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Dynamics and profiles of a diffusive host–pathogen system with distinct dispersal rates ☆

Yixiang Wu [a], Xingfu Zou [b,c,*]

[a] Department of Mathematics, Vanderbilt University, Nashville, TN 37212, USA

[b] Department of Applied Mathematics, Western University, London, Ontario N6A 3K7, Canada

[c] School of Mathematics and Statistics, Central South University, Changsha, Hunan 410083, PR China

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Abstract

In this paper, we investigate a diffusive host–pathogen model with *heterogeneous parameters* and *distinct dispersal rates* for the susceptible and infected hosts. We first prove that the solution of the model exists globally and the model system possesses a global attractor. We then identify the basic reproduction number $\mathcal{R}_0$ for the model and prove its threshold role: if $\mathcal{R}_0 \le 1$, the disease free equilibrium is globally asymptotically stable; if $\mathcal{R}_0 > 1$, the solution of the model is uniformly persistent and there exists a positive (pathogen persistent) steady state. Finally, we study the asymptotic profiles of the positive steady state as the dispersal rate of the susceptible or infected hosts approaches zero. Our result suggests that the infected hosts concentrate at certain points which can be characterized as the pathogen's most favoured sites when the mobility of the infected host is limited.

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* Corresponding author.

E-mail addresses: yixiang.wu@vanderbilt.edu (Y. Wu), xzou@uwo.ca (X. Zou).

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1. Introduction

Since the pioneering work of Anderson and May [3], host–pathogen models have attracted considerable attention from mathematical biologists and bio-mathematicians, as exploration of such model systems can help better understand the mechanisms of spread of infectious diseases. The original host–pathogen model proposed and studied by Anderson and May is the following ODE system

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

where $u_1(t)$ and $u_2(t)$ represent the densities of susceptible and infected hosts at time t respectively, $u_3(t)$ is the density of pathogen particles, r is the reproductive rate of the host, β is the transmission rate, α is the mortality rate of the infected hosts induced by the invaded pathogen, γ and δ are the reproduction and decay rates of the pathogen particles respectively.

The model (1.1) has two obvious drawbacks: (i) intra-species competition is ignored (hence there is no self-restriction mechanism in the model) so that even in the absence of pathogen, the host population would grow unbounded exponentially; (ii) spatial effects (e.g., spatial heterogeneity and mobility) are also neglected. Dwyer [9] made an attempt to overcome the above two drawbacks by considering spatial model with one dimensional Laplacian operator $\partial/\partial x^2$ accounting for the random movement of hosts and a logistic growth for the hosts, given by the following system

$$\begin{cases} \frac{\partial u_1}{\partial t} = ru_1\left(1 - \frac{u_1+u_2}{K}\right) - \beta u_1 u_3 + d\frac{\partial^2 u_1}{\partial x^2}, \\ \frac{\partial u_2}{\partial t} = \beta u_1 u_3 - \alpha u_2 - r\frac{u_1+u_2}{K} + d\frac{\partial^2 u_2}{\partial x^2}, \\ \frac{\partial u_3}{\partial t} = -\delta u_3 + \gamma u_2, \end{cases} \tag{1.2}$$

where $x \in \mathbb{R}$ is the spatial variable, and K is the carrying capacity. Here the consumption of the pathogen by the hosts is ignored, so there are only two terms in the third equation, and the pathogen is assumed to be immobile in the environment. In [9], Dwyer assumed that all parameters are constants and studied how these parameters affect the spatial spread of the pathogen by considering travelling wave solutions of (1.2).

Recently, based on the facts that the habitat of a host species is generally bounded and heterogenous, Wang et al. [25] considered a similar model but in an isolated bounded domain of general dimension and allowed space dependent parameters, represented by the following system

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d\Delta u_1 + ru_1\left(1 - \dfrac{u_1+u_3}{K(x)}\right) - \beta(x)u_1u_3, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_2}{\partial t} = d\Delta u_2 + \beta(x)u_1u_3 - \alpha u_2 - r\dfrac{u_1+u_2}{K(x)}u_2, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_3}{\partial t} = -\delta u_3 + \gamma(x)u_2 - \beta(x)(u_1+u_2)u_3, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_1}{\partial n} = \dfrac{\partial u_2}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u_i(x,0) = u_{i0}(x), & x \in \Omega,\ i = 1,2,3. \end{cases} \tag{1.3}$$

In [25], the authors showed that (1.3) has a global attractor, and it is uniformly persistent if the basic reproduction number is greater than one. In proving the existence of the global attractor (hence, also the uniform persistence of the model), the assumption that both susceptible and infectious hosts have the *same diffusion rate* d played a crucial role. Indeed, an essential step is to add up the first two equations in (1.3) and let $u = u_1 + u_2$ to prove the eventual uniform boundedness of u_2. This assumption of uniform dispersal rate and the strategy for proving the boundedness of solution have appeared in many recent articles (see, e.g., [14,23,25,26,28]). In reality, however, individuals in the two classes may disperse at different rates, and thus, it is natural to consider a model without this assumption. This constitutes one motivation of the present paper.

Our second motivation comes from a series of works on reaction–diffusion SIS epidemic models [2,4,17,18,20,19,22,24,27], which are devoted to understanding the joint effects of the spatial heterogeneity of the environment and the mobility of host species on the transmission of infectious diseases. Among those mentioned works is the pioneering work by Allen et al. [2] which proved that the disease component of the coexistence steady state vanishes as the dispersal rate of the susceptible individuals approaches zero, provided that the low-risk site is not empty (the low-risk site contains exactly the points on which the disease transmission rate is smaller than the recovery rate, or the local basic reproduction number is less than 1). This result has an interesting biological implication: the disease can be controlled by limiting the movement of the susceptible individuals. Later on, Peng [18] showed that, in general, one can not eradicate an infectious disease by limiting the movement of the *infected individuals*. These results reveal that diffusion rates of susceptible individuals and infectious individuals may have different impacts on the long time disease dynamics, and motivate us to consider *distinct diffusion rates* when exploring general host–pathogen interactions and investigate their respective effects on the long term dynamics and asymptotic profiles of steady states as one diffusion rate approaches zero.

Our goal in this paper is to investigate the effect of spatial heterogeneity and distinct diffusion rates on the dynamics of diffusive host–pathogen models. To make things not too complicated (as *non-uniformness of diffusion rates and spatial heterogeneity* have already made the problem very challenging), we compromise a little bit in the interaction term by considering the simplest growth term for host that support a stable positive equilibrium in the absence of pathogen. With these considerations, we consider the following diffusive host–pathogen system

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d_1\Delta u_1 + \gamma(x) - \mu(x)u_1 - \beta(x)u_1u_3, & \\ \dfrac{\partial u_2}{\partial t} = d_2\Delta u_2 + \beta(x)u_1u_3 - \nu(x)u_2, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_3}{\partial t} = \alpha(x)u_2 - \delta(x)u_3, & \end{cases} \tag{1.4}$$

where $\Omega \subset \mathbb{R}^n$ is a general open bounded domain with smooth boundary $\partial\Omega$. Here the pathogen transmission is modelled by the mass action mechanism $\beta(x)u_1u_3$ with transmission rate $\beta(x)$; $\gamma(x)$ is the recruitment rate of susceptible hosts; $\mu(x)$ is the natural death rate of susceptible hosts; $\nu(x)$ is the death rate of infected hosts; $\delta(x)$ is the decay rate of pathogen particles; $\alpha(x)$ is the production rate of pathogen particles from the infected hosts. We assume that these parameters are positive and Hölder continuous functions on $\bar{\Omega}$.

We consider an isolated habitat Ω, reflected by the homogeneous Neumann boundary condition

$$\frac{\partial u_1}{\partial n} = \frac{\partial u_2}{\partial n} = 0, \qquad x \in \partial\Omega, \quad t > 0. \tag{1.5}$$

For the initial condition, we assume

$$u_i(x,0) = u_{i0}(x), \qquad x \in \bar{\Omega}, \quad i = 1, 2, 3, \tag{1.6}$$

where $u_{i0}(x)$, $i = 1, 2, 3$, are nonnegative continuous functions.

The rest of this paper is organized as follows. In Section 2, we prove that the solution of the model exists globally and the model system possesses a global attractor. The *main difficulty* here lies in showing the eventual uniform boundedness of the solution, and this is caused by the facts that the dispersal rates of the susceptible and infected hosts are different and there is no diffusion term in the third equation of (1.4). In Section 3, we identify the basic reproduction number $\mathcal{R}_0$ for the model by following the procedure of next generation operator (see, e.g., [21,26]). We then prove that the pathogen free equilibrium is globally stable when $\mathcal{R}_0 \le 1$, and the model is uniformly persistent and has a positive (pathogen persistent) steady state when $\mathcal{R}_0 > 1$. In Section 4, we study the impact of the mobility of hosts and the spatial heterogeneity on the disease dynamics through considering the asymptotic profiles of positive steady state as one of dispersal rates of the hosts approaches zero. Our results suggest: (I) the pathogen can be eradicated by limiting the movement of the susceptible hosts only under certain conditions; (II) the infected hosts will concentrate on certain points which can be characterized as the pathogen's most favoured sites, provided that the dispersal rate of infected hosts is very small. We conclude the paper by Section 5, where some detailed conclusions and discussions are presented, together with some numeric simulations to demonstrate the concentration phenomenon.

2. Well-posedness of the model system

In this section, we prove that the model (1.4)–(1.6) has a unique global nonnegative solution and admits a connected global attractor. The main difficulty is due to the fact that there is no dissipation in the pathogen equation and the dispersal rates d_1 and d_2 are not necessarily equal. If $d_1 = d_2$, we can add the first two equations in (1.4) and set $v = u_1 + u_2$ to show the global boundedness of the solution. This approach to prove the global existence of solution has been extensively used for similar models in the literature ([14,23,25,26,28]). Nevertheless, this method does not work here because we are interested in the effects of different dispersal rates ($d_1 \neq d_2$) of susceptible and infected hosts on the disease dynamics. Our method here is inspired by Alikakos [1] (also see the works by Dung [7,8]).

Let $X := C(\bar{\Omega}, \mathbb{R}^3)$ be equipped with the supreme norm, and let $X^+ := C(\bar{\Omega}, \mathbb{R}^3_+)$ be its positive cone. Our main result in this section is the following theorem.

Theorem 2.1. *For any $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$, the model (1.4)–(1.6) has a unique global nonnegative classical solution. Moreover, (1.4)–(1.6) admits a connected global attractor in X^+.*

We will prove Theorem 2.1 by a number of lemmas. The first lemma is just a consequence of applying the general results in [15].

Lemma 2.2. *For any $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$, the model (1.4)–(1.6) has a unique nonnegative solution $u(\cdot, t) = (u_1(\cdot, t), u_2(\cdot, t), u_3(\cdot, t))$ defined on $\bar{\Omega} \times [0, t_{max})$ with $t_{max} \leq \infty$. Moreover if $t_{max} < \infty$, then*

$$\lim_{t \to t_{max}^-} (\|u_1(\cdot, t)\| + \|u_2(\cdot, t)\| + \|u_3(\cdot, t)\|) = \infty. \tag{2.1}$$

Lemma 2.3. *For any $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$, the model (1.4)–(1.6) has a unique nonnegative global solution defined on $\bar{\Omega} \times [0, \infty)$.*

Proof. Let $u = (u_1, u_2, u_3)$ be the solution corresponding to initial data $u_0 = (u_{10}, u_{20}, u_{30})$. Since $\partial u_1/\partial t \leq d_1 \Delta u_1 + \gamma(x) - \mu(x) u_1$, u_1 is a subsolution of the problem

$$\begin{cases} \dfrac{\partial \hat{u}_1}{\partial t} = d_1 \Delta \hat{u}_1 + \gamma(x) - \mu(x) \hat{u}_1, & x \in \Omega,\ t > 0, \\ \dfrac{\partial \hat{u}_1}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ \hat{u}_1(x, 0) = u_{10}(x), & x \in \Omega. \end{cases} \tag{2.2}$$

It is well known that (2.2) has a unique positive steady state, denoted by $U(x)$, which is globally attractive. This together with the comparison theorem implies that

$$\limsup_{t \to \infty} u_1(x, t) \leq \lim_{t \to \infty} \hat{u}_1(x, t) = U(x), \quad \text{uniformly for } x \in \bar{\Omega}. \tag{2.3}$$

Hence there exists $K > 0$, depending on initial data, such that

$$\|u_1\| \leq K, \quad t \geq 0. \tag{2.4}$$

Let $\{T_2(t)\}_{t \geq 0}$ be the semigroup generated by the operator $d_2 \Delta - \mu(\cdot)$ in $C(\bar{\Omega})$ (with Neumann boundary condition). By (1.4)–(1.6), we have

$$u_2(\cdot, t) = T_2(t) u_{20} + \int_0^t T_2(t - s) \beta u_1(\cdot, s) u_3(\cdot, s) ds. \tag{2.5}$$

It then follows that

$$\|u_2(\cdot, t)\| \leq e^{-\lambda t} \|u_{20}\| + K \|\beta\| \int_0^t e^{-\lambda(t-s)} \|u_3(\cdot, s)\| ds, \tag{2.6}$$

where $\lambda > 0$ denotes the principal eigenvalue of $-d_2\Delta + \mu(\cdot)$ (with Neumann boundary condition). By (1.4), we have

$$u_3(\cdot,t) = e^{-\delta t}u_{30} + \alpha \int_0^t e^{-\delta(t-s)}u_2(\cdot,s)ds.$$

Hence,

$$\|u_3(\cdot,t)\| \le e^{-\delta_m t}\|u_{30}\| + \|\alpha\| \int_0^t e^{-\delta_m(t-s)}\|u_2(\cdot,s)\|ds, \tag{2.7}$$

where $\delta_m = \min\{\lambda/2, \min\{\delta(x) : x \in \bar{\Omega}\}\}$. Combining (2.6)–(2.7), we have

$$\begin{aligned}
\|u_2(\cdot,t)\| &\le e^{-\lambda t}\|u_{20}\| \\
&\quad + K\|\beta\| \int_0^t e^{-\lambda(t-s)} \left(e^{-\delta_m s}\|u_{30}\| + \|\alpha\| \int_0^s e^{-\delta_m(s-r)}\|u_2(\cdot,r)\|dr \right) ds \\
&= e^{-\lambda t}\|u_{20}\| + K\|\beta\|\|u_{30}\| \int_0^t e^{-\lambda(t-s)}e^{-\delta_m s}ds \\
&\quad + K\|\alpha\|\|\beta\| \int_0^t e^{-\lambda(t-s)} \int_0^s e^{-\delta_m(s-r)}\|u_2(\cdot,r)\|drds \\
&\le \|u_{20}\| + K\|\beta\|\|u_{30}\|| \int_0^t e^{-\delta_m s}ds \\
&\quad + K\|\alpha\|\|\beta\|e^{-\lambda t} \int_0^t e^{\delta_m r}\|u_2(\cdot,r)\| \int_r^t e^{(\lambda-\delta_m)s}dsdr \\
&\le C_1 + C_2 e^{-\delta_m t} \int_0^t e^{\delta_m s}\|u_2(\cdot,s)\|ds,
\end{aligned}$$

where $C_1 = \|u_{20}\| + K\|\beta\|\|u_{30}\|/\delta_m$ and $C_2 = K\|\alpha\|\|\beta\|/(\lambda - \delta_m)$. In the last step of the computation, we have used the fact that $\delta_m < \lambda$. Then applying the Gronwall's inequality, we find

$$\|u_2(\cdot,t)\| \le C_1 e^{C_2 t}, \quad t \ge 0. \tag{2.8}$$

Combining (2.7) and (2.8), we obtain

$$\|u_3(\cdot,t)\| \le \|u_{30}\| + \frac{C_1\|\alpha\|}{C_2} e^{C_2 t}, \quad t \ge 0. \tag{2.9}$$

Therefore, by (2.4), (2.8)–(2.9) and Lemma 2.2, the solution exists globally. □

The following lemma establishes the boundedness of solution, the proof of which is *not trivial*, due to the fact that the two diffusion rates may be distinct.

Lemma 2.4. *There exists a positive constant M independent of $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$ such that the solution satisfies the following estimate*

$$\limsup_{t\to\infty} (\|u_1(\cdot,t)\| + \|u_2(\cdot,t)\| + \|u_3(\cdot,t)\|) \le M. \tag{2.10}$$

Proof. We prove this lemma by proving the following six claims, step by step.

Claim 0. *There exists a positive constant M_0, independent of initial conditions, such that*

$$\limsup_{t\to\infty} \|u_1(\cdot,t)\| \le M_0. \tag{2.11}$$

This claim directly follows from (2.3) with $M_0 = \|U\|$.

Claim 1. *There exists a positive constant M_1, independent of initial conditions, such that*

$$\limsup_{t\to\infty} (\|u_2(\cdot,t)\|_1 + \|u_3(\cdot,t)\|_1) \le M_1. \tag{2.12}$$

To prove this claim, we integrate both sides of the first two equations of (1.4) and add up to obtain

$$\begin{aligned}\frac{\partial}{\partial t}\int_\Omega (u_1+u_2)dx &= \int_\Omega \gamma dx - \int_\Omega \mu u_1 dx - \int_\Omega \nu u_2 dx \\ &\le |\Omega|\|\gamma\| - m\int_\Omega (u_1+u_2)dx,\end{aligned}$$

where $m = \min_{x\in\bar\Omega}\{\mu(x), \nu(x)\}$ and $|\Omega|$ is the volume of Ω. Hence (2.12) holds with $M_1 = |\Omega|\|\gamma\|/m$.

Claim 2. *For any $k \ge 0$, there exists a positive constant M_{2^k}, independent of initial conditions, such that*

$$\limsup_{t\to\infty} \left(\|u_2(\cdot,t)\|_{2^k}^{2^k} + \|u_3(\cdot,t)\|_{2^k}^{2^k}\right) \le M_{2^k}. \tag{2.13}$$

We prove this claim by induction. The case $k = 0$ is proved in Claim 1. Assume the statement is true for $k - 1$, that is, there exists $M_{2^{k-1}} > 0$ such that

$$\limsup_{t\to\infty}\left(\|u_2(\cdot,t)\|_{2^{k-1}}^{2^{k-1}} + \|u_3(\cdot,t)\|_{2^{k-1}}^{2^{k-1}}\right) \le M_{2^{k-1}}. \tag{2.14}$$

Multiplying both sides of the second equation of (1.4) by $u_2^{2^k-1}$ and integrating over Ω (see [1]), we have

$$\frac{1}{2^k}\frac{\partial}{\partial t}\int_\Omega u_2^{2^k}dx \le -\frac{2^k-1}{2^{2k-2}}d_2\int_\Omega |\nabla u_2^{2^{k-1}}|^2 dx + \int_\Omega \beta u_1 u_2^{2^k-1}u_3 dx - \int_\Omega \nu u_2^{2^k}dx.$$

By (2.11), there exists $t_0 > 0$ such that

$$\int_\Omega \beta u_1 u_2^{2^k-1}u_3 dx \le \|\beta\|(M_0+1)\int_\Omega u_2^{2^k-1}u_3 dx \quad \text{for } t \ge t_0.$$

To estimate $u_2^{2^k-1}u_3$, we apply Young's inequality:

$$ab \le \epsilon' a^p + C_{\epsilon'}b^q,$$

where $C_{\epsilon'} = (\epsilon' p)^{-q/p}q^{-1}$ and $1/p + 1/q = 1$. Setting $\epsilon_1' = \delta_m/(4\|\beta\|(M_0+1))$, $p = 2^k$, and $q = 2^k/(2^k-1)$ where $\delta_m = \min\{\delta(x) : x \in \bar{\Omega}\}$, we obtain

$$\int_\Omega u_3 u_2^{2^k-1}dx \le \frac{\delta_m}{4\|\beta\|(M_0+1)}\int_\Omega u_3^{2^k}dx + C_{\epsilon_1'}\int_\Omega u_2^{2^k}dx \quad \text{for } t \ge t_0.$$

Thus, for $t \ge t_0$, we have

$$\frac{1}{2^k}\frac{\partial}{\partial t}\int_\Omega u_2^{2^k}dx \le -D_k\int_\Omega |\nabla u_2^{2^{k-1}}|^2 dx + \frac{\delta_m}{4}\int_\Omega u_3^{2^k}dx + C_k\int_\Omega u_2^{2^k}dx, \tag{2.15}$$

where $D_k = d_2(2^k-1)/(2^{2k-2})$ and $C_k = \|\beta\|(M_0+1)C_{\epsilon_1'}$.

Multiplying both sides of the third equation in (1.4) by $u_3^{2^k-1}$ and integrating over Ω, we have

$$\begin{aligned}\frac{1}{2^k}\frac{\partial}{\partial t}\int_\Omega u_3^{2^k}dx &= -\int_\Omega \delta u_3^{2^k}dx + \int_\Omega \alpha u_2 u_3^{2^k-1}dx \\ &\le -\delta_m\int_\Omega u_3^{2^k}dx + \|\alpha\|\int_\Omega u_2 u_3^{2^k-1}dx.\end{aligned}$$

Again, applying Young's inequality with $\epsilon_2' = \delta_m/(4\|\alpha\|)$, $p = (2^k-1)/(2^k)$, and $q = 2^k$, we get

$$\int_\Omega u_3^{2^k-1} u_2 dx \le \frac{\delta_m}{4\|\alpha\|} \int_\Omega u_3^{2^k} dx + C_{\epsilon_2'} \int_\Omega u_2^{2^k} dx.$$

It then follows that

$$\frac{1}{2^k}\frac{\partial}{\partial t} \int_\Omega u_3^{2^k} dx \le -\frac{3\delta_m}{4} \int_\Omega u_3^{2^k} dx + \|\alpha\| C_{\epsilon_2'} \int_\Omega u_2^{2^k} dx. \tag{2.16}$$

Combining (2.15) and (2.16) leads to

$$\frac{1}{2^k}\frac{\partial}{\partial t} \int_\Omega (u_2^{2^k} + u_3^{2^k}) dx \le -D_k \int_\Omega |\nabla u_2^{2^{k-1}}|^2 dx + \hat{C}_k \int_\Omega u_2^{2^k} dx - \frac{\delta_m}{2} \int_\Omega u_3^{2^k} dx, \tag{2.17}$$

for $t \ge t_0$ with $\hat{C}_k = C_k + \|\alpha\| C_{\epsilon_2'}$. We now recall the interpolation inequality: for any $\epsilon > 0$, there exist $C_\epsilon > 0$ such that

$$\|\xi\|_2^2 \le \epsilon \|\nabla \xi\|_2^2 + C_\epsilon \|\xi\|_1^2 \quad \text{for any } \xi \in W^{1,2}(\Omega). \tag{2.18}$$

Applying this interpolation inequality with $\epsilon_3 = D_k/(2\hat{C}_k)$, we then have

$$\begin{aligned} \frac{1}{2^k}\frac{\partial}{\partial t} \int_\Omega (u_2^{2^k} + u_3^{2^k}) dx &\le -\hat{C}_k \int_\Omega u_2^{2^k} dx - \frac{\delta_m}{2} \int_\Omega u_3^{2^k} dx + B_k \left(\int_\Omega u_2^{2^{k-1}} dx \right)^2 \\ &\le -\delta' \int_\Omega (u_2^{2^k} + u_3^{2^k}) dx + B_k \left(\int_\Omega u_2^{2^{k-1}} dx \right)^2 \end{aligned} \tag{2.19}$$

for $t \ge t_0$ where $B_k = 2C_{\epsilon_3}\hat{C}_k/D_k$ and $\delta' = \min\{\hat{C}_k, \delta_m/2\}$. By (2.14),

$$\limsup_{t\to\infty} \int_\Omega u_2^{2^{k-1}} dx \le M_{2^{k-1}}^{2^{k-1}},$$

which, together with (2.19), leads to (2.13) with

$$M_{2^k} = \sqrt[2^k]{\frac{B_k}{\delta'}} M_{2^{k-1}}.$$

Claim 3. *For any $p \ge 1$, there exists a positive constant M_p, independent of initial conditions, such that*

$$\limsup_{t\to\infty} (\|u_2(\cdot,t)\|_p^p + \|u_3(\cdot,t)\|_p^p) \le M_p. \tag{2.20}$$

This easily follows from Claim 2 and the continuous embedding $L^q(\Omega) \subset L^p(\Omega)$, $q \ge p \ge 1$.

Claim 4. *There exists a positive constant M_∞, independent of initial conditions, such that*

$$\limsup_{t\to\infty} \|u_2(\cdot,t)\| \le M_\infty. \tag{2.21}$$

We use some well-known results for fractional power space to prove this claim. To this end, we denote by $T_2(t)$ the analytic semigroup generated by A in $Y = L^p(\Omega)$, where

$$A = d_2\Delta - \gamma,$$
$$D(A) = \left\{ u \in W^{2,p}(\Omega) \quad \text{and} \quad \frac{\partial u}{\partial n} = 0 \text{ on } \partial\Omega \right\}.$$

Let Y_a, $0 \le a \le 1$, be the fractional power space with graph norm. Choose $p > n/2$ and $a \ge n/(2p)$ so that $Y_a \subset C(\bar{\Omega})$. It is well known that there exists $M_a > 0$ such that $\|A^a T_2(t)\| \le M_a/t^a$ for all $t > 0$. By Claim 0 and Claim 3, there exists $t_\infty > 1$ such that

$$\|u_1(\cdot,t)\| \le M_0 + 1, \quad \|u_2(\cdot,t)\|_p \le (M_p + 1)^{1/p}, \quad \|u_3(\cdot,t)\|_p \le (M_p + 1)^{1/p}$$

for all $t \ge t_\infty - 1$. By the second equation of (1.4), for all $t \ge t_\infty - 1$, we have

$$u_2(t) = T_2(1)u_2(t-1) + \int_{t-1}^{t} T_2(t-s)\beta u_1(\cdot,s)u_3(\cdot,s)ds.$$

It then follows that for all $t \ge t_\infty - 1$

$$\begin{aligned}
\|A^a u_2(\cdot,t)\|_p &\le \|A^a T_2(1)u_2(t-1)\|_p + \int_{t-1}^{t} \|A^a T_2(t-s)\beta u_1(\cdot,s)u_3(\cdot,s)\|_p ds \\
&\le M_a\|u_2(\cdot,t-1)\|_p + \|\beta\|(M_0+1)(M_p+1)^{1/p} \int_{t}^{t-1} \frac{M_a}{(t-s)^a} ds \\
&\le M_a(M_p+1)^{1/p} + \frac{\|\beta\|(M_0+1)(M_p+1)^{1/p} M_a}{1-a}.
\end{aligned}$$

Then inequality (2.21) follows from the embedding $Y_a \subset C(\bar{\Omega})$.

Claim 5. *There exists a positive constant M, independent of initial conditions, such that* (2.10) *holds.*

To prove this claim, we note that by $\partial u_3/\partial t = -\delta u_3 + \alpha u_2$ and Claim 4, we have

$$\limsup_{t\to\infty} \|u_3(\cdot,t)\| \le \frac{\|\alpha\| M_\infty}{\delta_m}.$$

Hence inequality (2.10) holds with $M = M_0 + M_\infty + \|\alpha\| M_\infty/\delta_m$. □

In order to apply the theory in Hale [12] to prove Theorem 2.1, we need to verify the "asymptotically smoothness" of the solution semiflow. This weak compactness condition is implied by the so-called κ-contraction condition (see, e.g., Lemma 2.3.4 in [12]), which we now confirm below. Let $\Phi(t): X^+ \to X^+$, $t \geq 0$, be the semigroup induced by the solution of the (1.4)–(1.6), i.e. $\Phi(t)u_0 := u(\cdot, t; u_0) = (u_1(\cdot, t; u_0), u_2(\cdot, t; u_0), u_3(\cdot, t; u_0))$, $t \geq 0$, where $u(\cdot, t; u_0)$ is the solution of (1.4)–(1.6) with initial data $u_0 \in X^+$. Recall that for any bounded $B \subset X^+$, its Kuratowski measure of non-compactness κ is defined as

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

Then B is precompact if and only if $\kappa(B) = 0$. We now prove that $\Phi(t)$ is a κ-contraction, i.e. there exists a continuous function $k(t): \mathbb{R}^+ \to \mathbb{R}^+$ with $0 \leq k(t) < 1$ such that for any $t > 0$ and bounded set B, $\{\Phi(s)B,\ 0 \leq s \leq t\}$ is bounded and $\kappa(\Phi(t)B) \leq k(t)\kappa(B)$.

Lemma 2.5. *For any bounded $B \subset X^+$ and $t > 0$, the following set is precompact in $C(\bar{\Omega})$:*

$$\mathcal{S} := \left\{ \int_0^t e^{-\delta(t-s)} \alpha u_2(\cdot, s; u_0) ds : u_0 \in B \right\}.$$

Proof. We first claim that for any $l \in (0, t)$, the following set is precompact in $C(\bar{\Omega})$:

$$\mathcal{S}_l := \left\{ \int_l^t e^{-\delta(t-s)} \alpha u_2(\cdot, s; u_0) ds : u_0 \in B \right\}.$$

To see this, similar to the proof of (2.4), we choose $a > n/2p$ so that the imbeddings $Y_a \subset C^b(\bar{\Omega}) \subset C(\bar{\Omega})$ are compact. By (2.8)–(2.9) (one may use (2.2) to obtain a similar estimate for u_1), there exists $K > 0$ such that $\|u_i(\cdot, s; u_0)\| \leq K$, $i = 1, 2, 3$, for all $0 \leq s \leq t$ and $u_0 \in B$. By the second equation of (1.4), for any $\tilde{t} \in [l, t]$,

$$\begin{aligned}
\|A^a u_2(\cdot, \tilde{t})\|_p &\leq \|A^a T_2(\tilde{t}) u_{20}\|_p + \int_0^{\tilde{t}} \|A^a T_2(\tilde{t} - s) \beta u_1(\cdot, s) u_3(\cdot, s)\|_p ds \\
&\leq \frac{M_a \|u_{20}\|_p}{\tilde{t}^a} + \|\beta\| K^2 |\Omega|^{1/p} \int_0^{\tilde{t}} \frac{M_a}{(\tilde{t} - s)^a} ds \\
&\leq \frac{M_a \|u_{20}\|_p}{l^a} + \frac{\|\beta\| K^2 |\Omega|^{1/p} M_a t^{1-a}}{1 - a}.
\end{aligned}$$

Hence the set $\{u_2(\cdot, t; u_0) : u_0 \in B \text{ and } \tilde{t} \in [l, t]\}$ is bounded in Y_a. Noticing $\delta \in C^b(\bar{\Omega})$ and $Y_a \subset C^b(\bar{\Omega})$, $\mathcal{S}_l$ is bounded in $C^b(\bar{\Omega})$. By the compactness of the imbedding $C^b(\bar{\Omega}) \subset C(\bar{\Omega})$, $\mathcal{S}_l$ is precompact in $C(\bar{\Omega})$.

To prove $\mathcal{S}$ is precompact in $C(\bar{\Omega})$, by Arezela–Ascoli Theorem, it suffices to show that $\mathcal{S}$ is equicontinuous. Let $\epsilon > 0$ be given. We can choose $l > 0$ such that

$$\int_0^l e^{-\delta(x)(t-s)}\alpha(x)u_2(x,s;u_0)ds \le \frac{\epsilon}{3}, \text{ for all } x \in \bar{\Omega} \text{ and } u_0 \in B.$$

Since $\mathcal{S}_l$ is precompact in $C(\bar{\Omega})$, there exists $\epsilon' > 0$ such that

$$\left|\int_l^t e^{-\delta(x)(t-s)}\alpha(x)u_2(x,s;u_0)ds - \int_l^t e^{-\delta(y)(t-s)}\alpha(y)u_2(y,s;u_0)ds\right| \le \frac{\epsilon}{3}$$

for all $u_0 \in B$ and $x, y \in \bar{\Omega}$ with $|x-y| \le \epsilon'$. It then follows that

$$\begin{aligned}
&\left|\int_0^t e^{-\delta(x)(t-s)}\alpha(x)u_2(x,s;u_0)ds - \int_0^t e^{-\delta(y)(t-s)}\alpha(y)u_2(y,s;u_0)ds\right| \\
&\le \left|\int_0^l e^{-\delta(x)(t-s)}\alpha(x)u_2(x,s;u_0)ds\right| + \left|\int_0^l e^{-\delta(y)(t-s)}\alpha(y)u_2(y,s;u_0)ds\right| \\
&+ \left|\int_l^t e^{-\delta(x)(t-s)}\alpha(x)u_2(x,s;u_0)ds - \int_l^t e^{-\delta(y)(t-s)}\alpha(y)u_2(y,s;u_0)ds\right| \\
&\le \frac{\epsilon}{3} + \frac{\epsilon}{3} + \frac{\epsilon}{3} = \epsilon,
\end{aligned}$$

for all $u_0 \in B$ and $x, y \in \bar{\Omega}$ with $|x-y| \le \epsilon'$. Since $\epsilon > 0$ is arbitrary, $\mathcal{S}$ is equicontinuous. Hence $\mathcal{S}$ is precompact in $C(\bar{\Omega})$. □

Lemma 2.6. *The semigroup $\Phi(t)$ is a κ-contraction.*

Proof. Let $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$ and $u = (u_1(\cdot,t;u_0), u_2(\cdot,t;u_0), u_3(\cdot,t;u_0))$ be the solution of (1.4)–(1.6) with initial data u_0. Obviously Φ can be decomposed as $\Phi(t) = \Phi_1(t) + \Phi_2(t)$, $t \ge 0$, where

$$\Phi_1(t)u_0 = \left(u_1(\cdot,t;u_0), u_2(\cdot,t;u_0), \int_0^t e^{-\delta(t-s)}\alpha u_2(\cdot,s;u_0)ds\right), \quad t \ge 0,$$

and

$$\Phi_2(t)u_0 = \left(0, 0, e^{-\delta t}u_{30}\right), \quad t \ge 0.$$

Let $B \subseteq X^+$ be a bounded set. By (2.8)–(2.9), $\{\Phi(s)B, 0 \le s \le t\}$ is bounded for any $t > 0$ (one may use (2.2) to obtain a similar estimate for u_1). By Lemma 2.5, $\Phi_1(t)B$ is precompact for any $t > 0$ (we can do a similar computation as in the proof of Lemma 2.5 to show that $\{u_1(\cdot,t;u_0), u_0 \in B\}$ and $\{u_2(\cdot,t;u_0), u_0 \in B\}$ are precompact in $C(\bar{\Omega})$). Thus, we have $\kappa(\Phi_1(t)B) = 0$, $t > 0$. Moreover,

$$\kappa(\Phi_2(t)B) \le \|e^{-\delta t}\|\kappa(B) \le e^{-\delta_m t}\kappa(B), \quad t \ge 0,$$

where $\delta_m = \min\{\delta(x) : x \in \bar{\Omega}\} > 0$. It then follows that for $t > 0$

$$\kappa(\Phi(t)B) \le \kappa(\Phi_1(t)B) + \kappa(\Phi_2(t)B) \le e^{-\delta_m t}\kappa(B).$$

Therefore, $\Phi(t)$ is a κ-contraction. □

We are now in a position to prove Theorem 2.1 by the previous lemmas. The readers can consult [12] for the definitions of point dissipativeness, asymptotical smoothness, and global attractor.

Proof of Theorem 2.1. The global existence and uniqueness of solution of (1.4)–(1.6) follows from Lemma 2.2–2.3. By Lemma 2.4, $\Phi(t)$ is point dissipative. By Lemma 2.6, $\Phi(t)$ is asymptotically smooth. Hence problem (1.4)–(1.6) has a connected global attractor by Theorem 2.4.6 in [12]. □

3. Basic reproduction number and steady states

3.1. Basic reproduction number

A steady state of (1.4)–(1.5) is a solution of the elliptic system

$$\begin{cases} d_1\Delta u_1 + \gamma(x) - \mu(x)u_1 - \beta(x)u_1u_3 = 0, & x \in \Omega, \\ d_2\Delta u_2 + \beta(x)u_1u_3 - \nu(x)u_2 = 0, & x \in \Omega, \\ \alpha(x)u_2 - \delta(x)u_3 = 0, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial n} = \dfrac{\partial u_2}{\partial n} = 0 & x \in \partial\Omega. \end{cases} \tag{3.1}$$

It is easy to see that system (1.4)–(1.5) has a unique pathogen free steady state $E_0 = (U, 0, 0)$, where U is the unique positive solution of

$$\begin{cases} d_1\Delta u_1 + \gamma - \mu u_1 = 0, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{3.2}$$

A solution $E_1 = (u_1^*, u_2^*, u_3^*)$ of (3.1) with $u_i^*(x) \ge 0$ for $x \in \Omega$ and $i = 1, 2, 3$ and $u_2^* \not\equiv 0$ or $u_3^* \not\equiv 0$ is called an endemic steady state. Indeed, it follows from the maximum principle that for an endemic steady state, we must have $u_i^*(x) > 0$ for $x \in \Omega$ and $i = 1, 2, 3$, and hence, it is indeed a positive steady state (PSS).

The basic reproduction number $\mathcal{R}_0$ of the model (1.4)–(1.5) can be identified as the spectral radius of the next generation operator of the model as proceeded in, e.g., [11,21,23,25,26], which is closely related to the stability of E_0. Linearizing (1.4)–(1.5) at E_0, we get

$$\begin{cases} \dfrac{\partial u_1}{\partial t} = d_1 \Delta u_1 - \mu u_1 - \beta U u_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_2}{\partial t} = d_2 \Delta u_2 - \nu u_2 + \beta U u_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_3}{\partial t} = \alpha u_2 - \delta u_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_1}{\partial n} = \dfrac{\partial u_2}{\partial n} = 0, & x \in \partial\Omega, \ t > 0. \end{cases} \tag{3.3}$$

Note that in (3.3), the second and third equations are decoupled from the first. Let $T(t)$ be the semigroup associated to the problem

$$\begin{cases} \dfrac{\partial u_2}{\partial t} = d_2 \Delta u_2 - \nu u_2 + \beta U u_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_3}{\partial t} = \alpha u_2 - \delta u_3, & x \in \Omega, \ t > 0, \\ \dfrac{\partial u_2}{\partial n} = 0, & x \in \partial\Omega, \ t > 0. \end{cases} \tag{3.4}$$

It is easy to see that $T(t)$ has the generator

$$A = \begin{pmatrix} d_2\Delta - \nu & \beta U \\ \alpha & -\delta \end{pmatrix} = \begin{pmatrix} d_2\Delta - \nu & 0 \\ \alpha & -\delta \end{pmatrix} + \begin{pmatrix} 0 & \beta U \\ 0 & 0 \end{pmatrix} =: B + F.$$

Let $\tilde{T}(t)$ be the semigroup generated by B. Then, the next generation operator is $L := -FB^{-1}$, which has the expression

$$L(\phi)(x) = \int_0^\infty F(x)\tilde{T}(t)\phi(x)dt = F(x)\int_0^\infty \tilde{T}(t)\phi(x)dt \quad \phi \in C(\bar{\Omega}, \mathbb{R}^2), \ \ x \in \bar{\Omega}.$$

The *basic reproduction number* $\mathcal{R}_0$ is defined as the spectral radius of L, i.e.

$$\mathcal{R}_0 := r(L) = \sup\{|\lambda|, \lambda \in \sigma(L)\}.$$

We can check that A and B are resolvent-positive operators. By [21, Theorem 3.5] (also see [25, Lemma 2.9] or [26, Theorem 3.1-(i)]), we have

Lemma 3.1. *$\mathcal{R}_0 - 1$ has the same sign as $s(A)$, where $s(A) = \sup\{Re\lambda, \lambda \in \sigma(A)\}$ is the spectral bound of A.*

One can simply compute $-FB^{-1}$ or apply [26, Theorem 3.3 (ii)] to prove the following lemma.

Lemma 3.2. *Let $\tilde{\lambda}_0$ be the principal eigenvalue of the problem*

$$\begin{cases} d_2\Delta\phi - \nu\phi + \tilde{\lambda}\frac{\alpha\beta U}{\delta}\phi = 0, & x \in \Omega, \\ \frac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega, \end{cases} \tag{3.5}$$

then $\mathcal{R}_0 = 1/\tilde{\lambda}_0$.

Based on Lemma 3.2, $\mathcal{R}_0$ can also be expressed by the following variational formula:

$$\mathcal{R}_0 = \frac{1}{\tilde{\lambda}_0} = \sup_{\phi \in H^1(\Omega), \phi \neq 0} \left\{ \frac{\int_\Omega \frac{\alpha\beta U}{\delta}\phi^2 dx}{\int_\Omega \left(d_2|\nabla\phi|^2 + \nu\phi^2\right) dx} \right\}. \tag{3.6}$$

By this expression, one can easily obtain some information on how $\mathcal{R}_0$ depends the model parameters. In particular, by Theorem 2 in [2], we immediately have the following theorem on the impact of the diffusion coefficient d_2 on $\mathcal{R}_0$.

Theorem 3.3. *The following statements hold.*

(i) $\mathcal{R}_0$ is decreasing in d_2 with

$$\lim_{d_2 \to 0} \mathcal{R}_0 = \max\left\{ \frac{\alpha\beta U}{\delta\nu} : x \in \bar{\Omega} \right\} \quad \text{and} \quad \lim_{d_2 \to \infty} \mathcal{R}_0 = \frac{\int_\Omega \frac{\alpha\beta U}{\delta} dx}{\int_\Omega \nu\, dx}.$$

(ii) If Ω is a favourable environment for the pathogen in the sense that

$$\int_\Omega \frac{\alpha\beta U}{\delta} dx > \int_\Omega \nu\, dx, \tag{3.7}$$

then $\mathcal{R}_0 > 1$ for all $d_2 > 0$.

(iii) If Ω is a non-favourable environment for the pathogen in the sense that

$$\int_\Omega \frac{\alpha\beta U}{\delta} dx < \int_\Omega \nu\, dx, \tag{3.8}$$

and in the mean time, there is a favourable site x within the domain in the sense that $\alpha(x)\beta(x)U(x) > \delta(x)\nu(x)$, then there exists d_2^* such that $\mathcal{R}_0 > 1$ when $d_2 < d_2^*$, and $\mathcal{R}_0 < 1$ when $d_2 > d_2^*$.

$\mathcal{R}_0$ and $\tilde{\lambda}_0$ are closely related to another principal eigenvalue λ_0 of the eigenvalue problem (see [2, Lemma 2.3(d)])

$$\begin{cases} d_2\Delta\phi - \nu\phi + \dfrac{\alpha\beta U}{\delta}\phi = \lambda\phi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{3.9}$$

Lemma 3.4. $\mathcal{R}_0 - 1$ *and* $s(A)$ *have the same sign as* λ_0.

3.2. Exponential growth bound

The significance of $s(A)$ is that it is related to the exponential growth bound of $T(t)$, which is defined as

$$\omega = \omega(T) := \lim_{t\to\infty} \frac{\ln \|T(t)\|}{t}.$$

Actually ω is then the smallest real number such that $\|T(t)\| \le Me^{\omega t}$ for some M. It is well known (see [10]) that

$$\omega(T) = \max\{s(A), \omega_{ess}(T)\}, \tag{3.10}$$

where $\omega_{ess}(T)$ is the essential growth bound of T defined as

$$\omega_{ess}(T) := \lim_{t\to\infty} \frac{\ln \alpha(T(t))}{t}.$$

Here α is the measure of non-compactness, i.e. for any bounded linear operator L on $C(\bar{\Omega}, \mathbb{R}^2)$,

$$\alpha(L) := \inf_{K\in\mathcal{K}} \|L - K\|,$$

where $\mathcal{K}$ is the set of all compact linear operators on $C(\bar{\Omega}, \mathbb{R}^2)$.

We can compute $\omega_{ess}(T)$ to show:

Lemma 3.5. *Let* $\delta_m = \min\{\delta(x), x \in \bar{\Omega}\}$. *Then* $\omega_{ess}(T) \le -\delta_m$.

Proof. For any $(u_{20}, u_{30}) \in C(\bar{\Omega}, \mathbb{R}^2)$, let $(u_2(\cdot,t), u_3(\cdot,t)) := T(t)(u_{20}, u_{30})$. Then $T(t) = \hat{T}_2(t) + \hat{T}_3(t)$, where

$$\hat{T}_2(t)(u_{20}, u_{30}) = \left(u_2(\cdot,t), \int_0^t e^{-\delta(t-s)}\alpha u_2(\cdot,s)ds \right)$$

and $\hat{T}_3(t)(u_{20}, u_{30}) = (0, e^{-\delta t}u_{30})$. Similar to Lemma 2.5, we can prove that $\hat{T}_2(t)$ is compact. Hence we have

$$\alpha(T(t)) = \alpha(\hat{T}_2(t) + \hat{T}_3(t)) = \alpha(\hat{T}_3(t)) \le \|\hat{T}_3(t)\| \le e^{-\delta_m t}.$$

It then follows from the definition that $\omega_{ess}(T) \le -\delta_m$. □

Combining Lemmas 3.1 and 3.5 and (3.10) leads to the following lemma.

Lemma 3.6. *The following statements hold.*

(i) If $\mathcal{R}_0 < 1$*, then* $\omega(T) < 0$.
(ii) If $\mathcal{R}_0 = 1$*, then* $\omega(T) = s(A) = 0$.
(iii) If $\mathcal{R}_0 > 1$*, then* $\omega(T) = s(A) > 0$.

If $\mathcal{R}_0 \geq 1$, we are able to characterize $s(A)$ as the principal eigenvalue of A.

Lemma 3.7. *If* $\mathcal{R}_0 \geq 1$*,* $s(A)$ *is the principal eigenvalue of the problem*

$$\begin{cases} d_2\Delta\phi_2 - \nu\phi_2 + \beta U\phi_3 = \lambda\phi_2, & x \in \Omega, \\ \alpha\phi_2 - \delta\phi_3 = \lambda\phi_3, & x \in \Omega, \\ \dfrac{\partial\phi_2}{\partial n} = 0, & x \in \partial\Omega \end{cases} \tag{3.11}$$

associated with a strongly positive eigenfunction.

Proof. Let $\mathcal{L}_\lambda = d_2\Delta - \nu + \alpha\beta U/(\delta + \lambda)$ be a family of linear operators on $C(\bar{\Omega})$ (with Neumann boundary condition). We note that $s(\mathcal{L}_\lambda)$ is decreasing and continuously dependent on λ. Actually $s(\mathcal{L}_\lambda)$ is the principal eigenvalue of $\mathcal{L}_\lambda u = \tilde{\lambda} u$ with Neumann boundary condition, and hence has the following variational characterization

$$s(\mathcal{L}_\lambda) = \sup_{\phi \in H^1(\Omega), \phi \neq 0} \left\{ \frac{\int_\Omega (-d_2|\nabla\phi|^2 - \nu\phi^2 + \frac{\alpha\beta U}{\delta+\lambda}\phi^2) dx}{\int_\Omega \phi^2 dx} \right\}.$$

It is then clear that $s(\mathcal{L}_\lambda) < 0$ if λ is large. By $\mathcal{R}_0 \geq 1$ and Lemma 3.4, $s(\mathcal{L}_0) = \lambda_0 \geq 0$. Hence there exists a unique $\hat{\lambda} > 0$ such that $s(\mathcal{L}_{\hat{\lambda}}) = \hat{\lambda}$. Let $\phi_{20} > 0$ be an eigenvector associated with $s(\mathcal{L}_{\hat{\lambda}})$. So we have $\mathcal{L}_{\hat{\lambda}}\phi_{20} = \hat{\lambda}\phi_{20}$. Then we can apply [26, Theorem 2.3] to complete the proof (one can also prove $\hat{\lambda} = s(A)$ directly by applying the following characterization of resolvent positive operators: for any $\lambda \in \mathbb{R}$ the resolvent operator $(\lambda - A)^{-1}$ is positive if and only if $\lambda > s(A)$ [21, Theorem 3.2]). □

Remark 3.8. If δ is a constant, Lemma 3.7 is true without assuming $\mathcal{R}_0 \geq 1$ (see [25, Lemma 2.6]). If δ is dependent on x, it is not clear whether or not the conclusion of Lemma 3.7 still holds for $\mathcal{R}_0 < 1$. Since Lemma 3.7 is sufficient for our purpose, we will not further explore whether or not $s(A)$ is the principal eigenvalue of (3.11) for the case $\mathcal{R}_0 < 1$. Interested readers are referred to [13, Lemma 4.4] for a different approach of Lemma 3.7.

3.3. Stability of steady states

Our main results in this subsection are the following threshold property, in terms of $\mathcal{R}_0$, on the long-term dynamics of the model (1.4)–(1.6). We first prove the stability of E_0 when $\mathcal{R}_0 < 1$.

Theorem 3.9. *If $\mathcal{R}_0 < 1$, then E_0 is globally asymptotically stable.*

Proof. The local asymptotically stability of E_0 follows from [26, Theorem 3.1]. We then only need to prove the global attractivity of E_0. Fix $\epsilon_0 > 0$. By (2.3), there exists $t_1 > 0$ such that $0 \le u_1(\cdot, t) \le U + \epsilon$ for all $t \ge t_1$. By the comparison principle for cooperative systems (e.g. see [15]), we have $(u_2(x,t), u_3(x,t)) \le (\hat{u}_2(x,t), \hat{u}_3(x,t))$ on $\bar{\Omega} \times [t_1, \infty)$, where $(\hat{u}_2(x,t), \hat{u}_3(x,t))$ is the solution of the following problem

$$\begin{cases} \dfrac{\partial \hat{u}_2}{\partial t} = d_2 \Delta \hat{u}_2 - \nu \hat{u}_2 + \beta(U + \epsilon_0)\hat{u}_3, & x \in \Omega, \ t > t_1, \\ \dfrac{\partial \hat{u}_3}{\partial t} = \alpha \hat{u}_2 - \delta \hat{u}_3, & x \in \Omega, \ t > t_1, \\ \dfrac{\partial \hat{u}_2}{\partial n} = 0, & x \in \partial\Omega, \ t > t_1, \\ \hat{u}_2(x, t_1) = u_2(x, t_1), \quad \hat{u}_3(x, t_1) = u_3(x, t_1), & x \in \Omega. \end{cases} \tag{3.12}$$

Let $T_{\epsilon_0}(t)$ be the linear semigroup induced by (3.12) with generator A_{ϵ_0}. We can choose ϵ_0 small such that $\omega_{\epsilon_0} := \omega(T_{\epsilon_0}) < 0$. To see this, we note that $\omega_{ess}(T_{\epsilon_0}) \le -\delta_m$, which can be proved as Lemma 3.5. Hence, ω_{ϵ_0} has the same sign as $s(A_{\epsilon_0})$. Similar to Lemma 3.4, $s(A_{\epsilon_0})$ has the same sign as λ_{ϵ_0}, where λ_{ϵ_0} is the principal eigenvalue of the eigenvalue problem

$$\begin{cases} d_2 \Delta \phi - \nu \phi + \dfrac{\alpha\beta(U + \epsilon_0)}{\delta} \phi = \lambda \phi, & x \in \Omega, \\ \dfrac{\partial \phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{3.13}$$

The assumption $\mathcal{R}_0 < 1$ implies $\lambda_0 < 0$ by Lemma 3.4. Since λ_{ϵ_0} is continuously dependent on ϵ_0, we can choose $\epsilon_0 > 0$ such that $\lambda_{\epsilon_0} < 0$. And so we have $\omega_{\epsilon_0} < 0$. Since $\|T_{\epsilon_0}(t)\| \le M e^{\omega_{\epsilon_0} t}$ for some $M > 0$, we have $(\hat{u}_2(x,t), \hat{u}_3(x,t)) \to (0,0)$ as $t \to \infty$ uniformly for $x \in \bar{\Omega}$. Therefore, we have $(u_2(x,t), u_3(x,t)) \to (0,0)$ as $t \to \infty$ uniformly for $x \in \bar{\Omega}$. Moreover by the first equation of (1.4) and the global stability of U as the positive steady state of (2.2), we conclude that $u_1(x,t) \to U(x)$ as $t \to \infty$ uniformly for $x \in \bar{\Omega}$. This proves the global attractivity of E_0. □

Theorem 3.10. *If $\mathcal{R}_0 > 1$, then there exists $\delta > 0$ such that for any $u_0 = (u_{10}, u_{20}, u_{30}) \in X^+$ with $u_{20} \not\equiv 0$, or $u_{30} \not\equiv 0$, the solution $u = (u_1, u_2, u_3)$ of (1.4)–(1.6) satisfies*

$$\liminf_{t \to \infty} u_i(x,t) \ge \delta, \ \ \textit{uniformly for} \ \ x \in \bar{\Omega}. \tag{3.14}$$

Moreover, the model has at least one positive steady state (PSS).

Proof. The proof is similar to that of Theorem 2.3 in [25], but some revisions are needed to reflect the different demography for the host population from that in [25]; it is indeed simpler as the demography in (1.4) is simpler and there is no absorb term in the third equation. We proceed below.

Let

$$X_0 = \{(\phi_1, \phi_2, \phi_3) \in X^+ : \quad \phi_2 \not\equiv 0 \text{ and } \phi_3 \not\equiv 0\},$$

and

$$\partial X_0 = \{(\phi_1, \phi_2, \phi_3) \in X^+ : \quad \phi_2 \equiv 0 \text{ or } \phi_3 \equiv 0\}.$$

Then, $X^+ = X_0 \cup \partial X_0$ with X_0 being relatively open in X^+. Let $\Phi(t) : X^+ \to X^+$ be the semi-flow induced by the solution of the model (1.4)–(1.6), i.e. $\Phi(t)u_0 = u(\cdot, t)$ for all $t \geq 0$, where $u = (u_1, u_2, u_3)$ is the solution of (1.4)–(1.6) with initial data $u_0 \in X^+$. We prove the following claims.

Claim 1. *X_0 is positively invariant with respect to $\Phi(t)$, i.e. $\Phi(t)X_0 \subseteq X_0$ for all $t \geq 0$.*

Let $u_0 = (u_{10}, u_{20}, u_{30}) \in X_0$. Then $u_{20} \not\equiv 0$ and $u_{30} \not\equiv 0$. Since $\partial u_2/\partial t \geq d_2 \Delta u_2 - \nu u_2$, u_2 is an upper solution of the problem

$$\begin{cases} \dfrac{\partial \check{u}_2}{\partial t} = d_2 \Delta \check{u}_2 - \nu \check{u}_2, & x \in \Omega, \ t > 0, \\ \dfrac{\partial \check{u}_2}{\partial n} = 0, & x \in \partial\Omega, \ t > 0, \\ \check{u}_2(\cdot, 0) = u_2(\cdot, 0) = u_{20}, & x \in \Omega. \end{cases}$$

By the maximum principle and $u_{20} \not\equiv 0$, we have $\check{u}_2(x,t) > 0$ for all $x \in \bar{\Omega}$ and $t > 0$. So by the comparison principle, we have $u_2(x,t) \geq \check{u}_2(x,t) > 0$ for all $x \in \Omega$ and $t > 0$. Moreover, from the third equation of (1.4), we further have

$$u_3(x,t) = e^{-\delta(x)t} u_{30}(x) + \int_0^t e^{-\delta(x)(t-s)} \alpha(x) u_2(x,s) ds, \tag{3.15}$$

which implies $u_3(x,t) > 0$ for all $x \in \bar{\Omega}$ and $t > 0$. Thus, $\Phi(t)u_0 \in X_0$, proving Claim 1.

Claim 2. *For every $u_0 \in M_\partial := \{\phi \in \partial X_0 : \Phi(t)\phi \in \partial X_0, \ t > 0\}$, the ω limit set $\omega(u_0)$ of u_0 is the singleton $\{E_0\}$.*

We only need to prove $M_\partial \subseteq \{(u_{10}, 0, 0) : u_{10} \in C(\bar{\Omega})^+\}$. Suppose to the contrary that there exists $u_0 = (u_{10}, u_{20}, u_{30}) \in M_\partial$ but $u_0 \notin \{(u_{10}, 0, 0) : u_{10} \in C(\bar{\Omega})^+\}$. Then either "$u_{20} \not\equiv 0$ and $u_{30} \equiv 0$", or "$u_{20} \equiv 0$ and $u_{30} \not\equiv 0$". For the former case, by the proof of Claim 1, we still have $u_2(x,t) > 0$ and $u_3(x,t) > 0$ for all $x \in \bar{\Omega}$ and $t > 0$, meaning that $\Phi(t)u_0 \in X_0$ for $t > 0$ which contradicts the definition of M_∂. For the latter case, firstly by (3.15), we have $u_3(\cdot, t) \not\equiv 0$ for all $t > 0$. From the first equation (1.4), we have $\frac{\partial u_1}{\partial t} - d_1 \Delta u_1 + \mu u_1 + \beta u_1 u_3 = \gamma > 0$. By the comparison theorem (Theorem 2.1, P55, in [16]) and the fact that $u_1 \equiv 0$ does not satisfy this equation, we conclude that $u_1(x,t) > 0$ for all $x \in \bar{\Omega}$ and $t > 0$. Also by (2.5) and $u_1(\cdot, t)u_3(\cdot, t) \geq (\not\equiv)\ 0$, we have $u_2(x,t) > 0$ for all $x \in \bar{\Omega}$ and $t > 0$. Hence $\Phi(t)u_0 =$

$(u_1(\cdot,t), u_2(\cdot,t), u_3(\cdot,t)) \in X_0$ for $t > 0$, again a contradiction to the fact that $u_0 \in M_\partial$. Thus we have $M_\partial \subseteq \{(u_{10}, 0, 0) : u_1 \in C(\bar{\Omega})^+\}$. By the result on the dynamics of (2.2), we conclude that $\omega(u_0) = \{E_0\}$ for every $u_0 \in M_\partial$.

Now, as in [25], we define $\rho :\ X^+ \to [0, \infty)$ by

$$\rho(\phi) = \min\{\phi_i(x) : x \in \bar{\Omega}, i = 2, 3\},\ \ \phi \in X_+.$$

We easily see $\rho(\Phi(t)\phi) > 0$, $t > 0$, for every $\phi \in (X_0 \cap \rho^{-1}(0)) \cup \rho^{-1}(0, \infty)$. Thus, ρ is a generalized distance function for the semiflow $\Phi(t) : X^+ \to X^+$, which offers a more demanding measurement of distance for elements in X^+ to ∂X_0 than the maximum norm does.

Claim 3. *$W^s(E_0) \cap \rho^{-1}(0, \infty) = \emptyset$, where $W^s(E_0)$ denotes the stable manifold of E_0.*

Let $u_0 \in \rho^{-1}(0, \infty)$, meaning that $u_{10}(x) \geq 0$ and $u_{i0}(x) > 0$ for $x \in \Omega$ for both $i = 1, 2$, and let $u(x,t) = (u_1(x,t), u_2(x,t), u_3(x,t))$ be the corresponding solution. We need to show that $||u(\cdot,t) - E_0|| \nrightarrow 0$ as $t \to \infty$. To this end, we only need to show that there exists an $\epsilon > 0$ such that $\limsup_{t\to\infty} ||u(\cdot,t) - E_0|| > \epsilon$. Assume this is not true, then for any $\epsilon > 0$ there exists $t_1 > 0$ such that $u_1 \geq U - \epsilon$ and $u_i(\cdot,t) < \epsilon$ for $t \geq t_1$, $i = 2, 3$. Hence, for $t \geq t_1$, $(u_2(x,t), u_3(x,t))$ is actually an upper solution of the following auxiliary problem

$$\begin{cases} \dfrac{\partial \check{u}_2}{\partial t} = d_2\Delta\check{u}_2 - \nu\check{u}_2 + \beta(U-\epsilon)\check{u}_3, & x \in \Omega,\ \ t > t_1, \\ \dfrac{\partial \check{u}_3}{\partial t} = \alpha\check{u}_2 - \delta\check{u}_3, & x \in \Omega,\ \ t > t_1, \\ \dfrac{\partial \check{u}_2}{\partial n} = 0, & x \in \partial\Omega,\ \ t > t_1, \\ \check{u}_2(x,t_1) = \phi_2(x), \quad \check{u}_3(x,t_1) = \phi_3(x), & x \in \Omega, \end{cases} \tag{3.16}$$

with $\phi_i \leq u_i(\cdot,t_1)$, $i = 2, 3$. Denote by $\lambda_0(\epsilon)$ the principal eigenvalue of the following eigenvalue problem

$$\begin{cases} d_2\Delta\phi - \nu\phi + \dfrac{\alpha\beta(U-\epsilon)}{\delta}\phi = \lambda\phi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases}$$

Then $\lambda_0(\epsilon)$ is continuous in ϵ. By Lemma 3.4, the assumption $\mathcal{R}_0 > 1$ implies $\lambda_0(0) = \lambda_0 > 0$. So we can choose $\epsilon > 0$ sufficiently small such that $\lambda_0(\epsilon) > 0$. Then similar to Lemma 3.7, one can show that the following eigenvalue problem has a principal eigenvalue $\check{\lambda}_0(\epsilon)$ corresponding to which, there is a positive eigenvector $(\phi_2^\epsilon, \phi_3^\epsilon)$ with $i = 2, 3$.

$$\begin{cases} d_2\Delta\phi_2 - \nu\phi_2 + \beta(U-\epsilon)\phi_3 = \lambda\phi_2, & x \in \Omega, \\ \alpha\phi_2 - \delta\phi_3 = \lambda\phi_3, & x \in \Omega, \\ \dfrac{\partial\phi_2}{\partial n} = 0, & x \in \partial\Omega. \end{cases}$$

Choose $m > 0$ sufficiently small such that $m\phi_i^\epsilon \le u_i(\cdot, t_1)$, $i = 2, 3$, and let $\phi_i = m\phi_i^\epsilon$ in (3.16). Then the linear system (3.16) has the unique solution

$$(\check{u}_2, \check{u}_3) = (me^{\check{\lambda}_0(\epsilon)(t-t_1)}\phi_2^\epsilon,\ me^{\check{\lambda}_0(\epsilon)(t-t_1)}\phi_3^\epsilon).$$

By the comparison principle, we have $(u_2, u_3) \ge (\check{u}_2, \check{u}_3)$ on $\bar{\Omega} \times [t_1, \infty)$. This implies $u_i(\cdot, t) \to \infty$ as $t \to \infty$, $i = 2, 3$, a contradiction to Lemma 2.4, proving Claim 3.

Combining the above claims and Theorem 2.1 with the well-known abstract persistence theory (see, e.g., Theorem 1.3.2 in [29]), we conclude that there exists a $\delta > 0$ such that $\Phi(t)$ is uniformly persistent w.r.t. $(X_0, \partial X_0, \rho)$, meaning that there exists $\delta > 0$ such that for any $u_0 \in X^+$ with $\rho(u_0) > 0$ (i.e., $u_0 \in X_0$), there holds $\liminf \rho(\Phi(t)u_0) \ge \delta$. By the definition of ρ, we then obtain the second part of (ii). The existence of a positive steady state (third part of (ii)) is proved by repeating the corresponding argument in the proof of Theorem 2.3 in [25] (omitted here). □

The following lemma will be used in proving the global attractivity of the steady state when $\mathcal{R}_0 = 1$.

Lemma 3.11. *Let (Y, d) be a complete metric space, and $S(t) : Y \to Y$, $t \ge 0$, be a strongly continuous semiflow. Let $y_0 \in Y$ be a stable equilibrium of $S(t)$, and $A \subset Y$ be compact and invariant, i.e. $S(t)A = A$ for all $t \ge 0$. If $\lim_{t\to\infty} S(t)y = y_0$ for all $y \in A$, then $A = \{y_0\}$.*

Proof. Let $V \subset Y$ be any open neighbourhood of y_0. Since y_0 is stable, there exists an open neighbourhood $U \subset V$ of y_0 such that $S(t)U \subset U$ for all $t \ge 0$. For any $y \in A$, since $\lim_{t\to\infty} S(t)y = y_0$, there exists $t_y > 0$ such that $S(t)y \in U$ for all $t \ge t_y$. Since $S(t)y$ is continuous in y and $S(t)U \subset U$, there exists open set $O_y \subset Y$ with $y \in O_y$ such that $S(t)O_y \subset U$ for all $t \ge t_y$. Note that $\{O_y\}_{y\in A}$ is an open covering for A. By the compactness of A, there exist $y_1, y_2, ..., y_k \in A$ such that $A \subset \cup_{j=1}^k O_{y_j}$. It then follows that $S(t)A \subset S(t)(\cup_{j=1}^k O_{y_j}) \subset U$ for all $t \ge \max\{t_1, t_2, ..., t_k\}$. Since A is invariant, $A = S(t)A \subset U \subset V$. Since V is arbitrary, we have $A = \{y_0\}$. □

Using an idea in the recent work [5] and Lemma 3.11, we can also establish the global stability of E_0 for the critical case $\mathcal{R}_0 = 1$.

Theorem 3.12. *If $\mathcal{R}_0 = 1$, E_0 is also globally asymptotically stable.*

Proof. We first prove the *local stability* of E_0. Let $\epsilon > 0$ be given. Suppose $\delta > 0$ and let $u_0 = (u_{10}, u_{20}, u_{30})$ with $\|u_0 - E_0\| \le \delta$.

Define

$$w_1(x,t) = \frac{u_1(x,t)}{U(x)} - 1 \ \text{ and } \ b(t) = \max_{x\in\bar{\Omega}}\{w_1(x,t), 0\}.$$

Noticing $d_1\Delta U + \gamma - \mu U = 0$ and by the first equation of (1.4), we have

$$\frac{\partial w_1}{\partial t} - d_1\Delta w_1 - 2d_1\frac{\nabla U \cdot \nabla w_1}{U} + \frac{\gamma}{U}w_1 = -\frac{\beta u_1 u_3}{U}.$$

Let $\tilde{T}_1(t)$ be the positive semigroup generated by the following operator associated with Neumann boundary condition

$$d_1\Delta + 2d_1\frac{\nabla U\cdot\nabla}{U} - \frac{\gamma}{U}.$$

Then there exists $r>0$ such that $\|\tilde{T}_1(t)\| \le Me^{-rt}$ for some $M>0$. Hence, we have

$$w_1(\cdot,t) = \tilde{T}_1(t)w_{10} - \int_0^t \tilde{T}_1(t-s)\frac{\beta u_1(\cdot,s)u_3(\cdot,s)}{U}ds,$$

where $w_{10} = u_{10}/U - 1$. It then follows from the positivity of $\tilde{T}_1(t)$ that

$$\begin{aligned} b(t) = \max_{x\in\bar{\Omega}}\{w_1(x,t),0\} &= \max_{x\in\bar{\Omega}}\left\{\tilde{T}_1(t)w_{10} - \int_0^t \tilde{T}_1(t-s)\frac{\beta u_1(\cdot,s)u_3(\cdot,s)}{U}ds, 0\right\} \\ &\le \max_{x\in\bar{\Omega}}\left\{\tilde{T}_1(t)w_{10}, 0\right\} \le \|\tilde{T}_1(t)w_{10}\| \\ &\le Me^{-rt}\left\|\frac{u_{10}}{U} - 1\right\| \le \delta Me^{-rt}/U_m, \end{aligned}$$

where $U_m = \min_{x\in\bar{\Omega}} U(x)$.

Noticing that (u_2, u_3) satisfies

$$\begin{cases} \dfrac{\partial u_2}{\partial t} = d_2\Delta u_2 + \beta U u_3 - \nu u_2 + \beta U\left(\dfrac{u_1}{U} - 1\right)u_3, \\ \dfrac{\partial u_3}{\partial t} = \alpha u_2 - \delta u_3, \end{cases} \qquad x\in\Omega,\ \ t>0,$$

we have

$$\begin{pmatrix} u_2(\cdot,t) \\ u_3(\cdot,t)\end{pmatrix} = T(t)\begin{pmatrix} u_{20} \\ u_{30}\end{pmatrix} + \int_0^t T(t-s)\begin{pmatrix} \beta U\left(\frac{u_1(\cdot,s)}{U} - 1\right)u_3(\cdot,s) \\ 0\end{pmatrix}ds.$$

By $\mathcal{R}_0 = 1$ and Lemma 3.6, we have $\omega(T) = 0$, and hence $\|T(t)\| \le M$ for $t\ge 0$ for some constant $M>0$ where M can be chosen as large as needed in the sequel. Noticing $b(s) \le \delta Me^{-rs}/U_m$, we have

$$\begin{aligned} \max\{\|u_2(\cdot,t)\|, \|u_3(\cdot,t)\|\} &\le M\max\{\|u_{20}\|, \|u_{30}\|\} + M\|\beta\|\|U\|\int_0^t b(s)\|u_3(s)\|ds \\ &\le M\delta + M_1\delta\int_0^t e^{-rs}\|u_3(\cdot,s)\|ds, \end{aligned} \tag{3.17}$$

where $M_1 = M^2\|\beta\|\|U\|/U_m$. By Gronwall's inequality, we obtain

$$\|u_3(\cdot,t)\| \le M\delta e^{\int_0^t \delta M_1 e^{-rs}ds} \le M\delta e^{\delta M_1/r}. \tag{3.18}$$

Combining (3.17)–(3.18), we have

$$\|u_2(\cdot,t)\| \le M\delta + M_1\delta M\delta e^{\delta M_1/r}\int_0^t e^{-rs}ds \le M\delta(1+M_1\delta e^{\delta M_1/r}/r). \tag{3.19}$$

By the first equation of (1.4) and (3.18), we have

$$\frac{\partial u_1}{\partial t} - d_1\Delta u_1 > \gamma - \mu u_1 - M\delta e^{\delta M_1/r}\beta u_1.$$

Let $\hat{u}_1$ be the solution of the problem

$$\begin{cases} \dfrac{\partial \hat{u}_1}{\partial t} = d_1\Delta\hat{u}_1 + \gamma(x) - \mu(x)\hat{u}_1 - M\delta e^{\delta M_1/r}\beta\hat{u}_1, & x\in\Omega,\ t>0,\\ \dfrac{\partial \hat{u}_1}{\partial n} = 0, & x\in\partial\Omega,\ t>0,\\ \hat{u}_1(x,0) = u_{10}, & x\in\Omega. \end{cases} \tag{3.20}$$

By the comparison principle, we have $u_1(x,t) \ge \hat{u}_1(x,t)$ for all $x \in \bar{\Omega}$ and $t \ge 0$. Let U_δ be the positive steady state of (3.20) and $\hat{w} = \hat{u}_1 - U_\delta$. Then $\hat{w}$ satisfies

$$\begin{cases} \dfrac{\partial \hat{w}}{\partial t} = d_1\Delta\hat{w} - (\mu + M\delta e^{\delta M_1/r}\beta)\hat{w}, & x\in\Omega,\ t>0,\\ \dfrac{\partial \hat{w}}{\partial n} = 0, & x\in\partial\Omega,\ t>0,\\ \hat{w}(x,0) = u_{10} - U_\delta, & x\in\Omega. \end{cases} \tag{3.21}$$

Let $T_1(t)$ be the semigroup generated by $d_1\Delta - \mu$ with Neumann boundary condition. We can choose M large such that $\|T_1(t)\| \le Me^{-\mu_m t}$. By (3.21), we have

$$\hat{w}(\cdot,t) = T_1(t)(u_{10} - U_\delta) - \int_0^t T_1(t-s)M\delta e^{\delta M_1/r}\beta\hat{w}(\cdot,s)ds.$$

Therefore we have

$$\|\hat{w}(\cdot,t)\| \le M\|u_{10} - U_\delta\|e^{-\mu_m t} + \int_0^t Me^{-\mu_m(t-s)}M\delta e^{\delta M_1/r}\|\beta\|\|\hat{w}(\cdot,s)\|ds.$$

Let $K = M^2\delta e^{\delta M_1/r}||\beta||$. Then, applying the Gronwall's inequality to the above leads to

$$\|\hat{u}_1(\cdot,t) - U_\delta\| = \|\hat{w}(\cdot,t)\| \le M\|u_{10} - U_\delta\|e^{Kt-\mu_m t}$$

Choosing $\delta > 0$ sufficiently small such that $K < \mu_m/2$, the above inequality then further leads to

$$\|\hat{u}_1(\cdot,t) - U_\delta\| \le M\|u_{10} - U_\delta\|e^{-\mu_m t/2}. \tag{3.22}$$

Now by (3.22), we have

$$\begin{aligned} u_1(\cdot,t) - U \ge \hat{u}_1(\cdot,t) - U &= \hat{u}_1(\cdot,t) - U_\delta + U_\delta - U \\ &\ge -M\|u_{10} - U_\delta\|e^{-\mu_m t/2} + U_\delta - U \\ &\ge -M(\|u_{10} - U\| + \|U - U_\delta\|) - \|U_\delta - U\| \\ &\ge -M\delta - (M+1)\|U_\delta - U\|. \end{aligned} \tag{3.23}$$

On the other hand, noticing that $b(t) \le \delta M e^{-rt}/U_m \le \delta M/U_m$, we have

$$u_1(\cdot,t) - U = U\left(\frac{u_1(\cdot,t)}{U} - 1\right) \le \|U\|b(t) \le \delta M\|U\|/U_m. \tag{3.24}$$

Combining (3.23)–(3.24), we have

$$\|u_1(\cdot,t) - U\| \le \max\{M\delta + (M+1)\|U_\delta - U\|, \delta M\|U\|/U_m\}. \tag{3.25}$$

Finally, combining (3.18)–(3.19), (3.25) and $\lim_{\delta\to 0} U_\delta = U$, we can choose δ small such that for all $t > 0$

$$\|u_1(\cdot,t) - U\|, \|u_2(\cdot,t)\|, \|u_3(\cdot,t)\| \le \epsilon,$$

proving the local stability of $E_0 = (U, 0, 0)$.

Next we prove the *global attractivity* of E_0, i.e. $\mathcal{A} = \{E_0\}$. Let $\Phi(t)$ and X^+ be defined as in the proof of Theorem 3.10. By Theorem 2.1, $\Phi(t)$ has a connected global attractor $\mathcal{A}$. By Lemmas 3.6–3.7, the eigenvalue problem (3.11) has a positive eigenvector (ϕ_2, ϕ_3) associated with the principal eigenvalue which equals zero. Define

$$\partial X_1 = \{(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) \in X^+ : \tilde{u}_2 = \tilde{u}_3 = 0\}.$$

Claim 1. *For any $u_0 = (u_{10}, u_{20}, u_{30}) \in \mathcal{A}$, the omega limit set $\omega(u_0) \subset \partial X_1$.*

Noticing (2.3), we must have $u_{10} \le U$. If $u_{20} = u_{30} = 0$, the claim easily follows from the fact that ∂X_1 is invariant for $\Phi(t)$. So we can assume that either $u_{20} \ne 0$ or $u_{30} \ne 0$. It then follows that $u_i(x,t) > 0$, $i = 1, 2, 3$, for all $x \in \bar{\Omega}$ and $t > 0$ (see the proof of Theorem 3.10). Hence $u_1(x,t)$ satisfies that

$$\begin{cases} \dfrac{\partial u_1}{\partial t} < d_1 \Delta u_1 + \gamma(x) - \mu(x) u_1, & x \in \Omega,\ t > 0, \\ \dfrac{\partial u_1}{\partial n} = 0, & x \in \partial\Omega,\ t > 0, \\ u_1(x, 0) \le U, & x \in \Omega. \end{cases}$$

By the comparison principle, we must have $u_1(x,t) < U(x)$ for all $x \in \bar{\Omega}$ and $t > 0$.

Motivated by [5], we introduce

$$c(t; u_0) := \inf\{\tilde{c} \in \mathbb{R} : u_2(\cdot,t) \le \tilde{c}\phi_2 \text{ and } u_3(\cdot,t) \le \tilde{c}\phi_3\}.$$

Then $c(t; u_0) > 0$ for all $t > 0$. We claim that $c(t; u_0)$ is strictly decreasing. To see this, fix $t_0 > 0$ and let $\bar{u}_2(\cdot,t) = c(t_0; u_0)\phi_2$ and $\bar{u}_3(\cdot,t) = c(t_0; u_0)\phi_3$ for $t \ge t_0$. Noticing $u_1(\cdot,t) < U$, we have

$$\begin{cases} \dfrac{\partial \bar{u}_2}{\partial t} > d_2 \Delta \bar{u}_2 - \nu \bar{u}_2 + \beta u_1 \bar{u}_3, & x \in \Omega,\ \ t > t_0, \\ \dfrac{\partial \bar{u}_3}{\partial t} = \alpha \bar{u}_2 - \delta \bar{u}_3, & x \in \Omega,\ \ t > t_0, \\ \dfrac{\partial \bar{u}_2}{\partial n} = 0, & x \in \partial\Omega,\ \ t > t_0, \\ \bar{u}_2(x, t_0) \ge u_2(x, t_0), \quad \bar{u}_3(x, t_0) \ge u_3(x, t_0), & x \in \Omega. \end{cases} \tag{3.26}$$

By the comparison principle, we obtain $(\bar{u}_2(x,t), \bar{u}_3(x,t)) \ge (u_2(x,t), u_3(x,t))$ for all $x \in \bar{\Omega}$ and $t \ge t_0$. Then by the first equation of (3.26) and the strong comparison principle, we must have $c(t_0; u_0)\phi_2(x) = \bar{u}_2(x,t) > u_2(x,t)$ for all $x \in \bar{\Omega}$ and $t > t_0$. By the second equation of (3.26), we have $c(t_0; u_0)\phi_3(x) = \bar{u}_3(x,t) > u_3(x,t)$ for all $x \in \bar{\Omega}$ and $t > t_0$. Since $t_0 > 0$ is arbitrary, $c(t; u_0)$ is strictly decreasing.

Let $c_* = \lim_{t\to\infty} c(t; u_0)$. Then we must have $c_* = 0$. Actually let $\mathbb{U} = (U_1, U_2, U_3) \in \omega(u_0)$. Then there exists $\{t_k\}$ with $t_k \to \infty$ such that $\Phi(t_k)u_0 \to \mathbb{U}$. We must have that $c(t; \mathbb{U}) = c_*$ for all $t \ge 0$, since $\lim_{t_k\to\infty} \Phi(t + t_k)u_0 = \Phi(t) \lim_{t_k\to\infty} \Phi(t_k)u_0 = \Phi(t)\mathbb{U}$. If $U_2 \ne 0$ or $U_3 \ne 0$, we can repeat the previous arguments to show that $c(t; \mathbb{U})$ is strictly decreasing, which contradicts that $c(t; \mathbb{U}) = c_*$. Hence $U_2 = U_3 = 0$.

Claim 2. $\mathcal{A} = \{E_0\}$.

Since $\{E_0\}$ is globally attractive for (1.4)–(1.6) in ∂X_1, $\{E_0\}$ is the only compact invariant subset of (1.4)–(1.6) in ∂X_1. Now, for any $u_0 \in \mathcal{A}$, since the omega limit set $\omega(u_0)$ is compact invariant and $\omega(u_0) \subset \partial X_1$, we conclude that $\omega(u_0) = \{E_0\}$. Since the global attractor $\mathcal{A}$ is compact invariant in X^+, E_0 is stable, and by Lemma 3.11, we must have $\mathcal{A} = \{E_0\}$.

Global attractivity and local stability immediately lead to the globally asymptotical stability of $E_0 = (U, 0, 0)$, completing the proof of the theorem. □

4. Asymptotic profiles of the positive steady state

Theorem 3.10 established the existence of at least one positive steady state (PSS) of (1.4) under the condition $\mathcal{R}_0 > 1$, but no other information has been obtained about this PSS. In this section, we explore the asymptotic profiles of the PSS when one of the two diffusion rates tends to zero. Our study is mainly motivated by [2] where the authors proved that the disease component of the endemic (positive) steady state of the model vanishes as the diffusion rate of the susceptible individuals approaching zero under some conditions. It is then interesting to see whether similar results hold for our model.

By (3.1), we see that (u_1, u_2, u_3) is a PSS of (1.4) if and only if (u_1, u_2) is a positive solution of the problem

$$\begin{cases} d_1\Delta u_1 + \gamma - \mu u_1 - \dfrac{\alpha\beta}{\delta}u_1u_2 = 0, & x \in \Omega, \\ d_2\Delta u_2 + \dfrac{\alpha\beta}{\delta}u_1u_2 - \nu u_2 = 0, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial n} = \dfrac{\partial u_2}{\partial n} = 0, & x \in \partial\Omega, \end{cases} \tag{4.1}$$

and $u_3 = \alpha u_2/\delta$. Hence in the sequel, we will focus on (4.1) instead of (3.1). We remark that (4.1) is similar to the one species chemostat model in [6], where the authors considered the asymptotic profile of the positive solutions of the model as the diffusion rates d_1 and d_2 are both small. However motivated by [2,18,27], we are interested in the case when only one of the two diffusion rates d_1 and d_2 tends to zero. We also consider the case when $d_1 \to \infty$.

For convenience of notations, for any $d > 0$ and $h \in C(\bar{\Omega})$, we denote by $\lambda_0(d, h)$ the principal eigenvalue of the problem

$$\begin{cases} d\Delta\phi + h\phi = \lambda\phi, & x \in \Omega, \\ \dfrac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{4.2}$$

Then $\lambda_0(d, h)$ depends continuously on d and h, and it is given by the variational formula:

$$\lambda_0(d, h) = -\inf\left\{\int_\Omega (d|\nabla\phi|^2 - h\phi^2)dx : \ \phi \in H^1(\Omega) \text{ with } \int_\Omega \phi^2 dx = 1\right\}. \tag{4.3}$$

Moreover, $\lambda_0(d, h)$ is decreasing in d with $\lim_{d\to 0}\lambda_0(d, h) = \max\{h(x) : x \in \bar{\Omega}\}$, and it is increasing in h with $\lambda_0(d, h_1) > \lambda_0(d, h_2)$ if $h_1 \geq h_2$ and $h_1(x) > h_2(x)$ for some $x \in \bar{\Omega}$, where $h_i \in C(\bar{\Omega})$, $i = 1, 2$ (e.g. see [2]).

4.1. Profile as $d_1 \to 0$

We now study the asymptotic profile of the PSS as the diffusion rate of the susceptible hosts approaches zero. In the sequel, we denote

$$\Lambda_0 = \lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\gamma}{\mu} - \nu\right).$$

Lemma 4.1. *Consider the nonlinear problem*

$$\begin{cases} d_2\Delta u + \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu+\frac{\alpha\beta}{\delta}u} - \nu\right)u = 0, & x \in \Omega, \\ \frac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{4.4}$$

The following statements hold:

(i) if $\Lambda_0 \le 0$, *then* (4.4) *has no positive solution;*
(ii) if $\Lambda_0 > 0$, *then* (4.4) *has a unique positive solution.*

Proof. To prove (i), we suppose $\Lambda_0 \le 0$ and assume to the contrary that (4.4) has a positive solution u. Multiplying both sides of (4.4) by u, and integrating over Ω, we get

$$-d_2 \int_\Omega |\nabla u|^2 dx + \int_\Omega \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu+\frac{\alpha\beta}{\delta}u} - \nu\right)u^2 dx = 0,$$

which implies

$$-d_2 \int_\Omega |\nabla u|^2 dx + \int_\Omega \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu} - \nu\right)u^2 dx > 0. \tag{4.5}$$

By the variational formula and (4.5), we have

$$\Lambda_0 \ge \left(-d_2 \int_\Omega |\nabla u|^2 dx + \int_\Omega \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu} - \nu\right)u^2 dx\right) / \int_\Omega u^2 dx > 0,$$

which is a contradiction. Hence (4.4) has no positive solution if $\Lambda_0 \le 0$.

To prove (ii), we suppose $\Lambda_0 > 0$. Let ϕ be a positive eigenvector of (4.2) corresponding to Λ_0. Denote

$$f(u) = d_2\Delta u + \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu+\frac{\alpha\beta}{\delta}u} - \nu\right)u.$$

Let $\check{u} = \epsilon\phi$ with $\epsilon > 0$. Then since $\Lambda_0 > 0$, we have

$$\begin{aligned} f(\check{u}) &= \epsilon\left(d_2\Delta\phi + \left(\frac{\alpha\beta}{\delta}\frac{\gamma}{\mu+\epsilon\frac{\alpha\beta}{\delta}\phi} - \nu\right)\phi\right) \\ &= \epsilon\left(\Lambda_0 + \frac{\alpha\beta}{\delta}\left(\frac{\gamma}{\mu+\epsilon\frac{\alpha\beta}{\delta}\phi} - \frac{\gamma}{\mu}\right)\right)\phi > 0, \end{aligned}$$

if ϵ is small. Hence $\check{u}$ is a lower solution of (4.4) if $\epsilon > 0$ is small. Let $\hat{u} = M$ with M being a positive constant. Then $f(\hat{u}) < 0$ if M is large, which means $\hat{u}$ is an upper solution of (4.4). Thus by the method of upper/lower solution, (4.4) has at least one solution in $[\check{u}, \hat{u}]$, which is positive.

It remains to prove the uniqueness of the positive solution. Suppose to the contrary that (4.4) has two positive solutions u_1 and u_2. We can choose ϵ sufficiently small and M sufficiently large such that $u_i \in [\check{u}, \hat{u}]$, $i = 1, 2$. Then by the method of upper/lower solution, there exists a minimal solution u_m and a maximal solution u_M in $[\check{u}, \hat{u}]$ such that $u_m \le u_1, u_2 \le u_M$. Multiplying both sides of (4.4) with $u = u_M$ by u_m and multiplying both sides of (4.4) with $u = u_m$ by u_M, and subtracting the two resulting equations, we obtain

$$0 = \int_\Omega \frac{\alpha\beta}{\delta} u_M u_m \left(\frac{\gamma}{\mu + \frac{\alpha\beta}{\delta} u_M} - \frac{\gamma}{\mu + \frac{\alpha\beta}{\delta} u_m} \right) dx.$$

This implies $u_M = u_m$ as $u_M \ge u_m$. Hence $u_1 = u_2$, and the positive solution is unique. □

We are now in the position to present the main result in this section on the asymptotic profile of the PSS when the diffusion rate $d_1 \to 0$.

Theorem 4.2. *The following statements hold.*

(i) If $\Lambda_0 < 0$, then there exists $\check{d}_1 > 0$ such that (4.1) has no positive solution when $d_1 < \check{d}_1$;
(ii) If $\Lambda_0 > 0$, then there exists $\hat{d}_1 > 0$ such that (4.1) has a positive solution (u_1, u_2) when $d_1 < \hat{d}_1$; moreover, $(u_1, u_2) \to (u_1^*, u_2^*)$ as $d_1 \to 0$ uniformly on Ω, where u_2^* is the unique positive solution of (4.4) and $u_1^* = \gamma/(\mu + \alpha\beta u_2^*/\delta)$.

Proof. Noting that U is the unique solution of

$$\begin{cases} -d_1 \Delta u_1 = \gamma - \mu u_1, & x \in \Omega, \\ \dfrac{\partial u_1}{\partial n} = 0, & x \in \partial\Omega, \end{cases} \tag{4.6}$$

it is well-known that $U \to \gamma/\mu$ as $d_1 \to 0$. It then follows that

$$\lambda_0 = \lambda_0 \left(d_2, \frac{\alpha\beta U}{\delta} - \nu \right) \to \lambda_0 \left(d_2, \frac{\alpha\beta}{\delta} \frac{\gamma}{\mu} - \nu \right) = \Lambda_0, \quad \text{as } d_1 \to 0.$$

By Lemma 3.7, $\mathcal{R}_0 - 1$ and λ_0 have the same sign. Hence if $\Lambda_0 < 0$, there exists $\check{d}_1 > 0$ such that $\mathcal{R}_0 < 1$ if $d_1 < \check{d}_1$. By Theorem 3.10, E_0 is globally stable for (1.4)–(1.6) and hence, there can be no PSS if $d_1 < \check{d}_1$. Hence (4.1) has no positive solution if $d_1 < \check{d}_1$, proving (i).

If $\Lambda_0 > 0$, then there exists $\hat{d}_1 > 0$ such that $\mathcal{R}_0 > 1$ if $d_1 < \hat{d}_1$. By Theorem 3.10, (1.4)–(1.6) has an PSS and thus (4.1) has a positive solution (u_1, u_2) if $d_1 < \hat{d}_1$. It remains to prove the convergence of (u_1, u_2) to (u_1^*, u_2^*) as $d_1 \to 0$. To this end, we first give an *a priori* estimate of (u_1, u_2). By the first equation of (4.1), one has $-d_1 \Delta u_1 \le \gamma - \mu u_1$. Hence by the maximum principle, we have

$$\|u_1\| \le C_1 \quad \text{for all } d_1 > 0, \tag{4.7}$$

where

$$C_1 = \frac{\max\{\gamma(x) : x \in \bar{\Omega}\}}{\min\{\mu(x) : x \in \bar{\Omega}\}}.$$

Integrating both sides of the first two equations of (4.1) and adding them up, we have

$$\int_\Omega \nu u_2 dx = \int_\Omega (\gamma - \nu u_1) dx \le \|\gamma\| |\Omega|,$$

which implies that

$$\|u_2\|_1 \le \frac{\|\gamma\| |\Omega|}{\min\{\nu(x) : x \in \bar{\Omega}\}}.$$

Now for any $p > 0$, by the second equation of (4.1), the uniform boundedness of u_1, the elliptic estimate, and the well-known bootstrapping argument, there exists $C_2 > 0$ such that

$$\|u_2\|_{2,p} \le C_2, \quad \text{for all } d_1 > 0. \tag{4.8}$$

Fixing $p > n$, by (4.7)–(4.8), there exists a sequence $\{d_{1k}\}$ with $d_{1k} \to 0$ such that the corresponding positive solution $\{(u_{1k}, u_{2k})\}$ of (4.1) satisfies

$$\begin{aligned} &u_{1k} \to u_1^* \text{ weakly in } L^p(\Omega), \\ &u_{2k} \to u_2^* \text{ weakly in } W^{2,p}(\Omega) \text{ and strongly in } C(\bar{\Omega}), \end{aligned}$$

as $k \to \infty$, for some nonnegative u_1^* in $L^p(\Omega)$ and nonnegative u_2^* in $W^{2,p}(\Omega)$. By $u_{2k} \to u_2^*$ in $C(\bar{\Omega})$ and the first equation of (4.1), we have $u_{1k} \to u_1^*$ in $C(\bar{\Omega})$ as $n \to \infty$, where u_i^*, $i = 1, 2$, satisfies

$$\gamma - \mu u_1^* - \frac{\alpha\beta}{\delta} u_1^* u_2^* = 0.$$

Thus, we have

$$u_1^* = \frac{\gamma}{\mu + \frac{\alpha\beta}{\delta} u_2^*}. \tag{4.9}$$

By (4.9) and the second equation of (4.1), u_2^* is a nonnegative solution of (4.4). It follows from Lemma 4.1 that either $u_2^* = 0$ or u_2^* is the unique positive solution of (4.4). We now exclude the former case. Assume to the contrary that $u_2^* = 0$. Then by (4.9), we have $u_1^* = \gamma/\mu$. Let $\bar{u}_{2k} = u_{2k}/\|u_{2k}\|$ for all k. Then $\|\bar{u}_{2k}\| = 1$ and $\bar{u}_{2k}$ satisfies

$$\begin{cases} d_2 \Delta \bar{u}_{2k} + \dfrac{\alpha\beta}{\delta} u_{1k} \bar{u}_{2k} - \nu \bar{u}_{2k} = 0, & x \in \Omega, \\ \dfrac{\partial \bar{u}_{2k}}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{4.10}$$

Then by the elliptic estimate, $\{\bar{u}_{2k}\}$ is uniformly bounded in $W^{2,p}(\Omega)$. Then up to a subsequence, we have $\bar{u}_{2k} \to \bar{u}_2^*$ weakly in $W^{2,p}(\Omega)$ with $\bar{u}_2^*$ solving

$$\begin{cases} d_2 \Delta \bar{u}_2^* + \dfrac{\alpha\beta}{\delta}\dfrac{\gamma}{\mu}\bar{u}_2^* - \nu \bar{u}_2^* = 0, & x \in \Omega, \\ \dfrac{\partial \bar{u}_2^*}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{4.11}$$

Since $\bar{u}_{2k} \geq 0$, we have $\bar{u}_2^* \geq 0$. Moreover, $\|\bar{u}_2^*\| = 1$ as $\|\bar{u}_{2k}\| = 1$. Thus by (4.11), $\bar{u}_2^*$ is a positive eigenvector of (4.2) corresponding to the principal eigenvalue

$$\lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\gamma}{\mu} - \nu\right) = 0,$$

which contradicts the assumption that $\Lambda_0 > 0$. Hence u_2^* is nontrivial, and it must be the unique positive solution of (4.4). Moreover, u_1^* is given by (4.9). This completes the proof. □

4.2. *Profile as $d_2 \to 0$*

In this subsection, we investigate the asymptotic profile of the PSS when the diffusion rate of the infected host approaches 0. Since it is very challenging (if not impossible) to directly study the limit of the positive solution of (4.1) as $d_2 \to 0$, we will first consider behaviour of the PSS when $d_1 \to \infty$, then examine the shadow system for the process of $d_2 \to 0$.

For any $h \in C(\bar{\Omega})$, let $\bar{h}$ be the spatial average of h, i.e. $\bar{h} = (\int_\Omega h dx)/|\Omega|$. For convenience, we denote

$$\Lambda_1 = \lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}} - \nu\right).$$

Lemma 4.3. *Consider the nonlinear and nonlocal problem*

$$\begin{cases} d_2 \Delta u + \left(\dfrac{\alpha\beta}{\delta}\dfrac{\bar{\gamma}}{\bar{\mu} + \overline{\frac{\alpha\beta}{\delta}u}} - \nu\right) u = 0, & x \in \Omega, \\ \dfrac{\partial u}{\partial n} = 0, & x \in \partial\Omega. \end{cases} \tag{4.12}$$

The following statements hold:

(i) if $\Lambda_1 \leq 0$, then (4.12) has no positive solution;
(ii) if $\Lambda_1 > 0$, then (4.12) has a unique positive solution.

Proof. To prove (i), suppose $\Lambda_1 \geq 0$ and assume to the contrary that (4.12) has a positive solution u. Then the positiveness of u implies that it is a principal eigenvector of (4.2) corresponding to the principal eigenvalue

$$\lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+\overline{\frac{\alpha\beta}{\delta}u}} - \nu\right) = 0.$$

By the monotonicity of $\lambda_0(d,h)$ in h, this gives $\Lambda_1 > 0$, which is a contradiction. So (4.12) has no positive solution if $\Lambda_1 \le 0$.

To prove (ii), we suppose $\Lambda_1 > 0$ and define $\Lambda_1(b)$ as

$$\Lambda_1(b) = \lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+b} - \nu\right), \qquad b \ge 0.$$

Then $\Lambda_1(b)$ depends continuously on b with $\Lambda_1(0) = \Lambda_1 > 0$ and $\Lambda_1(\infty) = \lambda_0(d_2, -\nu) < 0$. Moreover, by the monotonicity of $\lambda_0(d,h)$ in h, $\Lambda_1(b)$ is strictly decreasing in b. Hence there exists a unique $b^* > 0$ such that $\Lambda_1(b^*) = 0$. Let ϕ be a positive eigenvector corresponding to $\Lambda_1(b^*)$. Then we have

$$\begin{cases} d_2\Delta\phi + \left(\frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+b^*} - \nu\right)\phi = 0, & x \in \Omega, \\ \frac{\partial\phi}{\partial n} = 0, & x \in \partial\Omega. \end{cases}$$

So $a\phi$ is a positive solution of (4.12) for some positive number a if

$$b^* = a\int_\Omega \frac{\alpha\beta}{\delta}\phi dx. \tag{4.13}$$

The uniqueness of the positive solution follows from the uniqueness of b^*, the simplicity of $\Lambda_1(b^*)$ and (4.13). □

We first consider the asymptotic profile of the PSS when $d_1 \to \infty$.

Theorem 4.4. *The following statements hold.*

(i) If $\Lambda_1 < 0$, then there exists $d_1^* > 0$ such that (4.1) *has no positive solution when $d_1 > d_1^*$;*
(ii) If $\Lambda_1 > 0$, then there exists $d_1^\dagger > 0$ such that (4.1) *has a positive solution (u_1, u_2) when $d_1 > d_1^\dagger$; moreover, $(u_1, u_2) \to (u_1^*, u_2^*)$ uniformly on Ω as $d_1 \to \infty$, where u_2^* is the unique positive solution of* (4.12) *and $u_1^* = \bar{\gamma}/(\bar{\mu} + \overline{\alpha\beta u_2^*/\delta})$.*

Proof. Noting that U solves (4.6), it is well-known that $U \to \bar{\gamma}/\bar{\mu}$ in $C(\bar{\Omega})$ as $d_1 \to \infty$. We then have $\lambda_0 = \lambda_0(d_2, \alpha\beta U/\delta - \nu) \to \Lambda_1$ as $d_1 \to \infty$. If $\Lambda_1 < 0$, then there exists $d_1^* > 0$ such that $\lambda_0 < 0$ for $d_1 > d_1^*$. Since λ_0 and $\mathcal{R}_0 - 1$ have the sign, $\mathcal{R}_0 < 1$ when $d_1 > d_1^*$. By Theorem 3.10, (4.1) has no positive solution if $d_1 > d_1^*$. Similarly if $\Lambda_1 > 0$, we can prove that there exists $d_1^\dagger > 0$ such that (4.1) has a positive solution (u_1, u_2) for $d_1 > d_1^\dagger$.

It then remains to prove the convergence of (u_1, u_2) as $d_1 \to \infty$. As in the proof of Theorem 4.2, $\{u_1\}_{d_1 > d_1^\dagger}$ is uniformly bounded in $C(\bar{\Omega})$ and $\{u_2\}_{d_1 > d_1^\dagger}$ is uniformly bounded in

$W^{2,p}(\Omega)$ for $d_1 > 0$. Then by the first equation of (4.1) and the elliptic estimate, $\{u_1\}$ is uniformly bounded in $W^{2,p}(\Omega)$. Hence there exists a sequence $\{d_{1k}\}$ with $d_{1k} \to \infty$ such that the corresponding positive solution (u_{1k}, u_{2k}) of (4.1) satisfies that $(u_{1k}, u_{2k}) \to (u_1^*, u_2^*)$ weakly in $W^{2,p}(\Omega) \times W^{2,p}(\Omega)$ as $n \to \infty$. By the first equation of (4.1), we have $\Delta u_1^* = 0$, which implies that u_1^* is constant. Integrating both sides of the first equation of (4.1), we have

$$u_1^* = \frac{\bar{\gamma}}{\bar{\mu} + \overline{\frac{\alpha\beta}{\beta} u_2^*}}. \tag{4.14}$$

Then by (4.14) and the second equation of (4.1), u_2^* is the unique positive solution (similar to Theorem 4.2, one can show that $u_2^* \neq 0$) of (4.12). □

We now study the solution of (4.12) when d_2 is small. Suppose that there exists $x \in \bar{\Omega}$ such that

$$\frac{\alpha(x)\beta(x)}{\delta(x)} \frac{\bar{\gamma}}{\bar{\mu}} - \nu(x) > 0. \tag{4.15}$$

Let $A > 0$ be given by

$$\max_{x \in \bar{\Omega}} \left\{ \frac{\alpha\beta}{\delta} \frac{\bar{\gamma}}{\bar{\mu} + A} - \nu \right\} = 0.$$

Then A is well defined with $A > 0$. For this A, define the following set which collects all realizing points for the above maximum:

$$\mathcal{M} = \left\{ x \in \bar{\Omega} : \quad \frac{\alpha(x)\beta(x)}{\delta(x)} \frac{\bar{\gamma}}{\bar{\mu} + A} - \nu(x) = 0 \right\}.$$

Obviously $\mathcal{M}$ is non-empty. It is indeed the set of locations in which infected hosts will stay when $d_2 \to 0$, in the sense stated in the following theorem.

Theorem 4.5. *Suppose that there exists $x \in \bar{\Omega}$ such that (4.15) holds. Then there exists $\hat{d}_2 > 0$ such that (4.12) has a positive solution u_2 when $d_2 < \hat{d}_2$ which satisfies $\overline{\alpha\beta u_2/\delta} \to A$ as $d_2 \to 0$. Moreover there exists a sequence $\{d_{2k}\}$ with $d_{2k} \to 0$ such that the corresponding solution $\{u_{2k}\}$ satisfies that $u_{2k} \to (A|\Omega|\delta/\alpha\beta)\mathfrak{m}$ weakly as $k \to \infty$, in the sense that*

$$\int_\Omega u_{2k}\psi dx \to A|\Omega| \int_\Omega \frac{\delta}{\alpha\beta} \psi d\mathfrak{m}, \quad \forall \psi \in C(\bar{\Omega}), \ \textit{as} \ k \to \infty, \tag{4.16}$$

where $\mathfrak{m}$ is a probability measure with support contained in $\mathcal{M}$.

Proof. Note that as $d_2 \to 0$,

$$\Lambda_1 = \lambda_0 \left(d_2, \frac{\alpha\beta}{\delta} \frac{\bar{\gamma}}{\bar{\mu}} - \nu \right) \to \max \left\{ x \in \bar{\Omega} : \quad \frac{\alpha(x)\beta(x)}{\delta(x)} \frac{\bar{\gamma}}{\bar{\mu}} - \nu(x) \right\} > 0.$$

Thus, there exists some $\hat{d}_2 > 0$ such that $\Lambda_1 > 0$ for all $d_2 < \hat{d}_2$. By Lemma 4.3, (4.12) has a unique positive solution u_2 if $d_2 < \hat{d}_2$.

By the positivity of u_2 and (4.12), u_2 is a principal eigenvector of (4.2) corresponding to the principal eigenvalue

$$\lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+\overline{\frac{\alpha\beta}{\delta}u_2}} - \nu\right) = 0. \tag{4.17}$$

Note that $\overline{\alpha\beta u_2/\delta}$ is decreasing in d_2. Hence $\overline{\alpha\beta u_2/\delta} \to A_0$ for some $A_0 \geq 0$ as $d_2 \to 0$. Moreover by (4.17), we have

$$0 = \lim_{d_2\to 0}\lambda_0\left(d_2, \frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+\overline{\frac{\alpha\beta}{\delta}u_2}} - \nu\right) = \max_{x\in\bar{\Omega}}\left\{\frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+A_0} - \nu\right\}.$$

Thus, by the definition of A, we have $A_0 = A$. Therefore, $\overline{\alpha\beta u_2/\delta} \to A$ as $d_2 \to 0$. So there exists a sequence $\{d_{2k}\}$ with $d_{2k} \to 0$ such that the corresponding positive solutions $\{u_{2k}\}$ of (4.12) satisfies that $u_{2k} \to (A|\Omega|\delta/\alpha\beta)\mathfrak{m}$ weakly as $n \to \infty$, where $\mathfrak{m}$ is a probability measure, leading to (4.16).

Finally, we show that the support of $\mathfrak{m}$ is contained in $\mathcal{M}$. If $\mathcal{M} = \bar{\Omega}$, the conclusion holds automatically. Suppose $\mathcal{M} \neq \bar{\Omega}$, and let $x_0 \in \bar{\Omega} \setminus \mathcal{M}$. We will show that x_0 is not in the support of $\mathfrak{m}$. We first consider the case that x_0 is an interior point of Ω. By the definition of $\mathcal{M}$, we can find $\varepsilon, \eta > 0$ such that

$$\frac{\delta}{\alpha\beta}\left(\frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+A} - \nu\right) < -\eta \quad \text{for all} \quad x \in B(x_0, \varepsilon),$$

where $B(x_0, \varepsilon)$ is the open ball centred at x_0 with radius ε, such that $B(x_0, \varepsilon) \subseteq \Omega/\mathcal{M}$. Choose a smooth cutoff function ψ with $0 \leq \psi \leq 1$ such that

$$\psi(x) = \begin{cases} 1, & \text{on } B(x_0, \varepsilon/3) \\ 0, & \text{on } \Omega/B(x_0, 2\varepsilon/3). \end{cases} \tag{4.18}$$

Multiplying both sides of (4.12) with $u = u_{2k}$ by ψ and integrating the resulting equation over $B(x_0, 2\varepsilon/3)$, we obtain

$$0 = d_{2k}\int_{B(x_0,2\varepsilon/3)} u_{2k}\Delta\psi\, dx + \int_{B(x_0,2\varepsilon/3)} \psi u_{2k}\left(\frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+\overline{\frac{\alpha\beta}{\delta}u_{2k}}} - \nu\right)dx.$$

Letting $k \to \infty$ then leads to

$$0 = \int_{B(x_0,2\varepsilon/3)} \psi\left(\frac{\alpha\beta}{\delta}\frac{\bar{\gamma}}{\bar{\mu}+A} - \nu\right)A|\Omega|\frac{\delta}{\alpha\beta}d\mathfrak{m} \leq -\eta A|\Omega|\mathfrak{m}(B(x_0, \varepsilon/3)),$$

which implies $\mathfrak{m}(B(x_0, \varepsilon/3)) = 0$. So x_0 is not in the support of $\mathfrak{m}$. For the case when $x_0 \in \partial\Omega$, replacing $B(x_0, \varepsilon)$ and $(x_0, \varepsilon/3)$ by the intersects of these two sets with Ω, the same arguments also get through, therefore, the proof is completed. □

5. Conclusion and discussion

In this paper, we have investigated a diffusive host–pathogen model with heterogeneous coefficients and different dispersal rates for susceptible and infected hosts. In addition to the global existence of solution, we have shown that the model possess a connected global attractor. To achieve this, we have used some subtle estimates to overcome the difficulty caused by the facts that the dispersal rates for susceptible and infected hosts are distinct and that there is no diffusion term in the pathogen equation. We have also identified the basic reproduction number $\mathcal{R}_0$ for the model and proved its threshold role: if $\mathcal{R}_0 < 1$, then the pathogen free steady state is globally asymptotically stable; if $\mathcal{R}_0 > 1$, then the model is uniformly persistent and it has a positive steady state (PSS), representing the persistence of pathogen.

Most importantly, we have also explored the asymptotic profiles of the PSS as the dispersal rate of susceptible or infected hosts tends to zero, and such results can help us better understand the role of the host's mobility plays in determining the spatial pattern of the pathogen. For example, Theorem 4.2 suggests that the pathogen can be eliminated by limiting the movement of the susceptible hosts, provided that $\Lambda_0 < 0$. By (4.3), we can rewrite $\Lambda_0 = \lambda_0(d_2, \nu(\mathcal{R}_0^l - 1))$ as

$$\Lambda_0 = \sup\left\{\int_\Omega \nu(\mathcal{R}_0^l - 1)\phi^2 dx - d_2 \int_\Omega |\nabla\phi|^2 dx : \phi \in H^1(\Omega) \text{ with } \int_\Omega \phi^2 dx = 1\right\}. \tag{5.1}$$

Here, $\mathcal{R}_0^l = \frac{\alpha\beta\gamma}{\delta\mu\nu}$ is nothing but the local basic reproduction number, and hence, if $\mathcal{R}_0^l(x) > 1$ (< 1), then x is a site that favours (does not favour) the pathogen. Thus, if $\mathcal{R}_0^l(x) \le 1$ for all $x \in \Omega$, then $\Lambda_0 < 0$ regardless of the value $d_2 > 0$, and thus, by Theorem 4.2, limiting d_1 can eradicate the pathogen. On the other hand, if there are location(s) $x \in \Omega$ at which $\mathcal{R}_0^l(x) > 1$ (such an x may be referred to as a pathogen favoured site), the first integral in (5.1) may be positive or negative. Note that Λ_0 is decreasing in d_2, and by Lemma 2.2 in [2], we have

$$\Lambda_0 \to \overline{\nu(\mathcal{R}_0^l - 1)} = \frac{1}{|\Omega|}\int_\Omega \nu(\mathcal{R}_0^l - 1)\, dx \quad \text{as } d_2 \to \infty.$$

Therefore, if there are pathogen favoured sites in Ω, but the domain Ω itself is not favourable as a whole for the pathogen in the sense that $\overline{\nu(\mathcal{R}_0^l - 1)} < 0$, then it is still possible to eradicate the pathogen in the domain by limiting mobility of the hosts. Note that $\overline{\nu(\mathcal{R}_0^l - 1)} < 0$ is equivalent to

$$\int_\Omega \frac{\alpha\beta(\gamma/\mu)}{\delta} < \int_\Omega \nu, \tag{5.2}$$

which is the limiting case (as $d_1 \to 0$) of (3.8) since $U \to \gamma/\mu$ as $d_1 \to 0$. The local condition $\mathcal{R}_0^l(x) > 1$ is also the limiting case (as $d_1 \to 0$) of $\alpha(x)\beta(x)U(x) > \delta(x)\nu(x)$, and thus, reflects

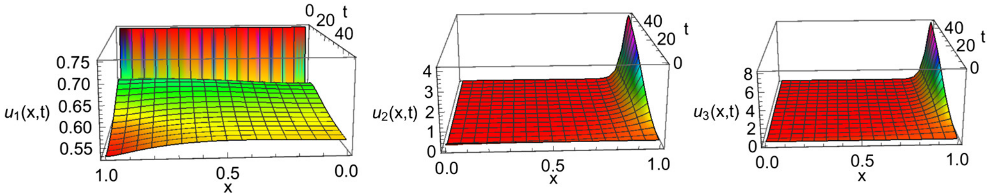

Fig. 1. The density of susceptible hosts, infected hosts and pathogen when d_2 is small.

the site suitability for the pathogen. In the context of infectious disease and for two diffusive SIS models *without demographic structure* for the host, similar results are obtained in [2] and [27], but with a difference in that large diffusion rate for the infected host is not required in [2] and [27].

On limiting the mobility of the infected hosts, we observe a very interesting concentration phenomenon: the infected hosts concentrate on certain points (denoted by $\mathcal{M}$) which are the pathogen's most favoured sites. We point out that we have only considered this case for the shadow system (4.12), rather than the original problem (4.1). Similar concentration phenomenon is also obtained for the model in [27], also for the shadow system. It remains an open (interesting and challenging) problem to study the asymptotic profile of the positive solution of the original system (4.1) as $d_2 \to 0$.

Lastly, to conclude the paper, we perform some numerical simulations to visually observe the concentration phenomenon (supporting Theorem 4.5). For this purpose, we choose the simplest domain $\Omega = (0, 1)$ and let $\alpha = 1 + x$, $\beta = \gamma = \delta = 1$, and $\mu = 2 - x$. Then we can calculate to obtain $\mathcal{M} = \{1\}$, meaning that the location $x = 1$ is the pathogen's most favoured site. The initial condition is $u_0 = (0.75, 0.28, 0.28)$. We consider the case when the diffusion rate d_2 is small by letting $d_1 = 1$ and $d_2 = 10^{-5}$. The solution of (1.4)–(1.6) is shown in Fig. 1, in which we can observe that the infected hosts and pathogen particles are both concentrated at $x = 1$.

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