Global Dynamics of Some Reaction and Diffusion Population Models in Heterogeneous Environments

by

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Abstract

This thesis is devoted to the study of the global dynamics of some reaction and diffusion models incorporating with spatial and/or temporal heterogeneities. We first investigate the spatial dynamics of a reaction-advection-diffusion model for a stream population in a time-periodic environment. Then we explore the propagation phenomena for a Lotka-Volterra reactionadvection-diffusion competition model in a periodic habitat. Moreover, we establish the theory of traveling waves and spreading speeds for time-space periodic monotone semiflows with monostable structure and apply it to a time-space version of the two-species competition model. To understand the effects of the spatial heterogeneity on the spread of Lyme disease, we propose a nonlocal and time-delayed reaction-diffusion model and obtain the global stability in terms of the basic reproduction ratio and the spreading speed of the disease. At the end of this thesis, some interesting problems are presented for further investigation.

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Chapter 1

Introduction

In spatial ecology and population biology, reaction and diffusion models are widely used to capture the spatial and temporal dynamics of species and to better understand biological invasions. In reality, the heterogeneous character of the environment plays an important role in the spread of the invasive species. Natural barriers like hills and rivers may bring more patterns of invasion fronts. It is also well known that seasonal change and geographic variations in temperature, rainfall and resource availability have crucial effects on the survival and reproduction of populations. Clearly, periodic environment of space and/or time is one of the useful approximations to understand the influence of the environmental heterogeneity on the spatially evolution and the persistence of species arising from ecological and biological processes. At times, an invading species is in the competition of the local species, resulting in the extinction of the latter. This explains why agricultural scientists sometimes try to introduce beneficial invasions to control local pest issues. Then the essential factors of biological invasions, spreading speeds and traveling waves, may help scientists to predict and evaluate the effectiveness of local pest control and further impacts on the local ecological balance.

This thesis is devote to study of the spatial dynamics of some diffusion and reaction models in heterogeneous environments. In the following, we will give a brief introduction of the research projects presented in the thesis.

I. *A stream population model*

In stream ecology, 'drift paradox' [65] is a crucial topic, which is concerned about why the aquatic insects have the ability to resist washout when they face with the downstream drift. A number of modeling works have been done to give positive answers for the drift paradox [65]. Pachepsky et al. [76] introduced a reaction-advection-diffusion model (called PA model) to handle the issue of persistence of benthic aquatic organisms. In this PA model, the population is divided into two interacting compartments: individuals living on the benthos and individuals drifting in the river, which has important implications for population persistence. Later, Lustscher and Seo [60] further developed this PA model by considering the temporal variability, and analytically studied the persistence conditions for the linearized PA model under the assumption that all parameters are T-periodic step functions and the average flow speed over one period is constant. Their model is governed by the following linear reaction-advection-diffusion system:

$$\begin{cases} \frac{\partial n_d}{\partial t} = -\sigma(t)n_d + \mu(t)n_b - v(t)\frac{\partial n_d}{\partial x} + D(t)\frac{\partial^2 n_d}{\partial x^2}, \\ \frac{\partial n_b}{\partial t} = \sigma(t)n_d - \mu(t)n_b + r(t)n_b, \quad t > 0, \ x \in \mathbb{R}, \end{cases}$$

where n_d is the population density in the drift; n_b is the population density on the benthos; $\mu(t)$ is the per capita rate at which individuals in the benthic population enter the drift; $\sigma(t)$ is the per capita rate at which the organisms return to the benthic population from drifting; $D(t)$ is the diffusion coefficient; $v(t)$ is the advection speed experienced by the organisms; and $r(t)$ is the maximum per capita growth rate of the benthic population.

The purpose of the first project in this thesis is to study the spatial dynamics of the following nonlinear periodic PA model:

$$\begin{cases} \frac{\partial n_d}{\partial t} = -\sigma(t)n_d + \mu(t)n_b - v(t)\frac{\partial n_d}{\partial x} + D(t)\frac{\partial^2 n_d}{\partial x^2}, \\ \frac{\partial n_b}{\partial t} = \sigma(t)n_d - \mu(t)n_b + f(t, n_b)n_b, \quad t > 0, \ x \in \mathbb{R}, \end{cases}$$

where $f(t, n_b)$ is the per capita growth rate of the benthic population with no Allee effect in the population. Biologically, our model here is more reasonable since it deals with seasonal variations in temperature, rainfall and resource availability. In the case of an unbounded domain, we establish the existence of spreading speeds and their coincidence with the minimal wave speeds for monotone periodic traveling waves, respectively. In the case of a bounded domain, we obtain a threshold result on the global stability of either zero or the positive periodic solution.

II. *A two-species competition model in a periodic habitat*

Over the past decade, there have been a number of research works concerning about traveling waves and spreading speeds in heterogeneous media, see, e.g., [100] and references therein. More specifically, Gätner and Friedlin [23, 24] studied the spreading speed for an equation of Fisher type in which the mobility and the growth function vary periodically in space via probabilistic methods. Shigesada et al. [84] first discussed the spread of a single species for a reaction-diffusion model in a patchy habitat with the periodic mobility and growth rate (see also [83]). Later, Berestycki, Hamel and Roques [6, 7] analyzed the following reaction-diffusion model in the periodically fragmented environment:

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

where $A(x)$ and $f(x, u)$ depend on $x = (x_1, .., x_N)$ in a periodic fashion, and obtained the existence of pulsating waves and a variational formula for the minimal wave speed.

A general theory of spreading speeds and traveling waves in a periodic habitat was developed by Weinberger [94] for a recursion with a periodic order-preserving compact operator, and by Liang and Zhao [55] for monotone semiflows with α-contraction compactness. Weng and Zhao [96] proposed a nonlocal and time-delayed reaction-diffusion model in a periodic habitat and studied its propagation phenomena by appealing to the abstract results in [55], which was further extended by Ouyang and Ou [75] to obtain the stability and convergence rate of traveling waves. It is worthy to point out that the theory in [55, 94] may not apply to scalar evolution equations with nonlocal dispersal in a periodic habitat since the associated solution maps are not compact. Recently, Shen and Zhang [81,82] and Coville, Dávila and Martínez [13] investigated spreading speeds and periodic traveling waves for a large class of such equations via quite different approaches.

For two species reaction-diffusion competition models in a spatially homogeneous environment, there have been quite a few papers on persistence, biological invasions of species, traveling wave solutions and the minimal wave speeds, see, e.g., [27, 33, 38, 39, 44, 51] and references therein. In particular, Lewis, Li and Weinberger [51] studied the spreading speed of two species Lotka-Volterra competition model and gave a set of sufficient conditions for its linear determinacy. Huang [38] and Guo and Liang [27] concerned about the minimal speed and the linear determinacy for more general cases. Huang and Han [39] further showed that the conjecture of linear determinacy is not true in general. Meanwhile, for a spatially heterogeneous environment, Dockery et al. [16] investigated the effect of different diffusion rates on the survival of two phenotypes of a species, and showed that the phenotype with the slower diffusion rate wins the competition. Recently, Lam and Ni [49] studied the global dynamics of two species Lotka-Volterra competition diffusion model with spatial heterogeneous growth rates in a bounded domain. Moreover, Lutscher, McCauley and Lewis [59] added the advection term into such a competition model to discuss spatial patterns and coexistence mechanisms for stream populations. However, it seems that there is no research on the propagation phenomena for two species reaction-diffusion competition model in a periodic habitat, which is the simplest form of the heterogeneous environment.

The purpose of the second project is to study the spatial dynamics of a two species competition reaction-advection-diffusion model in a periodic habitat:

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= L_1 u_1 + u_1(b_1(x) - a_{11}(x)u_1 - a_{12}(x)u_2),\\ \frac{\partial u_2}{\partial t} &= L_2 u_2 + u_2(b_2(x) - a_{21}(x)u_1 - a_{22}(x)u_2), \quad t>0,\ x\in\mathbb{R}.\end{aligned}$$

Here $L_i u = d_i(x)\frac{\partial^2 u}{\partial x^2} - g_i(x)\frac{\partial u}{\partial x}, i = 1, 2$, u_1 and u_2 denote the population densities of two competing species in an L-periodic habitat for some positive number L, $d_i(x)$, $g_i(x)$ and $b_i(x)$ are diffusion, advection and growth rates of the i-th species ($i = 1, 2$), respectively, and $a_{ij}(x)(1 \le i, j \le 2)$ are inter- and intra-specific competition coefficients. We establish the existence of the spreading speeds and its coincidence with the minimal wave speeds for spatially periodic traveling waves and obtain a set of sufficient conditions for the spreading speeds to be linearly determinate.

III. *Time-space periodic semiflows*

As in Part II, we have introduced the mathematical research works on the periodic habitat. There are also quite a few investigations on time-periodic fronts of reaction-diffusion equations, see, e.g., [1,2,22,61,102,104,105] and references therein. For time-periodic semiflows in one dimensional continuous medium, Liang, Yi and Zhao [53] used the wavefront $W(x - c\omega)$ obtained for the Poincaré map Q_ω to construct a two-variable function $U(t, \xi) := Q_t[W](\xi + ct)$, which is then shown to be a time-periodic traveling wave for the semiflow. However, when the medium is discrete, say $\mathbb{Z}$ for instance, such a construction may not give rise to a traveling wave since $Q_t[W](\xi)$ is not well defined for all $\xi \in \mathbb{R}$. We will obtain traveling waves in a strong sense for the associated Poincaré map so that this evolution approach is still applicable.

In the case where the time and space periodicity is incorporated into a reaction-diffusion equation, it remains unclear whether there exists a transition wave in the sense of Berestycki and Hamel [8], reflecting some interactions of time and space periods. Next we recall some works related to this question. Nolen, Rudd and Xin [69] used a three-variable function $\phi(\xi, t, x)$, which is periodic in the last two arguments, and an auxiliary equation to define a generalized pulsating wave. Nadin [67] introduced the following equivalent definition:

Definition 1.0.1. *A function $u(t, x)$ is a pulsating traveling front of speed c in the direction $-e$ that connects p^- to p^+ if it can be written as $u(t, x) = \phi(x \cdot e + ct, t, x)$, where $\phi \in L^\infty(\mathbb{R} \times \mathbb{R} \times \mathbb{R}^N)$ is such that for almost every $y \in \mathbb{R}$, the function $(t, x) \mapsto \phi(y + x \cdot e + ct, t, x)$ satisfies the above equation. The function ϕ is requested to be periodic in its second and third variables and to satisfy*

$$\begin{cases} \phi(z, t, x) - p^-(t, x) \to 0 & \text{as } z \to -\infty \text{ uniformly in } (t, x) \in \mathbb{R} \times \mathbb{R}^N, \\ \phi(z, t, x) - p^+(t, x) \to 0 & \text{as } z \to +\infty \text{ uniformly in } (t, x) \in \mathbb{R} \times \mathbb{R}^N. \end{cases} \tag{1.1}$$

One may observe that the solution $u(t, x) := \phi(y + x \cdot e - ct, t, x)$ is an almost planar wave under the setting of gerenalized transitions waves, for which we refer to [5, Definition 1.5]. It is also easy to see that such $u(t, x)$ is a classical pulsating wave in the sense of Xin [99] if $c\omega/L$ is a nonzero rational number.

In Nadin [67], for reaction-diffusion equations with time-space periodicity in $\mathbb{R}^N$:

$$\partial_t u - \nabla \cdot (A(t, x)\nabla u) + q(t, x) \cdot \nabla u = f(t, x, u), \tag{1.2}$$

the minimal wave speed of such pulsating fronts was established in [67] under a KPP type condition and the following monostability condition: (i) there is a positive continuous space-time periodic solution p; (ii) if u is a space periodic solution such that $u \leq p$ and $\inf_{(t,x)\in\mathbb{R}\times\mathbb{R}^N} u(t,x) > 0$, then $u \equiv p$; (iii) $u \equiv 0$ is an unstable solution in the sense that the associated generalized eigenvalue is positive, where the generalized eigenvalue was studied in [68]. Upper and lower bounds were given for the minimal wave speed (if it exists) when the KPP condition does not hold. The spreading speed as well as the tail behavior and the regularity of the wave were also studied there. One may ask the following questions: Does the minimal wave speed exist when the KPP type condition does not hold? Can $u(t,x;y) := \phi(y + x \cdot e + ct, t, x)$ satisfy the equation for any $y \in \mathbb{R}$? Can such a result be established for systems admitting possible semi-trivial time-space periodic solutions? We will give affirmative answers to these questions.

Most recently, Rawal, Shen and Zhang [78] introduced the following definition of time-space periodic traveling waves for a nonlocal dispersal Fisher-KPP equation:

Definition 1.0.2. *An entire solution $u(t,x)$ is called a traveling wave solution connecting $u^*(t,x)$ and 0 and propagating in the direction of e with speed c if there is a bounded function $\Phi : \mathbb{R}^N \times \mathbb{R} \times \mathbb{R}^N \to \mathbb{R}_+$ satisfying that Φ is locally Lebesgue measurable, $u(t,x;\Phi(\cdot,0,z))$ exists for all $t \in \mathbb{R}$,*

$$u(t,x;\Phi(\cdot,0,z)) = \Phi(x - cte, t, z + cte), \quad t \in \mathbb{R}, z \in \mathbb{R}^N$$

$$\lim_{x\cdot e\to-\infty}(\Phi(x,t,z) - u^*(t,x+z)) = 0, \quad \lim_{x\cdot e\to+\infty}\Phi(x,t,z) = 0, \text{ uniformly in } (t,z),$$

$$\Phi(x,t,z-x) = \Phi(x',t,z-x'), \quad x,x' \in \mathbb{R}^N \text{ with } x\cdot e = x'\cdot e,$$

and

$$\Phi(x,t+T,z) = \Phi(x,t,z+p_i e_i) = \Phi(x,t,z), \quad x,z \in \mathbb{R}^N.$$

Let $\phi(\xi, t, x) := \Phi(y, t, x - y)$ with $\xi = y \cdot e$. It then follows that for any $z \in \mathbb{R}^N$, $\phi(x \cdot e - ct, t, x + z)$ is a solution of the given evolution equation. Note that two quite different approaches were used in [67] and [78], respectively, to prove the existence of traveling waves. For further investigations on KPP type nonlocal evolution equations, we refer to Shen [80], Kong and Shen [47], and references therein.

The goal of the third project is to explore the propagation phenomena of the two-species competition model in time-space periodic environment. To do so, we first give a unified definition of traveling waves in a time-space periodic environment and then establish the theory of traveling waves, almost pulsating waves and spreading speed for time-space periodic monotone semiflows, which is further applied to the analysis of such time-space periodic systems.

IV. *A spatial model for Lyme disease*

Lyme disease is a worldwide vector-borne infection caused by the spriochete bacterium *Borrelia burgdorferi*, whose primary vector in North America is the black-legged tick (also known as Ixodes scapularis). The black-legged tick normally has a two-year life cycle including three feeding stages: larva, nymph and adult. In those stages, ticks could acquire blood meals from a variety of hosts like rodents and mammals. In particular, Larvae and nymphs mainly feed on white-footed mouse *Peromyscus leucopus*, and adult ticks obtain blood meals almost exclusively from the white-tailed deer *Odocoileus virginianus* [11]. Since nymphs are too tiny (less than 2mm) to detect, humans may carry Lyme disease through the bites of infectious nymphs. For more biological discussions about the infection of Lyme disease, we refer to [3, 45, 48, 62, 72, 89] and references therein.

To understand the invasion of Lyme disease, many mathematical modeling efforts are made through investigating the tick and host populations dynamics [25, 41, 56, 70, 79]. More specifically, Caraco et al. [12] proposed a reaction-diffusion model to study the effects of the tick's stage structure on the spatial expansion of Lyme disease in the northeast United States. The global dynamics and the spreading speed were obtained in [107] for the spatial model of [12]. To take the climate changes into account, Ogden et al. [73,74] presented simulation models, Wu et al. [98] established a temperature-driven map of the basic reproduction number of Lyme disease in Canada, and Zhang and Zhao [103] modified the model in [12] to a reaction-diffusion system with seasonality and studied its global dynamics and propagation phenomena. Note that the spatially homogeneous environment is basically assumed in these works, but the spatial heterogeneity is also vital. Geographic variations of food resources and climates could limit the activity and the population size of ticks and hosts. Biological studies [9, 50] show that spatial patterns of the disease is highly linked to the spatial configurations coupled with dispersal by vertebrates like mice. Furthermore, there are few mathematical models incorporating the spatial variation to estimate the Lyme disease risk. The patch models presented in [9, 34] considered the tick population dynamics with the dispersal of ticks on vertebrate hosts among multiple habitats, or between woodland and pasture, both of which are based on the assumption that the interactions are homogeneous in every habitat. To formulate a continuous-time model of Lyme disease including spatially dependent parameters, Wang and Zhao [92] took the model of Carco et.al. [12] as a basis and adapted it in the following aspects: (i) allow a spatial-dependent carrying capacity of hosts (mice), spatial-dependent diffusion rates of hosts and disease transmission coefficients; (ii) consider the influence of deers in disease transmissions; (iii) replace the random mobility of ticks in [12] with nonlocal terms to reveal the spatial movements of larvae, nymphs and adult ticks determined by their hosts (mice or deers).

Indeed, they proposed a nonlocal reaction-diffusion model and introduced the basic reproduction number R_0 of Lyme disease and revealed that R_0 can be a threshold value to describe the extinction and persistence of Lyme disease evolution under some appropriate assumptions. They also obtained a threshold result on the global dynamics in the case where the host diffusion rates and the carrying capacity of mice are constants.

The aim of the fourth project is to adopt the nonlocal spatial model in [92] by incorporating the self-regulation mechanism for the tick population as discussed in [11], and to study the spatial dynamics of Lyme disease while keeping the spatially heterogeneous structure of the model system. In the case of a bounded domain, we first prove the existence of the positive disease-free steady state and a threshold type result for the disease-free system, and then establish the global dynamics of the model system in terms of the basic reproduction number R_0. In the case of an unbound domain, we obtain the existence of the disease spreading speed and its coincidence with the minimal wave speed. At last, we use numerical simulations to verify our analytic results and investigate the influence of model parameters and spatial heterogeneity on the disease infection risk.

The rest of this thesis is organized as follows. In Chapter 2, we introduce some mathematical terminologies and theorems which are based on the theories of monotone dynamical systems, spreading speeds and traveling waves. Chapter 3 is devoted to the study of spatial dynamics of a periodic reaction-advection-diffusion model for a stream population. In Chapter 4, we study propagation phenomena for a Lotka-Volterra reaction-advection-diffusion competition model in a periodic habitat. In Chapter 5, we first establish the theory of traveling waves and spreading speeds for time-space periodic monotone semiflows with monostable structure and then apply it to the analysis of a two-species competition model in time-space periodic environment. In Chapter 6, we propose and investigate the global dynamics of a nonlocal and time-delayed reaction-diffusion model for Lyme disease with a spatially heterogeneous structure . A brief summary and some future works are presented in Chapter 7.

Chapter 2

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 monotone dynamical systems and the theory of spreading speeds and traveling waves.

2.1 Monotone dynamics

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 2.1.1. *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 2.1.1. *(Krein-Rutman theorem) [31, 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 2.1.2. *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 2.1.3. *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 $\lambda \in (0, 1)$.*

Theorem 2.1.2. *[106, 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.

Let X be a metric space with metric d. Recall that a continuous map $f : X \to X$ is said to be 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, that is,

$\lim_{n\to\infty} \sup_{x\in B}\{d(f^n(x), J)\} = 0$. 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 2.1.3. *(Threshold dynamics) [106, 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 bounded;

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

Then exists threshold dynamics:

(a) If $r(Df(0)) \le 1$, 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^*.

In the rest of this section, we introduce the result on abstract competitive systems. The basic setup is as follows. For $i = 1, 2$, let X_i be ordered Banach spaces with positive cones X_i^+ such that $\mathrm{Int}(X_i^+) \neq \emptyset$. Let $X = X_1 \times X_2$, $X^+ = X_1^+ \times X_2^+$, and $K = X_1^+ \times (-X_2^+)$. Then $\mathrm{Int}(X^+) = \mathrm{Int}(X_1^+) \times \mathrm{Int}(X_2^+) \neq \emptyset$ and $\mathrm{Int}(K^+) = \mathrm{Int}(X_1^+) \times (-\mathrm{Int}(X_2^+)) \neq \emptyset$. We can define $<, \le, \ll$ on X_i as we did in the beginning of this section. For any $x = (x_1, x_2), y = (y_1, y_2) \in X$, we write $x \le y$ if $x_i \le y_i$, $x \ll y$ if $x_i \ll y_i$, and $x < y$ if $x \le y$ but $x \neq y$, for $i = 1, 2$. For any $x = (x_1, x_2), y = (y_1, y_2) \in X$, we write $x \le_K y$ if $x_1 \le y_1$ and $y_2 \le x_2$, $x \ll_K y$ if $x_1 \ll y_1$ and $y_2 \ll x_2$, and $x <_K y$ if $x_1 \le y_1$ and $y_2 \le x_2$ but $x \neq y$.

Let $f : X^+ \to X^+$ be continuous and f^n be the n-fold composition of f. Recall that f is order compact if for every $(x_1, x_2) \in X^+$, it follows that $f([0, x_1] \times [0, x_2])$ has compact closure in X. We will make the following hypotheses on f, which capture the essence of competition between two adequate competitors:

(P1) f is order compact and strictly ordering-preserving with respect to $<_K$, that is, $x <_K y$ implies $f(x) <_K f(y)$.

(P2) 0 is a repelling fixed point of f in the sense that there exists a neighborhood U_0 of 0 in X^+ such that for each $x \in U_0$, $x \neq 0$, there is an integer $n = n(x)$ such that $f^n(x) \notin U_0$.

(P3) $f(X_1^+ \times \{0\}) \subset X_1^+ \times \{0\}$, and there exists $\hat{x}_1 \in \mathrm{Int}(X_1^+)$ such that $f((\hat{x}_1, 0)) = (\hat{x}_1, 0)$and $f^n((x_1, 0)) \to (\hat{x}_1, 0)$ for every $x_1 \in X_1^+ \setminus \{0\}$. The symmetric conditions hold for f on $\{0\} \times X_2$, and the fixed point is donated by $(0, \tilde{x}_2)$.

(P4) If $x, y \in X^+$ satisfy $x <_K y$ and either x or y belongs to $\mathrm{Int}(X^+)$, then $f(x) \ll_K f(y)$. If $x = (x_1, x_2) \in X^+$ with $x_i \neq 0$, $i = 1, 2$, then $T(x) \gg 0$.

Let $E_0 = (0, 0)$, $E_1 = (\hat{x}_1, 0)$, $E_2 = (0, \tilde{x}_2)$. We say that a fixed point E_* of f is positive if $E \in \mathrm{Int}(X^+)$. Let $I = [E_2, E_1]_K$. It is easy to see that $I \equiv [0, \hat{x}_1] \times [0, \tilde{x}_2]$. Given $x \in X^+$, we write $O(x) = \{f^n(x) : n \geq 0\}$ for the positive orbit of x. Its omega limit set is defined by

$$\omega(x) = \{y \in X^+ : f^{n_i}(x) \to y \quad \text{for some } \{n_i\} \text{ satisfying } n_i \to \infty\}.$$

The following result says that for a competitive system, either there is a positive fixed point of f, representing coexistence of the two populations, or one population drives the other to extinction.

Theorem 2.1.4. *(Trichotomy) [35, Theorem A] Let (P1)–(P4) hold. Then the omega limit set of every orbit is contained in I and exactly one of the following holds:*

(a) There exists a positive fixed E_* of f in I;

(b) $w(x) = E_1$ for every $x = (x_1, x_2) \in I$ with $x_i \neq 0$, $i = 1, 2$;

(c) $w(x) = E_2$ for every $x = (x_1, x_2) \in I$ with $x_i \neq 0$, $i = 1, 2$.

Finally, if (b) or (c) holds and $x = (x_1, x_2) \in X^+ \setminus I$ with $x_i \neq 0$, $i = 1, 2$, then either $\omega(x) = E_1$ or $\omega(x) = E_2$.

2.2 Propagation phenomena

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 $\mathrm{Int}(X_+) \neq \emptyset$. 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 $\varphi_1 - \varphi_2 \in \mathrm{Int}(X_+)$, 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

$$\|u\|_{\mathcal{C}} = \sum_{k=1}^{\infty} \frac{\max_{|x|\leq k} |u(x)|_X}{2^k}, \ \forall u \in \mathcal{C}, \tag{2.1}$$

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 $A(s) := \{u(s) : u \in A\}$. We use the Kuratowski measure of noncompactness in X, which is defined by

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

for any bounded set $B \subset X$. It is easy to see that B is precompact (i.e. the closure of B) is compact if and only if $\alpha(B) = 0$.

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 $\mathcal{R}[u](x) = u(-x)$.

2.2.1 Spreading speeds

In the subsection, we will present some results on spreading speeds for monotone semiflows in [53, 54].

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

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

(A2) Q is continuous with respect to the compact open topology.

(A3) $\{Q[u](x) : u \in \mathcal{C}_\beta, x \in \mathbb{R}\}$ is a precompact subset (i.e., the closure of set is compact) of X.

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

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

Theorem 2.2.1. *[54, Theorem 2.11, Theorem 2.15, Corollary 2.16] Assume that the map $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies assumptions (A1)–(A5). Let $u_0 \in \mathcal{C}_\beta$ and $u_n = Q(u_{n-1})$ for $n \geq 1$. Then there exists a real number c^* such that the following statements are valid:*

(1) For any $c > c^*$, if $0 \leq u_0 \ll \beta$ and $u_0(x) = 0$ for x outside a bounded interval, then $\lim_{n\to\infty |x|\geq cn} u_n(x) = 0$ in X.

(2) For any $c < c^*$ and any $\sigma \in X_\beta$ with $\sigma \gg 0$, there exists $r_\sigma > 0$ such that if $u_0(x) \geq \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{n\to\infty |x|\leq cn} u_n(x) = \beta$ in X. If, in additional, Q is subhomogeneous on $\mathcal{C}_\beta$, then r_σ can be chosen to be independent of $\sigma \gg 0$.

By Theorem 2.2.1, it follows that Q admits an asymptotic speed of spread c^* provided that (A1)–(A5) are valid. To estimate c^*, a linear operator approach was developed in [54]. Let $M : \mathcal{C} \to \mathcal{C}$ be a linear operator with the following properties:

(B1) M is continuous with respect to the compact open topology.

(B2) M is a positive operator, that is, $M[u] \geq 0$ whenever $u > 0$.

(B3) For any uniformly bounded subset A of $\mathcal{C}$, the set $\{M[u](x)(\theta) : u \in A, \theta \in \Omega, x \in \mathbb{R}\}$ is bounded in $\mathbb{R}^l$.

(B4) $\mathcal{T}_y \circ M = M \circ \mathcal{T}_y, \quad M \circ \mathcal{R} = \mathcal{R} \circ M, \quad \forall y \in \mathbb{R}$.

(B5) M can be extended to a linear operator on the linear space $\tilde{\mathcal{C}}$ of all functions $u \in C(\mathbb{R}, X)$ having the form

$$u(x) = v_1(x)e^{\mu_1 x} + v_2(x)e^{\mu_2 x}, \quad v_1, v_2 \in \mathcal{C},\ \mu_1, \mu_2, x \in \mathbb{R},$$

such that if $u_n, u \in \tilde{\mathcal{C}}$ and $u_n(x)(\theta) \to u(x)(\theta)$ uniformly on any bounded set of $\mathbb{R} \times \Omega$, then $M[u_n](x)(\theta) \to M[u](x)(\theta)$ uniformly on any bounded set of $\mathbb{R} \times \Omega$.

Note that hypothesis (B4) implies that M is also a linear operator on X. Define the linear map $B_\mu : X \to X$ by

$$B_\mu[\sigma](\theta) = M[\sigma e^{-\mu x}](0)(\theta), \quad \forall \theta \in \Omega.$$

In particular, $B_0 = M$ on X. If $\sigma_n, \sigma \in X$ and $\sigma_n \to \sigma$ as $n \to \infty$, then $\sigma_n(\theta)e^{-\mu x} \to \sigma(\theta)e^{-\mu x}$ uniformly on any bounded subset of $\Omega \times \mathbb{R}$. Thus,

$$B_\mu[\sigma_n] = M[\sigma_n e^{-\mu x}](0) \to M[\sigma e^{-\mu x}](0) = B_\mu[\sigma],$$

and hence, B_μ is continuous. Moreover, B_μ is a positive operator on X. Assume that

(B6) For any $\mu > 0$, B_μ is positive, and there is an n_0 such that $B_\mu^{n_0} = \underbrace{B_\mu \circ \cdots \circ B_\mu}_{n_0}$ is a compact and strongly positive linear operator on X.

It then follows from [54, Lemma 3.1] that B_μ has a principal eigenvalue $\lambda(\mu)$ with strongly positive eigenfunction. Moreover, we have the following property for $\lambda(\mu)$.

Lemma 2.2.1. *[54, Lemma 3.7] $\lambda(\mu)$ is log convex on $\mathbb{R}$.*

The next condition is needed for the estimate of the spreading speed c^*.

(B7) The principal eigenvalue $\lambda(0)$ of B_0 is larger than 1.

Define $\Psi(\mu) := \frac{\ln \lambda(\mu)}{\mu}$, $\forall \mu > 0$. Then, we can use the following result to estimate the spreading speed of map Q.

Theorem 2.2.2. *[54, Theorem 3.10] Let Q be an operator on $\mathcal{C}_\beta$ satisfying (A1)–(A5) and c^* be the asymptotic speed of Q. Assume that the linear operator M satisfies (B1)–(B7), and that the infimum of $\Psi(\mu)$ is attained at some finite value μ^* and $\Psi(+\infty) > \Psi(\mu^*)$. Then the following statements are valid:*

(1) If $Q[u] \leq M[u]$ for all $u \in \mathcal{C}_\beta$, then $c^* \leq \inf_{\mu>0} \Psi(\mu)$.

(2) If there exists some $\eta \in X$ with $\eta >> 0$ such that $Q[u] \geq M[u]$ for any $u \in \mathcal{C}_\eta$, then $c^* \geq \inf_{\mu>0} \Psi(\mu)$.

Recall that a family of operators $\{Q_t\}_{t\geq 0}$ is said to be a semiflow on $\mathcal{C}_\beta$ if the following three properties hold: (i) $Q_0 = I$, where I is the identity mapping; (ii) $Q_t \circ Q_s = Q_{t+s}$, $\forall t, s \geq 0$; (iii) $Q_t[u]$ is continuous jointly in $(t, u) \in [0, \infty) \times \mathcal{C}_\beta$.

Theorem 2.2.3. *[54, Theorem 2.17] Let $\{Q_t\}_{t\geq 0}$ be a semiflow on $\mathcal{C}_\beta$ with $Q_t[0] = 0$ and $Q_t[\beta] = \beta$ for all $t \geq 0$. Suppose that $Q = Q_1$ satisfies all hypotheses (A1)–(A5), and Q_t satisfies (A1) for any $t > 0$. Let c^* be the asymptotic speed of spread of Q_1. Then the following statements are valid:*

(i) For any $c > c^*$, if $v \in \mathcal{C}_\beta$ with $0 \leq v \ll \beta$ and $v(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\geq ct} Q_t[v](x) = 0$ in X.

(ii) For any $c < c^*$ and $\sigma \in X_\beta$ with $\sigma \gg 0$, there is a positive number r_σ such that if $v \in \mathcal{C}_\beta$ and $v(x) \gg \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{t\to\infty, |x|\leq ct} Q_t[v](x) =$

β in X. If, in addition, Q_1 is subhomogeneous, then r_σ can be chosen to be independent of $\sigma \gg 0$.

Recall that a family of operators $\{Q_t\}_{t\geq 0}$ is said to be a T-periodic semiflow on $\mathcal{C}$ if the following three properties hold: (i) $Q_0 = I$, where I is the identity mapping; (ii) $Q_t \circ Q_T = Q_{t+T}$, $\forall t \geq 0$; (iii) $Q_t[u]$ is continuous jointly in $(t, u) \in [0, \infty) \times \mathcal{C}$. The mapping Q_T is called the Poincaré map associated with this periodic semiflow.

Theorem 2.2.4. *[53, Theorem 2.1] Let $\{Q_t\}_{t\geq 0}$ be a T-periodic semiflow on $\mathcal{C}$ with two x-independent T-periodic orbits $0 \ll \beta(t)$. Suppose that the Poincaré map $Q = Q_T$ satisfies all hypotheses (A1)–(A5) with $\beta = \beta(0)$, and Q_t satisfies (A1) for any $t > 0$. Let c^* be the asymptotic speed of spread of Q_T. Then the following statements are valid:*

(i) For any $c > \frac{c^*}{T}$, if $v \in \mathcal{C}_\beta$ with $0 \leq v \ll \beta$ and $v(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\geq ct} Q_t[v](x) = 0$ in X.

(ii) For any $c < \frac{c^*}{T}$ and $\sigma \in X_\beta$ with $\sigma \gg 0$, there is a positive number r_σ such that if $v \in \mathcal{C}_\beta$ and $v(x) \gg \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{t\to\infty, |x|\leq ct} (Q_t[v](x) - \beta(t)) = 0$ in X. If, in addition, Q_T is subhomogeneous, then r_σ can be chosen to be independent of $\sigma \gg 0$.

Remark 2.2.1. *If the reflection invariance, i.e., $Q \circ \mathcal{R} = \mathcal{R} \circ Q$, is not assumed in (A1), then we have the existence of the leftward spreading speed c_-^* and rightward spreading speed c_+^*, respectively, see [93]. These spreading speeds can also be estimated by the linear operators approach.*

2.2.2 Traveling waves

In this subsection, we introduce the results in [19] on traveling waves for monotone semiflows with weak compactness.

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

(C1) $\mathcal{T}_y \circ Q = Q \circ \mathcal{T}_y, \quad \forall y \in \mathbb{R}$.

(C2) If $u_k \to u$ in $\mathcal{M}$, then $Q[u_k](x) \to Q[u](x)$ in X almost everywhere.

(C3) There exists $k \in [0,1)$ such that for any $\mathcal{U} \subset \mathcal{M}_\beta$, $\alpha(Q[\mathcal{U}](0)) \leq k\alpha(\mathcal{U}(0))$. Here α denotes the Kuratowski measure of noncompactness in X_β.

(C4) $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ is monotone (order preserving) in the sense that $Q[u] \geq Q[w]$ whenever $u \geq w$ in $\mathcal{M}_\beta$.

(C5) $Q : X_\beta \to X_\beta$ 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 (C1), it follows that (C3) is equivalent to

There exists $k \in [0,1)$ such that $\alpha(Q[\mathcal{U}](x)) \leq k\alpha(\mathcal{U}(x)), \quad \forall \mathcal{U} \subset \mathcal{M}_\beta,\ x \in \mathbb{R}$.

We call (C3) as the point-α-contraction assumption (see also (A3)(a')) in [53]). This condition is weaker than (A3). In the case that $X = \mathbb{R}^l$, (C3) is automatically satisfied and equivalent to the condition (A3).

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 2.2.2. *[19, 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 [19, 93], we define two numbers

$$c_+^* = \sup\{c : a(c,+\infty) = \beta\}, \quad \bar{c}_+ = \sup\{c : a(c,+\infty) > 0\}. \tag{2.2}$$

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 and continuous-time dynamical systems, the leftward case can be treated in a similar way.

Theorem 2.2.5. *[19, Theorem 3.8] Assume that $Q : \mathcal{M}_\beta \to \mathcal{M}_\beta$ satisfies (C1)–(C5). Let c_+^* and $\bar{c}_+$ with $c_+^* \leq \bar{c}_+$ be defined as in (2.2). 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*.*

Recall that a family of mappings $\{Q_t\}_{t\geq 0}$ is said to a continuous-time semiflow on $\mathcal{M}_\beta$ provide that $Q_0 = I$, $Q_t \circ Q_s = Q_{t+s}$, $\forall t, s \geq 0$ and the following continuity assumption holds:

(C2)′ If $u_n \to u$ in $\mathcal{M}_\beta$ and $t_n \to t$, then both $Q_{t_n}[u](x) \to Q_t[u](x)$ and $Q_t[u_n](x) \to Q_t[u](x)$ in X almost everywhere.

Theorem 2.2.6. *[19, Theorem 4.2] Let* $\{Q_t\}_{t\geq 0}$ *be a continuous-time semiflow on* $\mathcal{M}_\beta$*. Assume that for any* $t > 0$*,* Q_t *satisfies (C1), (C3)–(C5) with fixed points replaced by equilibria of* $\{Q_t\}_{t\geq 0}$ *in (A5). Let* c_+^* *and* $\bar{c}_+$ *with* $c_+^* \leq \bar{c}_+$ *be defined as in* (2.2) *with* $Q = Q_1$*. Then the following statements are valid:*

(1) *For any* $c \geq c_+^*$*, there is a left-continuous traveling wave* $W(x - ct)$ *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 $W(x - ct)$ 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 $W_1(x - ct)$ 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 $Q_t[W](x) = W(x - ct)$, $\forall x \in \mathbb{R}$ and $t \geq 0$. Finally, if $\{Q_t\}_{t \geq 0}$ admits exactly two equilibria in X_β, then $c_+^* = \bar{c}_+$ and c_+^* is the minimal wave speed of traveling waves connecting β to 0.

Theorem 2.2.7. *[19, Remark 3.7] and [53, Remark 2.1] Assume that the map $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies assumptions (A1)–(A5) with (A3) and (A5) replaced by (C3) and (C5) in $\mathcal{C}_\beta$. 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 (2.2) for Q. Then the following statements are valid:*

(1) For any $c > \bar{c}_+$, if $0 \leq u_0 \ll \beta$ and $u_0(x) = 0$ for x outside a bounded interval, then $\lim_{n\to\infty |x| \geq cn} u_n(x) = 0$ in X.

(2) For any $c < c_+^*$ and any $\sigma \in X_\beta$ with $\sigma \gg 0$, there exists $r_\sigma > 0$ such that if $u_0(x) \geq \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{n\to\infty |x| \leq cn} u_n(x) = \beta$ in X. If, in additional, Q is subhomogeneous on $\mathcal{C}_\beta$, then r_σ can be chosen to be independent of $\sigma \gg 0$.

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.

Theorem 2.2.7 will help to show that the coincidence of spreading speeds and minimal wave speeds of traveling waves for monotone semiflows with weak compactness, although we use the different phase spaces $\mathcal{C}_\beta$ and $\mathcal{M}_\beta$ to present the results.

Chapter 3

A Periodic Spatial Model for A Stream Population

In this chapter, we consider the following nonlinear stream population model:

$$\begin{cases} \frac{\partial n_d}{\partial t} = -\sigma(t)n_d + \mu(t)n_b - v(t)\frac{\partial n_d}{\partial x} + D(t)\frac{\partial^2 n_d}{\partial x^2}, \\ \frac{\partial n_b}{\partial t} = \sigma(t)n_d - \mu(t)n_b + f(t, n_b)n_b, \quad t > 0, \ x \in \mathbb{R}. \end{cases} \tag{3.1}$$

Here the biological explanation of parameters are as shown in Chapter 1. Note that system (3.1) is cooperative and its solution maps are monotone. Thus, we can use the general theory developed in [53, 93] (see also section 2.2.1) to study the spreading speeds for periodic system (3.1). However, the solution maps are not compact with respect to the compact open topology due to the lack of the diffusion term in the second equation of system (3.1). As a consequence, the theory in [53, 93] may not be applied to obtain the existence of time-periodic traveling waves for system (3.1). To overcome this difficulty, we will utilize the theory recently developed in [19] (see also section 2.2.2) for monotone semiflows with weak compactness. We should point out that the verification of some abstract assumptions in section 2.2.2 is highly nontrivial for the solution maps of system (3.1) since one needs to consider its mild solutions with discontinuous initial functions. It turns out that the spreading speeds are linearly determinate and coincide with the minimum wave speeds for monotone periodic traveling waves. For the global dynamics of system (3.1) in a bounded domain, we will appeal to the theory of monotone and subhomogeneous systems (see, e.g., [106]). Since we using Hostile boundary condition in a bounded domain, if we choose a space consisting of continuous functions vanishing at $x = L$, then its interior is empty, and hence, we cannot employ the strong monotonicity. To address this issue, we first carefully choose an appropriate function space. To avoid using the compactness for solution maps, we prove that every forward orbit of the Poincaré map associated with system (3.1) is asymptotically compact under an additional assumption. Those two enable us to establish a threshold type result on the global stability of either zero or the positive periodic solution.

This chapter is organized as follows. In section 3.1, we first obtain a threshold dynamics for the spatially homogeneous system of model (3.1) in terms of the principal Floquet multiplier of its linearized system at $(0, 0)$, and then we establish the existence of leftward and rightward spreading speeds and their coincidence with the minimal wave speeds for monotone periodic traveling waves for system (3.1). In section 3.2, we prove a threshold result on the global dynamics of system (3.1) in a bounded domain $[0, L]$. Section 3.3 presents some numerical simulations to verify our analytic results.

3.1 Spreading speeds and traveling waves

In this section, we establish the existence of spreading speeds and traveling waves for system (3.1), where $\mu(t)$, $\sigma(t)$, $v(t)$, $D(t)$ are nonnegative ω-periodic functions and

$f(t,u)$ is ω-periodic with respect to time t for some $\omega > 0$. For convenience, we use the notations $\mu_{\max} = \max\limits_{t\in[0,\omega]} \mu(t)$ and $\sigma_{\max} = \max\limits_{t\in[0,\omega]} \sigma(t)$. Throughout this paper, we assume that

(H1) $D(t) > 0$, $\mu(t) \not\equiv 0$, $\sigma(t) \not\equiv 0$, $f \in C(\mathbb{R}_+^2, \mathbb{R})$, and $f(t,u)$ is locally Lipschitz in u, uniformly for $t \in [0,\omega]$.

(H2) $\frac{\partial f(t,u)}{\partial u} < 0$ for all $(t,u) \in \mathbb{R}_+^2$, and there exists $K_0 > 0$ such that

$$\sigma(t)\int_{-\infty}^{t} e^{-\int_s^t \sigma(\tau)d\tau}\mu(s)ds - \mu(t) + f(t,K_0) \leq 0, \quad \forall t \geq 0.$$

Note that when $\sigma(t)$ and $\mu(t)$ are positive constants, the inequality in (H2) reduces to $f(t,K_0) \leq 0$, $\forall t \geq 0$. A prototypical example for (H2) is $f(t,u) = b(t) - a(t)u$ with $a(t) > 0$.

3.1.1 The spatially homogeneous system

We start with the global dynamics of the following spatially homogeneous system:

$$\begin{cases} \frac{dn_d}{dt} = -\sigma(t)n_d + \mu(t)n_b, \\ \frac{dn_b}{dt} = \sigma(t)n_d - \mu(t)n_b + f(t,n_b)n_b, \quad t > 0. \end{cases} \tag{3.2}$$

For convenience, we rewrite system (3.2) as

$$\frac{dy}{dt} = G(t,y) \tag{3.3}$$

with $y = \begin{pmatrix} n_d(t) \\ n_b(t) \end{pmatrix}$, and $G(t,y) = \begin{pmatrix} -\sigma(t)y_1 + \mu(t)y_2 \\ \sigma(t)y_1 - \mu(t)y_2 + f(t,y_2)y_2 \end{pmatrix}$.

Note that system (3.3) is cooperative and $f(t,u)u \leq f(t,0)u$, $\forall (t,u) \in \mathbb{R}_+^2$. It then follows that for any initial value $(y_1(0), y_2(0)) \in \mathbb{R}_+^2$, system (3.3) has a unique non-negative solution $(y_1(t), y_2(t))$ on $[0,\infty)$. We linearize system (3.3) at its ω-periodic solution $(0,0)$ to obtain

$$\frac{dz}{dt} = D_yG(t,0)z = \begin{bmatrix} -\sigma(t) & \mu(t) \\ \sigma(t) & -\mu(t)+f(t,0) \end{bmatrix} z. \tag{3.4}$$

Let ρ be the principal Floquet multiplier of the linear system (3.4), that is, ρ is the spectral radius of the matrix $Z(\omega)$, where $Z(t)$ satisfies $Z(0) = I$ and $\frac{d}{dt}Z(t) = D_yG(t,0)Z(t)$ for all $t > 0$. Then we have the following threshold type result on the global dynamics of system (3.2).

Lemma 3.1.1. *The following statements are valid:*

(i) If $\rho > 1$, then system (3.2) admits a unique positive ω-periodic solution $(u_1^*(t), u_2^*(t))$, and it is globally asymptotically stable for system (3.2) with initial values in $\mathbb{R}_+^2\backslash\{0\}$;

(ii) If $\rho \leq 1$, then $(0,0)$ is globally asymptotically stable for system (3.2) in $\mathbb{R}_+^2$.

Proof. Let $y_t(y_0) := y(t,y_0)$ be the unique solution of system (3.2) satisfying $y(0,y_0) = y_0$. Denote $X(t) = \frac{\partial y_t}{\partial y_0}(y_0)$ and $A(t) = D_y(G(t,y(t,y_0))) = (a_{ij}(t))_{2\times2}$. Then $X(t) = (x_{ij}(t))_{2\times2}$ satisfies

$$X'(t) = A(t)X(t),\ X(0) = I.$$

Since $a_{ij}(t) = \frac{\partial G_i}{\partial y_j} \geq 0,\ i \neq j, \forall (t,y) \in \mathbb{R}_+ \times \mathbb{R}_+^2$, we have $x'_{ik}(t) \geq a_{ii}(t)x_{ik}(t),\ \forall t \geq 0$ and $i,k \in \{1,2\}$. It then follows that $x_{ik}(t) > 0$ for all $t \geq t_0$ whenever $x_{ik}(t_0) > 0$ for some $t_0 \geq 0$. Since $x_{ii}(0) = 1$, we have $x_{ii}(t) > 0,\ \forall t \geq 0$. We further prove that $x_{ij}(t_{ij}) > 0$ for some $t_{ij} \in [0,\omega],\ \forall i \neq j$, and hence $x_{ij}(t) > 0, \forall t \geq \omega, i \neq j$. Suppose, by contradiction, that there exist $i_0, j_0 \in \{1,2\}$ and $i_0 \neq j_0$, such that $x_{i_0j_0}(t) = 0$ for all $t \in [0,\omega]$. Then we have

$$0 = x'_{i_0j_0}(t) = \sum_{l=1}^{2} a_{i_0l}(t)x_{lj_0}(t) = a_{i_0j_0}(t)x_{j_0j_0}(t),\ \forall t \in [0,\omega].$$

Since $x_{j_0 j_0}(t) > 0$, it then follows from that $a_{i_0 j_0}(t) \equiv 0$, $\forall t \in [0, \omega]$. Note that

$$A(t) = \begin{bmatrix} -\sigma(t) & \mu(t) \\ \sigma(t) & -\mu(t) + f(t, y_2(t, y_0)) + f_{y_2}(t, y_2(t, y_0))y_2(t, y_0) \end{bmatrix}.$$

We then obtain $a_{12}(t) = \mu(t) \not\equiv 0$ and $a_{21}(t) = \sigma(t) \not\equiv 0$, a contradiction. It follows that $\frac{\partial y_t}{\partial y_0}(y_0) \gg 0,\ t \geq \omega$. Thus, for any $a, b \in \mathbb{R}^2_+$ satisfy $a < b$, there holds

$$y(t, b) - y(t, a) = (b - a) \int_0^1 \frac{\partial y_t}{\partial y_0}(a + r(b - a))dr \gg 0, \quad \forall t \geq \omega.$$

This implies that $y(t, a) \ll y(t, b)$, $\forall t \geq \omega$. In particular, y_ω is strongly monotone. It is easy to verify that $G(t, y)$ has the following properties:

(a) $G_i(t, y) \geq 0$ whenever $(t, y) \in [0, \infty) \times \mathbb{R}^2_+$ with $y_i = 0, i = 1, 2$.

(b) For each $(t, y) \in [0, \infty) \times \mathbb{R}^2_+$, $G(t, y)$ is strictly subhomogeneous in y in the sense that $G(t, \alpha y) > \alpha G(t, y)$, $\forall y \in \mathbb{R}^2_+$ and $y \gg 0$, $\alpha \in (0, 1)$.

Note that for any given $M > 0$, the linear periodic equation

$$\frac{dx}{dt} = -\sigma(t)x + \mu(t)M$$

has a globally attractive positive ω-periodic solution

$$x_M(t) = M \int_{-\infty}^{t} e^{-\int_s^t \sigma(\tau)d\tau} \mu(s)ds.$$

By assumption (H2), we see that for any $M \geq K_0 > 0$, $(x_M(t), M)$ is an upper solution of the cooperative system (3.2). Thus, the comparison principle implies that solutions of system (3.2) are uniformly bounded. By Theorem 2.1.3, as applied to the Poincaré map associated with system (3.2) on the set $[0, x_M(0)] \times [0, M]$, it follows that system (3.2) admits a threshold dynamics (see also [106, Theorem 3.1.2]). Since M can be chosen as large as we wish, this threshold type result holds true on $\mathbb{R}^2_+$. $\square$

3.1.2 Spreading speeds

In the rest of this section, we always assume that $\rho > 1$. According to Lemma 3.1.1, there exist two periodic solutions, (0, 0) and $u^*(t) = (u_1^*(t), u_2^*(t))$, to the spatially homogeneous system (3.2). Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ and $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geq 0, \ \forall x \in \mathbb{R}\}$. Clearly, any vector in $\mathbb{R}^2$ can be regarded as a function in $\mathcal{C}$. For $u = (u_1, u_2), w = (w_1, w_2) \in \mathcal{C}$, we write $u \geq w (u \gg w)$ provided $u_j(x) \geq w_j(x) (u_j(x) > w_j(x)), \forall 1 \leq j \leq 2$, $x \in \mathbb{R}$, and $u > w$ provided $u \geq w$ but $u \neq w$. For any $r \in \mathbb{R}_+^2$ with $r \gg 0$, we set $[0, r] := \{u \in \mathbb{R}^2 : \ 0 \leq u \leq r\}$ and $\mathcal{C}_r := \{u \in \mathcal{C} : \ 0 \leq u \leq r\}$.

We equip $\mathcal{C}$ with the compact open topology and the norm defined in (2.1) with $X = \mathbb{R}^2$.

Let $\mathbb{Y}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$. Let $\Gamma(t, x)$ be the Green function associated with the heat equation $\frac{\partial u}{\partial t} = \Delta u$, and $T_1(t, s)$ and $T_2(t, s)$ be the evolution operators on $\mathbb{Y}$ generated by the following two linear equations:

$$\frac{\partial n_1}{\partial t} = -\sigma(t) n_1 - v(t) \frac{\partial n_1}{\partial x} + D(t) \frac{\partial^2 n_1}{\partial x^2} \quad \text{and} \quad \frac{\partial n_2}{\partial t} = (f(t, 0) - \mu(t)) n_2,$$

respectively. It then follows that

$$\begin{aligned} [T_1(t, s)\phi_1](x) &= e^{-\int_s^t \sigma(\tau) d\tau} \int_{\mathbb{R}} \Gamma \left(\int_s^t D(\tau) d\tau, x - \int_s^t v(\tau) d\tau - y \right) \phi_1(y) dy, \\ [T_2(t, s)\phi_2](x) &= e^{\int_s^t (f(\tau, 0) - \mu(\tau)) d\tau} \phi_2(x). \end{aligned} \tag{3.5}$$

Define $B : [0, \infty) \times \mathcal{C}_+ \to \mathcal{C}$ by

$$B(t, \phi)(x) := \begin{pmatrix} \mu(t)\phi_2 \\ \sigma(t)\phi_1 + F(t, \phi_2) \end{pmatrix}, \tag{3.6}$$

where $F(t,u) = u(f(t,u) - f(t,0))$. In view of (H1), $F(t,u)$ is also locally Lipschitz in u, uniformly for $t \in [0,\omega]$. Let $(u_1(t,x), u_2(t,x)) = (n_d(t,x), n_b(t,x))$. Then we can rewrite system (3.1) as

$$\begin{aligned} &\frac{\partial u}{\partial t} = A(t)u + B(t,u), \quad t > 0, \\ &u(0,\cdot) = \phi, \end{aligned} \tag{3.7}$$

where $A(t) = diag(-\sigma(t) - v(t)\frac{\partial}{\partial x} + D(t)\frac{\partial^2}{\partial x^2}, f(t,0) - \mu(t))$. Integrating two equations of system (3.7), we have

$$\begin{aligned} u_1(t,\cdot) &= T_1(t,0)\phi_1 + \textstyle\int_0^t T_1(t,s)B_1(s,u(s,\cdot))ds, \\ u_2(t,\cdot) &= T_2(t,0)\phi_2 + \textstyle\int_0^t T_2(t,s)B_2(s,u(s,\cdot))ds. \end{aligned}$$

It follows that system (3.7) with initial values can be written as an integral equation

$$\begin{aligned} &u(t) = T(t,0)\phi + \int_0^t T(t,s)B(s,u(s))ds, \\ &u(0) = \phi, \end{aligned} \tag{3.8}$$

where $T(t,s) = diag(T_1(t,s), T_2(t,s))$. As usual, solutions of (3.8) are called mild solutions to system (3.7).

Definition 3.1.1. *A function $u(t,x)$ is said to be an upper (a lower) solution of system* (3.7) *if it satisfies*

$$u(t) \geq (\leq) T(t,0)u(0) + \int_0^t T(t,s)B(s,u(s))ds.$$

To obtain the existence and uniqueness of the solution to system (3.7), we first establish a comparison theorem for the nonlinear integral equation (3.8) by similar arguments to those in [86, Lemma 3.2].

Proposition 3.1.1. *Let $T \in (0,\infty]$, and M_T be the set of all functions u from $[0,T)\times\mathbb{R}$ to $\mathbb{R}^2_+$ such that u is Borel measurable and bounded on $[0,T']\times\mathbb{R}$ for any $T' \in (0,T)$. Suppose w, $v \in M_T$ with $w(0,\cdot) \le v(0,\cdot)$, and w, v are lower and upper solutions of (3.7) on $[0,T)\times\mathbb{R}$, respectively. Then $w \le v$ on $[0,T)\times\mathbb{R}$.*

Proof. Let $T' \in (0,T)$ be given. Since $w(t,x)$ and $v(t,x)$ are bounded on $[0,T']\times\mathbb{R}$, there exist $B>0$ and $L>0$ such that $|w(t,x)| \le B$, $|v(t,x)| \le B$, and

$$|F(t,x) - F(t,y)| \le L|x-y|, \quad t \ge 0,\ |x| \le B, |y| \le B.$$

Set $m := w - v = (m_1, m_2)$. Then we see from the integral equation (3.8) that

$$\begin{aligned} m_1(t,x) &\le \int_0^t T_1(t,t-s)\mu(t-s)[m_2(t-s,x)]_+ ds, \\ m_2(t,x) &\le \int_0^t T_2(t,s)(\sigma(s)[m_1(s,x)]_+ + L[m_2(s,x)]_+) ds, \end{aligned} \tag{3.9}$$

where $[a]_+ = \max\{0,a\}$ for $a \in \mathbb{R}$. Let $\lambda > 0$, and set

$$\psi_\lambda(t) := \sup_{x\in\mathbb{R}}[m_1(t,x)]_+ e^{-\lambda t},\ \overline{\psi}_\lambda := \sup_{t\in[0,T']} \psi_\lambda(t).$$
$$\phi_\lambda(t) := \sup_{x\in\mathbb{R}}[m_2(t,x)]_+ e^{-\lambda t},\ \overline{\phi}_\lambda := \sup_{t\in[0,T']} \phi_\lambda(t).$$

By the first inequality of (3.9), we have

$$\psi_\lambda(t) \le \mu_{\max} \int_0^t T_1(t,t-s)\overline{\phi}_\lambda e^{-\lambda s} ds.$$

Since

$$T_1(t,s)(w(x)) = e^{-\int_s^t \sigma(\tau)d\tau} \int_{\mathbb{R}} \Gamma(\int_s^t D(\tau)d\tau, x - \int_s^t v(\tau)d\tau - y)w(y)dy,$$

it follows that

$$\overline{\psi}_\lambda \le \frac{\mu_{\max}\overline{\phi}_\lambda}{\lambda}. \tag{3.10}$$

Using the second inequality of (3.9) and (3.10), we further obtain

$$\begin{aligned} m_2(t,x) &\le \int_0^t T_2(t,s)(\sigma(s)[m_1(s,x)]_+ + L[m_2(s,x)]_+)ds \\ &\le \int_0^t T_2(t,t-s)(\sigma_{\max}[m_1(t-s,x)]_+ + L[m_2(t-s,x)]_+)ds, \end{aligned}$$

where $T_2(t,t-s) = e^{\int_{t-s}^t (f(\tau,0)-\mu(\tau))d\tau}$. Thus, we have

$$\begin{aligned} \phi_\lambda(t) &\le (\sigma_{\max}\overline{\psi}_\lambda + L\overline{\phi}_\lambda)\int_0^t e^{\int_{t-s}^t (f(\tau,0)-\mu(\tau))d\tau} e^{-\lambda s} ds \\ &\le e^{\int_0^{T'} (f(s,0)-\mu(s))ds}\overline{\phi}_\lambda \cdot \left(\frac{L}{\lambda} + \frac{\sigma_{\max}\mu_{\max}}{\lambda^2}\right). \end{aligned}$$

It follows that

$$\overline{\phi}_\lambda \le e^{\int_0^{T'} (f(s,0)-\mu(s))ds}\overline{\phi}_\lambda \cdot \left(\frac{L}{\lambda} + \frac{\sigma_{\max}\mu_{\max}}{\lambda^2}\right),$$

and hence, $\overline{\phi}_\lambda \le 0$ for sufficiently large λ, which implies $m_2(t,x) \le 0$ on $[0,T') \times \mathbb{R}$. Moreover, $\overline{\psi}_\lambda \le \frac{\mu_{\max}\overline{\phi}_\lambda}{\lambda} \le 0$ for sufficiently large λ, which implies $m_1(t,x) \le 0$ on $[0,T'] \times \mathbb{R}$. Since $T' \in (0,T)$ is arbitrary, we obtain $w \le v$ on $[0,T) \times \mathbb{R}$. □

Proposition 3.1.2. *Suppose that ϕ is nonnegative, bounded and Borel measurable. Then system (3.7) has a unique nonnegative, bounded and Borel measurable mild solution $u(t,\cdot,\phi) = (u_1(t,\cdot,\phi), u_2(t,\cdot,\phi))$ with $u(0,\cdot,\phi) = \phi$, $\forall t \ge 0$. If ϕ is continuous in x, so is $u(t,x,\phi)$. If ϕ is monotone in x, so is $u(t,x,\phi)$.*

Proof. Let ϕ be given as in the assumption. Then we have $\phi \in M_T$. Let $a = \max_{x\in\mathbb{R}} \phi(x)$. Define

$$\overline{M_T} := \{u \in M_T : u(t,x) \le v(t,a) \text{ on } [0,T) \times \mathbb{R},\ T < \infty\},$$

where $v(t,a)$ is a solution of system (3.4) with $v(0,a) = a$. Clearly, there exists $B_0 > 0$ such that $u \le B_0$ for any $u \in \overline{M_T}$. Let L be an appropriate local Lipschitz constant for $F(t,u)$ with $0 \le u \le B_0$. For convenience, we let

$$\hat{T}_1(t,s) = T_1(t,s),\ \hat{T}_2(t,s) = e^{-\alpha(t-s)}T_2(t,s),\ \hat{B}(t,\phi) = B(t,\phi) + \begin{pmatrix} 0 \\ \alpha\phi_2 \end{pmatrix}.$$

For any given $\alpha > L$, we can rewrite (3.7) as

$$\begin{aligned} u(t) &= \hat{T}(t,0)\phi + \int_0^t \hat{T}(t,s)\hat{B}(s,u(s))ds, \\ u(0) &= \phi, \end{aligned} \tag{3.11}$$

where $\hat{T}(t,s) = diag(\hat{T}_1(t,s), \hat{T}_2(t,s))$. Clearly, $\hat{B}(t,\phi) \ge \hat{B}(t,\varphi)$ whenever $\phi \ge \varphi$. Define

$$G(u)(t,x) := \hat{T}(t,0)\phi(x) + \int_0^t \hat{T}(t,s)\hat{B}(s,u(s))(x)ds.$$

Since $\hat{B}(t,\phi)$ is increasing in ϕ, and 0 and $v(t,a)$ are solutions of system (3.11), it follows that $G(\overline{M}_T) \subset \overline{M}_T$.

For any given $u, v \in \overline{M}_T$, we define

$$d_\lambda(u,v) := \sup_{[0,T)\times\mathbb{R}} |u(t,x) - v(t,x)|e^{-\lambda t},$$

where $\lambda > 0$ is a constant. Then $\overline{M}_T$ is a complete space with the metric d_λ. For any $u, v \in \overline{M}_T$, we have

$$d_\lambda(G(u), G(v)) \le \frac{\mu_{\max} + (\sigma_{\max} + \alpha + L)e^{\int_0^T (f(s,0)-\mu(s))ds}}{\lambda} \cdot d(u,v).$$

Choose sufficiently large $\lambda > 0$ such that $\frac{\mu_{\max}+(\sigma_{\max}+\alpha+L)e^{\int_0^T (f(s,0)-\mu(s))ds}}{\lambda} < 1$. It then follows that G is a contracting mapping on $(\overline{M}_T, d_\lambda)$. By the contracting mapping theorem, G has a unique fixed point in $\overline{M}_T$. Thus, system (3.11) has a unique nonnegative Borel measurable solution for all $t \in [0, T_\phi)$. Since $u(t,x,\phi) \le v(t,a)$ and $v(t,a)$ is bounded, it follows that $T = \infty$ and $u(t,x,\phi)$ is bounded on $[0,\infty) \times \mathbb{R}$.

In the case where ϕ is continuous in x, by including the continuity of u in the definition of $\overline{M}_T$, we see that the resulting space remains complete under the metric induced by $\|\cdot\|_\lambda$. Further, $G(\overline{M}_T) \subset \overline{M}_T$ still holds true, because $G(u)$ is continuous provided that ϕ and u are continuous.

In the case where ϕ is monotone in x, by including the monotonicity of u in the definition of $\overline{M}_T$, we see that the resulting space remains complete under the metric induced by $\|\cdot\|_\lambda$. Suppose that $u \in M_T$ is increasing in x, and define $v(x) = u(x+c)$ for any given $c > 0$. Clearly, $v \in M_T$ and $u \leq v$. Using the monotonicity of $\hat{B}(t, \phi)$ and $\hat{T}(t, 0)$ in ϕ, we obtain that $G(u)(x) \leq G(v)(x) = G(u(\cdot+c))(x) = G(u)(x+c), \forall x \in \mathbb{R}$. Consequently, we have $G(\overline{M}_T) \subset \overline{M}_T$. □

Theorem 3.1.1. *Let $u^*(t)$ be the ω-periodic solution given in Lemma 3.1.1. Then for any $\phi \in \mathcal{C}_{u^*(0)}$, system* (3.7) *has a unique nonnegative mild solution $u(t, \cdot, \phi) = (u_1(t, \cdot, \phi), u_2(t, \cdot, \phi)) \in \mathcal{C}_{u^*(t)}$ with $u(0, \cdot, \phi) = \phi \in \mathcal{C}_{u^*(0)}, \forall t \geq 0$. Moreover, if $\underline{u}(t, x)$ and $\overline{u}(t, x)$ are a pair of lower and upper solutions of system* (3.7)*, respectively, with $\underline{u}(0, \cdot) \leq \overline{u}(0, \cdot)$, then $\underline{u}(t, \cdot) \leq \overline{u}(t, \cdot), \forall t \geq 0$.*

Proof. By Proposition 3.1.2, it follows that for any $\varphi \in \mathcal{C}_+$, system (3.7) has a unique nonnegative mild solution $u(t, \cdot, \phi) \in \mathcal{C}_+$. Further, Proposition 3.1.1 implies the comparison principle holds for system (3.7). Since $u(t, \cdot, u^*(0)) = u^*(t)$ is a solution of system (3.7) with $u(0, \cdot) = u^*(0)$, our result follows from the comparison principle. □

Let $\{Q_t\}_{t\geq 0}$ be a family of solution maps from $\mathcal{C}_{u^*(0)}$ to $\mathcal{C}_{u^*(t)}$, that is,

$$Q_t(\phi)(x) = u(t, x, \phi) = (u_1(t, x, \phi), u_2(t, x, \phi)), \quad \forall \phi \in \mathcal{C}_{u^*(0)},\ x \in \mathbb{R},\ t \geq 0,$$

where $u(t, x, \phi)$ is the mild solution of system (3.7) with $u(0, \cdot, \phi) = \phi$. It is easy to see that $Q_0 = I$, and $Q_{t+\omega} = Q_t \circ Q_\omega$ for all $t \geq 0$. Further, we have the following observation.

Lemma 3.1.2. *$Q(t,\phi) = Q_t(\phi)$ is continuous in $(t,\phi) \in \mathbb{R}_+ \times \mathcal{C}_{u^*(0)}$ with respect to the compact open topology.*

Proof. Let $T(t,0) = diag(T_1(t,0), T_2(t,0))$, where $T_1(t,0)$ and $T_2(t,0)$ are defined as in (3.5). We first show that for any given $t_0 > 0$, $\varphi \in \mathcal{C}_\beta$ with $\beta = (\beta_1, \beta_2) \gg 0$, $T(t,0)\varphi$ is continuous at $\varphi = 0$ with respect to the compact open topology uniformly for $t \in [0, t_0]$. Indeed, define $\|\phi\|_{\Omega_\rho(z)} := \sup\limits_{x \in \Omega_\rho(z)} |\phi(x)|$, where $\Omega_\rho(z) := [z-\rho, z+\rho]$. Let $a = e^{\int_0^{t_0}[f(s,0)-\mu(s)]ds}$. For any $\varepsilon > 0$ and $K > 0$, there exists $A(\varepsilon) > 0$ such that $\int_{|x|>A} \frac{1}{\sqrt{\pi}} e^{-x^2} dx \leq \frac{\varepsilon}{2\beta_1}$. Choose $\delta = \frac{\varepsilon}{2}$ and $C(\varepsilon, t_0) = 2A\sqrt{\int_0^{t_0} D(s)ds} > 0$ such that for any $t \in (0, \int_0^{t_0} D(s)ds]$, we have

$$\begin{aligned} \int_{|y|>C} \frac{1}{\sqrt{4\pi t}} e^{-\frac{y^2}{4t}} dy &\leq \int_{|y|>2A\sqrt{t}} \frac{1}{\sqrt{4\pi t}} e^{-\frac{y^2}{4t}} dy \\ &\leq \int_{|x|>A} \frac{1}{\sqrt{\pi}} e^{-x^2} dx \leq \frac{\varepsilon}{2\beta_1}. \end{aligned}$$

Let $M = C + \int_0^{t_0} v(s)ds$. Since $0 \leq \varphi_1(x) \leq \beta_1$, we obtain

$$\int_{|y|>M} \frac{1}{\sqrt{4\pi \int_0^t D(s)ds}} e^{-\frac{(y-\int_0^t v(s)ds)^2}{4\int_0^t D(s)ds}} dy \leq \frac{\varepsilon}{2\beta_1},$$

$$\int_{\mathbb{R}} \frac{1}{\sqrt{4\pi \int_0^t D(s)ds}} e^{-\frac{(y-\int_0^t v(s)ds)^2}{4\int_0^t D(s)ds}} \varphi_1(x-y)dy \leq \frac{\varepsilon}{2} + \|\varphi_1\|_{\Omega_M(x)},$$

for all $t \in (0, t_0]$. It then follows that

$$\begin{aligned} T_1(t,0)\varphi_1(x) &= e^{-\int_0^t \sigma(s)ds} \int_{\mathbb{R}} \Gamma\Big(\int_0^t D(s)ds, y - \int_0^t v(s)ds\Big)\phi_1(x-y)dy \\ &\leq \frac{\varepsilon}{2} + \|\varphi_1\|_{\Omega_M(x)}, \end{aligned}$$

and hence, $T_1(t,0)\varphi_1(x) < \varepsilon$, $\forall x \in [-K, K]$, uniformly for $t \in (0, t_0]$ provided that $\varphi_1(x) < \delta$, $\forall x \in [-K-M, K+M]$. Since $\lim\limits_{t \to 0^+} T_1(t,0)\varphi_1 = \varphi_1$, we have $T_1(t,0)\varphi_1(x) <$

ε, $\forall x \in [-K, K]$, uniformly for $t \in [0, t_0]$ provided that $\varphi_1(x) < \delta$, $\forall x \in [-K - M, K + M]$. It then follows that for any $\overrightarrow{\varepsilon} = (\varepsilon, \varepsilon) \gg 0$ and $K > 0$, there exists $\overrightarrow{\delta} = (\frac{\varepsilon}{2}, \frac{\varepsilon}{a}) \gg 0$ and $M(\varepsilon, t_0) > 0$ such that $T(t, 0)\varphi(x) < \overrightarrow{\varepsilon}$,$\forall x \in [-K, K]$, uniformly for $t \in [0, t_0]$ provided that $\varphi(x) < \overrightarrow{\delta}$, $\forall x \in [-K - M, K + M]$. This proves the continuity of $T(t, 0)\varphi$ at $\varphi = 0$ uniformly for $t \in [0, t_0]$. We further prove the following claim.

Claim. For any $\varepsilon > 0$ and $t_0 > 0$, there exists $\delta = \delta(\varepsilon, t_0) > 0$ and $K = K(\varepsilon, t_0) > 0$ such that for any $z \in \mathbb{R}$, if $\phi, \hat{\phi} \in \mathcal{C}_{u^*(0)}$ with $|\phi(x) - \hat{\phi}(x)| < \delta$ for all $x \in [z - K, z + K]$, then $|u(z, t, \phi) - u(z, t, \hat{\phi})| < \varepsilon$, $\forall t \in [0, t_0]$.

Since system (3.1) admits the spatial translation invariance, it suffices to prove the claim for the case where $z = 0$. Let $\varphi(x) = \phi(x) - \hat{\phi}(x)$ and define $w(t, x) = u(t, x, \phi) - u(t, x, \hat{\phi})$. Then $w(t, x) = (w_1(t, x), w_2(t, x))$ satisfies

$$\begin{aligned} w_1(t, \cdot) = \;& T_1(t, 0)\varphi_1 + \textstyle\int_0^t T_1(t, s)\mu(s)w_2(s, \cdot)ds, \\ w_2(t, \cdot) = \;& T_2(t, 0)\varphi_2 + \textstyle\int_0^t T_2(t, s)\left(\sigma(s)w_1(s, \cdot) + f(s, u_2(s, \cdot, \phi))\right. \\ & \left. - f(s, u_2(s, \cdot, \hat{\phi}))\right)ds. \end{aligned}$$

We proceed by considering two cases.

Case 1. $\phi \geq \hat{\phi}$. By Theorem 3.1.1, $u(t, x, \phi) \geq u(t, x, \hat{\phi})$ for all $t \geq 0$, $x \in \mathbb{R}$. Then $w(t, x) \geq 0$ and

$$\begin{aligned} w_1(t, \cdot) &= T_1(t, 0)\varphi_1 + \textstyle\int_0^t T_1(t, s)\mu(s)w_2(s, \cdot)ds, \\ w_2(t, \cdot) &\leq T_2(t, 0)\varphi_2 + \textstyle\int_0^t T_2(t, s)\sigma(s)w_1(s, \cdot)ds. \end{aligned} \tag{3.12}$$

Now we consider the integral equations.

$$v(t, \cdot, \varphi) = T(t, 0)\varphi + \int_0^t T(t, s)M(s)v(s, \cdot, \varphi)ds, \tag{3.13}$$

where $T(t, s) = diag(T_1(t, s), T_2(t, s)), 0 \leq s \leq t$ and $M(t) = \begin{pmatrix} 0 & \mu(t) \\ \sigma(t) & 0 \end{pmatrix}$. Let

$Y(t)$ be the standard fundamental solution matrix associated with the linear equation $w' = M(t)w$. It is easy to see that $v(t, \cdot, \varphi) = Y(t)T(t,0)\varphi$ is the unique solution of (3.13) with $v(0, \cdot, \varphi) = \varphi$. Then the comparison principle implies that

$$0 \le w(t, \cdot) \le v(t, \cdot, \varphi) = Y(t)T(t,0)\varphi.$$

By the continuity of $T(t,0)\varphi$ at $\varphi = 0$ uniformly for $t \in [0, t_0]$, it follows that for any $\overrightarrow{\varepsilon} \gg 0$ and $t_0 > 0$, there exists $M > 0$ and $\overrightarrow{\delta} \gg 0$ such that

$$u(t, 0, \phi) - u(t, 0, \hat{\phi}) = w(t, 0) \le v(t, 0, \varphi) < \overrightarrow{\varepsilon}, \quad \forall t \in [0, t_0],$$

provided that $\varphi \in \mathcal{C}_{u^*(0)}$ with $\varphi(x) < \overrightarrow{\delta}$ for all $x \in [-M, M]$.

Case 2. $\phi \not\geq \hat{\phi}$. Let $\Phi_i(x) = \max\{\phi_i(x), \hat{\phi}_i(x)\}$, $\Psi(x) = \min\{\phi_i(x), \hat{\phi}_i(x)\}$, $i = 1, 2$. It then easily follows that

$$|\phi_i(x) - \hat{\phi}_i(x)| = \Phi_i(x) - \Psi_i(x), \ \forall x \in \mathbb{R}, \ i = 1, 2.$$

Using the comparison principle again, we further have

$$|u_i(0, t, \phi) - u_i(0, t, \hat{\phi})| \le u_i(0, t, \Phi) - u_i(0, t, \hat{\Psi}), \quad \forall t \in [0, \infty), \quad i = 1, 2.$$

By the conclusion in Case 1, it then follows that for any $\varepsilon > 0$ and $t_0 > 0$, there exists $M > 0$ and $\delta > 0$ such that

$$|u_i(0, t, \phi) - u_i(0, t, \hat{\phi})| < \frac{\varepsilon}{2}, \quad \forall t \in [0, t_0], \ i = 1, 2,$$

provided that $\varphi = (\varphi_1, \varphi_2) \in \mathcal{C}_{u^*(0)}$ with $|\varphi_i(x)| < \frac{\delta}{2}$ for all $x \in [-M, M]$.

From the claim above, we see that for any $t_0 > 0$, $\phi \in \mathcal{C}_{u^*(0)}$, $u(t, \cdot, \phi)$ is continuous in ϕ with respect to the compact open topology uniformly for $t \in [0, t_0]$. Clearly, $u(t, x, \phi)$ is continuous in t with respect to the compact open topology. By the triangle inequality, it then follows that $Q_t(\phi)$ is continuous in (t, ϕ) with respect to the compact open topology. $\square$

To use the result about the spreading speeds for monotone semiflows in section 2.2, we need verify $Q = Q_\omega : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies assumptions (A1)–(A5) with (A1) replaced by the following one without reflection invariance which is based on Remark 2.2.1:

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

Then the following lemma holds.

Lemma 3.1.3. *The poincaré map Q_ω satisfies all hypotheses (A1)′ and (A2)–(A5) with $\beta = u^*(0)$, $X = \mathbb{R}^2$ and $X_\beta = [0, u^*(0)]$.*

Proof. If $u(t,x)$ is a solution for system (3.7), then $u(t, x+y)$, $\forall y \in \mathbb{R}$, is also a solution, and hence (A1)′ holds. (A2) comes from Lemma 3.1.2. (A3) is automatically satisfied. (A4) follows directly from the comparison principle in Theorem 3.1.1, and Lemma 3.1.1(i) implies that (A5) is also valid. □

In view of Theorem 2.2.1 and Lemma 3.1.3, it follows that the map Q_ω admits a rightward spreading speed c_ω^+ and a leftward spreading speed c_ω^-. In order to estimate $c_\omega^\pm$, we consider the following linear system:

$$\begin{cases} \frac{\partial n_d}{\partial t} = -\sigma(t) n_d + \mu(t) n_b - v(t) \frac{\partial n_d}{\partial x} + D(t) \frac{\partial^2 n_d}{\partial x^2}, \\ \frac{\partial n_b}{\partial t} = \sigma(t) n_d - \mu(t) n_b + f(t,0) n_b, \quad t > 0,\ x \in \mathbb{R}. \end{cases} \tag{3.14}$$

Let $(u_1(t,x), u_2(t,x)) = e^{-\lambda x}(\overline{u}_1(t), \overline{u}_2(t))$ be a solution of (3.14) with $\lambda \in \mathbb{R}$. Then $(\overline{u}_1(t), \overline{u}_2(t))$ satisfies the following ordinary differential system in $\mathbb{R}^2$:

$$\begin{cases} \frac{d\overline{u}_1}{dt} = (-\sigma(t) + \lambda v(t) + \lambda^2 D(t))\overline{u}_1 + \mu(t)\overline{u}_2, \\ \frac{d\overline{u}_2}{dt} = \sigma(t)\overline{u}_1 - \mu(t)\overline{u}_2 + f(t,0)\overline{u}_2, \quad t > 0. \end{cases} \tag{3.15}$$

Let $\{M_t\}_{t\geq 0}$ be the solution map associated with (3.14). Define $B_\lambda^t : \mathbb{R}^2 \to \mathbb{R}^2$ as

$$B_\lambda^t(\phi) := M_t(\phi e^{-\lambda x})(0) = (\overline{u}_1(t), \overline{u}_2(t)).$$

Therefore, $B_\lambda^t(\phi)$ is the solution map of (3.15). Let $r(\lambda)$ be the spectral radius of the Poincaré map B_λ^ω. It is easy to verify that B_λ^ω is a compact and strongly positive operator (actually, B_λ^t is strongly positive for all $t \geq \omega$). By Theorem 2.1.1, it follows that $r(\lambda) > 0$ and it is a simple eigenvalue of B_λ^ω with a strongly positive eigenvector $w^* \gg 0$. Define $r_+(\lambda) = r(\lambda)$ and $r_-(\lambda) = r(-\lambda)$ for $\lambda \geq 0$. Then we have the following computation formulas for $c_\omega^\pm$.

Proposition 3.1.3. $c_\omega^\pm = \inf\limits_{\lambda>0} \frac{\ln r_\pm(\lambda)}{\lambda}$. *Moreover,* $c_\omega^+ + c_\omega^- > 0$.

Proof. Using an argument similar to that in the proof of [101, Lemma 2.1], we see that there exists a positive ω-periodic function $w(t)$ such that $\overline{v}(t) = e^{\rho_+(\lambda)t}w(t)$ is a solution of (3.15), where $\rho_+(\lambda) = \frac{1}{\omega}\ln r_+(\lambda)$ and $w(0) = w^*$. Thus, $B_\lambda^\omega(w(0)) = e^{\rho_+(\lambda)t}w(t)$. Letting $t = \omega$, we have $B_\lambda^\omega(w(0)) = e^{\rho_+(\lambda)\omega}w(0)$, which implies that $e^{\rho_+(\lambda)\omega}$ is the principal eigenvalue of B_λ^ω with strongly positive eigenvector $w(0)$. Define the function

$$\Phi_+(\lambda) := \frac{1}{\lambda}\ln(e^{\rho_+(\lambda)\omega}) = \frac{\rho_+(\lambda)\omega}{\lambda} = \frac{\ln r_+(\lambda)}{\lambda}, \quad \forall \lambda > 0. \tag{3.16}$$

When $\lambda = 0$, system (3.15) reduces to system (3.4). Since $\rho > 1$, we have $r_+(0) > 1$. Hence, condition $(C7)$ in [54] (see also (B7) in section 2.2) is satisfied. Now we prove that $\Phi_+(\infty) = \infty$. Since $\overline{v}(t) := e^{\rho_+(\lambda)t}w(t)$ is a solution of (3.15), it follows that

$$\overline{v}_1'(t) \geq (-\sigma(t) + \lambda v(t) + \lambda^2 D(t))\overline{v}_1(t),$$

and hence,

$$\frac{w_1'(t)}{w_1(t)} \geq -\sigma(t) + \lambda v(t) + \lambda^2 D(t) - \rho_+(\lambda).$$

Integrating the above inequality from 0 to ω, we have

$$0 = \int_0^\omega \frac{w_1'(t)}{w_1(t)} \geq -\int_0^\omega \sigma(t)dt + \lambda \int_0^\omega v(t)dt + \lambda^2 \int_0^\omega D(t)dt - \rho_+(\lambda)\omega.$$

Since $\int_0^\omega D(t)dt > 0$, it follows that

$$\Phi_+(\lambda) = \frac{\rho_+(\lambda)\omega}{\lambda} \geq -\frac{1}{\lambda}\int_0^\omega \sigma(t)dt + \int_0^\omega v(t)dt + \lambda \int_0^\omega D(t)dt,$$

which implies that $\Phi_+(\infty) = \infty$. Thus, $\Phi_+(\lambda)$ attains its minimum at some finite value λ^*. Since the solution $u(t,x,\phi)$ for system (3.7) is a lower solution of the linear system (3.14), we have $Q_t(\phi) \leq M_t(\phi)$ for all $\phi \in \mathcal{C}_{u^*(0)}, t \geq 0$. It then follows from Theorem 2.2.2(i) that $c_\omega^+ \leq \inf\limits_{\lambda>0} \Phi_+(\lambda)$. Note that the reflection invariance property is assumed for M_t in (B4) and Q_t in (A1), but this property is not needed in the proof of Theorem 2.2.2.

For $\lambda > 0$, let $r_+^\varepsilon(\lambda)$ be the spectral radius of the Poincaré map associated with the following differential system:

$$\begin{cases} \frac{d\overline{u}_1}{dt} = (-\sigma(t) + \lambda v(t) + \lambda^2 D(t))\overline{u}_1 + \mu(t)\overline{u}_2, \\ \frac{d\overline{u}_2}{dt} = \sigma(t)\overline{u}_1 - \mu(t)\overline{u}_2 + f(t,\varepsilon)\overline{u}_2, \quad t > 0. \end{cases} \tag{3.17}$$

Let $\{M_t^\varepsilon\}_{t\geq 0}$ be the solution map associated with

$$\begin{cases} \frac{\partial u_1}{\partial t} = -\sigma(t)u_1 + \mu(t)u_2 - v(t)\frac{\partial u_1}{\partial x} + D(t)\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} = \sigma(t)u_1 - \mu(t)u_2 + f(t,\varepsilon)u_2, \quad t > 0,\ x \in \mathbb{R}. \end{cases} \tag{3.18}$$

By the continuous dependence of the solutions on initial conditions, we know that for any small $\varepsilon \in (0, u^*(0))$, there exists $\eta > 0$ such that the solutions $\hat{w}(t,\overline{\eta})$ of system (3.2) with $w(0,\overline{\eta}) = \overline{\eta}$ satisfies $\hat{w}(t,\overline{\eta}) \leq \overline{\varepsilon}$ for all $t \in [0,\omega]$, where $\overline{\eta} = (\eta,\eta), \overline{\varepsilon} = (\varepsilon,\varepsilon)$. Then the comparison principle implies that

$$u(t,x,\phi) \leq \hat{w}(t,\overline{\eta}) \leq \overline{\varepsilon}, \quad \forall x \in \mathbb{R},\ \phi \in \mathcal{C}_{\overline{\eta}},\ t \in [0,\omega].$$

It follows that $u(t, x, \phi)$ satisfies

$$\begin{cases} \frac{\partial u_1}{\partial t} = -\sigma(t)u_1 + \mu(t)u_2 - v(t)\frac{\partial u_1}{\partial x} + D(t)\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} \geq \sigma(t)u_1 - \mu(t)u_2 + f(t,\varepsilon)u_2, \quad 0 < t \leq \omega, \ x \in \mathbb{R}. \end{cases} \tag{3.19}$$

This implies that $Q_t(\phi)$ is an upper solution of the linear system (3.18) for $t \in [0, \omega], \phi \in \mathcal{C}_{\overline{\eta}}$, and hence,

$$M_\omega^\varepsilon(\phi) \leq Q_\omega(\phi), \quad \forall \phi \in \mathcal{C}_{\overline{\eta}}.$$

Define the function

$$\Phi_+^\varepsilon(\lambda) := \frac{\ln r_+^\varepsilon(\lambda)}{\lambda}, \quad \forall \lambda > 0.$$

By performing an analysis on $\{M_t^\varepsilon\}_{t\geq 0}$ similar to that for $\{M_t\}_{t\geq 0}$, we obtain

$$\inf_{\lambda>0} \Phi_+^\varepsilon(\lambda) \leq c_\omega^+ \leq \inf_{\lambda>0} \Phi_+(\lambda)$$

for any sufficient small ε. Letting $\varepsilon \to 0$, we obtain that $c_\omega^+ = \inf\limits_{\lambda>0} \Phi_+(\lambda)$.

Let $\hat{v}_1(t, x) = n_d(t, -x)$ and $\hat{v}_2(t, x) = n_b(t, -x)$, we get

$$\begin{cases} \frac{\partial \hat{v}_1}{\partial t} = -\sigma(t)\hat{v}_1 + \mu(t)\hat{v}_2 + v(t)\frac{\partial \hat{v}_1}{\partial x} + D(t)\frac{\partial^2 \hat{v}_1}{\partial x^2}, \\ \frac{\partial \hat{v}_2}{\partial t} = \sigma(t)\hat{v}_1 - \mu(t)\hat{v}_2 + f(t,\hat{v}_2)\hat{v}_2, \quad t > 0, \ x \in \mathbb{R}. \end{cases} \tag{3.20}$$

If we denote c_ω^- as the leftward spreading speed of Q_ω, then c_ω^- is the rightward spreading speed of the map $\hat{Q}_\omega$, where $\hat{Q}_t$ is the solution map of system (3.20). By the similar arguments, we have $c_\omega^- = \inf\limits_{\lambda>0} \frac{\ln r_-(\lambda)}{\lambda}$. Moreover, we see from Lemma 2.2.1 and [57, Lemma 2.10] that $c_\omega^+ + c_\omega^- > 0$. □

Let $c_\pm^* := \frac{c_\omega^\pm}{\omega}$. Then the subsequent result shows that $c_\pm^*$ are the spreading speeds for system (3.7).

Theorem 3.1.2. *Assume that $\rho > 1$, and let $u(t, x, \phi)$ be the solution of system* (3.7) *with $u(0, \cdot, \phi) = \phi \in \mathcal{C}_{u^*(0)}$. Then the following statements are valid:*

(i) If $0 \le \phi \ll u^*(0)$*, and* $\phi = 0$ *for* x *outside a bounded interval, then we have* $\lim_{t\to\infty, x\ge ct} u(t,x,\phi) = 0$ *for all* $c > c_+^*$*, and* $\lim_{t\to\infty, x\le -ct} u(t,x,\phi) = 0$ *for all* $c > c_-^*$*;*

(ii) For any c *and* c' *satisfying* $-c_-^* < -c' < c < c_+^*$*, we have*

$\lim_{t\to\infty, -c't\le x\le ct}(u(t,x,\phi) - u^*(t)) = 0$ *for all* $\phi \in \mathcal{C}_{u^*(0)}$ *with* $\phi > 0$*.*

Proof. By Lemma 3.1.3, we know the Poincaré map Q_ω satisfies (A1)$'$, (A2)–(A5) with $\beta = u^*(0)$, and hence, statement (i) is a consequence of Theorem 2.2.4(i). For the second statement, since Q_t is subhomogeneous, by Theorem 2.2.4, r_σ can be chosen to be independent of $\sigma \gg 0$. Thus, we can denote r_σ by $\overline{r}$. By the arguments in Lemma 3.1.1 and the comparison principle for system (3.7), it follows that for every $\phi \in \mathcal{C}_{u^*(0)}$ with $\phi > 0$, $Q_t(\phi) \gg 0$ for all $t \ge \omega$. Thus, we have $Q_\omega(\phi) \gg 0$, and hence, there is a vector $\sigma \gg 0$ in $\mathbb{R}^2$ such that $Q_\omega(\phi) \gg \sigma$ for x on an interval of length $2\overline{r}$. Taking $Q_\omega(\phi)$ as a new initial data, we see from Theorem 2.2.4(ii) that statement (ii) holds. □

3.1.3 Traveling waves

In this section, we appeal to the theory of traveling waves for monotone semiflows with weak compactness developed in [19] (see also section 2.2.2) to prove the existence of leftward and rightward periodic traveling waves, and the coincidence of the spreading speeds $c_\pm^*$ with the minimal wave speeds for monotone periodic traveling waves.

Recall that $W(t, x-ct)$ is said to be a rightward periodic traveling wave of the ω-periodic semiflow $\{Q_t\}_{t\ge 0}$ provided that $Q_t(W(0,\cdot)) = W(t, x-ct)$, $\forall t \ge 0$, and the vector-valued function $W(t,z)$ is ω-periodic in t. We say that $W(t, x-ct)$ connects $\beta(t)$ to 0 if $W(t,-\infty) = \beta(t)$ and $W(t,\infty) = 0$ uniformly for $t \in \mathbb{R}_+$. A leftward periodic traveling wave $V(t, x+ct)$ can be defined for the ω-periodic semiflow $\{Q_t\}_{t\geq 0}$ in a similar way.

Since Q_ω satisfies (A1)$'$, (A2)–(A5) , we first have the following result on the nonexistence of periodic traveling waves of (3.7), which is the consequence of [53, Theorem 2.2].

Theorem 3.1.3. *Assume that $\rho > 1$, and let $c_\omega^\pm$ be defined as in Proposition 3.1.3 and $c_\pm^* = \frac{c_\omega^\pm}{\omega}$. Then for any $c < c_+^*$, system* (3.7) *admits no traveling wave solution $W(t, x-ct)$ connecting $u^*(t)$ to 0; and for any $c < c_-^*$, system* (3.7) *admits no traveling wave solution $V(t, x-ct)$ connecting 0 to $u^*(t)$.*

Next, we consider the existence of the rightward periodic traveling waves. Let $\mathcal{M}$ be the set of all non-increasing, left-continuous and bounded functions from $\mathbb{R}$ to $\mathbb{R}^2$. We equip $\mathcal{M}$ with the compact open topology. Let $\beta \in \mathbb{R}^2$ with $\beta \gg 0$, set $\mathcal{M}_\beta := \{u \in \mathcal{M} : 0 \leq u \leq \beta\}$ and $\mathcal{M}_+ := \{u \in \mathcal{M} : u \geq 0\}$.

By Propositions 3.1.1 and 3.1.2 and similar arguments to those in Theorem 3.1.1, we have the following result.

Proposition 3.1.4. *For any $\phi \in \mathcal{M}_{u^*(0)}$, system* (3.7) *has a unique Borel measurable mild solution $u(t, \cdot, \phi) = (u_1(t, \cdot, \phi), u_2(t, \cdot, \phi)) \in \mathcal{M}_{u^*(t)}$ with $u(0, \cdot, \phi) = \phi \in \mathcal{M}_{u^*(0)}$ for all $t \geq 0$, and the comparison principle holds for system* (3.7)*.*

Now we are ready to show the existence of periodic traveling waves based on the result in section 2.2.2.

Theorem 3.1.4. *Assume that $\rho > 1$, and let c_ω^+ be defined as in Proposition 3.1.3 and $c_+^* = \frac{c_\omega^+}{\omega}$. Then for any $c \geq c_+^*$, there exists a function $W(t, \xi) = (W_1(t, \xi), W_2(t, \xi)$ defined on $\mathbb{R}_+ \times \mathbb{R}$ such that $W(t, \xi)$ is non-increasing and left-continuous in ξ and* *that* $W(t, x - ct) = (W_1(t, x - ct), W_2(t, x - ct))$ *is a periodic traveling wave solution of system* (3.7) *connecting* $u^*(t)$ *to* 0.

Proof. We first prove that Q_ω: $\mathcal{M}_{u^*(0)} \to \mathcal{M}_{u^*(0)}$ satisfies (C1)–(C4) and (A5) with $X = \mathbb{R}^2$ and $X_\beta = [0, u^*(0)]$. Indeed, it is easy to see that for any $t > 0$, Q_t satisfies the translation invariance (C1). By the similar arguments to those in Lemma 3.1.2, we can verify that the continuity condition (C2) holds. (C3) is automatically satisfied with $k = 0$. The monotonicity of Q_ω in (C4) follows from Proposition 3.1.4. (A5) follows from Lemma 3.1.1. Since Q_ω satisfies (C1)–(C4) and (A5), and each Q_ω maps left-continuous functions to left-continuous functions. By [19, Remark 3.7 and theorem 3.8](see also Theorems 2.2.7 and 2.2.5), it follows that Q_ω admits a traveling wave $U(x - c\omega n) = (U_1(x - c\omega n), U_2(x - c\omega n))$ connecting $u^*(0)$ to 0 provided $c\omega \geq c_\omega^+$. Define $P_t = T_{-ct}Q_t$, $t \geq 0$. Then P_t is an ω-periodic semiflow on $\mathcal{M}_{u^*(0)}$, and U is a fixed point of the Poincaré map P_ω associated with the periodic semiflow P_t. It follows that $P_t[U]$ is an ω-periodic orbit of P_t, that is, $P_{t+\omega}[U] = P_t[U]$. Let $W(t, x) := P_t[U](x), \forall t \geq 0$. Then $Q_t[U](x) = T_{ct}P_t[U](x) = W(t, x - ct)$. Since $U(x)$ is left-continuous, non-increasing in x and connects $u^*(0)$ to 0, we see that $W(t, x - ct)$ connects $u^*(t)$ to 0, and $W(t, \xi)$ is left-continuous and non-increasing. □

By similar arguments to those in Theorem 3.1.4, we have the following result on leftward periodic traveling waves.

Theorem 3.1.5. *Assume that* $\rho > 1$, *and let* c_ω^- *be defined as in Proposition 3.1.3 and* $c_-^* = \dfrac{c_\omega^-}{\omega}$. *Then for any* $c \geq c_-^*$, *there exists a function* $V(t, \xi) = (V_1(t, \xi), V_2(t, \xi))$ *defined on* $\mathbb{R}_+ \times \mathbb{R}$ *such that* $V(t, \xi)$ *is non-decreasing and right-continuous in* ξ, *and that* $V(t, x + ct) = (V_1(t, x + ct), V_2(t, x + ct))$ *is a periodic traveling wave solution of system* (3.7) *connecting* 0 *to* $u^*(t)$.

3.2 Threshold dynamics in a bounded domain

In this section, we study the global dynamics of system (3.1) in a bounded spatial domain $[0, L]$ under the following zero-flux and hostile boundary condition for n_d:

$$v(t)n_d(t,0) - D(t)\frac{\partial n_d}{\partial x}(t,0) = 0 \quad \text{and} \quad n_d(t,L) = 0.$$

Let $(u_1, u_2) = (n_d, n_b)$. Then we consider the following PDE system:

$$\begin{cases} \frac{\partial u_1}{\partial t} = -\sigma(t)u_1 + \mu(t)u_2 - v(t)\frac{\partial u_1}{\partial x} + D(t)\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} = \sigma(t)u_1 - \mu(t)u_2 + f(t,u_2)u_2, \quad x \in (0,L),\ t > 0, \\ v(t)u_1(t,0) - D(t)\frac{\partial u_1}{\partial x}(t,0) = 0,\ u_1(t,L) = 0, \\ u_i(0,x) = \phi_i(x),\ x \in (0,L),\ i = 1,2. \end{cases} \tag{3.21}$$

Due to the non-compactness of solution maps, we need to impose the following additional condition:

(H3) $-\mu(t) + f(t,0) < 0, \quad \forall t \in [0,\omega]$.

Since $f(t,u) \leq f(t,0)$, $\forall u \geq 0$, (H3) implies that at time t, the leaving rate of the benthic population into the drift is higher than its growth rate.

Let $X = \{\phi \in C([0,L],\mathbb{R}^2) : \phi(L) = 0\}$ with the maximum norm $\|\cdot\|_X$ and $Y = \{\phi \in C^1([0,L],\mathbb{R}^2) : \phi(L) = 0\}$ with the usual norm in C^1. Then X and Y are ordered Banach spaces with positive cones X_+ and Y_+ consisting of all nonnegative functions in X and Y, respectively, and Y_+ has nonempty interior $\mathrm{Int}(\mathrm{Y}_+)$. Similarly, we define ordered Banach spaces X_1 and Y_1 with $\mathbb{R}^2$ replaced by $\mathbb{R}$ in the definition of X and Y, and $\mathrm{Int}(\mathrm{Y}_{1+}) \neq \emptyset$.

We can rewrite system (3.21) as an integral equation with $u(0,\cdot,\phi) = \phi \in X_+$, in view of last section's discussion, it is easy to see that system (3.21) has a unique solution $u(t,\cdot,\phi) \in X_+$ on $[0, t_\phi)$ with $u(0,\cdot,\phi) = \phi \in X_+$, and the comparison principle holds for (3.21). Since $(0,0)$ is the solution of (3.21) and $V(t,a)$ is the upper solution of (3.21) (also a solution of (3.2)), where $0 \le a = \|\phi\|_X < \infty$. Using the comparison principle, we can prove the positivity and L^∞-boundedness of $u(t,\cdot,\phi)$. Thus, system (3.21) has a unique solution $u(t,\cdot,\phi) \in X_+$ on $[0,\infty)$ with $u(0,\cdot,\phi) = \phi \in X_+$.

Define a family of maps $\{Q_t\}_{t\ge 0}$ from X_+ to X_+ by $Q_t(\phi) = u(t,\cdot,\phi)$, $\forall \phi \in X_+$, $t \ge 0$. Then $\{Q_t\}_{t\ge 0}$ is a monotone ω-periodic semiflow from X_+ to X_+.

Linearizing system (3.21) at its trivial periodic solution $(0,0)$, we have the following linear reaction-advection-diffusion system:

$$\begin{cases} \frac{\partial u_1}{\partial t} = -\sigma(t)u_1 + \mu(t)u_2 - v(t)\frac{\partial u_1}{\partial x} + D(t)\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} = \sigma(t)u_1 - \mu(t)u_2 + f(t,0)u_2, \quad x \in (0,L),\ t > 0, \\ v(t)u_1(t,0) - D(t)\frac{\partial u_1}{\partial x}(t,0) = 0,\ u_1(t,L) = 0, \\ u_i(0,x) = \phi_i(x),\ x \in (0,L),\ i = 1,2. \end{cases} \tag{3.22}$$

It follows that for any $\phi \in X(Y)$, system (3.22) has a unique solution $\tilde{u}(t,x,\varphi) \in X(Y)$ with $\tilde{u}(0,\cdot,\varphi) = \varphi$ and admits the comparison principle. Let P_1 be the Poincaré map associated with system (3.22). Then P_1 is a strongly positive and bounded linear operator from Y to Y. Let $r_1 = r(P_1)$ be the spectral radius of P_1. By substituting $u_1(t,x) = e^{-\lambda t}\varphi_1(t,x)$ and $u_2(t,x) = e^{-\lambda t}\varphi_2(t,x)$ into (3.22), we obtain the associated periodic eigenvalue problem:

$$\begin{cases} \frac{\partial \varphi_1}{\partial t} = -\sigma(t)\varphi_1 + \mu(t)\varphi_2 - v(t)\frac{\partial \varphi_1}{\partial x} + D(t)\frac{\partial^2 \varphi_1}{\partial x^2} + \lambda\varphi_1, \\ \frac{\partial \varphi_2}{\partial t} = \sigma(t)\varphi_1 - \mu(t)\varphi_2 + f(t,0)\varphi_2 + \lambda\varphi_2, \quad x \in (0,L),\ t > 0, \\ v(t)\varphi_1(t,0) - D(t)\frac{\varphi_1}{\partial x}(t,0) = 0,\ \varphi_1(t,L) = 0, \\ \varphi_1, \varphi_2 \text{ are } \omega\text{−periodic in } t, \end{cases} \tag{3.23}$$

Then we have the following result.

Lemma 3.2.1. *Let (H1)–(H3) hold. If $r_1 \geq 1$, then the eigenvalue problem (3.23) has a principal eigenvalue $\lambda^* = -\frac{1}{\omega}\ln r_1$ with a positive eigenfunction.*

Proof. Let $\Pi_t(\phi) = \tilde{u}(t, \cdot, \phi)$, $\phi \in Y$, $t \geq 0$. In view of (H3), there exists a positive number r_0 such that $\mu(t) - f(t, 0) \geq r_0$ for all $t \geq 0$. Let α be the Kuratowski measure of noncompactness in Y(see, e.g., [14]). By similar arguments to those in [36, Lemma 3.3], we can show that Π_t is an α-contraction on Y with a contracting function $e^{-r_0 t}$. In particular, we have $\alpha(P_1 B) \leq e^{-r_0\omega}\alpha(B)$ for any bounded set B in Y with $\alpha(B) > 0$. This implies that the essential spectral radius $r_e(P_1)$ of P_1 satisfies

$$r_e(P_1) \leq e^{-r_0\omega} < 1$$

Since $r_1 \geq 1$, we have $r_1 = r(P_1) > r_e(P_1)$. Note that P_1 is a strongly positive and bounded operator on Y. By the generalized Krein-Rutman Theorem (see, e.g., [71] and [37, Lemma 4.4]), there is an eigenfunction $\varphi^* = (\varphi_1^*, \varphi_2^*) \in \mathrm{Int}(\mathrm{Y}_+)$ corresponding to r_1, that is, $P_1(\varphi^*) = r_1\varphi^*$.

Let $\tilde{u}(t, \cdot, \varphi^*)$ be the solution of system (3.22) through φ^*, and denote $v(t, x) = e^{\lambda^* t}\tilde{u}(t, x, \varphi^*)$. Then $v(t, x)$ is positive for all $(t, x) \in [0, \infty) \times [0, L)$ and $\frac{\partial v_1(t,L)}{\partial x} < 0, \forall t \geq 0$. Since

$$\begin{aligned} &v(\omega, \cdot) = e^{\lambda^*\omega} P_1(\varphi^*) = e^{\lambda^*\omega} r_1 \varphi^* = v(0, \cdot), \\ &\frac{\partial v_2(t, L)}{\partial x} = T_2(t, 0)\varphi_2^{*'}(L) + \int_0^t T_2(t, s)\sigma(s)\frac{\partial v_1(s, L)}{\partial x} ds < 0, \quad t \geq 0, \end{aligned}$$

where $T_2(t, s)$ is defined as in (3.5). It then follows that $v(t, x)$ is the positive eigenfunction corresponding to the principle eigenvalue λ^* for problem (3.23). $\square$

We also consider the following perturbed system of (3.22):

$$\begin{cases} \frac{\partial u_1^\varepsilon}{\partial t} = -\sigma(t)u_1^\varepsilon + \mu(t)u_2^\varepsilon - v(t)\frac{\partial u_1^\varepsilon}{\partial x} + D(t)\frac{\partial^2 u_1^\varepsilon}{\partial x^2}, \\ \frac{\partial u_2^\varepsilon}{\partial t} = \sigma(t)u_1^\varepsilon - \mu(t)u_2^\varepsilon + f(t,\varepsilon)u_2^\varepsilon, \quad x \in (0,L),\ t > 0, \\ v(t)u_1^\varepsilon(t,0) - D(t)\frac{\partial u_1^\varepsilon}{\partial x}(t,0) = 0,\ u_1^\varepsilon(t,L) = 0, \\ u_i^\varepsilon(0,x) = \phi_i(x),\ i = 1,2, \end{cases} \tag{3.24}$$

and the associated eigenvalue problem:

$$\begin{cases} \frac{\partial \varphi_1}{\partial t} = -\sigma(t)\varphi_1 + \mu(t)\varphi_2 - v(t)\frac{\partial \varphi_1}{\partial x} + D(t)\frac{\partial^2 \varphi_1}{\partial x^2} + \lambda\varphi_1, \\ \frac{\partial \varphi_2}{\partial t} = \sigma(t)\varphi_1 - \mu(t)\varphi_2 + f(t,\varepsilon)\varphi_2 + \lambda\varphi_2, \quad x \in (0,L),\ t > 0, \\ v(t)\varphi_1^\varepsilon(t,0) - D(t)\frac{\partial \varphi_1^\varepsilon}{\partial x}(t,0) = 0,\ \varphi_1^\varepsilon(t,L) = 0, \\ \varphi_1, \varphi_2 \text{ are } \omega\text{-periodic in } t. \end{cases} \tag{3.25}$$

Let $u^\varepsilon(t,x,\varphi)$ be the solution of system (3.24) with $u^\varepsilon(0,x,\varphi) = \varphi(x)$, P_ε be the Poincaré map associated with system (3.24), and r_ε be the spectral radius of P_ε. By similar arguments to those [37, Lemma 4.5], we have the following result.

Lemma 3.2.2. *Let (H1)–(H3) hold. If $r_1 > 1$, then there exists a small $\varepsilon_0 > 0$ such that the eigenvalue problem (3.25) has a negative principal eigenvalue denoted by $\lambda_\varepsilon^* = -\frac{1}{\omega}\ln r_\varepsilon$, with a positive eigenfunction for all $\varepsilon \in [0,\varepsilon_0)$.*

Let $e \in \mathrm{Int}(Y_+)$. For any given $\phi \in X$, we define $\|\phi\|_e := \inf\{\rho \geq 0 : -\rho e(x) \leq \phi(x) \leq \rho e(x), \forall x \in [0,L]\}$. Let $E := \{x \in X : \|x\|_e < \infty\}$ and $E_+ = E \cap X_+$. It then follows that (E, E_+) is an ordered Banach space with $\mathrm{Int}(E_+) \neq \emptyset$, and E is independent of the choice of e. Similarly, we can define the ordered Banach space (E_1, E_{1+}) with $e \in \mathrm{Int}(Y_{1+})$. Note that we have $Y_1 \subset E_1$ with the continuous inclusion. It then follows that there exists $K > 0$ such that $\|a\|_{E_1} \leq K\|a\|_{Y_1}$ for any $a \in Y_1$. Now we are in a position to prove the main result of this section.

Theorem 3.2.1. *Let (H1)–(H3) hold. For any $\varphi \in X_+$, let $u(t, x, \varphi)$ be the solution of system* (3.21) *with $u(0, x, \varphi) = \varphi \in X_+$. Then the following statements are valid:*

(i) If $r_1 < 1$, then $\lim_{t\to\infty} \|u(t, \cdot, \varphi)\|_X = 0$ for any $\varphi \in X_+$.

(ii) If $r_1 > 1$, then either of the following statements holds true:

(a) There exists $\delta_0 > 0$ such that $\limsup_{n\to\infty} \|Q_{n\omega}(\varphi)\|_X \geq \delta_0$ for all $\varphi \in X_+\setminus\{0\}$.

(b) System (3.21) *has a unique positive ω-periodic solution $u^*(t, \cdot) \in \mathrm{Int}(\mathrm{E}_+)$ such that $\lim_{t\to\infty} \|u(t, \cdot, \varphi) - u^*(t, \cdot)\|_X = 0$ for any $\varphi \in E_+\setminus\{0\}$.*

Proof. In the case where $r_1 < 1$, we have $\lim_{n\to\infty} \|P_1^n\| = 0$, which implies that $\lim_{n\to\infty} \|P_1^n \varphi\|_X = 0$ for any $\varphi \in X_+$. It follows that $\lim_{t\to\infty} \|\hat{u}(t, \cdot, \varphi)\|_X = 0$. Thus, we have $\lim_{t\to\infty} \|u(t, \cdot, \varphi)\|_X = 0$ due to the comparison principle.

In the case where $r_1 > 1$, let $S = Q_\omega$. We then show that for any given $\varphi \in X_+\setminus\{0\}$, the forward orbit $\gamma^+(\varphi) := \{S^n(\varphi) : n \geq 0\}$ is asymptotically compact in the sense that for any sequence $n_k \to \infty$, there exist a subsequence n_{k_j} such that $S^{n_{k_j}}(\varphi)$ converges in X_+ as $j \to \infty$. Note that $Q_t(\varphi) = (u_1(t, x, \varphi), u_2(t, x, \varphi))$ is L^∞-bounded. Let $S_1(\varphi) = (u_1(\omega, x, \varphi), 0)$ and $S_2(\varphi) = (0, u_2(\omega, x, \varphi))$. Clearly, S_1 is compact on X. By assumptions (H2) and (H3), we have

$$\frac{\partial}{\partial u_2} [\sigma(t)u_1 - \mu(t)u_2 + f(t, u_2)u_2] \leq -\mu(t) + f(t, 0) < 0, \quad \forall (t, u) \in \mathbb{R}_+^3.$$

It then follows from the arguments in [36, Lemma 4.1] that $S_2^n(\varphi)$ is asymptotically compact for any $\varphi \in X_+$. Thus, for any sequence $n_k \to \infty$, there exists subsequence labeled as $n_k \to \infty$ such that $S_2^{n_k}(\varphi)$ converges in X_+. Further, there exists a subsequence n_{k_j} such that $S_1^{n_{k_j}}(\varphi)$ converges in X_+. Therefore, $S^{n_{k_j}}(\varphi)$ converges in X_+ as $j \to \infty$.

Let $\omega(\varphi)$ be the omega limit set of $\gamma^+(\varphi)$. It then follows that $\omega(\varphi)$ is nonempty, compact and invariant for Q_ω in X.

Now we prove statement (ii)(a). By virtue of Lemma 3.2.2, we fix an $\varepsilon \in [0, \varepsilon_0)$. Then there exists some $\delta > 0$ such that $\|u^\varepsilon(t, \cdot, \varphi)\|_X < \varepsilon$ for all $t \in [0, \omega]$ whenever $\|\varphi\|_X < \delta$. Let $\delta_0 = \delta$. Suppose, by contradiction, that $\lim_{n\to\infty} \sup \|Q_{n\omega}(\varphi_0)\|_X < \delta_0$ for some $\varphi_0 \in X_+\backslash\{0\}$. Then there exists $n_0 \geq 1$ such that

$$\|Q_{n\omega}(\varphi_0)\|_X < \delta, \quad \forall n \geq n_0.$$

For any $t \geq n_0\omega$, we can rewrite $t = n\omega + t'$ with $n \geq n_0$ and $t' \in [0, \omega)$. Thus, we have

$$\|Q_t(\varphi_0)\|_X = \|Q_{t'}(Q_{n\omega}(\varphi_0))\|_X < \varepsilon, \ \forall t \geq n_0\omega,$$

and hence, the solution $u(t, x, \varphi_0)$ of (3.21) satisfies the following system:

$$\begin{cases} \frac{\partial u_1}{\partial t} \geq -\sigma(t)u_1 + \mu(t)u_2 - v(t)\frac{\partial u_1}{\partial x} + D(t)\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} \geq \sigma(t)u_1 - \mu(t)u_2 + f(t, \varepsilon)u_2, \quad x \in (0, L), \end{cases} \tag{3.26}$$

for all $t \geq n_0\omega$. Let $\varphi_\varepsilon^*(t, \cdot) \in \mathrm{Int}(\mathrm{Y}_+)$ be the positive eigenfunction corresponding to the principal eigenvalue λ_ε^* of system (3.25). Then it is easy to see that $u^\varepsilon(t, x) = e^{-\lambda_\varepsilon^* t}\varphi_\varepsilon^*(t, x)$ is the solution for system (3.24). Note that $u_2(t, \cdot, \phi_0)$ is uniformly bounded on $t \in [0, \infty)$, there exist A and L such that $0 \leq u_2(t, \cdot, \phi_0) \leq A$ and $f(t, u) - f(t, 0) + Lu \geq 0$ for all $t \geq 0$ and $u \in [0, A]$. Define

$$\hat{u}_2(t, \cdot, \phi_0) = \int_{\frac{t}{2}}^{t} e^{-L(t-s)}T_2(t, s)\sigma(s)u_1(s, \cdot, \phi_0)ds.$$

Since $U_0(t, \cdot) = (u_1(t, \cdot, \phi_0), \hat{u}_2(t, \cdot, \phi_0)) \in \mathrm{Int}(\mathrm{Y}_+)$ and $U_0(t, \cdot) \leq u(t, \cdot, \phi_0)$ for $t > 0$. Then there exists a sufficiently small number $a > 0$ such that

$$u(n_0\omega, x, \varphi_0) \geq U_0(n_0\omega, x) \geq a\varphi_\varepsilon^*(n_0\omega, x), \quad \forall x \in [0, L].$$

By the comparison principle, it follows that

$$u(t,x,\varphi_0) \geq a\varphi_\varepsilon^*(n_0\omega,x)e^{-\lambda_\varepsilon^*(t-n_0\omega)},\ \forall t \geq n_0\omega,\ x \in [0,L].$$

Since $\lambda_\varepsilon^* < 0$, we see that $u(t,x,\varphi_0)$ is unbounded, a contradiction. This proves statement (ii)(a).

For (ii)(b), it is easy to see that for any $\phi \in E_+$, system (3.21) admits a unique solution $u(t,\cdot,\phi) \in E_+$ with $u(0,\cdot,\phi) = \phi$ and $S = Q_\omega$ is strongly monotone and strictly subhomogeneous in E_+. For any $\varphi \in E_+ \setminus \{0\} \subset X_+ \setminus \{0\}$, its omega set limit is non-empty, invariant and compact in X. In order to prove statement (ii)(b), we justify the following two claims.

Claim 1. For $\varphi \in X_+ \setminus \{0\}$ and $\phi^* \in \omega(\varphi)$, we have $\phi^* \in E_+ \setminus \{0\}$.

Since $\phi^* \in \omega(\varphi)$, there exists a sequence $\{n_k\}$ such that $u(n_k\omega,\cdot,\varphi) \to \phi^* = (\phi_1^*,\phi_2^*)$ as $k \to \infty$. For the sake of convenience, we choose $e = (e_1,e_1) \in \mathrm{Int}(\mathrm{Y}_+)$ with $e_1 \in \mathrm{Int}(\mathrm{Y}_{1+})$. Since $u(t,\cdot,\varphi)$ is uniformly bounded in X. There exists $M > 0$ such that $u_2(t,\cdot,\varphi) \leq M$. Now let $v(t,\cdot,m)$ be the solution of the following system

$$\begin{cases} \frac{\partial v}{\partial t} = -\sigma(t)v + \mu(t)M - v(t)\frac{\partial v}{\partial x} + D(t)\frac{\partial^2 v}{\partial x^2}, \\ v(t)v(t,0) - D(t)\frac{\partial v}{\partial x}(t,0) = 0,\ v(t,L) = 0, \\ v(0,\cdot) = m \in Y_{1+}. \end{cases}$$

Then by standard parabolic estimates, we see that there exists $C > 0$ such that $\|v(t,\cdot,m)\|_{Y_1} \leq C$ for all $t \geq 0$, and hence, $\|v(t,\cdot,m)\|_{E_1} \leq KC$, this implies there exists $M_0 > 0$ such that $v(t,\cdot,m) \leq M_0 e$ for all $t \geq 0$. Now take $m = u_1(\omega,\cdot,\varphi_1) \in Y_{1+}$. It follows that

$$0 \leq u_1(t,\cdot,\varphi) \leq v(t,\cdot,m) \leq M_0 e_1, \quad t \geq \omega,$$

and $\phi_1^* \in E_{1+}$.

$$u_2(n_k\omega,\cdot,\varphi) = T_2(n_k\omega,\omega)u_2(\omega,\cdot,\varphi_2) + \int_\omega^{n_k\omega} T_2(n_k\omega,s)(F(s,u_2)+\sigma(s)u_1(s,\cdot,\varphi))ds$$
$$\le T_2(n_k\omega,\omega)u_2(\omega,\cdot,\varphi_2) + \int_\omega^{n_k\omega} T_2(n_k\omega,s)\sigma(s)u_1(s,\cdot,\varphi)ds$$

Letting $k \to \infty$, we obtain that $\phi_2^* \in E_{1+}$, together with (ii)(a), it follows that $\phi^* \in E_+ \setminus \{0\}$.

Claim 2. There exists a unique ω- periodic solution $u^*(t,\cdot) \in \mathrm{Int(E_+)}$ of system (3.21).

Note that $S = Q_\omega$ is strongly monotone and strictly subhomogeneous in E_+. In view of Lemma 3.2.2, we fix $\epsilon \in (0,\epsilon_0)$ and choose a small $\delta > 0$ such that $\delta\phi_\epsilon^* \le \epsilon$. It then follows that $\delta\phi_\epsilon^*$ is a subsolution of system (3.21). Now the comparison principle implies that

$$u(\omega,\cdot,\delta\phi_\epsilon^*(0,\cdot)) \ge \delta\phi_\epsilon^*(\omega,\cdot) = \delta\phi_\epsilon^*(0,\cdot),$$

and hence, $u(n\omega,\cdot,\delta\phi_\epsilon^*)$ is nondecreasing in n. Since the positive orbit $\gamma^+(\delta\phi_\epsilon^*)$ is asymptotically compact in X, the omega limit set is nonempty, invariant and compact. Then we see that there exists $a^* \in X_+$ such that $\lim_{n\to\infty} u(n\omega,\cdot,\delta\phi_\epsilon^*) = a^* \ge \delta\phi_\epsilon^*(0,\cdot)$ in X. In view of Claim 1, we can easily deduce that $a^* \in E_+ \setminus \{0\}$, and hence, the strongly monotonicity of S and $S(a^*) = a^*$ yields that a^* is the unique fixed point of S in $\mathrm{Int(E_+)}$. Set $u^*(t,\cdot) := Q_t(a) \ge \delta\phi_\epsilon^*(t,\cdot)$. Then $u^*(t,\cdot) \in \mathrm{Int(E_+)}$ is the desired periodic solution for $t \in [0,\infty)$.

Now we are ready to state the proof of (ii)(b) by using the monotone iteration method. Recall that S is strongly monotone and subhomogeneous in E_+. Then it suffices to show that $\varphi \in \mathrm{Int(E_+)}$, the statement (ii)(b) holds true. For the sake of convenience, we take $e = a^*$. For any $\varphi \in \mathrm{Int(E_+)}$, there exist $\rho_1 \in (0,1)$ and $\rho_2 > 1$

such that $\rho_1 e \le \varphi \le \rho_2 e$ and

$$\rho_1 e = \rho_1 S(e) \le S(\rho_1 e) \le S(\varphi) \le S(\rho_2 e) \le \rho_2 S(e) = \rho_2 e.$$

It easily follows from Claim 1 and the argument in Claim 2 that

$$\lim_{n\to\infty} S^n(\rho_1 e) = \lim_{n\to\infty} S^n(\rho_2 e) = e \text{ in } X.$$

The squeeze theorem gives $\lim_{n\to\infty} S^n(\varphi) = e$ in X. Thus, we conclude that $u^*(t,\cdot,a^*)$ is an ω-periodic solution of system (3.21), and $\lim_{t\to\infty} \|u(t,\cdot,\varphi) - u^*(t,\cdot)\|_X = 0$ for any $\varphi \in E_+ \setminus \{0\}$. □

3.3 Simulations

In this section, we do some numerical simulations to illustrate our analytic results. We choose $\omega = 12$, $\sigma(t) = 0.7(1 - \sin(\frac{\pi t}{6}))$, $\mu(t) = 0.5(1 + \sin(\frac{\pi t}{6}))$, and consider the periodic logistic growth rate function $f(t,u) = r(1 + b\sin(\frac{\pi t}{6}) - u/K)$, and the advection velocity $v(t) = c_0(1.05 + \cos(\frac{\pi t}{6}))$. Assume that there is positive correlation between diffusivity and flow speed [60]. We choose $D(t) = c_1(1.05 + \cos(\frac{\pi t}{6}))$, where constants $r, b, K, c_1 > 0$, $c_0 \ge 0$.

For illustration, we choose $r = 0.15, b = 0.8, K = 50, c_0 = 1.1, c_1 = 0.5$. For a continuous periodic function $p(t)$ with the period ω, we define its average as

$$[p] := \frac{1}{\omega}\int_0^\omega p(t)dt.$$

Using Proposition 3.1.3, we can numerically compute $c_+^* = 0.7155$ and $c_-^* = -0.0962$. This implies the populations are washed downstream and therefore cannot persist. Figure 3.1 shows a plot of the spreading speed c_+^* and c_-^* as functions of $[v] = 1.05c_0$.

Figure 3.2 indicates that the rightward spreading speed c_+^* and leftward spreading speed c_-^* both increase with the average diffusion value $[D] = 1.05c_1$.

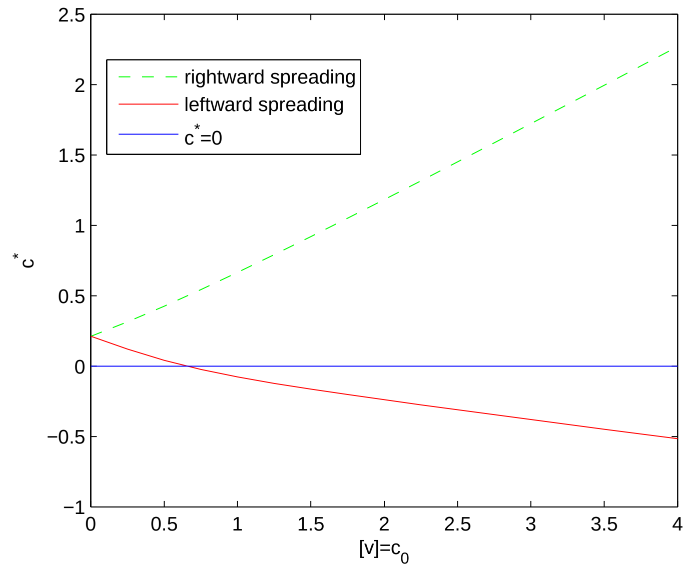

Figure 3.1: *Leftward and rightward spreading speeds as functions of the average advection velocity* $[v]$.

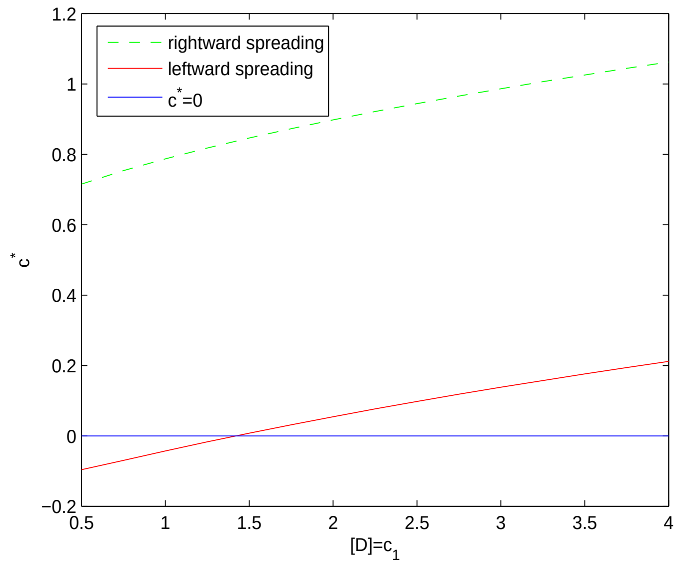

Figure 3.2: *Leftward and rightward spreading speeds as functions of the average diffusion coefficient* $[D]$.

To simulate the spatial spread of the model system, we discretize system (3.1) by the difference method on a finite interval $[-L, L]$ with the Neumann boundary condition, where L is sufficiently large. Figures 3.3 and 3.4 show numerical plots of the solution through the initial condition

$$n_d(0,x) = \begin{cases} 24, & \text{if } |x| \le 20 \\ \frac{4}{5}(50 - |x|), & \text{if } 20 \le |x| \le 50, \\ 0, & \text{if } |x| \ge 50 \end{cases} \quad n_b(0,x) = \frac{4}{3} \times n_d(0,x).$$

The population in the drift n_d and on the benthos n_b spread in one direction towards downstream.

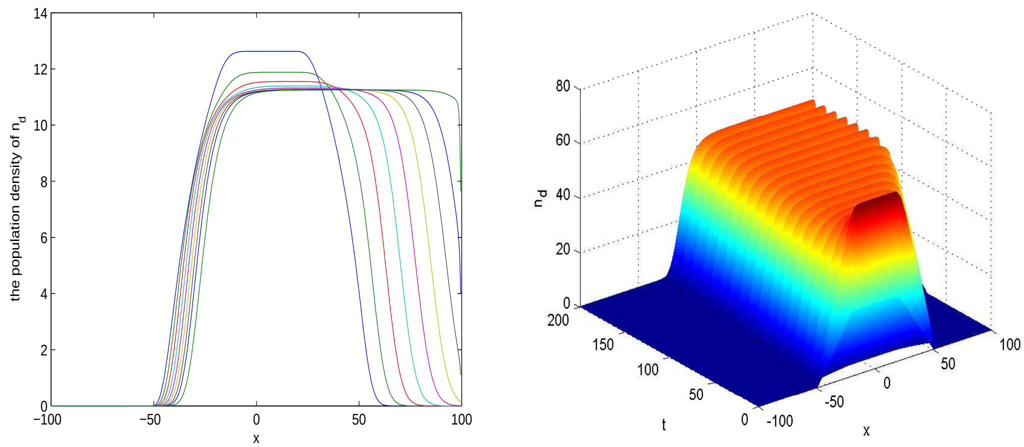

Figure 3.3: *The spread of n_d, and the left plot shows the density of n_d at different times $t = n\omega$, with $n = 1, 2, 3, 4, 5, 6, 7, 8$ and 9, respectively.*

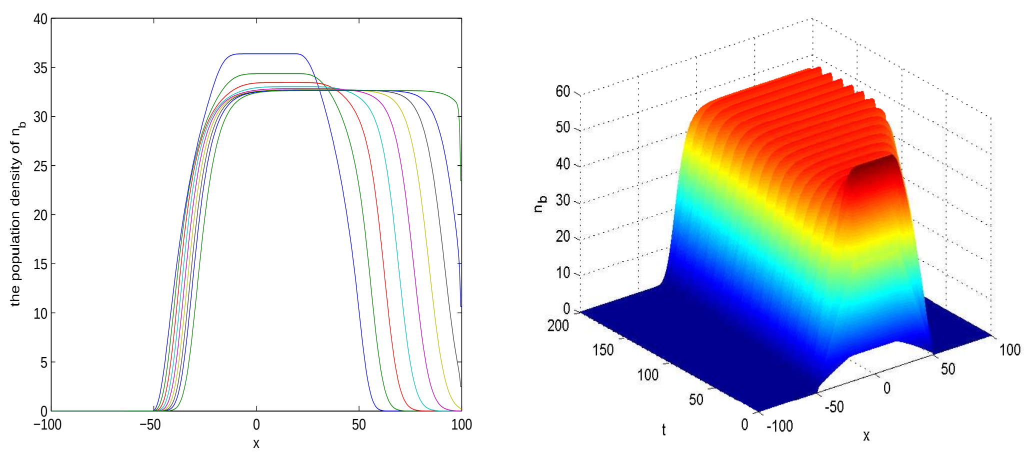

Figure 3.4: *The spread of n_b, and the left plot shows the density of n_b at different times $t = n\omega$, with $n = 1, 2, 3, 4, 5, 6, 7, 8$ and 9, respectively.*

To get rightward traveling waves, we choose the initial condition as

$$n_d(0,x) = \begin{cases} 30, & \text{if } x \le -20 \\ \frac{3}{4}(20-x), & \text{if } |x| \le 20, \\ 0, & \text{if } x \ge 20 \end{cases} \quad n_b(0,x) = \frac{9}{5} \times n_d(0,x).$$

The evolution of the solution is shown in Figure 3.5.

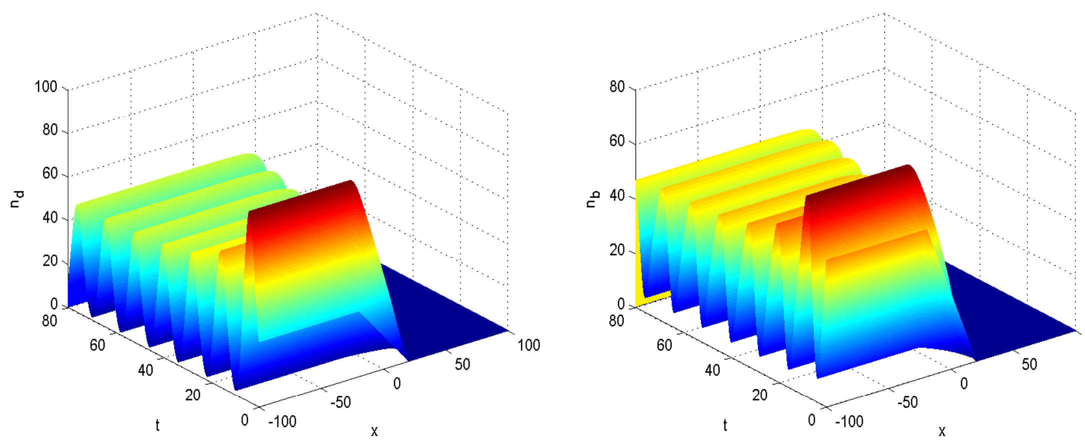

Figure 3.5: *The rightward periodic traveling waves observed for n_d and n_b, respectively.*

To simulate the global dynamics of system (3.1) in a bounded domain, we choose the initial condition as

$$n_d(0,x) = n_b(0,x) = 0.1x^2(L-x),$$

and the zero-flux and hostile boundary conditions as

$$1.1 \times n_d(t,0) - 0.5 \times \frac{\partial n_d}{\partial x}(t,0) = 0, \; n_d(t,L) = n_b(t,0) = n_b(t,L) = 0.$$

The evolution of the solution is shown in Figure 3.6 for $L = 10$ and $[v] = 0.4$. It indicates that in this case two components persist. The evolution of the solution is shown in Figure 3.7 for $L = 10$ and $[v] = 1.1$. It turns out that in this case two components cannot persist due to the large average advection velocity.

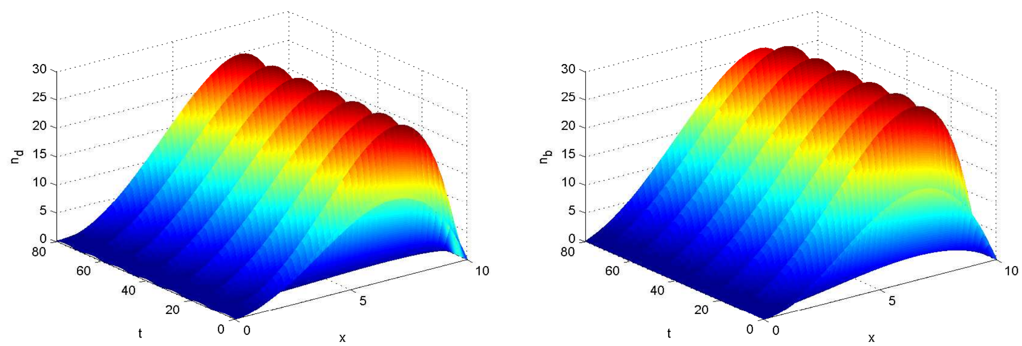

Figure 3.6: *The evolution of two components when $L = 10$ and $[v] = 0.4$.*

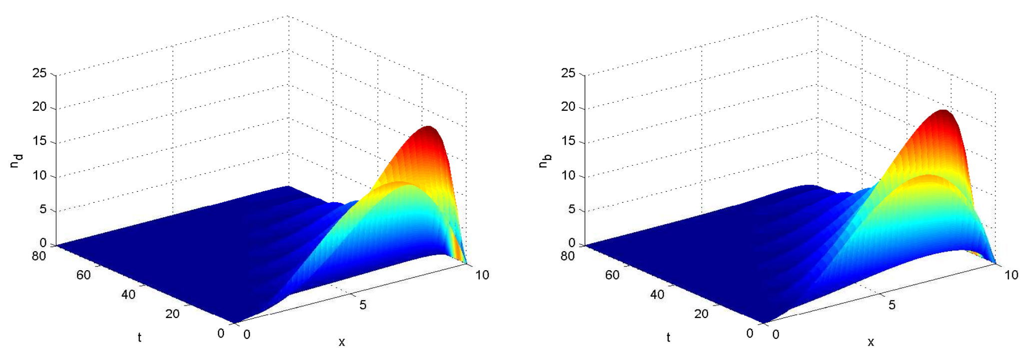

Figure 3.7: *The evolution of two components when $L = 10$ and $[v] = 1.1$.*

Chapter 4

A Two-species Competition Model in A Periodic Habitat

In this chapter, we investigate the following two-species competition model in a periodic habitat:

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= L_1 u_1 + u_1(b_1(x) - a_{11}(x)u_1 - a_{12}(x)u_2), \\ \frac{\partial u_2}{\partial t} &= L_2 u_2 + u_2(b_2(x) - a_{21}(x)u_1 - a_{22}(x)u_2), \quad t > 0,\ x \in \mathbb{R}.\end{aligned} \tag{4.1}$$

We first establish the existence of two semi-trivial periodic steady states $(u_1^*(x), 0)$ and $(0, u_2^*(x))$, and the global stability of $(u_1^*(x), 0)$ for system (4.1) with periodic initial data. Since the steady state $(0, 0)$ is between $(u_1^*(x), 0)$ and $(0, u_2^*(x))$ with respect to the competitive ordering, we cannot directly use the theory developed in [55] for monotone semiflows to study spreading speeds and spatially periodic traveling waves. Recently, Fang and Zhao [19] investigated traveling waves for monotone semiflows with weak compactness in the case where there may be boundary fixed points between two ordered unstable and stable fixed points. Accordingly, in the application of this theory one needs to determine whether the given system admits a single spreading speed and to identify the fixed points connected by traveling waves. Further, the abstract results in [19] (see also section 2.2.2) may not directly apply to the case of a periodic habitat. In the Appendix, we adapt this theory for such a case by combining the abstract results in [55] and [19]. We then prove the existence of the rightward spatially periodic traveling waves of system (4.1) connecting $(u_1^*(x), 0)$ to $(0, u_2^*(x))$, and show that system (4.1) admits a single rightward spreading speed via the method of upper solutions under appropriate assumptions. We also obtain a set of sufficient conditions for the rightward spreading speed to be linearly determinate. Since one more spreading speed is defined differently from the classical one, it is highly nontrivial to prove that those two speeds are identical.

This chapter is organized as follows. In section 4.1, we first obtain the existence of two semi-trivial periodic steady states and the global stability of one semi-trivial periodic steady state for system (4.1) with periodic initial data. In section 4.2, we establish the existence of the minimal wave speed of the rightward spatially periodic traveling waves and its coincidence with the minimal rightward spreading speed. In section 4.3, we show that the rightward spreading speed is linearly determinate under additional conditions. In section 4.4, we apply the obtained results to a prototypical class of reaction-diffusion systems, which were studied in [16, 49] in the case of a bounded domain. In the Appendix, we present the abstract results on traveling waves and spreading speeds for monotone semiflows in a periodic habitat to end this chapter.

4.1 The periodic initial value problem

In this section, we investigate the global dynamics of the spatially periodic Lotka-Volterra competition system with periodic initial values.

Throughout this paper, we assume that $d_i(x)$, $g_i(x)$, $a_{ij}(x)$ and $b_i(x)$ are L-periodic functions, $d_i, g_i, a_{ij}, b_i \in C^\nu(\mathbb{R})$, and $a_{ij}(\cdot) > 0$, $1 \leq i, j \leq 2$, where $C^\nu(\mathbb{R})$ is a Hölder continuous space with the Hölder exponent $\nu \in (0, 1)$; there exists a positive number α_0 such that $d_i(x) \geq \alpha_0, \forall x \in \mathbb{R}, i = 1, 2$, i.e., the operator $L_i u = d_i(x)\frac{\partial^2 u}{\partial x^2} - g_i(x)\frac{\partial u}{\partial x}$ is uniformly elliptic.

Let Y be the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}$, and $Y_+ = \{\psi \in Y : \psi(x) \geq 0, \forall x \in \mathbb{R}\}$ be a positive cone of Y. Equip Y with the maximum norm $\|\cdot\|_Y$, 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 $d, g, h \in C^\nu(\mathbb{R})$ and $d(\cdot) > 0$. It then follows that the scalar periodic eigenvalue problem

$$\begin{aligned} &\lambda\phi = d(x)\phi'' - g(x)\phi' + h(x)\phi, \quad x \in \mathbb{R}, \\ &\phi(x + L) = \phi(x), \quad x \in \mathbb{R} \end{aligned} \tag{4.2}$$

admits a principal eigenvalue $\lambda(d, g, h)$ associated with a positive L-periodic eigenfunction $\phi(x)$(see, e.g., [85, Theorem 7.6.1] and [96, Lemma 3.3]). By Theorem 2.1.3 and similar arguments to those in [96, Theorem 3.2], we have the following result.

Proposition 4.1.1. *Assume that L-periodic functions $d, g, c, e \in C^\nu(\mathbb{R})$, and $d(\cdot) > 0, e(\cdot) \geq 0$ but $\not\equiv 0$. Let $u(t, x, \phi)$ be the unique solution of the following parabolic equation:*

$$\begin{aligned} &\frac{\partial u}{\partial t} = d(x)\frac{\partial^2 u}{\partial x^2} - g(x)\frac{\partial u}{\partial x} + u(c(x) - e(x)u), \quad t > 0, \ x \in \mathbb{R}, \\ &u(0, x) = \phi(x) \in Y_+, \quad x \in \mathbb{R}. \end{aligned} \tag{4.3}$$

Then the following statements are valid:

(i) If $\lambda(d, g, c) \leq 0$, then $u = 0$ is globally asymptotically stable with respect to initial values in Y_+;

(ii) If $\lambda(d, g, c) > 0$, then (4.3) admits a unique positive L-periodic steady state $u^*(x)$, 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 $\|\cdot\|_{\mathbb{P}}$ by

$$\|\phi\|_{\mathbb{P}} = \max_{x\in\mathbb{R}} |\phi(x)|.$$

It then follows that $(\mathbb{P}, \|\cdot\|_{\mathbb{P}})$ is a Banach lattice.

Clearly, for any $\varphi \in \mathbb{P}$, (4.1) has a unique solution $u(t, \cdot, \varphi) \in \mathbb{P}$ defined on $[0, t_\varphi)$ with $t_\varphi \in (0, \infty]$. By the comparison principle for scalar reaction-diffusion equations in a period habitat (see, e.g., [96, Lemma 3.1]), together with the fact that $a_{ij}(x) > 0, \forall x \in \mathbb{R}, 1 \leq i, j \leq 2$, it follows that for any $\varphi \in \mathbb{P}_+$, system (4.1) has a unique nonnegative solution $u(t, \cdot, \varphi)$ defined on $[0, \infty)$, and $u(t, \cdot, \varphi) \in \mathbb{P}_+$ for all $t \geq 0$.

By Proposition 4.1.1, we see that there exists two positive L-periodic functions $u_1^*(x)$ and $u_2^*(x)$ such that $E_1 := (u_1^*(x), 0)$, $E_2 := (0, u_2^*(x))$ are semi-trivial steady states of system (4.1) provided that $\lambda(d_i, g_i, b_i) > 0,\ i = 1, 2$. Since we mainly concern about the case of the competition exclusion, we impose the following conditions on system (4.1):

(H1) $\lambda(d_i, g_i, b_i) > 0,\ i = 1, 2.$

(H2) $\lambda(d_1, g_1, b_1 - a_{12}u_2^*) > 0$.

(H3) System (4.1) has no steady state in $\text{Int}(\mathbb{P}_+)$.

(H1) guarantees the existence of two semi-trivial steady states of system (4.1). (H2) implies that $(0, u_2^*(x))$ is unstable. Moreover, by Lemma 4.4.1 with $\mu = 0, d(x) = d_1(x)$ and $g(x) = g_1(x), \forall x \in \mathbb{R}$, we see that (H2) implies $\lambda(d_1, g_1, b_1) > 0$. Thus, we can simply drop the assumption $\lambda_1(d_1, g_1, b_1) > 0$ from (H1).

Under assumptions (H1)–(H3), there are three steady states in $\mathbb{P}_+$: $E_0 = (0, 0)$, $E_1 := (u_1^*(x), 0)$, and $E_2 := (0, u_2^*(x))$. Next, we use the theory developed in [35] for abstract competitive systems (see also [32]) to prove the global stability of E_1.

Theorem 4.1.1. *Assume that (H1)–(H3) hold. Then $E_1 = (u_1^*(x), 0)$ is globally asymptotically stable for all initial values $\phi = (\phi_1, \phi_2) \in \mathbb{P}_+$ with $\phi_1 \not\equiv 0$.*

Proof. Let $u(t, x, \phi)$ be the solution of system (4.1) with $u(0, x) = \phi(x)$. In view of (H2), we can fix a real number $\varepsilon_0 \in (0, \lambda(d_1, g_1, b_1 - a_{12}u_2^*))$. By the uniform continuity of $F(x, u) := b_1(x) - a_{11}(x)u_1 - a_{12}(x)u_2$ on the set $\mathbb{R} \times [0, 1] \times [0, b]$, where $b = \max\limits_{x \in \mathbb{R}} u_2^*(x) + 1$, there exists $\delta_0 \in (0, 1)$ such that

$$|F(x, u) - F(x, v)| < \varepsilon_0, \quad \forall u = (u_1, u_2), v = (v_1, v_2) \in [0, 1] \times [0, b], \ x \in \mathbb{R}$$

provided that $|u_i - v_i| < \delta_0, i = 1, 2$. Then we have the following observation.

Claim. $\limsup_{t \to \infty} \|u(t, \cdot, \phi) - (0, u_2^*(\cdot))\|_{\mathbb{P}} \geq \delta_0$ for any $\phi \in \mathbb{P}_+$ with $\phi_1 \not\equiv 0$.

Suppose, by contradiction, that $\limsup\limits_{t \to \infty} \|u(t, \cdot, \hat{\phi}) - (0, u_2^*(\cdot))\|_{\mathbb{P}} < \delta_0$ for some $\hat{\phi} \in \mathbb{P}_+$ with $\hat{\phi}_1 \not\equiv 0$. Then there exists $t_0 > 0$ such that

$$\|u_1(t, \cdot, \hat{\phi})\|_Y < \delta_0, \ \|u_2(t, \cdot, \hat{\phi}) - u_2^*(\cdot)\|_Y < \delta_0, \ \forall t \geq t_0.$$

Consequently, we have

$$F(x,u(t,x,\hat{\phi})) > F(x,(0,u_2^*(x))) - \varepsilon_0 = b_1(x) - a_{12}(x)u_2^*(x) - \varepsilon_0, \quad t \geq t_0,\ x \in \mathbb{R}.$$

Let $\psi_1(x)$ be a positive eigenfunction corresponding to the principal eigenvalue $\lambda(d_1, g_1, b_1 - a_{12}u_2^*)$. Then $\psi_1(x)$ satisfies

$$\begin{aligned} &\lambda(d_1,g_1,b_1-a_{12}u_2^*)\psi_1 = d_1(x)\psi_1'' - g_1(x)\psi_1' + (b_1(x)-a_{12}(x)u_2^*(x))\psi_1, \quad x \in \mathbb{R}, \\ &\psi_1(x+L) = \psi_1(x), \quad x \in \mathbb{R}. \end{aligned} \tag{4.4}$$

Since $u_1(0,x) = \hat{\phi}_1 \not\equiv 0$, the comparison principle (see, e.g., [96, Lemma 3.1]), as applied to the first equation in system (4.1), implies that $u_1(t_0,x,\hat{\phi}) > 0,\ \forall x \in \mathbb{R}$. Then there exists small $\eta > 0$ such that $u_1(t_0,\cdot) \geq \eta\psi_1 \gg 0$. Thus, $u_1(t,x,\hat{\phi})$ satisfies

$$\begin{aligned} &\frac{\partial u_1}{\partial t} \geq L_1 u_1 + u_1(b_1(x) - a_{12}(x)u_2^*(x) - \varepsilon_0), \quad t > t_0,\ x \in \mathbb{R}, \\ &u_1(t_0,\cdot) \geq \eta\psi_1. \end{aligned} \tag{4.5}$$

In view of (4.4), it easily follows that $v(t,\cdot) = \eta e^{[\lambda(d_1,g_1,b_1-a_{12}u_2^*)-\varepsilon_0](t-t_0)}\psi_1$ satisfies

$$\begin{aligned} &\frac{\partial v}{\partial t} = L_1 v + v(b_1(x) - a_{12}(x)u_2^*(x) - \varepsilon_0), \quad t > t_0, x \in \mathbb{R}, \\ &u_1(t_0,\cdot) = \eta\psi_1. \end{aligned} \tag{4.6}$$

By (4.5) and (4.6), together with the standard comparison principle, it follows that

$$u_1(t,\cdot,\hat{\phi}) \geq \eta e^{[\lambda(d_1,g_1,b_1-a_{12}u_2^*)-\varepsilon_0](t-t_0)}\psi_1, \quad \forall t \geq t_0.$$

Letting $t \to \infty$, we see that $u_1(t,\cdot,\hat{\phi})$ is unbounded, a contradiction.

By the above claim and (H3), we rule out possibility (a) and (c) in [35, Theorem B]. Since E_2 is repellent in some neighborhood of itself, [35, Theorem B] implies that E_1 is globally asymptotically stable for all initial values $\phi = (\phi_1, \phi_2) \in \mathbb{P}_+$ with $\phi_1 \not\equiv 0$. $\square$

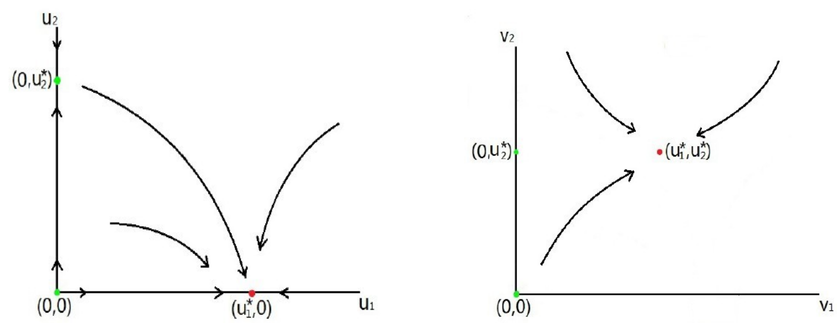

Figure 4.1: *The left and right plots are the competition system and the associated cooperative system, respectively.*

4.2 Spreading speeds and traveling waves

In this section, we study the spreading speeds and spatially periodic traveling waves for system (4.1). By a change of variables $v_1 = u_1, v_2 = u_2^*(x) - u_2$, we transform system (4.1) into the following cooperative system:

$$\begin{aligned} \frac{\partial v_1}{\partial t} &= L_1 v_1 + v_1(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)v_1 + a_{12}(x)v_2), \quad t>0,\ x\in\mathbb{R}, \\ \frac{\partial v_2}{\partial t} &= L_2 v_2 + a_{21}(x)v_1(u_2^*(x) - v_2) + v_2(b_2(x) - 2a_{22}(x)u_2^*(x) + a_{22}(x)v_2). \end{aligned} \tag{4.7}$$

Clearly, three steady states of (4.1), respectively, become

$$\hat{E}_0 = (0, u_2^*(x)),\ \hat{E}_1 = (u_1^*(x), u_2^*(x)),\ \hat{E}_2 = (0,0).$$

Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ and $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geq 0,\ \forall x \in \mathbb{R}\}$. Assume that β is a strongly positive L-periodic continuous function from $\mathbb{R}$ to $\mathbb{R}^2$. Set

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

Let $X = C([0, L], \mathbb{R}^2)$ equipped with the maximum norm $|\cdot|_X$, $X_+ = C([0, L], \mathbb{R}^2_+)$,

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

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.

Let $\beta = (u_1^*(\cdot), u_2^*(\cdot))$, $\mathbb{Y}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$, and $T_1(t)$ and $T_2(t)$ be the linear semigroups on $\mathbb{Y}$ generated by

$$\frac{\partial v}{\partial t} = L_1 v + v(b_1(x) - a_{12}(x)u_2^*(x)) \text{ and } \frac{\partial v}{\partial t} = L_2 v + v(b_2(x) - 2a_{22}(x)u_2^*(x)),$$

respectively. It follows that $T_1(t)$ and $T_2(t)$ are compact with the respect to the compact open topology for each $t > 0$ (see, e.g., [96]). For any $u = (u_1, u_2) \in \mathcal{C}_\beta$, define $F : \mathcal{C}_\beta \to \mathcal{C}$ by

$$F(u) = \begin{pmatrix} -a_{11}(x)u_1^2 + a_{12}(x)u_1u_2 \\ a_{21}(x)u_2^*(x)u_1 - a_{21}(x)u_1u_2 + a_{22}(x)u_2^2 \end{pmatrix}.$$

Then we can rewrite system (4.7) as an integral equation form:

$$\begin{aligned} v(t) &= T(t)v(0) + \int_0^t T(t-s)F(v(s))ds, \quad t > 0, \\ v(0) &= \phi \in \mathcal{C}_\beta, \end{aligned} \tag{4.8}$$

where $T(t) = diag(T_1(t), T_2(t))$.

As usual, a solution of (4.8) is called a mild solution of system (4.7). It then follows that for any $\phi \in \mathcal{C}_\beta$, system (4.7) has a mild solution $u(t, \cdot, \phi)$ defined on $[0, \infty)$ with $u(0, \cdot, \phi) = \phi$, and $u(t, \cdot, \phi) \in \mathcal{C}_\beta$ for all $t \geq 0$, and it is a classical solution when $t > 0$.

We say that $V(x - ct, x)$ is an L-periodic rightward traveling wave of system (4.7) if $V(\cdot + a, \cdot) \in \mathcal{C}_\beta$, $\forall a \in \mathbb{R}$, $u(t, x, V(\cdot, \cdot)) = V(x - ct, x)$, $\forall t \geq 0$, 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 $x \in \mathbb{R}$.

Definition 4.2.1. *A function $u(x, t)$ is said to be an upper (a lower) solution of system* (4.7) *if it satisfies*

$$u(t) \geq (\leq) T(t)u(0) + \int_0^t T(t - s)F(u(s))ds, \quad t \geq 0.$$

Define a family of operators $\{Q_t\}_{t \geq 0}$ on $\mathcal{C}_\beta$ by $Q_t(\phi) := u(t, \cdot, \phi)$, where $u(t, \cdot, \phi)$ is the solution of system (4.7) with $u(0, \cdot) = \phi \in \mathcal{C}_\beta$. It then easily follows that $\{Q_t\}_{t \geq 0}$ is a monotone semiflow on $\mathcal{C}_\beta$. Note that if $u(t, x, \phi)$ is a solution of (4.7), so is $u(t, x - a, \phi)$, $\forall a \in L\mathbb{Z}$. This implies that (D1) in the Appendix holds. By Theorem 4.1.1, we see that for each $t > 0$, (D5) holds for Q_t. Since $T(t)$ is compact with the compact open topology for each $t > 0$, (D2) and (D3) then follow from the same argument as in [63, Theorem 8.5.2]. Thus, we have the following observation.

Proposition 4.2.1. *Assume that (H1)–(H3) hold. Then for each $t > 0$, Q_t satisfies assumptions (D1)–(D5) in the Appendix.*

With the help of $\{Q_t\}_{t \geq 0}$, we can introduce a family of operators $\{\hat{Q}_t\}_{t \geq 0}$ on $\mathcal{X}_\beta$:

$$\hat{Q}_t[v](s)(\theta) := Q_t[v_s](\theta), \quad \forall v \in \mathcal{X}_\beta,\ s \in \mathbb{R},\ \theta \in [0, L],\ t \geq 0, \tag{4.9}$$

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

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

By Proposition 4.5.1, it is easy to see that $\{\hat{Q}_t\}_{t\geq 0}$ is a monotone semiflow on $\mathcal{X}_\beta$ and $\hat{Q}_t$ satisfies (A1)–(A5) with (A3) and (A5) replaced by (C3) and (C5) for each $t > 0$. Now we follow the procedure in the Appendix with $m = 2$. Let c_+^* and $\overline{c}_+$ be defined as in (4.49) with $\tilde{P} = \hat{Q}_1$. To show that $\overline{c}_+$ is the minimal wave speed for L-periodic rightward traveling waves of system (4.7) 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 of (4.10) and (4.12), respectively.

We remark that in the case where *either* $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ with $d_i \in C^{1+\nu}(\mathbb{R})$, *or* all the coefficient functions in (4.10) and (4.12) are even except g_i is odd, $i = 1, 2$, Lemma 4.4.2 shows that (H1) and (H2) guarantee (H4).

Theorem 4.2.1. *Assume that (H1)–(H4) hold. Then for any $c \geq \overline{c}_+$, system* (4.7) *admits an L-periodic traveling wave $(U(x-ct, x), V(x-ct, x))$ 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. In view of Theorem 4.5.2 (2) and (3), it suffices to rule out the second case in Theorem 4.5.2 (2). Suppose, by contradiction, that the statement in Theorem 4.5.2 (2)(ii) is valid for some $c \geq \overline{c}_+$. Since system (4.7) has exactly three L-periodic nonnegative steady states and $\hat{E}_0 = (0, u_2^*(x))$ is the only intermediate L-periodic steady state between $\hat{E}_1 = \beta$ and $\hat{E}_2 = 0$, it then follows that $\alpha_1 = \alpha_2 = \hat{E}_0$. Thus, by restricting system (4.7) on the order interval $[\hat{E}_0, \hat{E}_1]$ and $[\hat{E}_2, \hat{E}_0]$, respectively, we see that one scalar equation

$$u_t = L_1 u + u(b_1(x) - a_{11}(x)u) \tag{4.10}$$

admits an L-periodic traveling wave $U(x-ct,x)$ connecting $u_1^*(x)$ to 0 with $U(\xi,x)$ being continuous and nonincreasing in ξ, and the other scalar equation

$$v_t = L_2 v + v(b_2(x) - 2a_{22}(x)u_2^* + a_{22}(x)v) \tag{4.11}$$

also admits an L-periodic traveling wave $V(x-ct,x)$ connecting $u_2^*(x)$ to 0 with $V(\xi,x)$ being continuous and nonincreasing in ξ.

Let $W(x-ct,x) = u_2^*(x) - V(x-ct,x)$. Then $W(x-ct,x)$ is an L-periodic traveling wave connecting 0 to $u_2^*(x)$ of the following scalar equation with $W(\xi,x)$ being continuous and nondecreasing in ξ

$$w_t = L_2 w + w(b_2(x) - a_{22}(x)w). \tag{4.12}$$

Note that $W(x-ct,x)$ is an L-periodic leftward traveling wave connecting 0 to u_2^* with wave speed $-c$, and that systems (4.10) and (4.12) 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., [55, Theorem 5.3]). It then follows that $c \geq c_{1+}^*$ and $-c \geq c_{2-}^*$. This implies that $c_{1+}^* + c_{2-}^* \leq 0$, a contradiction. □

Let $\lambda_2(\mu)$ be the principle eigenvalue of the elliptic eigenvalue problem:

$$\lambda\psi = d_2(x)\psi'' - (2\mu d_2(x) + g_2(x))\psi' + \left(d_2(x)\mu^2 + g_2(x)\mu + b_2(x) - a_{22}(x)u_2^*(x)\right)\psi, \quad x \in \mathbb{R},$$
$$\psi(x+L) = \psi(x), \quad x \in \mathbb{R}. \tag{4.13}$$

In order to prove that system (4.7) admits a single rightward spreading speed, we impose the following assumption:

(H5) $\limsup_{\mu\to 0^+} \frac{\lambda_2(\mu)}{\mu} \leq c^*_{1+}$, where c^*_{1+} is the rightward spreading speed of (4.10).

By virtue of Lemma 4.4.2, it follows that in the case where *either* $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ with $d_i \in C^{1+\nu}(\mathbb{R})$, *or* all the coefficient functions of system (4.7) are even except g_i is odd, $i = 1, 2$, (H5) is automatically satisfied provided that (H1) and (H2) hold true.

Theorem 4.2.2. *Assume that (H1)–(H5) hold. Then the following statements are valid for system* (4.7)*:*

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

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi(x) \geq \sigma$, $\forall x \leq K$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim_{t\to\infty, x\leq ct}(u(t,x,\phi) - \beta(x)) = 0$ for any $c < \bar{c}_+$.

Proof. In view of Theorem 4.5.1, it suffices to show that $\bar{c}_+ = c^*_+$. If this is not valid, then the definition of $\bar{c}_+$ and c^*_+ implies that $\bar{c}_+ > c^*_+$. By Theorem 4.5.2 (1) and (3), it follows that system (4.7) admits an L-periodic traveling wave $(U_1(x - c^*_+ t, x), U_2(x - c^*_+ t, x))$ connecting $(u^*_1(x), u^*_2(x))$ to $(0, u^*_2(x))$ with $U_i(\xi, x) (i = 1, 2)$ being continuous and nonincreasing in ξ. Therefore, $U_2 \equiv u^*_2(x)$, and $U_1(x - c^*_+ t, x)$ is an L-periodic traveling wave connecting $u^*_1(x)$ to 0. This implies $c^*_+ \geq c^*_{1+}$ where c^*_{1+} is the rightward spreading of (4.10). By [5, Theorem 1.1], it follows that $c^*_{1+} = \inf_{\mu>0} \frac{\lambda_1(\mu)}{\mu}$, where $\lambda_1(\mu)$ is the principal eigenvalue of the scalar elliptic eigenvalue problem:

$$\lambda\psi = d_1(x)\psi'' - (2\mu d_1(x) + g_1(x))\psi' + (d_1(x)\mu^2 + g_1(x)\mu + b_1(x))\psi, \quad x \in \mathbb{R},$$
$$\psi(x + L) = \psi(x), \quad x \in \mathbb{R}. \tag{4.14}$$

For any given $c_1 \in (c^*_+, \bar{c}_+)$, there exists $\mu_1 > 0$ such that $c_1 = \frac{\lambda_1(\mu_1)}{\mu_1}$. Let $\phi^*_1(x)$ be the positive L-periodic eigenfunction associated with the principal eigenvalue $\lambda_1(\mu_1)$

of (4.14). Then it easily follows that

$$u_1(t,x) := e^{-\mu_1(x-c_1t)}\phi_1^*(x) = e^{-\mu_1 x}e^{\lambda_1(\mu_1)t}\phi_1^*(x), \quad t \geq 0,\ x \in \mathbb{R},$$

is a solution of the linear equation

$$\frac{\partial u_1}{\partial t} = L_1 u_1 + b_1(x)u_1.$$

Since $c_{1+}^* < c_1$ and (H5) holds, we can choose a small number $\mu_2 \in (0,\mu_1)$ such that $c_2 := \frac{\lambda_2(\mu_2)}{\mu_2} < c_1$. Let $\phi_2^*(x)$ be the positive L-periodic eigenfunction associated with the principal eigenvalue $\lambda_2(\mu_2)$ of (4.13). It is easy to see that

$$u_2(t,x) := e^{-\mu_2(x-c_2t)}\phi_2^*(x) = e^{-\mu_2 x}e^{\lambda_2(\mu_2)t}\phi_2^*(x)$$

is a solution of the linear equation

$$\frac{\partial u_2}{\partial t} = L_2 u_2 + (b_2(x) - a_{22}(x)u_2^*(x))u_2. \tag{4.15}$$

Since $c_1 > c_2$, it follows that the function

$$v_2(t,x) := e^{-\mu_2(x-c_1t)}\phi_2^*(x) = e^{\mu_2(c_1-c_2)t}u_2(t,x), \quad t \geq 0,\ x \in \mathbb{R},$$

satisfies

$$\frac{\partial v_2}{\partial t} \geq L_2 v_2 + (b_2(x) - a_{22}(x)u_2^*(x))v_2. \tag{4.16}$$

Define two wave-like functions:

$$\overline{u}_1(t,x) := \min\{m_0 e^{-\mu_1(x-c_1t)}\phi_1^*(x), u_1^*(x)\}, \quad t \geq 0,\ x \in \mathbb{R}, \tag{4.17}$$

and

$$\overline{u}_2(t,x) := \min\{q_0 e^{-\mu_2(x-c_1t)}\phi_2^*(x), u_2^*(x)\}, \quad t \geq 0,\ x \in \mathbb{R}, \tag{4.18}$$

where

$$q_0 := \max_{x\in[0,L]} \frac{u_2^*(x)}{\phi_2^*(x)} > 0, \quad m_0 := \min_{x\in[0,L]} \frac{q_0 a_{22}(x)\phi_2^*(x)}{a_{21}(x)\phi_1^*(x)} > 0.$$

Now, we are ready to verify that $(\overline{u}_1, \overline{u}_2)$ is an upper solution to system (4.7). Indeed, for all $x - c_1 t > \frac{1}{\mu_1} \ln \frac{m_0\phi_1^*(x)}{u_1^*(x)}$, we have $\overline{u}_1(t,x) = m_0 e^{-\mu_1(x-c_1t)}\phi_1^*(x)$, and hence,

$$\begin{aligned}&\frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)\overline{u}_1 + a_{12}(x)\overline{u}_2)\\ &\geq \frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - b_1(x)\overline{u}_1 = 0.\end{aligned}$$

For all $x - c_1 t < \frac{1}{\mu_1} \frac{m_0\phi_1^*(x)}{u_1^*(x)}$, we obtain $\overline{u}_1(t,x) = u_1^*(x)$, and hence,

$$\begin{aligned}&\frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)\overline{u}_1 + a_{12}(x)\overline{u}_2)\\ &\geq \frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(x) - a_{11}(x)\overline{u}_1) = 0.\end{aligned}$$

On the other hand, for all $x - c_1 t > \frac{1}{\mu_2} \ln \frac{q_0\phi_2^*(x)}{u_2^*(x)} > 0$, it follows that

$$\overline{u}_2(t,x) = q_0 e^{-\mu_2(x-c_1t)}\phi_2^*(x),$$

which satisfies inequality (4.16). Since

$$\overline{u}_1(t,x) \leq m_0 e^{-\mu_1(x-c_1t)}\phi_1^*(x), \quad \forall t \geq 0,\ x \in \mathbb{R},$$

and $\mu_2 \in (0, \mu_1)$, we obtain

$$\begin{aligned}&\tfrac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - a_{21}(x)(u_2^*(x) - \overline{u}_2)\overline{u}_1 - \overline{u}_2(b_2(x) - 2a_{22}(x)u_2^*(x) + a_{22}(x)\overline{u}_2)\\ &= \tfrac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - (b_2(x) - a_{22}(x)u_2^*(x))\overline{u}_2 + (u_2^*(x) - \overline{u}_2)(a_{22}(x)\overline{u}_2 - a_{21}(x)\overline{u}_1)\\ &\geq (u_2^*(x) - \overline{u}_2)e^{-\mu_1(x-c_1t)}a_{21}(x)\phi_1^*(x)\left(\tfrac{q_0a_{22}(x)\phi_2^*(x)}{a_{21}(x)\phi_1^*(x)} - m_0\right)\\ &\geq 0.\end{aligned}$$

For all $x - c_1 t < \frac{1}{\mu_2} \ln \frac{q_0\phi_2^*(x)}{u_2^*(x)}$, we have $\overline{u}_2(t,x) = u_2^*(x)$. Therefore,

$$\begin{aligned}&\frac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - a_{21}(x)(u_2^*(x) - \overline{u}_2)\overline{u}_1 - \overline{u}_2(b_2(x) - 2a_{22}(x)u_2^*(x) + a_{22}(x)\overline{u}_2)\\ &= -L_2u_2^* - u_2^*(b_2(x) - a_{22}(x)u_2^*) = 0.\end{aligned}$$

It then follows that $\overline{u} = (\overline{u}_1, \overline{u}_2)$ is a continuous upper solution of system (4.7).

Let $\phi \in \mathcal{C}_\beta$ with $\phi(x) \geq \sigma$, $\forall x \leq K$ 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 [95, Lemma 2.2] and the proof of Theorem 4.5.1, as applied to $\hat{Q}_1$, it follows that for any $c < \overline{c}_+$, there exists $\delta(c) > 0$ such that

$$\liminf_{n\to\infty, x\leq cn} |u(n, x, \phi)| \geq \delta(c) > 0. \tag{4.19}$$

Moreover, there exists a sufficiently large positive constant $A \in L\mathbb{Z}$ such that

$$\phi(x) \leq \overline{u}(0, x - A) := \psi(x), \quad \forall x \in \mathbb{R}.$$

By the translation invariance of Q_t, it follows that $\overline{u}(t, x-A)$ is still an upper solution of system (4.7), and hence,

$$0 \leq u(t, x, \phi) \leq u(t, x, \psi) = \overline{u}(t, x - A), \quad \forall x \in \mathbb{R},\ t \geq 0. \tag{4.20}$$

Fix a number $\hat{c} \in (c_1, \overline{c}_+)$. Letting $t = n$, $x = \hat{c}n$ and $n \to \infty$ in (4.20), together with (4.19), we have

$$0 < \delta(\hat{c}) \leq \liminf_{n\to\infty} |u(n, \hat{c}n, \phi)| \leq \lim_{n\to\infty} |\overline{u}(n, \hat{c}n - A)| = 0,$$

which is a contradiction. Thus, $c_+^* = \overline{c}_+$. □

Note that the leftward case can be addressed in a similar way. Indeed, by making a change of variable $v(t, x) = u(t, -x)$ for system (4.7), we obtain similar results for the rightward case of the resulting system, which is the leftward case for system (4.7).

Remark 4.2.1. *In the case where either* $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ *with* $d_i \in C^{1+\nu}(\mathbb{R})$ *in system* (4.7)*,* $i = 1, 2$*, or all the coefficient functions of system* (4.7) *are even except* g_i *is odd,* $i = 1, 2$*, it follows from Lemma 4.4.2 that system* (4.7) *admits a single rightward spreading speed which coincides with the minimal rightward wave speed provided that (H1)–(H3) hold.*

4.3 Linear determinacy of spreading speed

In this section, we give a set of sufficient conditions for the rightward spreading speed to be determined by the linearization of system (4.7) at $\hat{E}_2 = (0,0)$, which is

$$\begin{aligned}\frac{\partial v_1}{\partial t} &= L_1 v_1 + (b_1(x) - a_{12}(x)u_2^*(x))v_1, \\ \frac{\partial v_2}{\partial t} &= L_2 v_2 + a_{21}(x)u_2^*(x)v_1 + (b_2(x) - 2a_{22}(x)u_2^*(x))v_2, \quad t > 0,\ x \in \mathbb{R}.\end{aligned} \tag{4.21}$$

Clearly, under (H2) the following scalar equation

$$\frac{\partial u}{\partial t} = L_1 u + u(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)u), \quad t > 0, x \in \mathbb{R}, \tag{4.22}$$

admits a rightward spreading speed (also the minimal rightward wave speed) $c_+^0 = \inf\limits_{\mu>0} \frac{\lambda_0(\mu)}{\mu}$ (see, e.g., [5, Theorem 1.1]), where $\lambda_0(\mu)$ is the principle eigenvalue of the following elliptic eigenvalue problem:

$$\begin{aligned}&\lambda\psi = d_1(x)\psi'' - (2\mu d_1(x) + g_1(x))\psi' + (d_1(x)\mu^2 + g_1(x)\mu + b_1(x) - a_{12}(x)u_2^*(x))\psi, \quad x \in \mathbb{R}, \\ &\psi(x+L) = \psi(x), \quad x \in \mathbb{R}.\end{aligned} \tag{4.23}$$

The next result shows that c_+^0 is a lower bound of the slowest spreading c_+^* of system (4.7).

Proposition 4.3.1. *Let (H1)–(H3) hold. Then $c_+^* \geq c_+^0$.*

Proof. In the case where $\bar{c}_+ > c_+^*$, by the same arguments as in Theorem 4.2.2, we see that $c_+^* \geq c_{1+}^*$, where c_{1+}^* is the rightward spreading speed of (4.10). Since $b_1(x) > b_1(x) - a_{12}(x)u_2^*(x), \forall x \in \mathbb{R}$, by Lemma 4.4.1 with $d(x) = d_1(x)$ and $g(x) = g_1(x), \forall x \in \mathbb{R}$, it is easy to see that $\lambda_1(\mu) > \lambda_0(\mu), \forall \mu \geq 0$, where $\lambda_1(\mu)$ is the principal eigenvalue of (4.14). Thus, we have $c_+^* \geq c_{1+}^* > c_+^0$.

In the case where $\bar{c}_+ = c_+^*$, let $u(t,\cdot,\phi) = (u_1(t,\cdot,\phi), u_2(t,\cdot,\phi))$ be the solution of system (4.7) with $u(0,\cdot) = \phi = (\phi_1,\phi_2) \in \mathcal{C}_\beta$. Then the positivity of the solution implies that

$$\frac{\partial u_1}{\partial t} \geq L_1 u_1 + u_1(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)u_1), \quad t > 0, x \in \mathbb{R}.$$

Let $v(t,x,\phi_1)$ be the unique solution of (4.22) with $v(0,\cdot) = \phi_1$. Then the comparison principle yields that

$$u_1(t,x,\phi) \geq v(t,x,\phi_1), \quad \forall t \geq 0,\ x \in \mathbb{R}. \tag{4.24}$$

Since $\lambda(d_1, g_1, b_1 - a_{12}u_2^*) > 0$, Proposition 4.1.1 implies that there exists a unique positive L-periodic steady state $v_0(x)$ of (4.22). Let $\phi^0 = (\phi_1^0, \phi_2^0) \in \mathcal{C}_\beta$ be chosen as in Theorem 4.2.2 (i) and (ii) such that $\phi_1^0 \leq v_0$. Assume, by contradiction, that $c_+^* < c_+^0$. Then we can fix a real number $\hat{c} \in (\bar{c}_+, c_+^0)$. Thus, Theorem 4.2.2 implies that $\lim_{t\to\infty, x\geq \hat{c}t} u_1(t,x,\phi^0) = 0$. By Theorem 4.5.1, as applied to system (4.22), we further obtain $\lim_{t\to\infty, x\leq \hat{c}t}(v(t,x,\phi_1^0) - v_0(x)) = 0$. However, letting $x = \hat{c}t$ in (4.24), we get $\lim_{t\to\infty, x=\hat{c}t}(v(t,x,\phi_1^0)) = 0$, a contradiction. $\square$

For any given $\mu \in \mathbb{R}$, letting $v(t,x) = e^{-\mu x}u(t,x)$ in (4.21), we then have

$$\begin{aligned}
\frac{\partial u_1}{\partial t} &= L_1 u_1 - 2\mu d_1(x)\frac{\partial u_1}{\partial x} + (d_1(x)\mu^2 + g_1(x)\mu + b_1(x) - a_{12}(x)u_2^*(x))u_1, \\
\frac{\partial u_2}{\partial t} &= L_2 u_2 - 2\mu d_2(x)\frac{\partial u_2}{\partial x} + a_{21}(x)u_2^*(x)u_1 \\
&\quad + (d_2(x)\mu^2 + g_2(x)\mu + b_2(x) - 2a_{22}(x)u_2^*(x))u_2, \quad t > 0, x \in \mathbb{R}.
\end{aligned} \tag{4.25}$$

Substituting $u(t,x) = e^{\lambda t}\phi(x)$ into (4.25), we obtain the following periodic eigenvalue problem:

$$\lambda\phi_1 = d_1(x)\phi_1'' - (2\mu d_1(x) + g_1(x))\phi_1' + (d_1(x)\mu^2 + g_1(x)\mu + b_1(x) - a_{12}(x)u_2^*(x))\phi_1,$$
$$\lambda\phi_2 = d_2(x)\phi_2'' - (2\mu d_2(x) + g_2(x))\phi_2' + a_{21}(x)u_2^*(x)\phi_1$$
$$+ \left(d_2(x)\mu^2 + g_2(x)\mu + b_2(x) - 2a_{22}(x)u_2^*(x)\right)\phi_2, \quad x \in \mathbb{R}, \tag{4.26}$$
$$\phi_i(x) = \phi_i(x+L), \quad \forall x \in \mathbb{R},\ i = 1, 2.$$

Let $\overline{\lambda}(\mu)$ be the principal eigenvalue of the following periodic eigenvalue problem:

$$\lambda\psi = d_2(x)\psi'' - (2\mu d_2(x) + g_2(x))\psi'$$
$$+ \left(d_2(x)\mu^2 + g_2(x)\mu + b_2(x) - 2a_{22}(x)u_2^*(x)\right)\psi, \quad x \in \mathbb{R}, \tag{4.27}$$
$$\psi(x) = \psi(x+L), \quad x \in \mathbb{R}.$$

Then there exists $\mu_0 > 0$ such that $c_+^0 = \frac{\lambda_0(\mu_0)}{\mu_0}$. Now we introduce the following condition:

(M1) $\lambda_0(\mu_0) > \overline{\lambda}(\mu_0)$.

Proposition 4.3.2. *Let (H1)–(H3) and (M1) hold. Then the periodic eigenvalue problem* (4.26) *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 principle eigenvalue $\lambda_0(\mu_0)$ of (4.22). Since the first equation of (4.26) 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 (4.26), where ϕ_2^* is to be determined. Let $U(t)$ be the solution semigroup generated by the following linear scalar partial differential equation:

$$\frac{\partial u}{\partial t} = L_2 u - 2\mu_0 d_2(x)\frac{\partial u}{\partial x} + (d_2(x)\mu_0^2 + g_2(x)\mu_0 + b_2(x) - 2a_{22}(x)u_2^*(x))u, \quad t > 0, x \in \mathbb{R},$$
$$u(0, \cdot) = \varphi \in Y.$$

It is easy to see that $U(t)$ is a positive and compact semigroup on Y with its generator

$$A = L_2 - 2\mu_0 d_2(x)\frac{\partial}{\partial x} + (d_2(x)\mu_0^2 + g_2(x)\mu_0 + b_2(x) - 2a_{22}(x)u_2^*(x)).$$

By [86, Theorem 3.12], A is resolvent-positive and

$$(\lambda I - A)^{-1}\phi = \int_0^\infty e^{-\lambda t}U(t)\phi dt, \quad \forall \lambda > s(A),\ \phi \in Y,$$

where $s(A)$ is the spectral bound of A. Note that $\overline{\lambda}(\mu_0)$ is the principal eigenvalue of (4.27), that is, $s(A) = \overline{\lambda}(\mu_0)$. Since $\lambda_0(\mu_0) > \overline{\lambda}(\mu_0) = s(A)$, we can define $\phi_2^* = (\lambda_0(\mu_0)I - A)^{-1}a_{21}u_2^*\phi_1^* \gg 0$. It then follows that (ϕ_1^*, ϕ_2^*) satisfies (4.26) with $\mu = \mu_0$. Since $\lambda_0(\mu_0)$ is a simple eigenvalue for (4.22), we see that so is $\lambda_0(\mu_0)$ for (4.26). □

From Proposition 4.3.2, it is easy to see that for any given $M > 0$, the function

$$U(t,x) = Me^{-\mu_0 x}e^{\lambda_0(\mu_0)t}\phi^*(x), \quad t \geq 0,\ x \in \mathbb{R}, \tag{4.28}$$

is a positive solution of system (4.21). In order to obtain an explicit formula for the spreading speeding $\overline{c}_+$, we need the following additional condition:

(M2) $\frac{\phi_1^*(x)}{\phi_2^*(x)} \geq \max\left\{\frac{a_{12}(x)}{a_{11}(x)}, \frac{a_{22}(x)}{a_{21}(x)}\right\}, \quad \forall x \in \mathbb{R}.$

Now we are in a position to show that system (4.7) admits a single rightward spreading speed $\overline{c}_+$, which is linearly determinate.

Theorem 4.3.1. *Let (H1)–(H3) and (M1)–(M2) hold. Then* $\overline{c}_+ = c_+^* = c_+^0 = \inf_{\mu>0}\frac{\lambda_0(\mu)}{\mu}$.

Proof. First, we verify that $U(t,x)$, as defined in (4.28), is an upper solution of system

(4.7). Since $\frac{U_1}{U_2} = \frac{\phi_1^*}{\phi_2^*}$ and (M2) holds true, it follows that

$$\begin{aligned}
&\frac{\partial U_1}{\partial t} - L_1 U_1 - U_1(b_1(x) - a_{12}(x)u_2^*(x) - a_{11}(x)U_1 + a_{12}(x)U_2) \\
&= a_{11}(x)U_1U_2\left(\frac{U_1}{U_2} - \frac{a_{12}(x)}{a_{11}(x)}\right) \\
&= a_{11}(x)U_1U_2\left(\frac{\phi_1^*(x)}{\phi_2^*(x)} - \frac{a_{12}(x)}{a_{11}(x)}\right) \geq 0,
\end{aligned} \tag{4.29}$$

and

$$\begin{aligned}
&\frac{\partial U_2}{\partial t} - L_2U_2 - a_{21}(x)U_1(u_2^*(x) - U_2) - U_2(b_2(x) - 2a_{22}(x)u_2^*(x) + a_{22}(x)U_2). \\
&= a_{21}(x)U_2^2\left(\frac{U_1}{U_2} - \frac{a_{22}(x)}{a_{21}(x)}\right) \\
&= a_{21}(x)U_2^2\left(\frac{\phi_1^*(x)}{\phi_2^*(x)} - \frac{a_{22}(x)}{a_{21}(x)}\right) \geq 0.
\end{aligned} \tag{4.30}$$

Thus, $U(t, x)$ is an upper solution of (4.7). Choose some $\phi^0 \in \mathcal{C}_\beta$ satisfying the conditions in Theorem 4.2.2 (i) and (ii). Then there exists a sufficiently large number $M_0 > 0$ such that

$$0 \leq \phi^0(x) \leq M_0 e^{-\mu_0 x}\phi^*(x) = U(0, x), \quad \forall x \in \mathbb{R}.$$

Let $W(t, x)$ be the unique solution of system (4.7) with $W(0, \cdot) = \phi_0$. Then the comparison principle, together with the fact that $c_+^0 \mu_0 = \lambda_0(\mu_0)$, implies that

$$0 \leq W(t, x) \leq U(t, x) = M_0 e^{-\mu_0 x} e^{\lambda_0(\mu_0)t}\phi^*(x) = M_0 e^{-\mu_0(x - c_+^0 t)}\phi^*(x), \quad \forall t \geq 0, \ x \in \mathbb{R}.$$

It follows that for any given $\epsilon > 0$, there holds

$$0 \leq W(t, x) \leq U(t, x) \leq M_0 e^{-\mu_0 \epsilon t}\phi^*(x), \quad \forall t \geq 0, \ x \geq (c_+^0 + \epsilon)t,$$

and hence,

$$\lim_{t\to\infty, x \geq (c_+^0 + \epsilon)t} W(t, x) = 0.$$

By Theorem 4.2.2 (ii), we obtain $c_+^* \le c_+^0 + \epsilon$. Letting $\epsilon \to 0$, we have $c_+^* \le c_+^0$. Assume, by contradiction, that $\overline{c}_+ > c_+^*$. Then the proof of Proposition 4.3.1 shows that $c_+^* > c_+^0$, a contradiction. This implies that $\overline{c}_+ = c_+^*$. In view of Proposition 4.3.1, it follows that $\overline{c}_+ = c_+^* = c_+^0$. □

To finish this section, we consider the following classical Lotka-Volterra competition model:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + r_1 u_1 (1 - u_1 - a_1 u_2), \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + r_2 u_2 (1 - a_2 u_1 - u_2), \quad t > 0,\ x \in \mathbb{R}, \end{aligned} \tag{4.31}$$

where all parameters are positive constants. This system was investigated in [51]. By straightforward computations (see, e.g., [51]), it follows that if $a_1 < 1$, then there are only three constant steady states $E_0 = (0,0)$, $E_1 = (1,0)$ and $E_2 = (0,1)$, and hence, (H3) is valid. Since $\lambda(d_2, 0, r_2) = r_2 > 0$ and $\lambda(d_1, 0, r_1(1-a_1)) = r_1(1-a_1) > 0$, we see that (H1) and (H2) are also valid. Moreover, (H4) and (H5) are automatically satisfied due to Lemma 4.4.2. Thus, system (4.31) admits a single spreading speed $\overline{c}_+$ no matter whether it is linearly determinate.

Next, we find some conditions under which (M1)–(M2) hold for system (4.31). By substituting $d_i(x) = d_i$, $b_i(x) = r_i$, $a_{ii}(x) = r_i, i = 1, 2$, $a_{12}(x) = r_1 a_1$, and $a_{21}(x) = r_2 a_2$ into system (4.7), we can reduce the eigenvalue problems (4.23) and (4.27) to

$$\begin{aligned} &\lambda\psi = d_1 \psi'' - 2\mu d_1 \psi' + (d_1 \mu^2 + r_1 - r_1 a_1)\psi, \quad x \in \mathbb{R}, \\ &\psi(x+L) = \psi(x), \quad x \in \mathbb{R}, \end{aligned} \tag{4.32}$$

and

$$\lambda\psi = d_2\psi'' - 2\mu d_2\psi' + \left(d_2\mu^2 - r_2\right)\psi, \quad x \in \mathbb{R},$$
$$\psi(x) = \psi(x+L), \quad x \in \mathbb{R}. \tag{4.33}$$

Then it is easy to see that two principle eigenvalues

$$\lambda_0(\mu) = d_1\mu^2 + r_1 - r_1a_1,\ \overline{\lambda}(\mu) = d_2\mu^2 - r_2$$

have positive constant eigenfunctions. By virtue of

$$c_+^0 = \inf_{\mu>0} \frac{\lambda_0(\mu)}{\mu} = \min_{\mu>0} \left\{ d_1\mu + \frac{r_1(1-a_1)}{\mu} \right\},$$

it follows that

$$c_+^0 = 2\sqrt{d_1r_1(1-a_1)},\ \mu_0 = \sqrt{\frac{r_1(1-a_1)}{d_1}}.$$

Thus, (M1) is equivalent to

$$\lambda_0(\mu_0) = 2r_1(1-a_1) > \frac{d_2r_1(1-a_1)}{d_1} - r_2 = \overline{\lambda}(\mu_0).$$

On the other hand, the eigenvalue problem (4.26) can be simplified as

$$\lambda\phi_1 = d_1\phi_1'' - 2\mu d_1\phi_1' + (d_1\mu^2 + r_1 - r_1a_1)\phi_1,$$
$$\lambda\phi_2 = d_2\phi_2'' - 2\mu d_2\phi_2' + a_2r_2\phi_1 + (d_2\mu^2 - r_2)\phi_2, \quad x \in \mathbb{R}, \tag{4.34}$$
$$\phi_i(x) = \phi_i(x+L), \quad \forall x \in \mathbb{R},\ i = 1,2.$$

Substituting $(\phi_1^*, \phi_2^*) = (1, k)$ into the second equation of (4.34), we get

$$k = \frac{a_2}{(1-a_1)\frac{r_1}{r_2}(2 - \frac{d_2}{d_1}) + 1} > 0.$$

It then follows that (M2) is equivalent to

$$\frac{\phi_1^*}{\phi_2^*} = \frac{(1-a_1)\frac{r_1}{r_2}(2-\frac{d_2}{d_1}) + 1}{a_2} \geq \max\left\{a_1, \frac{1}{a_2}\right\},$$

and hence,

$$
\begin{aligned}
&(1-a_1)\frac{r_1}{r_2}(2-\frac{d_2}{d_1})+1 \geq a_1a_2,\\
&(1-a_1)\frac{r_1}{r_2}(2-\frac{d_2}{d_1}) \geq 0,
\end{aligned}
$$

that is,

$$
\begin{aligned}
&\frac{d_2}{d_1} \leq 2,\\
&\frac{a_1a_2-1}{1-a_1} \leq \frac{r_1}{r_2}(2-\frac{d_2}{d_1}),
\end{aligned}
\tag{4.35}
$$

which also guarantees that (M1) holds. Thus, under condition (4.35), we have $\bar{c}_+ = c_+^0 = 2\sqrt{d_1r_1(1-a_1)}$. This result is consistent with [51, Theorem 2.1].

Remark 4.3.1. *Consider a more general reaction-diffusion competition system in a periodic habitat, that is,*

$$
\begin{aligned}
&\frac{\partial u_1}{\partial t} = L_1u_1 + u_1f_1(x,u_1,u_2),\\
&\frac{\partial u_2}{\partial t} = L_2u_2 + u_2f_2(x,u_1,u_2), \quad t>0,\ x\in\mathbb{R},
\end{aligned}
\tag{4.36}
$$

where the operator $L_i := a_2^{(i)}(x)\frac{\partial^2}{\partial x^2} + a_1^{(i)}(x)\frac{\partial}{\partial x}$ *with* $a_2^{(i)}(x) > 0, \forall x \in \mathbb{R}$, *i.e.,* L_i *is uniformly elliptic,* $i = 1,2$. *Assume that* $a_j^{(i)}(x)$ *and* $f_i(x,u_1,u_2)$ *are periodic in* x *with the same period and Hölder continuous in* x *of order* $\nu \in (0,1)$, $1 \leq i,j \leq 2$, *and* $f_i(x,u_1,u_2)$ *are differentiable with respect to* u_1 *and* u_2, $i = 1,2$. *Moreover,* $\partial_{u_1}f_1(x,u_1,0) < 0$ *and* $\partial_{u_2}f_2(x,0,u_2) < 0$, $\forall x \in \mathbb{R}$, *and there exists* $M_1 > 0$ *and* $M_2 > 0$ *such that* $f_1(x,M_1,0) \leq 0$, $f_2(x,0,M_2) \leq 0$, $\partial_{u_2}f_1(x,u_1,u_2) < 0$ *and* $\partial_{u_1}f_2(x,u_1,u_2) < 0$ *for all* $(x,u_1,u_2) \in \mathbb{R}\times[0,M_1]\times[0,M_2]$. *Then we can obtain analogous results on traveling waves and spreading speeds under similar assumptions to (H1)–(H5) and (M1)–(M2).*

4.4 An application

In this section, we study the spatially periodic version of a well-known reaction diffusion model [16, 49]:

$$\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + u_1(a(x) - u_1 - cu_2), \tag{4.37}$$
$$\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + u_2(a(x) - u_1 - u_2), \quad t > 0, \ x \in \mathbb{R},$$

where $0 < d_1 < d_2$, $0 \leq c \leq 1$ and $a(x)$ is an L-periodic continuous function for some $L > 0$. Note that model (4.37) with $c = 1$ was proposed in [16].

For convenience, we use the same notations as in sections 2 and 3. We first present some results on the principle eigenvalue $\lambda_m(\mu)$ of (4.38).

Lemma 4.4.1. *Assume that L-periodic functions $d, g, m \in C^\nu(\mathbb{R})(\nu \in (0,1))$. Let $\lambda_m(\mu)(\mu \in \mathbb{R})$ be the principle eigenvalue of the following elliptic eigenvalue problem:*

$$\lambda\psi = d(x)\psi'' - (2\mu d(x) + g(x))\psi' + (d(x)\mu^2 + g(x)\mu + m(x))\psi, \quad x \in \mathbb{R},$$
$$\psi(x + L) = \psi(x), \quad x \in \mathbb{R}. \tag{4.38}$$

Then the following statements are valid:

(a) If $m_1(x) \geq m_2(x)$, $\forall x \in \mathbb{R}$, and $m_1(x) \not\equiv m_2(x)$, then $\lambda_{m_1}(\mu) > \lambda_{m_2}(\mu)$, $\forall \mu \in \mathbb{R}$.

(b) $\lambda_m(\mu)$ is a convex function of μ on $\mathbb{R}$.

(c) If either d, m are even and g is odd, or $d \in C^{1+\nu}(\mathbb{R})(\nu \in (0,1))$ and $g(x) = -d'(x), \forall x \in \mathbb{R}$, then $\lambda_m(\mu) = \lambda_m(-\mu), \forall \mu \in \mathbb{R}$.

Proof. By similar arguments to those in [31, Lemma 15.5] , it is easy to prove that (a) holds. (b) follows from the same arguments as in [96, Proposition 4.1].

In the case where d, m are even functions and g is odd, for any given $\mu \in \mathbb{R}$, let $\psi(x)$ be the positive and L-periodic eigenfunction associated with $\lambda_m(\mu)$. Then we have

$$\begin{aligned}\lambda_m(\mu)\psi(-x) =& d(-x)\psi''(-x) - (2\mu d(-x) + g(-x))\psi'(-x) \\ &+ (d(-x)\mu^2 + g(-x)\mu + m(-x))\psi(-x), \quad \forall x \in \mathbb{R}.\end{aligned} \tag{4.39}$$

Letting $\varphi(x) = \psi(-x), x \in \mathbb{R}$, we obtain $\varphi'(x) = -\psi'(-x), \varphi''(x) = \psi''(-x), \forall x \in \mathbb{R}$. Since $d(x) = d(-x), m(x) = m(-x), g(x) = -g(-x), \forall x \in \mathbb{R}$, it follows that

$$\lambda_m(\mu)\varphi = d(x)\varphi'' + (2\mu d(x) - g(x))\varphi' + (d(x)\mu^2 - g(x)\mu + m(x))\varphi, \quad \forall x \in \mathbb{R}.$$

By the uniqueness of the principal eigenvalue, we have $\lambda_m(-\mu) = \lambda_m(\mu), \forall \mu \in \mathbb{R}$.

In the case where $d \in C^{1+\nu}(\mathbb{R})(\nu \in (0,1))$ and $-g(x) = d'(x), \forall x \in \mathbb{R}$, for any given $\mu \in \mathbb{R}$, let $\psi(x)$ and $\phi(x)$ be the positive and L-periodic eigenfunctions associated with $\lambda_m(\mu)$ and $\lambda_m(-\mu)$, respectively, that is,

$$(d(x)\psi')' - 2\mu d(x)\psi' + (d(x)\mu^2 - d'(x)\mu + m(x))\psi = \lambda_m(\mu)\psi$$

and

$$(d(x)\phi')' + 2\mu d(x)\phi' + (d(x)\mu^2 + d'(x)\mu + m(x))\phi = \lambda_m(-\mu)\phi.$$

Using integration by parts, we have

$$\int_0^L (d(x)\psi'(x))'\phi(x)dx = \int_0^L (d(x)\phi'(x))'\psi(x)dx,$$

and

$$\begin{aligned}&-\mu\int_0^L [2d(x)\psi'(x)\phi(x) + d'(x)\psi(x)\phi(x)]dx \\ &= \mu\int_0^L [2(d(x)\phi(x))'\psi(x) - d'(x)\psi(x)\phi(x)]dx \\ &= \mu\int_0^L [2d(x)\phi'(x)\psi(x) + d'(x)\phi(x)\psi(x)]dx.\end{aligned}$$

It then follows that

$$\lambda_m(\mu) \int_0^L \psi(x)\phi(x)dx = \lambda_m(-\mu) \int_0^L \phi(x)\psi(x)dx. \tag{4.40}$$

Since $\int_0^L \psi(x)\phi(x)dx > 0$, we have $\lambda_m(\mu) = \lambda_m(-\mu), \forall \mu \in \mathbb{R}$. □

Lemma 4.4.2. *Assume that (H1) and (H2) hold. Then (H4) and (H5) are valid provided that either all the coefficient functions of system* (4.7) *are even except g_i is odd, or $d_i \in C^{1+\nu}(\mathbb{R})(\nu \in (0,1))$ and $g_i(x) = -d_i'(x), \forall x \in \mathbb{R}, i = 1, 2$.*

Proof. First, we prove that (H4) holds. Indeed, in either case, by Lemma 4.4.1(c) with $m(x) = b_1(x)$ and $d(x) = d_1(x)$, it is easy to see that the principle $\lambda_1(\mu)$ of (4.14) is an even function of μ on $\mathbb{R}$. Since $\lambda_1(\mu)$ is convex on $\mathbb{R}$ and $\lambda_1(0) > 0$, we have $\lambda_1(\mu) > 0, \forall \mu > 0$. It follows that $c_{1+}^* = \inf_{\mu>0} \frac{\lambda_1(\mu)}{\mu} > 0$. Similarly, we can show that $c_{2-}^* > 0$, this implies $c_{1+}^* + c_{2-}^* > 0$.

To verify (H5), it suffices to show that $\lim_{\mu \to 0^+} \frac{\lambda_2(\mu)}{\mu} = 0$, where $\lambda_2(\mu)$ is the principal eigenvalue of (4.13). In the case where all the coefficient functions of (4.7) are even except g_i is odd, $i = 1, 2$, we have

$$d_2(x)u_2^{*\prime\prime}(x) + g_2(x)u_2^{*\prime}(x) + u_2^*(x)(b_2(x) - a_{22}(x)u_2^*(x)) = 0, \quad x \in \mathbb{R}.$$

Let $u_2(x) = u_2^*(-x)$. Since d_2, b_2, a_{22} are even and g_2 is odd, it follows that

$$d_2(x)u_2''(x) + g_2(x)u_2'(x) + u_2(x)(b_2(x) - a_{22}(x)u_2(x)) = 0, \quad x \in \mathbb{R}.$$

This implies that $u_2^*(-x)$ is also an L-periodic positive steady state for scalar equation (4.3) with $d(x) = d_2(x)$, $g(x) = g_2(x)$, $c(x) = b_2(x)$ and $e(x) = a_{22}(x), \forall x \in \mathbb{R}$. In view of Proposition 4.1.1, the uniqueness of the L-periodic positive steady state implies that $u_2^*(-x) = u_2^*(x), \forall x \in \mathbb{R}$. Taking $d(x) = d_2(x)$, $m(x) = b_2(x) - a_{22}(x)u_2^*(x)$, and $g(x) = g_2(x)$, or $g(x) = -d_2'(x)$ in (4.38), we see from Lemma 4.4.1(c) that in two cases, $\lambda_2(\mu)$ is an even function on $\mathbb{R}$, and hence, $\lambda_2'(0) = 0$. Since $\lambda_2(0) = 0$, it follows that $\lim_{\mu \to 0^+} \frac{\lambda_2(\mu)}{\mu} = \lambda_2'(0) = 0 < c_{1+}^*$. □

Now we impose the following assumption on system (4.37):

(M) $a(x)$ is non-constant, and $\overline{a} = \frac{1}{L}\int_0^L a(x)dx \geq 0$.

Lemma 4.4.3. *Let (M) hold. Then (H1)–(H3) are valid for system* (4.37)*.*

Proof. Let ϕ be the positive periodic eigenfunction associated with the principal eigenvalue $\lambda(d_1, 0, a)$, that is,

$$d_1\phi'' + a(x)\phi = \lambda(d_1, 0, a)\phi.$$

Dividing the above equation by ϕ and integrating by parts on $[0, L]$, we get

$$\lambda(d_1, 0, a) = \frac{1}{L}\int_0^L a(x)dx + d_1\int_0^L \left[\frac{\phi'(x)}{\phi(x)}\right]^2 dx.$$

Since $a(x)$ is non-constant, a simple computation shows that $\phi(x)$ is also non-constant. Therefore, we have

$$\lambda(d_1, 0, a) > \frac{1}{L}\int_0^L a(x)dx \geq 0.$$

Similarly, we can show that $\lambda(d_2, 0, a) > 0$. It follows that (H1) holds, and hence, system (4.37) has three L-periodic steady states $E_0 := (0, 0)$, $E_1 := (u_1^*(x), 0)$ and $E_2 := (0, u_2^*(x))$ in $\mathbb{P}_+$. Note that

$$d_2 u_2^{*''}(x) + u_2^*(x)(a(x) - u_2^*(x)) = 0, \quad x \in \mathbb{R}. \tag{4.41}$$

It follows that $\lambda(d_2, 0, a - u_2^*) = 0$. If $a(x) - u_2^*(x)$ is a constant, then a straightforward computation shows that u_2^* must be a positive constant eigenfunction associated with

$\lambda(d_2, 0, a - u_2^*)$. Therefore, $a(x)$ is also a constant, a contradiction. This shows that $a(x) - u_2^*(x)$ is non-constant.

Note that for the eigenvalue problem (4.2) with $d_1(x) = d > 0$ and $g \equiv 0$, we have the variational formula for the principle eigenvalue (see, e.g., [6]):

$$\lambda(d, 0, h) = \min_{\phi \in E} \frac{-d \int_0^L [\phi'(x)]^2 dx + \int_0^L h(x)\phi^2(x)dx}{\int_0^L \phi^2(x)dx},$$

where $E := \{\phi \in C^2(\mathbb{R}) : \phi(x) = \phi(x + L) > 0, \ \forall x \in \mathbb{R}\}$. It easily follows that if $h(x)$ is non-constant, then $\lambda(d_1, 0, h) > \lambda(d_2, 0, h)$ provided $d_2 > d_1 > 0$. Therefore, we have $\lambda(d_1, 0, a - cu_2^*) > \lambda(d_2, 0, a - u_2^*) = 0$, that is, (H2) is valid for $c \in [0, 1]$. To verify (H3), we suppose, by contradiction, that there is an L-periodic coexistence steady state $(u_0, v_0) \gg 0$ in $\mathbb{P}_+$. Then we have

$$d_1 u_0^{''}(x) + u_0(x)(a(x) - u_0(x) - cv_0(x)) = 0, \quad x \in \mathbb{R},$$
$$d_2 v_0^{''}(x) + v_0(x)(a(x) - u_0(x) - v_0(x)) = 0, \quad x \in \mathbb{R}.$$

This implies that $\lambda(d_1, 0, a - u_0 - cv_0) = \lambda(d_2, 0, a - u_0 - v_0) = 0$. By way of contradiction, we further show that $a - u_0 - cv_0$ is non-constant, $\forall c \in [0, 1]$. It then follows that

$$\lambda(d_1, 0, a - u_0 - cv_0) > \lambda(d_2, 0, a - u_0 - cv_0) \geq \lambda(d_2, 0, a - u_0 - v_0), \forall c \in [0, 1],$$

a contradiction. □

As a consequence of Lemma 4.4.3 and Theorem 4.1.1, we have the following result.

Theorem 4.4.1. *Let (M) hold. Then* $E_1 := (u_1^*(x), 0)$ *is globally asymptotically stable for all initial values* $\phi = (\phi_1, \phi_2) \in \mathbb{P}_+$ *with* $\phi_1 \not\equiv 0$.

For simplicity, we transfer system (4.37) into the following cooperative system:

$$\begin{aligned}\frac{\partial u_1}{\partial t} &= d_1\frac{\partial^2 u_1}{\partial x^2} + u_1(a(x) - cu_2^*(x) - u_1 + cu_2), \\ \frac{\partial u_2}{\partial t} &= d_2\frac{\partial^2 u_2}{\partial x^2} + u_1(u_2^*(x) - u_2) + u_2(a(x) - 2u_2^*(x) + u_2), \quad t > 0,\ x \in \mathbb{R}.\end{aligned} \tag{4.42}$$

Let $u^* = (u_1^*(\cdot), u_2^*(\cdot))$. Define a family of operators $\{Q_t\}_{t\geq 0}$ on $\mathcal{C}_{u^*}$ by $Q_t(\phi) := u(t,\cdot,\phi)$, where $u(t,\cdot,\phi)$ is the unique solution of system (4.42) with $u(0,\cdot) = \phi \in \mathcal{C}_{u^*}$. Let $\{\hat{Q}_t\}_{t\geq 0}$ be defined as in (4.48) and $\bar{c}_+$ be denoted by (4.49) with $\tilde{P} = \hat{Q}_1$. By virtue of Lemma 4.4.1, Lemma 4.4.2 and Proposition 4.3.1, we see that $\bar{c}_+ \geq c_+^0 > 0$.

The next result is the consequence of Theorem 4.2.2 and Remark 4.2.1.

Theorem 4.4.2. *Assume that (M) holds. Let $u(t,\cdot,\phi)$ be the solution of system* (4.42) *with $u(0,\cdot) = \phi \in \mathcal{C}_{u^*}$. Then the following statements are valid for system* (4.42)*:*

(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 $\lim_{t\to\infty, x\geq ct} u(t,x,\phi) = 0$ for any $c > \bar{c}_+$.

(ii) If $\phi \in \mathcal{C}_\beta$ and $\phi(x) \geq \sigma$, $\forall x \leq K$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K \in \mathbb{R}$, then $\lim_{t\to\infty, x\leq ct}(u(t,x,\phi) - \beta(x)) = 0$ for any $c \in (0,\bar{c}_+)$.

In view of Theorem 4.2.1, we have the following result on periodic traveling waves for system (4.37).

Theorem 4.4.3. *Let (M) hold. Then for any $c \geq \bar{c}_+$, system* (4.37) *has an L-periodic rightward traveling wave $(U(x-ct,x), V(x-ct,x))$ connecting $(u_1^*(x),0)$ to $(0,u_2^*(x))$ 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 $c \in (0,\bar{c}_+)$, system* (4.37) *admits no L-periodic rightward traveling wave connecting $(u_1^*(x),0)$ to $(0,u_2^*(x))$.*

It is not easy to verify conditions (M1) and (M2). However, motivated by [58, 83, 84], we can formally compute the lower bound c_+^0 in the case where

$$d_1 = 1, d_2 > 1, a(x) = \begin{cases} 1, & ml < x < ml + l_1, \\ a < 1, & ml - l_2 \leq x < ml, \quad m \in \mathbb{Z}, \end{cases}$$

for system (4.37) with $l = l_1 + l_2$ and $\overline{a} = \frac{l_1 + a l_2}{l} > 0$. It is easy to see that $u_1^*(x) \approx a(x), u_2^*(x) \approx a(x)$, and hence, (4.23) becomes

$$\begin{aligned} \lambda\psi &= \psi'' - 2\mu\psi' + (\mu^2 + (1-c))\psi, \quad ml < x < ml + l_1, \\ \lambda\psi &= \psi'' - 2\mu\psi' + (\mu^2 + a(1-c))\psi, \quad ml + l_1 < x < (m+1)l. \end{aligned} \tag{4.43}$$

The matching conditions are

$$\lim_{x \to (ml)^-} \psi(x) = \lim_{x \to (ml)^+} \psi(x), \lim_{x \to (ml+l_1)^-} \psi(x) = \lim_{x \to (ml+l_1)^+} \psi(x), \quad m \in \mathbb{Z},$$

and

$$\lim_{x \to (ml)^-} \psi'(x) = \lim_{x \to (ml)^+} \psi'(x), \lim_{x \to (ml+l_1)^-} \psi'(x) = \lim_{x \to (ml+l_1)^+} \psi'(x), \quad m \in \mathbb{Z},$$

Set

$$\phi(x) = A_1 e^{\alpha_1 x} + A_2 e^{\alpha_2 x}, \quad x \in [0, l_1], \tag{4.44}$$

$$\phi(x) = A_3 e^{\beta_1 (l-x)} + A_4 e^{\beta_2 (l-x)}, \quad x \in [l_1, l], \tag{4.45}$$

where $\alpha_{1,2} = \mu \pm q_1$, $\beta_{1,2} = -\mu \pm q_2$, $q_1 = \sqrt{\lambda - (1-c)}$, and $q_2 = \sqrt{\lambda - a(1-c)}$. Then the matching conditions yield the following linear relationship between the coefficients

$$\begin{pmatrix} 1 & 1 & -1 & -1 \\ e^{\alpha_1 l_1} & e^{\alpha_2 l_2} & -e^{\beta_1 l_2} & -e^{\beta_2 l_2} \\ q_1 & -q_1 & q_2 & -q_2 \\ q_1 e^{\alpha_1 l_1} & -q_1 e^{\alpha_2 l_1} & q_2 e^{\beta_1 l_2} & -q_2 e^{\beta_2 l_2} \end{pmatrix} \begin{pmatrix} A_1 \\ A_2 \\ A_3 \\ A_4 \end{pmatrix} = 0.$$

Since we look for positive eigenfunctions, the determinant of the above matrix must be zero. Accordingly, straightforward computations show that

$$\cosh(\mu l) = \cosh(q_1 l_1)\cosh(q_2 l_2) + \frac{q_1^2 + q_2^2}{2q_1 q_2}\sinh(q_1 l_1)\sinh(q_2 l_2) := G(\lambda).$$

In view of

$$\cosh^{-1} z = \log\{z + (z^2 - 1)^{1/2}\}, \quad z > 1,$$

we then have

$$\mu(\lambda) = \frac{1}{l}\log\{G(\lambda) + \sqrt{[G(\lambda)]^2 - 1}\}.$$

Let λ_0 be the solution of the following equation:

$$\frac{d\mu(\lambda)}{d\lambda}\frac{\lambda}{\mu(\lambda)} = 1,$$

and $\mu_0 = \mu(\lambda_0)$. Thus, we obtain $c_+^0 = \frac{\lambda_0}{\mu_0}$.

If $l \ll 1$, by using $\cosh z \approx 1 + z^2/2$ and $\sinh z \approx z$, we get an approximation

$$1 + (\mu l)^2/2 \approx (1 + (q_1 l_1)^2/2)(1 + (q_2 l_2)^2/2) + l_1 l_2 \frac{q_1^2 + q_2^2}{2},$$

and hence,

$$c_+^0 = \inf_{\mu > 0} \frac{\lambda(\mu)}{\mu} \approx \inf_{\mu > 0}\left\{\mu + \frac{(1-c)\overline{a}}{\mu}\right\}.$$

It follows that $c_+^0 \approx 2\sqrt{(1-c)\overline{a}}$, $\mu_0 \approx \sqrt{(1-c)\overline{a}}$, $\overline{a} = \frac{l_1 + a l_2}{l} > 0$.

4.5 Appendix

In this section, we extend the abstract results in [19](see also section 2.2.2) and [55] on spreading speeds and traveling waves to the case of a periodic habitat.

Let $\mathcal{C}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^m$ with $m \geq 1$ and $\mathcal{C}_+ = \{\phi \in \mathcal{C} : \phi(x) \geq 0, \ \forall x \in \mathbb{R}\}$. Clearly, any vector in $\mathbb{R}^m$ can be regarded as a function in $\mathcal{C}$. For $u = (u_1, ..., u_m), w = (w_m, ..., w_m) \in \mathcal{C}$, we write $u \geq w (u \gg w)$ provided $u_j(x) \geq w_j(x)(u_j(x) > w_j(x)), \forall 1 \leq j \leq m$, $x \in \mathbb{R}$, and $u > w$ provided $u \geq w$ but $u \neq w$. 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

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

Let

$$\mathcal{K}_\beta := \{v \in BC(L\mathbb{Z}, X_\beta) : v(i)(L) = v(i+L)(0), \forall i \in L\mathbb{Z}\}.$$

Clearly, any element in $\overline{X}_\beta$ can be regarded as a constant function in $\mathcal{X}_\beta$, that is, any element in $\mathcal{C}_\beta^{per}$ corresponds to a constant function in $\mathcal{X}_\beta$. We equip $\mathcal{C}$ and $\mathcal{X}$ with the compact open topology, that is, $u_n \to u$ in $\mathcal{C}$ or $\mathcal{X}$ means that the sequence of $u_n(s)$ converges to $u(s)$ in $\mathbb{R}^m$ or X uniformly for s in any compact set. We equip $\mathcal{C}$ and $\mathcal{X}$ with the norm $\|\cdot\|_{\mathcal{C}}$ and $\|\cdot\|_{\mathcal{X}}$, respectively, which are defined by

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

where $|\cdot|$ denotes the usual norm in $\mathbb{R}^m$, and

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

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 $\beta \in \mathrm{Int}(\mathcal{C}_+)$ is L-periodic. In order to use the theory developed in [19] and [55], we need the following assumptions on Q:

(D1) Q is L-periodic, that is, $\mathcal{T}_a[Q[u]] = Q[\mathcal{T}_a[u]], \quad \forall u \in \mathcal{C}_\beta,\ a \in L\mathbb{Z}$.

(D2) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is continuous with respect to the compact open topology.

(D3) $Q[\mathcal{C}_\beta]$ is precompact in $\mathcal{C}_\beta$ with respect to the compact open topology.

(D4) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is monotone (order preserving) in the sense that $Q[u] \geq Q[w]$ whenever $u \geq w$.

(D5) Q admits two L-periodic fixed points 0 and β in $\mathcal{C}_+$, and for any $z \in \mathcal{C}_\beta^{per}$ with $0 \ll z \leq \beta$, there holds $\lim_{n\to\infty} Q^n[z](x) = \beta(x)$ uniformly for $x \in \mathbb{R}$.

Define a homeomorphsim $F : \mathcal{C} \to \mathcal{K}$ by

$$F[\phi](i)(\theta) = \phi(i+\theta),\ i \in L\mathbb{Z},\ \theta \in [0, L],$$

and an operator $P : \mathcal{K}_\beta \to \mathcal{K}_\beta$ by

$$P = F \circ Q \circ F^{-1}. \tag{4.46}$$

Next, we define $\tilde{P} : \mathcal{X} \to \mathcal{X}$ by

$$\tilde{P}[v](s) := P[v(\cdot + s)](0), \quad \forall v \in \mathcal{X},\ s \in \mathbb{R}. \tag{4.47}$$

We further claim that

$$\tilde{P}[v](s)(\theta) = Q[v_s](\theta), \quad \forall v \in \mathcal{X},\ s \in \mathbb{R},\ \theta \in [0, L], \tag{4.48}$$

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

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

Indeed, since

$$F[\phi](i)(\theta) = \phi(i + \theta), \quad F^{-1}[\psi](x) = \psi(n_x)(\theta_x),$$

it then follows that

$$\begin{aligned}\tilde{P}[v](s) \quad &= P[v(\cdot + s)](0) = FQF^{-1}[v(\cdot + s)](0) \\ &= F[Q[v(n. + s)(\theta.)]](0) = F[Q(v_s)](0),\end{aligned}$$

and hence,

$$\tilde{P}[v](s)(\theta) = F[Q(v_s)](0)(\theta) = Q[v_s](\theta).$$

In order to apply the results in [19] (see also section 2.2) to $\tilde{P}$, we need to verify that $\tilde{P}$ satisfies the following assumptions (C1)–(C5) in section 2.2 with $\mathcal{M} = \mathcal{X}$ and $\tilde{P} : \overline{X} \to \overline{X}$. Indeed, we prove the continuity assumption (A2) is valid for $\tilde{P}$.

Proposition 4.5.1. *Let $\beta \in \mathrm{Int}(\mathcal{C}_+)$ be L-periodic. Assume that $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ satisfies assumptions (D1)–(D5). Then $\tilde{P}$: $\mathcal{X}_\beta \to \mathcal{X}_\beta$ satisfies assumptions (C1)–(C5) with (C2) replaced by (A2).*

Proof. For any $c \in \mathbb{R}$, let $u(\cdot) = v(\cdot + c), \forall v \in \mathcal{X}$. Then

$$\begin{aligned} T_{-c}\tilde{P}[v](s) &= \tilde{P}[v](s + c) \\ &= Q[v_{s+c}] = Q[u_s] = \tilde{P}[u(\cdot)](s) \\ &= \tilde{P}[T_{-c}v](s), \quad \forall v \in \mathcal{X},\ s \in \mathbb{R}, \end{aligned}$$

and hence, (C1) holds. (A2) can be verified by similar arguments to those in [54, Lemma 2.1], and (C4) directly follows from (D4). Clearly, 0 is the fixed point of $\tilde{P}$

since $Q(0) = 0$. To verify (C5), we need to show that $\beta|_{[0,L]}$ is the fixed point of $\tilde{P}$. Note that $\beta(x)$ is a constant function in $\mathcal{X}$ with $x \in [0, L]$, we have

$$\beta_s(\cdot) = \beta(s + n.)(\theta.) = \beta(\theta.), \quad \forall s \in \mathbb{R}.$$

Therefore, $\beta_s = \beta$ in $\mathcal{C}, \forall s \in \mathbb{R}$. Moreover,

$$\tilde{P}[\beta](s)(\theta) = Q[\beta_s](\theta) = Q[\beta](\theta) = \beta(\theta), \quad \forall \theta \in [0, L].$$

This implies that $\tilde{P}[\beta] = \beta$ in $\mathcal{X}$. Thus, (C5) follows from (D5). Now we prove (C3) holds. For any given $\mathcal{U} \subset \mathcal{X}_\beta$, it is easy to see that $\tilde{P}(\mathcal{U})(0)$ is uniformly bounded. By (D3), it follows for any $\varepsilon > 0$, there exists $\delta > 0$ such that

$$|Q(v)(x_1) - Q(v)(x_2)| < \varepsilon, \quad \forall v \in \mathcal{C}_\beta$$

provided that $x_1, x_2 \in [0, L]$ with $|x_1 - x_2| < \delta$. So for any $v \in \mathcal{U}$,

$$|\tilde{P}(v)(0)(\theta_1) - \tilde{P}(v)(0)(\theta_2)| = |Q(v_0)(\theta_1) - Q(v_0)(\theta_2)| < \varepsilon$$

provided that $\theta_1, \theta_2 \in [0, L]$ with $|\theta_1 - \theta_2| < \delta$. This implies that $\tilde{P}(\mathcal{U})(0)$ is equicontinuous. By Arzelà–Ascoli theorem, it follows that $\tilde{P}(\mathcal{U})(0)$ is precompact in $X_{\hat{\beta}}$, and hence, $\alpha(\tilde{P}(\mathcal{U})(0)) = 0$, this proves (C3) with $k = 0$. $\square$

Let $\omega \in \overline{X}_\beta$ with $0 \ll \omega \ll \beta$. 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 $s \geq 0$;

(iii) $\phi(-\infty) = \omega$.

Let c be a given real number. According to [93], we define an operator R_c by

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

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

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

As a consequence of similar arguments to those in [19, Lemmas 3.1–3.3], we have the following result.

Lemma 4.5.1. *The following statements are valid:*

(1) 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 $a(c; \cdot) \in \mathcal{X}_\beta$.

(2) $a(c, -\infty) = \beta$ and $a(c, +\infty)$ existing in X is a fixed point of $\tilde{P}$.

Following [19, 95], we define two numbers

$$c_+^* = \sup\{c : a(c, +\infty) = \beta\}, \quad \bar{c}_+ = \sup\{c : a(c, +\infty) > 0\}. \tag{4.49}$$

Clearly, $c_+^* \leq \bar{c}_+$ due to the monotonicity of $a(c; \cdot)$ with respect to c. For each $t \geq 0$. Let P_t and $\tilde{P}_t$ be defined as in (4.46) and (4.48) with $Q = Q_t$, respectively. By [19, Remark 3.7], we have the following result.

Theorem 4.5.1. *Let $\{Q_t\}_{t\geq 0}$ be a continuous-time semifow on $\mathcal{C}_\beta$ with $Q_t[0] = 0, Q_t[\beta] = \beta$ for all $t \geq 0$ and $\{\tilde{P}_t\}_{t\geq 0}$ be defined as in (4.48) for each $t \geq 0$, and c_+^* and $\bar{c}_+$ be denoted by (4.49) with $\tilde{P} = \tilde{P}_1$. Suppose that Q_t satisfies (D1)–(D5) for each $t > 0$. Then the following statements are valid:*

(i) *If* $\phi \in \mathcal{C}_\beta$, $0 \le \phi \le \omega \ll \beta$ *for some* $\omega \in \mathcal{C}_\beta^{per}$, *and* $\phi(x) = 0, \forall x \ge H$, *for some* $H \in \mathbb{R}$, *then* $\lim_{t\to\infty, x\ge ct} Q_t(\phi) = 0$ *for any* $c > \bar{c}_+$.

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

Proof. Since $\{Q_t\}_{t\ge 0}$ is a continuous-time semifow on $\mathcal{C}_\beta$ with $Q_t(0) = 0$ and $Q_t(\beta) = \beta$ for all $t \ge 0$, it follows that $\{\tilde{P}_t\}_{t\ge 0}$ is a continuous-time semiflow on $\mathcal{X}_\beta$ with $\tilde{P}_t(0) = 0$ and $\tilde{P}_t(\beta) = \beta$ for all $t \ge 0$. By Proposition 4.5.1, $\tilde{P}_t$ satisfies (A1)–(A5). For any $\phi \in \mathcal{C}_\beta$, $0 \le \phi \le \omega \ll \beta$ with $\omega \in \mathcal{C}_\beta^{per}$, let

$$u(s)(\theta) = [\phi(n_s + L + \theta) - \phi(n_s + \theta)]\theta_s + \phi(n_s + \theta).$$

for $s \in \mathbb{R}$, $s = n_s + \theta_s$, $n_s = L\left[\dfrac{s}{L}\right]$, $\theta_s \in [0, L)$, $\theta \in [0, L]$. Then $u \in \mathcal{X}_\beta$, and $0 \le u \le \omega \ll \beta$.

To prove statement (i), we suppose that there exists some $H \in \mathbb{R}$ such that $\phi(x) = 0$, $x \ge H$ and $\phi(x) \not\equiv 0$ (otherwise, it is trivial). Thus, $u(s) = 0$, $s \ge H + L$. By Theorem 2.2.7, it follows that $\lim_{t\to\infty, s\ge ct} \tilde{P}_t(u)(s) = 0$ in X for any $c > \bar{c}_+$. On the other hand, we have

$$\begin{aligned}\tilde{P}_t[u](n_x)(\theta_x) &= Q_t[u_{n_x}](\theta_x) = Q_t[u(n_x + n.)(\theta.)](\theta_x), \\ &= Q_t[\phi(n_x + \cdot)](\theta_x) = Q_t[\phi(\cdot)](x), \quad x \in \mathbb{R},\end{aligned}$$

and for $s \in L\mathbb{Z}$, $\lim_{t\to\infty, s\ge ct} \tilde{P}_t(u)(s) = 0$ in X holds true for any $c > \bar{c}_+$. Choose a $c' \in (\bar{c}_+, c)$, we obtain

$$|Q_t[\phi](x)| \le |\tilde{P}_t[u](n_x)|_X, \quad \forall x \ge ct,\ t \ge \frac{L}{c - c'}, \tag{4.50}$$

and $n_x \ge ct - L \ge c't$. Letting $t \to \infty$ in (4.50), we have $\lim_{t\to\infty, x\ge ct} Q_t(\phi) = 0$ for any $c > \bar{c}_+$.

By similar arguments to the above, we can show that statement (ii) is also valid.

□

In view of the above theorem, we may regard $\overline{c}_+$ and c_+^*, respectively, as the fastest and slowest rightward spreading speeds for $\{Q_t\}_{t\geq 0}$ on $\mathcal{C}_\beta$. If $\overline{c}_+ = c_+^*$, then we say that this system admits a single rightward spreading speed.

Next, we address the existence and non-existence of traveling waves in a periodic habitat for the continuous-time semiflow $\{Q_t\}_{t\geq 0}$. Given a continuous-time semiflow $\{Q_t\}_{t\geq 0}$ on $\mathcal{C}_\beta$, we say that $V(x-ct,x)$ is an L-periodic rightward traveling wave of $\{Q_t\}_{t\geq 0}$ if $V(\cdot+a,\cdot)\in\mathcal{C}_\beta$, $\forall a\in\mathbb{R}$, $Q_t[U](x)=V(x-ct,x)$, $\forall t\geq 0$, and $V(\xi,x)$ is an L-periodic function in x for any fixed $\xi\in\mathbb{R}$, where $U(x):=V(x,x)$. 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 $x\in\mathbb{R}$.

Since we have only shown the weak compactness (C3) for $\tilde{P}_t$, we cannot directly apply [19, Theorem 4.2](see also Theorem 2.2.6) to $\{\tilde{P}_t\}_{t\geq 0}$ on $\mathcal{X}_\beta$. However, $\{P_t\}_{t\geq 0}$ on $\mathcal{K}_\beta$ has the compactness because any element in $\mathcal{K}_\beta$ is defined on the discrete domain. Following the proof of Case 1 in [55, Theorem 4.2] and the argument in [19, Theorem 3.8](see also Theorem 2.2.5), we obtain the existence and non-existence of traveling waves for the discrete-time dynamical system $\{P_1^n\}$ on $\mathcal{K}_\beta$. Thus, the existence and non-existence of traveling waves for the continuous-time dynamical system $\{P_t\}_{t\geq 0}$ on $\mathcal{K}_\beta$ follows from the arguments in [55, Theorem 4.4]. By similar arguments to those in [55, Theorem 5.3], we can extend Theorem 2.2.6 to the case of a periodic habitat so that the following result holds true.

Theorem 4.5.2. *Let* $\{Q_t\}_{t\geq 0}$ *be a continuous-time semifow on* $\mathcal{C}_\beta$ *with* $Q_t[0]=0, Q_t[\beta]=\beta$ *for all* $t\geq 0$, $\{\tilde{P}_t\}_{t\geq 0}$ *be defined as in* (4.48), *and* c_+^* *and* $\overline{c}_+$ *be de-*

noted by (4.49) *with* $\tilde{P} = \tilde{P}_1$. *Suppose that* Q_t *satisfies (D1)–(D5) for each* $t > 0$. *Then the following statements are valid:*

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

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

   (i) *there exists an L-periodic traveling wave* $W(x-ct, x)$ *connecting* β *to* 0 *with* $W(\xi, x)$ *be continuous and nonincreasing in* $\xi \in \mathbb{R}$.

   (ii) $\{Q_t\}_{t\geq 0}$ *has two ordered equilibria* α_1,$\alpha_2 \in C_\beta^{per} \backslash \{0, \beta\}$ *such that there exist an L-periodic traveling wave* $W_1(x-ct, x)$ *connecting* α_1 *and* 0 *and an L-periodic traveling wave* $W_2(x-ct, x)$ *connecting* β *and* α_2 *with* $W_i(\xi, x), i = 1, 2$ *be 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* $c < \overline{c}_+$, *there is no L-periodic traveling wave connecting* β *to* 0.

Chapter 5

Spatial Dynamics for Time-space Periodic Monotone Systems

This chapter consists of two parts. In the first one, we establish the traveling waves and spreading speeds for an ω-time periodic and L-space periodic monotone semiflow $\{Q_t\}_{t\in\mathcal{T}}$ of monostable type on some subsets of the space $\mathcal{C}$ consisting of all continuous functions from one-dimensional unbounded medium $\mathcal{H}$ to the Banach lattice $(X, X_+, \|\cdot\|)$ with $X = C(\Omega, \mathbb{R}^l)$, where Ω is a compact metric space, the evolution time $\mathcal{T}$ is $\mathbb{R}_+$ or $\mathbb{Z}_+$, and the medium $\mathcal{H}$ is $\mathbb{R}$ or $\mathbb{Z}$. In the second part, we address the aforementioned questions by applying the obtained results to a time-space periodic competition model in the medium $\mathbb{R}$.

Let us first introduce the definition of traveling wave with speed c for time-space periodic semiflows.

Definition 5.0.1. *A function $W : \mathcal{T} \times \mathcal{H} \times \mathbb{R} \to X$ is said to a traveling wave for* *the semiflow* $\{Q_t\}_{t\in\mathcal{T}}$ *provided that*

$$Q_t[W(0,\cdot,\cdot+y)](x) = W(t,x,x+y-ct), \quad \forall t\in\mathcal{T}, x\in\mathcal{H}, y\in\mathbb{R}, \tag{5.1}$$

$$W(t,x,\xi) \text{ is } \omega\text{-periodic in } t,\ L\text{-periodic in } x,\ \text{non-increasing in } \xi, \tag{5.2}$$

and

$$W(t,x,\pm\infty) \text{ exist such that } Q_t[W(0,\cdot,\pm\infty)] = W(t,\cdot,\pm\infty). \tag{5.3}$$

In (5.1), for any $y\in\mathbb{R}$, $W(0,\cdot,\cdot+y)$ is understood as a one variable function which is an element of $\mathcal{C}$. We say that $W(t,x,\xi)$ connects ω-time periodic and L-space periodic function β_1 to β_2 if $\lim_{\xi\to-\infty}|W(t,x,\xi)-\beta_1(t,x)| = 0$ and $\lim_{\xi\to+\infty}|W(t,x,\xi)-\beta_2(t,x)| = 0$ uniformly in $t\in\mathcal{T}$ and $x\in\mathcal{H}$.

One may observe the differences between Definitions 1.0.1 and 5.0.1. For instance, the medium is $\mathbb{R}^N$ in Definition 1.0.1 and $\mathbb{R}$ or $\mathbb{Z}$ in Definition 5.0.1. In section 5.1.1 we will explain how these two definitions are relevant, why (5.1) can hold for all $y\in\mathbb{R}$, and how the function W can be extended to obtain an entire orbit for the given semiflow.

To address the interaction of time and space periods, we introduce the following concept of almost pulsating waves.

Definition 5.0.2. *An entire solution* $u(t,x)$ *is said to be an almost pulsating wave with speed* c *provided that it has the following two properties:*

(i) If $c\omega/L$ *is a rational number, then there exist two integers* p *and* q *such that* $c\omega/L = p/q$ *and* $u(t+q\omega, x+pL) = u(t,x)$ *for all* $(t,x)\in\mathbb{R}^2$.

(ii) If $c\omega/L$ *is an irrational number, then there exists a sequence of integer pairs* (p_k,q_k) *with* $q_k\to+\infty$ *such that* $c\omega/L = \lim_{k\to\infty} p_k/q_k$ *and*

$$\lim_{k\to\infty} u(t+q_k\omega, x+p_kL) = u(t,x) \tag{5.4}$$

uniformly for all $t \in \mathbb{R}$ *and* x *in any compact subset of* $\mathbb{R}$.

We say that the almost pulsating wave $u(t,x)$ *connects two time-space periodic solutions* $\beta_\pm(t,x)$ *if* $\lim_{x-ct\to\pm\infty} |u(t,x) - \beta_\pm(t,x)| = 0$ *uniformly for all* $(t,x) \in \mathbb{R}^2$.

Such an almost pulsating wave will be constructed in terms of traveling wave $W(t,x,x-ct+y)$ with appropriate y defined in Definition 5.0.1.

Our strategy to construct traveling waves and almost pulsating waves is based on an evolution point of view. Firstly, for the Poincaré map Q_ω, we construct a family of classical pulsating waves $V(x,\xi+y)$ with any admissible speed c in the sense that $Q_\omega[V(\cdot,\cdot+y)] = V(x,x-c\omega+y), \forall y \in \mathbb{R}, x \in \mathcal{H}$. Secondly, the evolution form $W(t,x,\xi) = Q_t[V(\cdot,\cdot+\xi-x+ct)](x)$ gives rise to the desired traveling wave. Lastly, the periodic extension of $W(t,x,x-ct+y)$ in the first variable is shown to be an almost pulsating when y is appropriately chosen. An essential reason why such an approach works is that the family of pulsating waves $V(x,x-ct+y)$ has various properties. Such V is corresponding to the abstract monotone function ψ in Lemmas 5.1.6 and 5.1.7. In fact, the map Q_ω in the periodic medium $\mathcal{H}$ is topologically conjugate to another map P_ω in the homogeneous discrete medium $\mathbb{Z}$, and the abstract function ψ is a traveling wave of the extension $\tilde{P}_\omega$ of P_ω to the homogeneous continuous medium $\mathbb{R}$. The spreading speed will be obtained by a similar idea but the phase space for $\tilde{P}_\omega$ is selected in a different way.

The mono-stability of the semiflow will be defined later in section 5.1.1 by using its Poincaré map Q_ω restricted on the space of L-periodic functions. Since semi-trivial time-space periodic solutions may exist in certain non-scalar evolution systems, we need to introduce one more critical speed. In general, there are two kinds of spreading speeds (and minimal wave speeds) for semiflows and they are not necessarily identical or linearly determinate. For specific evolution systems, it is highly nontrivial to find appropriate conditions for the existence of a single spreading speed and its linear determinacy. We will illustrate this by considering a two species competition model.

Our strategy to establish the minimal wave speed for the semiflow is the following: (1) construct a map P_ω in homogeneous medium $\mathbb{Z}$ such that it is topologically conjugate to the Poincaré map Q_ω in periodic medium $\mathcal{H}$; (2) extend P_ω to a larger map $\tilde{P}_\omega$ in homogeneous medium $\mathbb{R}$ but with very weak compactness even if Q_ω is compact; (3) show that $\tilde{P}_\omega$ fits the framework of [19] to overcome the difficulty induced by non-compactness; (4) construct the wave for $\{Q_t\}_{t\in\mathcal{T}}$ using the evolution approach, which is applicable because the medium of $\tilde{P}_\omega$ is $\mathbb{R}$. The spreading speed will be obtained by a similar idea but the phase space for $\tilde{P}_\omega$ is selected in a different way.

In the second part, we apply the theory developed for monotone semiflows to the following two species competition reaction-advection-diffusion model with time and space periodicity:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= L_1 u_1 + u_1(b_1(t,x) - a_{11}(t,x)u_1 - a_{12}(t,x)u_2), \\ \frac{\partial u_2}{\partial t} &= L_2 u_2 + u_2(b_2(t,x) - a_{21}(t,x)u_1 - a_{22}(t,x)u_2), \quad t>0,\ x\in\mathbb{R}. \end{aligned} \tag{5.5}$$

Here $L_i u = d_i(t,x)\frac{\partial^2 u}{\partial x^2} - g_i(t,x)\frac{\partial u}{\partial x}$, $i=1,2$, u_1 and u_2 denote the population densities of two competing species in ω-time and L-space periodic environment, respectively, $d_i(t,x)$, $g_i(t,x)$ and $b_i(t,x)$ are diffusion, advection and growth rates of the i-th species ($i=1,2$), respectively, and $a_{ij}(t,x)(1\le i,j\le 2)$ are inter- and intra-specific competition coefficients. In order to verify the mono-stability assumption, we first find two semi-trivial time-space periodic solutions $(u_1^*(t,x),0)$ and $(0,u_2^*(t,x))$, one of which, under a set of conditions, is shown to be globally stable for system (5.5) with periodic initial datum. Since $(0,0)$ is always a solution between the two semi-trivial time-space periodic solutions with respect to the competitive ordering, there might be two spreading speeds in general. Due to the structure of competition, we can construct upper solutions to show these two speeds (having different definitions) are identical. Some sufficient conditions for the linear determinacy of the speed are also derived. For the reaction-diffusion competition model studied in [43] with unbounded domain, we obtain more explicit conditions for the existence of the minimal wave speed. In the case where there is no spatial heterogeneity in (5.5) (i.e., all coefficients are independent of x), our analysis shows that the minimal wave speed obtained in [104] is also the single spreading speed for such a system.

For two species time-periodic and space-dependent reaction-diffusion competition models in a bounded domain, Hess and Lazer [32] (see also [31]) studied the existence, stability and attractivity of nonnegative time-periodic solutions of model systems. Hutson, Mischaikow and Poláčik [43] investigated the effect of different diffusion rates on the survival of two phenotypes of a species, and showed that the interaction between temporal and spatial variability leads to a quite different result compared with the autonomous case [16], which concluded that the phenotype with the slower diffusion rate always wins the competition. Meanwhile, in an unbounded domain, Zhao and Ruan [104] obtained the existence, uniqueness and stability of time-periodic traveling waves for time-periodic but space-independent reaction-diffusion competition models. For a reaction-diffusion competition model with seasonal succession, Ma and Zhao [61] studied the existence of single spreading speed and its linear determinacy, and showed that the spreading speed coincides with the minimal wave speed of time-periodic traveling waves. More recently, Kong, Rawal and Shen [46] proposed a competition model with nonlocal dispersal in a time and space periodic habitats, and investigated the spreading speed and its linear determinacy. For traveling waves in a time-delayed reaction-diffusion competition model with nonlocal terms, we refer to Gourley and Ruan [26]. It is worthy to point out that our approach is quite different from those in [46, 67, 78].

This chapter is organized as follows. In the next section, we establish the theory of traveling waves, almost pulsating waves and spreading speeds for time-space periodic semiflows of monostable type. In section 5.2, we apply this theory to the model system (5.5) and explore its propagation phenomena by using the competition structure.

5.1 Time-space periodic semiflows

In this section, we first present some notations and assumptions and then study the existence of traveling waves and spreading speeds for time-space periodic semiflows.

5.1.1 Preliminaries

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 $\|\cdot\|$ and the partial ordering induced by the positive cone $X_+ := C(\Omega, \mathbb{R}^l_+)$. Then $(X, X_+, \|\cdot\|)$ is a Banach lattice. 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 $\varphi_1 - \varphi_2 \in \mathrm{Int}X_+$, and $\varphi_1 > \varphi_2$ if $\varphi_1 \geq \varphi_2$ but $\varphi_1 \neq \varphi_2$. For $\varphi_1, \varphi_2 \in X$, the least upper bound of the set $\{\varphi_1, \varphi_2\}$, denoted by $\max\{\varphi_1, \varphi_2\}$, is also an element of X. Moreover,

$$\max\{\varphi_1, \varphi_2\}(x) = \max\{\varphi_1(x), \varphi_2(x)\}.$$

Let $\mathcal{H} = \mathbb{R}$ or $\mathbb{Z}$. Define $[a, b]_{\mathcal{H}}$ as a closed subset of $\mathcal{H}$ in the sense that if $\mathcal{H} = \mathbb{R}$, then $[a, b]_{\mathcal{H}} = [a, b]$ with $a, b \in \mathbb{R}$ and $a \leq b$; and if $\mathcal{H} = \mathbb{Z}$, then $[a, b]_{\mathcal{H}} = \{a, a + 1, a + 2, ..., b\}$ with $a, b \in \mathbb{Z}$ and $a \leq b$. For $r \in \mathcal{H}$ with $r > 0$, define

$r\mathbb{Z} := \{rh : h \in \mathbb{Z}\}$. We use $\mathcal{C}$ to denote all continuous and bounded functions from $\mathcal{H}$ to X. We endow $\mathcal{C}$ with the compact open topology, which can be induced by the following metric

$$d(u,v) := \sum_{k=1}^{\infty} \frac{\max_{|x|\le k} \|u(x)-v(x)\|}{2^k}, \quad u,v \in \mathcal{C}. \tag{5.6}$$

A sequence u_n is said to be convergent to u in $\mathcal{C}$ provided that $u_n(x) \to u(x)$ in X uniformly locally in $x \in \mathcal{H}$ (that is, uniformly for x in any compact subset of $\mathcal{H}$). On the other hand, if $u_n \in \mathcal{C}$ is uniformly bounded and converges uniformly locally to some function u, then $u \in \mathcal{C}$. For $u_1, u_2 \in \mathcal{C}$, we write $u_1 \ge u_2$ if $u_1(x) \ge u_2(x)$ for all $x \in \mathcal{H}$. A subset U of $\mathcal{C}$ is bounded if $\sup_{u\in U} d(u,0)$ is finite. For $u \in \mathcal{C}$, define the function $u_{[0,L]_{\mathcal{H}}} \in C([0,L]_{\mathcal{H}}, X)$ by $u_{[0,L]_{\mathcal{H}}}(x) = u(x)$. Given a bounded set $U \subset \mathcal{C}$, we use $U_{[0,L]_{\mathcal{H}}}$ to denote the set $\{u_{[0,L]_{\mathcal{H}}} : u \in U\}$. We use the Kuratowski measure to define the noncompactness of $U_{[0,L]_{\mathcal{H}}}$ which is naturally endowed with the uniform topology. The measure is defined as follows.

$$\alpha(U_{[0,L]_{\mathcal{H}}}) := \inf\{r : U_{[0,L]_{\mathcal{H}}} \text{ has a finite open cover of diameter less than } r\}. \tag{5.7}$$

The set $U_{[0,L]_{\mathcal{H}}}$ is precompact if and only if $\alpha(U_{[0,L]_{\mathcal{H}}}) = 0$.

Let $L \in \mathcal{H}$ be a positive number, We use $\mathcal{C}^{per}$ to denote the set of all L-periodic functions in $\mathcal{C}$. We endow $\mathcal{C}^{per}$ with the same topology as $\mathcal{C}$. But the convergence of a sequence in $\mathcal{C}^{per}$ will be in the following stronger sense: u_n is said to be convergent to u in $\mathcal{C}^{per}$ provided that $u_n(x) \to u(x)$ in X uniformly in $x \in [0,L]_{\mathcal{H}}$. For $u_1, u_2 \in \mathcal{C}^{per}$, we write $u_1 \ge u_2$ if $u_1(x) - u_2(x) \in X_+$ for all $x \in \mathcal{H}$, $u_1 \gg u_2$ if $u_1(x) - u_2(x) \in \mathrm{Int}X_+$ for all $x \in \mathcal{H}$, and $u_1 > u_2$ if $u_1 \ge u_2$ but $u_1 \ne u_2$.

For $x \in \mathcal{H}$, there exist a unique $k_x \in \mathbb{Z}$ and a unique $\theta_x \in [0,L)$ such that $x = k_x L + \theta_x$. Define $[x]_L$ by

$$[x]_L = k_x L.$$

For $m \in \mathbb{Z}$, we have $[x + mL]_L = [x]_L + mL$.

Let $\omega \in \mathcal{T}$ be a positive number. Assume that $\beta : \mathcal{T} \times \mathcal{H} \to \mathrm{Int}X_+$ is continuous such that $\beta(t, x)$ is ω-periodic in $t \in \mathcal{T}$ and L-periodic in $x \in \mathcal{H}$. Then for any $t \in \mathcal{T}$, $\beta(t, \cdot) \in \mathcal{C}^{per}$ and $\beta(t, \cdot) \gg 0$. Define

$$\mathcal{C}_{\beta(t,\cdot)} := \{\phi \in \mathcal{C} : 0 \leq \phi(x) \leq \beta(t, x), x \in \mathcal{H}\}, \quad t \in \mathcal{T}$$

and

$$\mathcal{C}^{per}_{\beta(t,\cdot)} = \mathcal{C}_{\beta(t,\cdot)} \cap \mathcal{C}^{per}.$$

For $y \in \mathcal{H}$ and any function $u : \mathcal{H} \to X$, define the translation operator T_y by

$$T_y[u](x) = u(x - y).$$

For $t \in \mathcal{T}$, assume that the map $Q_t : \mathcal{C}_{\beta(0,\cdot)} \to \mathcal{C}_{\beta(t,\cdot)}$ satisfies $Q_t[0] = 0$ and $Q_t[\beta(0, \cdot)](x) = \beta(t, x)$.

Definition 5.1.1. $\{Q_t\}_{t\in\mathcal{T}}$ *is said to be an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$ provided that*

(i) $Q_0 = I$, *where I is the identity map.*

(ii) $Q_t \circ Q_\omega = Q_{t+\omega}, \quad \forall t \in \mathcal{T}$.

(iii) $T_y \circ Q_t = Q_t \circ T_y, \quad \forall t \in \mathcal{T},\ y \in L\mathbb{Z}$.

(iv) $Q_t[\phi]$ *is continuous jointly in* $(t, \phi) \in \mathcal{T} \times \mathcal{C}_{\beta(0,\cdot)}$

(v) $Q_t[\phi] \geq Q_t[\psi]$, $\forall t \in \mathcal{T}$, *whenever* $\phi \geq \psi$ *in* $\mathcal{C}_{\beta(0,\cdot)}$.

Properties (ii) and (iii) characterize the temporal and spatial periodicity, respectively, for the semiflow. In time-periodic dynamical systems, the period map Q_ω is often called the Poincaré map. We use E to denote the set of all ω-time periodic and L-space periodic solutions of the semiflow $\{Q_t\}_{t\in\mathcal{T}}$ from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$. Clearly, 0 and β are two elements of E. The following observation can be easily proved.

Lemma 5.1.1. *The following statements are valid:*

(i) $p \in E$ *if and only if* $p(0,\cdot)$ *is a fixed point of* $Q_\omega : \mathcal{C}^{per}_{\beta(0,\cdot)} \to \mathcal{C}^{per}_{\beta(0,\cdot)}$.

(ii) Let $u, v \in \mathcal{C}^{per}_{\beta(0,\cdot)}$. *If* u *is a fixed point of* Q_ω *and* $\lim_{n\to\infty} Q_{n\omega}[v] = u$, *then* $\lim_{t\to\infty} d(Q_t[v], Q_t[u]) = 0$, *where* d *is the metric defined in* (5.6).

In (5.1)-(5.3), we have defined the traveling wave for the semiflow $\{Q_t\}_{t\in\mathcal{T}}$. Here we explain it in the case where the semiflow is generated by the solution maps of a time-space periodic evolution system, including how to extend such a wave solution to an entire solution and how it relates to the one introduced by Nadin [67].

We first explain how to extend a wave to an entire solution. For $t \geq r$ with $t, r \in \mathcal{T} \cup (-\mathcal{T})$, let $S_{r,t} : \mathcal{C}_{\beta(r,\cdot)} \to \mathcal{C}_{\beta(t,\cdot)}$ be the solution map of a time-space periodic evolution equation in dimension one, where r is the initial time. Then $S_{r,t}$ has following time periodicity:

$$S_{r,t} = S_{r+\omega,t+\omega}, \quad t \geq r, \quad t, r \in \mathcal{T} \cup (-\mathcal{T}).$$

Suppose that we have already established the traveling wave $W(t, x, \xi)$ for $\{S_{0,t}\}_{t\in\mathcal{T}}$ in the sense of (5.1)-(5.3). In particular,

$$S_{0,t}[W(0, \cdot, \cdot + y)] = W(t, \cdot, \cdot + y - ct), \quad t \in \mathcal{T}, y \in \mathbb{R}.$$

For convenience, we still use $W(t, x, \xi)$ to denote the periodic extension of W in time. Note that for any $t \geq r$ with $t, r \in \mathcal{T} \cup (-\mathcal{T})$, there exists $k_r \in \mathbb{Z}_+$ such that

$r + k_r\omega \geq 0$. It then follows that

$$\begin{aligned}
&S_{r,t}[W(r,\cdot,\cdot+y-cr)] \\
&= S_{r+k_r\omega,t+k_r\omega}[W(r,\cdot,\cdot+y-cr)] \\
&= S_{r+k_r\omega,t+k_r\omega}[W(r+k_r\omega,\cdot,\cdot+y-cr)] \\
&= S_{r+k_r\omega,t+k_r\omega}S_{0,r+k_r\omega}[W(0,\cdot,\cdot+y-cr+c(r+k_r\omega))] \\
&= S_{0,t+k_r\omega}[W(0,\cdot,\cdot+y-cr+c(r+k_r\omega))] \\
&= W(t,\cdot,\cdot+y-ct), \quad \forall t \in \mathcal{T} \cup (-\mathcal{T}),\ y \in \mathbb{R}.
\end{aligned}$$

This shows that the periodic extension W gives rise to an entire wave solution.

Next, we point out there are many wave-like solutions satisfying (5.1). Indeed, for a decreasing function $\phi \in \mathcal{C}_{\beta(0,\cdot)}$, we define

$$U(t,x,\xi) := Q_t[\phi(\cdot+\xi+ct-x)](x).$$

Then one may easily verify that U is periodic in x, non-increasing in ξ and satisfies (5.1). However, U is in general not periodic in time and not extendable to be an entire solution. This suggests that we first look for a wave for the Poincaré map (i.e., period map) in a certain sense and then use it as the initial value to evolve under the semiflow to construct the traveling wave for the semiflow. We will show that $W(t,x,\xi) := Q_t[V(\cdot,\cdot+\xi+ct-x)](x)$ is a traveling wave of the semiflow $\{Q_t\}_{t\in\mathcal{T}}$ if $V(x,\xi)$ is L-periodic in x, non-increasing in ξ and satisfies

$$Q_\omega[V(\cdot,\cdot+y)] = V(\cdot,\cdot+y-c\omega), \quad \forall y \in \mathbb{R}. \tag{5.8}$$

The periodicity of W in time follows from (5.8). We call such V a traveling wave of Q_ω in a strong sense.

Now let us roughly explain why (5.8) may hold for all $y \in \mathbb{R}$. Indeed, we can employ the results in [19] to show that (5.8) holds for $y \in \mathbb{R} \setminus \Gamma$, where Γ is a countable set. Since V will be carefully constructed such that $V(\cdot, \xi + \cdot - [\cdot]_L)$ is left-continuous in ξ and for any $\xi \in \mathbb{R}$ it belongs to the same compact set in periodic function spaces, one is able to use the continuity of Q_ω to pass the limit so that (5.8) also holds for $y \in \Gamma$. This procedure will be presented in an abstract way in section 2.2.

To establish the existence of traveling waves and spreading speeds, we need the following two basic assumptions on time-space periodic semiflow $\{Q_t\}_{t\in\mathcal{T}}$:

(A1) (Monostability) $\lim_{n\to\infty} Q_{n\omega}[\phi] = \beta(0,\cdot)$ for any $\phi \in \mathcal{C}^{per}_{\beta(0,\cdot)}$ with $\phi \gg 0$.

(A2) (α-contraction) There exists $\kappa \in [0,1)$ such that

$$\alpha((Q_\omega[U])_{[0,L]_\mathcal{H}}) \leq \kappa\alpha(U_{[0,L]_\mathcal{H}}),\ \forall U \subset \mathcal{C}_{\beta(0,\cdot)}$$

where α is the Kuratowski measure defined in (5.7).

Suppose $u(t,x;\phi) := Q_t[\phi](x)$ solves a time-space periodic evolution equation. Since $u(t,x;\phi)$ is L-periodic in x if ϕ is, we only need to consider the evolution equation with periodic initial data. By Lemma 5.1.1, it follows that $\beta(t,x)$ is a time-space periodic solution of the evolution equation, and (A1) is equivalent to that the time-space periodic solution $\beta(t,x)$ attracts any solution with initial value $\phi \in \mathcal{C}^{per}_{\beta(0,\cdot)}$ and $\phi \gg 0$. For a scalar reaction-diffusion equation admitting the strong maximum principle, the condition $\phi \gg 0$ may be relaxed to be $\phi > 0$. For a system of reaction-diffusion equations, such a condition in general cannot be relaxed because there probably exist semi-trivial time-space periodic solutions.

Note that the assumption (A2) is for the Poincaré map on the phase space $\mathcal{C}_{\beta(0,\cdot)}$. If the Poincaré map $Q_\omega : \mathcal{C}_{\beta(0,\cdot)} \to \mathcal{C}_{\beta(0,\cdot)}$ is compact, then (A2) is satisfied by choosing $\kappa = 0$. For a time-space periodic evolution equation with delay, if the delay is larger than the time period ω, then Q_ω is not compact but satisfies (A2).

It is worthy to point out that we do not assume that the semflow is subhomogeneous (or sublinear in some literature), which is often understood as the KPP type condition for monostable semiflows. Thus, the expected minimal wave speed may not be linearly determinate in general.

5.1.2 Traveling waves

In this subsection, we establish the existence of traveling waves for time-space periodic and monotone semiflows under assumptions (A1) and (A2).

Let $\{Q_t\}_{t\in\mathcal{T}}$ be an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$. We define a family of mappings $\{S_t\}_{t\in\mathcal{T}}$ by

$$S_t[\phi](x) = \frac{Q_t[\phi\beta(0,\cdot)](x)}{\beta(t,x)}, \quad \forall \phi \in \mathcal{C}_{\mathbf{1}},\ x \in \mathcal{H}.$$

It easily follows that $\{S_t\}_{t\in\mathcal{T}}$ is an ω-time periodic and L-space periodic monotone semiflow on $\mathcal{C}_{\mathbf{1}}$. Without loss of generality, we then assume that $\beta(t,x)$ is a positive constant, denoted still by β, and hence, we may write $\mathcal{C}_\beta$ instead of $\mathcal{C}_{\beta(t,\cdot)}$ for any $t \geq 0$. We do not scale L to be one since the habitat has been scaled to be $\mathbb{Z}$ if it is discrete. We do not scale ω to be one since in delay differential equations, the relationship between the time period and the delay is important.

Our strategy is to first establish a traveling wave for the Poincaré map in a stronger sense than usual, and then use it as an initial value for the evolution to obtain the traveling wave for the given semiflow. To establish a traveling wave for the Poincaré map Q_ω, we first use the map Q_ω (in periodic habitat) to construct a topologically conjugate map P_ω (in homogeneous discrete habitat), and then extend P_ω into a larger map $\tilde{P}_\omega$ (in homogeneous continuous habitat), which was introduced by Weinberger [93] for the study of spreading speeds. In general, $\tilde{P}_\omega$ is not compact even if Q_ω is. To overcome the difficulty caused by the non-compactness, we show that $\tilde{P}_\omega$ fits the framework of [19] (see also in section 2.2) which deals with a large class of monotone semiflows with weak compactness.

To explain the operators P_ω and $\tilde{P}_\omega$ in detail, we need to introduce some notations. Let $\mathcal{M}$ be the set of all non-increasing and bounded functions from $\mathbb{R}$ to $Y := C([0, L]_{\mathcal{H}}, X)$, and

$$\mathcal{X} = \{v \in \mathcal{M} : v(s)(L) = v(s + L)(0), s \in \mathbb{R}\}.$$

Define order intervals X_β, Y_β and $\mathcal{X}_\beta$, respectively, by

$$X_\beta = [0, \beta]_X, \quad Y_\beta = [0, \beta]_Y, \quad \text{and} \quad \mathcal{X}_\beta = [0, \beta]_{\mathcal{X}}.$$

Let

$$\bar{Y}_\beta = \{\phi \in Y_\beta : \phi(0) = \phi(L)\}.$$

and

$$\mathcal{K}_\beta = \{\phi \in C(L\mathbb{Z}, Y_\beta) : \phi(iL + L)(0) = \phi(iL)(L), i \in \mathbb{Z}\}$$

Lemma 5.1.2. [20, Section 4] *The map $F : \mathcal{C}_\beta \to \mathcal{K}_\beta$ defined by*

$$F[\phi](iL)(\theta) = \phi(iL + \theta) \tag{5.9}$$

is a homeomorphism. Further, the semiflow $\{P_t\}_{t\in\mathcal{T}}$ on $\mathcal{K}_\beta$ defined by

$$P_t = F \circ Q_t \circ F^{-1} \tag{5.10}$$

is topologically conjugate to $\{Q_t\}_{t\in\mathcal{T}}$ on $\mathcal{C}_\beta$.

One can verify that

$$F^{-1}[v](x) = v(L[x])(x - L[x]), \quad v \in \mathcal{K}_\beta. \tag{5.11}$$

Define the identity map $G : \mathcal{X}_\beta \to \mathcal{K}_\beta$ by

$$G[\phi](iL) = \phi(iL). \tag{5.12}$$

and the t-parameterized map $\tilde{P}_t$ by

$$\tilde{P}_t[\phi](s) = P_t G[\phi(\cdot + s)](0). \tag{5.13}$$

Next we use two lemmas to prove that $\tilde{P}_\omega$ maps $\mathcal{X}_\beta$ to $\mathcal{X}_\beta$ and that it fits the framework of [19] (see also in section 2.2) in one-dimensional homogeneous continuous habitat.

Lemma 5.1.3. *The following statements on $\mathcal{X}$ are valid:*

(i) Any monotone or L-periodic function from $\mathbb{R}$ to X can be embedded into $\mathcal{X}$, and hence, $\mathcal{X} \neq \emptyset$.

(ii) For $r \in \mathbb{R} \setminus \{0\}$, $r\mathcal{X} = \mathcal{X}$ and $T_r\mathcal{X} = \mathcal{X}$.

(iii) For $v_1, v_2 \in \mathcal{X}$, $v_1 + v_2 \in \mathcal{X}$.

(iv) For $v_1, v_2 \in \mathcal{X}$, the function v, defined by $v(x) := \max\{v_1(x), v_2(x)\}$, is also in $\mathcal{X}$.

Proof. We only prove statement (i) since others are trivial. In the case where f is a monotone function from $\mathbb{R}$ to X, we define $v \in \mathcal{X}$ by

$$v(s)(\theta) = f(s + \theta). \tag{5.14}$$

Clearly, $v(s)$ is monotone in s. In the case where f is L-periodic, we define

$$v(s)(\theta) = f(L[s] + \theta). \tag{5.15}$$

Then it is easy to see that $v(s) = v(0)$ for all $s \in \mathbb{R}$ due to the periodicity of f. $\square$

Lemma 5.1.4. *Assume that the Poincaré map Q_ω satisfies (A1) and (A2). Then the map $\tilde{P}_\omega : \mathcal{X}_\beta \to \mathcal{X}_\beta$ has the following properties:*

(i) $\tilde{P}_\omega \circ T_y = T_y \circ \tilde{P}_\omega, \forall y \in \mathbb{R}$, where T_y is the y-length translation operator.

(ii) $\tilde{P}_\omega : \mathcal{X}_\beta \to \mathcal{X}_\beta$ is continuous with respect to the compact open topology.

(iii) There exists $\kappa \in [0, 1)$ such that for $V \subset \mathcal{X}_\beta$, $\alpha(\tilde{P}_\omega[V](0)) \leq \kappa\alpha(V(0))$, where α is the kuratowski measure of non-compactness for bounded sets in Y.

(iv) $\tilde{P}_\omega[\phi] \geq \tilde{P}_\omega[\psi]$ whenever $\phi \geq \psi$ in $\mathcal{X}_\beta$.

(v) $\tilde{P}_\omega : \bar{Y}_\beta \to \bar{Y}_\beta$ admits two fixed points 0 and β, and for any $\bar{\zeta} \in \bar{Y}_\beta$ with $\bar{\zeta} \gg 0$, $\lim_{n\to\infty} \tilde{P}_{n\omega}[\bar{\zeta}] = \beta$.

Proof. We first show that $\tilde{P}_\omega$ maps $\mathcal{X}_\beta$ into $\mathcal{X}_\beta$ and then verify the five properties one by one. Let $v \in \mathcal{X}_\beta$ be given. By definition, we have

$$\tilde{P}_\omega[v](s) = FQ_\omega F^{-1}G[v(\cdot + s)](0).$$

Then the monotonicity of $\tilde{P}_\omega[v](s)$ follows from the monotonicity of F, Q_ω, F^{-1} and G. Since

$$T_L Q_\omega = Q_\omega T_L \quad \text{and} \quad F[\phi](L)(0) = \phi(L) = F[\phi](0)(L),$$

we obtain

$$FQ_\omega F^{-1}G[v(\cdot+s+L)](0)(0) = FQ_\omega F^{-1}G[v(\cdot+s)](L)(0) = FQ_\omega F^{-1}G[v(\cdot+s)](0)(L),$$

which is equivalent to $\tilde{P}_\omega[v](s+L)(0) = \tilde{P}_\omega[v](s)(L)$. This shows that $\tilde{P}_\omega[v] \in \mathcal{X}_\beta$, and hence, $\tilde{P}_\omega$ maps $\mathcal{X}_\beta$ into $\mathcal{X}_\beta$.

Statement (i) follows directly from the definition of $\tilde{P}_\omega$. Statement (iv) follows directly from the monotonicity of F, Q_ω, F^{-1} and G. It remains to verify statements (ii),(iii) and (v).

To show the continuity, it suffices to prove that $\tilde{P}_\omega[v_n] \to \tilde{P}_\omega[v]$ locally uniformly if $v_n \to v$ locally uniformly. Indeed, $G[v_n(\cdot+s)](i) \to G[v(\cdot+s)](i)$ locally uniformly in i, s. By the topological conjugacy between Q_ω and P_ω as well as the continuity of Q_ω, it follows that $P_\omega G[v_n(\cdot+s)](0) \to P_\omega G[v(\cdot+s)](0)$ locally uniformly in s. The continuity is then proved.

For the statement on compactness, we note that

$$\tilde{P}_\omega[V](0)(\theta) = Q_\omega[F^{-1}G[V]](\theta).$$

It then follows from (A2) and definitions of F^{-1} and G that

$$\alpha(\tilde{P}_\omega[V](0)) = \alpha((Q_\omega[F^{-1}G[V]])_{[0,L]_\mathcal{H}}) \leq \alpha((F^{-1}G[V])_{[0,L]_\mathcal{H}}) = \alpha(V(0)).$$

For statement (v), it follows from statement (i) that

$$\tilde{P}_\omega[\bar{\zeta}](s)(\theta) = \tilde{P}_\omega[\bar{\zeta}(\cdot+s)](0)(\theta) = \tilde{P}_\omega[\bar{\zeta}](0)(\theta).$$

Further, by the definition of $\tilde{P}_\omega$, we have

$$\tilde{P}_\omega[\bar{\zeta}](0)(\theta) = Q_\omega F^{-1}G[\bar{\zeta}](\theta).$$

Note that $F^{-1}G : \bar{Y}_\beta \to C_\beta^{per}$ and $F^{-1}G[\bar{\zeta}] \gg 0$ due to $\bar{\zeta} \gg 0$. It then follows from (A1) that

$$\tilde{P}_{n\omega}[\bar{\zeta}] = Q_{n\omega}F^{-1}G[\bar{\zeta}] \to \beta, \quad as \quad n \to \infty.$$

This completes the proof. □

With Lemmas 5.1.3 and 5.1.4, we can proceed as in [19] (see also in section 2.2.2) to establish the existence of traveling waves for $\tilde{P}_\omega$. Indeed, let $\varpi \in \bar{Y}_\beta$ with $0 \ll \varpi \ll \beta$. Choose ϕ to be a continuous function from $\mathbb{R}$ to X with the following properties: (i) $\phi(x)$ is non increasing in x, (ii) $\phi(x) = 0$ for $x \geq 0$ and (iii) $\phi(-\infty) = \varpi$. Define $\tilde{\phi} \in \mathcal{X}_\beta$ by

$$\tilde{\phi}(s)(\theta) = \phi(s + \theta). \tag{5.16}$$

Then $\tilde{\phi}$ has the following properties:

(1) $\tilde{\phi}(s)$ is continuously non-increasing in s;

(2) $\tilde{\phi}(s) = 0$ for $s \geq 0$;

(3) $\tilde{\phi}(-\infty) = \varpi$.

Next we use $\tilde{\phi}$ to define two numbers $-\infty < c_+^* \leq \bar{c}_+ \leq +\infty$. For $c \in \mathbb{R}$ and integer $n \geq 1$, we define the map $R_{c,\frac{1}{n}} : \mathcal{X}_\beta \to \mathcal{X}_\beta$ by

$$R_{c,\frac{1}{n}}[a](s) = \max\left\{\frac{1}{n}\tilde{\phi}(s), T_{-c\omega}\tilde{P}_\omega[a](s)\right\}$$

and a sequence of functions $a_m\left(c, \frac{1}{n}; s\right)$ by the recursion

$$a_0\left(c, \frac{1}{n}; s\right) = \tilde{\phi}(s), \quad a_{m+1}\left(c, \frac{1}{n}; s\right) = R_{c,\frac{1}{n}}\left[a_m\left(c, \frac{1}{n}; \cdot\right)\right](s). \tag{5.17}$$

Define

$$A_0 = \mathcal{X}_\beta, \quad A_{i+1} = \overline{\cup_{n\geq 1} R_{c,\frac{1}{n}}[A_i]}, \quad i \geq 1. \tag{5.18}$$

Then we have the following result.

Lemma 5.1.5. [19, Lemmas 3.1 and 3.3] *The following two statements hold true:*

(i) The set $A := \cap_{i\geq 0} \cup_{s\in\mathbb{R}} A_i(s)$ *is non-empty and compact in* Y_β*, where* A_i *is defined as in* (5.18).

(ii) $\lim_{m\to\infty} a_m(c, \frac{1}{n}; s)$ *exists and the limit, denoted by* $a(c, \frac{1}{n}; \cdot)$*, is an element in* $\mathcal{X}_\beta$ *and satisfies*

$$R_{c,\frac{1}{n}}\left[a\left(c,\frac{1}{n};\cdot\right)\right](s) = a\left(c,\frac{1}{n};s\right), \quad a.e. \quad s\in\mathbb{R}$$

and

$$a\left(c,\frac{1}{n};-\infty\right)=\beta, \quad a\left(c,\frac{1}{n};+\infty\right)\in Y_\beta \text{ is a fixed point of } \tilde{P}_\omega.$$

According to [19], we define two numbers:

$$c_+^* := \sup\{c : a(c,1;+\infty)=\beta\}, \quad \bar{c}_+ := \sup\{c : a(c,1;+\infty)>0\}. \tag{5.19}$$

Let $\tilde{E}$ be the fixed point of $\tilde{P}_\omega$ on $\bar{Y}_\beta$. We say $\psi(s-c\omega)$ is a traveling wave of $\tilde{P}_\omega$ connecting $\beta_1 \in \tilde{E}$ to $\beta_2 \in \tilde{E}$ if there exits a countable set $\Gamma \subset \mathbb{R}$ such that

$$\tilde{P}_{n\omega}[\psi](s) = \psi(s-cn\omega), \quad n\geq 0, s\in\mathbb{R}\setminus\Gamma \tag{5.20}$$

and

$$\psi(-\infty)=\beta_1, \quad \psi(+\infty)=\beta_2. \tag{5.21}$$

Applying the same arguments as in the proof of [19, Theorem 3.8](Theorem 2.2.5) to the map $\tilde{P}_\omega : \mathcal{X}_\beta \to \mathcal{X}_\beta$, we have the following result.

Lemma 5.1.6. *The following statements are valid:*

(1) *For* $c \geq c_+^*$, $\tilde{P}_\omega$ *admits a traveling wave* ψ *connecting* β *to some elements* $\beta_1 \in \tilde{E}\setminus\{\beta\}$.

(2) *If, in addition,* 0 *is isolated in* $\tilde{E}$*, then for any* $c \geq \bar{c}_+$ *either of the following holds:*

(i) there exists a traveling wave ψ connecting β to 0.

(ii) there are two ordered elements β_1, β_2 in $\tilde{E} \setminus \{0, \beta\}$ such that there exist a traveling wave ψ_1 connecting β_1 to 0 and a traveling wave ψ_2 connecting β to β_2.

Before moving forward to construct the traveling waves for $\{Q_t\}_{t\in\mathcal{T}}$ in the sense of (5.1)-(5.3), we show that the set Γ can be chosen to be empty for all traveling waves of $\tilde{P}_\omega$ established in Lemma 5.1.6.

Lemma 5.1.7. *Let $\psi(s - c\omega)$ be a left continuous traveling wave of $\tilde{P}_\omega$ established in Lemma 5.1.6 in the sense of* (5.20)-(5.21). *Then $\tilde{P}_\omega[\psi](s)$ is also left continuous, and hence, $\tilde{P}_\omega[\psi](s) = \psi(s - c\omega), s \in \mathbb{R}$.*

Proof. It suffices to prove that $\tilde{P}_\omega[\psi](s)$ is left continuous. Indeed, for any given $s \in \mathbb{R}$ and a sequence $s_n \uparrow 0$, we need to show that $\tilde{P}_\omega[\psi](s + s_n) \to \tilde{P}_\omega[\psi](s)$ as $n \to \infty$, which is equivalent to

$$\lim_{n\to\infty} Q_\omega[\psi(L[\cdot] + s + s_n)(\cdot - L[\cdot])](\theta) = Q_\omega[\psi(L[\cdot] + s)(\cdot - L[\cdot])](\theta) \tag{5.22}$$

uniformly in $\theta \in [0, L]$ due to (5.9)-(5.13). Note that $x - L[x] \in [0, L]$ for all $x \in \mathbb{R}$ and $[x]$ takes finitely many values in $\mathbb{Z}$ for x in any compact set. It then follows from the left continuity of ψ that

$$\lim_{n\to\infty} \psi(L[x] + s + s_n)(x - L[x]) = \psi(L[x] + s)(x - L[x])$$

uniformly for x in any compact set. By the continuity of Q_ω with respect to the compact open topology, we obtain the equality (5.22). □

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

Theorem 5.1.1. *Let $\{Q_t\}_{t\in\mathcal{T}}$ be an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$, and assume that (A1) and (A2) hold. Then there are two numbers $-\infty < c_+^* \leq \bar{c}_+ \leq +\infty$ such that*

(1) For any $c \geq c_+^*$, $\{Q_t\}_{t\in\mathcal{T}}$ admits a traveling wave W connecting β to some elements $\beta_1 \in E \setminus \{\beta\}$.

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

(i) there exists a traveling wave W connecting β to 0.

(ii) there are two ordered elements α_1, α_2 in $E \setminus \{0, \beta\}$ such that there exist a traveling wave W_1 connecting α_1 to 0 and a traveling wave W_2 connecting β to α_2.

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

Proof. For each admissible speed c, we have already shown that $\tilde{P}_\omega : \mathcal{X}_\beta \to \mathcal{X}_\beta$ admits a wave ψ in the sense that

$$\tilde{P}_\omega[\psi](s) = \psi(s - c\omega), \quad \forall s \in \mathbb{R}. \tag{5.23}$$

Define $V(x,\xi)$ by

$$V(x,\xi) = \psi(\xi - x + [x]_L)(x - [x]_L).$$

It is not difficult to check V is L-periodic in x and non-increasing in ξ. Then we use the definitions of F, F^{-1}, P_ω and $\tilde{P}_\omega$ to obtain

$$\begin{aligned} V(x, x - c\omega + y) &= \psi(y - c\omega + [x]_L)(x - [x]_L) \\ &= \tilde{P}_\omega[\psi](y + [x]_L)(x - [x]_L) \\ &= P_\omega G[\psi(\cdot + y + [x]_L)](0)(x - [x]_L) \\ &= FQ_\omega F^{-1}G[\psi(\cdot + y + [x]_L)](0)(x - [x]_L) \\ &= Q_\omega F^{-1}G[\psi(\cdot + y + [x]_L)](x - [x]_L) \\ &= Q_\omega F^{-1}G[\psi(\cdot + y)](x) \\ &= Q_\omega[\psi([\cdot]_L + y)(\cdot - [\cdot]_L)](x) \\ &= Q_\omega[V(\cdot, \cdot + y)](x), \quad \forall x \in \mathcal{H},\ y \in \mathbb{R}. \end{aligned} \tag{5.24}$$

We claim that $W : \mathcal{T} \times \mathcal{H} \times \mathbb{R} \to X$ defined by

$$W(t, x, \xi) = Q_t[V(\cdot, \cdot + \xi + ct - x)](x), \tag{5.25}$$

is the desired traveling wave. It suffices to show that (5.1)-(5.3) hold true. Indeed, the space periodicity and (5.1) are easily verified. Also the limit equality (5.3) follows directly from the time periodicity. Thus, it remains to prove the time periodicity. By using (5.24), we obtain

$$\begin{aligned} W(t + \omega, x, \xi) &= Q_t Q_\omega[V(\cdot, \cdot + \xi + c(t + \omega) - x)](x) \\ &= Q_t[V(\cdot, \cdot - c\omega + \xi + c(t + \omega) - x)](x) \\ &= Q_t[V(\cdot, \cdot + \xi + ct - x)](x) \\ &= W(t, x, \xi), \quad t \in \mathcal{T}, x \in \mathcal{H}, \xi \in \mathbb{R}. \end{aligned} \tag{5.26}$$

This proves the existence of traveling waves.

Next we prove the non-existence of traveling waves. If the three-variable function W is a wave in the sense of (5.1)-(5.3) and it connects β to some other time-space periodic solution $\beta_1(t,x)$ with $\beta_1(0,\cdot) < \beta$, then we have

$$W(0,x,x+y-c\omega) = Q_\omega[W(0,\cdot,\cdot+y)](x), \quad x \in \mathcal{H}, y \in \mathbb{R}$$

with

$$W(0,\cdot,-\infty) = \beta, \quad W(0,\cdot,+\infty) = \beta_1(0,\cdot).$$

Recall that $\tilde{\phi}$ is defined in (5.16). Thus, we may choose $s_0 > 0$ such that

$$\tilde{\phi}(s)(\theta) \le W(0,\theta,\theta+s+s_0). \tag{5.27}$$

Note that

$$F^{-1}G[\tilde{\phi}(\cdot+s+c\omega)](x) = \tilde{\phi}([x]+s+c\omega)(x-[x]). \tag{5.28}$$

Combining (5.17), (5.27) and (5.28), we obtain

$$\begin{aligned} a_1(c,1,s)(\theta) \quad &= \max\{\tilde{\phi}(s)(\theta), T_{-c\omega}\tilde{P}_\omega[\tilde{\phi}](s)(\theta)\} \\ &= \max\{\tilde{\phi}(s)(\theta), FQ_\omega F^{-1}G[\tilde{\phi}(\cdot+s+c\omega)](0)(\theta)\} \\ &\le \max\{\tilde{\phi}(s)(\theta), FQ_\omega[W(0,\cdot,\cdot+s+s_0+cw)](0)(\theta)\} \\ &= \max\{\tilde{\phi}(s)(\theta), F[W(0,\cdot,\cdot+s+s_0)](0)(\theta)\} \\ &= W(0,\theta,\theta+s+s_0), \end{aligned}$$

and inductively, $a_n(c,1,s)(\theta) \le W(0,\theta,\theta+s+s_0)$, $\forall n \ge 1$. This implies that

$$a(c,1,+\infty) = \lim_{s\to+\infty}\lim_{n\to\infty} a_n(c,1,s) \le \lim_{s\to+\infty}\lim_{n\to\infty} W(0,\cdot,\cdot+s+s_0) = \beta_1(0,\cdot) < \beta,$$

which, together with the definition of c_+^*, implies that $c \ge c_+^*$. Similarly, if W is a traveling wave connecting β to 0 with speed c, then $c \ge \bar{c}_+$. □

We remark that there are examples arising from nonlocal or fractional diffusion equations such that $c_+^* = +\infty$. It is an interesting problem to find conditions to exclude such a possibility for semiflows, but it beyonds the purpose of this paper. When $c_+^* = +\infty$ (or $\bar{c}_+ = +\infty$), the condition $c \geq c_+^*$ (or $c \geq \bar{c}_+$) in Theorem 5.1.1 is vacuous, and hence, there are no traveling waves. Based on the constructions of V and W in the proof of Theorem 5.1.1, we further show the existence of almost pulsating waves in the sense of Definition 5.0.2.

Theorem 5.1.2. *Let $W(t, x, \xi)$ be a traveling wave with speed c, as established in Theorem 5.1.1, and $\hat{W}$ be its periodic extension in time. Define a family of entire solutions $u(t, x; y) := \hat{W}(t, x, x - ct + y)$ indexed by $y \in \mathbb{R}$. Then there exists a countable set $D \subset \mathbb{R}$ such that for any $y \in \mathbb{R} \setminus D$, $u(t, x; y)$ is an almost pulsating wave connecting two time-space periodic solutions.*

Proof. It suffices to consider positive time due to the periodicity. In the case where $c\omega/L = p/q$ for some integers p and q, the periodicity of W in the first two variables implies that

$$\begin{aligned} u(t + q\omega, x + pL; y) &= W(t + q\omega, x + pL; x + pL - ct - cq\omega + y) \\ &= W(t, x; x - ct + y) = u(t, x; y). \end{aligned}$$

In the case where $c\omega/L$ is irrational, since the set of rational numbers is dense in $\mathbb{R}$, we can choose a sequence of integer pairs (a_k, b_k) such that $b_k \geq k$, $\frac{a_k}{b_k} < c\omega/L$, and $\lim_{k\to\infty} \frac{a_k}{b_k} = c\omega/L$. Set

$$m_k := \min \left\{ m \in \mathbb{Z}_+ : \frac{a_k + m}{b_k} > c\omega/L \right\}.$$

It follows that

$$c\omega/L \in \left(\frac{a_k + m_k - 1}{b_k}, \frac{a_k + m_k}{b_k} \right), \quad \forall k \geq 1.$$

Letting $p_k = a_k + m_k$ and $q_k = b_k$, we then have

$$\lim_{k\to\infty} q_k = +\infty, \quad \left| c\omega/L - \frac{p_k}{q_k} \right| \le \frac{1}{q_k} \le 1, \quad \forall k \ge 1.$$

By the definition of $u(t, x; y)$ and (5.25), it easily follows that

$$\begin{aligned} u(t + q_k\omega, x + p_k L; y) &= W(t, x; x + p_k L - ct - cq_k\omega + y) \\ &= Q_t[V(\cdot, \cdot + y + p_k L - cq_k\omega)](x). \end{aligned} \tag{5.29}$$

Recall that $[t]_\omega = [\frac{t}{\omega}]\omega$, where $[s]$ is the integer part of real number s. In view of (5.24), we further infer that

$$u(t + q_k\omega, x + p_k L; y) = Q_{t-[t]_\omega}[V(\cdot, \cdot + y + p_k L - cq_k\omega - c[t]_\omega)](x). \tag{5.30}$$

Note that $V(x, \xi) = \psi(\xi - x + [x]_L)(x - [x]_L)$, where $\psi \in \mathcal{X}_\beta$ is an abstract non-increasing left continuous function from $\mathbb{R}$ to $C([0, L]_{\mathcal{H}}, X)$ (see Lemma 5.1.7), and it is continuous almost everywhere except for a countable set Γ. Define

$$D = \{c[t]_\omega - [x]_L + z \in \mathbb{R} : \ (t, x) \in \mathbb{R}^2, z \in \Gamma\}.$$

Clearly, D is a countable subset of $\mathbb{R}$. Now we claim that for any given $y \in \mathbb{R} \setminus D$,

$$V(x, x + y + p_k L - cq_k\omega - c[t]_\omega) \to V(x, x + y - c[t]_\omega) \tag{5.31}$$

uniformly for all $t \in \mathbb{R}$ and x in any compact subset of $\mathbb{R}$. Indeed, it is easy to see that (5.31) is equivalent to

$$\psi(y + p_k L - cq_k\omega - c[t]_\omega + [x]_L) \to \psi(y - c[t]_\omega + [x]_L) \quad \text{in } C([0, L]_{\mathcal{H}}, X) \tag{5.32}$$

uniformly for all $t \in \mathbb{R}$ and x in any compact subset of $\mathbb{R}$. Since $\psi(\pm\infty)$ exist and $p_k L - cq_k\omega \in [-L, L]$, it follows that for any $\epsilon > 0$ and $M > 0$, there exists $C_1 > 0$ such that

$$|\psi(y + p_k L - cq_k\omega - c[t]_\omega + [x]_L) - \psi(y - c[t]_\omega + [x]_L)| < \epsilon$$

for all $(t,x) \in \mathbb{R}^2$ satisfying

$$|y - c[t]_\omega + [x]_L| \geq C_1 \quad \text{and} \quad |x| \leq M,$$

which, due to $c \neq 0$, is true whenever $|t| \geq t_0$ for some large number $t_0 > 0$. It remains to show that there exists an integer k_0 such that for all $k \geq k_0$,

$$|\psi(y + p_k L - cq_k\omega - c[t]_\omega + [x]_L) - \psi(y - c[t]_\omega + [x]_L)| < \epsilon, \ \forall\, |t| \leq t_0, \ |x| \leq M,$$

which is implied by the continuity of $\psi(s)$ at finitely many points $s = y - c[t]_\omega + [x]_L \notin \Gamma$. This shows that (5.32) holds uniformly for all $t \in \mathbb{R}$ and x in any compact subset of $\mathbb{R}$. Note that $t - [t]_\omega \in [0,\omega]$ for all $t \in \mathbb{R}$ and $Q_t[\phi]$ is continuous in (t,ϕ) with respect to the compact open topology. It then follows from (5.30) and (5.31) that $\lim_{k\to\infty} u(t + q_k\omega, x + p_k L) = u(t,x)$ uniformly for all $t \in \mathbb{R}$ and x in any compact subset of $\mathbb{R}$. □

Remark 5.1.1. *The almost pulsating wave $u(t,x)$ constructed in Theorem 5.1.2 also has the property that $u(t + q_k\omega, x + p_k L) \to u(t,x)$ uniformly for all $x \in \mathbb{R}$ and t in any compact subset of $\mathbb{R}$ under the following additional continuity assumption:*

(A3) For any $\phi_n, \phi \in \mathcal{C}_\beta$ with $\lim_{n\to\infty} \phi_n(x) = \phi(x)$ uniformly for all $x \in \mathbb{R}$,

$$\lim_{n\to\infty} Q_t[\phi_n](x) = Q_t[\phi](x),$$

uniformly for all $(t,x) \in [0,\omega] \times \mathbb{R}$.

This is because for any given $y \in \mathbb{R} \setminus D$, the convergence in (5.32) are uniform for all $x \in \mathbb{R}$ and t in any compact subset of $\mathbb{R}$, and hence, the desired convergence follows from (5.30) and the assumption (A3).

5.1.3 Spreading speeds

So far, we have already proved that there exist two critical speeds c_+^* and $\bar{c}_+$ for non-increasing traveling waves. In this subsection, we use these two numbers to describe the rightward spreading property of solutions with appropriate initial datum.

Theorem 5.1.3. *Let $\{Q_t\}_{t\in\mathcal{T}}$ be an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$,, and assume that (A1) and (A2) hold. Then the following statements are valid:*

(i) For $c > \bar{c}_+$, we have $\lim_{x\geq ct} Q_t[\phi](x) = 0$ provided that $\phi \in \mathcal{C}_{\beta(0,\cdot)}$ vanishes when x is greater than some $x_0 \in \mathcal{H}$ and $\phi \leq \varpi \ll \beta(0,\cdot)$ for some $\varpi \in \mathcal{C}^{per}_{\beta(0,\cdot)}$ with $\varpi \gg 0$.

(ii) For $c < c_+^*$, we have $\lim_{t\to\infty, x\leq ct} |Q_t[\phi](x) - \beta(t,x)| = 0$ provided that $\phi \in \mathcal{C}_{\beta(0,\cdot)}$ satisfies $\phi(x) \geq \sigma$ when x is less than some $K \in \mathcal{H}$ for some $\sigma \in X$ with $\sigma \gg 0$.

Proof. To prove these spreading properties, we again use $\tilde{P}_\omega$ but on another phase space $\mathcal{Y}_\beta$, which is defined by

$$\mathcal{Y}_\beta = \{v \in C(\mathbb{R}, Y_\beta) : v(s)(L) = v(s+L)(0)\},$$

equipped with the compact open topology. It was shown in Proposition 4.5.1 that $\tilde{P}_\omega$ maps $\mathcal{Y}_\beta$ to $\mathcal{Y}_\beta$ and $\tilde{P}_\omega$ admits the five properties in Lemma 5.1.4 with $\mathcal{X}_\beta$ replaced by $\mathcal{Y}_\beta$. Note that different notations are used in Proposition 4.5.1. Thus, $\tilde{P}_\omega : \mathcal{Y}_\beta \to \mathcal{Y}_\beta$ has the same spreading property as in [19, Remark 3.7](see also Theorem 2.2.7). On the other hand, since the semiflow $\{\tilde{P}_t\}_{t\in\mathcal{T}}$ is time periodic and defined in the medium $\mathbb{R}$, one may see from [53, Theorem 2.3] that $\{\tilde{P}_t\}_{t\in\mathcal{T}}$ has the spreading properties stated in Theorem 5.1.3 with $\mathcal{C}_{\beta(0,\cdot)}, Q_t$, and X replaced by $\mathcal{Y}_\beta, \tilde{P}_t$ and Y respectively. Next we show how to derive the spreading property of $\{Q_t\}_{t\in\mathcal{T}}$ from $\tilde{P}_\omega$.

We look for the spreading properties of Q_t which are inherited from $\tilde{P}_t$. Indeed, for $\phi \in C(\mathcal{H}, X)$, define $v \in \mathcal{Y}_\beta$ by

$$v(s)(\theta) = \phi\left([s]_L + \theta\right).$$

Then for any $s \in \mathbb{R}, \theta \in [0, L]$ and $n \geq 1$, we have

$$\begin{aligned}
\tilde{P}_t[v](s)(\theta) \quad &= P_t G[v(\cdot + s)](0)(\theta) \\
&= F Q_t F^{-1} G[v(\cdot + s)](0)(\theta) \\
&= Q_t F^{-1} G[v(\cdot + s)](\theta) \\
&= Q_t[v([\cdot]_L + s)(\cdot - [\cdot]_L)](\theta).
\end{aligned}$$

In particular, setting $s = iL, i \in Z$, we obtain

$$\tilde{P}_t[v](iL)(\theta) = Q_t[v([\cdot]_L)(\cdot - [\cdot]_L)](\theta + iL) = Q_t[\phi](\theta + iL),$$

which is equivalent to

$$Q_t[\phi](x) = \tilde{P}_t[v]([x]_L)(x - [x]_L), \quad x \in \mathcal{H}, t \in \mathcal{T}.$$

Thus, the statements for $\{Q_t\}_{t \in \mathcal{T}}$ hold true. □

To finish this section, we note that similar arguments can be used to establish the existence of non-decreasing traveling waves $W(t, x, x + ct)$ and the leftward spreading property in terms of two critical speeds c_-^* and $\bar{c}_-$ satisfying $-\infty < c_-^* \leq \bar{c}_- \leq +\infty$.

5.2 Two species competition model

In this section, we first use the abstract results in last section to study the propagation phenomena for a two species competition reaction-advection-diffusion system in time-space periodic environment. Then we obtain sufficient conditions for these two speeds to be identical and linearly determinate, respectively. Two specific cases are also discussed in detail.

5.2.1 The periodic initial value problem

In this subsection, we investigate the global dynamics of the time and space periodic Lotka-Volterra competition system with the periodic initial values. Let ω and L be positive real numbers. We assume that

(a) $d_i(t,x)$, $g_i(t,x)$, $a_{ij}(t,x)$ and $b_i(t,x)$ are ω-periodic in t and L-periodic in x, $d_i, g_i, a_{ij}, b_i \in C^{\frac{\nu}{2},\nu}(\mathbb{R}\times\mathbb{R})$, $1 \le i,j \le 2$, where $C^{\frac{\nu}{2},\nu}(\mathbb{R}\times\mathbb{R})$ is a Hölder continuous space with the Hölder exponent $\frac{\nu}{2}$ for the first component and $\nu \in (0,1)$ for the second component.

(b) $a_{ij}(t,x) > 0$, $\forall (t,x) \in \mathbb{R}\times\mathbb{R}$, $1 \le i,j \le 2$.

(c) There exists a positive number α_0 such that $d_i(t,x) \ge \alpha_0, \forall (t,x) \in \mathbb{R}\times\mathbb{R}, i = 1,2$, i.e., the operator $L_i u = d_i(t,x)\frac{\partial^2 u}{\partial x^2} - g_i(t,x)\frac{\partial u}{\partial x}$ is uniformly elliptic.

In the sequel, if there is no specific mention, the periodicity will always refer to the time and space periods (ω, L).

Let $\mathcal{P}$ be the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}$ equipped with the maximum norm $\|\cdot\|_{\mathcal{P}}$, and $\mathcal{P}_+ = \{\psi \in \mathcal{P} : \ \psi(x) \ge 0, \forall x \in \mathbb{R}\}$ be a positive cone of $\mathcal{P}$. Then $(\mathcal{P}, \mathcal{P}_+)$ is a strongly ordered Banach lattice. Assume that time-space periodic functions $d, g, h \in C^{\frac{\nu}{2},\nu}(\mathbb{R}\times\mathbb{R})$ and $d(\cdot,\cdot) > 0$. By Theorem 2.1.1(see, e.g., [31, Theorem 7.2]) and the arguments similar to those in [31, II.14], it follows that the scalar parabolic eigenvalue problem

$$-\frac{\partial v}{\partial t} + d(t,x)\frac{\partial^2 v}{\partial x^2} - g(t,x)\frac{\partial v}{\partial x} + h(t,x)v = \lambda v, \quad (t,x) \in \mathbb{R}\times\mathbb{R},$$
$$v(t,x+L) = v(t,x),\ v(t+\omega,x) = v(t,x), \quad \forall (t,x) \in \mathbb{R}\times\mathbb{R} \tag{5.33}$$

admits a principal eigenvalue $\lambda(d,g,h)$ associated with a positive time-space periodic eigenfunction $\phi(t,x)$. Using the arguments similar to those in [106, Theorem 2.3.4] , as applied to the Poincaré map associated with system (5.34), we have the following result.

Proposition 5.2.1. *Assume that time-space periodic functions $d,g,c,e \in C^{\frac{\nu}{2},\nu}(\mathbb{R}\times\mathbb{R})$, and $d(\cdot,\cdot) > 0, e(\cdot,\cdot) \geq 0$ ($\not\equiv 0$). Let $u(t,x,\phi)$ be the unique solution of the following parabolic equation:*

$$\frac{\partial u}{\partial t} = d(t,x)\frac{\partial^2 u}{\partial x^2} - g(t,x)\frac{\partial u}{\partial x} + u(c(t,x) - e(t,x)u), \quad t>0,\ x\in\mathbb{R},$$
$$u(0,x) = \phi(x) \in \mathcal{P}_+, \quad x \in \mathbb{R}. \tag{5.34}$$

Then the following statements are valid:

(i) If $\lambda(d,g,c) \leq 0$, then $u = 0$ is globally asymptotically stable with respect to initial values in $\mathcal{P}_+$;

(ii) If $\lambda(d,g,c) > 0$, then (5.34) admits a unique positive time-space periodic solution $u^*(t,x)$, and it is globally asymptotically stable with respect to initial values in $\mathcal{P}_+\backslash\{0\}$.

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 $(\mathbb{P}, \|\cdot\|_{\mathbb{P}})$ is a Banach lattice.

Clearly, for any $\varphi \in \mathbb{P}_+$, (5.5) has a unique nonnegative solution $u(t,\cdot,\varphi)$ defined on $[0,\infty)$, and $u(t,\cdot,\varphi) \in \mathbb{P}_+$ for all $t \geq 0$.

By Proposition 5.2.1, we see that there exist two positive time-space periodic functions $u_1^*(t,x)$ and $u_2^*(t,x)$ such that $E_1 := (u_1^*(t,x),0)$, $E_2 := (0,u_2^*(t,x))$ are the time-space periodic solutions of system (5.5) provided that $\lambda(d_i,g_i,b_i) > 0,\ i=1,2$. Since we mainly concern about the case of the competition exclusion, we impose the following conditions on system (5.5):

(H1) $\lambda(d_i,g_i,b_i) > 0,\ i=1,2.$

(H2) $\lambda(d_1,g_1,b_1 - a_{12}u_2^*) > 0.$

(H3) System (5.5) has no positive time-space periodic solution.

Condition (H1) guarantees the existence of two semi-trivial time-space periodic solutions of system (5.5), and (H2) implies that $(0,u_2^*(t,x))$ is unstable. Moreover, by Lemma 4.4.1 with $\mu = 0, d(t,x) = d_1(t,x)$ and $g(t,x) = g_1(t,x), \forall (t,x) \in \mathbb{R}\times\mathbb{R}$, we know that (H2) implies $\lambda(d_1,g_1,b_1) > 0$. Thus, we could simply drop the assumption $\lambda_1(d_1,g_1,b_1) > 0$ from (H1).

Slightly modifying the arguments in [31, Example 34.2], we have the following observation.

Proposition 5.2.2. *Let $\underline{b}_1(t) := \min\limits_{x\in[0,L]} b_1(t,x)$, $\overline{b}_2(t) := \max\limits_{x\in[0,L]} b_2(t,x)$, and $\overline{a}_{11}(t)$, $\overline{a}_{12}(t)$, $\underline{a}_{21}(t)$, $\underline{a}_{22}(t)$ be defined in a similar way. Then (H3) holds true provided that*

$$\int_0^T \underline{b}_1(t)dt > \max_{t\in[0,\omega]} \frac{\overline{a}_{12}(t)}{\underline{a}_{22}(t)} \cdot \int_0^T \overline{b}_2(t)dt, \text{ and } \int_0^T \overline{b}_2(t)dt \leq \max_{t\in[0,\omega]} \frac{\underline{a}_{21}(t)}{\overline{a}_{11}(t)} \cdot \int_0^T \underline{b}_1(t)dt.$$

Under assumptions (H1)–(H3), there are three nonnegative time-space periodic solutions: $E_0 = (0,0)$, $E_1 := (u_1^*(t,x),0)$, and $E_2 := (0,u_2^*(t,x))$. Next, we use the theory developed in [35] for abstract competitive systems (see also [32]) to prove the global stability of E_1.

Theorem 5.2.1. *Assume that (H1)–(H3) hold. Then* $E_1(u_1^*(t,x),0)$ *is globally asymptotically stable for all initial values* $\phi=(\phi_1,\phi_2)\in\mathbb{P}_+$ *with* $\phi_1\not\equiv 0$.

Proof. Since (H2) holds true, the arguments similar to those in [106, Proposition 7.1.1] imply the following observation.

Claim. There exists $\delta_0>0$ such that $\limsup_{n\to\infty}\|u(n\omega,x,\phi)-(0,u_2^*(0,x))\|_{\mathbb{P}}\geq\delta_0$ for any $\phi\in\mathbb{P}_+$ with $\phi_1\not\equiv 0$.

By the above claim and (H3), we rule out possibility (a) and (c) in Theorem 2.1.4 with $T(\phi)=u(\omega,\cdot,\phi)$. Since E_2 is repellent in some neighborhood of itself, Theorem 2.1.4 implies that E_1 is globally asymptotically stable for all initial values $\phi\in\mathbb{P}_+$ with $\phi_1\not\equiv 0$. □

5.2.2 Spreading speeds and traveling waves

In this subsection, we study the spreading speeds and time-space periodic traveling waves for system (5.5). By a change of variables $v_1=u_1, v_2=u_2^*(t,x)-u_2$, we transform system (5.5) into the following cooperative system:

$$\begin{aligned}\frac{\partial v_1}{\partial t}&=L_1v_1+v_1(b_1(t,x)-a_{12}(t,x)u_2^*(t,x)-a_{11}(t,x)v_1+a_{12}(t,x)v_2),\quad t>0,\ x\in\mathbb{R},\\ \frac{\partial v_2}{\partial t}&=L_2v_2+a_{21}(t,x)v_1(u_2^*(t,x)-v_2)+v_2(b_2(t,x)-2a_{22}(t,x)u_2^*(t,x)+a_{22}(t,x)v_2).\end{aligned}\tag{5.35}$$

Note that three time-space solutions of (5.5), respectively, become

$$\hat{E}_0=(0,u_2^*(t,x)),\ \hat{E}_1=(u_1^*(t,x),u_2^*(t,x)),\ \hat{E}_2=(0,0).$$

To apply Theorems 5.1.1 and 5.1.3 to (5.35), we need to specify the meaning of the notations there. More precisely,

$$X = \mathbb{R}^2, \quad \mathcal{H} = \mathbb{R}, \quad \mathcal{T} = \mathbb{R}_+, \quad \beta(t,x) = \hat{E}_1, \quad 0 = \hat{E}_2.$$

Other notations such as $\mathcal{C}_{\beta(0,\cdot)}$ and $\mathcal{C}^{per}_{\beta(0,\cdot)}$ in Theorems 5.1.1 and 5.1.3 are then accordingly specified.

Let $\mathbb{Y}$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$, $T_1(t,s)$ and $T_2(t,s)$ be the linear semigroups on $\mathbb{Y}$ generated by

$$\frac{\partial v}{\partial t} = L_1 v + v(b_1(t,x) - a_{12}(t,x)u_2^*(t,x))$$

and

$$\frac{\partial v}{\partial t} = L_2 v + v(b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x)),$$

respectively. It follows that $T_1(t,s)$ and $T_2(t,s)$ are compact with the respect to the compact open topology for each $t > s \geq 0$ (see, e.g., [31]). For any $u = (u_1, u_2) \in \mathcal{C}$, define $F : [0, +\infty) \times \mathcal{C} \to \mathcal{C}$ by

$$F(t,u) = \begin{pmatrix} -a_{11}(t,\cdot)u_1^2 + a_{12}(t,\cdot)u_1u_2 \\ a_{21}(t,\cdot)u_2^*(t,\cdot)u_1 - a_{21}(t,\cdot)u_1u_2 + a_{22}(t,\cdot)u_2^2 \end{pmatrix}.$$

Then we rewrite system (5.35) as an integral equation form:

$$\begin{aligned} &v(t) = T(t,0)v(0) + \int_0^t T(t,s)F(s,v(s))ds, \quad t > 0, \\ &v(0) = \phi \in \mathcal{C}_{\beta(0,\cdot)}, \end{aligned} \tag{5.36}$$

where $T(t,s) = diag(T_1(t,s), T_2(t,s))$.

As usual, a solution of (5.36) is called a mild solution of system (5.35). It then follows that for any $\phi \in \mathcal{C}_{\beta(0,\cdot)}$, system (5.35) has a mild solution $u(t,\cdot,\phi)$ defined on $[0,\infty)$ with $u(0,\cdot,\phi)=\phi$, and $u(t,\cdot,\phi)\in\mathcal{C}_{\beta(t,\cdot)}$ for all $t\geq 0$, and it is a classical solution when $t>0$.

Definition 5.2.1. *A function $u(t):=u(t,\cdot)$ is said to be an upper (a lower) solution of system* (5.35) *if it satisfies*

$$u(t)\geq(\leq)T(t,0)u(0)+\int_0^t T(t,s)F(s,u(s))ds,\quad t\geq 0.$$

Define a family of operators $\{Q_t\}_{t\geq 0}$ from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$ by $Q_t(\phi):=u(t,\cdot,\phi)$, where $u(t,\cdot,\phi)$ is the solution of system (5.35) with $u(0,\cdot)=\phi\in\mathcal{C}_{\beta(0,\cdot)}$. Next we show that $\{Q_t\}_{t\geq 0}$ is an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$ in the sense of Definition 5.1.1. Indeed, since for any $a\in L\mathbb{Z}$, $v(t,x):=u(t,x-a,\phi)$ and $w(t,x):=u(t+\omega,x,\phi)$ are solutions of (5.35) with initial conditions $v(0,x)=u(0,x-a,\phi)$ and $w(0,x)=u(\omega,x,\phi)$, respectively, we see that Q_t satisfies the second and third properties in Definition 5.1.1. The fourth property and (A2) follow from the same argument as in [63, Theorem 8.5.2]. The fifth property is true since system (5.35) is cooperative and the comparison principle holds. Moreover, Theorem 5.2.1 implies (A1) is valid. Thus, we have the following observation.

Proposition 5.2.3. *Assume that (H1)–(H3) hold. Then $\{Q_t\}_{t\geq 0}$ is an ω-time periodic and L-space periodic monotone semiflow from $\mathcal{C}_{\beta(0,\cdot)}$ to $\mathcal{C}_{\beta(t,\cdot)}$, and Q_ω satisfies (A1) and (A2).*

By Proposition 5.2.3, we see that $\{Q_t\}_{t\geq 0}$ satisfies all conditions in Theorem 5.1.1. Thus, there exist two numbers $\bar{c}_+$ and c_+^* for the minimal speed of different kind of traveling waves. In Theorem 5.1.1, $\bar{c}_+$ might be plus infinite and the information of the limits of traveling waves at $\pm\infty$ is not fully understood for general semiflows. Below, we will use the structure of competition to show that $\bar{c}_+$ is finite and derive some conditions under which the limits of traveling waves at $\pm\infty$ can be figured out. By the comparison arguments, it is easy to see that $\bar{c}_+ \leq \max\{c^*_{1+}, c^*_{2+}\}$, where c^*_{i+} is the rightward spreading speed of the u_i species in the absence of the u_{3-i} species, $i = 1, 2$. Since c^*_{1+} and c^*_{2+} are determined by two Fisher-KPP type equations (see (5.37) and (5.39) below), it follows that $\bar{c}_+ < +\infty$.

To show that $\bar{c}_+$ is the minimal wave speed for periodic traveling waves of system (5.35) connecting $\beta(t, x)$ to 0, we propose the following assumption:

(H4) $c^*_{1+} + c^*_{2-} > 0$, where c^*_{1+} and c^*_{2-} are the rightward and leftward spreading speeds of two Fisher-KPP type equations (5.37) and (5.39), respectively.

Note that c^*_{1+} is the rightward spreading speed of u_1 species when u_2 species vanishes, and c^*_{2-} is the leftward spreading speed of u_2 species when u_1 species vanishes. When two species have opposite advection, they may separate even without competition. Assumption (H4) excludes such a possibility so that the competition plays a vital role. We remark that in the case where $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ with $d_i \in C^{\frac{v}{2}, 1+\nu}(\mathbb{R} \times \mathbb{R})$, or all the coefficient functions in (5.37) and (5.39) are even in x except g_i is odd in x, $i = 1, 2$, Lemma 5.2.2 in the forthcoming section 5.2.4 shows that (H1) and (H2) guarantee (H4).

Theorem 5.2.2. *Assume that (H1)–(H4) hold. Then for any $c \geq \bar{c}_+$, system* (5.35) *admits a periodic traveling wave $(U(t, x, x - ct), V(t, x, x - ct))$ connecting $\beta(t, x)$ to* 0*, with wave profile components $U(t, x, \xi)$ and $V(t, x, \xi)$ being continuous and non-increasing in ξ, and for any $c < \bar{c}_+$, there is no such traveling wave connecting $\beta(t, x)$ to* 0.

Proof. In view of Theorem 5.1.1 (2) and (3), it suffices to rule out the second case in Theorem 5.1.1 (2). Suppose, by contradiction, that the statement in Theorem 5.1.1

(2)(ii) is valid for some $c \geq \bar{c}_+$. Note that system (5.35) has exactly three time-space periodic solutions and $\hat{E}_0 = (0, u_2^*(t,x))$ is the only intermediate time-space periodic solution between $\hat{E}_1 = (u_1^*(t,x), u_2^*(t,x))$ and $\hat{E}_2 = (0,0)$, then we have $\alpha_1 = \alpha_2 = \hat{E}_0$. Thus, by restricting system (5.35) on the order interval $[\hat{E}_0, \hat{E}_1]$ and $[\hat{E}_2, \hat{E}_0]$, respectively, we see that one scalar equation

$$u_t = L_1 u + u(b_1(t,x) - a_{11}(t,x)u) \tag{5.37}$$

admits a periodic traveling wave $U(t,x,x-ct)$ connecting $u_1^*(t,x)$ to 0 with $U(t,x,\xi)$ being continuous and nonincreasing in ξ, and the other scalar equation

$$v_t = L_2 v + v(b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x) + a_{22}(t,x)v) \tag{5.38}$$

also admits a periodic traveling wave $V(t,x,x-ct)$ connecting $u_2^*(t,x)$ to 0 with $V(t,x,\xi)$ being continuous and nonincreasing in ξ.

Let $W(t,x,x-ct) = u_2^*(t,x) - V(t,x,x-ct)$. Then $W(t,x,x-ct)$ is a periodic traveling wave connecting 0 to $u_2^*(t,x)$ of the following scalar equation with $W(t,x,\xi)$ being continuous and nondecreasing in ξ

$$w_t = L_2 w + w(b_2(t,x) - a_{22}(t,x)w). \tag{5.39}$$

Note that $W(t,x,x-ct)$ is a periodic leftward traveling wave connecting 0 to $u_2^*(t,x)$ with wave speed $-c$, and that systems (5.37) and (5.39) 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., [53, Theorem 2.1–2.3]). It then follows that $c \geq c_{1+}^*$ and $-c \geq c_{2-}^*$. This implies that $c_{1+}^* + c_{2-}^* \leq 0$, a contradiction. $\square$

Let $\lambda_2(\mu)$ be the principle eigenvalue of the parabolic eigenvalue problem:

$$\begin{aligned}
&\lambda\psi = -\frac{\partial\psi}{\partial t} + d_2(t,x)\frac{\partial^2\psi}{\partial x^2} - (2\mu d_2(t,x) + g_2(t,x))\frac{\partial\psi}{\partial x} \\
&+ \big(d_2(t,x)\mu^2 + g_2(t,x)\mu + b_2(t,x) - a_{22}(t,x)u_2^*(t,x)\big)\,\psi, \quad (t,x)\in\mathbb{R}\times\mathbb{R}, \qquad (5.40)\\
&\psi(t,x+L)=\psi(t,x),\ \psi(t+\omega,x)=\psi(t,x), \quad (t,x)\in\mathbb{R}\times\mathbb{R}.
\end{aligned}$$

In order to prove that system (5.35) admits a single rightward spreading speed, we impose the following assumption:

(H5) $\limsup_{\mu\to 0^+}\frac{\lambda_2(\mu)}{\mu} \le c_{1+}^*$, where c_{1+}^* is the rightward spreading speed of (5.37).

By virtue of Lemma 4.4.2, it follows that in the case where $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ with $d_i \in C^{1+\nu}(\mathbb{R})$, or all the coefficient functions of system (5.35) are even in x except g_i is odd in x, $i=1,2$, (H5) is automatically satisfied provided that (H1) and (H2) hold true.

Theorem 5.2.3. *Assume that (H1)–(H5) hold. Then the following statements are valid for system* (5.35)*:*

(i) If $\phi \in \mathcal{C}_{\beta(0,\cdot)}$, $0 \le \phi \le \varpi \ll \beta(0,\cdot)$ for some $\varpi \in \mathcal{C}^{per}_{\beta(0,\cdot)}$, and $\phi(x)=0, \forall x \ge H$, for some $H\in\mathbb{R}$, then $\lim_{t\to\infty, x\ge ct} u(t,x,\phi)=0$ for any $c > \bar{c}_+$.

(ii) If $\phi \in \mathcal{C}_{\beta(0,\cdot)}$ and $\phi(x) \ge \sigma$, $\forall x \le K$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K\in\mathbb{R}$, then $\lim_{t\to\infty, x\le ct}(u(t,x,\phi)-\beta(t,x))=0$ for any $c<\bar{c}_+$.

Proof. In view of Theorem 5.1.3, it suffices to show that $\bar{c}_+ = c_+^*$. If this is not valid, then the definition of $\bar{c}_+$ and c_+^* implies that $\bar{c}_+ > c_+^*$. By Theorem 5.1.1 (1) and (3), it follows that system (5.35) admits a periodic traveling wave $(U_1(t,x,x-c_+^*t), U_2(t,x,x-c_+^*t))$ connecting $(u_1^*(t,x),u_2^*(t,x))$ to $(0,u_2^*(t,x))$ with $U_i(t,x,\xi)(i=$

$1, 2)$ being continuous and nonincreasing in ξ. Therefore, $U_2 \equiv u_2^*(t,x)$, and $U_1(t,x,x-c_+^*t)$ is a periodic traveling wave connecting $u_1^*(t,x)$ to 0. This implies $c_+^* \geq c_{1+}^*$ where c_{1+}^* is the rightward spreading of (5.37). By the linear operators approach as shown in [53, Theorem B] and [54, Theorem 3.10], it then follows that $c_{1+}^* = \inf_{\mu>0} \frac{\lambda_1(\mu)}{\mu}$, where $\lambda_1(\mu)$ is the principal eigenvalue of the scalar parabolic eigenvalue problem:

$$
\begin{aligned}
&\lambda\psi = -\frac{\partial\psi}{\partial t} + d_1(t,x)\frac{\partial^2\psi}{\partial x^2} - (2\mu d_1(t,x) + g_1(t,x))\frac{\partial\psi}{\partial x} \\
&+(d_1(t,x)\mu^2 + g_1(t,x)\mu + b_1(t,x))\psi, \quad (t,x) \in \mathbb{R}\times\mathbb{R}, \\
&\psi(t,x+L) = \psi(t,x),\ \psi(t+\omega,x) = \psi(t,x), \quad (t,x) \in \mathbb{R}\times\mathbb{R}.
\end{aligned} \tag{5.41}
$$

Note that $\frac{\lambda_1(\mu)}{\mu}$ is a continuous function and $\lim\limits_{\mu\to 0^+} \frac{\lambda_1(\mu)}{\mu} = +\infty$. For any given $c_1 \in (c_+^*, \bar{c}_+) \subseteq (c_{1+}^*, \bar{c}_+)$, there exists $\mu_1 > 0$ such that $c_1 = \frac{\lambda_1(\mu_1)}{\mu_1}$. Let $\phi_1^*(t,x)$ be the positive time and space periodic eigenfunction associated with the principal eigenvalue $\lambda_1(\mu_1)$ of (5.41). Then it easily follows that

$$
u_1(t,x) := e^{-\mu_1(x-c_1t)}\phi_1^*(t,x) = e^{-\mu_1 x}e^{\lambda_1(\mu_1)t}\phi_1^*(t,x), \quad t \geq 0,\ x \in \mathbb{R},
$$

is a solution of the linear equation

$$
\frac{\partial u_1}{\partial t} = L_1u_1 + b_1(t,x)u_1.
$$

Since $c_{1+}^* < c_1$ and (H5) holds, we can choose a small number $\mu_2 \in (0, \mu_1)$ such that $c_2 := \frac{\lambda_2(\mu_2)}{\mu_2} < c_1$. Let $\phi_2^*(t,x)$ be the positive time and space periodic eigenfunction associated with the principal eigenvalue $\lambda_2(\mu_2)$ of (5.40). It is easy to see that

$$
u_2(t,x) := e^{-\mu_2(x-c_2t)}\phi_2^*(x) = e^{-\mu_2 x}e^{\lambda_2(\mu_2)t}\phi_2^*(t,x)
$$

is a solution of the linear equation

$$
\frac{\partial u_2}{\partial t} = L_2u_2 + (b_2(t,x) - a_{22}(t,x)u_2^*(t,x))u_2.
$$

Since $c_1 > c_2$, it follows that the function

$$v_2(t,x) := e^{-\mu_2(x-c_1t)}\phi_2^*(t,x) = e^{\mu_2(c_1-c_2)t}u_2(t,x), \quad t \geq 0,\ x \in \mathbb{R},$$

satisfies

$$\frac{\partial v_2}{\partial t} \geq L_2 v_2 + (b_2(t,x) - a_{22}(t,x)u_2^*(t,x))v_2. \tag{5.42}$$

Define two wave-like functions:

$$\overline{u}_1(t,x) := \min\{m_0 e^{-\mu_1(x-c_1t)}\phi_1^*(t,x), u_1^*(t,x)\}, \quad t \geq 0,\ x \in \mathbb{R}, \tag{5.43}$$

and

$$\overline{u}_2(t,x) := \min\{q_0 e^{-\mu_2(x-c_1t)}\phi_2^*(t,x), u_2^*(t,x)\}, \quad t \geq 0,\ x \in \mathbb{R}, \tag{5.44}$$

where

$$q_0 := \max_{(t,x)\in[0,\omega]\times[0,L]} \frac{u_2^*(t,x)}{\phi_2^*(t,x)} > 0, \quad m_0 := \min_{(t,x)\in[0,\omega]\times[0,L]} \frac{q_0 a_{22}(t,x)\phi_2^*(t,x)}{a_{21}(t,x)\phi_1^*(t,x)} > 0.$$

Now, we are ready to verify that $(\overline{u}_1, \overline{u}_2)$ is an upper solution to system (5.35). Indeed, for all $x - c_1 t > \frac{1}{\mu_1}\ln\frac{m_0\phi_1^*(t,x)}{u_1^*(t,x)}$, we have $\overline{u}_1(t,x) = m_0 e^{-\mu_1(x-c_1t)}\phi_1^*(t,x)$, and hence,

$$\begin{aligned}
&\frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(t,x) - a_{12}(t,x)u_2^*(t,x) - a_{11}(t,x)\overline{u}_1 + a_{12}(t,x)\overline{u}_2) \\
&\geq \frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - b_1(t,x)\overline{u}_1 = 0.
\end{aligned}$$

For all $x - c_1 t < \frac{1}{\mu_1}\ln\frac{m_0\phi_1^*(t,x)}{u_1^*(t,x)}$, we obtain $\overline{u}_1(t,x) = u_1^*(t,x)$, and hence,

$$\begin{aligned}
&\frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(t,x) - a_{12}(t,x)u_2^*(t,x) - a_{11}(t,x)\overline{u}_1 + a_{12}(t,x)\overline{u}_2) \\
&\geq \frac{\partial \overline{u}_1}{\partial t} - L_1\overline{u}_1 - \overline{u}_1(b_1(t,x) - a_{11}(t,x)\overline{u}_1) = 0.
\end{aligned}$$

On the other hand, for all $x - c_1 t > \frac{1}{\mu_2}\ln\frac{q_0\phi_2^*(t,x)}{u_2^*(t,x)} > 0$, it follows that

$$\overline{u}_2(t,x) = q_0 e^{-\mu_2(x-c_1t)}\phi_2^*(t,x),$$

which satisfies inequality (5.42). Note that

$$\overline{u}_1(t,x) \le m_0 e^{-\mu_1(x-c_1 t)}\phi_1^*(t,x), \quad \forall t \ge 0,\ x \in \mathbb{R},$$

and $\mu_2 \in (0,\mu_1)$, we get

$$\begin{aligned}
&\tfrac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - a_{21}(t,x)(u_2^*(t,x)-\overline{u}_2)\overline{u}_1 - \overline{u}_2(b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x) + a_{22}(t,x)\overline{u}_2)\\
&= \tfrac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - (b_2(t,x) - a_{22}(t,x)u_2^*(t,x))\overline{u}_2 + (u_2^*(t,x)-\overline{u}_2)(a_{22}(t,x)\overline{u}_2 - a_{21}(t,x)\overline{u}_1)\\
&\ge (u_2^*(t,x)-\overline{u}_2)e^{-\mu_1(x-c_1t)}a_{21}(t,x)\phi_1^*(t,x)\left(\tfrac{q_0 a_{22}(t,x)\phi_2^*(t,x)}{a_{21}(t,x)\phi_1^*(t,x)} - m_0\right)\\
&\ge 0.
\end{aligned}$$

For all $x - c_1 t < \frac{1}{\mu_2}\ln\frac{q_0\phi_2^*(t,x)}{u_2^*(t,x)}$, we have $\overline{u}_2(t,x) = u_2^*(t,x)$. Therefore,

$$\begin{aligned}
&\frac{\partial \overline{u}_2}{\partial t} - L_2\overline{u}_2 - a_{21}(t,x)(u_2^*(t,x)-\overline{u}_2)\overline{u}_1 - \overline{u}_2(b_2(t,x) - 2a_{22}(x)u_2^*(t,x) + a_{22}(t,x)\overline{u}_2)\\
&= \frac{\partial u_2^*}{\partial t} - L_2 u_2^* - u_2^*(b_2(t,x) - a_{22}(t,x)u_2^*) = 0.
\end{aligned}$$

It then follows that $\overline{u} = (\overline{u}_1, \overline{u}_2)$ is a continuous upper solution of system (5.35).

Let $\phi \in \mathcal{C}_{\beta(0,\cdot)}$ with $\phi(x) \ge \sigma$, $\forall x \le K$ and $\phi(x) = 0$, $\forall x \ge H$, for some $\sigma \in \mathbb{R}^2$ with $\sigma \gg 0$ and $K, H \in \mathbb{R}$. By the arguments in [95, Lemma 2.2] and the proof of Theorem 5.1.3, as applied to $\tilde{P}_\omega$, it follows that for any $c < \bar{c}_+$, there exists $\delta(c) > 0$ such that

$$\liminf_{n\to\infty, x\le cn\omega} |u(n\omega, x, \phi)| \ge \delta(c) > 0. \tag{5.45}$$

Moreover, there exists a sufficiently large positive constant $A \in L\mathbb{Z}$ such that

$$\phi(x) \le \overline{u}(0, x-A) := \psi(x), \quad \forall x \in \mathbb{R}.$$

By the translation invariance of Q_t, it follows that $\overline{u}(t, x-A)$ is still an upper solution of system (5.35), and hence,

$$0 \le u(t,x,\phi) \le u(t,x,\psi) = \overline{u}(t, x-A), \quad \forall x \in \mathbb{R},\ t \ge 0. \tag{5.46}$$

Fix a number $\hat{c} \in (c_1, \bar{c}_+)$. Letting $t = n\omega$, $x = \hat{c}n\omega$ and $n \to \infty$ in (5.46), together with (5.45), we have

$$0 < \delta(\hat{c}) \leq \liminf_{n\to\infty} |u(n\omega, \hat{c}n\omega, \phi)| \leq \lim_{n\to\infty} |\overline{u}(n\omega, \hat{c}n\omega - A)| = 0,$$

which is a contradiction. Thus, $c_+^* = \bar{c}_+$. □

Note that the leftward case can be addressed in a similar way. Indeed, by making a change of variable $v(t,x) = u(t,-x)$ for system (5.35), we obtain similar results for the rightward case of the resulting system, which is the leftward case for system (5.35).

Remark 5.2.1. *In the case where $L_i u = \frac{\partial}{\partial x}(d_i(x)\frac{\partial u}{\partial x})$ with $d_i \in C^{1+\nu}(\mathbb{R})$ in system* (5.35)*, $i = 1, 2$, or all the coefficient functions of system* (5.35) *are even in x except g_i is odd in x, $i = 1, 2$, it follows from Lemma 4.4.2 that system* (5.35) *admits a single rightward spreading speed which is coincident with the minimal rightward wave speed provided that (H1)–(H3) hold.*

5.2.3 Linear determinacy of spreading speed

In this subsection, we give a set of sufficient conditions for the rightward spreading speed to be determined by the linearization of system (5.35) at $\hat{E}_2 = (0,0)$, which is

$$\begin{aligned}\frac{\partial v_1}{\partial t} &= L_1 v_1 + (b_1(t,x) - a_{12}(t,x)u_2^*(t,x))v_1, \qquad (5.47)\\ \frac{\partial v_2}{\partial t} &= L_2 v_2 + a_{21}(t,x)u_2^*(t,x)v_1 + (b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x))v_2, \quad t > 0,\ x \in \mathbb{R}.\end{aligned}$$

Clearly, under (H2) the following scalar equation

$$\frac{\partial u}{\partial t} = L_1 u + u(b_1(t,x) - a_{12}(t,x)u_2^*(t,x) - a_{11}(t,x)u), \quad t > 0, x \in \mathbb{R}, \qquad (5.48)$$

admits a rightward spreading speed (also the minimal rightward wave speed) $c_+^0 = \inf\limits_{\mu>0} \frac{\lambda_0(\mu)}{\mu}$, where $\lambda_0(\mu)$ is the principle eigenvalue of the following parabolic eigenvalue problem:

$$\lambda\psi = -\frac{\partial\psi}{\partial t} + d_1(t,x)\frac{\partial^2\psi}{\partial x^2} - (2\mu d_1(t,x) + g_1(t,x))\frac{\partial\psi}{\partial x} \tag{5.49}$$
$$+(d_1(t,x)\mu^2 + g_1(t,x)\mu + b_1(t,x) - a_{12}(t,x)u_2^*(t,x))\psi, \quad (t,x) \in \mathbb{R}\times\mathbb{R},$$
$$\psi(t,x+L) = \psi(t,x),\ \psi(t+\omega,x) = \psi(t,x), \quad (t,x) \in \mathbb{R}\times\mathbb{R}.$$

The next result shows that c_+^0 is a lower bound of the slowest spreading c_+^* of system (5.35).

Proposition 5.2.4. *Let (H1)–(H3) hold. Then* $c_+^* \geq c_+^0$.

Proof. In the case where $\bar{c}_+ > c_+^*$, by the same arguments as in Theorem 5.2.3, we see that $c_+^* \geq c_{1+}^*$ where c_{1+}^* is the rightward spreading speed of (5.37). Since $b_1(t,x) > b_1(t,x) - a_{12}(t,x)u_2^*(t,x), \forall (t,x) \in \mathbb{R}\times\mathbb{R}$, by Lemma 4.4.1 (a) with $d(t,x) = d_1(t,x)$ and $g(t,x) = g_1(t,x)$, it is easy to see that $\lambda_1(\mu) > \lambda_0(\mu), \forall \mu \geq 0$, where $\lambda_1(\mu)$ is the principal eigenvalue of (5.41). Thus, we have $c_+^* \geq c_{1+}^* > c_+^0$.

In the case where $\bar{c}_+ = c_+^*$, let $u(t,\cdot,\phi) = (u_1(t,\cdot,\phi), u_2(t,\cdot,\phi))$ be the solution of system (5.35) with $u(0,\cdot) = \phi = (\phi_1,\phi_2) \in \mathcal{C}_{\beta(0,\cdot)}$. Then the positivity of the solution implies that

$$\frac{\partial u_1}{\partial t} \geq L_1 u_1 + u_1(b_1(t,x) - a_{12}(t,x)u_2^*(t,x) - a_{11}(t,x)u_1), \quad t > 0, x \in \mathbb{R}.$$

Let $v(t,x,\phi_1)$ be the unique solution of (5.48) with $v(0,\cdot) = \phi_1$. Then the comparison principle yields that

$$u_1(t,x,\phi) \geq v(t,x,\phi_1), \quad \forall t \geq 0,\ x \in \mathbb{R}. \tag{5.50}$$

Since $\lambda(d_1, g_1, b_1 - a_{12}u_2^*) > 0$, Proposition 5.2.1 implies that there exists a unique positive time-space periodic solution $v_0(t,x)$ of (5.48). Let $\phi^0 = (\phi_1^0, \phi_2^0) \in \mathcal{C}_{\beta(0,\cdot)}$ be chosen as in Theorem 5.2.3 (i) and (ii) such that $\phi_1^0 \le v_0(0,\cdot)$. Suppose, by contradiction, $c_+^* < c_+^0$. Choose $\hat{c} \in (\bar{c}_+, c_+^0)$. Then Theorem 5.2.3 implies that $\lim_{t\to\infty, x\ge \hat{c}t} u_1(t,x,\phi^0) = 0$. By Theorem 5.1.3, as applied to system (5.48), we further obtain $\lim_{t\to\infty, x\le \hat{c}t}(v(t,x,\phi_1^0) - v_0(t,x)) = 0$. However, letting $x = \hat{c}t$ in (5.50), we get $\lim_{t\to\infty, x=\hat{c}t}(v(t,x,\phi_1^0)) = 0$, which is a contradiction. $\square$

For any given $\mu \in \mathbb{R}$, letting $v(t,x) = e^{-\mu x}u(t,x)$ in (5.47), we then have

$$
\begin{aligned}
\frac{\partial u_1}{\partial t} &= L_1 u_1 - 2\mu d_1(t,x)\frac{\partial u_1}{\partial x} + (d_1(t,x)\mu^2 + g_1(t,x)\mu + b_1(t,x) - a_{12}(t,x)u_2^*(t,x))u_1,\\
\frac{\partial u_2}{\partial t} &= L_2 u_2 - 2\mu d_2(t,x)\frac{\partial u_2}{\partial x} + a_{21}(t,x)u_2^*(x)u_1\\
&\quad + (d_2(t,x)\mu^2 + g_2(t,x)\mu + b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x))u_2, \quad t>0, x\in\mathbb{R}.
\end{aligned}
\tag{5.51}
$$

Substituting $u(t,x) = e^{\lambda t}\phi(t,x)$ into (5.51), we obtain the following periodic eigenvalue problem:

$$
\begin{aligned}
\lambda\phi_1 &= -\frac{\partial\phi_1}{\partial t} + d_1(t,x)\frac{\partial^2\phi_1}{\partial x^2} - (2\mu d_1(t,x) + g_1(t,x))\frac{\partial\phi_1}{\partial x}\\
&\quad + (d_1(t,x)\mu^2 + g_1(t,x)\mu + b_1(t,x) - a_{12}(t,x)u_2^*(t,x))\phi_1, \quad (t,x)\in\mathbb{R}\times\mathbb{R},\\
\lambda\phi_2 &= -\frac{\partial\phi_2}{\partial t} + d_2(t,x)\frac{\partial^2\phi_2}{\partial x^2} - (2\mu d_2(t,x) + g_2(t,x))\frac{\partial\phi_2}{\partial x} + a_{21}(t,x)u_2^*(t,x)\phi_1\\
&\quad + \left(d_2(t,x)\mu^2 + g_2(t,x)\mu + b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x)\right)\phi_2, \quad (t,x)\in\mathbb{R}\times\mathbb{R},\\
\phi_i(t,x+L) &= \phi_i(t,x),\ \phi_i(t+\omega,x) = \phi_i(t,x), \quad (t,x)\in\mathbb{R}\times\mathbb{R},\ i=1,2.
\end{aligned}
\tag{5.52}
$$

Let $\overline{\lambda}(\mu)$ be the principal eigenvalue of the following periodic eigenvalue problem:

$$\begin{aligned}\lambda\psi = &-\frac{\partial \psi}{\partial t} + d_2(t,x)\frac{\partial^2 \psi}{\partial x^2} - (2\mu d_2(t,x) + g_2(t,x))\frac{\partial \psi}{\partial x}\\ &+ \left(d_2(t,x)\mu^2 + g_2(t,x)\mu + b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x)\right)\psi, \quad (t,x) \in \mathbb{R}\times\mathbb{R},\\ \psi(t,x+L) = &\ \psi(t,x),\ \psi(t+\omega,x) = \psi(t,x), \quad (t,x)\in\mathbb{R}\times\mathbb{R}. \end{aligned} \tag{5.53}$$

Since there exists $\mu_0 > 0$ such that $c_+^0 = \frac{\lambda_0(\mu_0)}{\mu_0}$. In order to show that $\lambda_0(\mu_0)$ is the principle eigenvalue of (5.52), we introduce the following additional condition:

(D1) $\lambda_0(\mu_0) > \overline{\lambda}(\mu_0)$.

Proposition 5.2.5. *Let (H1)–(H3) and (D1) hold. Then the periodic eigenvalue problem* (5.52) *with* $\mu = \mu_0$ *has a simple eigenvalue* $\lambda_0(\mu_0)$ *associated with a positive periodic eigenfunction* $\phi^* = (\phi_1^*, \phi_2^*)$.

Proof. Clearly, there exists a positive eigenfunction ϕ_1^* associated with the principle eigenvalue $\lambda_0(\mu_0)$ of (5.48). Since the first equation of (5.52) 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 (5.52), where ϕ_2^* is to be determined. Let $U(t,s)$, $0 \le s < t$, be the evolution operator generated by (5.51) with $u(0,\cdot) \in \mathbb{P}$, and $U_1(t,s)$ and $U_2(t,s)$, $0 \le s < t$ be the evolution operators generated by the following scalar parabolic equations:

$$\begin{aligned}\frac{\partial u}{\partial t} =& L_1 u - 2\mu_0 d_1(t,x)\frac{\partial u}{\partial x}\\ &+ (d_1(t,x)\mu_0^2 + g_1(t,x)\mu_0 + b_1(t,x) - a_{12}(t,x)u_2^*(t,x))u, \quad t>0,\ x\in\mathbb{R},\\ u(0,\cdot) =& \varphi_1 \in \mathcal{P}\end{aligned}$$

and

$$\frac{\partial u}{\partial t} = L_2 u - 2\mu_0 d_2(t,x)\frac{\partial u}{\partial x}$$
$$+ (d_2(t,x)\mu_0^2 + g_2(t,x)\mu_0 + b_2(t,x) - 2a_{22}(t,x)u_2^*(t,x))u, \quad t>0,\ x\in\mathbb{R},$$
$$u(0,\cdot) = \varphi_2 \in \mathcal{P},$$

respectively. By the variation of constants formula for scalar parabolic equations, it then follows that

$$U(t,0)\begin{pmatrix}\varphi_1\\ \varphi_2\end{pmatrix} = \begin{pmatrix} U_1(t,0)\varphi_1 \\ U_2(t,0)\varphi_2 + \int_0^t U_2(t,s)a_{21}(s,\cdot)u_2^*(s,\cdot)U_1(s,0)\varphi_1 ds\end{pmatrix}, \quad \forall t>0.$$

And it is easy to see that $U_1(\omega,0)$ and $U_2(\omega,0)$ are strongly positive and compact linear operators on $\mathcal{P}$. Let r_1 and r_2 be the spectral radii of $U_1(\omega,0)$ and $U_2(\omega,0)$. Then Theorem 2.1.1 (see e.g., [31, Theorem 7.2]) implies r_i is the principle eigenvalue of $U_i(\omega,0), i=1,2$, and $r_1 = e^{\lambda_0(\mu_0)\omega}$ and $r_2 = e^{\overline{\lambda}(\mu_0)\omega}$. Moreover, $U_1(t,0)\phi_1^*(0,\cdot) = e^{\lambda_0(\mu_0)t}\phi_1^*(t,\cdot) > 0$, $\forall t>0$. By [31, Theorem 7.3] and (D1), it follows that

$$(r_1 - U_2(\omega,0))\varphi_2 = \int_0^\omega U_2(\omega,s)a_{21}(s,\cdot)u_2^*(s,\cdot)U_1(s,0)\phi_1^*(0,\cdot)ds > 0, \tag{5.54}$$

has a unique positive solution $\varphi_2^* \in \mathcal{P}$. Therefore, $\varphi^* = (\phi_1^*(0,\cdot),\varphi_2^*) \in \mathbb{P}$ is a positive eigenfunction of $U(\omega,0)$ with the eigenvalue $r_1 = e^{\lambda_0(\mu_0)\omega}$, that is, $U(\omega,0)\varphi^* = r_1\varphi^*$. Let

$$\phi_2^*(t,\cdot) = e^{-\lambda_0(\mu_0)t}U_2(t,0)\varphi_2^* + \int_0^t e^{-\lambda_0(\mu_0)(t-s)}U_2(t,s)a_{21}(s,\cdot)u_2^*(s,\cdot)\phi_1^*(s,\cdot)ds.$$

Clearly, $\phi_2^*(t,x)$ is positive for $(t,x)\in\mathbb{R}_+\times\mathbb{R}$, and satisfies the second equation of (5.52), and

$$\phi_2^*(\omega,\cdot) = e^{-\lambda_0(\mu_0)\omega}r_1\varphi_2^* = \varphi_2^* = \phi_2^*(0,\cdot).$$

This implies that $\phi^* = (\phi_1^*, \phi_2^*)$ is the positive time and space periodic eigenfunction associated with $\lambda_0(\mu_0)$. Since $\lambda_0(\mu_0)$ is a simple eigenvalue for (5.48), we see that so is $\lambda_0(\mu_0)$ for (5.52). $\square$

From Proposition 5.2.5, it is easy to see that for any given $M > 0$, the function

$$U(t,x) = Me^{-\mu_0 x} e^{\lambda_0(\mu_0)t} \phi^*(t,x), \quad t \geq 0,\ x \in \mathbb{R}, \tag{5.55}$$

is a positive solution of system (5.47). In order to obtain an explicit formula for the spreading speeding $\bar{c}_+$, we need one more additional condition:

(D2) $\frac{\phi_1^*(t,x)}{\phi_2^*(t,x)} \geq \max\left\{\frac{a_{12}(t,x)}{a_{11}(t,x)}, \frac{a_{22}(t,x)}{a_{21}(t,x)}\right\}, \quad \forall (t,x) \in \mathbb{R} \times \mathbb{R}.$

Now we are in a position to show that system (5.35) admits a single rightward spreading speed $\bar{c}_+$, which is linearly determinate.

Theorem 5.2.4. *Let (H1)–(H3) and (D1)–(D2) hold. Then* $\bar{c}_+ = c_+^* = c_+^0 = \inf_{\mu>0} \frac{\lambda_0(\mu)}{\mu}$.

Proof. First, we verify that $U(t,x)$, as defined in (5.55), is an upper solution of system (5.35). Since $\frac{U_1}{U_2} = \frac{\phi_1^*}{\phi_2^*}$ and (D2) holds true, it follows that

$$\begin{aligned}
&\frac{\partial U_1}{\partial t} - L_1 U_1 - U_1(b_1(t,x) - a_{12}(t,x)u_2^*(t,x) - a_{11}(t,x)U_1 + a_{12}(t,x)U_2) \\
&= a_{11}(t,x)U_1U_2\left(\frac{U_1}{U_2} - \frac{a_{12}(t,x)}{a_{11}(t,x)}\right) \\
&= a_{11}(t,x)U_1U_2\left(\frac{\phi_1^*(t,x)}{\phi_2^*(t,x)} - \frac{a_{12}(t,x)}{a_{11}(t,x)}\right) \geq 0,
\end{aligned}$$

and

$$\frac{\partial U_2}{\partial t}-L_2U_2-a_{21}(t,x)U_1(u_2^*(t,x)-U_2)-U_2(b_2(t,x)-2a_{22}(t,x)u_2^*(t,x)+a_{22}(t,x)U_2).$$
$$=a_{21}(t,x)U_2^2\left(\frac{U_1}{U_2}-\frac{a_{22}(t,x)}{a_{21}(t,x)}\right)$$
$$=a_{21}(t,x)U_2^2\left(\frac{\phi_1^*(t,x)}{\phi_2^*(t,x)}-\frac{a_{22}(t,x)}{a_{21}(t,x)}\right)\geq 0.$$

Thus, $U(t,x)$ is an upper solution of (5.35). Choose some $\phi^0\in\mathcal{C}_{\beta(0,\cdot)}$ satisfying the conditions in Theorem 5.2.3 (i) and (ii). Then there exists a sufficiently large number $M_0>0$ such that

$$0\leq\phi^0(x)\leq M_0e^{-\mu_0x}\phi^*(0,x)=U(0,x),\quad\forall x\in\mathbb{R}.$$

Let $W(t,x)$ be the unique solution of system (5.35) with $W(0,\cdot)=\phi^0$. Then the comparison principle, together with the fact that $c_+^0\mu_0=\lambda_0(\mu_0)$, leads that

$$0\leq W(t,x)\leq U(t,x)=M_0e^{-\mu_0x}e^{\lambda_0(\mu_0)t}\phi^*(t,x)=M_0e^{-\mu_0(x-c_+^0t)}\phi^*(t,x),\ \forall t\geq 0,\ x\in\mathbb{R}.$$

It follows that for any given $\epsilon>0$, there holds

$$0\leq W(t,x)\leq M_0e^{-\mu_0\epsilon t}\phi^*(t,x),\quad\forall t\geq 0,\ x\geq(c_+^0+\epsilon)t,$$

and hence,

$$\lim_{t\to\infty,x\geq(c_+^0+\epsilon)t}W(t,x)=0.$$

By Theorem 5.2.3 (ii), we obtain $c_+^*\leq c_+^0+\epsilon$. Letting $\epsilon\to 0$, we have $c_+^*\leq c_+^0$. In the case that $\bar{c}_+>c_+^*$, the proof of Proposition 5.2.4 shows that $c_+^*>c_+^0$, a contradiction. This implies that $\bar{c}_+=c_+^*=c_+^0$. $\square$

To finish this section, we consider the following time-periodic Lotka–Volterra competition model [104]:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= \frac{\partial^2 u_1}{\partial x^2} + u_1(b_1(t) - a_{11}(t)u_1 - a_{12}(t)u_2), \\ \frac{\partial u_2}{\partial t} &= d\frac{\partial^2 u_2}{\partial x^2} + u_2(b_2(t) - a_{21}(t)u_1 - a_{22}(t)u_2), \quad t > 0,\ x \in \mathbb{R}. \end{aligned} \tag{5.56}$$

Here $d > 0$ and all other coefficient functions are positive and ω-periodic in t.

For convenience, define $\overline{w} = \frac{1}{\omega}\int_0^\omega w(t)dt$ with any ω-periodic function $w(t)$. We first make the following assumption (see (A2) in [104]):

(P1) $\overline{b}_1 > \max\limits_{t\in[0,\omega]} \frac{a_{12}(t)}{a_{22}(t)} \cdot \overline{b}_2 > 0$, and $0 < \overline{b}_2 \le \max\limits_{t\in[0,\omega]} \frac{a_{21}(t)}{a_{11}(t)} \cdot \overline{b}_1$.

It is easy to see that if (P1) holds, then Proposition 5.2.2 implies that (H3) is valid. A straightforward computation shows that $\lambda(1,0,b_1) = \overline{b}_1 > 0$ and $\lambda(1,0,b_2) = \overline{b}_2 > 0$. Thus, (H1) holds true and system (5.56) admits three time periodic solutions $(0,0)$, $(u_1^*(t),0)$, and $(0,u_2^*(t))$. Moreover, we can show that

$$\lambda(1,0,b_1 - a_{12}u_2^*) = \overline{b_1 - a_{12}u_2^*} \ge \overline{b}_1 - \max_{t\in[0,\omega]} \frac{a_{12}(t)}{a_{22}(t)} \cdot \overline{a_{22}u_2^*} = \overline{b}_1 - \max_{t\in[0,\omega]} \frac{a_{12}(t)}{a_{22}(t)} \cdot \overline{b_2} > 0,$$

and hence, (H2) ia also valid. (H4) and (H5) are automatically satisfied since all coefficient functions are independent of x (treated as even functions of x). It then follows that system (5.56) admits a single spreading speed (also the minimal wave speed) $\bar{c}_+$ no matter whether it is linearly determinate. Next, we make another assumption (see [104, Theorem 2.5]):

(P2) $0 < d \le 1$, $a_{11}(t)u_1^*(t) - a_{12}(t)u_2^*(t) \ge a_{21}(t)u_1^*(t) - a_{22}(t)u_2^*(t) \ge 0, \forall t \in \mathbb{R}$.

In what follows, we show that (P2) is sufficient for (D1) and (D2) to hold. Clearly, $\lambda_0(\mu)$ and $\overline{\lambda}(\mu)$ become the principal eigenvalues of the following periodic eigenvalue problems:

$$\lambda\psi = -\frac{d\psi}{dt} + (\mu^2 + b_1(t) - a_{12}(t)u_2^*(t))\psi, \quad t \in \mathbb{R},$$
$$\psi(t+\omega) = \psi(t), \quad t \in \mathbb{R},$$

and

$$\lambda\psi = -\frac{d\psi}{dt} + \left(d\mu^2 + b_2(t) - 2a_{22}(t)u_2^*(t)\right)\psi, \quad t \in \mathbb{R},$$
$$\psi(t+\omega) = \psi(t), \quad t \in \mathbb{R}, \tag{5.57}$$

respectively. It is easy to see that

$$\lambda_0(\mu) = \mu^2 + \overline{b_1 - a_{12}u_2^*}, \quad \overline{\lambda}(\mu) = d\mu^2 + \overline{b_2 - 2a_{22}u_2^*}.$$

By virtue of (P2) and

$$c_+^0 = \inf_{\mu>0} \frac{\lambda_0(\mu)}{\mu} = \inf_{\mu>0} \left\{ \mu + \frac{\overline{b_1 - a_{12}u_2^*}}{\mu} \right\},$$

it follows that

$$c_+^0 = 2\sqrt{\overline{b_1 - a_{12}u_2^*}} > 0, \ \mu_0 = \sqrt{\overline{b_1 - a_{12}u_2^*}}.$$

We then see from (P2) that (D1) holds true.

Let $(\phi_1(t), \phi_2(t))$ be a positive eigenfunction, associated with $\lambda_0(\mu_0)$, of the following eigenvalue problem:

$$\lambda\phi_1 = -\frac{d\phi_1}{dt} + (\mu_0^2 + b_1(t) - a_{12}(t)u_2^*(t))\phi_1, \quad t \in \mathbb{R},$$
$$\lambda\phi_2 = -\frac{d\phi_2}{dt} + a_{21}(t)u_2^*(t)\phi_1 + \left(d\mu_0^2 + b_2(t) - 2a_{22}(t)u_2^*(t)\right)\phi_2, \quad t \in \mathbb{R},$$
$$\phi_i(t+\omega) = \phi_i(t), \quad t \in \mathbb{R}, \ i = 1, 2. \tag{5.58}$$

Next we verify that $\phi_2(t) \le \frac{u_2^*(t)}{u_1^*(t)}\phi_1(t) := v(t), \forall t \in \mathbb{R}$. Note that

$$\begin{aligned}
&-\frac{dv}{dt} + a_{21}(t)u_2^*(t)\phi_1(t) + (d\mu_0^2 + b_2(t) - 2a_{22}(t)u_2^*(t) - 2\mu_0^2)v \\
&= \frac{u_2^*(t)\phi_1(t)}{u_1^*(t)}\left[-\frac{u_1^*(t)}{u_2^*(t)}\left(\frac{u_2^*(t)}{u_1^*(t)}\right)' - \frac{\phi_1'(t)}{\phi_1(t)} + a_{21}(t)u_1^*(t) + d\mu_0^2\right. \\
&\left.+ b_2(t) - 2a_{22}(t)u_2^*(t) - 2\mu_0^2\right] \\
&= \frac{u_2^*(t)\phi_1(t)}{u_1^*(t)}\left[-\frac{u_1^*(t)}{u_2^*(t)}\left(\frac{u_2^*(t)}{u_1^*(t)}\right)' + b_2(t) - b_1(t) - a_{22}(t)u_2^*(t) + a_{11}(t)u_1^*(t)\right. \\
&\left.+ (d-1)\mu_0^2 - a_{11}(t)u_1^*(t) + a_{12}(t)u_2^*(t) + a_{21}(t)u_1^*(t) - a_{22}(t)u_2^*(t)\right] \\
&\le \frac{u_2^*(t)\phi_1(t)}{u_1^*(t)}\left[-\frac{u_1^*(t)}{u_2^*(t)}\left(\frac{u_2^*(t)}{u_1^*(t)}\right)' + b_2(t) - b_1(t) - a_{22}(t)u_2^*(t) + a_{11}(t)u_1^*(t)\right] \\
&= 0.
\end{aligned}$$

In view of the comparison principle and the periodicity of $\phi_2(t)$ and $v(t)$, it then suffices to show that $\phi_2(t_0) \le v(t_0)$ for some $t_0 \in \mathbb{R}$. Assume, by contradiction, that $\phi_2(t) > v(t)$, $\forall t \in \mathbb{R}$. Thus, we have $w(t) := v(t) - \phi_2(t) < 0$, and

$$\frac{dw(t)}{dt} + \left(2\mu_0^2 - d\mu_0^2 - b_2(t) + 2a_{22}(t)u_2^*(t)\right) w(t) \ge 0, \ \forall t \in \mathbb{R}.$$

This implies that

$$\int_0^\omega (2\mu_0^2 - d\mu_0^2 - b_2(t) + 2a_{22}(t)u_2^*(t))dt \le 0.$$

On the other hand, we know that $\bar{b}_2 = \overline{a_{22}u_2^*}$, and

$$\frac{1}{\omega}\int_0^\omega (2\mu_0^2 - d\mu_0^2 - b_2(t) + 2a_{22}(t)u_2^*(t))dt = (2-d)\mu_0^2 + \overline{a_{22}u_2^*} > 0,$$

which leads to a contradiction. This shows that $\frac{\phi_1(t)}{\phi_2(t)} \ge \frac{u_1^*(t)}{u_2^*(t)}$, $\forall t \in \mathbb{R}$. It then follows from (P2) that

$$\frac{\phi_1(t)}{\phi_2(t)} \ge \frac{u_1^*(t)}{u_2^*(t)} \ge \max\left\{\frac{a_{12}(t)}{a_{11}(t)}, \frac{a_{22}(t)}{a_{21}(t)}\right\}, \quad \forall t \in \mathbb{R},$$

which implies that (D2) is also valid. Therefore, if (P1) and (P2) hold, then the spreading speed $\bar{c}_+$ is linearly determinate, equal to $2\sqrt{b_1 - a_{12}u_2^*}$.

Remark 5.2.2. *Consider a more general reaction-diffusion competition system in a periodic habitat, that is,*

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= L_1 u_1 + u_1 f_1(t, x, u_1, u_2), \\ \frac{\partial u_2}{\partial t} &= L_2 u_2 + u_2 f_2(t, x, u_1, u_2), \quad t \in \mathbb{R},\ x \in \mathbb{R}, \end{aligned} \tag{5.59}$$

where the operator $L_i := a_2^{(i)}(t,x)\frac{\partial^2}{\partial x^2} + a_1^{(i)}(t,x)\frac{\partial}{\partial x}$ *with* $a_2^{(i)}(t,x) > 0, \forall (t,x) \in \mathbb{R} \times \mathbb{R}$, *i.e.,* L_i *is uniformly elliptic,* $i = 1, 2$. *Assume that* $a_j^{(i)}(t,x)$ *and* $f_i(t, x, u_1, u_2)$ *are periodic in* t *and* x *with the same periods, respectively, Hölder continuous in* x *of order* $\nu \in (0,1)$ *and in* t *of order* $\frac{\nu}{2}$, $1 \le i, j \le 2$, *and* $f_i(t, x, u_1, u_2)$ *are differentiable with respect to* u_1 *and* u_2, $i = 1, 2$. *Moreover,* $\partial_{u_1} f_1(t, x, u_1, 0) < 0$ *and* $\partial_{u_2} f_2(t, x, 0, u_2) < 0$, $\forall (t,x) \in \mathbb{R} \times \mathbb{R}$, $u_1 \in \mathbb{R}_+$, $u_2 \in \mathbb{R}_+$, *and there exist* $M_1 > 0$ *and* $M_2 > 0$ *such that* $f_1(t, x, M_1, 0) \le 0$, $f_2(t, x, 0, M_2) \le 0$, $\partial_{u_2} f_1(t, x, u_1, u_2) < 0$ *and* $\partial_{u_1} f_2(t, x, u_1, u_2) < 0$ *for all* $(t, x, u_1, u_2) \in \mathbb{R} \times \mathbb{R} \times [0, M_1] \times [0, M_2]$. *Then we can obtain analogous results on traveling waves and spreading speeds under similar assumptions to (H1)–(H5) and (D1)–(D2).*

5.2.4 An example

In this section, we study the time periodic version of a well-known reaction diffusion model [43]:

$$\begin{aligned} \frac{\partial u_1}{\partial t} &= d_1 \Delta u_1 + u_1(a_\omega(t,x) - u_1 - u_2), \\ \frac{\partial u_2}{\partial t} &= d_2 \Delta u_2 + u_2(a_\omega(t,x) - u_1 - u_2), \quad t > 0,\ x \in \mathbb{R}, \end{aligned} \tag{5.60}$$

where $0 < d_1 < d_2$, $a_\omega(t,x) = a(t/\omega, x)$ and $a(t,x)$ is a continuous function on $\mathbb{R} \times \mathbb{R}$ and it is 1-periodic in t and L-periodic in x.

For convenience, we use the same notations as in sections 2 and 3. We first present some results on the principle eigenvalue $\lambda_m(\mu)$ of (5.61).

Lemma 5.2.1. *Assume that time and space periodic functions $d, g, m \in C^{\frac{\nu}{2},\nu}(\mathbb{R} \times \mathbb{R})(\nu \in (0,1))$. Let $\lambda_m(\mu)(\mu \in \mathbb{R})$ be the principle eigenvalue of the following parabolic eigenvalue problem:*

$$\begin{aligned} &\lambda\psi = -\frac{\partial \psi}{\partial t} + d(t,x)\frac{\partial^2 \psi}{\partial x^2} - (2\mu d(t,x) + g(t,x))\frac{\partial \psi}{\partial x} \\ &+(d(t,x)\mu^2 + g(t,x)\mu + m(t,x))\psi, \quad (t,x) \in \mathbb{R} \times \mathbb{R}, \\ &\psi(t, x+L) = \psi(t,x),\ \psi(t+\omega, x) = \psi(t,x), \quad (t,x) \in \mathbb{R} \times \mathbb{R}. \end{aligned} \tag{5.61}$$

Then the following statements are valid:

(a) If $m_1(t,x) \geq m_2(t,x)$ with $m_1(t,x) \not\equiv m_2(t,x), \forall (t,x) \in [0,\omega] \times [0,L]$, then $\lambda_{m_1}(\mu) > \lambda_{m_2}(\mu)$, $\forall \mu \in \mathbb{R}$.

(b) $\lambda_m(\mu)$ is a convex function of μ on $\mathbb{R}$.

(c) If either d, m are even in x and g is odd in x, or $d \in C^{\frac{\nu}{2},1+\nu}(\mathbb{R} \times \mathbb{R})(\nu \in (0,1))$ and $g(t,x) = -\frac{\partial d(t,x)}{\partial x}, \forall (t,x) \in \mathbb{R} \times \mathbb{R}$ and d, m are even in t, then $\lambda_m(\mu) = \lambda_m(-\mu), \forall \mu \in \mathbb{R}$.

Proof. By similar arguments to those in [31, Lemma 15.5] , it is easy to prove that (a) holds. (b) follows from the same arguments as in [54].

In the case where d, m are even functions in x and g is odd in x. Let $\psi(t,x)$ be eigenfunction associated with $\lambda_m(\mu)$. Set $\phi(t,x) = \psi(t,-x)$, we then have

$$\begin{aligned} &\lambda\phi = -\frac{\partial \phi}{\partial t} + d(t,-x)\frac{\partial^2 \phi}{\partial x^2} + (2\mu d(t,-x) + g(t,-x))\frac{\partial \phi}{\partial x} \\ &+(d(t,-x)\mu^2 + g(t,-x)\mu + m(t,-x))\phi, \quad (t,x) \in \mathbb{R} \times \mathbb{R}. \end{aligned}$$

Since $d(t,x) = d(t,-x), m(t,x) = m(t,-x), g(t,x) = -g(t,-x), \forall (t,x) \in \mathbb{R}\times\mathbb{R}$, we obtain

$$\begin{aligned}&\lambda\phi = -\frac{\partial\phi}{\partial t} + d(t,x)\frac{\partial^2\phi}{\partial x^2} + (2\mu d(t,x) - g(t,x))\frac{\partial\phi}{\partial x}\\&+(d(t,x)\mu^2 - g(t,x)\mu + m(t,x))\phi, \quad (t,x)\in\mathbb{R}\times\mathbb{R}.\end{aligned}$$

By the uniqueness of the principal eigenvalue, it follows that $\lambda_m(-\mu) = \lambda_m(\mu), \forall \mu \in \mathbb{R}$.

In the case where $d \in C^{\frac{\nu}{2},1+\nu}(\mathbb{R}\times\mathbb{R})(\nu \in (0,1))$ and $g(t,x) = -\frac{\partial d(t,x)}{\partial x}, \forall (t,x) \in \mathbb{R}\times\mathbb{R}$, d, m is even in t, for any given $\mu \in \mathbb{R}$, it is easy to see that $\lambda_m(\mu)$ is also the principle eigenvalue of

$$\begin{aligned}&\lambda\psi = \frac{\partial\psi}{\partial t} + \frac{\partial}{\partial x}\left(d(t,x)\frac{\partial\psi}{\partial x}\right) - 2\mu d(t,x)\frac{\partial\psi}{\partial x}\\&+(d(t,x)\mu^2 - \frac{\partial d(t,x)}{\partial x}\mu + m(t,x))\psi, \quad (t,x)\in\mathbb{R}\times\mathbb{R}, \qquad (5.62)\\&\psi(t,x+L) = \psi(t,x),\ \psi(t+\omega,x) = \psi(t,x), \quad (t,x)\in\mathbb{R}\times\mathbb{R}.\end{aligned}$$

Let $\varphi(t,x)$ and $\phi(t,x)$ be the positive periodic eigenfunctions associated with $\lambda_m(\mu)$ and $\lambda_m(-\mu)$, respectively, and $\psi(t,x) = \varphi(-t,x), \forall (t,x)\in\mathbb{R}\times\mathbb{R}$. Note that d, m are even in t, so is $\frac{\partial d(t,x)}{\partial x}$, it then follows that,

$$\lambda_m(\mu)\psi = \frac{\partial\psi}{\partial t} + \frac{\partial}{\partial x}\left(d(t,x)\frac{\partial\psi}{\partial x}\right) - 2\mu d(t,x)\frac{\partial\psi}{\partial x} + (d(t,x)\mu^2 - \frac{\partial d(t,x)}{\partial x}\mu + m(t,x))\psi$$

and

$$\lambda_m(-\mu)\phi = -\frac{\partial\phi}{\partial t} + \frac{\partial}{\partial x}\left(d(t,x)\frac{\partial\phi}{\partial x}\right) + 2\mu d(t,x)\frac{\partial\phi}{\partial x} + (d(t,x)\mu^2 + \frac{\partial d(t,x)}{\partial x}\mu + m(t,x))\phi$$

Using integration by parts, we have

$$\int_0^\omega\int_0^L \frac{\partial\psi(t,x)}{\partial t}\phi(t,x)dxdt = -\int_0^\omega\int_0^L \frac{\partial\phi(t,x)}{\partial t}\psi(t,x)dxdt,$$

$$\int_0^\omega \int_0^L \frac{\partial}{\partial x}\left(d(t,x)\frac{\partial \psi(t,x)}{\partial x}\right)\phi(t,x)dxdt = \int_0^\omega \int_0^L \frac{\partial}{\partial x}\left(d(t,x)\frac{\partial \phi(t,x)}{\partial x}\right)\psi(t,x)dxdt,$$

and

$$\begin{aligned}
-\mu \int_0^\omega \int_0^L & \left[2d(t,x)\frac{\partial \psi(t,x)}{\partial x}\phi(t,x) + \frac{\partial d(t,x)}{\partial x}\psi(t,x)\phi(t,x)\right] dxdt \\
&= \mu \int_0^\omega \int_0^L \left[2\frac{\partial d(t,x)\phi(t,x)}{\partial x}\psi(t,x) - \frac{\partial d(t,x)}{\partial x}\psi(t,x)\phi(t,x)\right] dxdt \\
&= \mu \int_0^\omega \int_0^L \left[2d(t,x)\frac{\partial \psi(t,x)}{\partial x}\phi(t,x) + \frac{\partial d(t,x)}{\partial x}\psi(t,x)\phi(t,x)\right] dxdt.
\end{aligned}$$

It then follows that

$$\lambda_m(\mu) \int_0^\omega \int_0^L \psi(t,x)\phi(t,x)dxdt = \lambda_m(-\mu) \int_0^\omega \int_0^L \phi(t,x)\psi(t,x)dxdt.$$

Since $\int_0^\omega \int_0^L \phi(t,x)\psi(t,x)dxdt > 0$, we have $\lambda_m(\mu) = \lambda_m(-\mu), \forall \mu \in \mathbb{R}$. □

With the aid of Lemma 5.2.1, we are able to provide sufficient conditions for (H4) and (H5) to hold.

Lemma 5.2.2. *Assume that (H1) and (H2) hold. Then (H4) and (H5) are valid provided that either all the coefficient functions of system* (5.35) *are even in x except g_i is odd in x, or all the coefficient functions of system* (5.35) *are independent of t, $d_i \in C^{1+\nu}(\mathbb{R})(\nu \in (0,1))$ and $g_i(t,x) = -d_i'(x), \forall (t,x) \in \mathbb{R}\times\mathbb{R}, i = 1,2$.*

Proof. First, we prove that (H4) holds. Indeed, in either case, by Lemma 5.2.1(c) with $m(t,x) = b_1(t,x)$ and $d(t,x) = d_1(t,x)$, it is easy to see that the principle $\lambda_1(\mu)$ of (5.41) is an even function of μ on $\mathbb{R}$. Since $\lambda_1(\mu)$ is convex on $\mathbb{R}$ and $\lambda_1(0) > 0$, we have $\lambda_1(\mu) > 0, \forall \mu > 0$. It follows that $c_{1+}^* = \inf_{\mu>0} \frac{\lambda_1(\mu)}{\mu} > 0$. Similarly, we can show that $c_{2-}^* > 0$, this implies $c_{1+}^* + c_{2-}^* > 0$.

To verify (H5), it suffices to show that $\lim_{\mu\to 0^+} \frac{\lambda_2(\mu)}{\mu} = 0$, where $\lambda_2(\mu)$ is the principal eigenvalue of (5.40). In the case where all the coefficient functions of (5.35) are even in x except g_i is odd in x, $i = 1, 2$, we have

$$\frac{\partial u_2^*}{\partial t} = d_2(t,x)\frac{\partial^2 u_2^*}{\partial x^2} + g_2(t,x)\frac{\partial u_2^*}{\partial x} + u_2^*(b_2(t,x) - a_{22}(t,x)u_2^*), \quad (t,x) \in \mathbb{R} \times \mathbb{R}.$$

Let $u_2^0(t,x) = u_2^*(t,-x)$. Since d_2, b_2, a_{22} are even in x and g_2 is odd in x, it follows that

$$\frac{\partial u_2^0}{\partial t} = d_2(t,x)\frac{\partial^2 u_2^0}{\partial x^2} + g_2(t,x)\frac{\partial u_2^0}{\partial x} + u_2^0(b_2(t,x) - a_{22}(t,x)u_2^0), \quad (t,x) \in \mathbb{R} \times \mathbb{R}.$$

This implies that $u_2^0(t,-x)$ is also a time and space periodic positive solution for scalar equation (5.34) with $d(t,x) = d_2(t,x)$, $g(t,x) = g_2(t,x)$, $c(t,x) = b_2(t,x)$ and $e(t,x) = a_{22}(t,x), \forall(t,x) \in \mathbb{R} \times \mathbb{R}$. In view of Proposition 5.2.1, the uniqueness of the time and space periodic positive solution implies that $u_2^*(t,-x) = u_2^*(t,x), \forall(t,x) \in \mathbb{R}\times\mathbb{R}$. Taking $d(t,x) = d_2(t,x)$, $m(t,x) = b_2(t,x) - a_{22}(t,x)u_2^*(t,x)$, and $g(t,x) = g_2(t,x)$ in (5.61), we see from the former case in Lemma 5.2.1(c) that $\lambda_2(\mu)$ is an even function on $\mathbb{R}$, and hence, $\lambda_2'(0) = 0$. Since $\lambda_2(0) = 0$, it follows that $\lim_{\mu\to 0^+} \frac{\lambda_2(\mu)}{\mu} = \lambda_2'(0) = 0 < c_{1+}^*$.

In the case where all the coefficient functions of system (5.35) are independent of t, $d_i \in C^{1+\nu}(\mathbb{R})(\nu \in (0,1))$ and $g_i(t,x) = -d_i'(x), \forall(t,x) \in \mathbb{R}\times\mathbb{R}, i = 1, 2$, it easily follows from the latter case in Lemma 5.2.1(c) or the proof of Lemma 4.4.2. □

Now we introduce the following assumptions on system (5.60):

(M) $a(t,x)$ is non-trivial and even in x, and $\overline{a} = \frac{1}{L}\int_0^1\int_0^L a(t,x)dxdt \geq 0$.

Lemma 5.2.3. *Let (M) hold. Then (H1)–(H3) are valid for system* (5.60) *if either of the following holds:*

(a) d_2 *is large enough;*

(b) ω is small enough.

Proof. Since we consider the periodic initial value problem. We may regard system (5.60) as in the following system:

$$\begin{aligned}
&\frac{\partial u_1}{\partial t} = d_1\Delta u_1 + u_1(a_\omega(t,x) - u_1 - u_2), \\
&\frac{\partial u_2}{\partial t} = d_2\Delta u_2 + u_2(a_\omega(t,x) - u_1 - u_2), \quad t>0,\ x\in(0,L), \\
&u_i(0,x) = \phi_i(x) \in \overline{X} := \{\phi\in C([0,L],\mathbb{R}) : \phi(0)=\phi(L)\}, i=1,2.
\end{aligned} \tag{5.63}$$

Let $\phi(t,x)$ be the positive time-space periodic eigenfunction associated with the principal eigenvalue $\lambda(d_1,0,a)$, that is,

$$-\phi_t + d_1\phi_{xx} + a_\omega(t,x)\phi = \lambda(d_1,0,a)\phi, \quad (t,x)\in\mathbb{R}\times\mathbb{R}.$$

Dividing the above equation by ϕ and integrating by parts on $[0,L]\times[0,\omega]$, we get

$$\lambda(d_1,0,a) = \frac{1}{L}\int_0^1\int_0^L a(t,x)dxdt + \frac{d_1}{\omega L}\int_0^\omega\int_0^L\left[\frac{\phi_x(t,x)}{\phi(t,x)}\right]^2 dxdt.$$

Since $a(t,x)$ is non-trivial in x, a simple computation shows that $\phi(t,x)$ is also non-trivial in x. Therefore, we have

$$\lambda(d_1,0,a) > \frac{1}{L}\int_0^1\int_0^L a(t,x)dxdt = \overline{a} \geq 0.$$

Similarly, we can show that $\lambda(d_2,0,a)>0$. It follows that (H1) holds provided that (M) is valid.

In the case where d_2 is large enough, let A_{d_2} denote the unbounded closed operator on $\overline{X}$ with the maximum norm defined by

$$D(A_{d_2}) = \{u : u, u', u'' \in \overline{X}\}, \quad A_{d_2}u = d_2u'', \forall u\in D(A_{d_2}).$$

Then [77, Chapter 8, Lemma 2.1] implies that A_{d_2} generates an analytic semigroup $e^{A_{d_2}t}$ on $\overline{X}$. By the essentially same arguments as in [43, Lemmas 3.6(c)–3.7 and Theorem 5.3(a)], it follows that (H2) and (H3) hold true.

In the case where ω is small enough, by the arguments similar to those in [43, Lemma 3.6(b) and Theorem 5.3(b)], we can also show that (H2) and (H3) are valid, and hence, system (5.60) has three time-space periodic solutions $E_0 := (0,0)$, $E_1 := (u_1^*(t,x),0)$ and $E_2 := (0,u_2^*(t,x))$ in $\mathbb{P}_+$. □

As a consequence of Lemma 5.2.3 and Theorem 5.2.1, we have the following result.

Theorem 5.2.5. *Let (M) and either case (a) or (b) in Lemma 5.2.3 hold. Then* $E_1 := (u_1^*(t,x),0)$ *is globally asymptotically stable for all initial values* $\phi = (\phi_1,\phi_2) \in \mathbb{P}_+$ *with* $\phi_1 \not\equiv 0$.

For simplicity, we transfer system (5.60) into the following cooperative system:

$$
\begin{aligned}
\frac{\partial u_1}{\partial t} &= d_1\frac{\partial^2 u_1}{\partial x^2} + u_1(a_\omega(t,x) - u_2^*(t,x) - u_1 + u_2), \\
\frac{\partial u_2}{\partial t} &= d_2\frac{\partial^2 u_2}{\partial x^2} + u_1(u_2^*(t,x) - u_2) + u_2(a_\omega(t,x) - 2u_2^*(t,x) + u_2), \quad t>0,\ x\in\mathbb{R}.
\end{aligned}
\tag{5.64}
$$

The next result is the consequence of Theorem 5.2.3, Remark 5.2.1 and Proposition 5.2.4.

Theorem 5.2.6. *Assume that (M) and either case (a) or (b) in Lemma 4.4.3 hold. Let* $u(t,\cdot,\phi)$ *be the solution of system* (5.64) *with* $u(0,\cdot) = \phi \in \mathcal{C}_{\beta(0,\cdot)}$. *Then there exists a positive real number* $\bar{c}_+$ *such that the following statements are valid for system* (5.64)*:*

(i) If $\phi \in \mathcal{C}_{\beta(0,\cdot)}$, $0 \le \phi \le \omega \ll \beta$ *for some* $\omega \in \mathcal{C}^{per}_{\beta(0,\cdot)}$, *and* $\phi(x) = 0, \forall x \ge H$, *for some* $H \in \mathbb{R}$, *then* $\lim_{t\to\infty, x\ge ct} u(t,x,\phi) = 0$ *for any* $c > \bar{c}_+$.

(ii) If $\phi \in \mathcal{C}_{\beta(0,\cdot)}$ *and* $\phi(x) \geq \sigma$, $\forall x \leq K$, *for some* $\sigma \in \mathbb{R}^2$ *with* $\sigma \gg 0$ *and* $K \in \mathbb{R}$, *then* $\lim_{t\to\infty, x\leq ct}(u(t,x,\phi) - u^*(t,x)) = 0$ *for any* $c \in (0, \bar{c}_+)$.

In view of Theorem 5.2.2, we have the following result on periodic traveling waves for system (5.60).

Theorem 5.2.7. *Let (M) and either case (a) or (b) in Lemma 5.2.3 hold. Then for any* $c \geq \bar{c}_+$, *system* (5.60) *has time-space periodic traveling wave* $(U(t,x,x-ct), V(t,x,x-ct))$ *connecting* $(u_1^*(t,x),0)$ *to* $(0,u_2^*(t,x))$ *with the wave profile component* $U(t,x,\xi)$ *being continuous and non-increasing in* ξ, *and* $V(t,x,\xi)$ *being continuous and non-decreasing in* ξ. *While for any* $c \in (0,\bar{c}_+)$, *system* (5.60) *admits no periodic rightward traveling wave connecting* $(u_1^*(t,x),0)$ *to* $(0,u_2^*(t,x))$.

Chapter 6

A Nonlocal Spatial Model for Lyme Disease

In this chapter, we consider the Lyme disease transmission in a bounded habitat $\Omega \subset \mathbb{R}^2$ with a smooth boundary $\partial\Omega$. Let $\Gamma(t, x, y, D)$ be the Green function associated with the linear parabolic equation:

$$\frac{\partial u}{\partial t} = \nabla \cdot (D(x)\nabla u),\ t > 0, x \in \Omega,$$
$$\frac{\partial u}{\partial \nu} = 0,\ t > 0, x \in \partial\Omega,$$

where ν is the outward normal vector to $\partial\Omega$. Then $\int_\Omega \Gamma(t, x, y, D)\varphi(y)dy$ denotes the distribution at time t through the diffusion with the given initial distribution $\varphi(x)$. Let $M(t, x)$ and $m(t, x)$ be the densities of susceptible and pathogen-infected mice, $L(t, x)$ be the density of questing larvae, $N(t, x)$ and $n(t, x)$ be the densities of susceptible and infectious questing nymphs, $A(t, x)$ and $a(t, x)$ be the densities of uninfected and pathogen-infected adult ticks, and $H(t, x)$ be the density of deers, at time t and location x. Based on the attached rates of larvae to mice and disease transmission mechanisms in the model of [12], the authors of [92] introduced the following drop-off rate of susceptible larvae from a mouse:

$$N_b = P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)[M(t-\tau_l, y) + (1-\beta_T(y))m(t-\tau_l, y)]L(t-\tau_l, y)dy,$$

where $P_l = \alpha e^{-(\mu_L+\mu_M)\tau_l}$, and the definition of unstated parameters is referred to Table 6.1. The drop-off rates of infected larvae, susceptible nymphs and infectious nymphs from mice can be described in a similar way. Moreover, the density of egg-laying adult ticks, that is, the drop-off rate of adult ticks from deers after blood meals is given by

$$T_b = \xi e^{-(\mu_A+\mu_h)\tau_a} \int_\Omega \Gamma(\tau_a, x, y, D_H)(A(t-\tau_a, y) + a(t-\tau_a, y))H(t-\tau_a, y)dy.$$

The per capita birth rate B_M of mice is taken in [92] as the negative exponential function:

$$B_M(x, M+m) = r_M \exp\left(-\frac{M+m}{K_M(x)}\right),$$

where $K_M(x)$ is a continuous and positive function on $\overline{\Omega}$. Unlike the model in [92], we use the linear birth rate rT_b for the tick population. Assume that the self-regulation process for adult ticks is mainly due to some density-dependent death terms and intra-competition. Then terms $\delta_A(A+a)A$ and $\delta_A(A+a)a$ represent the self-regulation for uninfected and infected adult ticks, respectively. Let $P_n = \alpha e^{-(\mu_L+\mu_M)\tau_n}$. Accordingly, the earlier model in [92] can be modified as

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla\cdot(D_M(x)\nabla M) + (M+m)B_M(x, M+m) - \mu_M M - \alpha\beta(x)Mn,\\
\frac{\partial m}{\partial t} &= \nabla\cdot(D_M(x)\nabla m) + \alpha\beta(x)Mn - \mu_M m,\\
\frac{\partial L}{\partial t} &= rT_b - \mu_L L - \alpha L(M+m),\\
\frac{\partial N}{\partial t} &= N_b - [\gamma + \alpha(M+m) + \mu_N]N,\\
\frac{\partial n}{\partial t} &= n_b - [\gamma + \alpha(M+m) + \mu_N]n,\\
\frac{\partial A}{\partial t} &= A_b - (\mu_A + \xi H)A - \delta_A(A+a)A,\\
\frac{\partial a}{\partial t} &= a_b - (\mu_A + \xi H)a - \delta_A(A+a)a,\\
\frac{\partial H}{\partial t} &= \nabla\cdot(D_H(x)\nabla H) + r_h - \mu_h H,
\end{aligned} \tag{6.1}$$

where three terms

$$\begin{aligned}
n_b &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)m(t-\tau_l, y)L(t-\tau_l, y)dy,\\
A_b &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)[M(t-\tau_n, y) + (1-\beta_T(y))m(t-\tau_n, y)]N(t-\tau_n, y)dy,\\
a_b &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)[(M(t-\tau_n, y) + m(t-\tau_n, y))n(t-\tau_n, y)\\
&\qquad + \beta_T(y)m(t-\tau_n, y)N(t-\tau_n, y)]dy
\end{aligned}$$

describe the drop-off rates of infected larvae, susceptible and infectious nymphs from mice, respectively. Figure 6.1 is the schematic diagram for tick population to illustrate the tick-mouse cycle of infection.

We suppose that all constant parameters in (6.1) are positive, $D_M(x)$, $D_H(x)$ are positive and continuous on $\overline{\Omega}$, and $\beta(x)$ is a continuous function on $\overline{\Omega}$ with $0 \leq \beta(x) \leq 1$ but $\beta(x) \not\equiv 0$, so is $\beta_T(x)$. Further, we impose the Neumann boundary condition

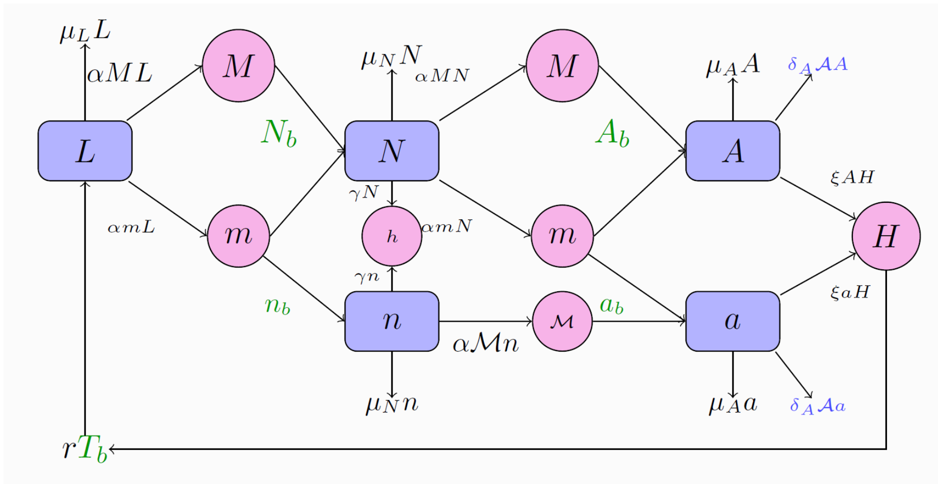

Figure 6.1: The schematic diagram for tick population.

for M, m and H:

$$\frac{\partial M}{\partial \nu} = \frac{\partial m}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0, \quad \forall t > 0, x \in \partial \Omega.$$

The biological interpretations for the parameters in system (6.1) are listed in Table 6.1.

This chapter is organized as follows. In section 6.1, we focus on the global stability of disease-free steady state of the associated system. In section 6.2, we introduce the basic reproduction number and obtain a threshold result on the global dynamics of the model system with spatial heterogeneity in a bounded habitat. In section 6.3, we investigate the propagation phenomena for a limiting system in an unbounded habitat. Numerical simulations are given in section 6.4 to verify our analytic results. And a short discussion section completes the paper.

Table 6.1: Biological interpretations of parameters in model (6.1).

r_M	Maximal individual birth rate of mice.
r	Individual birth rate of ticks.
r_h	Birth rate of deers.
μ_M	Mortality rate per mouse.
μ_L	Mortality rate per tick larva.
μ_N	Mortality rate per tick nymph.
μ_A	Mortality rate per adult tick.
μ_h	Mortality rate per deer.
α	Attack rate, juvenile ticks on mice.
γ	Attack rate, tick nymphs on humans.
ξ	Coefficient of an adult tick to attach to deers.
δ_A	Self-regulation coefficient for adult ticks.
τ_l	Feeding duration of tick larvae on mice.
τ_n	Feeding duration of tick nymphs on mice.
τ_a	Feeding duration of adult ticks on deers.
$D_M(x)$	Diffusion coefficient for mice at location x.
$D_H(x)$	Diffusion coefficient for deers at location x.
$K_M(x)$	Carrying capacity for mice at location x.
$\beta(x)$	Susceptibility to infection in mice at location x.
$\beta_T(x)$	Susceptibility to infection in ticks at location x.

6.1 Disease-free dynamics

In this section, we study the existence of the positive disease-free steady state and its global attractiveness. Note that in the absence of infection of Lyme disease, system (6.1) reduces to

$$\begin{aligned}
\frac{\partial M}{\partial t} &= \nabla \cdot (D_M(x)\nabla M) + MB(x,M) - \mu_M M,\\
\frac{\partial L}{\partial t} &= P_a \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t-\tau_a, y) H(t-\tau_a, y)dy - (\mu_L + \alpha M)L,\\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M(t-\tau_l, y) L(t-\tau_l, y)dy - (\gamma + \alpha M + \mu_N)N, \qquad (6.2)\\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M(t-\tau_n, y) N(t-\tau_n, y)dy - (\mu_A + \xi H)A - \delta_A A^2,\\
\frac{\partial H}{\partial t} &= \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H,
\end{aligned}$$

where $P_a = r\xi e^{-(\mu_A+\mu_h)\tau_a}$, and M and H are subject to the Neumann boundary condition:

$$\frac{\partial M}{\partial \nu} = \frac{\partial H}{\partial \nu} = 0, \quad \forall t > 0, x \in \partial\Omega.$$

It is easy to see that

$$\begin{aligned}
&\frac{\partial H}{\partial t} = \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H, \quad t > 0,\ x \in \Omega,\\
&\frac{\partial H}{\partial \nu} = 0, \quad \forall t > 0,\ x \in \partial\Omega
\end{aligned}$$

has a positive steady state $H^* = \frac{r_h}{\mu_h}$, which is globally stable in $C(\overline{\Omega}, \mathbb{R}_+)$. Moreover, we assume that

(H1) $r_M > \mu_M$.

By a standard convergence result on the logistic type reaction-diffusion equation (see, e.g., [10] and [106, Theorems 2.3.4 and 3.1.6]), it then follows that the following reaction-diffusion system

$$\begin{aligned}
&\frac{\partial M}{\partial t} = \nabla \cdot (D_M(x)\nabla M) + MB_M(x, M) - \mu_M M, \quad t > 0,\ x \in \Omega,\\
&\frac{\partial M}{\partial \nu} = 0, \quad \forall t > 0,\ x \in \partial\Omega
\end{aligned}$$

admits a globally stable positive steady state $M^*(x)$ in $C(\overline{\Omega}, \mathbb{R}_+)\backslash\{0\}$. Thus, we first study the global dynamics of the following limiting system:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)A(t-\tau_a, y)dy - [\mu_L + \alpha M^*(x)]L,\\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)M^*(y)L(t-\tau_l, y)dy - [\gamma + \alpha M^*(x) + \mu_N]N, \qquad (6.3)\\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)M^*(y)N(t-\tau_n, y)dy - (\mu_A + \xi H^*)A - \delta_A A^2.
\end{aligned}$$

Let $\tau_0 = \max\{\tau_a, \tau_l, \tau_n\}$, $X = C(\overline{\Omega}, \mathbb{R}^3)$, $X_+ = C(\overline{\Omega}, \mathbb{R}^3_+)$, $Y = C([-\tau_0, 0], X)$ and $Y_+ = C([-\tau_0, 0], X_+)$. Then (X, X_+) and (Y, Y_+) are ordered Banach spaces. As usual, we identify an element $\varphi \in Y$ with a function from $[-\tau_0, 0] \times \mathbb{R}$ into $\mathbb{R}^3$ defined by $\varphi(\theta, x) = \varphi(\theta)(x)$. For any function $u \in C([-\tau_0, a), X)$ with some $a > 0$ and any $t \in [0, a)$, we define $u_t \in Y$ by $u_t(\theta) = u(t + \theta), \forall \theta \in [-\tau_0, 0]$.

Define linear semigroups $T_i(t)$, $1 \le i \le 3$ on $C(\overline{\Omega}, \mathbb{R})$ by

$$T_1(t)\phi_1 = e^{-[\mu_L + \alpha M^*(x)]t}\phi_1,\ T_2(t)\phi_2 = e^{-[\gamma + \alpha M^*(x) + \mu_N]t}\phi_2,\ T_3(t)\phi_3 = e^{-(\mu_A + \xi H^*)t}\phi_3,$$

respectively. Let A_i^0 be the generator of $T_i(t)$. Then $T(t) = (T_1(t), T_2(t), T_3(t)) : X \to X$ is a semigroup generated by the operator $A^0 = (A_1^0, A_2^0, A_3^0)$. Define $F = (F_1, F_2, F_3) : Y \to X$ by

$$\begin{aligned}
F_1(\phi)(x) &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(-\tau_a, y)dy,\\
F_2(\phi)(x) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)M^*(y)\phi_1(-\tau_l, y)dy,\\
F_3(\phi)(x) &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)M^*(y)\phi_2(-\tau_n, y)dy - \delta_A \phi_3^2(0, x),
\end{aligned}$$

for $x \in \overline{\Omega}$ and $\phi = (\phi_1, \phi_2, \phi_3)^T \in Y$. Then system (6.3) can be written as the following abstract functional differential equation:

$$\begin{aligned}
&\frac{du}{dt} = A^0 u + F(u_t), \quad t > 0,\\
&u_0 = \phi \in Y_+.
\end{aligned} \tag{6.4}$$

From the expression of F, we see that $F(\phi)$ is locally Lipschitz continuous on Y_+, and $F(\phi)$ is quasi-monotone on Y_+ in the sense that whenever $\phi \le \psi$ and $\phi_i(0) = \psi_i(0)$ for some $i \in \{1, 2, 3\}$, then $F_i(\phi) \le F_i(\psi)$.

In view of [64, Corollary 5] (see also [97, Theorem 2.1.1 and Remark 2.1.5]), it follows that for any $\phi \in Y_+$, system (6.4) admits a unique nonnegative continuous solution

$$u(t,x,\phi) = (L(t,x,\phi), N(t,x,\phi), A(t,x,\phi))$$

on $[0,t_\phi)$ with $u(\theta,x,\phi)=\phi(\theta,x)$ for all $(\theta,x)\in[-\tau_0,0]\times\overline{\Omega}$ and $u_t\in Y_+$ for $t\geq 0$, and the comparison principle holds for upper and lower solutions of system (6.4). Note that there exists a positive vector $\zeta=(\zeta_1,\zeta_2,\zeta_3)\in\mathbb{R}^3$ such that

$$P_a H^*\zeta_3-\mu_L\zeta_1=0,\ P_l M^*_{\max}\zeta_1-(\gamma+\mu_N)\zeta_2=0,\ P_n M^*_{\max}\zeta_2-\delta_A\zeta_3^2\leq 0,$$

where $M^*_{\max}=\max_{\overline{\Omega}} M^*(x)$. Then it is easy to see that for any $k\geq 1$, $k\zeta$ is an upper solution of system (6.4). This implies that $t_\phi=\infty$ and the solution of (6.4) is uniformly bounded. We further have the following result on the asymptotic compactness of forward orbits.

Proposition 6.1.1. *For any $\phi\in Y_+$, the forward orbit $\gamma^+(\phi):=\{u(t,\cdot,\phi),t\geq 0\}$ for system* (6.3) *is asymptotically compact in the sense that for any sequence $t_n\to\infty$, there exists a subsequence t_{n_k} such that $u(t_{n_k},\cdot,\phi)$ converges in X as $k\to\infty$.*

Proof. Our arguments are motivated by [36, Lemma 4.1]. Note that for any given $\phi=(\phi_1,\phi_2,\phi_3)\in Y_+$, there exists $\eta>0$ such that

$$|L(t,x,\phi)|\leq\eta,\ |N(t,x,\phi)|\leq\eta,\ |A(t,x,\phi)|\leq\eta,\quad \forall t\geq 0,\ x\in\overline{\Omega}.$$

In view of the Arezla-Ascoli theorem, it suffices to prove that $\{u(t_n,x,\phi)\}_{n\geq 1}$ is equicontinuous in $x\in\overline{\Omega}$ for all $n\geq 1$. We first show that $\{A(t_n,x,\phi)\}_{n\geq 1}$ is equicontinuous in $x\in\overline{\Omega}$ for all $n\geq 1$. By the uniform boundedness of $N(t,x,\phi)$, it is easy to see that $f(x,t):=P_n\int_\Omega\Gamma(\tau_n,x,y,D_M)M^*(y)N(t-\tau_n,y,\phi)dy$ is uniformly continuous in $x\in\overline{\Omega}$ uniformly for $t\geq 0$, that is, $\forall\varepsilon>0$, there exists $\delta>0$ such that

$$|f(x_1,t)-f(x_2,t)|<\varepsilon^2$$

provided that $|x_1 - x_2| < \delta, \forall t \geq 0, x_1, x_2 \in \overline{\Omega}$. As in the proof of [36, Lemma 4.1], we let $v_n(t_n, x) = A(t_n, x, \phi)$, $t \geq 0, x \in \overline{\Omega}$. Define $\overline{v}_n(t, x) = v_n(t + t_n, x), \forall t \geq -t_n, x \in \overline{\Omega}$. Set $r = \mu_A + \xi H^* > 0$. Clearly,

$$\begin{aligned}
&\frac{\partial}{\partial t}[\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2)]^2 \\
&= 2(\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2))[f(x_1, t + t_n) - f(x_2, t + t_n) \\
&\quad -r(\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2)) - \delta_A(\overline{v}_n^2(t, x_1) - \overline{v}_n^2(t, x_2))] \\
&\leq 4\eta|f(x_1, t + t_n) - f(x_2, t + t_n)| - 2r(\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2))^2 \\
&\leq 4\eta\varepsilon^2 - 2r(\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2))^2
\end{aligned}$$

for all $t \geq -t_n$, $|x_1 - x_2| < \delta, x_1, x_2 \in \overline{\Omega}$. By the variation of constants formula and the comparison argument, we have

$$|\overline{v}_n(t, x_1) - \overline{v}_n(t, x_2)|^2 \leq e^{-2r(t-s)}|\overline{v}_n(s, x_1) - \overline{v}_n(s, x_2)|^2 + 4\eta\varepsilon^2 \int_s^t e^{-2r(t-\theta)} d\theta.$$

Letting $t = 0$ and $s = -t_n$ in the above inequality, we further obtain

$$|\overline{v}_n(0, x_1) - \overline{v}_n(0, x_2)|^2 \leq e^{-2rt_n}|\overline{v}_n(-t_n, x_1) - \overline{v}_n(-t_n, x_2)|^2 + \frac{2\eta\varepsilon^2}{r},$$

that is,

$$|A(t_n, x_1, \phi) - A(t_n, x_2, \phi)|^2 \leq |\phi_3(0, x_1) - \phi_3(0, x_2)|^2 + \frac{2\eta\varepsilon^2}{r},$$

for all $n \geq 1$, $|x_1 - x_2| < \delta$, $x_1, x_2 \in \overline{\Omega}$. Since $\phi_3(0, x)$ is uniformly continuous for $x \in \overline{\Omega}$, there exists $\delta_1 > 0$ such that $|\phi_3(0, x_1) - \phi_3(0, x_2))| < \varepsilon$ whenever $|x_1 - x_2| < \delta_1$. Thus, for any $|x_1 - x_2| < \delta_0 := \min\{\delta_1, \delta\}$, $x_1, x_2 \in \overline{\Omega}$, we have

$$|A(t_n, x_1, \phi) - A(t_n, x_2, \phi)|^2 \leq \varepsilon^2 + \frac{2\eta\varepsilon^2}{r} \leq (1 + \frac{2\eta}{r})\varepsilon^2.$$

Similarly, we can verify that $\{L(t_n, x, \phi)\}_{n\geq 1}$ and $\{N(t_n, x, \phi)\}_{n\geq 1}$ are also equicontinuous in $x \in \overline{\Omega}$ for all $n \geq 1$. □

Linearizing (6.3) at its zero solution, we obtain

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t-\tau_a, y)dy - [\mu_L + \alpha M^*(x)]L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t-\tau_l, y)dy - [\gamma + \alpha M^*(x) + \mu_N]N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t-\tau_n, y)dy - (\mu_A + \xi H^*)A.
\end{aligned} \tag{6.5}$$

Define an operator $A = (A_1, A_2, A_3)$ on X by

$$\begin{aligned}
A_1(\phi) &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y)dy - [\mu_L + \alpha M^*(x)]\phi_1, \\
A_2(\phi) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(y)dy - [\gamma + \alpha M^*(x) + \mu_N]\phi_2, \\
A_3(\phi) &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y)\phi_2(y)dy - (\mu_A + \xi H^*)\phi_3.
\end{aligned} \tag{6.6}$$

Clearly, A is closed and resolvent-positive operator (see, e.g., [88, Theorem 3.12]). Let $s(\tilde{A})$ be the spectral bound of an operator $\tilde{A}$, that is, $s(\tilde{A}) = \sup\{\text{Re}\lambda : \lambda \in \sigma(\tilde{A})\}$, where $\sigma(\tilde{A})$ is the spectral set of an operator, and $\mathcal{N}(\lambda I - \tilde{A})$ and $\mathcal{R}(\lambda I - \tilde{A})$ be the null space and range space of $\lambda I - \tilde{A}$, respectively, where I is the identity operator. Then we have the following observation.

Lemma 6.1.1. *Assume that (H1) holds. Then $s(A)$ is a geometrically simple eigenvalue of A with a positive eigenfunction.*

Proof. Let $M_m^* = \min_{x\in\overline{\Omega}} M^*(x)$ and $c_0 := \min\{\mu_L + \alpha M_m^*, \gamma + \alpha M_m^* + \mu_N, \mu_A + \xi H^*\}$. For any $\phi = (\phi_1, \phi_2, \phi_3) \in \mathcal{N}(\lambda I - A)$, we have

$$\begin{aligned}
\lambda\phi_1 &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y)dy - (\mu_L + \alpha M^*(x))\phi_1, \\
\lambda\phi_2 &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y)\phi_1(y)dy - (\gamma + \alpha M^*(x) + \mu_N)\phi_2, \\
\lambda\phi_3 &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y)\phi_2(y)dy - (\mu_A + \xi H^*)\phi_3.
\end{aligned} \tag{6.7}$$

For $\lambda > -c_0$, we obtain from the first and second equations of (6.7) that

$$\phi_1(x) = \frac{P_a H^*}{\lambda + \mu_L + \alpha M^*(x)} \int_\Omega \Gamma(\tau_a, x, y, D_H)\phi_3(y)dy,$$
$$\phi_2(x) = \frac{P_l}{\lambda + \gamma + \alpha M^*(x) + \mu_N} \int_\Omega \Gamma(\tau_l, x, y, D_M)M^*(y)\phi_1(y)dy. \qquad (6.8)$$

It then follows that

$$\begin{aligned}\phi_2(x) \quad = \quad & \int_\Omega \Gamma(\tau_l, x, y, D_M)\frac{M^*(y)}{\lambda + \mu_L + \alpha M^*(y)}\int_\Omega \Gamma(\tau_a, y, s, D_H)\phi_3(s)dsdy \\ & \cdot \frac{P_a P_l H^*}{\lambda + \gamma + \alpha M^*(x) + \mu_N} := F(\lambda, \phi_3)(x) \qquad (6.9)\end{aligned}$$

Substituting this into the third equation of (6.7), we obtain

$$L_\lambda(\phi_3) := P_n \int_\Omega \Gamma(\tau_n, \cdot, y, D_M)M^*(y)F(\lambda, \phi_3)(y)dy - (\mu_A + \xi H^*)\phi_3 = \lambda\phi_3. \quad (6.10)$$

Let $G(\lambda) := (\lambda+\gamma+\alpha M_m^*+\mu_N)(\lambda+\mu_A+\xi H^*)(\lambda + \mu_L + \alpha M_m^*) - P_a P_n P_l H^* M_m^{*2}$. Since $G(-c_0) = -P_a P_n P_l H^* M_m^{*2} < 0$, $G(+\infty) = +\infty$, and $G(\lambda)$ is strictly increasing on $[-c_0, +\infty)$, it follows that there exists a unique $\lambda_0 \in (-c_0, \infty)$ such that $G(\lambda_0) = 0$. Note that for any $x \in \overline{\Omega}$,

$$\frac{M^*(x)}{\lambda_0 + \mu_L + \alpha M^*(x)} \geq \frac{M_m^*}{\lambda_0 + \mu_L + \alpha M_m^*},$$

and

$$\frac{M^*(x)}{\lambda_0 + \gamma + \alpha M^*(x) + \mu_N} \geq \frac{M_m^*}{\lambda_0 + \gamma + \alpha M_m^* + \mu_N}.$$

Thus, if we choose $\phi_3 = 1$, then we have

$$L_{\lambda_0}(\phi_3) \geq \frac{P_a P_n P_l H^* M_m^{*2}}{(\lambda_0 + \gamma + \alpha M_m^* + \mu_N)(\lambda_0 + \mu_L + \alpha M_m^*)} - (\mu_A + \xi H^*) = \lambda_0 \phi_3$$

Since L_λ admits a principle eigenvalue $\mu(\lambda)$, by the essentially same arguments as in [91, Theorem 2.3], it follows that $s(A)$ is a geometrically simple eigenvalue with a positive eigenfunction. □

Now we are in position to prove a threshold type result on the global dynamics of system (6.2) in terms of $s(A)$.

Theorem 6.1.1. *Let (H1) hold. Then the following statements are valid:*

(i) If $s(A) < 0$, then $(M^*(x), 0, 0, 0, H^*)$ is globally attractive for positive solutions of system (6.2).

(ii) If $s(A) > 0$, then system (6.2) admits a unique positive steady state $E_0 := (M^*(x), L^*(x), N^*(x), A^*(x), H^*)$, and E_0 is globally attractive for positive solutions of system (6.2).

Proof. Note that $M^*(x)$ and H^* are globally stable for positive solutions of the first equation and the last equation of system (6.2), respectively. By the theory of asymptotically autonomous semiflows (see, e.g., [87]), it suffices to prove the threshold type result on the global dynamics of system (6.3). To do so, we first consider the following nonlocal evolution system without time delay:

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^*) A - \delta_A A^2.
\end{aligned} \tag{6.11}$$

It then easily follows that for each $t > 0$, the time-t map of (6.11) is strongly monotone and strictly subhomogeneous on X_+. Since the linearized system of (6.11) at $(0, 0, 0)$

is

$$
\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^*) A,
\end{aligned}
\tag{6.12}
$$

we see that A is the generator of solution semigroup of (6.12). By Lemma 6.1.1, there exists a positive function ϕ^* such that $A\phi^* = s(A)\phi^*$, that is,

$$
\begin{aligned}
s(A)\phi_1^* &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) \phi_3^*(y) dy - (\mu_L + \alpha M^*(x))\phi_1^*, \\
s(A)\phi_2^* &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) \phi_1^*(y) dy - (\gamma + \alpha M^*(x) + \mu_N)\phi_2^*, \\
s(A)\phi_3^* &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) \phi_2^*(y) dy - (\mu_A + \xi H^*)\phi_3^*.
\end{aligned}
$$

In the case where $s(A) < 0$, let u_t be the solution semiflow of linear time-delayed system (6.5), that is, $u_t(\varphi)(\theta) = u(t+\theta, \cdot, \varphi)$, $\forall t \geq 0$, $\theta \in [-\tau_0, 0], \varphi \in Y$. It then follows from the arguments similar to those in Proposition 6.1.1 that the bounded forward orbit $\gamma^+(\phi^*) = \{u_t(\phi^*) : t \geq 0\}$ is asymptotically compact, and hence, its omega limit set $\omega(\phi^*)$ is nonempty, compact and invariant for the solution semiflow u_t. Adapting the proof in [92, Theorem 3.6], we see that every solution of linear system (6.5) converges to zero. Thus, the fact that every nonnegative solution of system (6.3) satisfies

$$
\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t - \tau_a, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t - \tau_l, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &\leq P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t - \tau_n, y) dy - (\mu_A + \xi H^*) A,
\end{aligned}
\tag{6.13}
$$

that is, every nonnegative solution of system (6.3) is a lower solution of system (6.5), implies that statement (i) is valid.

Next we consider the case where $s(A) > 0$. Note that the solution semiflow of system (6.3) is monotone and subhomogeneous. In view of the comparison arguments shown in [92, Proposition 3.7], it suffices to verify that system (6.11) admits a globally stable positive steady state $(L^*(x),\ N^*(x), A^*(x))$. For small $\epsilon > 0$, we consider the following linear system without time delay:

$$
\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &= P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^* + \epsilon \delta_A) A.
\end{aligned}
\tag{6.14}
$$

Let A_ϵ be the generator of the solution semigroup of (6.14). By virtue of Lemma 6.1.1, we obtain that $s(A_\epsilon)$ is also a geometrically simple eigenvalue with a positive eigenfunction ϕ_ϵ. Note that when $\epsilon > 0$ is small enough, the spectral bound depends continuously on ϵ. It then follows that there exists a sufficiently small $\epsilon_0 > 0$ such that $s(A_{\epsilon_0}) > 0$. We further prove the following two claims.

Claim 1. Let $\hat{u}(t, \cdot, \phi)$ is the solution of system (6.11). Then $\limsup_{t\to\infty} \|\hat{u}(t, \cdot, \phi)\| \geq \epsilon_0,\ \forall \phi \in X_+ \setminus \{0\}$.

For the sake of contradiction, we assume that $\limsup_{t\to\infty} \|\hat{u}(t, \cdot, \phi)\| < \epsilon_0$ for some $\phi_0 \in X_+ \setminus \{0\}$. Then there exists $t_0 > 0$ such that $\hat{u}(t, \cdot, \phi_0) < \boldsymbol{\epsilon_0} := (\epsilon_0, \epsilon_0, \epsilon_0)$, $\forall t \geq t_0$.

It follows that for all $t \geq t_0$, $\hat{u}(t, \cdot, \phi_0)$ satisfies

$$\begin{aligned}
\frac{\partial L}{\partial t} &= P_a H^* \int_\Omega \Gamma(\tau_a, x, y, D_H) A(t, y) dy - [\mu_L + \alpha M^*(x)] L, \\
\frac{\partial N}{\partial t} &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M) M^*(y) L(t, y) dy - [\gamma + \alpha M^*(x) + \mu_N] N, \\
\frac{\partial A}{\partial t} &\geq P_n \int_\Omega \Gamma(\tau_n, x, y, D_M) M^*(y) N(t, y) dy - (\mu_A + \xi H^* + \epsilon_0 \delta_A) A.
\end{aligned} \tag{6.15}$$

Since $\hat{u}(t_0, \cdot, \phi_0) \gg 0$, we can choose a small number $\rho > 0$ such that $\hat{u}(t_0, x, \phi_0) \geq \rho e^{s(A_{\epsilon_0})t_0} \phi_{\epsilon_0}(x)$, $\forall x \in \overline{\Omega}$. Note that $\rho e^{s(A_{\epsilon_0})t} \phi_{\epsilon_0}(x)$ is the solution of linear system (6.14) with $\epsilon = \epsilon_0$ and $s(A_{\epsilon_0}) > 0$. It follows from (6.15) and the comparison principle that $\hat{u}(t, x, \phi_0) \geq \rho e^{s(A_{\epsilon_0})t} \phi_{\epsilon_0}(x)$, $\forall t \geq t_0$, $x \in \overline{\Omega}$. Letting $t \to \infty$, we see that $\hat{u}(t, x, \phi_0)$ is unbounded, a contradiction to the boundedness of $\hat{u}(t, x, \phi_0)$.

Claim 2. Let $\omega(\phi)$ be the omega limit set of the forward orbit $\gamma^+(\phi) := \{\hat{u}(t, \cdot, \phi) : t \geq 0\}$. Then $\omega(\phi) \subset \mathrm{Int}(X_+)$, $\forall \phi \in X_+ \backslash \{0\}$. .

By adapting the proof in Proposition 6.1.1, we see that $\gamma^+(\phi)$ is asymptotically compact, and hence, $\omega(\phi)$ is nonempty, compact and invariant. Let $\phi \in X_+ \backslash \{0\}$ be given and $Q(t)\phi := \hat{u}(t, \cdot, \phi)$. It then follows from *Claim 1* that set $A := \{0\}$ is an isolated invariant set for the semiflow $Q(t)$ and $\omega(\phi) \not\subseteq A$. Thus, the generalized Butler-McGehee lemma (see, e.g., [106, Lemma 1.2.7]) implies that $\omega(\phi) \cap A = \emptyset$, and hence, $\omega(\phi) \subset X_+ \backslash \{0\}$. By the strong monotonicity of $Q(t)$ and the invariant of $\omega(\phi)$ for $Q(t)$, it follows that $\omega(\phi) \subset \mathrm{Int}(X_+)$.

Let $t_1 > 0$ be fixed. Then $Q(t_1)$ is strongly monotone and strictly subhomogeneous on $X_+ \backslash \{0\}$. Note that $\omega(\phi)$ is a compact and invariant set for Q_{t_1}. It then follows from Claim 2 and [106, Theorem 2.3.2] with $K = \omega(\phi)$ that Q_{t_1} has a unique fixed point $u_e = (L^*(\cdot), N^*(\cdot), A^*(\cdot)) \gg 0$ such that $\omega(\phi) = \{u_e\}$, $\forall \varphi \in X_+ \backslash \{0\}$. Since $Q(t)\omega(\phi) = \omega(\phi)$ for all $t \geq 0$, we see that u_e is a positive steady state of system (6.11). This shows that system (6.11) admits a unique positive steady state $(L^*(x)$,

$N^*(x), A^*(x))$, which is globally asymptotically stable in $X_+\backslash\{0\}$. Consequently, the same comparison arguments as in [92, Proposition 3.7(ii)] imply that statement (ii) holds true for system (6.2). □

6.2 Global dynamics

In this section, we introduce the basic reproduction number for model (6.1) and study the global dynamics of Lyme disease invasion. Throughout this section, we assume that (H1) holds and $s(A) > 0$, where A is defined as in (6.6).

By Theorem 6.1.1, system (6.2) admits a globally stable positive steady state $(M^*(x), L^*(x), N^*(x), A^*(x), H^*)$, and hence, system (6.1) has a unique disease-free steady state

$$E_1 = (M^*(x), 0, L^*(x), N^*(x), 0, A^*(x), 0, H^*).$$

Linearizing (6.1) at E_1 and then considering only the equations of infective compartments, we get

$$\begin{aligned}
\frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)M^*(x)n - \mu_M m, \\
\frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)m(t-\tau_l, y)dy - [\gamma + \alpha M^*(x) + \mu_N]n, \\
\frac{\partial a}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)K_a^*(t-\tau_n, y)dy - [\mu_A + \xi H^* + \delta_A A^*(x)]a,
\end{aligned} \tag{6.16}$$

where m is subject to the Neumann boundary condition and

$$K_a^*(t-\tau_n, y) = M^*(y)n(t-\tau_n, y) + \beta_T(y)N^*(y)m(t-\tau_n, y).$$

Note that the third equation of system (6.16) is decoupled from the first two equations. Thus, we can simply use the first two equations to define the basic reproduction number for model (6.1). Let $\tilde{X} = C(\overline{\Omega}, \mathbb{R}^2)$ and $\tilde{X}_+ = C(\overline{\Omega}, \mathbb{R}_+^2)$. Following the procedure in [92], we assume that the state variables are near the disease-free steady state E_1. Then we introduce infected individuals with the spatial distribution $\phi = (\phi_1, \phi_2) \in \tilde{X}_+$ into the population at $t = 0$. As time evolves, the spatial distribution of the infective individuals m and n under the synthetical influences of mortality, mobility and transfer of individuals among the infected compartments is described by

$$\begin{aligned} \frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) - \mu_M m, \\ \frac{\partial n}{\partial t} =& -[\gamma + \alpha M^*(x) + \mu_N]n, \end{aligned}$$

where m satisfies the Neumann boundary condition. Let $(m(t, \phi), n(t, \phi))$ denote the distribution of the infective individuals at time $t > 0$. Then we have

$$\begin{aligned} m(t, \phi)(x) &= e^{-\mu_M t} \int_\Omega \Gamma(t, x, y, D_M)\phi_1(y)dy, \\ n(t, \phi)(x) &= e^{-(\gamma+\alpha M^*(x)+\mu_N)t}\phi_2(x). \end{aligned}$$

Evidently, the distribution of new infection rate of mice induced by the infective agents at time t is

$$F_1(t, \phi)(x) = \alpha\beta(x)M^*(x)n(t, \phi)(x).$$

The distribution of new infection rate of nymphs induced by the infective agents at time t is

$$F_2(t, \phi)(x) = \begin{cases} 0 & \text{if } 0 < t < \tau_l, \\ P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)m(t - \tau_l, \phi)(y)dy, & \text{if } t \geq \tau_l. \end{cases}$$

Consequently, the distribution of total new infections of mice is

$$\int_0^\infty F_1(t, \phi)dt := \hat{F}_1(\phi),$$

the distribution of total new infections of nymphs is

$$\int_0^\infty F_2(t,\phi)dt = P_l \int_0^\infty \int_\Omega \Gamma(\tau_l, \cdot, y, D_M)\beta_T(y)L^*(y)m(t,\phi)(y)dydt := \hat{F}_2(\phi), \quad (6.17)$$

Clearly, $\hat{F} = (\hat{F}_1, \hat{F}_2)$ is a continuous and positive operator, which maps the initial infection distribution ϕ to the distribution of the total infective members produced during the infection period. Following the idea of next generation operators (see, e.g., [15, 90, 92]), we define the spectral radius of $\hat{F}$, $r(\hat{F})$, as the basic reproduction number R_0 for model (6.1). Direct calculations lead to

$$\hat{F}_1(\phi)(x) = \frac{\alpha\beta(x)M^*(x)}{\gamma + \alpha M^*(x) + \mu_N}\phi_2(x).$$

Define the operator B_1 on $C(\overline{\Omega}, \mathbb{R})$ by

$$B_1(\phi_1) = \nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1$$

By [88, Theorem 3.12], we have

$$\int_0^\infty m(t,\phi)dt = \int_0^\infty m(t,\phi_1)dt = -B_1^{-1}\phi_1.$$

It then follows from (6.17) that

$$\hat{F}_2(\phi)(x) = -P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)B_1^{-1}\phi_1(y)dy,$$

By the same arguments as in [92, Theorem 3.1 and Corollary 3.2], we have the following result.

Theorem 6.2.1. *The spectral radius $R_0 := r(\hat{F})$ is a geometrically simple eigenvalue of $\hat{F}$ with a positive eigenfunction. Moreover, let μ be the principal eigenvalue of the following problem:*

$$\begin{aligned} &-\nabla \cdot (D_M(x)\nabla\varphi) + \mu_M\varphi = \mu g(\varphi)(x), \qquad x \in \Omega, \\ &\frac{\partial\varphi}{\partial\nu} = 0, \quad x \in \partial\Omega, \end{aligned} \quad (6.18)$$

where

$$g(\varphi)(x) = P_l \frac{\alpha\beta(x)M^*(x)}{\gamma + \alpha M^*(x) + \mu_N} \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\varphi(y)dy.$$

Then $R_0 = 1/\sqrt{\mu}$.

To show that R_0 is a threshold value for disease invasion, we first suppress time delays in (6.16) and then consider the following subsystem without time delay:

$$\begin{aligned} \frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)M^*(x)n - \mu_M m, \\ \frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)m(t, y)dy - [\gamma + \alpha M^*(x) + \mu_N]n, \end{aligned} \tag{6.19}$$

where m is subject to the Neumann boundary condition. For $\phi = (\phi_1, \phi_2) \in \tilde{X}_+$, we define two operators $C = (C_1, C_2)$ by

$$\begin{aligned} C_1(\phi)(x) &= \alpha\beta(x)M^*(x)\phi_2(x), \\ C_2(\phi)(x) &= P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy, \end{aligned}$$

and $B = (B_1, B_2)$ by

$$\begin{aligned} B_1(\phi)(x) &= \nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1(x), \\ B_2(\phi)(x) &= -[\gamma + \alpha M^*(x) + \mu_N]\phi_2(x), \end{aligned}$$

and set $\mathcal{A} = C + B$. It is easy to see that the spectral bound $s(B)$ is negative. Our next goal is to reveal that $s(\mathcal{A})$ is not only an eigenvalue with the finite multiplicity but also has the same sign as $R_0 - 1$. To do so, we need the following assumption:

(H2) There exists some $x_0 \in \overline{\Omega}$ such that $\beta(x_0)$ and $\beta_T(x_0)$ are positive.

Biologically, this means there exists some small region that infectious nymphs can infect mice and pathogen-infected mice also can infect ticks in return.

Theorem 6.2.2. *Let (H1) and (H2) hold. Then the spectral bound $s(\mathcal{A})$ is a geometrically simple eigenvalue of $\mathcal{A}$ with a positive eigenfunction, and $s(\mathcal{A})$ has the same sign as $R_0 - 1$.*

Proof. By [88, Theorem 3.5], we see that $s(\mathcal{A})$ has the same sign as $r(-CB^{-1})$. Then it follows from [92, Lemma 3.3] that $r(-CB^{-1}) = r(\hat{F}) = R_0$. To verify $s(\mathcal{A})$ is an eigenvalue, letting $\phi = (\phi_1, \phi_2) \in \mathcal{N}(\lambda I - \mathcal{A})$, we have

$$\begin{aligned} &\nabla \cdot (D_M(x)\nabla\phi_1) + \alpha\beta(x)M^*(x)\phi_2 - \mu_M\phi_1 = \lambda\phi_1, \\ &P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy - [\gamma + \alpha M^*(x) + \mu_N]\phi_2 = \lambda\phi_2. \end{aligned} \tag{6.20}$$

For $\lambda > -(\gamma+\alpha M_m^*+\mu_N)$ with $M_m^* = \min_{x\in\overline{\Omega}} M^*(x)$, we obtain from the second equation of (6.20) that

$$\phi_2(x) = \frac{P_l}{\lambda + \gamma + \alpha M^*(x) + \mu_N} \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi_1(y)dy := \zeta(\lambda, \phi_1)(x).$$

Substituting it into the first equation of (6.20), we get

$$L_\lambda(\phi_1)(x) := \nabla\cdot(D_M(x)\nabla\phi_1)+\alpha\beta(x)M^*(x)\zeta(\lambda, \phi_1)(x)-\mu_M\phi_1(x) = \lambda\phi_1(x). \tag{6.21}$$

It easily follows from (H2) that there exists an open neighborbood $U \subset \Omega$ such that $\beta(x) > 0, \beta_T(x) > 0$, $\forall x \in \overline{U} \subset \Omega$. Let λ_1 be the principal eigenvalue of the elliptic eigenvalue problem

$$\begin{aligned} &\nabla \cdot (D_M(x)\nabla\phi) - \mu_M\phi = \lambda\phi, \quad x \in U, \\ &\phi = 0, \quad x \in \partial U, \end{aligned}$$

with the positive eigenfunction $\phi^*(x)$. Now define a continuous function ϕ^0 as follows

$$\phi^0(x) = \begin{cases} \phi^*(x) & \text{if} \quad x \in \overline{U} \\ 0 & \text{if} \quad x \in \overline{\Omega} \setminus \overline{U}. \end{cases}$$

Since $\beta_T(x)L^*(x)\phi^0(x) \geq 0(\not\equiv 0), \forall x \in \overline{\Omega}$, the standard maximum principle implies that $\int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi^0(y)dy > 0$, $\forall x \in \overline{\Omega}$. Set

$$A = \min_{x\in\overline{\Omega}} \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)L^*(y)\phi^0(y)dy, \quad \underline{\beta} = \min_{x\in\overline{U}} \beta(x), \quad \phi^*_{\max} = \max_{x\in\overline{U}} \phi^*(x),$$

and

$$\begin{aligned}
\lambda_0 &= \frac{\lambda_1 - (\gamma + \alpha M^*_m + \mu_N) + \sqrt{(\lambda_1 + \gamma + \alpha M^*_m + \mu_N)^2 + 4\frac{\alpha\underline{\beta}M^*_m A}{\phi^*_{\max}}}}{2} \\
&> \frac{\lambda_1 - (\gamma + \alpha M^*_m + \mu_N) + |\lambda_1 + \gamma + \alpha M^*_m + \mu_N|}{2} \\
&= \max\{\lambda_1, -(\gamma + \alpha M^*_m + \mu_N)\}.
\end{aligned}$$

Clearly for $x \in \Omega \setminus \overline{U}$, we have $L_{\lambda_0}(\phi^0)(x) \geq \lambda_0\phi^0(x)$. Moreover, for any $x \in U$

$$\begin{aligned}
L_{\lambda_0}(\phi^0)(x) &= \nabla \cdot (D_M(x)\nabla\phi^0) + \alpha\beta(x)M^*(x)\zeta(\lambda, \phi^0)(x) - \mu_M\phi^0(x) \\
&\geq \lambda_1\phi^*(x) + \frac{\alpha\underline{\beta}M^*_m A}{\lambda_0 + \gamma + \alpha M^*_m + \mu_N} \\
&= \lambda_1\phi^*(x) + \phi^*_{\max}(\lambda_0 - \lambda_1) \\
&\geq \lambda_1\phi^*(x) + \phi^*(x)(\lambda_0 - \lambda_1) \\
&= \lambda_0\phi^*(x) = \lambda_0\phi^0(x).
\end{aligned}$$

Thus, $e^{\lambda_0 t}\phi^0(x)$ is a subsolution of the integral form of the linear system $u_t = L_{\lambda_0}u$. By the arguments similar to those in [91, Theorem 2.3 and Remark 2.1], we conclude that $s(\mathcal{A})$ is a geometrically simple eigenvalue with a positive eigenfunction. □

Remark 6.2.1. *Let λ_1^Ω be the principal eigenvalue of the elliptic eigenvalue problem*

$$\nabla \cdot (D_M(x)\nabla\phi_1) - \mu_M\phi_1(x) = \lambda\phi_1(x), \quad x \in \Omega$$

subject to the Neumann boundary condition, and $\phi_1^*(x)$ be the associated positive eigenfunction. Instead of (H2), we assume that $\lambda_1^\Omega > -(\gamma + \alpha M^*_m + \mu_N)$. It then follows *that $L_{\lambda_1^\Omega}(\phi_1^*)(x) \geq \lambda_1^\Omega \phi_1^*(x)$, and hence, $s(\mathcal{A})$ is a geometrically simple eigenvalue with a positive eigenfunction (see also [91, Corollary 2.4]).*

Now we are in a position to show that the basic reproduction number R_0 determines the global dynamics of system (6.1). Let $\mathcal{M} = M + m$, $\mathcal{N} = N + n$, $\mathcal{A} = A + a$. Then system (6.1) is equivalent to the following system:

$$
\begin{aligned}
\frac{\partial \mathcal{M}}{\partial t} =& \nabla \cdot (D_M(x)\nabla \mathcal{M}) + \mathcal{M}B(x,\mathcal{M}) - \mu_M \mathcal{M}, \\
\frac{\partial L}{\partial t} =& P_a \int_\Omega \Gamma(\tau_a, x, y, D_H)\mathcal{A}(t-\tau_a, y)H(t-\tau_a, y)dy - (\mu_L + \alpha\mathcal{M})L, \\
\frac{\partial \mathcal{N}}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\mathcal{M}(t-\tau_l, y)L(t-\tau_l, y)dy - (\gamma + \alpha\mathcal{M} + \mu_N)\mathcal{N}, \\
\frac{\partial \mathcal{A}}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)\mathcal{M}(t-\tau_l, y)\mathcal{N}(t-\tau_l, y)dy - (\mu_A + \xi H)\mathcal{A} - \delta_A \mathcal{A}^2, \\
\frac{\partial H}{\partial t} =& \nabla \cdot (D_H(x)\nabla H) + r_h - \mu_h H, \\
\frac{\partial m}{\partial t} =& \nabla \cdot (D_M(x)\nabla m) + \alpha\beta(x)(\mathcal{M} - m)n - \mu_M m, \\
\frac{\partial n}{\partial t} =& P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\beta_T(y)m(t-\tau_l, y)L(t-\tau_l, y)dy - (\gamma + \alpha\mathcal{M} + \mu_N)n, \\
\frac{\partial a}{\partial t} =& P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)K_a(t-\tau_n, y)dy - (\mu_A + \xi H)a - \delta_A \mathcal{A} a,
\end{aligned}
\tag{6.22}
$$

where $\mathcal{M}$, H and m are subject to the Neumann boundary condition, and

$$K_a(t,y) = \mathcal{M}(t,y)n(t,y) + \beta_T(y)m(t,y)(\mathcal{N}(t,y) - n(t,y)).$$

By virtue of Theorem 6.1.1, $(M^*(x), L^*(x), N^*(x), A^*(x), H^*)$ is a globally attractive steady state of system (6.2), which is exactly the same as the first five equations of system (6.22). By similar discussions to those in the last section, we may confine ourselves into

$$\begin{aligned}\frac{\partial m}{\partial t} =&\nabla\cdot(D_M(x)\nabla m)+\alpha\beta(x)(M^*(x)-m)n-\mu_M m,\\ \frac{\partial n}{\partial t} =&P_l\int_\Omega \Gamma(\tau_l,x,y,D_M)\beta_T(y)m(t-\tau_l,y)L^*(y)dy-[\gamma+\alpha M^*(x)+\mu_N]n,\\ \frac{\partial a}{\partial t} =&P_n\int_\Omega \Gamma(\tau_n,x,y,D_M)K_a^*(t-\tau_n,y)dy-(\mu_A+\xi H^*+\delta_A A^*(x))a,\end{aligned}\tag{6.23}$$

where m is subject to the Neumann boundary condition, and

$$K_a^*(t,y)=M^*(y)n(t,y)+\beta_T(y)m(t,y)(N^*(y)-n(t,y)).$$

Since the first two equations in (6.23) do not depend on the variable a, we first consider the following subsystem:

$$\begin{aligned}\frac{\partial m}{\partial t} =&\nabla\cdot(D_M(x)\nabla m)+\alpha\beta(x)(M^*(x)-m)n-\mu_M m,\\ \frac{\partial n}{\partial t} =&P_l\int_\Omega \Gamma(\tau_l,x,y,D_M)\beta_T(y)m(t-\tau_l,y)L^*(y)dy-[\gamma+\alpha M^*(x)+\mu_N]n.\end{aligned}\tag{6.24}$$

Let $\mathbb{C}_{M^*}=\{\varphi\in C(\overline{\Omega},\mathbb{R}_+):\varphi(x)\le M^*(x),\ \forall x\in\overline{\Omega}\}$, and

$$\mathcal{X}:=C([-\tau_l,0],\mathbb{C}_{M^*})\times C(\overline{\Omega},\mathbb{R}_+).$$

Note that

$$\nabla\cdot(D_M(x)\nabla M^*)-\mu_M M^*(x)=-M^*B(x,M^*)=-r_M M^*(x)\exp\left(-\frac{M^*(x)}{K_M(x)}\right)\le 0.$$

By [64, Corollary 4], it follows that for any $\phi\in\mathcal{X}$, system (6.24) admits a unique mild solution $\hat{u}(t,\cdot,\phi)=(\hat{u}_1(t,\cdot,\phi),\hat{u}_2(t,\cdot,\phi))$ on $[0,\infty)$ with $\hat{u}_1(\theta,\cdot,\phi)=\phi_1(\theta)$, $\hat{u}_2(0,\cdot,\phi)=\phi_2$, $\theta\in[-\tau_l,0]$, and $(\hat{u}_{1t}(\phi),\hat{u}_2(t,\cdot,\phi))\in\mathcal{X}$ for all $t\ge 0$. Note that system (6.24) is eventually strongly monotone and strictly subhomogeneous on $\mathcal{X}$. By the arguments similar to those for system (6.3) in Theorem 6.1.1 (see also the proof of [92, Proposition 3.7]), together with Theorem 6.2.2, we have the following result for system (6.24).

Lemma 6.2.1. *Assume that (H1)–(H2) hold and $s(A) > 0$. Then the following statements are valid:*

(i) If $R_0 < 1$, then $(0, 0)$ is globally attractive for system (6.24) in $\mathcal{X}$.

(ii) If $R_0 > 1$, then system (6.24) admits a positive steady state $(\bar{m}(x), \bar{n}(x))$ which is globally attractive in $\mathcal{X}\backslash\{0\}$.

Now we are ready to prove the main result of this section on the global dynamics of system (6.1) on $W := C([-\tau_0, 0], C(\overline{\Omega}, \mathbb{R}^8_+))$.

Theorem 6.2.3. *Assume that (H1) and (H2) hold and $s(A) > 0$. Then the following statements are valid:*

(i) If $R_0 < 1$, then every positive solution $v(t, x, \varphi)$ of system (6.1) satisfies $lim_{t\to\infty} v(t, x, \varphi) = (M^*(x), 0, L^*(x), N^*(x), 0, A^*(x), 0, H^*)$ uniformly for $x \in \overline{\Omega}$.

(ii) If $R_0 > 1$, then system (6.1) admits a positive steady state $\bar{v}(x) = (M^*(x) - \bar{m}(x), \bar{m}(x), L^*(x), N^*(x) - \bar{n}(x), \bar{n}(x), A^*(x) - \bar{a}(x), \bar{a}(x), H^*)$, and every positive solution $v(t, x, \varphi)$ satisfies $lim_{t\to\infty} v(t, x, \varphi) = \bar{v}(x)$ uniformly for $x \in \overline{\Omega}$.

Proof. By using the theory of chain transitive sets, as illustrated in [92, Theorem 3.8], we can lift the threshold type result for system (6.24) to the full system (6.22) and show that every positive solution of system (6.22) converges to either

$$(M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, 0, 0, 0)$$

or

$$(M^*(\cdot), L^*(\cdot), N^*(\cdot), A^*(\cdot), H^*, \bar{m}(\cdot), \bar{n}(\cdot), \bar{a}(\cdot))$$

in terms of R_0. It remains to prove the positivity of the steady state of model (6.1) in the case where $R_0 > 1$. Let $\overline{M}(x) = M^*(x) - \overline{m}(x)$. It suffices to prove that $\overline{M}(x) := M^*(x) - \overline{m}(x) > 0, \forall x \in \bar{\Omega}$. Clearly, we have $M^*(x) \geq \overline{m}(x), \forall x \in \bar{\Omega}$. In view of the integral form of the following equation

$$\begin{aligned}
&\frac{\partial M}{\partial t} = \nabla \cdot (D_M(x)\nabla M) + M^* B(x, M^*) - [\mu_M + \alpha\beta(x)\overline{n}(x)]M, \; x \in \Omega, \; t > 0,\\
&\frac{\partial M}{\partial \nu} = 0, \quad x \in \partial\Omega, \; t > 0,
\end{aligned}$$

we have

$$\begin{aligned}
\overline{M}(x) = &\int_\Omega \Gamma(0, x, y, D_M)\overline{M}(y)dy\\
&+ \int_0^t e^{-(\mu_M + \alpha\beta(x)\overline{n}(x)(t-s)} \int_\Omega \Gamma(t-s, x, y, D_M)M^*(y)B(y, M^*(y))dydt.
\end{aligned}$$

By the standard maximum principle (see e.g., [85, Theorem 7.2.2 and Corollary 7.2.3]), it easily follows that $\overline{M}(x) > 0, \forall x \in \overline{\Omega}$. Thus, a straightforward computation implies that

$$\begin{aligned}
N^*(x) - \overline{n}(x) &= \frac{P_l \int_\Omega \Gamma(\tau_l, x, y, D_M)\tilde{K}_N(y)dy}{\gamma + \alpha M^*(x) + \mu_N}, \quad x \in \overline{\Omega}\\
A^*(x) - \overline{a}(x) &= \frac{P_n \int_\Omega \Gamma(\tau_n, x, y, D_M)\tilde{K}_A(y)dy}{\mu_A + \xi H^* + \delta_A A^*(x)}, \quad x \in \overline{\Omega}
\end{aligned}$$

with

$$\begin{aligned}
\tilde{K}_N(y) &= [M^*(y) - \beta_T(y)\overline{m}(y)]L^*(y),\\
\tilde{K}_A(y) &= [M^*(y) - \beta_T(y)\overline{m}(y)](N^*(y) - \overline{n}(y)).
\end{aligned}$$

Since $0 \leq \beta_T(y) \leq 1$, it follows that $\tilde{K}_N(y) > 0, \forall y \in \overline{\Omega}$, and hence, $N^*(x) - \overline{n}(x) > 0$, and $\tilde{K}_A(x) > 0$, $\forall x \in \overline{\Omega}$. Thus, we obtain $A^*(x) - \overline{a}(x) > 0$, $\forall x \in \overline{\Omega}$. □

Remark 6.2.2. *The results in sections 5.2 and 5.3 are still valid if we take a general per capita birth rate function $B(x,u)$ satisfying the following conditions:*

(C1) $B(x,u) \geq 0 (\not\equiv 0), \quad \forall (x,u) \in \overline{\Omega} \times [0,+\infty)$.

(C2) $B(x,u)$ *is continuous on* $\overline{\Omega} \times [0,+\infty)$, *and strictly decreasing in* $u \in [0,c_0)$ *for some* $c_0 > 0$.

(C3) There exists $M > 0$ *such that* $\frac{1}{|\Omega|}\int_\Omega B(x,0)dx > \mu_M > B(x,u)$ *for all* $u > M$ *and* $x \in \overline{\Omega}$.

It is easy to see that the birth rate function $B(x,u) = r_M \exp\left(-\frac{u}{K_M(x)}\right)$ satisfies (C1)–(C3). Another prototypical birth rate function (see, e.g., [12, 90]) is

$$B(x,u) = \begin{cases} r_M \left[1 - \dfrac{u}{k_M(x)}\right], & 0 \leq u \leq K_M(x), x \in \overline{\Omega}, \\ 0, & u > K_M(x),\ x \in \overline{\Omega}. \end{cases}$$

6.3 Propagation phenomena

In this section, we consider the spreading speed and traveling waves for system (6.23) in an unbounded habitat. Since the first two equations in (6.23) are decoupled from the third one, it suffices to consider system (6.24).

Assume that all the coefficients in system (6.1) are constant. Without loss of generality, we suppose that the spatial domain $\Omega = \mathbb{R}$. As such, the Green function $\Gamma(\tau_l, x, y, D_M)$ can be expressed as

$$\Gamma(\tau_l, x, y, D_M) = \frac{1}{\sqrt{4\pi D_M \tau_l}} e^{-\frac{(x-y)^2}{4D_M\tau_l}}.$$

In the case where $r_M > \mu_M$, we have $M^* = K_M \ln \frac{r_M}{\mu_M} > 0$. Let

$$\chi := P_a P_n P_l H^* M^{*2} - (\gamma + \alpha M^* + \mu_N)(\mu_A + \xi H^*)(\mu_L + \alpha M^*). \tag{6.25}$$

Then a straightforward computation shows that system (6.2) admits a unique constant positive steady state $E_0 = (M^*, L^*, N^*, A^*, H^*)$ with

$$L^* = \frac{P_a H^*}{\mu_L + \alpha M^*} A^*,\ \ N^* = \frac{P_l M^*}{\gamma + \alpha M^* + \mu_N} L^*,\ \ A^* = \frac{\chi}{\delta_A(\gamma + \alpha M^* + \mu_N)(\mu_L + \alpha M^*)}$$

provided that $r_M > K_M$ and $\chi > 0$.

Consider the spatially homogeneous system associated with (6.24):

$$\begin{aligned} \frac{dm}{dt} =& \alpha\beta(M^* - m)n - \mu_M m, \\ \frac{dn}{dt} =& P_l \beta_T L^* m(t - \tau_l) - (\gamma + \alpha M^* + \mu_N)n. \end{aligned} \tag{6.26}$$

Linearizing system (6.26) at $(0, 0)$, we get

$$\begin{aligned} \frac{dm}{dt} =& \alpha\beta M^* n - \mu_M m, \\ \frac{dn}{dt} =& P_l \beta_T L^* m(t - \tau_l) - (\gamma + \alpha M^* + \mu_N)n. \end{aligned} \tag{6.27}$$

Following [108], we introduce the basic reproduction number for system (6.26). Clearly, system (6.27) is of the form $\frac{du}{dt} = F u_t - V u$ with

$$F \begin{pmatrix} \phi_1 \\ \phi_2 \end{pmatrix} = \begin{pmatrix} \alpha\beta M^* \phi_2(0) \\ P_l \beta_T L^* \phi_1(-\tau_l) \end{pmatrix}, \quad \phi \in C([-\tau_l, 0], \mathbb{R}^2)$$

and

$$V = \begin{pmatrix} \mu_M & 0 \\ 0 & \gamma + \alpha M^* + \mu_N \end{pmatrix}.$$

Then [108, Corollary 2.1] implies that the basic reproduction number $\mathcal{R}_0 = r(\hat{F} V^{-1})$ with $\hat{F} = \begin{pmatrix} 0 & \alpha\beta M^* \\ P_l \beta_T L^* & 0 \end{pmatrix}$, and hence, we obtain

$$\mathcal{R}_0 = \sqrt{\frac{P_l \alpha\beta\beta_T M^* L^*}{\mu_M(\gamma + \alpha M^* + \mu_N)}}. \tag{6.28}$$

If $\mathcal{R}_0 > 1$, then system (6.24) admits a unique positive steady state $u^* := (\overline{m}, \overline{n})$ with

$$\overline{m} = M^*(1 - \frac{1}{\mathcal{R}_0^2}), \quad \overline{n} = \frac{P_l \beta_T L^*}{\gamma + \alpha M^* + \mu_N} \overline{m}. \tag{6.29}$$

By [109, Theorem 3.2], as applied to system (6.26) on $C([-\tau_l, 0], [0, M^*]) \times \mathbb{R}_+$, we conclude that every positive solution of (6.26) converges to u^*.

In order to use the theory of spreading speeds developed in [54], we first introduce some basic notations. Let $Z = C([-\tau_l, 0], \mathbb{R}^2)$. We equip Z with the maximum norm and the partial ordering induced by the positive cone $Z_+ := C([-\tau_l, 0], \mathbb{R}^2_+)$. For any $u, v \in Z$, we write $u \geq v$ if $u - v \in Z_+$, $u > v$ if $u \geq v$ but $u \neq v$, and $u \gg v$ if $u - v \in \mathrm{Int}(Z_+)$. Define $\mathcal{C}$ as the set of all bounded and continuous functions from $\mathbb{R}$ to Z equipped with the compact open topology, that is, $u^m \to u$ in $\mathcal{C}$ means that the sequence of $u^m(x)$ converges to $u(x)$ in Z as $m \to \infty$ uniformly for x in any compact subset of $\mathbb{R}$. For $u, w \in \mathcal{C}$, we write $u \geq w (u \gg w)$ provided $u(x) \geq w(x) (u(x) > w(x))$, $\forall x \in \mathbb{R}$ and $u > w$ provided $u \geq w$ but $u \neq w$. Clearly, any element in Z can be regarded as a constant function in $\mathcal{C}$. For each $r \in Z$ with $r \gg 0$, we set $Z_r := \{u \in Z : 0 \leq u \leq r\}$ and $\mathcal{C}_r := \{u \in \mathcal{C} : u(x) \in Z_r, \forall x \in \mathbb{R}\}$. We also identify an element $\phi \in \mathcal{C}$ as a function from $[-\tau_l, 0] \times \mathbb{R}$ into $\mathbb{R}$ by $\phi(\theta, x) = \phi(x)(\theta)$.

Recall that a family of operators $\{Q_t\}_{t \geq 0}$ is said to be a semiflow on $\mathcal{C}_r$ provided Q_t has the following properties: (i) $Q_0 = I$, where I is the identity map; (ii) $Q_{t_1} \circ Q_{t_2} = Q_{t_1 + t_2}$; (iii) $Q_t[\phi]$ is jointly continuous in (t, ϕ) on $[0, \infty) \times \mathcal{C}_r$.

Now let $\{Q_t\}_{t \geq 0}$ be a family of solution maps of system (6.24) from $\mathcal{C}_{u^*}$ to $\mathcal{C}_{u^*}$, that is,

$$[Q_t(\phi)](\theta, x) = u_t(\theta, x, \phi) = (m_t(\theta, x, \phi), n_t(\theta, x, \phi)), \quad \forall \phi \in \mathcal{C}_{u^*}, x \in \mathbb{R}, \theta \in [-\tau_l, 0],$$

where $u(t, x, \phi)$ is the mild solution of system (6.24) with an initial function $\phi \in \mathcal{C}_{u^*}$

and $u_t(\theta, x, \phi) = u(t+\theta, x, \phi)$, $\theta \in [-\tau_l, 0]$. The following result shows that system (6.24) admits a spreading speed.

Theorem 6.3.1. *Assume that $r_M > K_M$, $\chi > 0$ and $\mathcal{R}_0 > 1$. Then there exists a positive number c^* such that the following statements are valid:*

(i) For any $c > c^*$, if $\phi \in \mathcal{C}_{u^*}$ with $0 \le \phi \le \varpi$ for some $\varpi \in Z_+$ and $\varpi \ll u^*$, and $\phi(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\ge ct} u(t, x, \phi) = 0$;

(ii) For any $c \in (0, c^*)$, if $\phi := (\phi_1, \phi_2) \in \mathcal{C}_{u^*}$ and either $\phi_1 \not\equiv 0$ or $\phi_2(0, \cdot) \not\equiv 0$ holds, then $\lim_{t\to\infty, |x|\le ct} u(t, x, \phi) = u^*$.

Proof. Without loss of generality, we assume that $\tau_l < 1$. Otherwise, we do the time rescaling $s = \frac{t}{\tau}$ for a fixed $\tau > \tau_l$ and then consider the resulting system. Using arguments similar to those in [17, Lemma 4.3], we prove that $\{Q_t\}_{t\ge 0}$ is a monotone semiflow on $\mathcal{C}_{u^*}$ with the time-one map Q_1 satisfying (A1)–(A5) in section 2.2.1. By the similar proofs to those in [54, Theorems 2.11 and 2.15](see also Theorem 2.2.1), we know that Q_1 admits a spreading speed $c^* > 0$. The following claim gives the eventual strong positivity of $\{Q_t\}_{t\ge 0}$ on $\mathcal{C}_{u^*}$.

Claim. For any $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{u^*}$, if either $\phi_1 \not\equiv 0$ or $\phi_2(0, \cdot) \not\equiv 0$, then $u(t, x, \phi) \gg 0$ for all $t > \tau_l, x \in \mathbb{R}$, and hence, $Q_t(\phi) \gg 0$ for all $t > 2\tau_l$.

If $\phi_1 \not\equiv 0$, then there exists a number $\eta > 0$ and an interval $[a_1, a_2] \times [b_1, b_2] \subset [-\tau_l, 0] \times \mathbb{R}$ such that

$$\phi_1(\theta, x) \ge \eta, \quad \forall (\theta, x) \in [a_1, a_2] \times [b_1, b_2].$$

In view of the integral form of system (6.24), we have

$$\begin{aligned}
n(\tau_l,x,\phi) &= e^{-(\gamma+\alpha M^*+\mu_N)\tau_l}\phi_2(0,x)\\
&\quad + P_l L^*\beta_T\int_0^{\tau_l}\int_{\mathbb{R}} e^{-(\gamma+\alpha M^*+\mu_N)(\tau_l-s)}\Gamma(\tau_l,x,y,D_M)\phi_1(s-\tau_l,y)dyds\\
&\geq P_l L^*\beta_T\int_0^{\tau_l}\int_{\mathbb{R}} e^{-(\gamma+\alpha M^*+\mu_N)(\tau_l-s)}\Gamma(\tau_l,x,y,D_M)\phi_1(s-\tau_l,y)dyds\\
&\geq P_l L^*\beta_T\eta\int_{a_1}^{a_2}\int_{b_1}^{b_2} e^{-(\gamma+\alpha M^*+\mu_N)(\tau_l-s)}\Gamma(\tau_l,x,y,D_M)dyds>0,\ \forall x\in\mathbb{R}.
\end{aligned}$$

It follows that $n(t,x,\phi)\geq e^{-(\gamma+\alpha M^*+\mu_N)(t-\tau_l)}n(\tau_l,x,\phi)>0$, $\forall t>\tau_l, x\in\mathbb{R}$. Note that $\tilde{F}(t,x):=\alpha\beta(M^*-m(t,x,\phi))n(t,x,\phi)\geq\alpha\beta(M^*-\overline{m})n(t,x,\phi)>0$, $\forall t>\tau_l, x\in\mathbb{R}$. Then the standard maximum principle of parabolic equations implies that $m(t,x,\phi)>0$, $\forall t>\tau_l, x\in\mathbb{R}$.

If $\phi_2(0,x)\geq 0$ with $\phi_2(0,x)\not\equiv 0$, then we have

$$n(t,x,\phi)\geq e^{-(\gamma+\alpha M^*+\mu_N)t}\phi_2(0,x)\geq 0(\not\equiv 0),\quad \forall t\geq 0, x\in\mathbb{R}.$$

Thus, $\tilde{F}(t,x)\geq 0(\not\equiv 0)$, $t\geq 0, x\in\mathbb{R}$. It follows from the maximum principle of parabolic equations (see, e.g., [85, Corollary 7.2.3]) that $m(t,x,\phi)>0$ for all $t>0$. Then similar to the first case, for $t>\tau_l$, $x\in\mathbb{R}$, we have

$$\begin{aligned}
n(t,x,\phi) &\geq P_l L^*\beta_T\int_0^{t}\int_{\mathbb{R}} e^{-(\gamma+\alpha M^*+\mu_N)(t-s)}\Gamma(\tau_l,x,y,D_M)m(s-\tau_l,y)dyds\\
&\geq P_l L^*\beta_T\int_{\tau_l}^{t}\int_{\mathbb{R}} e^{-(\gamma+\alpha M^*+\mu_N)(t-s)}\Gamma(\tau_l,x,y,D_M)m(s-\tau_l,y)dyds>0.
\end{aligned}$$

It follows that $u(t,x,\phi)>0$ for all $t>\tau_l, x\in\mathbb{R}$, and hence, $Q_t(\phi)\gg 0$ for all $t>2\tau_l$.

Now statement (i) follows from Theorem 2.2.3(i). For statement (ii), since Q_t is subhomogeneous, then r_σ in Theorem 2.2.3(ii) can be chosen to be independent of $\sigma\gg 0$. Thus, we can write r_σ as $\bar{r}$. If $\phi\in\mathcal{C}_{u^*}$ and $\phi(\theta,x)\gg 0$ for all $\theta\in[-\tau_l,0]$ and x on an interval I of length $2\bar{r}$, then there exists a vector $\sigma\gg 0$ in $\mathbb{R}^2$ such that $\phi(\theta, x) \gg \sigma$, $\forall(\theta, x) \in [-\tau_l, 0] \times I$, and hence, Theorem 2.2.3(ii) implies that $\lim_{t\to\infty, |x|\le ct} u(t, x, \phi) = u^*$. For any given $\phi = (\phi_1, \phi_2) \in \mathcal{C}_{u^*}$ with either $\phi_1 \not\equiv 0$ or $\phi_2(0, \cdot) \not\equiv 0$, the above claim implies that $u(t, x, \phi) > 0, \forall t > \tau_l, x \in \mathbb{R}$. Fix a $t_0 > 2\tau_l$. Then $u_{t_0}(\phi) \gg 0$. By taking u_{t_0} as a new initial data, we see that statement (ii) is valid. □

Next we show that c^* is linearly determinate and give a formula of it. Consider the linearized system of (6.24) at its zero solution:

$$\begin{aligned}\frac{\partial v_1}{\partial t} =& D_M \frac{\partial^2 v_1}{\partial x^2} + \alpha\beta M^* v_2 - \mu_M v_1,\\ \frac{\partial v_2}{\partial t} =& P_l \beta_T L^* \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) v_1(t - \tau_l, y) dy - (\gamma + \alpha M^* + \mu_N) v_2.\end{aligned} \tag{6.30}$$

Let $\{L(t)\}_{t\ge 0}$ be the linear solution maps associated with (6.30), that is, $L(t)\phi = v_t(\phi)$. Letting $v(t, x) = e^{-\mu x} u(t, x)$ in (6.30), we see that $u(t, x)$ satisfies

$$\begin{aligned}\frac{\partial u_1}{\partial t} =& D_M \frac{\partial^2 u_1}{\partial x^2} + \alpha\beta M^* u_2 + (D_M \mu^2 - \mu_M) u_1,\\ \frac{\partial u_2}{\partial t} =& P_l \beta_T L^* \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) e^{\mu(x-y)} u_1(t - \tau_l, y) dy - (\gamma + \alpha M^* + \mu_N) u_2.\end{aligned} \tag{6.31}$$

Furthermore, letting $u(t, x) = e^{\lambda t} w(x)$, we obtain the following nonlocal eigenvalue problem of delay type:

$$\begin{aligned}\lambda w_1 =& D_M w_1'' + \alpha\beta M^* w_2 + (D_M \mu^2 - \mu_M) w_1,\\ \lambda w_2 =& P_l \beta_T L^* e^{-\lambda\tau_l} \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) e^{\mu(x-y)} w_1(y) dy - (\gamma + \alpha M^* + \mu_N) w_2.\end{aligned} \tag{6.32}$$

Clearly, $-(\gamma + \alpha M^* + \mu_N)$ is not an eigenvalue, so we solve w_2 in terms of w_1 from the second equation, and then substitute it into the first one to obtain:

$$\lambda w_1 = D_M w_1'' + \frac{\alpha\beta M^* P_l \beta_T L^* e^{-\lambda\tau_l} \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) e^{\mu(x-y)} w_1(y) dy}{\lambda + \gamma + \alpha M^* + \mu_N} + (D_M \mu^2 - \mu_M) w_1. \tag{6.33}$$

Let $b(\mu) = \max\{D_M\mu^2 - \mu_M, -\gamma - \alpha M^* - \mu_N\}$. Note that

$$\int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) e^{\mu(x-y)} dy = \frac{1}{\sqrt{4\pi D_M \tau_l}} \int_{\mathbb{R}} e^{-\frac{y^2}{4D_M\tau_l} + \mu y} dy = e^{D_M \tau_l \mu^2}.$$

By Lemma 6.1.1 and [91, Theorem 2.3], it then follows that (6.33) admits a principle eigenvalue $\lambda(\mu) \in (b(\mu), \infty)$ with the constant positive eigenfunction, and $\lambda(\mu)$ satisfies the following equation

$$\Delta(\lambda, \mu) := (\lambda - D_M\mu^2 + \mu_M)(\lambda + \gamma + \alpha M^* + \mu_N) - \alpha\beta M^* P_l \beta_T L^* e^{-\lambda\tau_l + D_M\tau_l\mu^2} = 0. \tag{6.34}$$

Since $\Delta(\lambda, \mu)$ is even in $\mu \in \mathbb{R}$, we only consider the case $\mu \geq 0$. Since $\mathcal{R}_0 = \sqrt{\frac{P_l\alpha\beta\beta_T M^* L^*}{\mu_M(\gamma + \alpha M^* + \mu_N)}} > 1$, it is easy to see that

$$\begin{aligned}
\Delta(0, \mu) &= (-D_M\mu^2 + \mu_M)(\gamma + \alpha M^* + \mu_N) - \alpha\beta M^* P_l\beta_T L^* e^{D_M\tau_l\mu^2} \\
&= -D_M\mu^2(\gamma + \alpha M^* + \mu_N) - \alpha\beta M^* P_l \beta_T L^* e^{D_M\tau_l\mu^2}\left(\frac{1}{\mathcal{R}_0^2} - e^{D_M\tau_l\mu^2}\right) < 0, \forall\, \mu \geq 0,
\end{aligned}$$

and

$$\frac{\partial \Delta(\lambda, \mu)}{\partial \lambda} \geq 2(\lambda - b(\mu)) + \alpha\beta M^* P_l \beta_T L^* \tau_l e^{-\lambda\tau_l + D_M\tau_l\mu^2} > 0, \quad \forall \lambda > b(\mu),\, \mu \geq 0.$$

If $b(\mu) < 0$, then there exists a unique positive $\lambda(\mu)$ such that $\Delta(\lambda, \mu) = 0$. If $b(\mu) \geq 0$, since $\Delta(b(\mu), \mu) < 0$, we also get a uniquely positive $\lambda(\mu)$ being the root of $\Delta(\lambda, \mu)$. Moreover, since $\frac{\lambda(\mu)}{\mu} > \frac{b(\mu)}{\mu} \geq D_M\mu - \frac{\mu_M}{\mu}$, it follows that $\lim_{\mu\to\infty} \frac{\lambda(\mu)}{\mu} = \infty$. Note that $\frac{\lambda(\mu)}{\mu}$ has the same properties as stated in [54, Lemma 3.8], and $\frac{\lambda(\mu)}{\mu} \to \infty$ as $\mu \to \infty$. It follows that there exists a unique $\mu_0 > 0$ such that $\frac{d}{d\mu}\frac{\lambda(\mu)}{\mu} = 0$ and $\frac{\lambda(\mu_0)}{\mu_0} = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu} > 0$.

Let ϕ be the positive constant eigenfunction associated with $\lambda(\mu_0)$ and $c_0 = \frac{\lambda(\mu_0)}{\mu_0}$. In view of systems (6.24) and (6.30), it is easy to see that for any $M > 0$, $u(x,t) = Me^{-\mu_0(x - c_0 t)}\phi$ is an upper solution for system (6.24). Now we are in position to give a computational formula for the spreading spreed.

Lemma 6.3.1. *Let c^* be the spreading speed of $\{Q_t\}_{t\geq 0}$. Then*

$$c^* = \frac{\lambda(\mu_0)}{\mu_0} = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu} > 0.$$

Moreover, (c^*, μ_0) is uniquely determined as the solution of the system

$$\mu > 0, \quad \tilde{\Delta}(c,\mu) = 0, \quad \partial_\mu \tilde{\Delta}(c,\mu) = 0.$$

where $\tilde{\Delta}(c,\mu) = \Delta(c\mu,\mu)$ with $\Delta(\lambda,\mu)$ defined as in (6.34).

Proof. Note that for any $M > 0$, $u(x,t) = Me^{-\mu_0(x-c_0t)}\phi$ is an upper solution for system (6.24). Then Theorem 2.2.2(i), together with Theorem 6.3.1, implies that $c^* \leq c_0 = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu}$. On the other hand, let $\{L^\epsilon(t)\}_{t\geq 0}$ be the solution semigroup of the following linear system with small $\epsilon \in (0, M^*)$:

$$\begin{aligned} \frac{\partial u_1}{\partial t} =& D_M \Delta u_1 + \alpha\beta(M^* - \epsilon)u_2 - \mu_M u_1, \\ \frac{\partial u_2}{\partial t} =& P_l \beta_T L^* \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) u_1(t-\tau_l, y) dy - (\gamma + \alpha M^* + \mu_N) u_2. \end{aligned} \tag{6.35}$$

Define $\lambda^\epsilon(\mu)$ be the principal eigenvalue of the following eigenvalue problem for small $\epsilon \in (0, M^*)$:

$$\begin{aligned} \lambda w_1 =& D_M w_1'' + \alpha\beta(M^* - \epsilon)w_2 + (D_M\mu^2 - \mu_M)w_1, \\ \lambda w_2 =& P_l \beta_T L^* e^{-\lambda\tau_l} \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) e^{\mu(x-y)} w_1(y) dy - (\gamma + \alpha M^* + \mu_N) w_2. \end{aligned} \tag{6.36}$$

Since $Q_t(0) \equiv 0$, by the continuous dependence of the solutions on initial conditions, it follows that for any sufficiently small $\epsilon \in (0, M^*)$, there exists $\eta \in \mathrm{Int}(Z_+)$ with $\eta \leq u^*$ such that $Q_t(\eta) \leq \bar{\epsilon}$ for all $t \in [0,1]$, where $\bar{\epsilon} = (\epsilon, \epsilon)$. Then the comparison principle implies that

$$Q_t(\phi) \leq Q_t(\eta) \leq \bar{\epsilon}, \quad \phi \in \mathcal{C}_\eta,\ t \in [0,1].$$

Thus, $Q_t(\phi)$ satisfies

$$\begin{aligned}\frac{\partial u_1}{\partial t} \geq & D_M \Delta u_1 + \alpha\beta(M^* - \epsilon)u_2 - \mu_M u_1,\\ \frac{\partial u_2}{\partial t} = & P_l \beta_T L^* \int_{\mathbb{R}} \Gamma(\tau_l, x, y, D_M) u_1(t - \tau_l, y) dy - (\gamma + \alpha M^* + \mu_N) u_2,\end{aligned} \tag{6.37}$$

for all $t \in [0, 1]$. This implies that $Q_t(\phi)$ is an upper solution of the linear system (6.35) for $t \in [0, 1], \phi \in \mathcal{C}_\eta$, and hence,

$$L^\epsilon(1)(\phi) \leq Q_1(\phi), \quad \forall \phi \in \mathcal{C}_\eta.$$

Using the convexity of $\lambda^\epsilon(\mu)$ and the arguments similar to those in [54, Theorem 3.10(ii)](see also Theorem 2.2.2(ii)), we have $\inf\limits_{\mu>0} \frac{\lambda^\epsilon(\mu)}{\mu} \leq c^*$ for all sufficiently small ε. Letting $\epsilon \to 0$, we obtain that $\inf\limits_{\mu>0} \frac{\lambda(\mu)}{\mu} \leq c^*$. Thus, $c^* = \inf_{\mu>0} \frac{\lambda(\mu)}{\mu} > 0$. Since $\lambda(\mu)$ can be explicitly expressed from (6.34), it follows that $\lambda'(\mu) = -\frac{\partial_\mu \Delta(\lambda,\mu)}{\partial_\lambda \Delta(\lambda,\mu)}$, $\forall \mu > 0$, and

$$\frac{d}{d\mu} \frac{\lambda(\mu)}{\mu} = \frac{\mu \lambda'(\mu) - \lambda(\mu)}{\mu^2} = -\frac{\mu \partial_\mu \Delta(\lambda, \mu) + \lambda(\mu) \partial_\lambda \Delta(\lambda, \mu)}{\mu^2 \partial_\lambda \Delta(\lambda, \mu)}.$$

Consequently, $(\lambda(\mu_0), \mu_0)$ is a unique solution to the system

$$\mu > 0, \quad \Delta(\lambda, \mu) = 0, \quad \partial_\mu \Delta(\lambda, \mu) + \frac{\lambda}{\mu} \partial_\lambda \Delta(\lambda, \mu) = 0.$$

Replacing λ with a new variable $c := \frac{\lambda}{\mu}$, we then have

$$\partial_c \tilde{\Delta}(c, \mu) = \partial_\mu \Delta(c\mu, \mu) + c \partial_\lambda \Delta(c\mu, \mu) = \partial_\mu \Delta(\lambda, \mu) + \frac{\lambda}{\mu} \partial_\lambda \Delta(\lambda, \mu).$$

It follows that (c^*, μ_0) is uniquely determined as the solution of the system

$$\mu > 0, \quad \tilde{\Delta}(c, \mu) = 0, \quad \partial_\mu \tilde{\Delta}(c, \mu) = 0.$$

This completes the proof. □

Since the solution maps of system (6.24) do not satisfy the compactness assumption in [54], we cannot use the theory of traveling waves there. We will appeal to the theory recently developed in [19] (see also in section 2.2.2) to prove the existence of the minimal wave speed for monotone traveling waves.

Recall that $W(x-ct)$ is said to be a traveling wave of the semiflow $\{Q_t\}_{t\geq 0}$ provided that $Q_t[W](x) = W(x-ct)$, $\forall t \geq 0$, and we say that $W(x-ct)$ connects β to 0 if $W(-\infty) = \beta$ and $W(+\infty) = 0$.

Let $\mathcal{M}$ be the set of all non-increasing, left-continuous and bounded functions from $\mathbb{R}$ to Z. We equip $\mathcal{M}$ with the compact open topology. Let $\beta \in Z_+$ with $\beta \gg 0$, set $\mathcal{M}_\beta := \{u \in \mathcal{M} : u(x) \in Z_\beta, \forall x \in \mathbb{R}\}$ and $\mathcal{M}_+ := \{u \in \mathcal{M} : u \geq 0\}$.

It is easy to show that for any initial data $\phi \in \mathcal{M}_{u^*}$, system (6.24) admits a unique solution $u(t,x,\phi)$ on $[0,\infty)$, and $u_t(\phi) \in \mathcal{M}_{u^*}$ for each $t \geq 0$. Moreover, we can verify that for each $t > 0$, Q_t: $\mathcal{M}_{u^*} \to \mathcal{M}_{u^*}$ satisfies (C1) and (C4). (C2)$'$ follows from the similar proof to that in [17, Lemma 4.3]. By the arguments in [19, Theorem 5.2] and [17, Theorem 5.3], we see that for each $t > 0$, (C3) is also satisfied for Q_t. Finally, Lemma 6.2.1 implies that for each $t > 0$, (A5) is valid for Q_t. It follows that for each $t > 0$, Q_t satisfies (C1), (C3), (C4), (A5) and $\{Q_t\}_{t\geq 0}$ satisfying (C2)$'$ is a semiflow on $\mathcal{M}_\beta$ (see section 2.2.2). Then we have the following result.

Theorem 6.3.2. *Assume that $r_M > K_M$, $\chi > 0$ and $\mathcal{R}_0 > 1$, and let c^* be defined as in Lemma 6.3.1. Then the following statements are valid:*

(i) For any $c \geq c^*$, system (6.24) *admits a monotone traveling wave solution $W(x-ct)$ connecting u^* to* 0.

(ii) For any $c \in (0, c^*)$, system (6.24) *has no such traveling wave solution.*

Proof. The existence and nonexistence of the monotone and left-continuous wave profiles with speed in terms of c^* follows from [19, Theorem 4.2 and Remark 3.7] (see also Theorems 2.2.6 and 2.2.7). It suffices to prove the smoothness of wave profiles. Note that $W = (W_1, W_2)$ solves the following integral equations:

$$\begin{aligned} W_1(x-ct) &= e^{-\mu_M t}\int_{\mathbb{R}}\Gamma(0,x,y,D_M)W_1(y)dy \\ &\quad + \alpha\beta\int_0^t\int_{\mathbb{R}} e^{-\mu_M(t-s)}\Gamma(t-s,x,y,D_M)(M^*-W_1(y-cs))W_2(y-cs)dyds, \\ W_2(x-ct) &= e^{-(\gamma+\alpha M^*+\mu_N)t}W_2(x) \\ &\quad + P_l L^*\beta_T\int_0^t\int_{\mathbb{R}} e^{-(\gamma+\alpha M^*+\mu_N)(t-s)}\Gamma(\tau_l,x,y,D_M)W_1(y-c(s-\tau_l))dyds, \end{aligned}$$

where $c \geq c^* > 0$. From the first equation, we see that the right-hand side is twice differentiable with respect to x, and hence, W_1 is twice differentiable. Meanwhile, the right-hand side of the second equation is differentiable with respect to t, and hence, W_2 is differentiable. □

To finish this section, we point out that the third equation in system (6.23) can be regarded as the following non-homogeneous evolution equation:

$$\frac{\partial a}{\partial t} = -(\mu_A + \xi H^* + \delta_A A^*)a + P_n\int_{\mathbb{R}}\Gamma(\tau_n,x,y,D_M)K_a^*(t-\tau_n,y)dy,$$

with

$$K_a^*(t,y) = M^* n(t,y) + \beta_T m(t,y)(N^* - n(t,y)).$$

By the same arguments as in [18, Theorems 3.1 and 3.2], it then follows that the similar conclusions in Theorems 6.3.1–6.3.2 also hold for $a(t,x)$, and hence, the number c^* is the spreading speed and the minimal wave speed for system (6.23).

6.4 Numerical simulations

In this section, we use numerical computations to verify our analytic results in sections 6.2–6.4 and reveal the biological insights into the invasion of Lyme disease.

In the case of a bounded habitat, we choose $\Omega = (0, 1)$. According to biological data in [74], we take basic parameters $\mu_M = 0.012\,\text{day}^{-1}, \mu_L = 0.006\,\text{day}^{-1}, \mu_N = 0.006\,\text{day}^{-1}, \mu_A = 0.003\,\text{day}^{-1}$, $\tau_L = 3\,\text{days}, \tau_N = 5\,\text{days}, \tau_A = 10\,\text{days}$. We also adapt the parameter values from [12] by choosing $\alpha = 0.02$ and $\gamma = 0.005\,\text{day}^{-1}$. For illustration, we choose $\xi = 0.01, \mu_h = 0.001\text{day}^{-1}$, $r = 10$ and $H^* = 8$. In [92], the authors numerically studied the effects of host population sizes and spatial configurations, and the spatial control of Lyme disease. Since our model is motivated by [92], we only explore new phenomena in the bounded habitat $[0, 1]$ such as influences of self-regulation mechanism and host diffusion rates on the risk of Lyme disease infection. More precisely, we first investigate the case where the demographic environment for mice and deers is spatially homogeneous, but the disease transmission environment for mice and ticks is spatially heterogeneous. To do so, we let $\beta(x) = 0.4(1 + \cos \pi x)$, $\beta_T(x) = 0.35(1 + \cos \pi x)$, and mice population size $M^* = 100$.

Fix $D_M = 0.01\,\text{km}^2 \cdot day^{-1}$, $D_H = 0.22\,\text{km}^2 \cdot day^{-1}$ and $\delta_A = 0.065$, we use Theorem 6.2.1 to numerically compute the basic reproduction number R_0 and obtain $R_0 = 1.0543$. While we retake $\beta = 0.4$ and $\beta_T = 0.35$, exactly the spatial average of $\beta(x)$ and $\beta_T(x)$, it follows that $R_0 = 0.8647$. This suggests that spatially averaged system may underestimate the disease outbreak risk.

To observe the sensitivity of R_0 on model parameters, we vary δ_A and keep all other parameters the same as above, the left panel of Figure 6.2 shows that the basic reproduction number R_0 is a decreasing function of δ_A and goes down through the threshold value 1. This means the self-regulation mechanism for adult ticks could reduce the infection risk via intrinsically controlling the population size of adult ticks. Fix $\delta_A = 0.065$ and let D_M vary. Then the right panel of Figure 6.2 indicates that the basic reproduction number R_0 is also a decreasing function of D_M, which indicates that the higher random diffusion movement of mice may lower the infection risk.

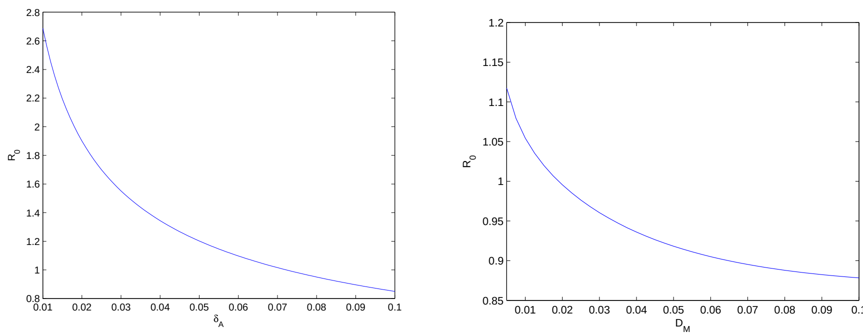

Figure 6.2: R_0 as functions of δ_A and D_M.

Clearly, when $M^*(x)$ is spatially homogeneous, the random diffusion movement of deers D_H has no evident influence on the control of the infection risk. Now let us include the feature of spatially dependent mice distribution. Take $K_M(x) = 80(1.1 + \delta \sin(k\pi x))$ with $\delta \in [-1, 1]$ and $k = 1, 2$, $r_M = 0.036$, $\delta_A = 0.065$, $D_M = 0.01$. A simple computation shows that the positive disease-free steady state exists uniquely for $\delta \in [-1, 1], k = 1, 2$. Figure 6.3 shows that R_0 is an increasing function of D_H with $K_M = 80(1.1 + \sin(2\pi x))$, but the difference of R_0 values for $D_H = 0.25$ and $D_H = 0.01$ is 6.2177×10^{-5}, which could result from the error of computation. A further numerical calculation indicates that R_0 almost remains the same in the case that $K_M = 80(1.1 + \sin(\pi x))$, and hence, the random diffusion movement of deers might have little impact on the control of the disease outbreak. This may arise from the fact that adult ticks don't amplify the disease directly and deers, the host of adult ticks, do not disperse the pathogen and cannot be infected. Next, we vary δ to estimate the spatially heterogeneous effects on the basic reproduction number R_0. Figure 6.4 shows the different spatial dependent carrying capacity distributions of

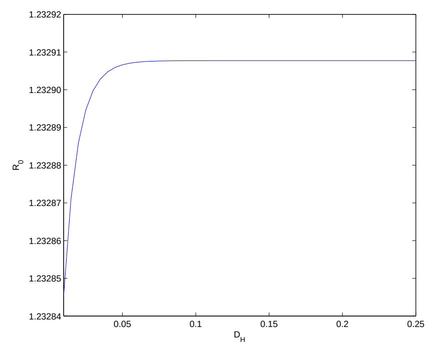

Figure 6.3: R_0 as functions of D_H with $K_M(x) = 80(1.1 + \sin(2\pi x))$.

mice may dilute or amplify the disease infection. A possible explanation is that too large mouse population size could cause intensive intra-competition and the decrease of the ratio of tick to host, ending in the dilution of infections [25,79]. When $k = 1$, the spatial average of K_M is increasing as δ increases, so is the population size of mice in this whole interval. When $k = 2$, although the average of the carrying capacity size on the whole area remains the same, it is very likely that when the sharply heterogeneous carrying capacity distribution of mice occurs, the ratio of tick to mice increases on the interval $[\frac{1}{2}, 1]$ with $\delta > 0$, or $[0, \frac{1}{2}]$ with $\delta < 0$, which has a predominant effect on the infection risk, leading to the worse disease burden.

In order to simulate the long-time behavior of system (6.24), we discretize it by the difference method on $[0, 1]$. Here we should point out that the idea of the discretization of the non-local term in system (6.24) follows from [52, Appendix]. Figure 6.5 gives the plot of two disease infectious components, $m(t, x)$ and $n(t, x)$, with the initial

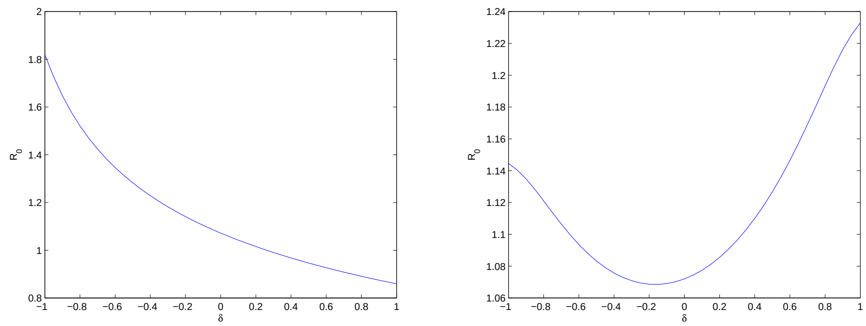

Figure 6.4: Left panel: R_0 decreases as δ increases with $K_M(x) = 80(1.1 + \delta \sin(\pi x))$. Right panel: R_0 is a function of δ with $K_M(x) = 80(1.1 + \delta \sin(2\pi x))$.

data

$$m(\theta, x) = 20 - 5\cos(2\pi x),\ n(\theta, x) = \frac{1}{5}m(\theta, x),\ \forall \theta \in [-\tau_l, 0], x \in [0, 1].$$

It turns out the both infectious components can persist in that situation.

In the case of an unbounded habitat, we take $\Omega = \mathbb{R}$, $\beta = 0.4$, $\beta_T = 0.35$, $D_M = 0.03$, $M^* = 100$ and $\delta_A = 0.004$. It follows that χ defined in (6.25) equals to $2.3273 > 0$, and the basic reproduction number $\mathcal{R}_0 = 3.4857 > 1$. Moreover, using Lemma 6.3.1, we numerically obtain the spreading spreed $c^* = 0.1039$. Figure 6.6 suggests that c^* is decreasing in δ_A, and increasing in D_M.

To observe traveling waves of system (6.24), we truncate the infinite domain $\mathbb{R}$ to be $[-200, 200]$. Choose the initial data as

$$m(\theta, x) = \begin{cases} 80, & \text{if} \quad -200 \le x < -50,\ \theta \in [-\tau_l, 0], \\ 40 - \frac{4}{5}x, & \text{if} \quad |x| \le 50,\ \theta \in [-\tau_l, 0], \\ 0, & \text{if} \quad 50 < x \le 200,\ \theta \in [-\tau_l, 0]. \end{cases}$$

and $n(\theta, x) = \frac{1}{8}m(\theta, x), \forall x \in [-200, 200], \theta \in [-\tau_l, 0]$. Then the evolution of the

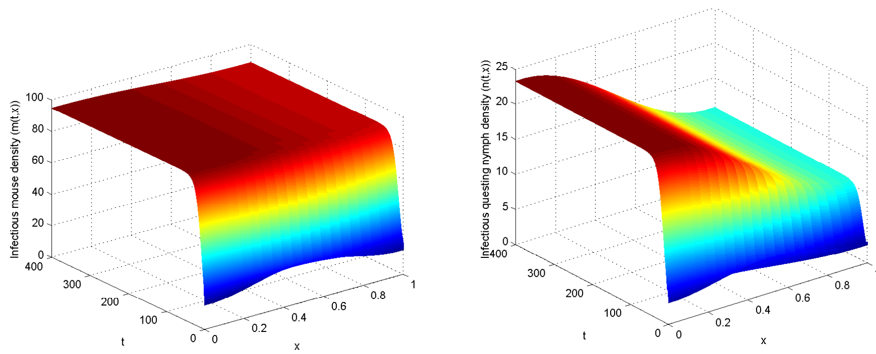

Figure 6.5: The long-time behavior of disease infectious components with $R_0 = 3.8720$ and $\chi = 2.3273$. Here $D_M = 0.03$, $M^* = 100$, $\delta_A = 0.004$, $\beta(x) = 0.4(1 + \cos \pi x)$ and $\beta_T(x) = 0.35(1 + \cos \pi x)$.

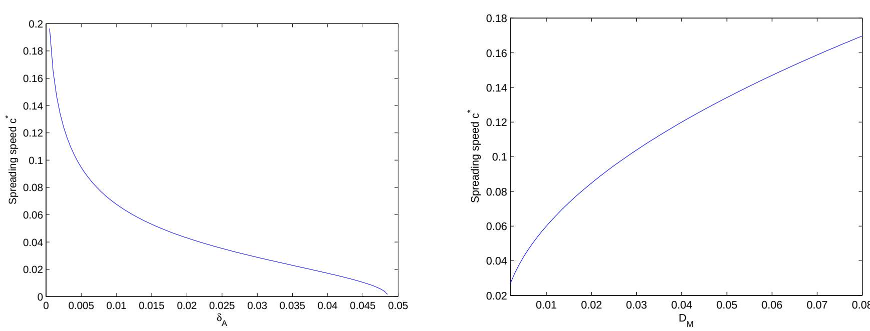

Figure 6.6: Spreading speed c^* as functions of δ_A and D_M.

solution is as shown in Figure 6.7 .

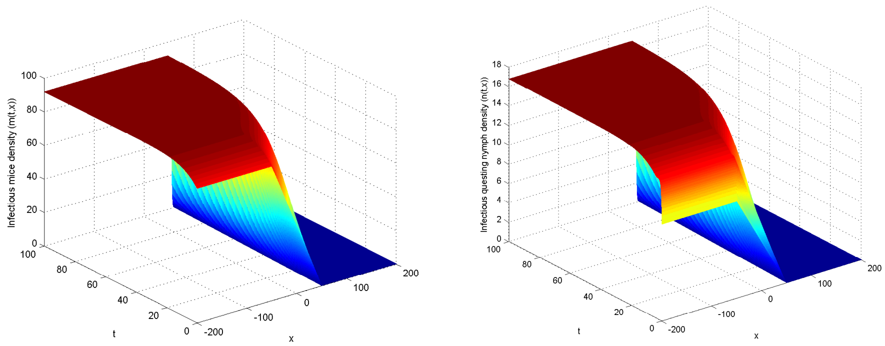

Figure 6.7: The rightward traveling waves observed for m and n.

6.5 Discussion

In this chapter, we have modified the nonlocal spatial model of Lyme disease presented in [92] to take into account of the self-regulation mechanism. In a bounded domain, we first investigated the disease-free dynamics of system (6.2) and then the global dynamics of the model system (6.1) with spatially dependent parameters in terms of the basic reproduction number R_0. In an unbounded domain, we established the existence of the spreading speed for the disease infection and its coincidence with the minimal wave speed for the limiting system (6.24).

Our analytic results in sections 6.2 and 6.3 greatly improved the main results in [92], where they required more technical assumptions for the existence of principal eigenvalues and global attractivity. Specifically, with the spatially homogeneous diffusion rates and one assumption on the spatial distribution $M^*(x)$ of mice population, they obtained the persistence result in term of the basic reproduction number R_0, and proved the sharp global dynamics under the structure of these spatially homogeneous quantities and one additional condition.

Numerically, we found that the spatial averaged system would underestimate the disease risk, and we also numerically pursued the influences of self-regulation mechanism of ticks and host diffusion rates on the infection risk. It turned out that both self-regulation mechanism of ticks and random movements of mice would alleviate the infection, but random movements of deers would take no evident effect. Moreover, the carrying capacity of mice with strong spatial heterogeneity would increase the infection risk. In order to study the spatial invasion of the disease in an unbounded domain, we also computed the spreading speed numerically and plotted the traveling waves of two infectious components. Our results show that the spreading speed is decreased when the self-regulation of adult ticks is appropriately enhanced, and is increasing with the random diffusion rate of mice. Combining with the numerical results in a bounded domain, we see that the intensive self-regulation of ticks would force disease to spread more slowly and even to go extinct, and cooling down the random movements of mice could deteriorate the infection locally, but this might slow down the invasion of the disease in a large area.

Chapter 7

Summary and Future Works

In this chapter, we first briefly summarize the main results in this thesis, and then suggest some future research works.

In this thesis, we studied three reaction-diffusion models in the spatial and/or temporal heterogeneous environments. We mainly focused on the threshold dynamics, spreading speeds, and monostable traveling waves, which are the crucial factors to characterize and predict the evolution of species.

To study the population persistence with the temporal heterogeneity in a stream ecology, we modified the early models in [60,76] to a time-periodic reaction-advection-diffusion systems (3.1) in Chapter 3. We first investigated a threshold dynamics for the spatially homogeneous system of model (3.1) in terms of the principal Floquet multiplier of its linearized system at $(0,0)$, and then we established the existence of leftward and rightward spreading speeds and their coincidence with the minimal wave speeds for monotone periodic traveling waves in an unbounded domain. We also proved a threshold result on the global dynamics of the model system in a bounded domain, at last we presented some numerical simulations to verify our analytic results.

In Chapter 4, we extended the theory of traveling waves (and spreading speeds) for monotone semiflows to the case of a periodic habitat, and applied this theory to the two species competition reaction-advection-diffusion models in a spatially periodic environment. We 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 shown that the rightward spreading speed is linearly determinate under additional conditions. A prototypical class of reaction-diffusion systems, which were studied in [16, 49] in the case of a bounded domain was used to illustrate our results. Furthermore, we established the theory of traveling waves, almost pulsating waves and spreading speeds for time-space periodic semiflows of monostable type in Chapter 5, and then applied this theory to the two species competition model in the time-space environment and explored its propagation phenomena.

In Chapter 6, we modified the nonlocal spatial model of Lyme disease presented in [92] to take into account of the self-regulation mechanism. In a bounded domain, we first investigated the disease-free dynamics of the associated system and then the global dynamics of the model system with spatially dependent parameters in terms of the basic reproduction number R_0. In an unbounded domain, we studied the spatial spread of disease and the existence of traveling waves. We established the existence of the spreading speed for the limiting system and its coincidence with the minimal wave speed. we also numerically pursued the influences of self-regulation mechanism of ticks and host diffusion rates on the infection risk. This project could give some insights into the control of the disease spread.

Related to the projects in this thesis, there are some open and challenging issues for future investigation. In the first project, I considered the stream population model in time periodic environment. However, motivated by [58], it is worthy to study the model in time-space periodic environment and investigate the spatial dynamics and the propagation phenomena. For the second project, It will be more interesting if we consider the age structure of the population and derive a reaction-diffusion and nonlocal time-delayed competition model in a periodic habitat. Moreover, I only discussed the traveling waves with the monostable structure in Chapter 4. It could be much more challenging to study the bistable traveling waves for two-species competition model in a periodic habitat. For the last project, we could incorporate the seasonal succession into the model system in Chapter 6 and investigate the spatial dynamics of the model system. Since the full model system in Chapter 6 is non-monotone, it will be subtle but interesting to study the existence of traveling waves.

Bibliography

[1] N. D. Alikakos, P. W. Bates and X. Chen, Periodic traveling waves and locating oscillating patterns in multidimensions domains, *Trans. Amer. Math. Soc.*, 351 (1999), 2777–2805.

[2] X. Bao and Z.-C. Wang, Existence and stability of time periodic traveling waves for a periodic bistable Lotka-Volterra competition system, *J. Diff. Eqns.*, 255(2013), 2402–2435.

[3] A. G. Barbour, D. Fish, The biological and social phenomenon of Lyme disease, *Science*, 260(1993), 1610–1616.

[4] H. Berestycki and F. Hamel, Front propagation in periodic excitable media, *Comm. Pure Appl. Math.*, 55(2002), 949–1032.

[5] H. Berestycki, F. Hamel and N. Nadirashvili, The speed of propagation for KPP type problems: I. Periodic framework, *J. Eur. Math. Soc.*, 7(2005), 173–213.

[6] H. Berestycki, F. Hamel and L. Roques, Analysis of the periodically fragmented environment model: I-Species persistence, *J. Math. Biol.*, 51(2005), 75–113.

[7] H. Berestycki, F. Hamel and L. Roques, Analysis of the periodically fragmented environment model: II-Biological invasions and pulsating traveling fronts, *J. Math. Pures Appl.*, 84(2005), 1101–1146.

[8] H. Berestycki and F. Hamel, Generalized transition waves and their properties, *Comm. Pure Appl. Math.*, 65(2012), 592-648.

[9] J. V. Buskirk and R. S. Ostfeld, Habitat heterogeneity, dispersal, and local risk of exposure to Lyme disease, *Ecological Applications*, 8 (1998), 365–378.

[10] R.S. Cantrell and C. Cosner, *Spatial Ecology via Reaction-Diffusion Equations*, Ser. Math. Comput. Biol., Wiley, Chichester, UK, 2003.

[11] T. Caraco, G. Gardner, W. Maniatty, E. Deelman and B. K. Szymanski, Lyme disease: self-regulation and pathogen invasion, *J. Theor. Biol.*, 193 (1998), 561–575.

[12] T. Caraco, S. Glavanakov, G. Chen, J. E. Flaherty, T. K. Ohsumi, and B. K. Szymanski, Stage-structured infection transmission and a spatial epidemic: a model for Lyme disease, *The American Naturalist*, 160 (2002), 348–359.

[13] J. Coville, J. Dávila and S. Martínez, Pulsating fronts for nonlocal dispersion and KPP nonlinearity, *Ann. Inst. H. Poincaré Anal. Non Linéaire*, 30(2013), 179–223.

[14] K. Deimling, *Nonlinear Functional Analysis*, Springer-Verlag, Berlin, 1988.

[15] O. Diekmann, J. A. P. Heesterbeek and J. A. J. Metz, On the definition and the computation of the basic reproduction ratio R_0 in the models for infectious disease in heterogeneous populations, *J. Math. Biol.*, 28 (1990), 365–382.

[16] J. Dockery, V. Hutson, K. Mischaikow and M. Pernarowski, The evolution of slow dispersal rates: a reaction diffusion model, *J. Math. Biol.*, 37(1998), 61–83.

[17] J. Fang, K. Lan, G. Seo and J. Wu, Spatial dynamics of an age-structured population model of Asian clams, *SIAM J. Appl. Math.*, 74(2014), 959–979.

[18] J. Fang, J. Wei, and X.-Q. Zhao, Spatial dynamics of a nonlocal and time-delayed reaction-diffusion system, *J. Diff. Eqns.*, 245 (2008), 2749–2770.

[19] J. Fang and X.-Q. Zhao, Traveling waves for monotone semiflows with weak compactness, *SIAM J. Math. Anal.*, 46(2014), 3678–3704.

[20] J. Fang and X.-Q. Zhao, Bistable waves for monotone semiflows with applications, *J. Euro. Math. Soc.*, 17(2015), 2243–2288.

[21] H. Freedman and X.-Q. Zhao, Globa asymptotics in some quasimonotone reaction–diffusion systems with delays, *J. Diff. Eqns.*, 137(1997), 340–362.

[22] G. Frejacques, Travelling waves in infinite cylinders with time-periodic coefficients, PhD thesis, 2006.

[23] M. I. Friedlin, On wavefront propagation in periodic media, stochastic analysis and applications, in "Adv. Probab. Related Topics, 7", Dekker, New York, 1984, 147–166.

[24] J. Gärtner and M. I. Freidlin, The propagation of concentration waves in periodic and random media, *Soviet Math. Dokl.*, 20(1979), 1282–1286.

[25] M. Ghosh and A. Pugliese, Seasonal population dynamics of ticks, and its influence on infection transmission: a semi-discrete approach, *Bull. Math. Biol.*, 66 (2004), 1659–1684.

[26] S. A. Gourley and S. Ruan, Convergence and travelling fronts in functional differential equations with nonlocal terms: a competition model, *SIAM J. Math. Anal.*, 35(2003), 806–822.

[27] J.-S. Guo and X. Liang, The minimal speed of traveling fronts for the Lotka-Volterra competition system, *J. Dynam. Diff. Eqns*, 23(2011), 353–363.

[28] J. K. Hale, *Asymptotic Behavior of Dissipative Systems*, American Mathematical Society, Providence, RI, 1988.

[29] F. Hamel and L. Roques, Uniqueness and stability properties of monostable pulsating fronts, *J. Euro. Math. Soc.*, 13 (2011), 345–390.

[30] F. Hamel and L. Roques, Persistence and propagation in periodic reaction-diffusion models. *Tamkang J. Math.*, 45(2014), 217–228.

[31] P. Hess, *Periodic-Parabolic Boundary Value Problems and Positivity*, Pitman Search Notes in Mathematics Series, Vol. 247, Longman Scientific Technical, Harlow, UK, 1991.

[32] P. Hess and A. C. Lazer, On an abstract competition model and applications, *Nonlinear Analysis T.M.A.*, 16(1991), 917–940.

[33] Y. Hosono, The minimal speed of traveling fronts for a diffusive Lotka-Volterra competition model, *Bull. Math. Biol.*, 60(1998), 435–448.

[34] T. Hoch, Y. Monnet and A. Agoulon, Influence of host migration between woodland and pasture on the population dynamics of the tick *Ixodes ricinus*: A modelling approach, *Ecological Modelling*, 221 (2010), 1798–1806.

[35] S. B. Hsu, H. L. Smith and P. Waltman, Competitive exclusion and coexistence for competitive systems on ordered Banach spaces, *Trans. Amer. Math. Soc.*, 348(1996), 4083–4094.

[36] S.-B. Hsu, F.-B. Wang and X.-Q. Zhao, Dynamics of a periodically pulsed bioreactor model with a hydraulic storage zone, *J. Dyn. Diff. Eqns*, 23 (2011), 817–842.

[37] S.-B. Hsu, F.-B. Wang and X.-Q. Zhao, Global dynamics of zooplankton and harmful algae in flowing habitats, *J. Diff. Eqns.*, 255(2013), 265–297.

[38] W. Huang, Problem on minimum wave speed for a Lotka-Volterra reaction-diffusion competition model, *J. Dyn. Diff. Eqns.*, 22(2010), 285–297.

[39] W. Huang and M. Han, Non-linear determinacy of minimum wave speed for a Lotka-Volterra competition model, *J. Diff. Eqns.*, 251(2011), 1549–1561.

[40] Y. Jin and X.-Q. Zhao, Spatial dynamics of a periodic population model with dispersal, *Nonlinearity*, 22(2009), 1167–1189.

[41] P. J. Hudson, R. Norman, M. K. Laurenson, D. Newborn, M. Gaunt, L. Jones, H. Reid, E. Gould, R. Bowers and A. P. Dobson, Persistence and transmission of tick-borne viruses: Ixodes ricinus and louping-ill virus in red grouse populations, *Parasitology*, 111 (1995), (Suppl.) S49–S58.

[42] W. Hudson and B. Zinner, Existence of traveling waves for reaction diffusion equations of Fisher type in periodic media, in Boundary Problems for Functional Differential Equations, World Scientific, Singapore, 1995, 187–199.

[43] V. Hutson, K. Mischaikow and P. Poláčik, The evolution of dispersal rates in a heterogeneous time-periodic environment, *J. Math. Biol.*, 43(2001), 501–533.

[44] Y. Kan-on, Fisher wave fronts for the Lotka-Volterra competition model with diffusion, *Nonlinear Analysis*, TMA 28(1997), 145–164.

[45] M. E Killilea, A. Swei, R. S Lane, C. J. Briggs and R. S. Ostfeld, Spatial dynamics of Lyme disease: a review, *EcoHealth*, 5(2008), 167–195.

[46] L. Kong, N. Rawal and W. Shen, Spreading speeds and linear determinacy for two species competition systems with nonlocal dispersal in periodic habitats, preprint, http://arxiv.org/pdf/1410.0317v1.pdf, 2014.

[47] L. Kong and W. Shen, Liouville type property and spreading speeds of KPP equations in periodic media with localized spatial inhomogeneity, *J. Dyn. Diff. Eqns*, 26(2014), 181–215.

[48] K. Kurtenbach, K Hanincová, J. I. Tsao, C. Margos, D. Fish and N. H. Ogden, Fundamental processes in the evolutionary ecology of Lyme borreliosis, *Nature Reviews Microbiology*, 4 (2006), 660–669.

[49] K.-Y. Lam and W.-M. Ni, Uniqueness and complete dynamics of the Lotka-Volterra competition diffusion system, *SIAM J. Appl. Math.*, 72(2012), 1695–1712.

[50] E. F. Lambin, A. Tran, S. O. Vanwambeke, C. Linard and V. Soti, Pathogenic landscapes: Interactions between land, people, disease vectors, and their animal hosts, *International Journal of Health Geographics*, 9 (2010), 1–13.

[51] M. A. Lewis, B. Li, and H. F. Weinberger, Spreading speeds and linear determinacy for two-species competition models, *J. Math. Biol.*, 45(2002), 219–233.

[52] J. Li and X. Zou, Modeling spatial spread of infectious diseases with a fixed latent period in a spatially continuous domain, *Bull. Math. Biol.*, 71(2009), 2048–2079.

[53] X. Liang, Y. Yi and X.-Q. Zhao, Spreading speeds and traveling waves for periodic evolution systems, *J. Diff. Eqns*, 231(2006), 57–77.

[54] X. Liang and X.-Q. Zhao, Asymptotic speeds of spread and traveling waves for monotone semiflows with applications, *Comm. Pure Appl. Math.*, 60(2007), 1–40.

[55] X. Liang and X.-Q. Zhao, Spreading speeds and traveling waves for abstract monostable evolution systems, *J. Funt. Anal.*, 259(2010), 857–903.

[56] Y. Lou and J. Wu, Tick seeking assumptions and their implications for Lyme disease predictions, *Ecological Complexity*, 17 (2014), 99–106.

[57] Y. Lou and X.-Q. Zhao, The periodic Ross-Macdonald model with diffusion and advection, *Applicable Analysis*, 89(2010), 1067–1089.

[58] F. Lutscher, M. A. Lewis, and E. McCauley, Effects of heterogeneity on spread and persistence in rivers, *Bull. Math. Biol.*, 68(2006), 2129–2160.

[59] F. Lutscher, E. McCauley, and M. A. Lewis, Spatial patterns and coexistence mechanisms in systems with unidirectional flow, *Theor. Popul. Biol.*, 71(2007), 267–277.

[60] F. Lutscher and G. Seo, The effect of temporal variability on persistence conditions in rivers, *J. Theor. Biol.*, 283(2011), 53–59.

[61] M. Ma and X.-Q. Zhao, Monostable waves and spreading speed for a reaction-diffusion model with seasonal succession, *Discrete Contin. Dyn. Syst. Ser. B*, in press.

[62] N. K. Madhav, J. S. Brownstein, J. I. Tsao, and D. Fish, A dispersal model for the range expansion of blacklegged tick (Acari: Ixodidae), *J. Med. Entomol.*, 41 (2004), 842–852.

[63] R. H. Martin, Nonlinear Operators and Differential Equations in Banach Spaces, Wiley-Interscience, New York, 1976.

[64] R. H. Martin and H. L. Smith, Abstract functional differential equations and reaction-diffusion systems, *Trans. Amer. Math. Soc.*, 321(1990), 1–44.

[65] K. M̈uller, The colonization cycle of fresh water insects, *Oecologica 53*, 1982, 202–207.

[66] J. D. Murray, *Mathematical Biology, I: An introduction*, Springer-Verlag, New York, 2002.

[67] G. Nadin, Traveling fronts in space-time periodic media, *J. Math. Pures Appl.*, 92(2009), 232-262.

[68] G. Nadin, The principal eigenvalue of a space-time periodic parabolic operator, *Ann. Mat. Pura Appl.*, 188(2009), 269–295.

[69] J. Nolen, M. Rudd and J. Xin, Existence of KPP fronts in spatially-temporally periodic advection and variational principle for propagation speeds, *Dyn. Partial Diff. Eqn.*, 2(2005), 1–24.

[70] R. Norman, B. G. Bowers, M. Begon and P. J. Hudson, Persistence of tick-borne virus in the presence of multiple host species: tick reservoirs and parasite mediated competition, *J. Theor. Biol.*, 200 (1999), 111–118.

[71] R. D. Nussbaum, Eigenvectors of nonlinear positive operator and the linear Krein-Rutman theorem, in: E. Fadell, G. Fournier (Eds.), *Fixed Point Theory*, Lecture Notes in Mathematics, Vol. 886, Springer, New York/Berlin, (1981), 309–331.

[72] N. H. Ogden, L. R. Lindsay, G. Beauchamp, D. Charron, A. Maarouf, C. J. OCallaghan, D. Waltner-Toews, and I. K. Barker, Investigation of relationships between temperature and developmental rates of tick Ixodes scapularis (Acari: Ixodidae) in the laboratory and field, *J. Med. Entomol.*, 41 (2004), 622–633.

[73] N. H. Ogden, M. Bigras-Poulin, C. J. Oćallaghan, I. K. Barker, L. R. Lindsay, A. Maarouf, K. E. Smoyer-Tomic, D. Waltner-Toews and D. F. Charron, A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*, *International Journal for Parasitology*, 35 (2005), 375–389.

[74] N. H. Ogden, M. Bigras-Poulin, C. J. Oćallaghan, I. K. Barker, K. Kurtenbach, L. R. Lindsay and D. F. Charron, Vector seasonality, host infection dynamics and fitness of pathogens transmitted by the tick Ixodes scapularis, *Parasitology*, 134 (2007), 209–227.

[75] Z. Ouyang and C. Ou, Global stability and convergence rate of traveling waves for a nonlocal model in periodic media, *Discrete Contin. Dyn. Syst. Ser. B*, 17(2012), 993–1007.

[76] E. Pachepsky, F. Lutscher, R. Nisbet and M. A. Lewis, Persistence, spread and the drift paradox, *Theor. Popul. Biol.*, 67(2005), 61–73.

[77] A. Pazy, *Semigroups of Linear Operators and Application to Partial Differential Equations*, Springer-Verlag, 1983.

[78] N. Rawal, W. Shen and A. Zhang, Spreading speeds and traveling waves of nonlocal monostable equations in time and space periodic habitats, preprint, arXiv:1307.6576v3 (2014).

[79] R. Rosà and A. Pugliese, Effects of tick population dynamics and host densities on the persistence of tick-borne infections, *Math. Biosci.*, 208 (2007), 216–240.

[80] W. Shen, Variational principle for spreading speeds and generalized propagating speeds in time almost periodic and space periodic KPP models, *Trans. Amer. Math. Soc.*, 362(2010), 5125–5168.

[81] W. Shen and A. Zhang, Spreading speeds for monostable equations with nonlocal dispersal in space periodic habitats, *J. Diff. Eqns*, 249(2010), 747–795.

[82] W. Shen and A. Zhang, Traveling wave solutions of spatially periodic nonlocal monostable equations, *Comm. Appl. Nonlinear Anal.*, 19(2012), 73–101.

[83] N. Shigesada, K. Kawasaki, *Biological invasions: theory and practice*, Oxford Series in Ecology and Evolution, Oxford : Oxford University Press, 1997.

[84] N. Shigesada, K. Kawasaki and E. Teramoto, Traveling periodic waves in heterogeneous environments, *Theor. Popul. Biol.*, 30(1986), 143–160.

[85] H. L. Smith, *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*, Mathematical Surveys and Monographs, Vol. 41, American Mathematical Society, Providence, RI (1995).

[86] H. R. Thieme, Asymptotic estimates of the solutions of nonlinear integral equations and asymptotic speeds for the spread of populations, *J. Reine Angew. Math*, 306 (1979), 94–121.

[87] H. R. Thieme, Convergence results and Poincaré-Bendixson trichotomy for asymptotically autonomous differential equations, *J. Math. Biol.*, 30(1992), 755–763.

[88] H. R. Thieme, Spectral bound and reproduction number for infinite dimensional population structure and time heterogeneity, *SIAM J. Appl. Math.*, 70(2009), 188–211.

[89] L. A. Waller, B. J. Goodwin, M. L. Wilson, R. S. Ostfeld, S. L. Marshall and E. B. Hayes, Spatio-temporal patterns in county-level incidence and reporting of Lyme disease in the northeastern United States, 1990-2000, *Environmental and Ecological Statistics*, 14 (2007), 83–100.

[90] W. Wang and X.-Q. Zhao, A nonlocal and time-delayed reaction-diffusion model of Dengue transmission, *SIAM J. Appl. Math.*, 71(2011),147–168.

[91] W. Wang and X.-Q. Zhao, Basic reproduction numbers for reaction-diffusion epidemic models, *SIAM J. Appl. Math.*, 11(2012), 1652–1673.

[92] W. Wang and X.-Q. Zhao, Spatial invasion threshold of Lyme disease, *SIAM J. Appl. Math.*, 75(2015), 1142-1170.

[93] H. F. Weinberger, Long-time behavior of a class of biological models, *SIAM J. Math. Anal.*, 13(1982), 353–396.

[94] H. F. Weinberger, On spreading speeds and traveling waves for growth and migration models in a periodic habitat, *J. Math. Biol.*, 45(2002), 511–548; *J. Math. Biol.*, 46 (2003), 190 (Erratum).

[95] H. F. Weinberger, M. A. Lewis, and B. Li, Analysis of linear determinacy for spread in cooperative models, *J. Math. Biol.*, 45(2002), 183–218.

[96] P. Weng and X.-Q. Zhao, Spatial dynamics of a nonlocal and delayed population model in a periodic habitat, *Discrete Contin. Dyn. Syst. Ser. A*, 29(2011), 343–366.

[97] J. Wu, *Theory and Applications of Partial Functional Differential Equations*, Springer, New York, 1996.

[98] X. Wu, V. R. Duvvuri, Y. Lou, N. H. Ogden, Y. Pelcat, H. Nicholas, Y. Pelcat, and J. Wu, Developing a temperature-driven map of the basic reproductive number of the emerging tick vector of Lyme disease *Ixodes scapularis* in Canada, *J. Theor. Biol.*, 319 (2013), 50–61.

[99] J. Xin, Existence and stability of travelling waves in periodic media governed by a bistable nonlinearity, *J. Dyn. Diff Eqns*, 3 (1991), 541–573.

[100] J. Xin, Front propagation in heterogeneous media, *SIAM Rev.*, 42 (2000), 161–230.

[101] F. Zhang and X.-Q. Zhao, A periodic epidemic model in a patchy environment, *J. Math. Anal. Appl.* 325 (2007), 496–516.

[102] Y. Zhang and X.-Q. Zhao, Bistable travelling waves for a reaction and diffusion model with seasonal succession, *Nonlinearity*, 26(2013), 691–709.

[103] Y. Zhang and X.-Q. Zhao, A reaction-diffusion Lyme disease model with seasonality, *SIAM J. Appl. Math.*, 73 (2013), 2077–2099.

[104] G. Zhao and S. Ruan, Existence, uniqueness and asymptotic stability of time periodic traveling solutions for a periodic Lotka–Volterra competition system with diffusion, *J. Math. Pures Appl.*, 95(2011), 627–671.

[105] G. Zhao and S. Ruan, Time periodic traveling wave solutions for periodic advection-reaction-diffusion systems, *J. Diff. Eqns.*, 257(2014),1078–1147.

[106] X.-Q. Zhao, *Dynamical Systems in Population Biology*, Springer-Verlag, New York, 2003.

[107] X.-Q. Zhao, Global dynamics of a reaction and diffusion model for Lyme disease, *J. Math. Biol.*, 65(2012), 787–808.

[108] X.-Q. Zhao, Basic reproduction ratios for periodic compartmental models with time delay, *J. Dyn. Diff. Eqns*, 2015, DOI 10.1007/s10884-015-9425-2.

[109] X.-Q. Zhao and Z.-J. Jing, Global asymptotic behavior in some cooperative systems of functional-differential equations, *Canad. Appl. Math. Quart.*, 4(1996), 421–444.