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DYNAMICS OF A HOST-PATHOGEN SYSTEM ON A BOUNDED SPATIAL DOMAIN

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Abstract. We study a host-pathogen system in a bounded spatial habitat where the environment is closed. Extinction and persistence of the disease are investigated by appealing to theories of monotone dynamical systems and uniform persistence. We also carry out a bifurcation analysis for steady state solutions, and the results suggest that a backward bifurcation may occur when the parameters in the system are spatially dependent.

1. Introduction.

Mathematical disease models play an important role in studying the mechanism of infectious disease. Recent evidences have shown that diseases can affect the dynamics of animal populations and communities. In classical epidemiological models, the host population is divided into infected and susceptible classes, with one differential equation representing each class. Anderson and May [3] introduced an additional class representing the population of infectious pathogen particles. These particles are found in invertebrate pathogens and they allow pathogens to survive in the environment for several decades. The following host-pathogen system was proposed by Anderson and May [3]:

$$\begin{cases} \dfrac{du_1}{dt} = r\,(u_1+u_2) - \beta u_1 u_3, \\ \dfrac{du_2}{dt} = \beta u_1 u_3 - \alpha u_2, \\ \dfrac{du_3}{dt} = -\delta u_3 + \lambda u_2 - \beta (u_1+u_2) u_3, \end{cases} \tag{1.1}$$

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where $u_1(t)$ is the density of susceptible hosts, $u_2(t)$ is the density of infected hosts, $u_3(t)$ is the density of pathogen particles, r is the reproductive rate of the host, β is the transmission coefficient, α is the rate of disease-induced mortality, λ is the rate of production of pathogen particles by infected hosts, and δ is the decay rate of the pathogens.

Dwyer [9] revised the system (1.1) and obtained a mathematical disease model that includes density-dependent host population dynamics:

$$\begin{cases} \dfrac{du_1}{dt} = r\left(1 - \dfrac{u_1+u_2}{K}\right)u_1 - \beta u_1 u_3, \\ \dfrac{du_2}{dt} = \beta u_1 u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K}u_2, \\ \dfrac{du_3}{dt} = -\delta u_3 + \lambda u_2 - \beta(u_1+u_2)u_3, \end{cases} \tag{1.2}$$

where the new parameter K is the carrying capacity for the hosts. In order to simplify the system (1.2), Dwyer [9] further ignored the consumption of the pathogen by the hosts and investigated the following system:

$$\begin{cases} \dfrac{du_1}{dt} = r\left(1 - \dfrac{u_1+u_2}{K}\right)u_1 - \beta u_1 u_3, \\ \dfrac{du_2}{dt} = \beta u_1 u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K}u_2, \\ \dfrac{du_3}{dt} = -\delta u_3 + \lambda u_2. \end{cases} \tag{1.3}$$

In many situations ordinary differential equations are appropriate mathematical models for the progress of infectious diseases. However, it has been recognized that spatial structure is also a central factor that affects the spatial spreading of a disease. Taking into consideration the host movement, the author in [9] modified (1.3) to a reaction-diffusion model in a spatial environment:

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d\Delta u_1 + r\left(1 - \dfrac{u_1+u_2}{K}\right)u_1 - \beta u_1 u_3, \\ \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + \beta u_1 u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K}u_2, \\ \dfrac{\partial u_3}{\partial t} = -\delta u_3 + \lambda u_2. \end{cases} \tag{1.4}$$

Here the host movement is described by the diffusion terms $d\Delta u_1$ and $d\Delta u_2$ where Δ is the usual Laplacian operator; $d > 0$ denotes the diffusion coefficient, which represents the rate of host movement; x and t represent location and time, respectively. All coefficients in (1.4) are positive constants. Dwyer [9] assumed that the habitat in (1.4) is *one-dimensional* and *unbounded*, and accordingly, investigated the existence of travelling wave and spreading speed.

In the real world, a habitat in which a host population settles is typically bounded, and this motivates us to consider a mathematical system modelling the dynamics of a disease in a *bounded spatial domain (not necessarily one-dimensional)*. Also, the parameters in a model involving space are typically *space dependent* due to the spatial heterogeneity. Based on these basic facts, we will, in this paper, further modify the more general (than (1.4)) model system (1.2) by replacing the constant parameters with spatial dependent parameters, and consider the solution dynamics on a general bounded domain with zero-flux boundary condition. In other words, we consider the following problem:

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d\Delta u_1 + r\left(1 - \dfrac{u_1+u_2}{K(x)}\right)u_1 - \beta(x)u_1u_3, & x \in \Omega,\ t>0, \\ \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + \beta(x)u_1u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K(x)}u_2, & x \in \Omega,\ t>0, \\ \dfrac{\partial u_3}{\partial t} = -\delta u_3 + \lambda(x)u_2 - \beta(x)(u_1+u_2)u_3, & x \in \Omega,\ t>0, \\ \dfrac{\partial u_1}{\partial \nu} = \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega,\ t>0, \\ u_i(x,0) = u_i^0(x), & x \in \Omega,\ i=1,2,3. \end{cases} \tag{1.5}$$

Here $\Omega \subset \mathbb{R}^m$ is a bounded open set with smooth boundary $\partial\Omega$; $\frac{\partial}{\partial\nu}$ denotes the differentiation along the unit outward normal ν to $\partial\Omega$; $K(x)$ is the carrying capacity. The spatially dependent functions $\beta(x),\ \lambda(x),\ K(x)$ are assumed to be continuous and positive in Ω.

We point out that although there have been numerous ODE models for disease and/or pathogen dynamics in literature, the studies of PDE models with spatial variables are much fewer, among which are Allen *et. al.* [2], Capasso and Maddalena [4], Capasso and Wilson [5], Guo *et. al.* [12], Li and Zou [18], Peng [24], Peng and Yi [25], Vaidya *et. al.* [34], Wang and Zhao [36, 37]. The main reason is that a PDE model with spatial variables (important in disease spread), such as (1.5), is infinite dimensional, and thus, is much harder to analyze. Taking basic reproduction number as an example, for an ODE model, following the "recipe" given in [33], the basic reproduction number can be easily identified as the spectral radius of the next generation that enjoys some nice properties, and can be conveniently calculated in most cases. However, for a PDE model, one needs to work on operators between function spaces in order to obtain the next generation operator. Moreover the spectral radius of a general operator is very hard, or even impossible in most cases, to calculate, and thus, one has to heavily depend on numerical simulations. See, e.g., [2, 4, 12, 24, 25, 34, 36, 37] for a taste of what is stated above. Furthermore, unlike in [2, 4, 12, 24, 25, 34, 36, 37] where all equations in the models have diffusion terms and hence the solution semiflows are alway compact, here in our model (1.5), the compactness is an issue because of the lack of diffusion term in the u_3 equation, and this makes analysis more challenging. In [5], a model on temporal and spatial evolution of orofecal transmitted disease with immobile human population and Dirichlet boundary condition was considered, but our approach is quite different.

In the rest of this paper, we will investigate the dynamics of this modified model. In Section 2, we explore the solution properties of the system (1.5) by appealing to the theories of monotone dynamical systems and uniform persistence. In Section 3, we utilize bifurcation theory to investigate the steady state solutions of the system (1.5). A brief discussion section concludes the paper.

2. **Basic properties of solutions.**

This section is devoted to establishing some basic properties of (1.5), starting with the well-posedness.

2.1. **Well-posedness.**

We first show the existence of solutions to (1.5) via a semigroup approach. Let $\mathbb{X} := C(\overline{\Omega}, \mathbb{R}^3)$ be the Banach space with the supremum norm $\|\cdot\|_{\mathbb{X}}$. Define $\mathbb{X}^+ := C(\overline{\Omega}, \mathbb{R}^3_+)$, then $(\mathbb{X}, \mathbb{X}^+)$ is a strongly ordered Banach space. Let Γ be the Green function associated with the parabolic equation $\frac{\partial v}{\partial t} = \Delta v$ in Ω subject to the Neumann boundary condition. Suppose that $T_1(t),\ T_2(t) : C(\overline{\Omega}, \mathbb{R}) \to C(\overline{\Omega}, \mathbb{R})$ are the C_0 semigroups associated with $d\Delta$ and $d\Delta - \alpha$ subject to the Neumann boundary condition, respectively. It then follows that for any $\varphi \in C(\overline{\Omega}, \mathbb{R})$, $t \geq 0$,

$$(T_1(t)\varphi)(x) = \int_\Omega \Gamma(dt, x, y)\varphi(y)dy,$$

and

$$(T_2(t)\varphi)(x) = e^{-\alpha t}\int_\Omega \Gamma(dt, x, y)\varphi(y)dy. \tag{2.1}$$

From [29, Section 7.1 and Corollary 7.2.3], it follows that $T_i(t) : C(\overline{\Omega}, \mathbb{R}) \to C(\overline{\Omega}, \mathbb{R})$ is compact and strongly positive for any $t > 0$ and $i = 1, 2$. We also define

$$(T_3(t)\varphi)(x) = e^{-\delta t}\varphi(x).$$

Then $T(t) := (T_1(t), T_2(t), T_3(t)) : \mathbb{X} \to \mathbb{X},\ t \geq 0$, defines a C_0 semigroup (see, e.g., [23]). Define $F = (F_1, F_2, F_3) : \mathbb{X}^+ \to \mathbb{X}$ by

$$\begin{aligned}
F_1(\phi)(x) &= r\left(1 - \frac{\phi_1+\phi_2}{K(x)}\right)\phi_1 - \beta(x)\phi_1\phi_3,\\
F_2(\phi)(x) &= \beta(x)\phi_1\phi_3 - r\frac{\phi_1+\phi_2}{K(x)}\phi_2,\\
F_3(\phi)(x) &= \lambda(x)\phi_2 - \beta(x)(\phi_1+\phi_2)\phi_3,
\end{aligned}$$

for $x \in \overline{\Omega}$ and $\phi = (\phi_1, \phi_2, \phi_3) \in \mathbb{X}^+$. Then (1.5) can be rewritten as the following integral equation

$$u(t) = T(t)\phi + \int_0^t T(t-s)F(u(\cdot, s))ds.$$

The following lemma gives some basic properties of the local solution flow on $\mathbb{X}^+$.

Lemma 2.1. *For any $\phi := (\phi_1, \phi_2, \phi_3) \in \mathbb{X}^+$, the system (1.5) has a unique mild solution $u(\cdot, t; \phi) := (u_1(\cdot, t), u_2(\cdot, t), u_3(\cdot, t))$ on $(0, \tau_\phi)$ with $u(\cdot, 0; \phi) = \phi$, where $\tau_\phi \leq \infty$. Furthermore for $t \in (0, \tau_\phi)$, $u(\cdot, t; \phi) \in \mathbb{X}^+$ and $u(\cdot, t; \phi)$ is a classical solution of (1.5).*

Proof. By [19, Corollary 4] or [29, Theorem 7.3.1], it suffices to show that for any $\phi \in \mathbb{X}^+$,

$$\lim_{h\to 0^+} dist(\phi + hF(\phi), \mathbb{X}^+) = 0. \tag{2.2}$$

Let $\bar{\beta} := \max_{x\in\overline{\Omega}} \beta(x)$ and $\tilde{K} := \min_{x\in\overline{\Omega}} K(x)$. Then for any $\phi \in \mathbb{X}^+$ and $h \geq 0$, we have

$$\begin{aligned}
\phi + hF(\phi) &= \begin{pmatrix} \phi_1 + h\left(r(1-\dfrac{\phi_1+\phi_2}{K(x)})\phi_1 - \beta(x)\phi_1\phi_3\right)\\ \phi_2 + h\left(\beta(x)\phi_1\phi_3 - r\dfrac{\phi_1+\phi_2}{K(x)}\phi_2\right)\\ \phi_3 + h[\lambda(x)\phi_2 - \beta(x)(\phi_1+\phi_2)\phi_3]\end{pmatrix}\\
&\geq \begin{pmatrix} \phi_1[1 - h(\dfrac{r}{\tilde{K}}(\phi_1+\phi_2) + \bar{\beta}\phi_3)]\\ \phi_2[1 - h\dfrac{r}{\tilde{K}}(\phi_1+\phi_2)]\\ \phi_3[1 - h\bar{\beta}(\phi_1+\phi_2)]\end{pmatrix}.
\end{aligned}$$

The above inequalities imply that (2.2) holds and thus the lemma is proved. $\square$

For convenience of discussions later, we recall some well-known results for some auxiliary systems. First consider the following equation

$$\frac{\partial w(x,t)}{\partial t} = \lambda(x) - A(x)w(x,t),\ x \in \overline{\Omega},\ t > 0. \tag{2.3}$$

It is easy to see that system (2.3) has a unique positive steady state $\frac{\lambda(x)}{A(x)}$ if $A(x) > 0$. By [38, Theorem 2.2.1], we have the following result:

Lemma 2.2. *Suppose that $A(x) > 0$ and $\lambda(x) > 0$ for $x \in \overline{\Omega}$, then the system (2.3) admits a unique positive steady state $\frac{\lambda(x)}{A(x)}$ which is globally asymptotically stable in $C(\overline{\Omega}, \mathbb{R})$.*

Secondly we consider the dynamics of the following diffusive logistic equation:

$$\begin{cases} \dfrac{\partial W}{\partial t} = d\Delta W + r\left(1 - \dfrac{W}{K(x)}\right)W, & x \in \Omega,\ t > 0, \\ \dfrac{\partial W}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0, \\ W(x,0) = W^0(x), & x \in \Omega. \end{cases} \tag{2.4}$$

The dynamics of the system (2.4) is well-known (see for example, [38, Theorem 3.1.5 and the proof of Theorem 3.1.6]):

Lemma 2.3. *For any $d, r > 0$ and $W^0(x) \not\equiv 0$, the diffusive logistic equation (2.4) admits a unique positive steady state $u_1^*(x)$ which is globally asymptotically stable in $C(\overline{\Omega}, \mathbb{R})$.*

Now we are in a position to show that solutions of the system (1.5) exist globally for $t \in [0, \infty)$ in $\mathbb{X}^+$.

Lemma 2.4. *For every initial value function $\phi \in \mathbb{X}^+$, the system (1.5) has a unique solution $u(x,t;\phi)$ defined on $[0,\infty)$ with $u(\cdot,0;\phi) = \phi$ and a semiflow $\Psi(t) : \mathbb{X}^+ \to \mathbb{X}^+$ is generated by (1.5) which is defined by*

$$\Psi(t)\phi = u(\cdot, t; \phi),\ \ t \geq 0. \tag{2.5}$$

Furthermore $\Psi(t) : \mathbb{X}^+ \to \mathbb{X}^+$ is point dissipative.

Proof. Let $U(x,t) := u_1(x,t) + u_2(x,t)$. Then $U(x,t)$ satisfies

$$\begin{cases} \dfrac{\partial U}{\partial t} \leq d\Delta U + r\left(1 - \dfrac{U}{K(x)}\right)U, & x \in \Omega,\ t > 0, \\ \dfrac{\partial U}{\partial \nu} = 0, & x \in \partial\Omega,\ t > 0. \end{cases} \tag{2.6}$$

The system (2.6) is bounded from above by the system (2.4) and the standard parabolic comparison theorem (see, e.g., [29, Theorem 7.3.4]) implies that $U(x,t)$ is uniformly bounded. By Lemma 2.1, it follows that $u_1(x,t)$ and $u_2(x,t)$ are uniformly bounded. This, together with the comparison arguments, implies that $u_3(x,t)$ is also uniformly bounded.

Comparing (2.6) with (2.4), we see from Lemma 2.3 and the comparison principle that

$$\limsup_{t\to\infty} U(x,t) \leq u_1^*(x) \text{ uniformly for } x \in \overline{\Omega}. \tag{2.7}$$

More precisely, there exist $t_1 > 0$ and $a > 0$ such that

$$U(\cdot, t) \leq u_1^*(\cdot) + a, \ \forall\, t \geq t_1.$$

This implies that $U(x,t)$ is ultimately bounded. It follows from Lemma 2.1 that $u_i(x,t)$ is also ultimately bounded, $i = 1, 2$. Then there exists a positive number A such that the third equation of system (1.5) for u_3 satisfies

$$\frac{\partial u_3(x,t)}{\partial t} \leq A - \delta u_3(x,t), \ \forall\, x \in \Omega, \ t \geq t_1. \tag{2.8}$$

By standard comparison theorem and Lemma 2.2, it follows that u_3 is also ultimately bounded. Thus, the solution exists globally, i.e., for all $t \in [0, \infty)$, and moreover, the solution semiflow generated by (1.5) is point dissipative. □

Since the third equation in (1.5) has no diffusion term, the solution map $\Psi(t)$ is not compact. In order to overcome this problem, we introduce the Kuratowski measure of noncompactness κ (see [7]), which is defined by

$$\kappa(B) := \inf\{r : B \text{ has a finite cover of diameter} < r\}, \tag{2.9}$$

for any bounded set B. We set $\kappa(B) = \infty$ whenever B is unbounded. It is easy to see that B is precompact (*i.e.* $\bar{B}$ is compact) if and only if $\kappa(B) = 0$. Then the solution map $\Psi(t)$ has some partial compactness in the following sense.

Lemma 2.5. *$\Psi(t)$ is κ-contracting in the sense that*

$$\lim_{t\to\infty} \kappa(\Psi(t)B) = 0 \text{ for any bounded set } B \subset \mathbb{X}^+.$$

Proof. Let

$$G(u_1, u_2, u_3) = -\delta u_3 + \lambda(x) u_2 - \beta(x)(u_1 + u_2) u_3$$

represent the reaction term for the third equation of (1.5). Then

$$\frac{\partial G(u_1, u_2, u_3)}{\partial u_3} = -\delta - \beta(x)(u_1 + u_2) \leq -\delta, \ \ (u_1, u_2, u_3) \in \mathbb{X}^+.$$

With this inequality, the rest of the proof is similar to the one in [15, Lemma 4.1] (see also [15, Lemma 3.2]). □

Now we are ready to show that solutions of system (1.5) converge to a compact attractor in $\mathbb{X}^+$.

Theorem 2.1. *$\Psi(t)$ admits a connected global attractor on $\mathbb{X}^+$.*

Proof. By Lemma 2.4 and Lemma 2.5, it follows that $\Psi(t)$ is point dissipative and κ-contracting on $\mathbb{X}^+$. From the proof of Lemma 2.4 (see (2.6) and (2.8)), we also know that the positive orbits of bounded subsets of $\mathbb{X}^+$ for $\Psi(t)$ are (uniformly) bounded. By [20, Theorem 2.6], $\Psi(t)$ has a global attractor that attracts every bounded set in $\mathbb{X}^+$. □

2.2. **Extinction.** In this subsection, an extinction result for large α is established. We first consider the following linear system:

$$\begin{cases} \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + \beta(x) u_1^*(x) u_3 - \alpha u_2, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_3}{\partial t} = -\delta u_3 + \lambda(x) u_2, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ u_i(x, 0) = u_i^0(x), & x \in \Omega, \ i = 2, 3. \end{cases} \tag{2.10}$$

Denote by $\Sigma(t)$ the solution semiflow $\Sigma(t)$ of (2.10), that is, $\Sigma(t) : \mathbf{C} \to \mathbf{C}$ is defined by

$$\Sigma(t)(\phi) = (u_2(\cdot, t, \phi), u_3(\cdot, t, \phi)),\ \phi \in \mathbf{C},\ t \geq 0,$$

where $(u_2(\cdot, t, \phi), u_3(\cdot, t, \phi))$ is the solution of (2.10) with initial function $\phi \in \mathbf{C}$ where $\mathbf{C} = C(\overline{\Omega}, \mathbb{R}^2)$. Since (2.10) is cooperative, $\Sigma(t)$ is a positive C_0-semigroup on $\mathbf{C}$, and its generator $\mathcal{B}$ can be written as

$$\mathcal{B} = \begin{pmatrix} d\Delta - \alpha & \beta(x)u_1^*(x) \\ \lambda(x) & -\delta \end{pmatrix}.$$

Further, $\mathcal{B}$ is a closed and resolvent positive operator (see, e.g., [32, Theorem 3.12]). Substituting $u_i(x, t) = e^{\mu t}\psi_i(x)$, $i = 2, 3$, into (2.10), we get the following associated eigenvalue problem:

$$\begin{cases} \mu\psi_2(x) = d\Delta\psi_2 + \beta(x)u_1^*(x)\psi_3 - \alpha\psi_2, & x \in \Omega, \\ \mu\psi_3(x) = -\delta\psi_3 + \lambda(x)\psi_2, & x \in \Omega, \\ \dfrac{\partial\psi_2(x)}{\partial\nu} = 0, & x \in \partial\Omega. \end{cases} \tag{2.11}$$

We point out that $\Sigma(t)$ is not compact since the second equation in (2.10) has no diffusion term and its sign.

The following lemma concerns with the existence of the principal eigenvalue of (2.11).

Lemma 2.6. *Let $s(\mathcal{B})$ be the spectral bound of $\mathcal{B}$. Then*

(i) *$s(\mathcal{B})$ is the principal eigenvalue of the eigenvalue problem (2.11) which has a strongly positive eigenfunction;*

(ii) *$s(\mathcal{B})$ has the same sign as ξ^0, where ξ^0 is the principal eigenvalue of the eigenvalue problem*

$$\begin{cases} d\Delta\varphi + \left(\dfrac{\beta(x)\lambda(x)u_1^*(x)}{\delta} - \alpha\right)\varphi = \xi\varphi, & x \in \Omega, \\ \dfrac{\partial\varphi(x)}{\partial\nu} = 0, & x \in \partial\Omega. \end{cases} \tag{2.12}$$

Proof. In order to make use of the results in [37, Theorem 2.3 (i)], we define an one-parameter family of linear operators on $C(\bar{\Omega}, \mathbb{R})$:

$$\mathcal{L}_\mu = d\Delta - \alpha + \frac{\beta(x)\lambda(x)u_1^*(x)}{\mu + \delta},\ \mu > -\delta.$$

Let $A := \min_{x\in\bar{\Omega}}[\beta(x)\lambda(x)u_1^*(x)] > 0$. It is easy to see that the eigenvalue problem

$$\begin{cases} \hat{\eta}\phi(x) = d\Delta\varphi(x) - \alpha\varphi(x), & x \in \Omega, \\ \dfrac{\partial\varphi(x)}{\partial\nu} = 0, & x \in \partial\Omega, \end{cases}$$

admits a principal eigenvalue, denoted by $\hat{\eta}^0 = -\alpha$, with an associated eigenvector $\varphi^0 \gg 0$. Let μ^* be the larger root of the algebraic equation

$$\mu^2 + (\delta - \hat{\eta}^0)\mu - (A + \hat{\eta}^0\delta) = 0.$$

Then $\mu^* = \frac{1}{2}[(\hat{\eta}^0 - \delta) + \sqrt{(\hat{\eta}^0 + \delta)^2 + 4A}] > -\delta$. It is easy to see that

$$\mathcal{L}_{\mu^*}\varphi^0 = d\Delta\varphi^0 - \alpha\varphi^0 + \frac{\beta(x)\lambda(x)u_1^*(x)}{\mu^* + \delta}\varphi^0 \geq (\hat{\eta}^0 + \frac{A}{\mu^* + \delta})\varphi^0 = \mu^*\varphi^0.$$

By [37, Theorem 2.3 (i)], we complete the proof of (i).

Since $-\delta < 0$, it follows from [37, Theorem 2.3 (ii)] that $s(\mathcal{B})$ has the same sign as $s(\mathcal{L}_0)$, where

$$\mathcal{L}_0 = d\Delta - \alpha + \frac{\beta(x)\lambda(x)u_1^*(x)}{\delta}.$$

□

Now we are ready to show that $s(\mathcal{B})$ is an index for disease extinction.

Theorem 2.2. *Let $\hat{\mu} = s(\mathcal{B})$ be the principal eigenvalue of the eigenvalue problem (2.11). If $\hat{\mu} < 0$, then the disease free equilibrium $(u_1^*(x), 0, 0)$ is globally attractive for the system (1.5). More precisely, if $u(x,t;\phi)$ is the solution of system (1.5) with $u(\cdot, 0; \phi) = \phi \in \mathbb{X}^+$, we have*

$$\lim_{t\to\infty} (u_1(x,t), u_2(x,t), u_3(x,t)) = (u_1^*(x), 0, 0), \text{ uniformly for all } x \in \overline{\Omega}.$$

Proof. For $\varepsilon \geq 0$, one can use the same arguments to those in Lemma 2.6 to show that the eigenvalue problem

$$\begin{cases} \mu\psi_2(x) = d\Delta\psi_2 + \beta(x)\left(u_1^*(x) + \varepsilon\right)\psi_3 - \alpha\psi_2, & x \in \Omega, \\ \mu\psi_3(x) = -\delta\psi_3 + \lambda(x)\psi_2, & x \in \Omega, \\ \dfrac{\partial\psi_2(x)}{\partial\nu} = 0, & x \in \partial\Omega, \end{cases} \tag{2.13}$$

has a principal eigenvalue, denoted by $\hat{\mu}_\varepsilon$, with an associated eigenvector $(\psi_2^\varepsilon(x), (\psi_3^\varepsilon(x)) \gg 0$. Since $\hat{\mu} < 0$, there exists a small $\varepsilon_0 > 0$ such that $\hat{\mu}_{\varepsilon_0} < 0$ and it corresponds to an associated eigenvector $(\psi_2^{\varepsilon_0}(x), \psi_3^{\varepsilon_0}(x)) \gg 0$.

From (2.7), it follows that

$$\limsup_{t\to\infty} u_1(x,t) \leq u_1^*(x) \text{ uniformly for } x \in \overline{\Omega}.$$

This implies that there exists a large $t_0 > 0$ such that

$$u_1(x,t) \leq u_1^*(x) + \varepsilon_0, \ t \geq t_0, \ x \in \overline{\Omega}.$$

From the second and third equations of (1.5), it follows that

$$\begin{cases} \dfrac{\partial u_2}{\partial t} \leq d\Delta u_2 + \beta(x)(u_1^*(x) + \varepsilon_0)u_3 - \alpha u_2, & x \in \Omega, \ t \geq t_0, \\ \dfrac{\partial u_3}{\partial t} \leq -\delta u_3 + \lambda(x)u_2, & x \in \Omega, \ t \geq t_0, \\ \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega, \ t \geq t_0. \end{cases} \tag{2.14}$$

For any given $\phi \in \mathbb{X}^+$, there exists some $a > 0$ such that $(u_2(x,t_0;\phi), u_3(x,t_0;\phi)) \leq a(\psi_2^{\varepsilon_0}(x), \psi_3^{\varepsilon_0}(x))$, for all $x \in \bar{\Omega}$. Note that the following linear system

$$\begin{cases} \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + \beta(x)(u_1^*(x) + \varepsilon_0)u_3 - \alpha u_2, & x \in \Omega, \ t \geq t_0, \\ \dfrac{\partial u_3}{\partial t} = -\delta u_3 + \lambda(x)u_2, & x \in \Omega, \ t \geq t_0, \\ \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega, \ t \geq t_0, \end{cases}$$

admits a solution $ae^{\hat{\mu}_{\varepsilon_0}(t-t_0)}(\psi_2^{\varepsilon_0}(x), \psi_3^{\varepsilon_0}(x))$, for all $t \geq t_0$. The comparison principle implies that

$$(u_2(x,t;\phi), u_3(x,t;\phi)) \leq ae^{\hat{\mu}_{\varepsilon_0}(t-t_0)}(\psi_2^{\varepsilon_0}(x), \psi_3^{\varepsilon_0}(x)), \ t \geq t_0,$$

which implies that $\lim_{t\to\infty}(u_2(x,t;\phi), u_3(x,t;\phi)) = 0$ uniformly for $x \in \bar\Omega$. Then the equation for u_1 is asymptotic to the system (2.4) and we get $\lim_{t\to\infty} u_1(x,t;\phi) = u_1^*(x)$ uniformly for $x \in \bar\Omega$ by Lemma 2.3 and the theory for asymptotically autonomous semiflows (see, e.g., [31, Corollary 4.3]). The proof is completed. $\square$

Remark 2.1. *From Lemma 2.6 (ii), it follows that $s(\mathcal{B}) < 0$ if*

$$\max_{x\in\bar\Omega}[\beta(x)\lambda(x)u_1^*(x)] < \alpha\delta. \tag{2.15}$$

By Theorem 2.2 and (2.15), it follows that the disease will become extinct if $\alpha\delta$ is large or $\max_{x\in\bar\Omega}[\beta(x)\lambda(x)]$ is small.

2.3. **Persistence.** Next we show the persistence for small α in the system (1.5). We establish some lemmas for that purpose. First we show the strict positiveness of solutions of (1.5).

Lemma 2.7. *Suppose that $u(x,t;\phi)$ is the solution of system (1.5) with $u(\cdot,0;\phi) = \phi \in \mathbb{X}^+$.*

(i) *If there exists some $t_0 \geq 0$ such that $u_1(\cdot,t_0;\phi) \not\equiv 0$, then $u_1(x,t;\phi) > 0$ for all $x \in \overline{\Omega}$, $t > t_0$;*
(ii) *If there exists some $t_0 \geq 0$ such that $u_2(\cdot,t_0;\phi) \not\equiv 0$, then $u_i(x,t;\phi) > 0$ for all $x \in \overline{\Omega}$, $t > t_0$, and $i = 2,3$.*

Proof. (i) From Lemma 2.1, it follows that $u_1(x,t)$ satisfies

$$d\Delta u_1(x,t) - \frac{\partial u_1(x,t)}{\partial t} + h_1(x,t)u_1(x,t) = -ru_1(x,t) \leq 0,\ x \in \Omega,\ t > 0,$$

where $h_1(x,t) := -\frac{r}{K(x)}[u_1(x,t)+u_2(x,t)] - \beta(x)u_3(x,t) \leq 0$. By similar arguments to that in [14, Lemma 2.1] and [35, Proposition 3.1], it follows from the strong maximum principle (see, e.g., [26, p. 172, Theorem 4]) and the Hopf boundary lemma (see, e.g., [26, p. 170, Theorem 3]) that part (i) holds.

(ii) From Lemma 2.1, it follows that $u_2(x,t)$ satisfies

$$d\Delta u_2(x,t) - \frac{\partial u_2(x,t)}{\partial t} + h_2(x,t)u_2(x,t) = -\beta(x)u_1(x,t)u_3(x,t) \leq 0,\ x \in \Omega,\ t > 0,$$

where $h_2(x,t) := -\alpha - \frac{r}{K(x)}[u_1(x,t) + u_2(x,t)] \leq 0$. Since $u_2(\cdot,t_0;\phi) \not\equiv 0$, it follows from the strong maximum principle and the Hopf boundary lemma that

$$u_2(x,t;\phi) > 0,\ \ x \in \overline{\Omega},\ \ t > t_0. \tag{2.16}$$

For fixed $x \in \overline{\Omega}$, $u_3(\cdot,t)$ satisfies an ordinary differential equation, then $u_3(x,t) > 0$ for $x \in \overline{\Omega}$, $t > t_0$ from $u_2 > 0$ and the equation of u_3. This completes the proof of part (ii). $\square$

It is easy to see that system (1.5) has a trivial equilibrium at $M_1 = (0,0,0)$ and a disease-free equilibrium at $M_2 = (u_1^*(\cdot),0,0)$, where $u_1^*(x)$ is the unique positive steady state of (2.4) which is globally asymptotically stable in $C(\overline{\Omega},\mathbb{R})$ for the dynamics of (2.4). Linearizing system (1.5) at the disease-free equilibrium

$(u_1^*(x),0,0)$, we get the following linear system:

$$\begin{cases} \dfrac{\partial w_1}{\partial t} = d\Delta w_1 + \dfrac{r}{K(x)}\left(K(x)-2u_1^*(x)\right)w_1 \\ \qquad\qquad -\dfrac{r}{K(x)}u_1^*(x)w_2 - \beta(x)u_1^*(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_2}{\partial t} = d\Delta w_2 - \alpha w_2 - \dfrac{r}{K(x)}u_1^*(x)w_2 + \beta(x)u_1^*(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_3}{\partial t} = -\delta w_3 + \lambda(x)w_2 - \beta(x)u_1^*(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_1}{\partial \nu} = \dfrac{\partial w_2}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0, \\ w_i(x,0) = w_i^0(x), & x\in\Omega,\ i=1,2,3. \end{cases} \tag{2.17}$$

Note that the equations for the infected host (w_2) and pathogen populations (w_3) decouple from the that for uninfected host population (w_1) in (2.17), forming the following subsystem which is cooperative:

$$\begin{cases} \dfrac{\partial w_2}{\partial t} = d\Delta w_2 - \alpha w_2 - \dfrac{r}{K(x)}u_1^*(x)w_2 + \beta(x)u_1^*(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_3}{\partial t} = -\delta w_3 + \lambda(x)w_2 - \beta(x)u_1^*(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_2}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0, \\ w_i(x,0) = w_i^0(x), & x\in\Omega,\ i=2,3. \end{cases} \tag{2.18}$$

The perturbation of the eigenvalue problem (2.18) will play a central role in proving the persistence of the system (1.5). To proceed further, we first consider the following more general linear parabolic system:

$$\begin{cases} \dfrac{\partial w_2}{\partial t} = d\Delta w_2 - \alpha w_2 - \dfrac{r}{K(x)}h_1(x)w_2 + \beta(x)h_2(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_3}{\partial t} = -\delta w_3 + \lambda(x)w_2 - \beta(x)h_1(x)w_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial w_2}{\partial \nu} = 0, & x\in\partial\Omega,\ t>0, \\ w_i(x,0) = w_i^0(x), & x\in\Omega,\ i=2,3. \end{cases} \tag{2.19}$$

where $h_1(x)>0$ and $h_2(x)>0$ for $x\in\overline{\Omega}$.

Denote by Π_t the solution semiflow of (2.17) on $\mathbf{C}$. The it is easy to see that Π_t is a positive C_0-semigroup on $\mathbf{C}$, and its generator $\mathcal{B}^{h_1,h_2}$ can be written as

$$\mathcal{B}^{h_1,h_2} = \begin{pmatrix} d\Delta - \alpha - \dfrac{r}{K(x)}h_1(x) & \beta(x)h_2(x) \\ \lambda(x) & -\delta-\beta(x)h_1(x) \end{pmatrix}.$$

Furthermore $\mathcal{B}^{h_1,h_2}$ is a closed and resolvent positive operator (see, e.g., [32, Theorem 3.12]). Again, Π_t is not compact since the second equation in (2.19) has no diffusion term.

Substituting $w_i(x,t) = e^{\Lambda t}\psi_i(x)$, $i = 2,3$, into (2.19), we obtain the following eigenvalue problem:

$$\begin{cases} \Lambda\psi_2 = d\Delta\psi_2 - \alpha\psi_2 - \dfrac{r}{K(x)}h_1(x)\psi_2 + \beta(x)h_2(x)\psi_3, & x \in \Omega, \\ \Lambda\psi_3 = -\delta\psi_3 + \lambda(x)\psi_2 - \beta(x)h_1(x)\psi_3, & x \in \Omega, \\ \dfrac{\partial\psi_2}{\partial\nu} = 0, & x \in \partial\Omega. \end{cases} \tag{2.20}$$

The following lemma concerns with the existence of the principal eigenvalue of (2.20).

Lemma 2.8. *Suppose that $h_1(x) > 0$ and $h_2(x) > 0$ for $x \in \overline{\Omega}$ and let $s(\mathcal{B}^{h_1,h_2})$ be the spectral bound of $\mathcal{B}^{h_1,h_2}$. If $s(\mathcal{B}^{h_1,h_2}) \geq 0$, then $s(\mathcal{B}^{h_1,h_2})$ is the principal eigenvalue of the eigenvalue problem (2.20), corresponding to which, there is a strongly positive eigenfunction.*

Proof. We first show that for each $t > 0$, Π_t is an κ-contraction on $\mathbf{C}$ in the sense that

$$\kappa(\Pi_t B) \leq e^{-\delta t}\kappa(B) \tag{2.21}$$

for any bounded set B in $\mathbf{C}$, where κ is the Kuratowski measure of noncompactness as defined in (2.9). Recall that $T_2(t)$ is the analytic semigroup on $C(\overline{\Omega}, \mathbb{R})$ defined by (2.1). Let $U_2(t) = T_2(t)$ and $U_3(t)\phi_3 = e^{-(\delta+\beta(\cdot)h_1(\cdot))t}\phi_3$ for $\phi_3 \in C(\overline{\Omega}, \mathbb{R})$. Obviously, $U(t) = (U_2(t), U_3(t))$ is a linear semigroup on $\mathbf{C}$.

Define a linear operator

$$I(t)\phi = (0, U_3(t)\phi_3), \quad \phi = (\phi_2, \phi_3) \in \mathbf{C}, \tag{2.22}$$

and a nonlinear operator

$$Q(t)\phi = \left(w_2(\cdot,t,\phi), \int_0^t U_3(t-s)[\lambda(\cdot)w_2(.,s,\phi))]ds\right), \ \phi = (\phi_2,\phi_3) \in \mathbf{C},$$

where

$$w_2(\cdot,t,\phi) = U_2(t)\phi_2 + \int_0^t U_2(t-s)g(w_2(\cdot,s,\phi), w_3(\cdot,s,\phi))ds,$$

where $g(w_2,w_3) = -\frac{r}{K(\cdot)}h_1(\cdot)w_2 + \beta(\cdot)h_2(\cdot)w_3$. It is easy to see that

$$\Pi_t(\phi) = I(t)\phi + Q(t)\phi, \ \phi \in \mathbf{C}, \ t \geq 0.$$

By (2.22), it follows that

$$\sup_{\phi\in\mathbf{C},||\phi||\neq 0}\frac{\|I(t)\phi\|}{\|\phi\|} \leq \sup_{\phi\in\mathbf{C},||\phi||\neq 0}\frac{\|e^{-(\delta+\beta(\cdot)h_1(\cdot))t}\phi_3\|}{\|\phi\|} \leq \sup_{\phi\in\mathbf{C},||\phi||\neq 0}\frac{\|e^{-\delta t}\phi_3\|}{\|\phi\|} \leq e^{-\delta t},$$

and hence $\|I(t)\| \leq e^{-\delta t}$.

From the boundedness of Π_t and the compactness of $U_2(t)$ for $t > 0$, it follows that $Q(t) : \mathbf{C} \to \mathbf{C}$ is compact for each $t > 0$. For any bounded set B in $\mathbf{C}$, there holds $\kappa(Q(t)B) = 0$ since $Q(t)B$ is precompact, and consequently,

$$\kappa(\Pi_t B) \leq \kappa(I(t)B) + \kappa(Q(t)B) \leq \|I(t)\|\kappa(B) \leq e^{-\delta t}\kappa(B), \ t > 0.$$

In the above inequality, we have used the fact that

$$\kappa(I(t)B) \leq \|I(t)\|\kappa(B), \quad t > 0,$$

since $I(t)$ is a linear operator. Thus, Π_t is an κ-contraction on $\mathbf{C}$ with a contracting function $e^{-\delta t}$. From (2.21), it follows that the essential spectral radius $r_e(\Pi_t)$ of Π_t satisfies

$$r_e(\Pi_t) \leq e^{-\delta t} < 1, \ \ t > 0.$$

On the other hand, the spectral radius $r(\Pi_t)$ of Π_t satisfies

$$r(\Pi_t) = e^{s(\mathcal{B}^{h_1,h_2})t} \geq 1, \ \ t > 0.$$

This implies that $r_e(\Pi_t) < r(\Pi_t)$ for any $t > 0$. Since Π_t is a strongly positive and bounded operator on $\mathbf{C}$, it follows from a generalized Krein-Rutman Theorem (see, e.g., [21]) that the stated conclusion holds. $\square$

Now we are ready to prove the main result of this section, which indicates that $s(\mathcal{B}^{u_1^*,u_1^*})$ is a crucial index for disease persistence.

Theorem 2.3. *Assume that $s(\mathcal{B}^{u_1^*,u_1^*}) > 0$. Then, the infection is uniformly persistent in the sense that there exists an $\eta > 0$ such that for any $\phi \in \mathbb{X}^+$ with $\phi_i \not\equiv 0$ for $i = 1, 2$, we have*

$$\liminf_{t\to\infty} u_i(x,t) \geq \eta, \ \forall\ i = 1, 2, \quad \textit{uniformly for all} \quad x \in \overline{\Omega}.$$

Moreover, System (1.5) admits at least one (componentwise) positive steady state $\hat{u}(x)$.

Proof. Let

$$\mathbb{W}_0 = \{\phi \in \mathbb{X}^+ : \phi_i(\cdot) \not\equiv 0, \ \forall\ i = 1, 2.\},$$

and

$$\partial\mathbb{W}_0 = \mathbb{X}^+ \backslash \mathbb{W}_0 = \{\phi \in \mathbb{X}^+ : \phi_1(\cdot) \equiv 0 \text{ or } \phi_2(\cdot) \equiv 0\}.$$

By Lemma 2.7, it follows that for any $\phi \in \mathbb{W}_0$, we have $u_i(x,t,\phi) > 0, \ \forall\ x \in \overline{\Omega}, \ t > 0, \ i = 1, 2, 3$. In other words, $\Psi(t)\mathbb{W}_0 \subseteq \mathbb{W}_0, \ \forall\ t \geq 0$.

Let

$$M_\partial := \{\phi \in \partial\mathbb{W}_0 : \Psi(t)\phi \in \partial\mathbb{W}_0, \forall\ t \geq 0\},$$

and $\omega(\phi)$ be the omega limit set of the orbit $\Gamma^+(\phi) := \{\Psi(t)\phi : t \geq 0\}$.

Claim: $\omega(\psi) = M_1 \cup M_2, \ \forall\ \psi \in M_\partial$, where $M_1 = \{(0,0,0)\}$ and $M_2 = \{(u_1^*, 0, 0)\}$.

Since $\psi \in M_\partial$, we have $\Psi(t)\psi \in M_\partial, \ \forall\ t \geq 0$. Thus $u_1(\cdot,t,\psi) \equiv 0$ or $u_2(\cdot,t,\psi) \equiv 0, \ \forall\ t \geq 0$. In the case where $u_2(\cdot,t,\psi) \equiv 0, \ \forall\ t \geq 0$, it follows from the second equation of (1.5) that $\beta(\cdot)u_1(\cdot,t,\psi)u_3(\cdot,t,\psi) \equiv 0$. From the third equation of (1.5), it follows that

$$\frac{\partial u_3(\cdot,t,\psi)}{\partial t} = -\delta u_3(\cdot,t,\psi), \ x \in \Omega, \ t > 0. \tag{2.23}$$

This implies that $\lim_{t\to\infty} u_3(x,t,\psi) = 0$ uniformly for $x \in \overline{\Omega}$. Thus, the equation for u_1 is asymptotic to the reaction-diffusion equation (2.4), and the theory for asymptotically autonomous semiflows (see, e.g., [31, Corollary 4.3]) and Lemma 2.3 imply that $\lim_{t\to\infty} u_1(x,t,\phi) = u_1^*(x)$ or $\lim_{t\to\infty} u_1(x,t,\phi) = 0$ uniformly for $x \in \overline{\Omega}$. In the case where $u_2(\cdot,\tilde{t}_0,\psi) \not\equiv 0$, for some $\tilde{t}_0 \geq 0$, Lemma 2.7 implies that $u_2(x,t,\psi) > 0, \ \forall\ x \in \overline{\Omega}, \ t > \tilde{t}_0$. Hence, $u_1(\cdot,t,\psi) \equiv 0, \ \forall\ t > \tilde{t}_0$. It follows from the second equation of (1.5) that

$$\begin{cases} \dfrac{\partial u_2}{\partial t} = d\Delta u_2 - \alpha u_2 - \dfrac{r}{K(x)}(u_2)^2, & x \in \Omega,\ t > \tilde{t}_0, \\ \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega,\ t > \tilde{t}_0, \\ u_2(x,0) = \psi(x), & x \in \Omega. \end{cases}$$

It is easy to see that $\lim_{t\to\infty} u_2(x,t,\psi) = 0$ uniformly for $x \in \overline{\Omega}$. Hence, the equation for u_3 is asymptotic to the reaction-diffusion equation (2.23) and the theory for asymptotically autonomous semiflows (see, e.g., [31, Corollary 4.3]) implies that $\lim_{t\to\infty} u_3(x,t,\psi) = 0$ uniformly for $x \in \overline{\Omega}$. Thus, $\omega(\psi) = M_1 \cup M_2,\ \forall\ \psi \in M_\partial$.

For convenience, we let $\Lambda(h_1,h_2) = s(\mathcal{B}^{h_1,h_2})$. By similar arguments to that in Lemma 2.8 and [16, Lemma 4.5], we can show that there is a small $\sigma_0 > 0$ such that $\tilde{\Lambda} := \Lambda(u_1^* + \sigma_0, u_1^* - \sigma_0)$ is the principal eigenvalue of the eigenvalue problem (2.20) with $h_1 \equiv u_1^* + \sigma_0$, $h_2 \equiv u_1^* - \sigma_0$ and $\tilde{\Lambda} := \Lambda(u_1^* + \sigma_0, u_1^* - \sigma_0) > 0$. Let $\tilde{\psi} := (\tilde{\psi}_2, \tilde{\psi}_3)$ be the strongly positive eigenfunction corresponding to $\tilde{\Lambda}$. We may further assume σ_0 satisfies

$$1 - \sigma_0 \max_{x\in\overline{\Omega}}(\frac{1}{K(x)} + \beta(x)) > 0.$$

Claim: $\limsup_{t\to\infty} \|\Psi(t)\phi - M_i\| \geq \frac{\sigma_0}{2},\ \forall\ \phi \in \mathbb{W}_0,\ \forall\ i = 1,2.$

Suppose, by contradiction, there exists $\phi_0 \in \mathbb{W}_0$ such that

$$\limsup_{t\to\infty} \|\Psi(t)\phi_0 - M_1\| < \frac{\sigma_0}{2} \text{ or } \limsup_{t\to\infty} \|\Psi(t)\phi_0 - M_2\| < \frac{\sigma_0}{2}.$$

In the case that $\limsup_{t\to\infty} \|\Psi(t)\phi_0 - M_2\| < \frac{\sigma_0}{2}$, there exists $t_1 > 0$ such that $u_1^*(x) + \frac{\sigma_0}{2} > u_1(x,t,\phi_0) > u_1^*(x) - \frac{\sigma_0}{2}$ and $u_2(x,t,\phi_0) < \frac{\sigma_0}{2}$, $\forall\ t \geq t_1$, $x \in \overline{\Omega}$. Thus $u_2(x,t,\phi_0)$ and $u_3(x,t,\phi_0)$ satisfies

$$\begin{cases} \dfrac{\partial u_2}{\partial t} \geq d\Delta u_2 - \alpha u_2 - \dfrac{r}{K(x)}(u_1^*(x) + \sigma_0)u_2 + \beta(x)(u_1^*(x) - \sigma_0)u_3, & x \in \Omega, t > t_1, \\ \dfrac{\partial u_3}{\partial t} \geq -\delta u_3 + \lambda(x)u_2 - \beta(x)(u_1^*(x) + \sigma_0)u_3, & x \in \Omega, t > t_1, \\ \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega, t > t_1. \end{cases} \tag{2.24}$$

By Lemma 2.7, it follows that $u_i(x,t,\phi_0) > 0,\ \forall\ x \in \overline{\Omega},\ t > 0,\ i = 2,3$, and hence, there exists $\epsilon_0 > 0$ such that $(u_2(x,t_1,\phi_0), u_3(x,t_1,\phi_0)) \geq \epsilon_0\tilde{\psi}$. Note that $\epsilon_0 e^{\tilde{\Lambda}(t-t_1)}\tilde{\psi}$ is a solution of the following linear system:

$$\begin{cases} \dfrac{\partial v_2}{\partial t} = d\Delta v_2 - \alpha v_2 - \dfrac{r}{K(x)}(u_1^*(x) + \sigma_0)v_2 + \beta(x)(u_1^*(x) - \sigma_0)v_3, & x \in \Omega, t > t_1, \\ \dfrac{\partial v_3}{\partial t} = -\delta v_3 + \lambda(x)v_2 - \beta(x)(u_1^*(x) + \sigma_0)v_3, & x \in \Omega, t > t_1, \\ \dfrac{\partial v_2}{\partial \nu} = 0, & x \in \partial\Omega, t > t_1. \end{cases} \tag{2.25}$$

The comparison principle implies that

$$(u_2(x,t,\phi_0), u_3(x,t,\phi_0)) \geq \epsilon_0 e^{\tilde{\Lambda}(t-t_1)}\tilde{\psi},\ \forall\ t > t_1,\ x \in \overline{\Omega}.$$

Since $\tilde{\Lambda} > 0$, it follows that $u(x,t,\phi_0)$ is unbounded. This is a contradiction.

In the case that $\limsup_{t\to\infty} \|\Psi(t)\phi_0 - M_1\| < \frac{\sigma_0}{2}$, there exists $t_2 > 0$ such that $u_1^*(x) < \frac{\sigma_0}{2}$ and $u_2(x,t,\phi_0) < \frac{\sigma_0}{2}$, $\forall\ t \geq t_2$, $x \in \overline{\Omega}$. From the u_1 equation in (1.5), it follows that

$$\begin{cases} \dfrac{\partial u_1(x,t)}{\partial t} \geq d\Delta u_1 + r[1-\sigma_0(\dfrac{1}{K(x)}+\beta(x))]u_1 & \\ \qquad\qquad \geq d\Delta u_1 + r[1-\sigma_0\theta]u_1, & x\in\Omega,\ t>t_2, \\ \dfrac{\partial u_1}{\partial \nu} = 0, & x \in \partial\Omega, \end{cases} \tag{2.26}$$

where $\theta := \max_{x\in\overline{\Omega}}(\frac{1}{K(x)} + \beta(x))$. It is easy to see that $(\tilde{\eta}^0, \varphi^0(x)) = (0,1)$ is the pair of principal eigenvalue-eigenfunction of

$$\begin{cases} \tilde{\eta}\phi(x) = d\Delta\phi(x), & x\in\Omega, \\ \dfrac{\partial\phi(x)}{\partial\nu} = 0, & x\in\partial\Omega. \end{cases}$$

Since $u_1(x,t_2,\phi_0) > 0$, $\forall\ x \in \overline{\Omega}$, it follows that there exists $b > 0$ such that $u_1(x,t_2,\phi_0) \geq b\varphi^0(x)$. By the standard comparison principle, it follows that

$$u_1(x,t) \geq e^{r[1-\sigma_0\theta](t-t_2)}\varphi^0(x),\ t > t_2,\ x\in\overline{\Omega}.$$

Since $1-\sigma_0\theta > 0$, it follows that $u_1(x,t,\phi_0)$ is unbounded. This contradiction completes the proof of the claim.

Define a continuous function $\rho : \mathbb{X}^+ \to [0,\infty)$ by

$$\rho(\phi) := \min_{1\leq i\leq 2}\{\min_{x\in\overline{\Omega}} \phi_i(x)\},\ \forall\ \phi\in\mathbb{X}^+.$$

By Lemma 2.7, it follows that $\rho^{-1}(0,\infty) \subseteq \mathbb{W}_0$ and ρ has the property that if $\rho(\phi) > 0$ or $\phi \in \mathbb{W}_0$ with $\rho(\phi) = 0$, then $\rho(\Psi(t)\phi) > 0$, $\forall\ t > 0$. That is, ρ is a generalized distance function for the semiflow $\Psi(t) : \mathbb{X}^+ \to \mathbb{X}^+$ (see, e.g., [30]). From the above claims, it follows that any forward orbit of $\Psi(t)$ in M_∂ converges to $M_1 \cup M_2$ which is isolated in $\mathbb{X}^+$ and $W^S(M_i) \cap \mathbb{W}_0 = \emptyset$, $\forall\ i = 1,2$, where $W^S(M_i)$ is the stable set of M_i, $i = 1,2$ (see [30]). It is obvious that there is no cycle in M_∂ from $M_1 \cup M_2$ to $M_1 \cup M_2$. By [30, Theorem 3], it follows that there exists an $\eta > 0$ such that

$$\min_{\psi\in\omega(\phi)} \rho(\psi) > \eta,\ \forall\ \phi\in\mathbb{W}_0.$$

Hence, $\liminf_{t\to\infty} u_i(\cdot,t,\phi) \geq \eta$, $\forall\ \phi \in \mathbb{W}_0$, $i = 1,2$. Therefore, the uniform persistence stated in the theorem is valid. By [20, Theorem 3.7 and Remark 3.10], it follows that $\Psi(t) : \mathbb{W}_0 \to \mathbb{W}_0$ has a global attractor A_0. It then follows from [20, Theorem 4.7] that $\Psi(t)$ has an equilibrium $\tilde{u}(\cdot) := (\tilde{u}_1(\cdot), \tilde{u}_2(\cdot), \tilde{u}_3(\cdot)) \in \mathbb{W}_0$. Further, Lemma 2.7 implies that $\tilde{u}_i(\cdot) > 0$, $\forall\ i = 1,2$. It remains to show that $\tilde{u}_3(\cdot) > 0$. Indeed, from the third equation of (1.5), it follows that

$$\tilde{u}_3(\cdot) = \frac{\lambda(x)\tilde{u}_2(\cdot)}{\delta + \beta(\cdot)(\tilde{u}_1(\cdot)+\tilde{u}_2(\cdot))} > 0.$$

This implies that $\tilde{u}(\cdot)$ is a positive steady state of (1.5). The proof is completed. □

Remark 2.2. We regret to point out that when $s(\mathcal{B}^{u_1^*,u_1^*}) < 0$, we are unable to determine the dynamics of the system (1.5) at the present.

2.4. **The basic reproduction number.** In this subsection, we adopt the approach of next generation operators (see, e.g., [8, 32], also see more recent work [12, 34, 36, 37]) to define the basic reproduction number for the system (1.5). The cooperative system (2.18) is the linearized system of (1.5) at the disease-free equilibrium $(u_1^*, 0, 0)$. Thus, the matrices $\mathbb{F}$ and $\mathbb{V}$ defined in [37, Eq. (3.4)] become

$$\mathbb{F}(x) = \begin{pmatrix} 0 & \beta(x)u_1^*(x) \\ 0 & 0 \end{pmatrix}, \ \mathbb{V}(x) = \begin{pmatrix} \alpha + \frac{r}{K(x)}u_1^*(x) & 0 \\ -\lambda(x) & \delta + \beta(x)u_1^*(x) \end{pmatrix}.$$

Let $\mathbb{S}(t) : C(\bar{\Omega}, \mathbb{R}^2) \to C(\bar{\Omega}, \mathbb{R}^2)$ be the C_0-semigroup generated by the following system

$$\begin{cases} \dfrac{\partial w_2}{\partial t} = d\Delta w_2 - \alpha w_2 - \dfrac{r}{K(x)}u_1^*(x)w_2, & x \in \Omega, \ t > 0, \\ \dfrac{\partial w_3}{\partial t} = -\delta w_3 + \lambda(x)w_2 - \beta(x)u_1^*(x)w_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial w_2}{\partial \nu} = 0, & x \in \partial\Omega, \ t > 0, \\ w_i(x, 0) = w_i^0(x), & x \in \Omega, \ i = 2, 3. \end{cases} \tag{2.27}$$

It is easy to see $\mathbb{S}(t)$ is a positive C_0-semigroup on $C(\bar{\Omega}, \mathbb{R}^2)$.

In order to define the basic reproduction number for the system (1.5), we assume that the state variables are near the disease-free steady state $(u_1^*(x), 0, 0)$. Then with an given initial distribution of infections described by $(\varphi_2(\cdot), \varphi_3(\cdot)) \in C(\bar{\Omega}, \mathbb{R}^2)$, solving (2.27) with this given initial distribution will give a distribution of total infections caused by $(\varphi_2(\cdot), \varphi_3(\cdot))$, which is

$$\int_0^\infty \mathbb{F}(x)\mathbb{S}(t)(\varphi_2, \varphi_3)(x)dt.$$

Let $\mathbb{L} : C(\bar{\Omega}, \mathbb{R}^2) \to C(\bar{\Omega}, \mathbb{R}^2)$ be defined by the above integral, i.e.,

$$\mathbb{L}(\varphi_2, \varphi_3)(x) = \int_0^\infty \mathbb{F}(x)\mathbb{S}(t)(\varphi_2, \varphi_3)(x)dt.$$

Then $\mathbb{L}$ is nothing but the next generation operator of the model system (see, e.g., [8, 12, 32, 34, 36, 37]), the spectral radian of $\mathbb{L}$ we gives the basic reproduction number of the model, that is,

$$\mathcal{R}_0 := r(\mathbb{L}). \tag{2.28}$$

By [37, Theorem 3.1 (i) and Remark 3.1], we then have the following result.

Lemma 2.9. *$\mathcal{R}_0 - 1$ and $s(\mathcal{B}^{u_1^*, u_1^*})$ have the same sign, where $s(\mathcal{B}^{u_1^*, u_1^*})$ is the generator associated with the linear system (2.18).*

By Lemma 2.9, we may restate Theorem 2.3 as follows:

Theorem 2.4. *Assume that $\mathcal{R}_0 > 1$. Then, the infection is uniformly persistent in the sense that there exists an $\eta > 0$ such that such that for any $\phi \in \mathbb{X}^+$ with $\phi_i \not\equiv 0$ for $i = 1, 2$, we have*

$$\liminf_{t\to\infty} u_i(x, t) \geq \eta, \ \forall \ i = 1, 2, \quad \textit{uniformly for all} \quad x \in \overline{\Omega}.$$

Moreover, System (1.5) admits at least one (componentwise) positive steady state $\hat{u}(x)$.

By the same arguments as in [37, Lemma 4.2 and Theorem 3.2 (ii)], we have the following observation.

Lemma 2.10. *Let η_0 be the principal eigenvalue of the following eigenvalue problem:*

$$\begin{cases} -d\Delta\psi + \left(\alpha + \dfrac{r}{K(x)}u_1^*(x)\right)\psi = \eta\dfrac{\beta(x)\lambda(x)u_1^*(x)}{\delta+\beta(x)u_1^*(x)}\psi, & x\in\Omega, \\ \dfrac{\partial\psi(x)}{\partial\nu} = 0, & x\in\partial\Omega. \end{cases} \tag{2.29}$$

Then $\mathcal{R}_0 = \frac{1}{\eta_0}$.

Remark 2.3. When all parameters in (1.5) are constants, one can easily see that $u_1^*(x) \equiv K$, and one can actually calculate the spectral radius to obtain

$$\mathcal{R}_0 = \frac{1}{\eta_0} = \frac{\beta\lambda K}{\delta+\beta K} \Big/ \left(\alpha + \frac{r}{K}K\right) = \frac{\beta\lambda K}{(\delta+\beta K)(\alpha+r)}. \tag{2.30}$$

At the end of this section, we briefly mention a modified version of system (1.5). We may assume that susceptible and infected classes have different movement rates, and pathogen also adopts movement. Then system (1.5) can be modified as follows:

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d_1\Delta u_1 + r\left(1-\dfrac{u_1+u_2}{K(x)}\right)u_1 - \beta(x)u_1u_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_2}{\partial t} = d_2\Delta u_2 + \beta(x)u_1u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K(x)}u_2, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_3}{\partial t} = d_3\Delta u_3 - \delta u_3 + \lambda(x)u_2 - \beta(x)(u_1+u_2)u_3, & x\in\Omega,\ t>0, \\ \dfrac{\partial u_1}{\partial\nu} = \dfrac{\partial u_2}{\partial\nu} = \dfrac{\partial u_3}{\partial\nu} = 0, & x\in\partial\Omega,\ t>0, \\ u_i(x,0) = u_i^0(x), & x\in\Omega,\ i=1,2,3. \end{cases} \tag{2.31}$$

We note that our arguments used in the analysis of (1.5) can be applied to system (2.31), except those in Lemma 2.4. Due to the fact that $d_1 \neq d_2$, the arguments used in Lemma 2.4 do NOT work. Next, we sketch an approach in proving the boundedness of $u_i(x,t)$, $i=1,2,3$. From the first equation of (2.31), it follows that

$$\frac{\partial u_1}{\partial t} \le d_1\Delta u_1 + r\left(1-\frac{u_1}{K(x)}\right)u_1,$$

which implies that $u_1(x,t)$ is uniformly bounded. Let $V(t) := \int_\Omega (u_1(x,t)+u_2(x,t))dx$. Then it is easy to see that

$$\frac{dV(t)}{dt} + \alpha V(t) \le (\alpha+r)\int_\Omega u_1(x,t)dx \le \rho, \text{ for some } \rho>0.$$

By Gronwall's inequality we get the L^1 estimates,

$$V(t) \le V(0)e^{-\alpha t} + \frac{\rho}{\alpha}(1-e^{-\alpha t}).$$

With the L^1 estimates, one can show that $u_2(x,t)$ is uniformly bounded (see e. g. [1, 17]). Since $u_2(x,t)$ is uniformly bounded, it follows from the third equation of (2.31) that $u_3(x,t)$ is uniformly bounded. Thus, the results in Lemma 2.4 can be obtained when system (1.5) is replaced by (2.31). We also note that $d_i > 0$, $i = 1,2,3$, and hence, it follows that the solution maps generated by system (2.31) are compact, and hence, Lemma 2.5 is automatically valid. In other words, when we assume that susceptible and infected classes have different movement rates and pathogen also adopts movement, the mathematical analysis is similar to those in (1.5).

3. **Bifurcation Analysis.** In Theorem 2.4 we have proved that system (1.5) is uniformly persistent when $\mathcal{R}_0 > 1$, thus (1.5) admits at least one positive steady state solution. In this section, we consider the steady state equation directly to obtain more information on the set of positive steady state solutions. The steady state solutions of (1.5) satisfy

$$\begin{cases} d\Delta u_1 + r\left(1 - \dfrac{u_1+u_2}{K(x)}\right)u_1 - \beta(x)u_1u_3 = 0, & x \in \Omega, \\ d\Delta u_2 + \beta(x)u_1u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K(x)}u_2 = 0, & x \in \Omega, \\ -\delta u_3 + \lambda(x)u_2 - \beta(x)(u_1+u_2)u_3 = 0, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial \nu} = \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.1}$$

From the third equation of (3.1), it follows that u_3 satisfies

$$u_3(x) = \frac{\lambda(x)u_2(x)}{\delta + \beta(x)(u_1(x)+u_2(x))}. \tag{3.2}$$

Then (3.1) is equivalent to

$$\begin{cases} d\Delta u_1 + r\left(1 - \dfrac{u_1+u_2}{K(x)}\right)u_1 - \dfrac{\beta(x)\lambda(x)u_1u_2}{\delta + \beta(x)(u_1+u_2)} = 0, & x \in \Omega, \\ d\Delta u_2 + \dfrac{\beta(x)\lambda(x)u_1u_2}{\delta + \beta(x)(u_1+u_2)} - \alpha u_2 - r\dfrac{u_1+u_2}{K(x)}u_2 = 0, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial \nu} = \dfrac{\partial u_2}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.3}$$

It is easy to see that $(u_1^*(x), 0)$ is a semi-trivial steady state solution of (3.3), where $u_1^*(x)$ is the unique positive steady state solution of the diffusive logistic equation (2.4).

We use the rate of disease-induced mortality α as the main bifurcation parameter. Denote α^0 to be the principal eigenvalue of the following eigenvalue problem:

$$\begin{cases} d\Delta\psi + \left[\dfrac{\beta(x)\lambda(x)}{\delta + \beta(x)u_1^*(x)} - \dfrac{r}{K(x)}\right]u_1^*(x)\psi = \alpha\psi, & x \in \Omega, \\ \dfrac{\partial\psi(x)}{\partial\nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.4}$$

with the corresponding positive eigenfunction $\psi_0(x)$ uniquely determined by the normalization $\max_{\overline{\Omega}} \psi_0(x) = 1$. Notice that $\alpha = \alpha^0$ is equivalent to $\eta_0 = 1$ or $\mathcal{R}_0 = 1$ in (2.29). Let

$$H(x) = \left[\frac{\beta(x)\lambda(x)}{\delta + \beta(x)u_1^*(x)} - \frac{r}{K(x)}\right]u_1^*(x). \tag{3.5}$$

It is easy to see that $\alpha^0 = H$ if $H(x) \equiv H$ is a constant. We next consider the case where $H(x) \not\equiv$ constant and it could change sign in Ω. Consider the eigenvalue problem with indefinite weight:

$$\begin{cases} \Delta\varphi(x) + \Lambda H(x)\varphi = 0, & x \in \Omega, \\ \dfrac{\partial\varphi(x)}{\partial\nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.6}$$

It follows from [22, Theorem 4.2] that the problem (3.6) has a nonzero principal eigenvalue $\Lambda_0 = \Lambda_0(H)$ if and only if $H(x)$ changes sign in Ω and $\int_\Omega H(x)dx \neq 0$.

The following lemma concerns with the sign of the principal eigenvalue α^0.

Lemma 3.1. [22, Proposition 4.4] *The principal eigenvalue α^0 of the problem (3.4) has the following properties:*

(i) *If $\int_\Omega H(x)dx \geq 0$, then $\alpha^0 > 0$ for all $d > 0$;*

(ii) *If $\int_\Omega H(x)dx < 0$, then*

$$\begin{cases} \alpha^0 > 0 & \text{for all } \ d < \frac{1}{\Lambda_0(H)}. \\ \alpha^0 < 0 & \text{for all } \ d > \frac{1}{\Lambda_0(H)}. \end{cases}$$

Remark 3.1. Assume that the coefficients of (3.1) are all constants, that is, $u_1^*(x) \equiv K$ and

$$H(x) \equiv H = \left[\frac{\beta\lambda}{\delta + \beta K} - \frac{r}{K}\right] K = \frac{\beta K(\lambda - r) - \delta r}{\delta + \beta K}. \tag{3.7}$$

Then $\alpha^0 = H > 0$ if (a) λ is large, or (b)$\lambda > r$, δ is small, and β is large.

We use α as a bifurcation parameter and show that a local branch (and also a global continuum) of positive solutions of (3.3) bifurcates from the branch of semi-trivial solutions $\{(\alpha, u_1^*(x), 0) : \alpha > 0\}$. We note that $u_1^*(x)$ is independent of the parameter α. Let $u = u_1$ and $w = u_2$. Then (3.3) becomes

$$\begin{cases} d\Delta u + \dfrac{r}{K(x)}\left(K(x) - u - w\right) u - \dfrac{\beta(x)\lambda(x)uw}{\delta + \beta(x)(u + w)} = 0, & x \in \Omega, \\ d\Delta w + \dfrac{\beta(x)\lambda(x)uw}{\delta + \beta(x)(u + w)} - \alpha w - \dfrac{r}{K(x)}(u + w)w = 0, & x \in \Omega, \\ \dfrac{\partial u(x)}{\partial \nu} = \dfrac{\partial w(x)}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.8}$$

For $p > n$, let $X = \{u \in W^{2,p}(\Omega) : \frac{\partial u(x)}{\partial \nu} = 0,\ x \in \partial\Omega\}$, and $Y = L^p(\Omega)$. We define the set of positive solutions of (3.3) to be

$$\Sigma = \{\alpha, u, w) \in \mathbf{R}^+ \times X \times X : (\alpha, u, w) \text{ is a positive solution of (3.3).}\} \tag{3.9}$$

We now state the main result of this section regrading the set of steady state solutions of (3.3).

Theorem 3.1. *Assume that α^0 is the principal eigenvalue of the eigenvalue problem (3.4). Then*

(i) *There is a connected component Σ_1 of $\overline{\Sigma}$ containing $(\alpha^0, u_1^*, 0)$, and the projection $proj_\alpha \Sigma_1$ of Σ_1 into the α-axis satisfies $(0, \alpha^0] \subset proj_\alpha \Sigma_1 \subset (0, M]$ for*

$$M = \frac{\max\limits_{x \in \overline{\Omega}}[\beta(x)\lambda(x)u_1^*(x)]}{\delta}. \tag{3.10}$$

In particular, (3.3) admits at least one positive steady state solution for $0 < \alpha < \alpha^0$.

(ii) *Near $\alpha = \alpha^0$, Σ_1 is a smooth curve*

$$C_1 = \{(\alpha(s), u(s), w(s)) : s \in (0, \varepsilon)\}, \tag{3.11}$$

where $u(s) = u_1^*(\cdot) + s\phi_0(\cdot) + o(s)$, $w(s) = s\psi_0(\cdot) + o(s)$ where $\psi_0(x) > 0$ is the principal eigenfunction of (3.4), and $\phi_0(x) < 0$ satisfies

$$\begin{cases} -d\Delta\phi_0(x) - \dfrac{r}{K(x)}\left[K(x) - 2u_1^*(x)\right]\phi_0(x) = -q(x)\psi_0(x), & x \in \Omega, \\ \dfrac{\partial \phi_0(x)}{\partial \nu} = 0, & x \in \partial\Omega. \end{cases} \tag{3.12}$$

Moreover

$$\alpha'(0) = \frac{I}{\int_\Omega \psi_0^2(x)dx}, \tag{3.13}$$

where

$$I = \int_\Omega \frac{\beta(x)\lambda(x)\delta\phi_0(x)\left(\psi_0(x)\right)^2}{\left[\delta+\beta(x)u_1^*(x)\right]^2}dx - \int_\Omega \frac{r\left[\phi_0(x)\left(\psi_0(x)\right)^2 + \left(\psi_0(x)\right)^3\right]}{K(x)}dx$$
$$- \int_\Omega \frac{(\beta(x))^2\lambda(x)u_1^*(x)\left(\psi_0(x)\right)^3}{\left[\delta+\beta(x)u_1^*(x)\right]^2}dx. \tag{3.14}$$

Proof. We apply a global bifurcation theorem in [28] to consider the solutions of (3.3). Define $F : \mathbf{R} \times X \times X \to Y \times Y$ by

$$F(\alpha, u, w) = \begin{pmatrix} d\Delta u + \dfrac{r}{K(x)}\left(K(x) - u - w\right)u - p(u,w) \\ d\Delta w + p(u,w) - \alpha w - \dfrac{r}{K(x)}(u+w)w \end{pmatrix},$$

where $p(u,w) := \frac{\beta(x)\lambda(x)uw}{\delta+\beta(x)(u+w)}$. By direct calculations,

$$F_{(u,w)}(\alpha,u,w)[\phi,\psi]$$
$$= \begin{pmatrix} d\Delta\phi \\ d\Delta\psi \end{pmatrix} + \begin{pmatrix} \dfrac{r}{K(x)}\left(K(x) - 2u - w\right) - p_u & -\dfrac{r}{K(x)}u - p_w \\ p_u - \dfrac{r}{K(x)}w & p_w - \alpha - \dfrac{r}{K(x)}(u+2w) \end{pmatrix}\begin{pmatrix} \phi \\ \psi \end{pmatrix},$$

where the partial derivatives of p are given by

$$p_u := p_u(u,w) = \frac{\beta(x)\lambda(x)(\delta+\beta(x)w)w}{\left[\delta+\beta(x)(u+w)\right]^2}, \quad p_w := p_w(u,w) = \frac{\beta(x)\lambda(x)(\delta+\beta(x)u)u}{\left[\delta+\beta(x)(u+w)\right]^2}.$$

Note that

$$p_u(u_1^*,0) = 0, \; p_w(u_1^*,0) = \frac{\beta(x)\lambda(x)u_1^*(x)}{\delta+\beta(x)u_1^*(x)}.$$

Furthermore,

$$F_\alpha(\alpha,u,w) = \begin{pmatrix} 0 \\ -w \end{pmatrix}, \quad F_{\alpha,(u,w)}(\alpha,u,w)[\phi,\psi] = \begin{pmatrix} 0 \\ -\psi \end{pmatrix},$$

and

$$F_{(u,w),(u,w)}(\alpha,u,w)[\phi,\psi]^2$$
$$= \begin{pmatrix} -\left(\dfrac{2r}{K(x)} + p_{uu}\right)\phi^2 - 2\left(\dfrac{r}{K(x)} + p_{uw}\right)\phi\psi - p_{ww}\psi^2 \\ p_{uu}\phi^2 + 2\left(p_{uw} - \dfrac{r}{K(x)}\right)\phi\psi + \left(p_{ww} - \dfrac{2r}{K(x)}\right)\psi^2 \end{pmatrix},$$

where the second derivatives of p are given by

$$p_{uu} := p_{uu}(u,w) = \frac{-2\lambda(x)\left(\beta(x)\right)^2(\delta+\beta(x)w)w}{\left[\delta+\beta(x)(u+w)\right]^3},$$
$$p_{uw} := p_{uw}(u,w) = \frac{\beta(x)\lambda(x)\left(\delta^2 + \beta(x)\delta u + \beta(x)\delta w + 2\left(\beta(x)\right)^2 uw\right)}{\left[\delta+\beta(x)(u+w)\right]^3},$$
$$p_{ww} := p_{ww}(u,w) = \frac{-2\lambda(x)\left(\beta(x)\right)^2(\delta+\beta(x)u)u}{\left[\delta+\beta(x)(u+w)\right]^3}.$$

Note that

$$\begin{cases} p_{uu}(u_1^*,0)=0,\ p_{uw}(u_1^*,0)=\dfrac{\beta(x)\lambda(x)\delta}{[\delta+\beta(x)u_1^*(x)]^2}, \\ p_{ww}(u_1^*,0)=-\dfrac{2(\beta(x))^2\lambda(x)u_1^*(x)}{[\delta+\beta(x)u_1^*(x)]^2}. \end{cases} \tag{3.15}$$

In particular,

$$F_{(u,w)}(\alpha^0,u_1^*,0)[\phi,\psi]=\begin{pmatrix} d\Delta\phi+\dfrac{r}{K(x)}\left[K(x)-2u_1^*(x)\right]\phi-q(x)\psi \\ d\Delta\psi-\alpha^0\psi+H(x)\psi \end{pmatrix},$$

where α^0 is the principal eigenvalue of the eigenvalue problem (3.4), $H(x)$ is defined as in (3.5) and

$$q(x)=\frac{r}{K(x)}u_1^*(x)+\frac{\beta(x)\lambda(x)u_1^*(x)}{\delta+\beta(x)u_1^*(x)}>0. \tag{3.16}$$

It is easy to verify that the kernel $N(F_{(u,w)}(\alpha^0,u_1^*,0))=span\{(\phi_0,\psi_0)\}$, where ψ_0 is the positive eigenfunction of (3.4) and ϕ_0 satisfies (3.12). By Lemma 2.3, it follows that $u_1^*(x)$ is globally asymptotically stable in $C(\overline{\Omega},\mathbb{R})$ for the diffusive logistic equation (2.4). This implies that

$$\left[-d\Delta-\frac{r}{K(x)}\left(K(x)-2u_1^*(x)\right)\right]^{-1}$$

exists and it is a positive operator. Thus, $\phi_0(x)<0$ for $x\in\Omega$.

Next we show that the range

$$R(F_{(u,w)}(\alpha^0,u_1^*,0))=\left\{(h_1,h_2)\in Y^2:\int_\Omega h_2(x)\psi_0(x)dx=0\right\}. \tag{3.17}$$

In fact, $(h_1,h_2)\in R(F_{(u,w)}(\alpha^0,u_1^*,0))$ if and only if there exists $(\phi,\psi)\in X\times X$ such that

$$\begin{aligned} h_1&=d\Delta\phi+\frac{r}{K(x)}\left[K(x)-2u_1^*(x)\right]\phi-q(x)\psi, \\ h_2&=d\Delta\psi-\alpha^0\psi+H(x)\psi, \end{aligned}$$

where $q(x)$ and $H(x)$ are defined as in (3.16) and (3.5). It then follows that

$$\int_\Omega h_2(x)\psi_0(x)dx=d\int_\Omega\Delta\psi(x)\psi_0(x)dx+\int_\Omega\left[-\alpha^0\psi_0(x)+H(x)\psi_0(x)\right]\psi(x)dx. \tag{3.18}$$

By integration by parts and the boundary conditions of ψ and ψ_0, it follows that

$$\int_\Omega\Delta\psi(x)\psi_0(x)dx=\int_\Omega\Delta\psi_0(x)\psi(x)dx. \tag{3.19}$$

From (3.4), (3.19) and (3.18), it follows that $\int_\Omega h_2(x)\psi_0(x)dx=0$ which implies (3.17). Since

$$F_{\alpha,(u,w)}(\alpha^0,u_1^*,0)[\phi_0,\psi_0]=(0,-\psi_0), \tag{3.20}$$

and $\int_\Omega[-\psi_0(x)]\psi_0(x)dx<0$. This implies that

$$F_{\alpha,(u,w)}(\alpha^0,u_1^*,0)[\phi_0,\psi_0]\notin R(F_{(u,w)}(\alpha^0,u_1^*,0)).$$

Thus we can apply the theorem of bifurcation from a simple eigenvalue by Crandall and Rabinowitz [6] (see also [27]) to conclude that the set of positive solutions to

(3.8) near $(\alpha^0, u_1^*(x), 0)$ is a curve in form (3.11), with $(u'(0), w'(0)) = (\phi_0, \psi_0)$. Moreover $\alpha'(0)$ can be calculated as follows (see [27] and Refs. [10, 11]):

$$\alpha'(0) = -\frac{\langle l, F_{(u,w),(u,w)}(\alpha^0, u_1^*, 0)[\phi_0, \psi_0]^2\rangle}{2\langle l, F_{\alpha,(u,w)}(\alpha^0, u_1^*, 0)[\phi_0, \psi_0]\rangle},$$

where l is a linear functional on Y^2 defined as $\langle l, [h_1, h_2]\rangle = \int_\Omega h_2(x)\psi_0(x)dx$. Note that the second component of $F_{(u,w),(u,w)}(\alpha^0, u_1^*, 0)[\phi_0, \psi_0]^2$ takes the form

$$G(x) := 2\left(p_{uw}(u_1^*(x), 0) - \frac{r}{K(x)}\right)\phi_0(x)\psi_0(x) + \left(p_{ww}(u_1^*(x), 0) - \frac{2r}{K(x)}\right)(\psi_0(x))^2,$$

where $p_{uw}(u_1^*, 0)$ and $p_{ww}(u_1^*, 0)$ are defined in (3.15). Thus,

$$\alpha'(0) = \frac{\int_\Omega G(x)\psi_0(x)dx}{2\int_\Omega \psi_0^2(x)dx} := \frac{I}{\int_\Omega \psi_0^2(x)dx}, \tag{3.21}$$

where I is defined as in (3.14).

Next we apply [28, Theorem 4.4] to $F(\alpha, u, w) = 0$ with $V = \mathbf{R}_+ \times (X^+)^2$ where $X^+ = \{u \in X : u > -\epsilon\}$ for some $\epsilon > 0$. From the remarks after [28, Theorem 4.4] and discussions above, all conditions in [28, Theorem 4.4] are satisfied. Therefore there exists a connected component Σ_1 of Σ containing the curve C_1, and Σ_1 satisfies either (i) it is not compact; or (ii) it contains a point $(\alpha^*, u_1^*, 0)$ with $\alpha^* \neq \alpha^0$; or (iii) it contains a point $(\alpha, u_1^* + U, W)$, where $(U, W) \neq 0$ and (U, W) is in a compliment of $span\{(\phi_0, \psi_0)\}$. Note that the equations of u and w are all in a form of $d\Delta V + g(x)V = 0$ for $V = u$ or w thus a weak form of maximum principle holds, and all solutions on the connected component Σ_1 are necessarily positive. Since $\psi_0 > 0$, then W must be sign-changing and such $(\alpha, u_1^* + U, W)$ cannot be on Σ_1 hence (iii) is not possible. Similarly (ii) is also impossible as the eigenvalue of (3.4) with positive eigenfunction is unique. Therefore Σ_1 is not compact.

From Theorem 2.2 and Remark 2.1, (3.3) has no positive steady state solution for $\alpha \geq M$ where M is defined in (3.10), and from (2.7), all positive steady state solutions are uniformly bounded for $\alpha \geq 0$. Thus we must have $(0, \alpha^0] \subset proj_\alpha \Sigma_1 \subset (0, M]$. □

With the above discussions, we have the following observations:

Remark 3.2. The quantity I determines the direction of bifurcation near $(\alpha^0, u_1^*, 0)$. Assume that the coefficients of (3.1) are all constants. This implies that $u_1^*(x) \equiv K$. From (3.4), it follows that

$$\psi_0(x) \equiv 1,\ \alpha^0 = \left[\frac{\beta\lambda}{\delta + \beta K} - \frac{r}{K}\right] K = \frac{\beta\lambda K}{\delta + \beta K} - r.$$

From (3.12), it follows that

$$\phi_0(x) \equiv -1 - \frac{\beta\lambda K}{r\,(\delta + \beta K)}.$$

From (3.14), it deduces that

$$I = \left[\frac{\beta\lambda}{\delta + \beta K}\right]\left[-\frac{\beta\lambda\delta K}{r\,(\delta + \beta K)^2}\right]|\Omega| < 0,$$

which implies that

$$\alpha'(0) < 0.$$

But if $\lambda(x)$, $\beta(x)$ and $K(x)$ are not all constants, then $I > 0$ is possible which implies that $\alpha'(0) > 0$. Thus a backward bifurcation occurs, and there exist positive steady state solutions of system (3.3) for $\alpha > \alpha^0$.

4. **Discussion.** In this paper, we investigate the long-term behavior of a model system (1.5) that describes the transmission dynamics of an insect disease with spatial structure in a bounded habitat of general spatial dimension. Assuming that the host insects are mobile, the first two equations of (1.5) include the diffusion terms. The absence of the pathogen mobility results in the absence of diffusion in the third equation for the pathogen population in (1.5), and this causes some mathematical difficulties as the solution semiflow of (1.5) is not compact. For instance, because of the lack of compactness, the classical Theorem 3.4.8 in [13] cannot be applied, and we need to address the existence of "global compact attractor" for system (1.5) (see Lemma 2.5 and Theorem 2.1). The linearized stability of the trivial and semi-trivial steady states of the model are determined by the associated linearized system at these states. The associated linear system is cooperative, but compactness condition of the classical Krein–Rutman theory is not satisfied. We have established the existence of the principal eigenvalue of two eigenvalue problems by the approach of [37, Theorem 2.3](see Lemma 2.6) and a generalized Krein–Rutman Theorem [21] (see Lemma 2.8), respectively.

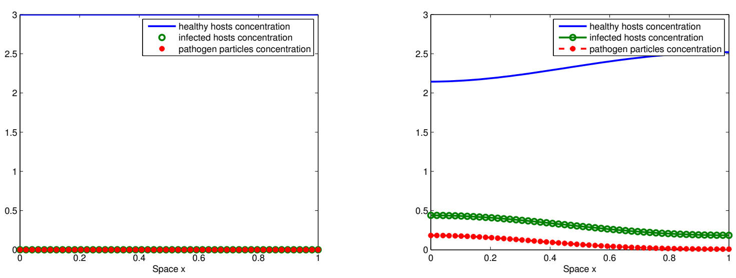
Basic reproduction number, $\mathcal{R}_0$, is an important notion in epidemiology and it can be used to predict persistence or extinction of a disease. This quantity is defined as the expected number of secondary infections generated by a single infected individual introduced into a completely susceptible population. For a model system describing the disease dynamics, $\mathcal{R}_0$ is mathematically defined as the spectral radius of the so-called next generation operator of the model system. For a next generation theory, see [8, 33, 32]; particularly for models with spatial structure, see more recent works [12, 34, 36, 37]. In this paper, we mainly follow the approach in the above works to identify the basic reproduction number for (1.5), leading to (2.28).

The local stability of the disease-free equilibrium $(u_1^*(x), 0, 0)$ is determined by the sign of $s(\mathcal{B}^{u_1^*,u_1^*})$, which is the principal eigenvalue of (2.20) with $h_1(\cdot) \equiv u_1^*(\cdot)$ and $h_2(\cdot) \equiv u_1^*(\cdot)$. Applying the abstract results in Thieme [32], we conclude that the local stability of the disease-free equilibrium is also determined by the sign of $\mathcal{R}_0 - 1$ (see Lemma 2.9). Then the uniform persistence of the disease can be established by appealing to the abstract persistence theory if $\mathcal{R}_0 > 1$ (see Theorem 2.3 and Theorem 2.4). However, we cannot prove the extinction of the disease if $\mathcal{R}_0 < 1$. Another index $s(\mathcal{B})$, spectral bound, is defined in Lemma 2.6 and it can determine the extinction of the disease (see Theorem 2.2). From our dynamical approach, it seems that $\mathcal{R}_0$ (or $s(\mathcal{B}^{u_1^*,u_1^*})$) is not a threshold value for the extinction of the disease. This observations motivate us to conduct a bifurcation analysis of the steady state solutions for the system (1.5). We suspect that backward bifurcation may occur when the parameters in System (1.5) are spatially dependent (see Remark 3.2).

Our dynamical approach and bifurcation analysis both suggest that the parameter α plays an important role in determining the extinction and persistence of the disease. We perform some numerical simulations which confirm our analytical results, that is, the disease will die out if α is large (see (a) in Fig. 4.1) and the disease will persist if α is small (see (b) in Fig. 4.1).

When model parameters are spatially dependent, it does not seem to be possible to obtain an explicit form for $\mathcal{R}_0$ (in contrast to the constant parameter case, see

Remark 2.3). In such a case, the impact of the model parameters on $\mathcal{R}_0$ can only be explored numerically. To demonstrate this, we fix parameter values $\Omega = (0,1)$, $\alpha = 0.02$, $d = 0.137$, $r = 1$, $\delta = 0.0137$, $K(x) \equiv 3$, $\beta(x) \equiv 1.5$, but let $\lambda(x) = 0.9[1 + c\cos(2\pi x + x_0)]$, where $c \in [0,1]$. The spatial average of $\lambda(x)$ on $[0,1]$ is always the constant 0.9 regardless of the values of c and x_0, but the dependence of $\mathcal{R}_0$ on c varies for different values of x_0, as shown in Fig. 4.2. This indicates that the spatial variation can also affect the persistence/extinction of the disease. In order to understand the spatial effect of $\beta(x)$ on $\mathcal{R}_0$, we take $\Omega = (0,1)$, and parameter values are $\alpha = 0.02$, $d = 0.137$, $r = 1$, $\delta = 0.0137$, $K(x) \equiv 3$, $\lambda(x) \equiv 0.9$, and $\beta(x) = 1.5[1 + c_1\cos(2\pi x)]$. The dependence of $\mathcal{R}_0$ on c_1 is shown in Fig. 4.3.



(a) (b)

FIGURE 4.1. Simulations of disease dynamics. Parameter values are $\Omega = (0,1)$, $d = 0.137$, $r = 1$, $\delta = 0.0137$, $K(x) \equiv 3$, $\beta(x) \equiv 1.5$, and $\lambda(x) = 0.9(1 + 0.5\cos(\pi x))$. (a) $\alpha = 1.2$, leading to $\mathcal{R}_0 < 1$ and hence the disease dies out; (b) $\alpha = 0.02$, leading to $\mathcal{R}_0 > 1$, and hence disease persists.

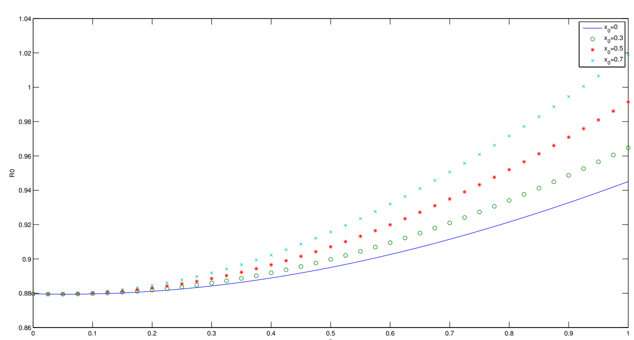


FIGURE 4.2. Impact of $\lambda(x)$ on $\mathcal{R}_0$. Parameter values are $\Omega = (0,1)$, $\alpha = 0.02$, $d = 0.137$, $r = 1$, $\delta = 0.0137$, $K(x) \equiv 3$, $\beta(x) \equiv 1.5$, and $\lambda(x) = 0.9[1 + c\cos(2\pi x + x_0)]$. The values of x_0 are $x_0 = 0, 0.3, 0.5$ and 0.7. Horizontal axis is c value in the above form of $\lambda(x)$, and vertical axis is $\mathcal{R}_0$ value.

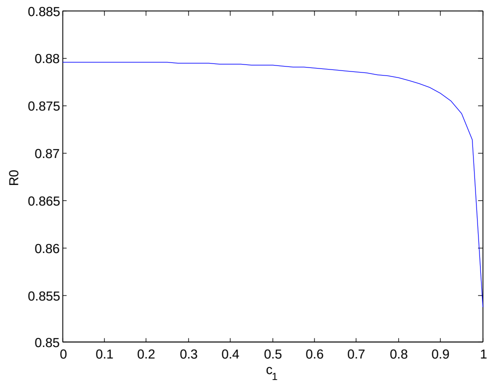


FIGURE 4.3. Spatial effect of $\beta(x)$ on $\mathcal{R}_0$. Parameter values are $\Omega = (0,1)$, $\alpha = 0.02$, $d = 0.137$, $r = 1$, $\delta = 0.0137$, $K(x) \equiv 3$, $\lambda(x) \equiv 0.9$, and $\beta(x) = 1.5[1 + c_1 \cos(2\pi x)]$. Horizontal axis is c_1 value in the above form of $\beta(x)$, and vertical axis is $\mathcal{R}_0$ value.

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