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Spatial dynamics of a partially degenerate reaction–diffusion system with pair formation

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Abstract. This article is devoted to the study of the mosquito growth incorporating metamorphic stages (including aquatic stage and adult stage), mating behavior, and the spatial movement of adult mosquitoes in a seasonal environment. Our model is a reaction–diffusion system that describes the dynamics of aquatic mosquitoes, mature male mosquitoes, and mature female mosquitoes. In the case of a bounded habitat, we establish the threshold dynamics of the model system in terms of the basic reproduction ratio, which is defined by a time-periodic homogeneous evolution system without compactness. In the case of a spatially periodic habitat, we show that the system admits the leftward and rightward spreading speeds that coincide with the minimal wave speeds of leftward and rightward time–space periodic traveling waves, respectively. Further, we derive a formula to compute the spreading speed via the homogeneous systems approach and quantitatively investigate the effects of parameters on it in the autonomous case.

1 Introduction

A typical mechanism of mosquito-borne diseases involves a mosquito feeding on the blood of an infected host and ingesting the viruses or parasites, which can then be transferred to the next host bitten by the mosquito. Common mosquito-borne diseases include malaria, dengue, West Nile virus, chikungunya, yellow fever, and Zika, which are directly responsible for more than a million deaths per year. Mathematical models serve as valuable tools for understanding the transmission dynamics of mosquito-borne diseases. Most existing models overlook the compartment of male mosquitoes, focusing solely on female mosquitoes, and typically assume that either the total number of female mosquitoes or their recruitment rate is a constant or a given function. However, the life cycle of mosquitoes is quite complicated, as their reproduction is

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influenced by various stages of metamorphosis, along with pair formation and mating behaviors [3, 8, 18].

The main purpose of this article is to study mosquito growth by incorporating metamorphic stages (including aquatic and adult stages), pair formation, and the spatial movement of adult mosquitoes in a time-periodic environment. Let Ω be a spatial habitat with smooth boundary $\partial\Omega$, and we consider a closed environment with the Neumann boundary conditions for subpopulations on the boundary. Let $u_A(x,t)$ be the population size of the aquatic mosquitoes, and $u_M(x,t)$ (resp. $u_F(x,t)$) be the population size of matured male mosquitoes (resp. matured female mosquitoes). The reproductive rate at location x and time t of adult female mosquitoes is denoted by $\rho(x,t)$. According to the law of harmonic mean [3, 8, 18], we set

$$H(a,b) := \begin{cases} \dfrac{ab}{a+b}, & a+b>0, \\ 0, & a=b=0, \end{cases}$$

and the mating function takes the following form:

$$\rho(x,t)H(u_M,u_F),$$

which satisfies preservation of positivity, homogeneity, and monotonicity. Note that the aquatic mosquito population is constrained by the environmental carrying capacity $K(x,t)$, as female mosquitoes lay their eggs in clusters on the surface of stagnant water. As in [18], the growth rate of the aquatic mosquito population can be described by

$$\rho(x,t)H(u_M,u_F)\left(1-\frac{u_A}{K(x,t)}\right).$$

This motivates us to consider the following reaction–diffusion system describing the growth of mosquitoes with pair formation in a time-varying environment:

(1.1)
$$\begin{cases} \dfrac{\partial u_A}{\partial t} = \rho(x,t)H(u_M,u_F)\left(1-\dfrac{u_A}{K(x,t)}\right) - d(x,t)u_A - \gamma(x,t)u_A, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_M(x,t)}{\partial \nu} = 0, \dfrac{\partial u_F(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0, \end{cases}$$

where Δ is the usual Laplacian operator and ν is the unit outward normal vector to the boundary $\partial\Omega$; D is the diffusion coefficient of matured mosquitoes, $d(x,t)$ (resp. $\hat{d}(x,t)$) represents the natural death rate of aquatic (resp. matured) mosquitoes; $\gamma(x,t)$ is the maturation rate; and θ is the probability of the aquatic mosquitoes maturing into male. With the seasonality, we further assume that there exists a $T>0$ such that $w(x,t+T)=w(x,t)$, $\forall\, x\in\Omega, t\in\mathbb{R}$, and there exists $\kappa\in(0,1)$ such that $w\in C^{\kappa,\frac{\kappa}{2}}(\overline{\Omega}\times[0,T])$ for $w=\rho,\ K,\ d,\ \gamma,\ \hat{d}$, and all these functions are strictly positive. We should point out that a similar reaction–diffusion model of mosquito growth was studied in [3] under the assumption that each of three equations contains a diffusion term. Biologically, aquatic mosquitoes typically stay within specific regions, and their

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movements can be ignored. Consequently, the first equation in (1.1) does not include a diffusion term, which leads to a lack of compactness for the solution maps of system (1.1).

In order to investigate the influence of the spatial heterogeneity on the spreading of the invading mosquitoes, we also modify system (1.1) into the following reaction–diffusion system in a time–space periodic habitat:

(1.2)
$$\begin{cases} \dfrac{\partial u_A}{\partial t} = \rho(x,t)H(u_M,u_F)\left(1-\dfrac{u_A}{K(x,t)}\right) - d(x,t)u_A - \gamma(x,t)u_A, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x\in\mathbb{R},\ t>0, \end{cases}$$

where the coefficient functions $\rho(x,t)$, $K(x,t)$, $d(x,t)$, $\gamma(x,t)$, and $\hat{d}(x,t)$ are positive L-periodic in x and T-periodic in t, and of class $C^{\kappa,\frac{\kappa}{2}}([0,L]\times[0,T])$ for appropriate $L>0$, $T>0$, and $\kappa\in(0,1)$. We will study the spreading properties and time–space periodic traveling wave solutions for system (1.2). Since the linearization of $H(u_M,u_F)$ at $(0,0)$ exhibits a singularity, we cannot employ the linear operators approach to estimate the spreading speed. To overcome this difficulty, we need to study how to use an associated homogeneous system to determine the spreading speed.

In addition to the evolution dynamics of systems (1.1) and (1.2), we further quantitatively analyze the effects of the model parameters on basic reproduction ratios and spreading speeds. Notably, when the diffusion coefficient is sufficiently large, the spreading speed can either tend toward infinity or approach zero, which depends on the limiting behavior of the basic reproduction ratio in the case of a sufficiently large diffusion coefficient. To the best of our knowledge, this is the first analytic work to relate the limiting behavior of the spreading speed to that of the basic reproduction ratio.

The rest of this article is organized as follows. In Section 2, we prove the continuity of the cone spectral radius with respect to perturbations of the cone norm, without assuming compactness. In Section 3, we overcome the non-compactness of associated solution maps to establish the threshold dynamics of system (1.1) in a bounded habitat in terms of the basic reproduction ratio, which is defined by a time-periodic homogeneous evolution system without compactness. In Section 4, we study the propagation properties and traveling waves of system (1.2) and quantitatively investigate the spreading speed in the autonomous case.

2 Preliminaries

Let E be a Banach space with the norm $\|\cdot\|$. A closed convex set D is called a cone if $\lambda D\subseteq D$ for all $\lambda\geq 0$ and $D\cap(-D)=\{0\}$. A cone D is called solid if it contains an interior point (i.e., $\mathrm{Int}(D)\neq\varnothing$), and normal if there exists $c>0$ such that

$$\|x\|\leq c\|x+y\|,\ \text{whenever } x\in D,\ y\in D.$$

We write $y\geq_D x$ if $y-x\in D$; $y>_D x$ if $y-x\in D$ and $y-x\neq 0$; and $y\gg_D x$ if $y-x\in\mathrm{Int}(D)$.

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Next, we recall some basic definitions (see, e.g., [4, 17, 19]). An operator A is called positive on D if $A(D) \subseteq D$; homogeneous (of degree one) if $A(\alpha x) = \alpha Ax$ for all $\alpha \geq 0$, $x \in D$; D-order-preserving if $Ax \geq_D Ay$ whenever $x \geq_D y \geq_D 0$; and D-strongly-order-preserving if $Ax \gg_D Ay$ whenever $x >_D y \geq_D 0$. Let $A : D \to D$ be a homogeneous map, define

$$\|A\|_D = \sup\{\|Ax\| : x \in D \text{ with } \|x\| \leq 1\}.$$

If the supremum exists, then A is said to be bounded and $\|A\|_D$ is called the cone norm of A. Furthermore,

$$r_D(A) = \inf_{n\in\mathbb{N}} \|A^n\|_D^{\frac{1}{n}} = \lim_{n\to+\infty} \|A^n\|_D^{\frac{1}{n}}$$

is called the cone spectral radius on D.

In the following, we extend the elementary results in [20, Lemma 2.4] to the case of non-compact homogeneous maps.

Lemma 2.1 *Let E be a Banach space with a solid and normal cone D. Assume that C is a cone with $C \subseteq D$. Let $L : C \to C$ be a bounded, continuous, homogeneous, and D-order-preserving map such that $r_C(L) > 0$ and $Lu = r_C(L)u$ for some $u \in \mathrm{Int}(D) \cap C$, and let $\{L_n\}_{n\geq 1}$ be a sequence of bounded, continuous, homogeneous, and D-order-preserving maps from C to C. If $\lim_{n\to\infty} \|L - L_n\|_C = 0$, then $\lim_{n\to\infty} r_C(L_n) = r_C(L)$.*

Proof Define

$$\|x\|_u = \inf\{\alpha : -\alpha u \leq_D x \leq_D \alpha u\}, \ \forall x \in E.$$

Since D is normal and $u \in \mathrm{Int}(D)$, $\|\cdot\|_u$ is an equivalent norm on E (see, e.g., [2, Theorem 2.4]). Let $u_n := L_n u$ for all $n \geq 1$. It is easy to see that

$$\lim_{n\to\infty} \|u_n - r_C(L)u\|_u = \lim_{n\to\infty} \|L_n u - Lu\|_u = 0.$$

Then there exists a sequence ϵ_n with $\epsilon_n \to 0^+$ as $n \to \infty$ and $\|u_n - r_C(L)u\|_u \leq \epsilon_n r_C(L)$ for all $n \geq 1$. Therefore, for each $n \geq 1$,

$$(1 - \epsilon_n)r_C(L)u \leq_D u_n \leq_D (1 + \epsilon_n)r_C(L)u.$$

An easy computation yields that

$$(1 - \epsilon_n)r_C(L)u_n = (1 - \epsilon_n)r_C(L)L_n u \leq_D L_n u_n \leq_D (1 + \epsilon_n)r_C(L)L_n u = (1 + \epsilon_n)r_C(L)u_n.$$

In view of [20, Lemma 2.1 and Corollary 2.7], it follows that

$$(1 - \epsilon_n)r_C(L) \leq r_C(L_n) \leq (1 + \epsilon_n)r_C(L), \forall n \geq 1.$$

Letting $n \to \infty$, we then obtain

$$r_C(L) \leq \liminf_{n\to\infty} r_C(L_n) \leq \limsup_{n\to\infty} r_C(L_n) \leq r_C(L),$$

which implies that $\lim_{n\to\infty} r_C(L_n) = r_C(L)$. ∎

Proposition 2.1 *Let E be a Banach space with a solid cone D. Assume that C is a cone with $C \subseteq D$. Let $L : C \to C$ be a bounded, continuous, homogeneous, and D-order-*

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preserving map such that $Lu = r_C(L)u$ *for some* $u \in \mathrm{Int}(D) \cap C$. *If* $r_C(L) = 0$, *then* $Lv = 0$ *for all* $v \in C$.

Proof Let $v \in C$ be given. Since $u \in \mathrm{Int}(D)$ and $v \in C \subseteq D$, there exists $\delta = \delta(v) > 0$ such that $u \geq_D \delta v$. As L is D-order-preserving and homogeneous, we have $Lu \geq_D L(\delta v) = \delta Lv$. It follows from $Lu = r_C(L)u = 0$ that $Lv \leq_D 0$. On the other hand, $Lv \in C \subseteq D$. Hence, $Lv \in D \cap (-D) = \{0\}$, and therefore $Lv = 0$. ∎

As a consequence of [15, Corollary 4.6], we have the following observation.

Lemma 2.2 *Let* E *be a Banach space with a total cone* D, *and* α *be the Kuratowski measure of noncompactness in* E. *Assume that* C *is a cone with* $C \subseteq D$. *Let* $L : C \to C$ *be a bounded, continuous, homogeneous, and* D*-order-preserving map. If* $r_C(L) \geq 1$ *and there exists* $k \in (0,1)$ *such that* $\alpha(LB) \leq k\alpha(B)$ *for any bounded subset* B *of* C, *then* $r_C(L)$ *is an eigenvalue of* L *with an eigenvector in* $C\backslash\{0\}$.

Proof For readers' convenience, we provide the idea how to choose r and μ. In the case of $r_C(L) > 1$, we can choose $r = r_C(L) > 1$ and $\mu = 1$; and in the case of $r_C(L) = 1$, we can choose $r = r_C(L) = 1$ and $\mu \in (k, 1)$. ∎

3 Global stability in a bounded habitat

In this section, we study the global dynamics of system (1.1) in a bounded habitat. In order to establish a threshold-type result, we proceed with three sections.

3.1 A nonlinear eigenvalue problem

We consider the following homogeneous and partially degenerate reaction–diffusion system:

$$
\begin{cases}
\dfrac{\partial u_A}{\partial t} = \rho(x,t)H(u_M,u_F) - d(x,t)u_A - \gamma(x,t)u_A, & x \in \Omega,\ t > 0,\\
\dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x \in \Omega,\ t > 0,\\
\dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x \in \Omega,\ t > 0,\\
\dfrac{\partial u_M(x,t)}{\partial \nu} = 0,\ \dfrac{\partial u_F(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0.
\end{cases}
\tag{3.1}
$$

Let $X = C(\overline{\Omega}, \mathbb{R}^3)$, $P = C(\overline{\Omega}, \mathbb{R}^3_+)$, and $\{U(t,s) : t \geq s\}$ be the T-periodic evolution family on X associated with (3.1). We substitute $u_N(x,t) = e^{-\lambda t}w_N(x,t)$, $N = A, M, F$,

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into (3.1), to obtain the associated nonlinear eigenvalue problem:

(3.2)
$$\begin{cases} \dfrac{\partial w_A}{\partial t} = \rho(x,t)H(w_M,w_F) - d(x,t)w_A - \gamma(x,t)w_A + \lambda w_A, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial w_M}{\partial t} = D\Delta w_M + \theta\gamma(x,t)w_A - \hat{d}(x,t)w_M + \lambda w_M, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial w_F}{\partial t} = D\Delta w_F + (1-\theta)\gamma(x,t)w_A - \hat{d}(x,t)w_F + \lambda w_F, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial w_M(x,t)}{\partial \nu} = 0,\ \frac{\partial w_F(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t\in\mathbb{R},\\ w_N \text{ is } T\text{-periodic in } t,\ N = A,M,F. \end{cases}$$

Define $p(x,t) := -d(x,t) - \gamma(x,t)$, $\forall (x,t)\in\overline{\Omega}\times\mathbb{R}$, $\tilde{p}(x) = T^{-1}\int_0^T p(x,t)\mathrm{d}t$, $\forall x\in\overline{\Omega}$ and $\eta = -\max_{x\in\Omega}\tilde{p}(x)$. By using the arguments similar to those in [9], we have the following observation.

Lemma 3.1 *$\alpha(U(T,0)B) \le e^{-\eta T}\alpha(B)$ for any bounded $B\subseteq P$.*

Motivated by [11, Theorem 2.16 and Lemma 3.3], we are able to prove the following result for the nonlinear eigenvalue problem (3.2).

Lemma 3.2 *$U(T,0)$ admits the principal eigenvalue with an eigenvector $\boldsymbol{\phi}^* = (\phi_A^*,\phi_M^*,\phi_F^*)^T \in \mathrm{Int}(P)$ provided that one of the following two conditions holds true:*

(i) $r_P(U(T,0)) \ge 1$.

(ii) *There exists a nonempty C^2 subdomain $\Omega_0\subseteq\Omega$ such that $\tilde{p}(x) = \max_{x\in\Omega}\tilde{p}(x)$ for all $x\in\Omega_0$,*

Proof (i) In view of Lemma 2.2, $U(T,0)$ admits the principal eigenvalue $r_P(U(T,0))$ corresponding to an eigenvector $\boldsymbol{\phi}^* = (\phi_A^*,\phi_M^*,\phi_F^*)^T \in P\backslash\{0\}$. It suffices to show that $\boldsymbol{\phi}^*\in\mathrm{Int}(P)$. Write $\lambda^* = -\frac{\ln r_P(U(T,0))}{T}\le 0$ and $\boldsymbol{w}^*(x,t) = [e^{\lambda^* t}U(t,0)\boldsymbol{\phi}^*](x)$, $\forall (x,t)\in\overline{\Omega}\times\mathbb{R}$. It is easy to see that $\boldsymbol{w}^* = (w_A^*,w_M^*,w_F^*)^T$ is T-periodic in $t\in\mathbb{R}$.

We first show that $\phi_M^*(x) > 0$, $\forall x\in\overline{\Omega}$. Suppose that $\phi_M^*(x_M) = 0$ for some $x_M\in\overline{\Omega}$. We claim that $w_M^*(x,t) = 0$, $\forall (x,t)\in\overline{\Omega}\times\mathbb{R}$. Otherwise, $w_M^*(x_0,t_0) > 0$ for some $x_0\in\overline{\Omega}$ and $t_0\in[0,T)$, it then follows from $[e^{\lambda^* T}U(T,0)\boldsymbol{\phi}^*](x) = \boldsymbol{\phi}^*(x)$ and the strong maximum principle on the second equation of (3.2) that $\phi_M^*(x) > 0$, $\forall x\in\overline{\Omega}$, which contradicts $\phi_M^*(x_M) = 0$. Thus, $w_M^*(x,t) = 0$, $\forall (x,t)\in\overline{\Omega}\times\mathbb{R}$. Thanks to the second equation of (3.2) again with λ replaced by λ^*, we have $w_A^*(x,t) = 0$, $\forall (x,t)\in\overline{\Omega}\times\mathbb{R}$. This further implies that

$$\begin{cases} \dfrac{\partial w_F^*}{\partial t} = D\Delta w_F^* - \hat{d}(x,t)w_F^* + \lambda^* w_F^*, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial w_F^*}{\partial \nu} = 0, & x\in\partial\Omega,\ t\in\mathbb{R}. \end{cases}$$

Integrating both sides of the above equation over $\Omega\times[0,T]$ and using the T-periodicity in t together with the Neumann boundary condition, we obtain $0 = \int_0^T\int_\Omega(-\hat{d}(x,t)+\lambda^*)w_F^*(x,t)\,\mathrm{d}x\mathrm{d}t$. Since $w_F^*\ge 0$, $\lambda^*\le 0$, and $\hat{d}(x,t) > 0$, it

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follows that $w_F^* \equiv 0$ on $\overline{\Omega} \times \mathbb{R}$, which implies $\boldsymbol{\phi}^* \equiv 0$. This contradicts $\boldsymbol{\phi}^* \in P\backslash\{0\}$. Therefore, $\phi_M^*(x) > 0$ for all $x \in \overline{\Omega}$.

Similarly, we can prove that $\phi_F^*(x) > 0$, $\forall x \in \overline{\Omega}$. It suffices to show that $\phi_A^*(x) > 0$, $\forall x \in \overline{\Omega}$. Suppose that $\phi_A^*(x_A) = 0$ for some $x_A \in \overline{\Omega}$. If $\phi_M^*(x_A)\phi_F^*(x_A) > 0$, then $w_A^*(x_A, t) > 0$, $\forall t > 0$, which contradicts $\phi_A^*(x_A) = w_A^*(x_A, T) = 0$. If $\phi_M^*(x_A)\phi_F^*(x_A) = 0$, then $\phi_M^*(x_A) = 0$ or $\phi_F^*(x_A) = 0$, which is impossible. Therefore, $\phi_A^*(x) > 0$, $\forall x \in \overline{\Omega}$, and hence, $\boldsymbol{\phi}^* = (\phi_A^*, \phi_M^*, \phi_F^*)^T \in \mathrm{Int}(P)$.

(ii) Define

$$C_T(\overline{\Omega} \times \mathbb{R}, \mathbb{R}_+^2) = \{\boldsymbol{w} \in C(\overline{\Omega} \times \mathbb{R}, \mathbb{R}_+^2) : \boldsymbol{w}(x,t) = \boldsymbol{w}(x, t+T),\ \forall (x,t) \in \overline{\Omega} \times \mathbb{R}\}.$$

For any $\lambda < \eta$, define $p_\lambda(x,t) = p(x,t) + \lambda$, $\forall (x,t) \in \overline{\Omega} \times \mathbb{R}$, $\tilde{p}_\lambda = \tilde{p} + \lambda$ and let $R_\lambda[\boldsymbol{w}]$ be the unique nonnegative T-periodic solution of

$$\frac{\partial u_A}{\partial t} = \rho(x,t)H(u_M, u_F) - d(x,t)u_A - \gamma(x,t)u_A + \lambda u_A,\ x \in \overline{\Omega},\ t \in \mathbb{R},$$

where $\boldsymbol{w} = (w_M, w_F)^T \in C_T(\overline{\Omega} \times \mathbb{R}, \mathbb{R}_+^2)$. It is easy to verify that for any $(x,t) \in \overline{\Omega} \times \mathbb{R}$ and $\lambda < \eta$, there holds

$$[R_\lambda \boldsymbol{w}](x,t) = e^{\int_0^t p_\lambda(x,\tau)\mathrm{d}\tau}(u_A)_0 + \int_0^t e^{\int_s^t p_\lambda(x,\tau)\mathrm{d}\tau}\rho(x,s)H(w_M(x,s), w_F(x,s))\mathrm{d}s,$$

where

$$(u_A)_0 = \frac{\int_0^T e^{\int_s^T p_\lambda(x,\tau)\mathrm{d}\tau}\rho(x,s)H(w_M(x,s), w_F(x,s))\mathrm{d}s}{1 - e^{\int_0^T p_\lambda(x,\tau)\mathrm{d}\tau}}.$$

Let $G = C_0^1(\overline{\Omega}_0)$ and $G_+ = \{w \in G : w(x) \geq 0,\ \forall x \in \overline{\Omega}_0\}$. Then (G, G_+) is an ordered Banach space with

$$\mathrm{Int}(G_+) = \{w \in G : w(x) > 0,\ \forall x \in \Omega_0,\ \frac{\partial w}{\partial \nu} < 0,\ \forall x \in \partial\Omega_0\}.$$

We denote by $C_T(\mathbb{R}, G)$ the Banach space of continuous T-periodic functions from $\mathbb{R}$ to G, which is equipped with the maximum norm and the positive cone $C_T(\mathbb{R}, G_+)$. It is easy to see that $\mathrm{Int}(C_T(\mathbb{R}, G_+))$ is nonempty.

Define two linear operators $\mathcal{L}_M$ and $\mathcal{L}_F$ by

$$\mathcal{L}_M u_M = \frac{\partial u_M}{\partial t} - D\Delta u_M + \hat{d}u_M, \quad \mathcal{L}_F u_F = \frac{\partial u_F}{\partial t} - D\Delta u_F + \hat{d}u_F,$$

with their domains $\mathcal{D}(\mathcal{L}_M) = \mathcal{D}(\mathcal{L}_F) \subset C_T(\overline{\Omega}_0 \times \mathbb{R}, \mathbb{R})$ being

$$C_T^{2,1}(\overline{\Omega}_0 \times \mathbb{R}, \mathbb{R}) := \{u \in C^{2,1}(\overline{\Omega}_0 \times \mathbb{R}, \mathbb{R}) : u(x,t) = u(x, t+T),\ \forall (x,t) \in \overline{\Omega}_0 \times \mathbb{R}\}.$$

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For convenience, let $q_M = \theta\gamma$ and $q_F = (1-\theta)\gamma$. Next, we find a suitable $\overline{\lambda} < \eta$ such that

$$\begin{cases} \mathcal{L}_M \tilde{w}_M - q_M R_{\overline{\lambda}} \tilde{\boldsymbol{w}} \le \overline{\lambda} \tilde{w}_M, & x \in \Omega_0,\ t \in \mathbb{R}, \\ \mathcal{L}_F \tilde{w}_F - q_F R_{\overline{\lambda}} \tilde{\boldsymbol{w}} \le \overline{\lambda} \tilde{w}_F, & x \in \Omega_0,\ t \in \mathbb{R}, \\ \tilde{w}_M = 0, \tilde{w}_F = 0, & x \in \partial\Omega_0,\ t \in \mathbb{R}, \\ \tilde{w}_M \text{ and } \tilde{w}_F \text{ are } T\text{-periodic}, \end{cases} \tag{3.3}$$

where $\tilde{\boldsymbol{w}} = (\tilde{w}_M, \tilde{w}_F)^T \in C_T(\overline{\Omega}_0 \times \mathbb{R}, \mathbb{R}^2_+)$.

For $N = M, F$, let λ_N be the principal eigenvalue of

$$\begin{cases} \mathcal{L}_N w = \lambda_N w, & x \in \Omega_0,\ t \in \mathbb{R}, \\ w = 0, & x \in \partial\Omega_0,\ t \in \mathbb{R}, \\ w \text{ is } T\text{-periodic}, \end{cases}$$

with the positive eigenvector $\tilde{w}_N \in \mathrm{Int}(C_T(\mathbb{R}, G_+))$, where $\max_{(x,t)\in\overline{\Omega}_0\times\mathbb{R}} |\tilde{w}_N(x,t)| = 1$. It is easy to verify that there exist $a > 0$ and $b > 0$ such that $a\tilde{w}_M \le \tilde{w}_F \le b\tilde{w}_M$. Hence, there exist $c_M > 0$, $c_F > 0$, $\hat{c}_M > 0$, and $\hat{c}_F > 0$ such that

$$\begin{aligned} &H(\tilde{w}_M(x,t), \tilde{w}_F(x,t)) \ge c_M \tilde{w}_M(x,t), \\ &H(\tilde{w}_M(x,t), \tilde{w}_F(x,t)) \ge c_F \tilde{w}_F(x,t),\ \forall (x,t) \in \overline{\Omega}_0 \times \mathbb{R}, \end{aligned}$$

and

$$\frac{1}{T}\int_0^T \tilde{w}_M(x,s)\mathrm{d}s \ge \hat{c}_M \tilde{w}_M(x,t), \quad \frac{1}{T}\int_0^T \tilde{w}_F(x,s)\mathrm{d}s \ge \hat{c}_F \tilde{w}_F(x,t),\ \forall (x,t) \in \overline{\Omega}_0 \times \mathbb{R}.$$

Choose $\hat{\eta} < \eta$ such that $\lambda_M > \hat{\eta}$ and $\lambda_F > \hat{\eta}$. For any $\lambda \in [\hat{\eta}, \eta)$, there exists $\hat{c}_1 > 0$ independent of λ such that $e^{\int_s^t p_\lambda(x,\tau)\mathrm{d}\tau} > \hat{c}_1$, $\forall s, t \in \mathbb{R}$ with $0 \le s \le t \le T$, $x \in \overline{\Omega}_0$. Moreover, there exist $\hat{c}_2 > 0$, $\tilde{c}_M > 0$, and $\tilde{c}_F > 0$ such that $\rho(x,t) > \hat{c}_2$, $\theta\gamma(x,t) \ge \tilde{c}_M$, $(1-\theta)\gamma(x,t) \ge \tilde{c}_F$, $\forall (x,t) \in \overline{\Omega}_0 \times \mathbb{R}$. An easy computation yields that

$$\begin{aligned} [R_\lambda \tilde{\boldsymbol{w}}](x,t) &\ge \frac{\int_0^T \hat{c}_1^2 \hat{c}_2 c_M \tilde{w}_M(x,s)\mathrm{d}s}{1 - e^{-(\eta-\lambda)T}} \ge \hat{c}_1^2 \hat{c}_2 c_M \frac{\int_0^T \tilde{w}_M(x,s)\mathrm{d}s}{(\eta-\lambda)T} \\ &\ge \frac{\hat{c}_1^2 \hat{c}_2 c_M \hat{c}_M}{\eta - \lambda} \tilde{w}_M(x,t), \quad (x,t) \in \overline{\Omega}_0 \times \mathbb{R},\ \lambda \in [\hat{\eta}, \eta), \end{aligned}$$

and

$$[R_\lambda \tilde{\boldsymbol{w}}](x,t) \ge \frac{\hat{c}_1^2 \hat{c}_2 c_F \hat{c}_F}{\eta - \lambda} \tilde{w}_F(x,t),\ \forall (x,t) \in \overline{\Omega}_0 \times \mathbb{R},\ \lambda \in [\hat{\eta}, \eta).$$

Therefore,

$$q_N R_\lambda \tilde{\boldsymbol{w}} \ge \frac{b_N}{\eta - \lambda} \tilde{w}_N,\ \forall \lambda \in [\hat{\eta}, \eta),$$

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where $b_N = \hat{c}_1^2\hat{c}_2\tilde{c}_N c_N \hat{c}_N$ for $N = M, F$. We set $\tilde{\lambda}_N = \frac{b_N}{\hat{\eta}-\lambda_N} + \eta$ for $N = M, F$, $\overline{\lambda} = \max(\tilde{\lambda}_M, \tilde{\lambda}_F, \hat{\eta})$. It is easy to see that $\overline{\lambda} < \eta$. A straightforward computation gives rise to

$$\begin{aligned}\mathcal{L}_M\tilde{w}_M - q_M R_{\overline{\lambda}}\tilde{\boldsymbol{w}} &\le \lambda_M\tilde{w}_M - \frac{b_M}{\eta-\overline{\lambda}}\tilde{w}_M \le \lambda_M\tilde{w}_M - \frac{b_M}{\eta-\tilde{\lambda}_M}\tilde{w}_M\\ &= \hat{\eta}\tilde{w}_M \le \overline{\lambda}\tilde{w}_M,\ \forall (x,t)\in\Omega_0\times\mathbb{R}.\end{aligned}$$

By similar arguments, we also get

$$\mathcal{L}_F\tilde{w}_F - q_F R_{\overline{\lambda}}\tilde{\boldsymbol{w}} \le \overline{\lambda}\tilde{w}_F,\ \forall (x,t)\in\Omega_0\times\mathbb{R}.$$

Therefore, (3.3) holds true.

Letting $\tilde{w}_A = R_{\overline{\lambda}}\tilde{\boldsymbol{w}}$, we then have

$$\begin{cases}\dfrac{\partial\tilde{w}_A}{\partial t} = \rho(x,t)H(\tilde{w}_M,\tilde{w}_F) - d(x,t)\tilde{w}_A - \gamma(x,t)\tilde{w}_A + \overline{\lambda}\tilde{w}_A, & x\in\Omega_0,\ t\in\mathbb{R},\\ \dfrac{\partial\tilde{w}_M}{\partial t} \le D\Delta\tilde{w}_M + \theta\gamma(x,t)\tilde{w}_A - \hat{d}(x,t)\tilde{w}_M + \overline{\lambda}\tilde{w}_M, & x\in\Omega_0,\ t\in\mathbb{R},\\ \dfrac{\partial\tilde{w}_F}{\partial t} \le D\Delta\tilde{w}_F + (1-\theta)\gamma(x,t)\tilde{w}_A - \hat{d}(x,t)\tilde{w}_F + \overline{\lambda}\tilde{w}_F, & x\in\Omega_0,\ t\in\mathbb{R},\\ \tilde{w}_M = 0,\ \tilde{w}_F = 0, & x\in\partial\Omega_0,\ t\in\mathbb{R},\\ \tilde{w}_N \text{ is } T\text{-periodic in } t,\ N = A, M, F.\end{cases}$$

For $N = A, M, F$, define

$$\tilde{\phi}_N(x) = \begin{cases}\tilde{w}_N(x,0), & x\in\overline{\Omega}_0,\\ 0, & x\in\overline{\Omega}\backslash\overline{\Omega}_0.\end{cases}\quad\text{and } \tilde{\boldsymbol{\phi}} = (\tilde{\phi}_A,\tilde{\phi}_M,\tilde{\phi}_F)^T.$$

We then obtain that $e^{\overline{\lambda}T}U(T,0)\tilde{\boldsymbol{\phi}} \ge \tilde{\boldsymbol{\phi}}$. Choose $\sigma\in(0,\eta-\overline{\lambda})$ small enough. It follows from [20, Lemma 2.1] that $r_P(e^{\overline{\lambda}T}U(T,0)) \ge 1$, and hence, $r_P(e^{(\eta-\sigma)T}U(T,0)) > r_P(e^{\overline{\lambda}T}U(T,0)) \ge 1$. With Lemma 3.1, we have $\alpha(e^{(\eta-\sigma)T}U(T,0)B) \le e^{-\sigma T}\alpha(B)$ for any bounded set $B\subseteq P$. It then follows from Lemma 2.2 that $e^{(\eta-\sigma)T}U(T,0)$, and hence, $U(T,0)$ admits the principal eigenvalue with an eigenvector $\phi^*\in P\backslash\{0\}$.

For $N = M, F$, let $\hat{\lambda}_N$ be the principal eigenvalue of

$$\begin{cases}\mathcal{L}_N w = \hat{\lambda}_N w, & x\in\Omega,\ t\in\mathbb{R},\\ \frac{\partial w}{\partial\nu} = 0, & x\in\partial\Omega,\ t\in\mathbb{R},\\ w \text{ is } T\text{-periodic},\end{cases}$$

with the positive eigenvector $\hat{w}_N\in\mathrm{Int}(C_T(\overline{\Omega}\times\mathbb{R},\mathbb{R}_+))$ satisfying $\max_{(x,t)\in\overline{\Omega}\times\mathbb{R}}|\hat{w}_N(x,t)| = 1$. Note that $\lambda^* = -\frac{\ln r_P(U(T,0))}{T} \le \min(\eta,\hat{\lambda}_M,\hat{\lambda}_F)$. Since $r_P(e^{(\eta-\sigma)T}U(T,0)) > 1$, we have $\lambda^* < \eta-\sigma$. In view of $\lambda_0 := \hat{\lambda}_M = \hat{\lambda}_F$, choosing

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$\hat{w}_A = 0$, we then have

$$\begin{cases} \dfrac{\partial \hat{w}_A}{\partial t} \le \rho(x,t)H(\hat{w}_M,\hat{w}_F) - d(x,t)\hat{w}_A - \gamma(x,t)\hat{w}_A + \lambda_0\hat{w}_A, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial \hat{w}_M}{\partial t} = D\Delta\hat{w}_M + \theta\gamma(x,t)\hat{w}_A - \hat{d}(x,t)\hat{w}_M + \lambda_0\hat{w}_M, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial \hat{w}_F}{\partial t} = D\Delta\hat{w}_F + (1-\theta)\gamma(x,t)\hat{w}_A - \hat{d}(x,t)\hat{w}_F + \lambda_0\hat{w}_F, & x\in\Omega,\ t\in\mathbb{R},\\ \dfrac{\partial \hat{w}_M(x,t)}{\partial \nu} = 0,\ \frac{\partial \hat{w}_F(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t\in\mathbb{R},\\ \hat{w}_N \text{ is } T\text{-periodic in } t,\ N = A,M,F. \end{cases}$$

Define

$$\hat{\psi}_A(x) = 0,\ \hat{\psi}_M(x) = \hat{w}_M(x,0),\ \hat{\psi}_F(x) = \hat{w}_F(x,0),\ \text{and } \hat{\boldsymbol{\psi}} = (\hat{\psi}_A,\hat{\psi}_M,\hat{\psi}_F)^T.$$

By the comparison arguments, it is not hard to verify that $e^{\lambda_0 T}U(T,0)\hat{\boldsymbol{\psi}} \gg \hat{\boldsymbol{\psi}}$. Using [20, Lemma 2.1] again, we have $r_P(e^{\lambda_0 T}U(T,0)) > 1$, which implies that $\lambda^* < \lambda_0$. Therefore, $\lambda^* < \min(\eta, \hat{\lambda}_M, \hat{\lambda}_F)$. Now one can easily obtain $\boldsymbol{\phi}^* \in \mathrm{Int}(P)$ by using the arguments similar to those in case (i). ∎

Remark 3.1 If we replace the bounded domain Ω and the Neumann boundary condition in the eigenvalue problem (3.2) with the region $\mathbb{R}$ and the periodic boundary condition, respectively, then Lemma 3.2 is still valid.

3.2 Basic reproduction ratio

In this section, we introduce and characterize the basic reproduction ratio $\mathcal{R}_0$ for system (1.1), and then quantitatively analyze the effects of parameters on $\mathcal{R}_0$.

Following the notations and procedure in [20, Section 3], we choose

$$X = C(\overline{\Omega},\mathbb{R}^3),\ P = K = \tilde{P} = C(\overline{\Omega},\mathbb{R}^3_+),\ \mathbb{X} = C_T(\mathbb{R},X),\ \mathbb{P} = \mathbb{K} = \tilde{\mathbb{P}} = C_T(\mathbb{R},P),$$

where $C_T(\mathbb{R},X)$ is the Banach space of all T-periodic and continuous functions from $\mathbb{R}$ to X. Let $\{\Phi(t,s),\ t\ge s\}$ be the evolution family on X associated with the following linear system:

$$\begin{cases} \dfrac{\partial u_A}{\partial t} = -d(x,t)u_A - \gamma(x,t)u_A, & x\in\Omega,\ t>0,\\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x\in\Omega,\ t>0,\\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x\in\Omega,\ t>0,\\ \dfrac{\partial u_M(x,t)}{\partial \nu} = 0,\ \frac{\partial u_F(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0. \end{cases}$$

It is easy to verify that $\omega(\Phi) < 0$. For each $t\in\mathbb{R}$, we define $F(t): P\to P$ by

$$F(t)\begin{pmatrix} w_A\\ w_M\\ w_F\end{pmatrix} = \begin{pmatrix} \rho(\cdot,t)H(w_M,w_F)\\ 0\\ 0\end{pmatrix},$$

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where $(w_A, w_M, w_F)^T \in P$. Thus, the operator $\mathcal{L}$ on $\mathbb{P}$ is defined by

$$[\mathcal{L}\boldsymbol{v}](t) = \int_0^{+\infty} \Phi(t, t-s)F(t-s)\boldsymbol{v}(t-s)\mathrm{d}s, \ \forall\ t \in \mathbb{R}, \ \boldsymbol{v} \in \mathbb{P},$$

and the basic reproduction ratio of mosquitoes is given by

$$\mathcal{R}_0 = r_{\mathbb{P}}(\mathcal{L}).$$

For any $\mu > 0$, let $\{U(t,s;\mu)\}$ be the evolution family on X of the following system:

$$\begin{cases} \dfrac{\partial w_A}{\partial t} = \mu\rho(x,t)H(w_M, w_F) - d(x,t)w_A - \gamma(x,t)w_A, & x \in \Omega,\ t > 0, \\ \dfrac{\partial w_M}{\partial t} = D\Delta w_M + \theta\gamma(x,t)w_A - \hat{d}(x,t)w_M, & x \in \Omega,\ t > 0, \\ \dfrac{\partial w_F}{\partial t} = D\Delta w_F + (1-\theta)\gamma(x,t)w_A - \hat{d}(x,t)w_F, & x \in \Omega,\ t > 0, \\ \dfrac{\partial w_M(x,t)}{\partial \nu} = 0, \ \frac{\partial w_F(x,t)}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0. \end{cases}$$

Proposition 3.1 *$\mathcal{R}_0 - 1$ and $r_P(U(T,0)) - 1$ have the same sign. Moreover, $\mathcal{R}_0^{-1}$ is the unique solution of $r_P(U(T,0;\mu)) = 1$.*

Proof It is easy to see that (H1)–(H4) in [20, Section 3] hold true. Thanks to Lemma 3.2, if there exists a domain $\Omega_0 \subseteq \Omega$ such that $\tilde{p}(x) = -\eta$ for all $x \in \Omega_0$, then (H5) in [20, Section 3] is true. Thus, the desired conclusion follows from Lemma 2.1 and [20, Theorem 3.4].

To prove the conclusion in the general case, we first take a series of functions d_ϵ and domains $\Omega_\epsilon \subseteq \Omega$ such that $d_\epsilon \le d \le d_\epsilon + \epsilon$ and $\tilde{p}^\epsilon(x) = \max_{x\in\Omega} \tilde{p}^\epsilon(x)$, $\forall x \in \overline{\Omega}_\epsilon$, where $\tilde{p}^\epsilon(x) = T^{-1}\int_0^T [-d_\epsilon(x,t) - \gamma(x,t)]\mathrm{d}t$, $\forall x \in \overline{\Omega}$.

We can define $\mathcal{R}_0^\epsilon$ and $\{U^\epsilon(t,s) : t \ge s\}$ (resp. $\mathcal{R}_{0,\epsilon}$ and $\{U_\epsilon(t,s) : t \ge s\}$) in the same way as $\mathcal{R}_0$ and $\{U(t,s) : t \ge s\}$ with d replaced by d_ϵ (resp. $d_\epsilon + \epsilon$). It is easy to see that $\mathcal{R}_{0,\epsilon} \le \mathcal{R}_0 \le \mathcal{R}_0^\epsilon$ and $r_P(U_\epsilon(T,0)) \le r_P(U(T,0)) \le r_P(U^\epsilon(T,0)) \le r_P(U_\epsilon(T,0))e^{\epsilon T}$. Moreover, $\mathcal{R}_{0,\epsilon} - 1$ and $r_P(U_\epsilon(T,0)) - 1$ have the same sign, and $\mathcal{R}_0^\epsilon - 1$ and $r_P(U^\epsilon(T,0)) - 1$ share the same sign.

If $r_P(U(T,0)) = 1$, then $\mathcal{R}_0 = 1$ by [20, Lemma 3.2(i)]. If $r_P(U(T,0)) > 1$, one can choose $\epsilon > 0$ small enough such that $r_P(U(T,0))e^{-\epsilon T} > 1$. We then have $r_P(U_\epsilon(T,0)) \ge r_P(U(T,0))e^{-\epsilon T} > 1$, and hence, $\mathcal{R}_0 \ge \mathcal{R}_{0,\epsilon} > 1$. By the similar arguments, we can also prove that $\mathcal{R}_0 < 1$ whenever $r_P(U(T,0)) < 1$.

Repeating the above arguments, we see that $\mu\mathcal{R}_0 - 1$ and $r_P(U(T,0;\mu)) - 1$ have the same sign for all $\mu > 0$. By the comparison arguments, it is not hard to prove that $\mathcal{R}_0 \ge \theta(1-\theta)\underline{\rho}\underline{\gamma}[\overline{d}(\overline{d} + \overline{\gamma})]^{-1} > 0$, where $\underline{\rho} = \min_{(x,t)\in\overline{\Omega}\times\mathbb{R}} \rho(x,t)$, $\underline{\gamma} = \min_{(x,t)\in\overline{\Omega}\times\mathbb{R}} \gamma(x,t)$, $\overline{\gamma} = \max_{(x,t)\in\overline{\Omega}\times\mathbb{R}} \gamma(x,t)$, and $\overline{d} = \max_{(x,t)\in\overline{\Omega}\times\mathbb{R}} \max(d(x,t), \hat{d}(x,t))$. Therefore, $\mathcal{R}_0^{-1}$ is the unique solution of $r_P(U(T,0;\mu)) = 1$. ∎

Theorem 3.1 *The following statements are valid:*

(i) *$\frac{\mathcal{R}_0}{\theta(1-\theta)}$ is independent of θ. In particular, $\mathcal{R}_0$ is increasing with respect to $\theta \in (0, \frac{1}{2}]$ and decreasing with respect to $\theta \in [\frac{1}{2}, 1)$, and goes to 0 as $\theta \to 0^+$ or $\theta \to 1^-$.*

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(ii) *If, in addition, all parameters are independent of t, then* $\mathcal{R}_0$ *is decreasing with respect to D. Moreover,* $\mathcal{R}_0 \to \theta(1-\theta)\max_{x\in\overline{\Omega}} \frac{\rho(x)\gamma(x)}{(d(x)+\gamma(x))\hat{d}(x)}$ *as* $D \to 0^+$ *and* $\mathcal{R}_0 \to \theta(1-\theta)\frac{\int_\Omega \frac{\rho(x)\gamma(x)}{d(x)+\gamma(x)}\mathrm{d}x}{\int_\Omega \hat{d}(x)\mathrm{d}x}$ *as* $D \to +\infty$.

Proof (i) It suffices to prove that $\mathcal{R}_0^{-1}$ is an eigenvalue of the weighted eigenvalue problem

$$
\begin{cases}
\dfrac{\partial w_A}{\partial t} = \lambda\rho(x,t)\theta(1-\theta)w_S - d(x,t)w_A - \gamma(x,t)w_A, & x\in\Omega,\ t\in\mathbb{R},\\
\dfrac{\partial w_S}{\partial t} = D\Delta w_S + \gamma(x,t)w_A - \hat{d}(x,t)w_S, & x\in\Omega,\ t\in\mathbb{R},\\
\dfrac{\partial w_S(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t\in\mathbb{R},\\
w_A \text{ and } w_S \text{ are } T\text{-periodic in } t,
\end{cases}
\tag{3.4}
$$

with a strongly positive eigenvector. With Proposition 3.1, we have $r_P(U(T,0;\mathcal{R}_0^{-1})) = 1$. Thanks to Lemma 3.2, there exists a strongly positive eigenvector $(w_A^*, w_M^*, w_F^*)^T$ such that

$$
\begin{cases}
\dfrac{\partial w_A^*}{\partial t} = \mathcal{R}_0^{-1}\rho(x,t)H(w_M^*, w_F^*) - d(x,t)w_A^* - \gamma(x,t)w_A^*, & x\in\Omega,\ t>0,\\
\dfrac{\partial w_M^*}{\partial t} = D\Delta w_M^* + \theta\gamma(x,t)w_A^* - \hat{d}(x,t)w_M^*, & x\in\Omega,\ t>0,\\
\dfrac{\partial w_F^*}{\partial t} = D\Delta w_F^* + (1-\theta)\gamma(x,t)w_A^* - \hat{d}(x,t)w_F^*, & x\in\Omega,\ t>0,\\
\frac{\partial w_M^*(x,t)}{\partial \nu} = 0,\ \frac{\partial w_F^*(x,t)}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0,\\
w_N^* \text{ is } T\text{-periodic in } t,\ N = A, M, F.
\end{cases}
\tag{3.5}
$$

Multiplying the second and third equations by $1-\theta$ and θ, respectively, and then making difference, we obtain

$$
\begin{cases}
\dfrac{\partial z}{\partial t} = D\Delta z - \hat{d}(x,t)z, & x\in\Omega,\ t>0,\\
\dfrac{\partial z(x,t)}{\partial \nu} = 0 & x\in\partial\Omega,\ t>0,\\
z \text{ is } T\text{-periodic in } t,
\end{cases}
$$

where $z = (1-\theta)w_M^* - \theta w_F^*$. It is easy to verify that $z \equiv 0$ due to the Krein–Rutman theorem. Let $w_S^* = \theta^{-1}w_M^* = (1-\theta)^{-1}w_F^*$. Then (3.4) holds with $\mu = \mathcal{R}_0^{-1}$, $w_A = w_A^*$, and $w_S = w_S^*$.

(ii) If all parameters are independent of t, then so are w_A^* and w_S^*. By the first equation of (3.4), it then follows that

$$
w_A^* = \mathcal{R}_0^{-1}\theta(1-\theta)\frac{\rho(x)}{d(x)+\gamma(x)}w_S^*,
$$

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which yields that $\mathcal{R}_0^{-1}$ is an eigenvalue of the weighted eigenvalue problem

$$\begin{cases} D\Delta\hat{w} + \lambda\theta(1-\theta)\frac{\rho(x)\gamma(x)}{d(x)+\gamma(x)}\hat{w} - \hat{d}(x)\hat{w} = 0, & x \in \Omega, \\ \dfrac{\partial \hat{w}(x)}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases}$$

Now the desired conclusion follows from the same arguments as in [1, Lemma 2.3]. ■

3.3 Threshold dynamics

In this section, we establish the threshold dynamics for system (1.1) in terms of the basic reproduction ratio $\mathcal{R}_0$. For this purpose, we choose the feasible domain of system (1.1) as

$$\Sigma(t) := \{\boldsymbol{\phi} := (\phi_A, \phi_M, \phi_F) \in C(\bar{\Omega}, \mathbb{R}^3_+) : 0 \le \phi_A(x) \le K(x,t),\ \forall\ x \in \bar{\Omega}\}.$$

To guarantee the positive invariance of $\Sigma(t)$ for system (1.1), we further assume that

(A) $\frac{\partial K(x,t)}{\partial t} \ge -(d(x,t)+\gamma(x,t))K(x,t)$ for all $x \in \overline{\Omega}$, $t > 0$.

Note that assumption (A) holds true automatically in the autonomous case. For convenience, we also let

$$\tilde{\Sigma} := \{\boldsymbol{\phi} := (\phi_A, \phi_M, \phi_F) \in \Sigma(0) : \phi_A(\cdot) \not\equiv 0 \text{ or } \phi_M(\cdot)\phi_F(\cdot) \not\equiv 0\}.$$

Then we have the following threshold-type result on the global dynamics of system (1.1).

Theorem 3.2 *Let $\boldsymbol{u}(x,t;\boldsymbol{\phi})$ be the unique solution of system (1.1) with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi} \in \Sigma(0)$. Then the following statements are valid:*

(i) *If $\mathcal{R}_0 \le 1$, then $\lim_{t\to+\infty} \|\boldsymbol{u}(\cdot,t;\boldsymbol{\phi})\|_{C(\overline{\Omega},\mathbb{R}^3)} = 0$ for all $\boldsymbol{\phi} \in \Sigma(0)$.*

(ii) *If $\mathcal{R}_0 > 1$, then system (1.1) admits a unique positive T-periodic solution $\boldsymbol{u}^*(x,t)$, and $\lim_{t\to+\infty} \|\boldsymbol{u}(\cdot,t;\boldsymbol{\phi}) - \boldsymbol{u}^*(\cdot,t)\|_{C(\overline{\Omega},\mathbb{R}^3)} = 0$ for all $\boldsymbol{\phi} \in \tilde{\Sigma}$.*

Proof By [16, Corollary 4] and assumption (A), it follows that for every initial value function $\boldsymbol{\phi} := (\phi_A, \phi_M, \phi_F)^T \in \Sigma(0)$, system (1.1) admits a unique non-continuable solution $\boldsymbol{u}(\cdot,t;\boldsymbol{\phi}) := (u_A, u_M, u_F)^T(\cdot,t;\boldsymbol{\phi})$ on its maximal interval of existence $[0, t_{\boldsymbol{\phi}})$ with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi}$, where $t_{\boldsymbol{\phi}} \le \infty$, and $\boldsymbol{u}(\cdot,t;\boldsymbol{\phi}) \in \Sigma(t)$ for all $t \in [0, t_{\boldsymbol{\phi}})$. Thus, $0 \le u_A(x,t;\boldsymbol{\phi}) \le K(x,t)$, $\forall\ x \in \bar{\Omega}$, $t \ge 0$. Then we can use standard comparison arguments to further show that solutions of system (1.1) are ultimately bounded and uniformly bounded. Hence, we can define the solution maps $S(t) : \Sigma(0) \to \Sigma(t)$ associated with system (1.1) by

$$S(t)\boldsymbol{\phi} = \boldsymbol{u}(\cdot,t;\boldsymbol{\phi}),\ \forall\ \boldsymbol{\phi} \in \Sigma(0),$$

where $\boldsymbol{u}(x,t;\boldsymbol{\phi})$ is the unique solution of system (1.1) with $\boldsymbol{u}(x,0;\boldsymbol{\phi}) = \boldsymbol{\phi}(x)$, $\forall\ x \in \bar{\Omega}$. Let $S := S(T) : \Sigma(0) \to \Sigma(0)$ be the Poincaré map associated with system (1.1) on $\Sigma(0)$. By the theory of periodic semiflows (see [22]), it suffices to prove a threshold-type result on the global dynamics for S on $\Sigma(0)$ in terms of $\mathcal{R}_0$. By using the arguments similar to those in [9], we see that S is α-contracting in the sense that $\lim_{n\to\infty} \alpha(S^n(B)) = 0$ for any bounded set $B \subset \Sigma(0)$. It follows from [14, Theorem

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2.6] that S admits a strong global attractor that attracts each bounded set in $\Sigma(0)$. By the essentially same arguments as those for [3, Theorem 3.1], we can easily show that the desired statements are valid in the case where $\mathcal{R}_0 < 1$ or $\mathcal{R}_0 > 1$.

It remains to consider the critical case where $\mathcal{R}_0 = 1$. In view of Proposition 3.1, we have $r_P(U(T,0)) = 1$. It follows from Lemma 3.2 that 0 is the principal eigenvalue of system (3.2), which corresponds to an eigenvector $\boldsymbol{\psi} = (\psi_A, \psi_M, \psi_F)^T \in \mathrm{Int}(P)$. Motivated by [5, 10], we define

$$c(t;\boldsymbol{\phi}) := \max\left\{\max_{x\in\bar{\Omega}} \frac{u_A(x,t;\boldsymbol{\phi})}{\psi_A(x,t)}, \max_{x\in\bar{\Omega}} \frac{u_M(x,t;\boldsymbol{\phi})}{\psi_M(x,t)}, \max_{x\in\bar{\Omega}} \frac{u_F(x,t;\boldsymbol{\phi})}{\psi_F(x,t)}\right\},\ t \geq 0.$$

Then we have the following observation.

Claim. $c(nT;\boldsymbol{\phi})$ is non-increasing in n, and $c(nT;\boldsymbol{\phi})$ is not a constant sequence whenever $\boldsymbol{\phi} \in \tilde{\Sigma}$.

Indeed, since $\phi_A(\cdot) \leq K(\cdot,0)$, we have $u_A(\cdot,t,\boldsymbol{\phi}) \leq K(\cdot,t)$ for all $t \geq 0$. Fix $n_0 > 0$, we let

$$\begin{cases} \tilde{u}_A(x,t;\boldsymbol{\phi}) := c(n_0T;\boldsymbol{\phi})\psi_A(x,t),\ x \in \bar{\Omega},\ t \geq n_0T, \\ \tilde{u}_M(x,t;\boldsymbol{\phi}) := c(n_0T;\boldsymbol{\phi})\psi_M(x,t),\ x \in \bar{\Omega},\ t \geq n_0T, \\ \tilde{u}_F(x,t;\boldsymbol{\phi}) := c(n_0T;\boldsymbol{\phi})\psi_F(x,t),\ x \in \bar{\Omega},\ t \geq n_0T. \end{cases}$$

Then $(\tilde{u}_A(x,t;\boldsymbol{\phi}), \tilde{u}_M(x,t;\boldsymbol{\phi}), \tilde{u}_F(x,t;\boldsymbol{\phi}))$ satisfies (3.2) with $\lambda = 0$. Since $(u_A, u_M, u_F)(x,t;\boldsymbol{\phi})$ satisfies system (1.1), it follows that

$$\begin{cases} \dfrac{\partial u_A}{\partial t} \leq \rho(x,t)H(u_M,u_F) - d(x,t)u_A - \gamma(x,t)u_A, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_M(x,t,\boldsymbol{\phi})}{\partial \nu} = 0, \dfrac{\partial u_F(x,t,\boldsymbol{\phi})}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{3.6}$$

and

$$\begin{cases} u_A(x,n_0T;\boldsymbol{\phi}) \leq \tilde{u}_A(x,n_0T;\boldsymbol{\phi}), & x \in \overline{\Omega}, \\ u_M(x,n_0T;\boldsymbol{\phi}) \leq \tilde{u}_M(x,n_0T;\boldsymbol{\phi}), & x \in \overline{\Omega}, \\ u_F(x,n_0T;\boldsymbol{\phi}) \leq \tilde{u}_F(x,n_0T;\boldsymbol{\phi}), & x \in \overline{\Omega}. \end{cases}$$

By the comparison principle, we have

$$(u_A(\cdot,t;\boldsymbol{\phi}), u_M(\cdot,t;\boldsymbol{\phi}), u_F(\cdot,t;\boldsymbol{\phi})) \leq (\tilde{u}_A(\cdot,t;\boldsymbol{\phi}), \tilde{u}_M(\cdot,t;\boldsymbol{\phi}), \tilde{u}_F(\cdot,t;\boldsymbol{\phi})),\ \forall\ t \geq n_0T.$$

This implies that

$$c(nT;\boldsymbol{\phi}) \leq c(n_0T;\boldsymbol{\phi}),\ \forall\ n \geq n_0.$$

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Moreover, $c(nT;\boldsymbol{\phi})$ is non-increasing in n. In addition, if $\boldsymbol{\phi} := (\phi_A, \phi_M, \phi_F) \in \tilde{\Sigma}$, then one can show that

$$(u_A(x,t;\boldsymbol{\phi}), u_M(x,t;\boldsymbol{\phi}), u_F(x,t;\boldsymbol{\phi})) \gg (0,0,0),\ \forall x \in \bar{\Omega},\ t>0,$$

and hence,

$$1 - \frac{u_A(x,t;\boldsymbol{\phi})}{K(x,t)} < 1,\ \forall\, x \in \bar{\Omega},\ t>0,$$

which implies that the first inequality in (3.6) must be strict. Thus, the strong comparison principle ensures

$$(u_A(\cdot,t;\boldsymbol{\phi}), u_M(\cdot,t;\boldsymbol{\phi}), u_F(\cdot,t;\boldsymbol{\phi})) \ll (\bar{u}_A(\cdot,t;\boldsymbol{\phi}), \bar{u}_M(\cdot,t;\boldsymbol{\phi}), \bar{u}_F(\cdot,t;\boldsymbol{\phi})),\ \forall\ t > n_0 T.$$

It then follows that $c(nT;\boldsymbol{\phi}) < c(n_0 T;\boldsymbol{\phi})$ whenever $n > n_0$, and hence, $c(nT;\boldsymbol{\phi})$ is not a constant sequence whenever $\boldsymbol{\phi} \in \tilde{\Sigma}$.

Now we show that $\lim_{n\to\infty} S^n\boldsymbol{\phi} = 0$ for all $\boldsymbol{\phi} \in \tilde{\Sigma}$. Clearly, $\lim_{n\to\infty} c(nT;\boldsymbol{\phi}) = c_0 \geq 0$. Let $\omega(\boldsymbol{\phi})$ be the omega limit set of the forward orbit through $\boldsymbol{\phi}$ for S. For any given $\boldsymbol{\varphi} \in \omega(\boldsymbol{\phi})$, there is a sequence $n_k \to \infty$ such that $\lim_{k\to\infty} S^{n_k}\boldsymbol{\phi} = \boldsymbol{\varphi}$. It then follows that

$$\lim_{k\to\infty} S^{m+n_k}\boldsymbol{\phi} = \lim_{k\to\infty} S^m S^{n_k}\boldsymbol{\phi} = S^m\boldsymbol{\varphi},\ \forall m \geq 0.$$

By the definition of $c(t;\boldsymbol{\varphi})$, we have

$$c(mT;\boldsymbol{\varphi}) = \lim_{k\to\infty} c((m+n_k)T;\boldsymbol{\phi}) = c_0,\ \forall m \geq 0.$$

It then follows from the above claim that $\boldsymbol{\varphi} = (0,0,0)$, and hence, $\omega(\boldsymbol{\phi}) = \{(0,0,0)\}$. The desired conclusion can be derived easily for all $\boldsymbol{\phi} \in \Sigma(0)\backslash\tilde{\Sigma}$. ∎

Remark 3.2 In view of [21, Lemma 2.1], it turns out that the zero solution is globally asymptotically stable for system (1.1) in $\Sigma(0)$ if $\mathcal{R}_0 \leq 1$, and the positive periodic solution $u^*(x,t)$ is globally asymptotically stable for system (1.1) in $\tilde{\Sigma}$ if $\mathcal{R}_0 > 1$.

4 Propagation in a periodic habitat

In this section, we investigate the spreading properties and time–space periodic traveling waves for system (1.2) in a spatially periodic habitat. Throughout this section, we always assume that the function $K(x,t)$ satisfies condition (A) as stated in Section 3.3.

4.1 The periodic initial value problem

We first consider the following reaction–diffusion system with periodic initial value:

(4.1)
$$\begin{cases} \dfrac{\partial u_A}{\partial t} = \rho(x,t)H(u_M,u_F)\left(1-\frac{u_A}{K(x,t)}\right) - d(x,t)u_A - \gamma(x,t)u_A, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x\in\mathbb{R},\ t>0,\\ (u_A(\cdot,0),u_M(\cdot,0),u_F(\cdot,0)) \in \mathcal{X}_+, \end{cases}$$

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where $\mathcal{X} = PC(\mathbb{R}, \mathbb{R}^3)$ represents the set of all continuous and L-periodic functions from $\mathbb{R}$ to $\mathbb{R}^3$ with the maximum norm $\|\cdot\|_{\mathcal{X}}$, and $\mathcal{X}_+ = \{\psi \in \mathcal{X} : \psi(x) \geq 0, \forall x \in \mathbb{R}\}$ is a positive cone of $\mathcal{X}$. Clearly, $(\mathcal{X}, \mathcal{X}_+)$ is a strongly ordered Banach space.

Let $\{\mathcal{U}(t,s) : t \geq s\}$ be the evolution family associated with homogeneous system on $\mathcal{X}$:

$$\begin{cases} \dfrac{\partial u_A}{\partial t} = \rho(x,t)H(u_M, u_F) - d(x,t)u_A - \gamma(x,t)u_A, & x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial u_M}{\partial t} = D\Delta u_M + \theta\gamma(x,t)u_A - \hat{d}(x,t)u_M, & x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial u_F}{\partial t} = D\Delta u_F + (1-\theta)\gamma(x,t)u_A - \hat{d}(x,t)u_F, & x \in \mathbb{R},\ t > 0, \end{cases} \tag{4.2}$$

that is, $\mathcal{U}(t,0)\boldsymbol{\phi} = \boldsymbol{u}(\cdot, t; \boldsymbol{\phi})$, where $\boldsymbol{u}(x,t;\boldsymbol{\phi}) := (u_A(x,t;\boldsymbol{\phi}), u_M(x,t;\boldsymbol{\phi}), u_F(x,t;\boldsymbol{\phi}))$ is the unique solution of system (4.2) with $\boldsymbol{u}(\cdot, 0; \boldsymbol{\phi}) = \boldsymbol{\phi} \in \mathcal{X}$.

According to [20, Section 3], we choose

$$X = \mathcal{X},\ P = K = \tilde{P} = \mathcal{X}_+,\ \mathbb{X} = C_T(\mathbb{R}, \mathcal{X}),\ \mathbb{P} = \mathbb{K} = \tilde{\mathbb{P}} = C_T(\mathbb{R}, \mathcal{X}_+),$$

where $C_T(\mathbb{R}, \mathcal{X})$ is the Banach space of all T-periodic and continuous functions from $\mathbb{R}$ to $\mathcal{X}$. Then we can use the arguments similar to those in Section 3.2 to define the basic reproduction ratio $\mathcal{R}_0$ and obtain the following result.

Lemma 4.1 *$\mathcal{R}_0 - 1$ and $r_{\mathcal{X}_+}(\mathcal{U}(T,0)) - 1$ have the same sign.*

Note that the feasible domain of system (1.2) takes the form

$$\Upsilon(t) := \{\boldsymbol{\varphi} := (\varphi_A, \varphi_M, \varphi_F) \in \mathcal{X}_+ : 0 \leq \varphi_A(x) \leq K(x,t),\ \forall\, x \in \mathbb{R}\},\ t \geq 0.$$

For convenience, we also let

$$\tilde{\Upsilon} := \{\boldsymbol{\varphi} := (\varphi_A, \varphi_M, \varphi_F) \in \Upsilon(0) : \varphi_A(\cdot) \not\equiv 0 \text{ or } \varphi_F(\cdot)\varphi_M(\cdot) \not\equiv 0\}.$$

By the arguments similar to those for Theorem 3.2, we have the following threshold-type result on the global dynamics of system (4.1).

Lemma 4.2 *Let $\boldsymbol{u}(x,t;\boldsymbol{\varphi})$ be the unique solution of system (4.1) with $\boldsymbol{u}(\cdot,0;\boldsymbol{\varphi}) = \boldsymbol{\varphi} \in \Upsilon(0)$. Then the following statements are valid:*

(i) *If $\mathcal{R}_0 \leq 1$, then $\lim_{t\to+\infty} \|\boldsymbol{u}(\cdot,t;\boldsymbol{\varphi})\|_{\mathcal{X}} = 0$ for all $\boldsymbol{\varphi} \in \Upsilon(0)$.*

(ii) *If $\mathcal{R}_0 > 1$, then system (4.1) admits a unique positive time–space periodic solution $\boldsymbol{u}^*(x,t)$ with $\boldsymbol{u}_A^*(x,t) \leq K(x,t)$ for all $(x,t) \in \mathbb{R}^2$, and $\lim_{t\to+\infty} \|\boldsymbol{u}(\cdot,t;\boldsymbol{\varphi}) - \boldsymbol{u}^*(\cdot,t)\|_{\mathcal{X}} = 0$ for all $\boldsymbol{\varphi} \in \tilde{\Upsilon}$.*

4.2 Spreading speeds and traveling waves

In this section, we first establish the well-posedness of system (1.2), and then investigate the spreading speeds and traveling waves of system (1.2) in the case where $\mathcal{R}_0 > 1$.

Let $\mathcal{C}$ be the space of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^3$. It is easy to see that $\mathcal{C}^+ := \{\boldsymbol{u} \in \mathcal{C} : \boldsymbol{u}(x) \geq \boldsymbol{0},\ \forall x \in \mathbb{R}\}$ is a positive cone of $\mathcal{C}$. For $\boldsymbol{u} := (u_1, u_2, u_3)$ and $\boldsymbol{v} := (v_1, v_2, v_3) \in \mathcal{C}$, we write $\boldsymbol{u} \geq \boldsymbol{v}$ provided that $u_i(x) \geq v_i(x)$, $\forall\, i = 1,2,3, x \in \mathbb{R}$, and $\boldsymbol{u} > \boldsymbol{v}$ if $\boldsymbol{u} \geq \boldsymbol{v}$ and $\boldsymbol{u} \neq \boldsymbol{v}$. We equip $\mathcal{C}$ with the compact open topology, that is,

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$\boldsymbol{u}^m \to \boldsymbol{u}$ in $\mathcal{C}$ means that the sequence of $\boldsymbol{u}^m(x)$ converges to $\boldsymbol{u}(x)$ as $m \to \infty$ uniformly for x in any compact set of $\mathbb{R}$. Define

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

where $|\cdot|$ denotes the usual norm in $\mathbb{R}^3$. Then $(\mathcal{C}, \|\cdot\|)$ is a normed space. For $\boldsymbol{r} \in \mathcal{C}^+$, we define $\mathcal{C}_{\boldsymbol{r}} := \{\boldsymbol{u} \in \mathcal{C} : \boldsymbol{0} \le \boldsymbol{u} \le \boldsymbol{r}\}$. Besides, we let

$$\|\boldsymbol{u}\|_\infty = \sup_{x\in\mathbb{R}} \mid \boldsymbol{u}(x) \mid, \ \forall\ \boldsymbol{u} \in \mathcal{C},$$

where $|\cdot|$ denotes the usual norm in $\mathbb{R}^3$.

Assume that $\mathcal{R}_0 > 1$. In view of Lemma 4.2, there exist two periodic solutions $\boldsymbol{0} := (0,0,0)$ and $\boldsymbol{u}^*(x,t) := (u_1^*(x,t), u_2^*(x,t), u_3^*(x,t))$ for system (1.2). Then we have the following result.

Lemma 4.3 *For any initial value $\boldsymbol{\phi} \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$, system (1.2) admits a unique solution $\boldsymbol{u}(x,t;\boldsymbol{\phi})$ with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi}$ and $\boldsymbol{u}(\cdot,t;\boldsymbol{\phi}) \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,t)}$ for $t \in [0,\infty)$. Moreover, $\boldsymbol{u}(x,t;\boldsymbol{\phi}) \ge \boldsymbol{u}(x,t;\boldsymbol{\psi})$ for all $x \in \mathbb{R}$ and $t \ge 0$ provided that $\boldsymbol{\phi} \ge \boldsymbol{\psi}$ in $\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$.*

Proof Following the arguments similar to those for[23, Lemma 4.1], we first rewrite system (1.2) as an abstract integral equation in the Banach space $(\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}, \|\cdot\|_\infty)$, and then apply [16, Corollary 5] with $\tau = 0$ to obtain the desired conclusions. ∎

In Lemma 4.3, we use the Banach space $(\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}, \|\cdot\|_\infty)$ to establish the existence and uniqueness of solutions and the comparison principle for system (1.2). Further, one can use the same arguments as in [23, Theorem 4.4 and Remark 1] to show that the solution maps of system (1.2) induce a monotone semiflow on $(\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}, \|\cdot\|)$ with respect to the compact open topology. Thus, we can define a family of operators $\{Q_t\}_{t\ge0}$ from $\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$ to $\mathcal{C}_{\boldsymbol{u}^*(\cdot,t)}$ by

$$Q_t[\boldsymbol{\phi}] = \boldsymbol{u}(\cdot,t;\boldsymbol{\phi}),$$

where $\boldsymbol{u}(\cdot,t;\boldsymbol{\phi})$ is the solution of system (1.2) with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi} \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$.

By the arguments similar to those in [6, Section 4], we have the following two results on the continuity and α-contraction property for Q_t.

Lemma 4.4 *$Q_t[\boldsymbol{\phi}]$ is continuous in $(t,\boldsymbol{\phi})$ in the sense that if $\boldsymbol{\phi}_n \to \boldsymbol{\phi}$ in $\mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$ and $t_n \to t$ as $n \to \infty$, then $Q_{t_n}[\boldsymbol{\phi}_n] \to Q_t[\boldsymbol{\phi}]$ in $\mathcal{C}$.*

Lemma 4.5 *For any $I = [a,b] \subset \mathbb{R}$ and $t > 0$, there exists $\zeta(t) \in (0,1)$ such that $\alpha((Q_t[B])_I) \le \zeta(t)\alpha(B_I)$ for any bounded $B \subseteq \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$.*

As a consequence of [7, Theorem 2.1], we have the following result on time–space periodic traveling waves of system (1.2).

Theorem 4.1 *Assume that $\mathcal{R}_0 > 1$. Then there exist two numbers c_+^* and c_-^* such that the following statements are valid:*

(i) *For any $c \ge c_+^*$, system (1.2) admits rightward traveling waves $\boldsymbol{U}(x,t,x-ct)$ connecting $\boldsymbol{u}^*(x,t)$ to $\boldsymbol{0}$, that is, $\boldsymbol{U}(x,t,-\infty) = \boldsymbol{u}^*(x,t)$ and $\boldsymbol{U}(x,t,+\infty) = \boldsymbol{0}$, with the wave profile $\boldsymbol{U}(x,t,\xi) = \boldsymbol{U}(x+L,t+T,\xi)$ being continuous and non-increasing in*

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ξ. For any $c < c^*_+$, system (1.2) admits no such traveling waves connecting $\boldsymbol{u}^*(x,t)$ to $\mathbf{0}$.

(ii) *For any $c \geq c^*_-$, system (1.2) admits leftward traveling waves $\boldsymbol{V}(x,t,x+ct)$ connecting $\mathbf{0}$ to $\boldsymbol{u}^*(x,t)$, that is, $\boldsymbol{V}(x,t,-\infty) = \mathbf{0}$ and $\boldsymbol{V}(x,t,+\infty) = \boldsymbol{u}^*(x,t)$, with the wave profile $\boldsymbol{V}(x,t,\xi) = \boldsymbol{V}(x+L,t+T,\xi)$ being continuous and non-decreasing in ξ. For any $c < c^*_-$, system (1.2) admits no such traveling waves connecting $\mathbf{0}$ to $\boldsymbol{u}^*(x,t)$.*

The following result shows that the minimum wave speed coincides with the spreading speed, which follows from [7, Theorem 2.3].

Theorem 4.2 *Assume that $\mathcal{R}_0 > 1$ and let $c^*_\pm$ be given in Theorem 4.1. Let $\boldsymbol{u}(x,t;\boldsymbol{\phi})$ be a solution of (1.2) with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi} = (\phi_A,\phi_M,\phi_F)^T \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$. Then the following statements are valid:*

(i) *If $0 \leq \boldsymbol{\phi}(\cdot) \leq \boldsymbol{\varphi}(\cdot) \ll \boldsymbol{u}^*(\cdot,0)$, for some $\boldsymbol{\varphi}(\cdot) \in \mathcal{X}$, and there exist x_1, $\tilde{x}_1$, and $\delta_1 > 0$ with $x_1 < \tilde{x}_1$ such that $\phi_N(x) > \delta_1$ for $x < x_1$ and $\phi_N(x) = 0$ for $x > \tilde{x}_1$, $N = A,M,F$, then*

$$\lim_{t\to\infty} \sup_{x\geq ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi})\| = 0, \ \forall c > c^*_+, \quad \lim_{t\to\infty} \sup_{x\leq ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi}) - \boldsymbol{u}^*(x,t)\| = 0, \ \forall c < c^*_+.$$

(ii) *If $0 \leq \boldsymbol{\phi}(\cdot) \leq \boldsymbol{\varphi}(\cdot) \ll \boldsymbol{u}^*(\cdot,0)$, for some $\boldsymbol{\varphi}(\cdot) \in \mathcal{X}$, and there exist x_2, $\tilde{x}_2$, and $\delta_2 > 0$ with $x_2 > \tilde{x}_2$ such that $\phi_N(x) > \delta_2$ for $x > x_2$ and $\phi_N(x) = 0$ for $x < \tilde{x}_2$, $N = A,M,F$, then*

$$\lim_{t\to\infty} \sup_{x\leq -ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi})\| = 0, \ \forall c > c^*_-,$$
$$\lim_{t\to\infty} \sup_{x\geq -ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi}) - \boldsymbol{u}^*(x,t)\| = 0, \ \forall c < c^*_-.$$

Since (4.1) cannot be linearized at the zero solution, we are unable to use the linear operators approach in [12] to estimate c^*_+ and c^*_-. Next, we show that the spreading speeds can be determined by an associated homogeneous system.

For $\mu \in \mathbb{R}$, substituting $(u_A(x,t),u_M(x,t),u_F(x,t)) = e^{-\mu x}(v_A(x,t),v_M(x,t),v_F(x,t))$ into (4.2), we obtain

(4.3)
$$\begin{cases} \dfrac{\partial v_A}{\partial t} = \rho(x,t)H(v_M,v_F) - d(x,t)v_A - \gamma(x,t)v_A, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial v_M}{\partial t} = D\dfrac{\partial^2 v_M}{\partial x^2} - 2\mu D\dfrac{\partial v_M}{\partial x} + \mu^2 D v_M(x,t) + \theta\gamma(x,t)v_A - \hat{d}(x,t)v_M, & x\in\mathbb{R},\ t>0,\\ \dfrac{\partial v_F}{\partial t} = D\dfrac{\partial^2 v_F}{\partial x^2} - 2\mu D\dfrac{\partial v_F}{\partial x} + \mu^2 D v_F(x,t) + (1-\theta)\gamma(x,t)v_A - \hat{d}(x,t)v_F, & x\in\mathbb{R},\ t>0,\\ (v_A(x,0),v_M(x,0),v_F(x,0)) = e^{\mu x}(u_A(x,0),u_M(x,0),u_F(x,0)), & x\in\mathbb{R}. \end{cases}$$

Let $\{L_\mu(t,s)\}_{t\geq s}$ be the evolution family on $\mathcal{C}$ generated by system (4.3), that is, $L_\mu(t,0)\boldsymbol{\varphi} = \boldsymbol{v}(\cdot,t;\boldsymbol{\varphi})$, where $\boldsymbol{v}(x,t;\boldsymbol{\varphi})$ is the unique solution of system (4.3) with $\boldsymbol{v}(x,0;\boldsymbol{\varphi}) = \boldsymbol{\varphi}$. It is not hard to see that for any $\mu \geq 0$, $L_\mu(t,0)\mathcal{X}_+ \subset \mathcal{X}_+$, and

$$L_0(t,0)[e^{-\mu x}\boldsymbol{\varphi}](x) = e^{-\mu x}L_\mu(t,0)[\boldsymbol{\varphi}](x), \ x\in\mathbb{R}, \ t\geq 0, \ \boldsymbol{\varphi}\in\mathcal{X}_+.$$

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Substituting $(v_A(x,t), v_M(x,t), v_F(x,t)) = e^{-\lambda t}(w_A(x,t), w_M(x,t), w_F(x,t))$ into (4.3), we obtain the following periodic eigenvalue problem:

(4.4)
$$\begin{cases} \dfrac{\partial w_A}{\partial t} = \rho(x,t)H(w_M, w_F) - d(x,t)w_A - \gamma(x,t)w_A + \lambda w_A, & (x,t) \in \mathbb{R}\times\mathbb{R}, \\ \dfrac{\partial w_M}{\partial t} = D\dfrac{\partial^2 w_M}{\partial x^2} - 2\mu D\dfrac{\partial w_M}{\partial x} + \mu^2 D w_M + \theta\gamma(x,t)w_A \\ \quad -\hat{d}(x,t)w_M + \lambda w_M, & (x,t) \in \mathbb{R}\times\mathbb{R}, \\ \dfrac{\partial w_F}{\partial t} = D\dfrac{\partial^2 w_F}{\partial x^2} - 2\mu D\dfrac{\partial w_F}{\partial x} + \mu^2 D w_F + (1-\theta)\gamma(x,t)w_A \\ \quad -\hat{d}(x,t)w_F + \lambda w_F, & (x,t) \in \mathbb{R}\times\mathbb{R}, \\ w_N(x+L,t) = w_N(x,t),\ w_N(x,t+T) = w_N(x,t),\ (x,t) \in \mathbb{R}\times\mathbb{R},\ N = A, M, F. \end{cases}$$

Using the arguments in Lemma 3.2(i), we have the following observation.

Lemma 4.6 *If $r_{\mathcal{X}_+}(L_\mu(T,0)) \geq 1$, then eigenvalue problem (4.4) admits a principal eigenvalue, $\lambda^*(\mu)$, which is associated with an eigenvector $\boldsymbol{\phi}^* = (\phi_A^*, \phi_M^*, \phi_F^*)^T \in \mathrm{Int}(\mathcal{X}_+)$. Further, $\lambda^*(\mu)$ can be expressed as $\lambda^*(\mu) = -\frac{1}{T}\log r_{\mathcal{X}_+}(L_\mu(T,0))$, and $e^{-\lambda^*(\mu)t}\boldsymbol{\phi}^*(x,t)$ is a positive solution of system (4.3).*

We define

$$\lambda^*(\mu) := -\frac{1}{T}\log r_{\mathcal{X}_+}(L_\mu(T,0))$$

no matter whether it is the principal eigenvalue of (4.4) or not. Now we can give a computation formula for two spreading speeds.

Theorem 4.3 *Assume that $\mathcal{R}_0 > 1$. Then there holds*

$$c_+^* = \inf_{\mu>0} -\frac{\lambda^*(\mu)}{\mu}, \quad c_-^* = \inf_{\mu>0} -\frac{\lambda^*(-\mu)}{\mu}.$$

Proof We first introduce the following evolution system:

(4.5)
$$\begin{cases} \dfrac{\partial u_A}{\partial t} = \rho(x,t)\theta(1-\theta)u_S\left(1-\frac{u_A}{K(x,t)}\right) - d(x,t)u_A - \gamma(x,t)u_A, & x \in \mathbb{R},\ t > 0, \\ \dfrac{\partial u_S}{\partial t} = D\dfrac{\partial^2 u_S}{\partial x^2} + \gamma(x,t)u_A - \hat{d}(x,t)u_S, & x \in \mathbb{R},\ t > 0, \end{cases}$$

and the associated linear eigenvalue problem:

(4.6)
$$\begin{cases} \dfrac{\partial w_A}{\partial t} = \rho(x,t)\theta(1-\theta)w_S - d(x,t)w_A - \gamma(x,t)w_A + \lambda w_A, & x \in \mathbb{R},\ t \in \mathbb{R}, \\ \dfrac{\partial w_S}{\partial t} = D\dfrac{\partial^2 w_S}{\partial x^2} - 2D\mu\dfrac{\partial w_S}{\partial x} + \gamma(x,t)w_A + D\mu^2 w_S - \hat{d}(x,t)w_S + \lambda w_S, & x \in \mathbb{R},\ t \in \mathbb{R}, \\ w_A \text{ and } w_S \text{ are } T-\text{periodic in } t \text{ and } L-\text{periodic in } x. \end{cases}$$

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We next prove $c_+^* = \inf_{\mu>0} -\frac{\lambda^*(\mu)}{\mu}$ by dividing the proof into four steps, and $c_-^* = \inf_{\mu>0} -\frac{\lambda^*(-\mu)}{\mu}$ can be obtained similarly.

Step 1: The principal eigenvalue of the nonlinear eigenvalue problem (4.4) coincides with that of the linear eigenvalue problem (4.6). It then suffices to show the following two claims.

Claim 1. If λ^* is the principal eigenvalue of eigenvalue problem (4.4), then it is also the principal eigenvalue of (4.6).

Claim 2. If $\hat{\lambda}$ is the principal eigenvalue of (4.6), then it is also the principal eigenvalue of (4.4).

We only prove Claim 1, and Claim 2 can be derived similarly. For any given $\mu \geq 0$, let $(w_A^*, w_M^*, w_F^*)^T$ be the principal eigenvector of (4.4) corresponding to λ^*, and let $\hat{\lambda}$ be the principal eigenvalue of

$$\begin{cases} \dfrac{\partial \hat{w}}{\partial t} = D\dfrac{\partial^2 \hat{w}}{\partial x^2} - 2D\mu\dfrac{\partial \hat{w}}{\partial x} + D\mu^2\hat{w} - \hat{d}(x,t)\hat{w} + \lambda\hat{w}, & x \in \mathbb{R},\ t \in \mathbb{R}, \\ \hat{w} \text{ is } T-\text{periodic in } t \text{ and } L-\text{periodic in } x. \end{cases} \tag{4.7}$$

Thanks to the Krein–Rutman theorem, it is easy to verify that $\lambda^* < \hat{\lambda}$. Multiplying $1-\theta$ and θ on the second and third equations of (4.4), respectively, and then making difference, we obtain

$$\frac{\partial z}{\partial t} = D\frac{\partial^2 z}{\partial x^2} - 2D\mu\frac{\partial z}{\partial x} + D\mu^2 z - \hat{d}(x,t)z + \lambda^* z, \qquad x \in \mathbb{R},\ t \in \mathbb{R}.$$

Here, $z = (1-\theta)w_M^* - \theta w_F^*$ is T-periodic in t and L-periodic in x. In view of $\lambda^* < \hat{\lambda}$, we have $z \equiv 0$ due to the Krein–Rutman theorem. Then we have

$$\frac{1}{\theta}w_M^* = \frac{1}{1-\theta}w_F^* = w_M^* + w_F^*.$$

An easy computation yields that λ^* and $(w_A^*, w_M^* + w_F^*)$ satisfy (4.6), and the desired conclusion follows from [20, Corollary 2.6] or the Krein–Rutman theorem again.

Step 2. Systems (1.2) and (4.5) admit the same minimum wave speed of rightward time–space periodic traveling waves.

Let

$$(u_A, u_M, u_F)(x,t) := (U_A, U_M, U_F)(x,t,\xi) \text{ with } \xi = x - ct.$$

An easy computation yields that

$$\frac{\partial u_M}{\partial t} = \frac{\partial U_M}{\partial t} - c\frac{\partial U_M}{\partial \xi}, \quad \frac{\partial u_M}{\partial x} = (U_M)_x + \frac{\partial U_M}{\partial \xi},$$
$$\frac{\partial^2 u_M}{\partial x^2} = \frac{\partial^2 U_M}{\partial x^2} + 2\frac{\partial^2 U_M}{\partial \xi \partial x} + \frac{\partial^2 U_M}{\partial \xi^2}.$$

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Then system (1.2) becomes

(4.8)
$$\begin{cases} \dfrac{\partial U_A}{\partial t} = \rho(x,t)H(U_M,U_F)\big(1-\frac{U_A}{K(x,t)}\big) - d(x,t)U_A - \gamma(x,t)U_A + c\dfrac{\partial U_A}{\partial \xi}, \ (x,t,\xi)\in\mathbb{R}^3, \\ \dfrac{\partial U_M}{\partial t} = D\big(\frac{\partial^2 U_M}{\partial x^2} + 2\frac{\partial^2 U_M}{\partial \xi \partial x} + \frac{\partial^2 U_M}{\partial \xi^2}\big) + \theta\gamma(x,t)U_A - \hat{d}(x,t)U_M + c\dfrac{\partial U_M}{\partial \xi}, \quad (x,t,\xi)\in\mathbb{R}^3, \\ \dfrac{\partial U_F}{\partial t} = D\big(\frac{\partial^2 U_F}{\partial x^2} + 2\frac{\partial^2 U_F}{\partial \xi \partial x} + \frac{\partial^2 U_F}{\partial \xi^2}\big) + (1-\theta)\gamma(x,t)U_A - \hat{d}(x,t)U_F + c\dfrac{\partial U_F}{\partial \xi}, (x,t,\xi)\in\mathbb{R}^3, \\ U_N(x+L,t+T,\xi) = U_N(x+L,t,\xi) = U_N(x,t,\xi), \qquad (x,t,\xi)\in\mathbb{R}^3, \ N = A,M,F. \end{cases}$$

Substituting $(u_A,u_S)(x,t) := (U_A,U_S)(x,t,\xi)$ with $\xi = x - ct$ into (4.5), we obtain

(4.9)
$$\begin{cases} \dfrac{\partial U_A}{\partial t} = \rho(x,t)\theta(1-\theta)U_S\big(1-\frac{U_A}{K(x,t)}\big) - d(x,t)U_A - \gamma(x,t)U_A + c\dfrac{\partial U_A}{\partial \xi}, (x,t,\xi)\in\mathbb{R}^3, \\ \dfrac{\partial U_S}{\partial t} = D\big(\frac{\partial^2 U_S}{\partial x^2} + 2\frac{\partial^2 U_S}{\partial \xi \partial x} + \frac{\partial^2 U_S}{\partial \xi^2}\big) + \gamma(x,t)U_A - \hat{d}(x,t)U_S + c\dfrac{\partial U_S}{\partial \xi}, \qquad (x,t,\xi)\in\mathbb{R}^3, \\ U_N(x+L,t+T,\xi) = U_N(x+L,t,\xi) = U_N(x,t,\xi), \qquad (x,t,\xi)\in\mathbb{R}^3, \ N = A,S. \end{cases}$$

We then have the following two claims:

Claim 3. If (U_A,U_S,c) satisfies (4.9), then $(U_A,\theta U_S,(1-\theta)U_S,c)$ satisfies (4.8).

Claim 4. If (U_A,U_M,U_F,c) satisfies (4.8), then (U_A,U_M+U_F,c) satisfies (4.9).

Claim 3 can be obtained via a straightforward computation, and so we only prove Claim 4. Multiplying $1-\theta$ and θ on the second and third equations of (4.8), respectively, and then making difference, we obtain

$$\frac{\partial Z}{\partial t} = D\left(\frac{\partial^2 Z}{\partial x^2} + 2\frac{\partial^2 Z}{\partial \xi \partial x} + \frac{\partial^2 Z}{\partial \xi^2}\right) - \hat{d}(x,t)Z + c\frac{\partial Z}{\partial \xi}, \qquad (x,t,\xi)\in\mathbb{R}^3, \tag{4.10}$$

where $Z = (1-\theta)U_M - \theta U_F$. Since Z is a bounded entire solution of (4.10), it is not hard to verify that Z converges to 0 uniformly for $(x,\xi)\in\mathbb{R}^2$ as $t\to+\infty$. Notice that Z is T-periodic in t. It then follows that $Z\equiv 0$ for $(x,t,\xi)\in\mathbb{R}^3$. This implies that $(1-\theta)U_M \equiv \theta U_F$, $(x,t,\xi)\in\mathbb{R}^3$. Let $U_S = \frac{1}{\theta}U_M = \frac{1}{1-\theta}U_F = U_M + U_F$. A straightforward computation shows that Claim 4 holds.

Step 3. Prove the conclusion when $\lambda^*(\mu)$ is the principal eigenvalue of (4.4).

For any $\mu\in\mathbb{R}$, let $\{Q_\mu(t,s)\}_{t\geq s}$ be the evolution family on $\mathcal{X}$ generated by system (4.6) with $\lambda = 0$ and define

$$\tilde{\lambda}(\mu) = -\frac{1}{T}\log r(Q_\mu(T,0)).$$

By the arguments similar to those for [6, Theorem 5.1] (see also [7, 13]), the rightward spreading speed of (4.5) can be characterized by $\inf_{\mu>0} -\frac{\tilde{\lambda}(\mu)}{\mu}$, which coincides with the minimum wave speed of rightward almost pulsating waves of (4.5). By Step 2, systems (1.2) and (4.5) have the same minimum wave speed of rightward

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almost pulsating waves. It then follows from Step 1 that

$$c_+^* = \inf_{\mu>0} -\frac{\tilde{\lambda}(\mu)}{\mu} = \inf_{\mu>0} -\frac{\lambda^*(\mu)}{\mu}.$$

Step 4. Complete the proof.

We take a series of functions d_ϵ and domains $\Omega_\epsilon \subseteq \Omega := [0, L]$ such that $d_\epsilon \le d \le d_\epsilon + \epsilon$ and $\tilde{p}^\epsilon(x) = \max_{x\in\Omega} \tilde{p}^\epsilon(x)$, $\forall x \in \overline{\Omega}_\epsilon$, where $\tilde{p}^\epsilon(x) = T^{-1}\int_0^T [-d_\epsilon(x,t) - \gamma(x,t)]\mathrm{d}t$, $\forall x \in \overline{\Omega}$. Then (4.4) admits the principal eigenvalue $\lambda^\epsilon(\mu)$ and $\lambda_\epsilon(\mu)$ with d replaced by d_ϵ and $d_\epsilon + \epsilon$, respectively. It is not hard to verify that

$$|\lambda^\epsilon(\mu) - \lambda_\epsilon(\mu)| \le \epsilon, \quad -\lambda_\epsilon(\mu) \le -\lambda^*(\mu) \le -\lambda^\epsilon(\mu), \ \forall \mu > 0.$$

Therefore, the two corresponding perturbed systems admit the rightward spreading speeds c_+^ϵ and $c_{+,\epsilon}$, respectively. Repeating the above three steps, we conclude that

$$c_+^\epsilon = \inf_{\mu>0} -\frac{\lambda^\epsilon(\mu)}{\mu}, \text{ and } c_{+,\epsilon} = \inf_{\mu>0} -\frac{\lambda_\epsilon(\mu)}{\mu}.$$

Notice that $-\frac{\lambda^\epsilon(\mu)}{\mu} \to +\infty$ and $-\frac{\lambda_\epsilon(\mu)}{\mu} \to +\infty$ as $\mu \to 0$ and $\mu \to +\infty$. Thus, the two infima are attained at some finite values of μ. It follows that $c_+^\epsilon \to c_+^*$ and $c_{+,\epsilon} \to c_+^*$ as $\epsilon \to 0^+$, which implies the desired result. ∎

By the arguments similar to those in [13, Proposition 7.4], we further have the following result.

Lemma 4.7 *Assume that $\mathcal{R}_0 > 1$. Then $c_+^* + c_-^* > 0$.*

As a consequence of Lemmas 4.3, 4.5, and 4.7 and [13, Theorem 5.1], we have the following result, which indicates that c_+^* and c_-^* are the rightward and leftward spreading speeds for system (1.2) with initial functions having compact supports, respectively.

Proposition 4.1 *Assume that $\mathcal{R}_0 > 1$. Let $\boldsymbol{u}(x,t;\boldsymbol{\phi})$ be a solution of (1.2) with $\boldsymbol{u}(\cdot,0;\boldsymbol{\phi}) = \boldsymbol{\phi} = (\phi_A, \phi_M, \phi_F)^T \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$. Then the following statements are valid:*

(i) *If $0 \le \boldsymbol{\phi}(\cdot) \le \boldsymbol{\varphi}(\cdot) \ll \boldsymbol{u}^*(\cdot,0)$, for some $\boldsymbol{\varphi}(\cdot) \in \mathcal{X}$, and $\phi_N(x) = 0$ for x outside a bounded interval and $N = A, M, F$, then*

$$\lim_{t\to\infty} \sup_{x\ge ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi})\| = 0, \text{ for any } c > c_+^*,$$

and

$$\lim_{t\to\infty} \sup_{x\le -ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi})\| = 0, \text{ for any } c > c_-^*.$$

(ii) *If $\boldsymbol{\phi} \in \mathcal{C}_{\boldsymbol{u}^*(\cdot,0)}$ and $\boldsymbol{\phi} \not\equiv \mathbf{0}$, then for any c and c' satisfying $-c_-^* < -c' < c < c_+^*$, there holds*

$$\lim_{t\to\infty} \sup_{-c't\le x\le ct} \|\boldsymbol{u}(x,t;\boldsymbol{\phi}) - \boldsymbol{u}^*(x,t)\| = 0.$$

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4.3 Spreading speeds in autonomous case

In this section, we discuss the spreading speed quantitatively under the assumption that all parameters are independent of time (i.e., in the autonomous case).

Proposition 4.2 *Assume all parameters are independent of time and $\mathcal{R}_0 > 1$. Then for any $\mu \in \mathbb{R}$, eigenvalue problem (4.4) admits a principal eigenvalue $\lambda^*(\mu)$ such that $\lambda^*(\mu) = \lambda^*(-\mu)$, $\mu \in \mathbb{R}$. Moreover, $c_+^* = c_-^* = \inf_{\mu>0} -\frac{\lambda^*(\mu)}{\mu} > 0$.*

Proof Since $\mathcal{R}_0 > 1$ and $L_0(T,0) = \mathcal{U}(T,0)$ restricted on $\mathcal{X}_+$, we have $r_{\mathcal{X}_+}(L_0(T,0)) > 1$ due to Lemma 4.1. In view of Lemma 2.1, there exists $\tilde{\mu}$ such that $r_{\mathcal{X}_+}(L_\mu(T,0)) > 1$ for $\mu \in (0,\tilde{\mu})$. Thus, Lemma 4.6 implies that eigenvalue problem (4.4) admits a principal eigenvalue $\lambda^*(\mu) = -\frac{1}{T}\log r_{\mathcal{X}_+}(L_\mu(T,0))$ for any $\mu \in (0,\tilde{\mu})$. We still let $\{Q_\mu(t,s)\}_{t\geq s}$ be the evolution family on $\mathcal{X}$ generated by system (4.6) with $\lambda = 0$ and write $\tilde{\lambda}(\mu) = -\frac{1}{T}\log r(Q_\mu(T,0))$. According to Claim 1 in the proof of Theorem 4.3, $\tilde{\lambda}(\mu) = \lambda^*(\mu)$ is the principal eigenvalue of eigenvalue problem (4.6) for any $\mu \in (0,\tilde{\mu})$. We only need to prove that $\tilde{\mu}$ can be extended to $+\infty$. It then suffices to prove the following three claims:

Claim 1. $-\tilde{\lambda}(\mu)$ is convex on $\mathbb{R}$.

Claim 2. $\lim_{\mu\to+\infty} -\tilde{\lambda}(\mu) = +\infty$.

Claim 3. $\tilde{\lambda}(\mu) = \tilde{\lambda}(-\mu)$, $\forall \mu \in \mathbb{R}$.

If these claims are valid, then $\tilde{\lambda}(\mu)$ is non-increasing with respect to $\mu \in (0,+\infty)$, and hence, $r(Q_\mu(T,0)) \geq 1$ for all $\mu \geq 0$. Thus, [6, Lemma 3.1] implies that $\tilde{\lambda}(\mu)$ is the principal eigenvalue of (4.6). By Claim 2 in the proof of Theorem 4.3, we see that $\lambda^*(\mu) = \tilde{\lambda}(\mu)$ is the principal eigenvalue of eigenvalue problem (4.4) for any $\mu \in (0,+\infty)$. Combining with Claim 3, we can obtain the desired conclusions.

Indeed, Claim 1 follows from the proof of Theorem 4.3. For readers' convenience, we provide more details. We take a series of functions d_ϵ and define $\lambda^\epsilon(\mu)$ and $\lambda_\epsilon(\mu)$ as those in the proof of Theorem 4.3. By Step 1 of Theorem 4.3, it is known that $\lambda^\epsilon(\mu)$ and $\lambda_\epsilon(\mu)$ are also the principal eigenvalues of (4.6) with d replaced by d_ϵ and $d_\epsilon + \epsilon$, respectively. According to [12], we obtain that $-\lambda^\epsilon(\mu)$ and $-\lambda_\epsilon(\mu)$ are convex on $\mathbb{R}$, so is $-\tilde{\lambda}(\mu)$ by letting $\epsilon \to 0^+$.

In order to prove Claim 2, we choose four constants a_{11}, a_{12}, a_{21}, and a_{22} such that

$$0 \geq a_{11} \geq -d(x) - \gamma(x), a_{12} \geq \rho(x)\theta(1-\theta) > 0, a_{21} \geq \gamma(x) > 0, 0 \geq a_{22} \geq -\hat{d}(x), \forall x \in \mathbb{R},$$

and four constants b_{11}, b_{12}, b_{21}, and b_{22} such that

$$b_{11} \leq -d(x) - \gamma(x), 0 < b_{12} \leq \rho(x)\theta(1-\theta), 0 < b_{21} \leq \gamma(x), b_{22} \leq -\hat{d}(x), \forall x \in \mathbb{R}.$$

By the arguments in Lemma 3.2, it then follows that the following two eigenvalue problems

$$\begin{cases} a_{11}\phi_1 + a_{12}\phi_2 = -\lambda\phi_1, & x \in \mathbb{R}, \\ D\dfrac{\partial^2\phi_2}{\partial x^2} - 2D\mu\dfrac{\partial\phi_2}{\partial x} + a_{21}\phi_1 + D\mu^2\phi_2 + a_{22}\phi_2 = -\lambda\phi_2, & x \in \mathbb{R}, \\ \phi_1 \text{ and } \phi_2 \text{ are } L-\text{periodic in } x, \end{cases} \tag{4.11}$$

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and

$$\begin{cases} b_{11}\phi_1 + b_{12}\phi_2 = -\lambda\phi_1, & x \in \mathbb{R}, \\ D\dfrac{\partial^2\phi_2}{\partial x^2} - 2D\mu\dfrac{\partial\phi_2}{\partial x} + b_{21}\phi_1 + D\mu^2\phi_2 + b_{22}\phi_2 = -\lambda\phi_2, & x \in \mathbb{R}, \\ \phi_1 \text{ and } \phi_2 \text{ are } L-\text{periodic in } x \end{cases} \tag{4.12}$$

have the principal eigenvalues, which are denoted by $\overline{\lambda}(\mu)$ and $\underline{\lambda}(\mu)$, respectively. By the comparison arguments, we have $\overline{\lambda}(\mu) \le \tilde{\lambda}(\mu) \le \underline{\lambda}(\mu)$, $\forall \mu \in \mathbb{R}_+$. A direct computation shows that $\lim\limits_{\mu\to+\infty} -\frac{\overline{\lambda}(\mu)}{\mu^2} = \lim\limits_{\mu\to+\infty} -\frac{\underline{\lambda}(\mu)}{\mu^2} = D > 0$. This yields that $\lim\limits_{\mu\to+\infty} -\tilde{\lambda}(\mu) = +\infty$.

Finally, we prove Claim 3. Write $m_{11}(x) = -d(x) - \gamma(x)$, $m_{12}(x) = \rho(x)\theta(1-\theta)$, $m_{21}(x) = \gamma(x)$, $m_{22}(x) = -\hat{d}(x)$, $\tilde{m}_{12}(x) = \tilde{m}_{21}(x) = [m_{12}(x)m_{21}(x)]^{\frac{1}{2}}$, $\forall x \in \mathbb{R}$. Clearly, if λ, ϕ_1, and ϕ_2 satisfy the following eigenvalue problem:

$$\begin{cases} m_{11}\phi_1 + m_{12}\phi_2 = -\lambda\phi_1, & x \in \mathbb{R}, \\ D\dfrac{\partial^2\phi_2}{\partial x^2} - 2D\mu\dfrac{\partial\phi_2}{\partial x} + m_{21}\phi_1 + D\mu^2\phi_2 + m_{22}\phi_2 = -\lambda\phi_2, & x \in \mathbb{R}, \\ \phi_1 \text{ and } \phi_2 \text{ are } L-\text{periodic in } x, \end{cases}$$

then λ, $\psi_1 = [m_{12}(x)]^{-\frac{1}{2}}[m_{21}(x)]^{\frac{1}{2}}\phi_1$, and $\psi_2 = \phi_2$ satisfy the following eigenvalue problem:

$$\begin{cases} m_{11}\psi_1 + \tilde{m}_{12}\psi_2 = -\lambda\psi_1, & x \in \mathbb{R}, \\ D\dfrac{\partial^2\psi_2}{\partial x^2} - 2D\mu\dfrac{\partial\psi_2}{\partial x} + \tilde{m}_{21}\psi_1 + D\mu^2\psi_2 + m_{22}\psi_2 = -\lambda\psi_2, & x \in \mathbb{R}, \\ \psi_1 \text{ and } \psi_2 \text{ are } L-\text{periodic in } x. \end{cases} \tag{4.13}$$

Now Claim 3 follows from this observation and the adjoint eigenvalue problem. ∎

In the rest of this section, we study the effects of diffusion coefficient on the spreading speeds. We use $c^*(D) = c^*_+(D) = c^*_-(D)$ and $\mathcal{R}_0(D)$ to denote the spreading speed and basic reproduction ratio of system (1.2), respectively, to emphasize that they depend on the diffusion coefficient D. From the analysis in Theorem 3.1, we have the following observation.

Lemma 4.8 *Assume all parameters are independent of time. Then the following statements are valid:*

(i) $\mathcal{R}_0(D)$ *is decreasing with respect to* $D \in (0, +\infty)$.

(ii) $\mathcal{R}_0(D) \to \theta(1-\theta)\max_{x\in[0,L]} \frac{\rho(x)\gamma(x)}{(d(x)+\gamma(x))\hat{d}(x)} =: \mathcal{R}_0(0)$ *as* $D \to 0^+$.

(iii) $\mathcal{R}_0(D) \to \theta(1-\theta)\frac{\int_0^L \frac{\rho(x)\gamma(x)}{d(x)+\gamma(x)}\mathrm{d}x}{\int_0^L \hat{d}(x)\mathrm{d}x} := \tilde{\mathcal{R}}_0$ *as* $D \to +\infty$.

We are ready to prove the following result on the spreading speed $c^*(D)$.

Theorem 4.4 *Assume all parameters are independent of time. Then the following statements are valid:*

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(i) *If* $\mathcal{R}_0(0) > 1$, *then there exists* $\underline{D} > 0$ *such that* $c^*(D) > 0$ *for all* $D \in (0, \underline{D})$, *and* $\lim_{D\to 0^+} c^*(D) = 0$.

(ii) *If* $\mathcal{R}_0(0) > 1 > \tilde{\mathcal{R}}_0$, *then there exists a unique* $D^* > 0$ *such that* $c^*(D) > 0$ *for all* $D \in (0, D^*)$ *and* $\lim_{D\to(D^*)^-} c^*(D) = 0$.

(iii) *If* $\tilde{\mathcal{R}}_0 > 1$, *then* $c^*(D) > 0$ *for all* $D \in (0, +\infty)$, *and* $\lim_{D\to+\infty} c^*(D) = +\infty$.

Proof We denote $\lambda^*(D, \mu)$ the principal eigenvalue of (4.4) which depends on D and μ. We remark that $\lambda^*(D, \mu)$ is also the principal eigenvalue of (4.6) due to Step 1 of Theorem 4.3.

(i) In view of Lemma 4.8(ii), there exists $\underline{D} > 0$ such that for all $D \in (0, \underline{D})$, $\mathcal{R}_0(D) > 1$, and hence, $c^*(D) > 0$ due to Proposition 4.2. Let $\overline{\lambda}^*(D, \mu)$ be the principal eigenvalue of eigenvalue problem (4.11). By the comparison arguments, it is easy to see that $\overline{\lambda}^*(D, \mu) \le \lambda^*(D, \mu)$, $\forall (D, \mu) \in \mathbb{R}^2_+$. Combining with $c^*(D) = \inf_{\mu>0} -\frac{\lambda^*(D,\mu)}{\mu}$, we only need to show that

$$\lim_{D\to 0^+} \inf_{\mu>0} -\frac{\overline{\lambda}^*(D, \mu)}{\mu} = 0.$$

It is easy to verify that $\lim_{D\to 0^+} \overline{\lambda}^*(D, \mu)$ exists for any $\mu \ge 0$, which is the smaller solution of the equation $(\lambda + a_{11})(\lambda + a_{22}) - a_{12}a_{21} = 0$. For convenience, we denote this limit by $\overline{\lambda}$. In view of $\mathcal{R}_0(0) > 1$, it then follows that $\frac{a_{12}a_{21}}{a_{11}a_{22}} > 1$, which implies $\overline{\lambda} < 0$.

For any $\epsilon > 0$, there exists $M > 0$ such that $-\epsilon \le \frac{-\overline{\lambda}+\epsilon}{M} \le \epsilon$. Moreover, there exists $D_0 > 0$ such that $|\overline{\lambda}^*(D, M) - \overline{\lambda}| \le \epsilon$ for all $D \in (0, D_0)$. Therefore,

$$-\frac{\overline{\lambda}^*(D, M)}{M} \le \frac{-\overline{\lambda} + \epsilon}{M} \le \epsilon,$$

which implies that $\lim_{D\to 0^+} \inf_{\mu>0} -\frac{\overline{\lambda}^*(D,\mu)}{\mu} = 0$.

(ii) In view of Lemma 4.8, there exists $D^* > 0$ such that $\mathcal{R}_0(D^*) = 1$, and $\mathcal{R}_0(D) > 1$ for all $D \in (0, D^*)$ and $\mathcal{R}_0(D) < 1$ for all $D > D^*$. Proposition 4.2 implies that $c^*(D) > 0$ for all $D \in (0, D^*)$.

We next show that $\frac{\partial}{\partial\mu}\lambda^*(D^*, 0) = 0$. For convenience, we use $\dot{\lambda}$, $\dot{\psi}_1$, and $\dot{\psi}_2$ to represent $\frac{\partial}{\partial\mu}\lambda$, $\frac{\partial}{\partial\mu}\psi_1$, and $\frac{\partial}{\partial\mu}\psi_2$, respectively. Differentiating (4.13) with respect to μ, we obtain

$$\begin{cases} m_{11}\dot{\psi}_1 + \tilde{m}_{12}\dot{\psi}_2 = -\lambda\dot{\psi}_1 - \dot{\lambda}\psi_1, & x \in \mathbb{R}, \\ D\dfrac{\partial^2\dot{\psi}_2}{\partial x^2} - 2D\mu\dfrac{\partial\dot{\psi}_2}{\partial x} + \tilde{m}_{21}\dot{\psi}_1 + D\mu^2\dot{\psi}_2 + m_{22}\dot{\psi}_2 - 2D\dfrac{\partial\psi_2}{\partial x} + 2D\mu\psi_2 \\ \quad = -\lambda\dot{\psi}_2 - \dot{\lambda}\psi_2, & x \in \mathbb{R}, \\ \dot{\psi}_1 \text{ and } \dot{\psi}_2 \text{ are } L-\text{periodic in } x. \end{cases} \tag{4.14}$$

Multiplying the first equation of (4.14) by ψ_1 and the second equation of (4.14) by ψ_2 and summing them together, and multiplying the first equation of (4.13) by $\dot{\psi}_1$ and the second equation of (4.13) by $\dot{\psi}_2$ and summing them together, and integrating them

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from 0 to L, and then making a difference, we further have

$$-\dot{\lambda}\int_0^L[\psi_1^2+\psi_2^2]\mathrm{d}x = -4D\mu\int_0^L\frac{\partial\dot{\psi}_2}{\partial x}\psi_2\mathrm{d}x - 2D\int_0^L\frac{\partial\psi_2}{\partial x}\psi_2\mathrm{d}x + 2D\mu\int_0^L\psi_2^2\mathrm{d}x$$
$$= -4D\mu\int_0^L\frac{\partial\dot{\psi}_2}{\partial x}\psi_2\mathrm{d}x + 2D\mu\int_0^L\psi_2^2\mathrm{d}x.$$

Letting $\mu = 0$ and $D = D^*$, we see that $\frac{\partial}{\partial\mu}\lambda^*(D^*,0) = 0$.

Notice that $\lambda^*(D^*,0) = 0$ due to $\mathcal{R}_0(D^*) = 1$. For any sequence $D_n \to D^*$ with $D_n < D^*$ as $n\to\infty$, there exists $\mu_n \to 0^+$ such that $\frac{\lambda^*(D_n,\mu_n)}{\mu_n} \to 0$ as $n\to\infty$. It follows that $\inf_{\mu>0} -\frac{\lambda^*(D_n,\mu)}{\mu} \le 0$ as $n\to\infty$. Therefore, $c^*(D_n)\to 0$ as $n\to\infty$.

(iii) In view of Lemma 4.8(i) and (iii), we have $\mathcal{R}_0(D) > 1$, which implies that $c^*(D) > 0$ for all $D\in(0,+\infty)$ by Proposition 4.2. We next prove the following two claims:

Claim 1. There exist $\rho_0 > 0$ and $\overline{D}_1 > 0$ such that $-\lambda^*(D,\mu)\ge\rho_0$ holds uniformly for $\mu\in[0,+\infty)$ when $D > \overline{D}_1$.

Claim 2. For any given $\epsilon_0 > 0$, $\lim\limits_{D\to+\infty} -\frac{\lambda^*(D,\mu)}{D} = \mu^2$ holds uniformly on $[\epsilon_0,+\infty)$, that is, for every $\epsilon > 0$, there exists $\overline{D}_2 > 0$ large enough such that $|-\frac{\lambda^*(D,\mu)}{D} - \mu^2| \le \epsilon$ for all $\mu\in[\epsilon_0,+\infty)$ when $D > \overline{D}_2$.

We postpone the proof of these two claims and complete the proof in a few lines. For any given $M > 0$, there exists $\delta_0 > 0$ such that $\frac{\rho_0}{\delta_0} \ge M$ due to $\rho_0 > 0$. Thus, $\frac{\rho_0}{\mu} \ge M$, $\mu\in[0,\delta_0]$. According to Claim 1, there exists D_1 such that $\frac{-\lambda^*(D,\mu)}{\mu} \ge \frac{\rho_0}{\mu} \ge M$ holds for all $\mu\in(0,\delta_0]$ when $D\ge D_1$. By Claim 2, we can choose D_2 large enough such that $\frac{M}{D_2} \le \frac{\delta_0}{2}$, and $-\frac{\lambda^*(D,\mu)}{D} \ge \frac{\delta_0}{2}\mu \ge \frac{M}{D_2}\mu$ for all $\mu\in[\delta_0,+\infty)$ when $D\ge D_2$. Therefore, $-\frac{\lambda^*(D,\mu)}{\mu} \ge \frac{MD}{D_2} \ge M$ for all $\mu\in[\delta_0,+\infty)$ when $D\ge D_2$. Thus, $\frac{-\lambda^*(D,\mu)}{\mu} \ge M$ for all $\mu\in(0,\infty)$ when $D\ge\max(D_1,D_2)$.

Note that $-\lambda^*(D,0)$ is the principal eigenvalue of (4.13) with $\mu = 0$. It is easy to verify that $-\lambda^*(D,0)$ is non-increasing with respect to $D\in(0,+\infty)$. In view of $\tilde{\mathcal{R}}_0 > 1$, we have $\theta(1-\theta)\int_0^L\frac{\rho(x)\gamma(x)}{d(x)+\gamma(x)}\mathrm{d}x > \int_0^L\hat{d}(x)\mathrm{d}x$. This implies that $\theta(1-\theta)\int_0^L\frac{\rho(x)\gamma(x)}{d(x)+\gamma(x)+\rho}\mathrm{d}x = \int_0^L\hat{d}(x)\mathrm{d}x + \rho L$ has a unique positive root ρ_1. It then follows that $-\lambda^*(D,0)$ converges to ρ_1 as $D\to+\infty$. Thus, there exists $\overline{D}_1$ such that $-\lambda^*(D,0) > \rho_0$ whenever $D > \overline{D}_1$ for some $\rho_0 > 0$. By the proof of Proposition 4.2, we see that $-\lambda^*(D,\mu)$ is non-decreasing with respect to $\mu\in(0,+\infty)$. This proves Claim 1.

Let $\underline{\lambda}^*(D,\mu)$ be the principal eigenvalue of the eigenvalue problem (4.12). By the comparison arguments, it is easy to see that

$$\overline{\lambda}^*(D,\mu) \le \lambda^*(D,\mu) \le \underline{\lambda}^*(D,\mu),\ \forall(D,\mu)\in\mathbb{R}^2_+,$$

where $\overline{\lambda}^*(D,\mu)$ is the principal eigenvalue of (4.11). It suffices to show that $\lim\limits_{D\to+\infty} -\frac{\overline{\lambda}^*(D,\mu)}{D} = \lim\limits_{D\to+\infty} -\frac{\underline{\lambda}^*(D,\mu)}{D} = \mu^2$ holds uniformly on $[\epsilon_0,+\infty)$. Here, we prove that $\lim\limits_{D\to+\infty} -\frac{\underline{\lambda}^*(D,\mu)}{D} = \mu^2$ holds uniformly on $[\epsilon_0,+\infty)$, and the other limit can be

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proved similarly. Since $\underline{\lambda}^*(D,\mu)$ is the smaller solution of the equation

$$(\lambda + b_{11})(\lambda + b_{22} + D\mu^2) - b_{12}b_{21} = 0,$$

it follows that

$$\begin{aligned}&\underline{\lambda}^*(D,\mu)\\ &= \frac{1}{2}\left(-b_{11} - b_{22} - D\mu^2 - \sqrt{(b_{11} + b_{22} + D\mu^2)^2 - 4b_{11}b_{22} - 4b_{11}D\mu^2 + 4b_{12}b_{21}}\right).\end{aligned}$$

A straightforward computation gives rise to

$$-\frac{\underline{\lambda}^*(D,\mu)}{D} - \mu^2 = \frac{2\frac{b_{12}b_{21}}{D\mu^2} - 2\frac{b_{11}b_{22}}{D\mu^2} + 2b_{22}}{D\left(\sqrt{(\frac{b_{11}}{D\mu^2} - \frac{b_{22}}{D\mu^2} - 1)^2 + 4\frac{b_{12}b_{21}}{D^2\mu^4}} - \frac{b_{11}}{D\mu^2} - \frac{b_{22}}{D\mu^2} + 1\right)},$$

which implies Claim 2. ∎

Finally, we remark that it remains an unsolved problem to determine the limiting behavior of the propagation speed as the diffusion coefficient approaches infinity in the critical case where $\tilde{\mathcal{R}}_0 = 1$.

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