 0)$ to $(0, q^*(x))$.*

The above results shows that if $a_1^M < \dfrac{C_m}{C_M} < 1 < \dfrac{C_M}{C_m} < a_2^m$, i.e., 1-th species is always a better and strong competitor, then 1-th species can invade and further replace 2-th species in a oscillating way no matter what movement strategy is taken. Below we present some simulations results for the process of invasion. For this purpose, we truncate the infinite domain $\mathbb{R}$ to a finite domain $[-M, M]$, where M is sufficiently large. The evolution of the solution is shown in figures. Let $r_1 = r_2 = e$,

$$a_1(x) = \begin{cases} 0.3, & 0 \leqslant x < 5.5, \\ 0.4, & 5.5 \leqslant x < 10, \end{cases} \quad a_2(x) = \begin{cases} 2, & 0 \leqslant x < 5.5, \\ 1.5, & 5.5 \leqslant x < 10, \end{cases}$$

$$C(x) = \begin{cases} 1, & 0 \leqslant x < 5.5, \\ 0.5, & 5.5 \leqslant x < 10. \end{cases}$$

Fig. 5.1 shows that under the same type dispersal kernel, taking a small dispersal, i.e., trying to stay in the patch, cannot help to reduce the loss induced by the intra-competition. Fig. 5.2 shows that the success of invasion of 1-th species into 2-th species is independent of the particular type of dispersal kernels.



(a) p_n with dispersal distance=1 (b) q_n with dispersal distance=0.1

Figure 5.1: The evolution of p_n and q_n with a Laplace kernel, when $n = 2, 4, 6, 8$

To obtain the linear determinacy of c^*, we need to verify (D1) and (D2). Below we provide an example with simple scenario where two species have same growth ability and competition ability, but their responses to environment changing are different. We assume that species-1, always has better response towards the varying environment conditions than species-2, that is, $C_1(x) > C_2(x) > 0,\ \forall x \in \mathbb{R}$.

Proposition 5.5.1. *We consider the following spatially periodic competition model*

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} \frac{rp_n(y)}{1+b_1(y)(p_n(y)+q_n(y))} k(x-y)\mathrm{d}y, \\ q_{n+1}(x) &= \int_{\mathbb{R}} \frac{rq_n(y)}{1+b_2(y)(q_n(y)+p_n(y))} k(x-y)\mathrm{d}y,\ x \in \mathbb{R}, \end{aligned} \tag{5.5.5}$$

where $b_i(x) = \dfrac{r-1}{C_i(y)}$, $C_i(x)$ *is* L*-periodic with* $C_1(x) > C_2(x) > 0$, $a_1 = a_2 = 1$ *and* $r > 1$ *are constant,* $k(x-y)$ *satisfies (K2)-(K3). Then (H1)-(H5) and (D1)-(D2) are valid.*

Proof. (H1) holds immediately by Proposition 5.3.2 (i) with $m_i(x) = r > 1,\ (i = 1, 2)$.

Now we verify (H2). Let $(0, q^*)$ be the L-periodic semi-trivial steady state of system (5.5.1), which is guaranteed by (H1), and $q_0 = \max\limits_{x\in[0,L]} q^*(x)$. By a comparison argument, we have

$$\int_{\mathbb{R}} \frac{rq_0}{1+\frac{r-1}{C_2(y)}q_0} k(x-y)\mathrm{d}y \geqslant \int_{\mathbb{R}} \frac{rq^*}{1+\frac{r-1}{C_2(y)}q^*} k(x-y)\mathrm{d}y = q^*.$$

It then follows that

$$\int_{\mathbb{R}} \frac{rq_0}{1+\frac{r-1}{C_2(y)}q_0} k(x-y)\mathrm{d}y \geqslant q_0,$$

and hence,

$$\int_{\mathbb{R}} \frac{rq_0}{1+\frac{r-1}{C_2^M}q_0} k(x-y)\mathrm{d}y \geqslant \int_{\mathbb{R}} \frac{rq_0}{1+\frac{r-1}{C_2^M(y)}q_0} k(x-y)\mathrm{d}y \geqslant q_0,$$

that is,

$$\frac{r}{1+\frac{r-1}{C_2^M}q_0} \geqslant 1, \text{ i.e., } q^* \leqslant q_0 \leqslant C_2^M.$$

Taking $m_1(x) = \dfrac{r}{1+b_1(x)q^*(x)} = \dfrac{r}{1+\frac{r-1}{C_1(y)}q^*(x)}$, we have

$$\frac{r}{1+\frac{r-1}{C_1(y)}q^*(x)} \geqslant \frac{r}{1+\frac{r-1}{C_2(y)}q^*(x)} \geqslant \frac{r}{1+\frac{r-1}{C_2^m}C_2^M} > \frac{r}{1+r-1} = 1.$$

Thus, $\lambda\Big(k, \dfrac{r}{1+b_1q^*}\Big) > 1$ due to Proposition 5.3.2 (i).

We prove (H3) by a way of contradiction. Suppose that $(\tilde{p}, \tilde{q})$ is a positive L-periodic steady state. Since

$$\begin{aligned} \tilde{p}(x) &= \int_{\mathbb{R}} \frac{r\tilde{p}(y)}{1+b_1(y)(\tilde{p}(y)+\tilde{q}(y))} k(x-y)\mathrm{d}y, \\ \tilde{q}(x) &= \int_{\mathbb{R}} \frac{r\tilde{q}(y)}{1+b_2(y)(\tilde{q}(y)+\tilde{p}(y))} k(x-y)\mathrm{d}y, \ x \in \mathbb{R}, \end{aligned} \tag{5.5.6}$$

it follows that

$$\lambda\Big(k, \frac{r}{1+b_1(\tilde{p}+\tilde{q})}\Big) = \lambda\Big(k, \frac{r}{1+b_2(\tilde{p}+\tilde{q})}\Big) = 1.$$

Note that

$$\frac{r}{1+b_1(\tilde{p}+\tilde{q})} > \frac{r}{1+b_2(\tilde{p}+\tilde{q})}.$$

Then Proposition 5.3.2 (i) implies that

$$\lambda\Big(k, \frac{r}{1+b_1(\tilde{p}+\tilde{q})}\Big) > \lambda\Big(k, \frac{r}{1+b_2(\tilde{p}+\tilde{q})}\Big),$$

which is a contradiction.

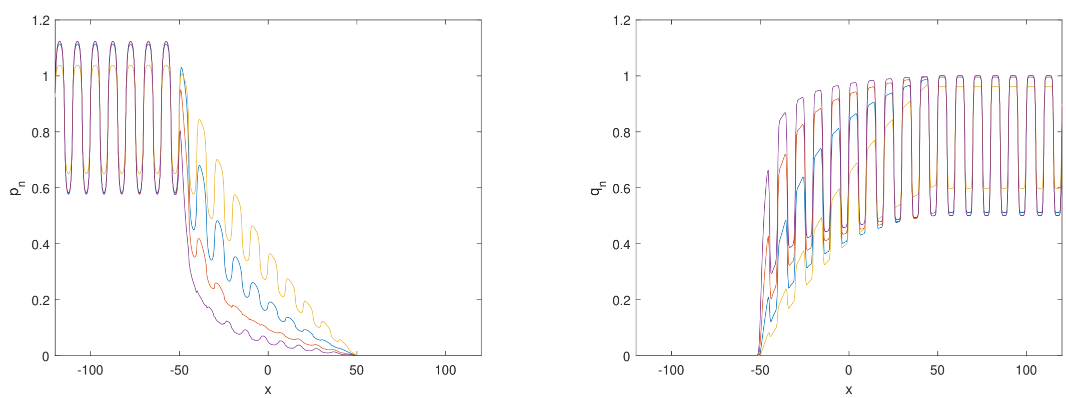
Assumptions (H4) and (H5) can be verified by arguments similar to those in the proof of Lemma 5.5.1.

Condition (D1) is easy to verify. Since $1 + b_1 q^* < (1 + b_1 q^*)^2 < (1 + b_2 q^*)^2$ with $C_1(x) > C_2(x),\ \forall x \in \mathbb{R}$, it follows that for eigenvalue problems (5.4.3) and (5.4.6), we have $\lambda_0(\mu) > \overline{\lambda}(\mu)$ due to Proposition 5.3.2 (i).

Regarding condition (D2), since $a_1 = a_2 = 1$, we have $\max\{a_1(x), \frac{1}{a_2(x)}\} = 1$. Let $\phi^* = (\phi_1^*, \phi_2^*)$ be the associated positive eigenfunctions associated with the principal eigenvalue λ of the periodic eigenvalue problem (5.4.5). Since

$$\begin{aligned}
&\lambda\phi_1^* - \int_{\mathbb{R}} \frac{r}{1 + b_2(y)q^*(y)} \cdot \frac{b_2(y)q^*(y)\phi_1^*(y) + \phi_1^*(y)}{1 + b_2(y)q^*(y)} e^{-\mu(y-x)} k(x-y)\mathrm{d}y, \\
&= \lambda\phi_1^* - \int_{\mathbb{R}} \frac{r}{1 + b_2(y)q^*(y)} \phi_1^*(y) e^{-\mu(y-x)} k(x-y)\mathrm{d}y \\
&\geqslant \lambda\phi_1^* - \int_{\mathbb{R}} \frac{r}{1 + b_1(y)q^*(y)} \phi_1^*(y) e^{-\mu(y-x)} k(x-y)\mathrm{d}y \\
&= \lambda\phi_1^* - \lambda\phi_1^* = 0,
\end{aligned}$$

it follows that ϕ_1^* is a upper solution, and hence, $\phi_1^* \geqslant \phi_2^*$, i.e., $\frac{\phi_1^*}{\phi_2^*} \geqslant 1$. □



(a) The evolution of p_n with a Gaussian kernel. (b) The evolution of q_n with a Laplace kernel.

Figure 5.2: The evolution of p_n and q_n with $k_1(x-y) = \frac{1}{\sqrt{2\pi \times 0.1}} e^{\frac{-(x-y)^2}{0.2}}$, $k_2(x-y) = \frac{1}{2 \times 0.5} e^{\frac{-|x-y|}{0.5}}$, when $n = 2, 4, 6, 8$

To finish this chapter, we remark that in the case where system (5.1.2) admits a unique positive steady state, its spatial dynamics is relatively simple from the viewpoint of mathematical analysis, as we can apply the theory developed in [81, 132] directly to the existence of two different spatially periodic traveling waves connecting $(0, q^*)$ and $(\tilde{p}, \tilde{q})$, $(p^*, 0)$ and $(\tilde{p}, \tilde{q})$, respectively, under appropriate conditions.

Chapter 6

Summary and future works

In this chapter, we first briefly summarize the main results in this thesis, and then present some possible future research works.

6.1 Research summary

In Chapters 2 and 3, we studied global dynamics of some climate-based vector-borne infectious disease models. In Chapters 4 and 5, we mainly focused on the propagation phenomena of some invading species, including the threshold dynamics, spreading speeds, and monostable traveling waves.

We presented and analyzed a time-periodic WNv compartment model with vertical infection and stage-structure in vector populations in Chapter 2. Moreover, we incorporated temperature-dependent incubation periods in both vectors and reservoirs. We then derived the mosquito reproduction number $\mathcal{R}_0^V$ and basic reproduction number $\mathcal{R}_0$, and showed these two numbers serve as threshold parameters that determine whether WNv will spread, that is, the mosquito-free equilibrium is globally attractive if $\mathcal{R}_0^V < 1$; the disease-free periodic solution is globally attractive if $\mathcal{R}_0^V > 1$ and $\mathcal{R}_0 < 1$; the model system is uniformly persistent if $\mathcal{R}_0^V > 1$ and $\mathcal{R}_0 > 1$. As an application, we conducted a case study for the disease transmission in Los Angeles County, California. We also carried out numerical simulations to identify the situations that require time-periodic delays. Moreover, we found that rising temperatures may potentially increase the risk of disease outbreaks.

In Chapter 3, we proposed a nonlocal reaction-diffusion model of vector-borne disease with periodic delays to investigate the multiple effects of the spatial heterogeneity, the temperature sensitivity of extrinsic and intrinsic incubation periods, and the seasonality on disease transmission. We introduced the basic reproduction number $\mathcal{R}_0$ for this model and then established a threshold type result on its global dynamics in terms of $\mathcal{R}_0$, that is, that the disease-free periodic solution is globally attractive if

$\mathcal{R}_0 < 1$; the model system is uniformly persistent and admits a positive periodic solution if $\mathcal{R}_0 > 1$. In the case where all the coefficients are constants, we also proved the global attractivity of the positive constant steady state when $\Re_0 > 1$. Numerically, we studied the malaria transmission in Maputo Province, Mozambique.

In Chapter 4, we developed an impulsive integro-differential model to describe an invading species with a birth pulse in the reproductive stage and a nonlocal dispersal stage. We first established a threshold-type result on the global dynamics for the model system in a bounded domain, and presented an application to insect pests outbreak in terms of the critical domain size. For the spatial spread in an unbounded domain, we proved the existence of the invasion speed and its coincidence with the minimal speed for monotone traveling waves. Numerical simulations were also carried out to illustrate our analytical results.

To study the propagation phenomena of two competing invaders in a spatially periodic habitat, we modified the early models in [25, 73, 110, 143] to a spatial-periodic integro-difference competitive population model in Chapter 5. We first obtained the existence of two semi-trivial periodic steady states and the global stability of one semi-trivial periodic steady state for the model system with periodic initial data. We established the existence of the minimal wave speed of the rightward spatially periodic traveling waves and its coincidence with the minimal rightward spreading speed. We also showed that the rightward spreading speed is linearly determinate under additional conditions. We presented some numerical simulations to verify our analytic results.

6.2 Future work

Related to the projects in this thesis, there are some open and challenging issues for future investigation.

The data used to describe the mosquito dynamics in a vector-borne disease model, as shown in Chapters 2 and 3, e.g., the mosquito biting rate, mortality rate, recruitment rate, and the extrinsic incubation period, are mainly temperature-driven. However, there exists other environmental drivers, like rainfalls and winds. For example, it has been shown that precipitation can be a limiting factor for mosquito populations [48, 111]. And hence, it would be interesting to incorporate these environmental drivers into the model and study their influence on the spread of vector-borne diseases. In addition to weather factors, other complex factors in the mosquito-bird interactions, such as bird migration [105, 140], feather-picking of sick birds [13], asymptomatic carriers [3, 21], avian host immunity [49], the mutualistic nature between mistletoes and birds [125, 126], non-viremic transmission via vector co-feeding [54], may affect disease transmission patterns, and their effects are worth exploring as well.

The world's first generation malaria vaccine, known as RTS,S/AS01 (RTS,S) was piloted in Africa in 2018 (http://www.who.int/ malaria/media/malaria-vaccine-implementation-qa/en/). According to the report by WHO, children receiving four does of RTS,S experienced significant reductions in malaria and malaria-related complications, in comparison with those who did not receive RTS,S (https://www.who.int/malaria/publications/atoz/first-malaria-vaccine/en/). Whether the current vaccine strategy is optimal to control the spread of malaria, or whether the vaccine program is sensitive to seasonality and spatial heterogeneity is still unknown, but of great health interest. To explore these, we plan to introduce the vaccination, as a new state variable, into the existing model systems, and study the combined effects of the vaccine efficacy and vaccination rate.

The concept of generation speed was introduced by Lewis *et al.* [14], to study a stage-structured, dispersal population. Naturally, we are curious to know whether there exists a generation speed for the scaler impulsive integro-differential model system (4.1.1), which appeared in Chapter 4. Since most landscapes are heterogeneous, to explore the invasion dynamics in the case of spatial heterogeneities (e.g., in a spatial periodic habitat) will be interesting and challenging. In addition, some birds, like bats, have hibernation and birth pulse happened at different time of a year [42]. This motivates us to incorporate the hibernation into our current model system.

We proposed sufficient conditions (D1) and (D2) such that the rightward spreading speed is linearly determinate in Chapter 5. Recently, the speed selection mechanism (linear *vs* nonlinear) for traveling wave solutions to a two-species Lokta-Velterra competition model was discussed in [4, 88], which motives to investigate the nonlinear selection for model system (5.1.2).

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