Asymptotic Profiles of the Steady States for an SIS Epidemic Reaction-Diffusion Model

Dedicated to Norman Dancer on the occasion of his 60th birthday

December 31, 2006

L.J.S. Allen[1], B.M. Bolker[2], Y. Lou[3], and A.L. Nevai[4†]

Abstract

To understand the impact of spatial heterogeneity of environment and movement of individuals on the persistence and extinction of a disease, a spatial SIS reaction-diffusion model is studied, with the focus on the existence, uniqueness and particularly the asymptotic profile of the steady-states. First, the basic reproduction number $\mathcal{R}_0$ is defined for this SIS PDE model. It is shown that if $\mathcal{R}_0 < 1$, the unique disease-free equilibrium is globally asymptotic stable and there is no endemic equilibrium. If $\mathcal{R}_0 > 1$, the disease-free equilibrium is unstable and there is a unique endemic equilibrium.

A domain is called high (low) risk if the average of the transmission rates is greater (less) than the average of the recovery rates. It is shown that the disease-free equilibrium is always unstable ($\mathcal{R}_0 > 1$) for high-risk domains. For low-risk domains, the disease-free equilibrium is stable ($\mathcal{R}_0 < 1$) if and only if infected individuals have mobility above a threshold value. The endemic equilibrium tends to a spatially inhomogeneous disease-free equilibrium as the mobility of susceptible individuals tends to zero. Surprisingly, the density of susceptible for this limiting disease-free equilibrium, which is always positive on the subdomain where the transmission rate is less than the recovery rate, must also be positive at some, but not all, places where the transmission rates are greater than the recovery rates.

Keywords: Spatial heterogeneity, Dispersal, Basic reproduction number, Disease-free equilibrium, Endemic equilibrium.

[1]Department of Mathematics and Statistics, Texas Tech University, Lubbock, TX 79409-1042.
[2]Department of Zoology, University of Florida, P.O. Box 118525, Gainesville, FL 32611-8525.
[3]Department of Mathematics, The Ohio State University, Columbus, OH 43210.
[4]Mathematical Biosciences Institute, The Ohio State University, Columbus, OH 43210.
[†]Corresponding author: `anevai@mbi.osu.edu`.

1 Introduction

There have been some recent theoretical studies on SI-type reaction-diffusion models. For references to other spatial deterministic epidemic models, we refer the reader to excellent surveys by Fitzgibbon and Langlais (to appear), Ruan (to appear), and Thieme (2006).

In two papers, Fitzgibbon et al. (2001, 2004) study a family of SIR (susceptible-infected-recovered) models that can include spatially-dependent terms for diffusion, convection, disease transmission, and population demography. They include novel model features such as the presence of an additional state variable to denote the fraction of the environment which is contaminated (and can therefore cause infection) as well as the inclusion of "compartmental" or "diffractive diffusion" appropriate for populations living in fragmented habitats. Some of their results include the existence of unique solutions which are nonnegative and bounded, gradient estimates, and the existence of global attractors.

Beardmore and Beardmore (2003) model disease dynamics on a one-dimensional interval for a species which moves both randomly according to spatially-dependent diffusion and also by spatially-dependent convection towards a "focal point" (or den). Their model incorporates population demography and their main theoretical results concern the outcome of the disease for different relative values of birth rate, uninfected death rate, and infected death rate. They numerically simulated diseases which can make infected individuals "dumb" (reducing their diffusion coefficients) or "furious" (increasing their diffusion coefficients), a theme which we consider in depth in this paper. Gudelj et al. (2004) and Gudelj and White (2004) combine social structure and movement by including two mutant species which differ only in the location of their focal points. These species are social in that an infected individual of either group can infect any susceptible individual by making contact according to a mass action law. They study the stability of steady-state solutions and the existence of invariant regions. These papers are based on an earlier non-spatial model by Beardmore and White (2001).

In theoretical investigations of a continuous time SIS (susceptible-infected-susceptible) epidemic patch model, Allen et al. (2006) showed that when susceptible and infected individuals can move between patches, then an endemic equilibrium is reached in every patch. But if the movement pattern is changed so that only infected individuals disperse between the patches a surprising result occurs. The disease does not persist in any patch at equilibrium. Moreover, at equilibrium, all low-risk patches (where the patch reproduction numbers are less than one) contain susceptibles, and in some cases, high-risk patches (where the patch reproduction numbers are greater than one) can also contain susceptibles. In this paper, we investigate these phenomena in a continuous-time and continuous-space SIS model that includes both low-risk and high-risk sites.

Here, we consider a frequency-dependent SIS reaction-diffusion model for a population inhabiting a continuous spatial habitat. The habitat is characterized as *low-risk* (or *high-risk*) if the spatial average of the transmission rates is less than (or greater than) the spatial average of the recovery rates, respectively. Individual site is also characterized as *low-risk* (or *high-risk*) if the local transmission rate is less than (or greater than) the local recovery rate, which is equivalent to the local reproduction number being less than (or greater than) one, respectively.

Our results link spatial heterogeneity and rates of movement to disease persistence and extinction. In our first theorem, a unique disease-free equilibrium is shown to exist, a basic reproduction number $\mathcal{R}_0$ is determined by a variational problem, and we show that if $\mathcal{R}_0 < 1$ then the disease-free equilibrium is globally asymptotically stable. The second theorem relates the basic reproduction number to the heterogeneity of the spatial domain. It is shown that for low-risk domains, the disease-free equilibrium is stable ($\mathcal{R}_0 < 1$) if and only if the mobility of infected

individuals lies above a threshold value. For high-risk domains the disease-free equilibrium is always unstable ($\mathcal{R}_0 > 1$). In the third theorem we show that if the disease-free equilibrium is unstable ($\mathcal{R}_0 > 1$) then a unique endemic equilibrium exists. The fourth theorem demonstrates that when the endemic equilibrium exists, it approaches a spatially inhomogeneous disease-free equilibrium as the mobility of susceptible individuals approaches zero. This limiting disease-free equilibrium has a positive number of susceptible individuals at all low-risk sites and also on some (but not all) high-risk sites. These results have important implications for disease control. If the spatial environment can be modified to include low-risk sites (i.e., low transmission rates or high recovery rates) and if the movement of susceptible individuals can be restricted then it may be possible to eliminate the disease.

1.1 The model

Let Ω be a bounded domain in $\mathbb{R}^m$ ($m \geq 1$) with smooth boundary $\partial\Omega$ (when $m > 1$). Consider the SIS reaction-diffusion model

$$\frac{\partial \bar{S}}{\partial t} = d_S \Delta \bar{S} - \frac{\beta \bar{S}\bar{I}}{\bar{S}+\bar{I}} + \gamma \bar{I}, \quad x \in \Omega, \quad t > 0, \tag{1.1a}$$

$$\frac{\partial \bar{I}}{\partial t} = d_I \Delta \bar{I} + \frac{\beta \bar{S}\bar{I}}{\bar{S}+\bar{I}} - \gamma \bar{I}, \quad x \in \Omega, \quad t > 0, \tag{1.1b}$$

where $\bar{S}(x,t)$ and $\bar{I}(x,t)$ denote the density of susceptible and infected individuals at location x and time t; d_S and d_I are positive diffusion coefficients for the susceptible and infected populations; and $\beta(x)$ and $\gamma(x)$ are positive Hölder-continuous functions on $\overline{\Omega}$ that represent the rates of disease transmission and recovery at x, respectively. Because $\bar{S}\bar{I}/(\bar{S}+\bar{I})$ is a Lipschitz continuous function of $\bar{S}$ and $\bar{I}$ in the open first quadrant, we extend its definition to the entire first quadrant by defining it to be zero when either $\bar{S} = 0$ or $\bar{I} = 0$. We will assume no-flux boundary conditions

$$\frac{\partial \bar{S}}{\partial n} = \frac{\partial \bar{I}}{\partial n} = 0, \quad x \in \partial\Omega, \quad t > 0, \tag{1.1c}$$

and that there are initially a positive number of infected individuals, i.e.,

(A1) $\int_\Omega \bar{I}(x,0)\,dx > 0$, with $\bar{S}(x,0) \geq 0$ and $\bar{I}(x,0) \geq 0$ for $x \in \Omega$.

By the maximum principle (Protter and Weinberger 1984), both $\bar{S}(x,t)$ and $\bar{I}(x,t)$ are positive for $x \in \overline{\Omega}$ and $t \in (0, T_{\max})$, where $T_{\max}$ is the maximal existence time for solutions of (1.1). Again by the maximum principle, both $\bar{S}(x,t)$ and $\bar{I}(x,t)$ are bounded on $\overline{\Omega} \times (0, T_{\max})$. Hence, it follows from the standard theory for semilinear parabolic systems that $T_{\max} = \infty$ and that a unique classical solution $(\bar{S}, \bar{I})$ of (1.1) exists for all time (Henry 1981). Let

$$N \stackrel{\text{def}}{=} \int_\Omega \left[\bar{S}(x,0) + \bar{I}(x,0)\right] dx \tag{1.2}$$

be the total number of individuals in Ω at $t = 0$. Summing (1.1a) and (1.1b) and then integrating over Ω gives

$$\frac{\partial}{\partial t}\int_\Omega \left(\bar{S}+\bar{I}\right) = \int_\Omega \Delta\left(d_S\bar{S} + d_I\bar{I}\right) = \int_{\partial\Omega} \frac{\partial}{\partial n}\left(d_S\bar{S} + d_I\bar{I}\right) = 0, \quad t > 0.$$

We conclude that the total population size is constant, i.e.,

$$\int_\Omega \left(\bar{S} + \bar{I}\right) = N, \quad t \geq 0. \tag{1.3}$$

We say that x is a *low-risk site* if the local disease transmission rate $\beta(x)$ is lower than the local disease recovery rate $\gamma(x)$. A *high-risk site* is defined in a similar manner. Let

$$H^- = \{x \in \Omega : \beta(x) < \gamma(x)\} \quad \text{and} \quad H^+ = \{x \in \Omega : \beta(x) > \gamma(x)\}$$

denote the set of these low- and high-risk sites, respectively. For reference, these sets are illustrated in Figure 1. Let $\mathcal{R}_0(x) = \beta(x)/\gamma(x)$ be the *local reproduction number* at $x \in \Omega$. Then $\mathcal{R}_0(x) < 1$ for low-risk sites ($x \in H^-$) and $\mathcal{R}_0(x) > 1$ for high-risk sites ($x \in H^+$). It is well-known that without movement, the disease can persist at high-risk sites but not at low-risk sites. We say that Ω is a *low-risk domain* if $\int_\Omega \beta < \int_\Omega \gamma$ and a *high-risk domain* if $\int_\Omega \beta \geq \int_\Omega \gamma$.

We assume that $\beta - \gamma$ changes sign on Ω, i.e.,

(A2) H^- and H^+ are nonempty.

By continuity, the set $H^\circ = \{x \in \Omega : \beta(x) = \gamma(x)\}$ is also nonempty. We will sometimes assume that

(A3) H° consists of finitely many disjoint C^1-surfaces (or finitely many points if $m = 1$, each of which is a simple root of $\beta - \gamma$).

1.2 The equilibrium problem

We will be interested primarily in equilibrium solutions of (1.1), i.e., solutions of the elliptic problem

$$d_S \Delta \tilde{S} - \frac{\beta \tilde{S} \tilde{I}}{\tilde{S} + \tilde{I}} + \gamma \tilde{I} = 0, \quad x \in \Omega, \tag{1.4a}$$

$$d_I \Delta \tilde{I} + \frac{\beta \tilde{S} \tilde{I}}{\tilde{S} + \tilde{I}} - \gamma \tilde{I} = 0, \quad x \in \Omega, \tag{1.4b}$$

with boundary conditions

$$\frac{\partial \tilde{S}}{\partial n} = \frac{\partial \tilde{I}}{\partial n} = 0, \quad x \in \partial\Omega. \tag{1.4c}$$

Here, $\tilde{S}(x)$ and $\tilde{I}(x)$ denote the density of susceptible and infected individuals, respectively, at $x \in \Omega$ at equilibrium. In view of (1.3), we impose the additional condition

$$\int_\Omega \left(\tilde{S} + \tilde{I}\right) = N. \tag{1.4d}$$

We are only interested in solutions $(\tilde{S}, \tilde{I})$ of (1.4) which satisfy $\tilde{S} \geq 0$ and $\tilde{I} \geq 0$ on Ω. A *disease-free equilibrium* (DFE) is a solution in which $\tilde{I}(x) = 0$ for every $x \in \Omega$. An *endemic equilibrium* (EE) is a solution in which $\tilde{I}(x) > 0$ for some $x \in \Omega$. To distinguish between these two types of equilibria, we will for notational convenience denote a DFE by $(\hat{S}, 0)$ and an EE by $(\tilde{S}, \tilde{I})$.

1.3 Statement of the main results

We consider in Sect. 2 properties of the DFE, including its existence, uniqueness, and stability. We also define a basic reproduction number $\mathcal{R}_0$ for (1.1).

Theorem 1. *Suppose that* (A1)-(A2) *hold and N is fixed. There exists a DFE, it is unique, and it is given by $(\hat{S}, 0) = (N/|\Omega|, 0)$. Let*

$$\mathcal{R}_0 = \sup_{\substack{\varphi \in H^1(\Omega) \\ \varphi \neq 0}} \left\{ \frac{\int_\Omega \beta \varphi^2}{\int_\Omega d_I |\nabla \varphi|^2 + \gamma \varphi^2} \right\}.$$

If $\mathcal{R}_0 < 1$ then the DFE is globally asymptotically stable, but if $\mathcal{R}_0 > 1$ then it is unstable.

Our variational characterization of the basic reproduction number $\mathcal{R}_0$ is in keeping with the next generation approach for heterogeneous populations (Diekmann et al. 1990, Diekmann and Heesterbeek 2000) which occupy a continuous spatial habitat, and it was inspired by earlier disease models with movement between discrete patches (van den Driessche and Watmough 2002, Allen et al. 2006). It is also interesting to note that $\mathcal{R}_0$ does not depend on the value of the diffusion coefficient d_S for susceptibles.

In Sect. 2, we also show that the basic reproductive number $\mathcal{R}_0$ is a monotone decreasing function of the diffusion coefficient d_I for infected individuals which tends to the maximum local reproduction number as d_I becomes arbitrarily small and to the average transmission rate divided by the average recovery rate as d_I becomes arbitrarily large. We also find an equivalent characterization for the stability of the DFE in terms of d_I rather than $\mathcal{R}_0$. In particular, the DFE in a low-risk domain is stable if and only if d_I lies above a certain threshold value, but in a high-risk domain, the DFE is always unstable.

Theorem 2. *Suppose that* (A1)-(A2) *hold and N is fixed.*

(a) *$\mathcal{R}_0$ is a monotone decreasing function of d_I with $\mathcal{R}_0 \to \max\{\beta(x)/\gamma(x) : x \in \overline{\Omega}\}$ as $d_I \to 0$ and $\mathcal{R}_0 \to \int_\Omega \beta / \int_\Omega \gamma$ as $d_I \to \infty$;*

(b) *In a low-risk domain ($\int_\Omega \beta < \int_\Omega \gamma$), there exists a threshold value $d_I^* \in (0, \infty)$ such that $\mathcal{R}_0 > 1$ for $d_I < d_I^*$ and $\mathcal{R}_0 < 1$ for $d_I > d_I^*$;*

(c) *In a high-risk domain ($\int_\Omega \beta \geq \int_\Omega \gamma$), we have $\mathcal{R}_0 > 1$ for all d_I.*

Some comments about d_I^*. If $\int_\Omega \beta < \int_\Omega \gamma$ then

$$d_I^* = \sup \left\{ \frac{\int_\Omega (\beta - \gamma)\varphi^2}{\int_\Omega |\nabla \varphi|^2} : \varphi \in W^{1,2}(\Omega) \text{ and } \int_\Omega (\beta - \gamma)\varphi^2 > 0 \right\}. \tag{1.5}$$

We refer to Cantrell and Cosner (2003) for such characterizations and related references. Observe that if $\int_\Omega \beta \geq \int_\Omega \gamma$ then the right-hand side of (1.5) is equal to zero. In this case, we can define $d_I^* = \infty$.

In Sect. 3, we show that when the DFE is unstable, then there exists a unique EE. Moreover, the disease persists everywhere.

Theorem 3. *Suppose that* (A1)-(A2) *hold and N is fixed. An EE exists if and only if the DFE is unstable ($\mathcal{R}_0 > 1$). Furthermore, when it exists, the EE is unique and both $\tilde{S}$ and $\tilde{I}$ are positive on Ω.*

Observe from (1.4) that in the limiting case $d_S = 0$ there also exists a family of infinitely many spatially inhomogeneous DFEs $(\hat{S}, 0)$, each of which satisfies

$$\hat{S} \geq 0 \text{ on } \Omega, \quad \frac{\partial \hat{S}}{\partial n} = 0 \text{ on } \partial\Omega, \quad \text{and} \quad \int_\Omega \hat{S} = N. \tag{1.6}$$

It is natural to inquire about the connection between these spatially inhomogeneous DFEs and the unique EE as d_S approaches zero. In Sect. 4, we show that if $\mathcal{R}_0 > 1$ then the EE approaches such a spatially inhomogeneous DFE as the mobility of susceptible individuals becomes very small. We write this limiting DFE as $(S^*, 0)$ and also consider the distribution of sites for which S^* is either positive or zero (see Figure 2).

Theorem 4. *Suppose that* (A1)-(A2) *hold and N is fixed.*

(a) $(\tilde{S}, \tilde{I}) \to (S^*, 0)$ *in* $C^1(\overline{\Omega})$ *as* $d_S \to 0$ *for some* $S^*(x) \in C^1(\overline{\Omega})$ *satisfying* (1.6)*;*

(b) $J^- \stackrel{\text{def}}{=} \{x \in \overline{\Omega} : S^*(x) > 0\}$ *contains* H^-*;*

(c) $J^+ \stackrel{\text{def}}{=} \{x \in \overline{\Omega} : S^*(x) = 0\}$ *has positive measure and is contained in* $\overline{H^+}$*;*

(d) *If* (A3) *also holds, then* J^- *contains* $\overline{H^-}$*, and the set* $J^- \setminus H^-$ *has positive measure. Moreover, if* $m = 1$*, then the measure of* $J^- \setminus H^-$ *tends to zero as* $d_I \to 0$*.*

Some comments about Theorem 4. First, this theoretical study is motivated primarily by the question of how the long time behavior of $(\bar{S}, \bar{I})$ depends upon the susceptible diffusion coefficient d_S. We conjecture that if d_S is sufficiently small, then the EE is globally asymptotically stable and it closely approximates some spatially inhomogeneous DFE. Theorem 4 (a) confirms the second part of this conjecture. Another prediction of Theorem 4 is that, in the limiting DFE, susceptibles will not only occupy all low-risk sites but will also occupy some high-risk sites. It remains to show the global asymptotic stability of the EE for small values of d_S. However, it is unknown whether the EE is even locally stable, and we hope that Theorem 4 will guide future attempts to prove stability of the EE when d_S is very small.

Second, it can be shown that the function S^* belongs to $C^1(\overline{\Omega}) \cap C^2(J^-)$ and satisfies the free boundary problem

$$d_I \Delta S^* + (S^* - C)(\beta - \gamma) = 0 \quad \text{in } J^-, \quad S^* = \nabla S^* = 0 \quad \text{on } \partial J^-, \quad \int_{J^-} S^* = N,$$

where C is a positive constant. One technical difficulty to extend Theorem 4 (d) to $m \geq 2$ is our lack of understanding of the regularity of the free boundary ∂J^-.

2 The Disease-Free Equilibrium

Throughout this section, we assume that (A1) and (A2) hold and that N is fixed. Theorem 1 follows from Lemmas 2.1, 2.4, and 2.5, and Theorem 2 is a consequence of Lemmas 2.3 and 2.4.

2.1 Existence and uniqueness of the DFE

Eq. (1.4) has a unique disease-free solution, and it is spatially homogeneous.

Lemma 2.1. *A DFE* $(\hat{S}, 0)$ *exists, it is unique, and it is given by* $\hat{S} \equiv N/|\Omega|$ *on* Ω*.*

Proof. It is clear from (1.4) that $(N/|\Omega|, 0)$ is a DFE. Now, let $(\tilde{S}, 0)$ be any DFE. It follows from (1.4) with $\tilde{I} = 0$ that $\Delta\tilde{S} = 0$ for $x \in \Omega$ and $\partial\tilde{S}/\partial n = 0$ for $x \in \partial\Omega$. The maximum principle implies that $\tilde{S}$ is constant on Ω. In view of (1.4d) with $\tilde{I} = 0$, we obtain $\tilde{S} \equiv N/|\Omega|$ on Ω. □

2.2 An eigenvalue problem

So that we may study the stability of the DFE in Lemma 2.1, it will be useful to consider first an eigenvalue problem which is associated with (1.1). We linearize (1.1a) and (1.1b) around the DFE to obtain

$$\frac{\partial \eta}{\partial t} = d_S \Delta \eta - (\beta - \gamma)\xi, \quad x \in \Omega \text{ and } t > 0,$$
$$\frac{\partial \xi}{\partial t} = d_I \Delta \xi + (\beta - \gamma)\xi, \quad x \in \Omega \text{ and } t > 0.$$

Here, $\eta(x,t) = \bar{S}(x,t) - \hat{S}(x)$ and $\xi(x,t) = \bar{I}(x,t)$. Suppose that $(\eta, \xi) = (e^{-\lambda t}\phi, e^{-\lambda t}\psi)$ is a solution of the linear system where $\lambda \in \mathbb{R}$, $\phi = \phi(x)$, and $\psi = \psi(x)$. We substitute this solution into the linearized equations and divide by $e^{-\lambda t}$ to get the following linear eigenvalue problem

$$d_S \Delta \phi - (\beta - \gamma)\psi + \lambda \phi = 0, \quad x \in \Omega, \tag{2.1a}$$
$$d_I \Delta \psi + (\beta - \gamma)\psi + \lambda \psi = 0, \quad x \in \Omega. \tag{2.1b}$$

Observe that (2.1b) decouples from (2.1a). In view of (1.1c), we must have that

$$\frac{\partial \phi}{\partial n} = \frac{\partial \psi}{\partial n} = 0, \quad x \in \partial\Omega. \tag{2.1c}$$

Observe from (1.3) and Lemma 2.1 that

$$e^{-\lambda t} \int_\Omega (\phi + \psi) = \int_\Omega (\eta + \xi) = 0.$$

Therefore,

$$\int_\Omega (\phi + \psi) = 0. \tag{2.1d}$$

By the Krein-Rutman Theorem (Krein and Rutman 1962), if (λ, ψ) is a solution of (2.1b) with $\psi \not\equiv 0$ on Ω then λ is real. Furthermore, there exists a least eigenvalue λ^*, its corresponding eigenfunction ψ^* can be chosen to be positive on Ω, and no other eigenvalue λ has an eigenfunction ψ which is positive everywhere. Observe that (λ^*, ψ^*) satisfies

$$d_I \Delta \psi^* + (\beta - \gamma)\psi^* + \lambda^* \psi^* = 0 \text{ for } x \in \Omega \quad \text{and} \quad \frac{\partial \psi^*}{\partial n} = 0 \text{ for } x \in \partial\Omega. \tag{2.2}$$

It is well-known that λ^* is given by the following variational characterization:

$$\lambda^* = \inf \left\{ \int_\Omega \left[d_I |\nabla \varphi|^2 + (\gamma - \beta)\varphi^2 \right] : \varphi \in W^{1,2}(\Omega) \text{ and } \int_\Omega \varphi^2 = 1 \right\}. \tag{2.3}$$

It can be shown also that λ^* and ψ^* are both differentiable functions of d_I (Cantrell and Cosner 2003).

Lemma 2.2. *The following statements about $\lambda^* = \lambda^*(d_I)$ hold.*

(a) *λ^* is a strictly monotone increasing function of $d_I > 0$;*

(b) *$\lambda^* \to \min\{\gamma(x) - \beta(x) : x \in \overline{\Omega}\} < 0$ as $d_I \to 0$;*

(c) *$\lambda^* \to \frac{1}{|\Omega|} \int_\Omega (\gamma - \beta)$ as $d_I \to \infty$;*

(d) *If* $\int_\Omega \beta \geq \int_\Omega \gamma$ *then* $\lambda^* < 0$ *for all* $d_I > 0$*;*

(e) *If* $\int_\Omega \beta < \int_\Omega \gamma$ *then the equation* $\lambda^*(d_I) = 0$ *has a unique positive root denoted by* d_I^**. Furthermore, if* $d_I < d_I^*$ *then* $\lambda^* < 0$ *and if* $d_I > d_I^*$ *then* $\lambda^* > 0$*.*

Proof. We need only to prove parts (a)-(c), because parts (d) and (e) follow immediately from them.

(a) The fact that λ^* is a monotone increasing function of d_I is clear by inspection of (2.3). We now show that this dependence is strict. We differentiate both sides of (2.2) by d_I to get

$$\Delta\psi^* + d_I\Delta(\psi^*)' + (\beta-\gamma)(\psi^*)' + (\lambda^*)'\psi^* + \lambda^*(\psi^*)' = 0, \quad x \in \Omega, \tag{2.4}$$

and $\partial(\psi^*)'/\partial n = 0$ for $x \in \partial\Omega$. Here, the prime notation denotes differentiation by d_I. We now multiply (2.2) by $(\psi^*)'$ and (2.4) by ψ^*, subtract the resulting equations, and then integrate by parts over Ω to get $(\lambda^*)' \int_\Omega (\psi^*)^2 = \int_\Omega |\nabla\psi^*|^2$. Since $\psi^* > 0$ on Ω, it follows that $(\lambda^*)' \geq 0$, with equality possible only if ψ^* is constant on Ω. But if ψ^* is constant on Ω then it must be a positive constant. Eq. (2.2) implies then that $\beta(x) - \gamma(x) + \lambda^* = 0$ for every $x \in \Omega$, a contradiction because the function $\beta - \gamma$ changes sign on Ω. We conclude that $(\lambda^*)' > 0$.

(b) This result appears as Lemma 3.1 in (Lou and Nagasaki 2006).

(c) It is easy to see from (2.3) with $\varphi^2 \equiv 1/|\Omega|$ that $\lambda^* \leq \max\{\gamma(x) - \beta(x) : x \in \overline{\Omega}\}$ for all $d_I > 0$. By part (a), λ^* is uniformly bounded for $d_I \geq 1$. Thus, it has a finite limit $\hat{\lambda}$ as $d_I \to \infty$. We divide both sides of (2.2) by d_I to get

$$\Delta\psi^* + \frac{\beta - \gamma + \lambda^*}{d_I}\psi^* = 0, \quad x \in \Omega.$$

By elliptic regularity (Gilbarg and Trudinger 1983), $\psi^* \to \bar{\psi}$ in $C(\Omega)$ as $d_I \to \infty$ for some positive constant $\bar{\psi}$. We integrate (2.2) by parts over Ω to get $\int_\Omega (\beta-\gamma)\psi^* + \lambda^* \int_\Omega \psi^* = 0$. Letting $d_I \to \infty$ produces the desired relation $\hat{\lambda} = \frac{1}{|\Omega|}\int_\Omega (\gamma - \beta)$. □

2.3 Stability of the DFE and properties of $\mathcal{R}_0$

Applying Lemmas 2.1 and 2.2, and the linear eigenvalue problem just described, we can define a basic reproduction number $\mathcal{R}_0$ for the system (1.1) using the next generation approach for heterogenous populations (Diekmann et al. 1990, Diekmann and Heesterbeek 2000). It is known in non-spatial models and in patch models (van den Driessche and Watmough 2002) that if $\mathcal{R}_0 < 1$ then the DFE is locally asymptotically stable, and if $\mathcal{R}_0 > 1$ then the DFE is unstable. We now extend this theory to our reaction-diffusion model.

Lemma 2.3. *Define the basic reproduction number* $\mathcal{R}_0$ *for* (1.1) *by*

$$\mathcal{R}_0 = \sup_{\substack{\varphi \in H^1(\Omega) \\ \varphi \neq 0}} \left\{ \frac{\int_\Omega \beta\varphi^2}{\int_\Omega d_I|\nabla\varphi|^2 + \gamma\varphi^2} \right\}. \tag{2.5}$$

Then

(a) $\mathcal{R}_0$ *is a positive and monotone decreasing function of* $d_I > 0$*;*

(b) $\mathcal{R}_0 \to \max\{\beta(x)/\gamma(x) : x \in \overline{\Omega}\}$ *as* $d_I \to 0$*;*

(c) $\mathcal{R}_0 \to \int_\Omega \beta / \int_\Omega \gamma$ *as* $d_I \to \infty$*;*

(d) $\mathcal{R}_0 > 1$ *when* $\lambda^* < 0$*,* $\mathcal{R}_0 = 1$ *when* $\lambda^* = 0$*, and* $\mathcal{R}_0 < 1$ *when* $\lambda^* > 0$*.*

Proof. The right-hand side of (2.5) exists and is positive because the functions β and γ are positive on $\overline{\Omega}$. The rest of part (a) is clear by inspection of (2.5). The proof for part (b) is similar to that of Lemma 3.1 (Lou and Nagasaki 2006), and the argument for part (c) is similar to the one given in Lemma 2.2 (c). It remains to establish part (d). It is a well-known fact that there exists a positive function $\Phi(x) \in C^2(\overline{\Omega})$ such that

$$-d_I \Delta \Phi + \gamma \Phi = \frac{\beta}{\mathcal{R}_0} \Phi \ \text{ for } \ x \in \Omega \quad \text{and} \quad \frac{\partial \Phi}{\partial n} = 0 \ \text{ for } \ x \in \partial\Omega. \tag{2.6}$$

Now consider (2.2) and (2.6),

$$d_I \Delta \psi^* + (\beta - \gamma)\psi^* + \lambda^* \psi^* = 0, \quad x \in \Omega, \tag{2.7}$$

$$d_I \Delta \Phi - \gamma \Phi + \frac{\beta}{\mathcal{R}_0} \Phi = 0, \quad x \in \Omega. \tag{2.8}$$

Recall that ψ^* and Φ are both positive on Ω and that $\partial\psi^*/\partial n = \partial\Phi/\partial n = 0$ on $\partial\Omega$. We multiply (2.7) by Φ and (2.8) by ψ^*, integrate by parts on Ω, and subtract the resulting equations to obtain

$$\left(1 - \frac{1}{\mathcal{R}_0}\right) \int_\Omega \beta \psi^* \Phi + \lambda^* \int_\Omega \psi^* \Phi = 0.$$

Since $\int_\Omega \beta\psi^*\Phi$ and $\int_\Omega \psi^*\Phi$ are both positive, we conclude that $1 - (1/\mathcal{R}_0)$ and λ^* have opposite signs. That is, $\mathcal{R}_0 > 1$ when $\lambda^* < 0$, $\mathcal{R}_0 = 1$ when $\lambda^* = 0$, and $\mathcal{R}_0 < 1$ when $\lambda^* > 0$. □

We now show that the stability of the DFE is determined entirely by the magnitude of $\mathcal{R}_0$.

Lemma 2.4. *If* $\mathcal{R}_0 < 1$ *then the DFE is stable, but if* $\mathcal{R}_0 > 1$ *then it is unstable.*

Proof.

(a) Suppose first that $\mathcal{R}_0 < 1$. We will show that the DFE is linearly stable, that is, if (λ, ϕ, ψ) is any solution of (2.1), with at least one of ϕ or ψ not identically zero on Ω, then $\mathrm{Re}(\lambda)$ must be positive. We argue by contradiction. Suppose that (λ, ϕ, ψ) is a solution of (2.1), with at least one of ϕ or ψ not identically zero, and that $\mathrm{Re}(\lambda) \le 0$. We first show that $\psi \not\equiv 0$ on Ω. For suppose otherwise. Then $\phi \not\equiv 0$ on Ω. Furthermore, (2.1a) with $\psi \equiv 0$ and (2.1c) imply that

$$d_S \Delta \phi + \lambda \phi = 0 \ \text{ for } \ x \in \Omega \quad \text{and} \quad \frac{\partial \phi}{\partial n} = 0 \ \text{ for } \ x \in \partial\Omega.$$

This equation implies that λ is real and nonnegative, and therefore that $\lambda = 0$. We conclude from the maximum principle that ϕ takes a constant value, say ϕ_0, on $\overline{\Omega}$. It follows from (2.1d) with $\psi \equiv 0$ that $\phi_0 = 0$. But this implies that $\phi \equiv 0$ on Ω, a contradiction. We conclude then that $\psi \not\equiv 0$ on Ω. Thus, λ must be real and nonpositive in (2.1b) because $d_I \Delta + \beta - \gamma$ is a self-adjoint operator. It follows from this and the minimality of λ^* that $\lambda^* \le \lambda \le 0$. Lemma 2.3 (d) implies that $\mathcal{R}_0 \ge 1$, a contradiction. We conclude that if (λ, ϕ, ψ) is a solution of (2.1), with at least one of ϕ or ψ not identically zero on Ω, then $\mathrm{Re}(\lambda) > 0$. This proves linear stability of the DFE. Stability of the DFE follows from its linear stability (Henry 1981).

(b) Suppose now that $\mathcal{R}_0 > 1$. We will show that the DFE is linearly unstable. In fact, we will establish that there exists a solution (λ, ϕ, ψ) of (2.1) with $\mathrm{Re}(\lambda) < 0$ and $\psi > 0$ on Ω. Recall that (λ^*, ψ^*) satisfies (2.2) and that we may take $\psi^* > 0$ on Ω. Lemma 2.3 (d) implies that $\lambda^* < 0$. Hence, the inhomogeneous linear equation (2.1a) with $(\lambda, \psi) = (\lambda^*, \psi^*)$, i.e.,

$$d_S \Delta \phi + \lambda^* \phi = (\beta - \gamma)\psi^*, \quad x \in \Omega, \tag{2.9}$$

has a unique solution ϕ^* satisfying $\partial \phi^*/\partial n = 0$ for $x \in \partial\Omega$ (Gilbarg and Trudinger 1983). Finally, we add (2.9) with $\phi = \phi^*$ to (2.2) and then integrate by parts over Ω to get $\lambda^* \int_\Omega (\phi^* + \psi^*) = 0$. Since λ^* is negative, we conclude that $\int_\Omega (\phi^* + \psi^*) = 0$. Thus, (2.1) has a solution $(\lambda^*, \phi^*, \psi^*)$ satisfying $\lambda^* < 0$ and $\psi^* > 0$ on Ω. Hence, the DFE is linearly unstable. Instability of the DFE follows from its linear instability (Henry 1981). □

We now show that if $\mathcal{R}_0 < 1$ then the disease always becomes extinct, i.e., the DFE is globally asymptotically stable.

Lemma 2.5. *If $\mathcal{R}_0 < 1$ then $(\bar{S}, \bar{I}) \to (\hat{S}, 0)$ in $C(\Omega)$ as $t \to \infty$.*

Proof. Suppose that $\mathcal{R}_0 < 1$. We will use the comparison principle to show that $\bar{I}(x,t) \to 0$ as $t \to \infty$ for every $x \in \Omega$. To begin, observe from (1.1b) that

$$\frac{\partial \bar{I}}{\partial t} \le d_I \Delta \bar{I} + (\beta - \gamma)\bar{I}, \quad x \in \Omega \text{ and } t > 0.$$

Next, let us define $u(x,t) = Me^{-\lambda^* t}\psi^*(x)$ where $\lambda^* > 0$ by Lemma 2.3(d), $\psi^* > 0$ on Ω, and M is chosen so large that $\bar{I}(x,0) \le u(x,0)$ for every $x \in \Omega$. It can be easily shown, by making use of (2.2), that u satisfies

$$\frac{\partial u}{\partial t} = d_I \Delta u + (\beta - \gamma)u, \quad x \in \Omega \text{ and } t > 0$$

and $\partial u/\partial n = 0$ for $x \in \partial\Omega$ and $t > 0$. By the comparison principle, $\bar{I}(x,t) \le u(x,t)$ for every $x \in \Omega$ and $t \ge 0$. Since $u(x,t) \to 0$ as $t \to \infty$ for every $x \in \Omega$, we also have that $\bar{I}(x,t) \to 0$ as $t \to \infty$ for every $x \in \Omega$.

We now show that $\bar{S}$ tends to $\hat{S}$ as $t \to \infty$. Observe from (1.1a) that

$$\frac{\partial \bar{S}}{\partial t} - d_S \Delta \bar{S} = \left[\gamma - \frac{\beta \bar{S}}{\bar{S} + \bar{I}}\right] \bar{I}, \quad x \in \Omega \text{ and } t > 0.$$

The continuity of β and γ on $\overline{\Omega}$, together with the preceding remarks about $\bar{I}(x,t)$ and $u(x,t)$, imply that

$$\left| \frac{\partial \bar{S}}{\partial t} - d_S \Delta \bar{S} \right| \le C_1 e^{-\lambda^* t}, \quad x \in \Omega \text{ and } t > 0,$$

for some positive constant C_1. Since the right-hand side tends to 0 exponentially, it follows that $\bar{S}(x,t)$ tends to a positive constant as $t \to \infty$. To see this, write $\bar{S}(x,t) = S_1(t) + S_2(x,t)$, where $S_1(t) = \frac{1}{|\Omega|}\int_\Omega \bar{S}(x,t)\,dx$. Observe that $|\partial S_1/\partial t| \le C_2 e^{-\lambda^* t}$ for some positive constant C_2. Therefore, S_2 satisfies $\partial S_2/\partial t = d_S \Delta S_2 + f(x,t)$ on $\Omega \times (0,\infty)$ with $|f(x,t)| \le C_3 e^{-\lambda^* t}$ for some positive constant C_3, $\partial S_2/\partial n = 0$ on $\partial\Omega \times (0,\infty)$, and $\int_\Omega S_2(x,t)\,dx \equiv 0$ for every $t \ge 0$. By (1.3) and $\bar{I}(x,t) \to 0$ as $t \to \infty$, we have $S_1(t) \to \hat{S}$ as $t \to \infty$. Let $0 = \lambda_0 < \lambda_1 \le \lambda_2 \le \cdots$ denote the eigenvalues of $-\Delta$ with zero Neumann boundary condition, and $\{\varphi_k\}_{k=0}^\infty$ be corresponding normalized eigenfunctions. Set $S_2 = \sum_{k=0}^\infty a_k(t)\varphi_k(x)$ and $f = \sum_{k=0}^\infty f_k(t)\varphi_k(x)$. Note that $a_0 = f_0 = 0$ as $\int_\Omega S_2(x,t)\,dx \equiv 0$. Since $|f_k(t)| \le C_4 e^{-\lambda^* t}$ for every $k \ge 1$, we see that $|a_k(t)| \le$

$C_5 e^{-\lambda^{**}t}$ for every $k \geq 1$, where C_4 and C_5 are positive constants and $\lambda^{**} = \min\{\lambda^*, \lambda_1\} > 0$. Hence, $S_2(x,t) \to 0$ for $x \in \Omega$ as $t \to \infty$ for every $x \in \Omega$. We conclude that $\bar{S}(x,t) \to \hat{S}$ as $t \to \infty$ for every $x \in \Omega$. □

The global asymptotic stability of the DFE when $\mathcal{R}_0 < 1$ implies that there can be no EE in this case. In Sect. 3, we consider what happens when $\mathcal{R}_0 > 1$.

3 The Endemic Equilibrium

Throughout this section, we again assume that (A1) and (A2) hold and that N is fixed. Theorem 3 follows from Lemma 3.4.

3.1 Equivalent problems

We will consider several alternative statements of the equilibrium problem. The first such statement is as follows.

Lemma 3.1. *The pair $(\tilde{S}, \tilde{I})$ is a solution of (1.4) if and only if $(\tilde{S}, \tilde{I})$ is a solution of*

$$\kappa = d_S \tilde{S} + d_I \tilde{I}, \qquad x \in \Omega, \tag{3.1a}$$

$$0 = d_I \Delta \tilde{I} + \tilde{I}\left(\beta - \gamma - \frac{\beta \tilde{I}}{\tilde{S} + \tilde{I}}\right), \quad x \in \Omega, \tag{3.1b}$$

$$0 = \frac{\partial \tilde{S}}{\partial n} = \frac{\partial \tilde{I}}{\partial n}, \qquad x \in \partial\Omega, \tag{3.1c}$$

$$N = \int_\Omega (\tilde{S} + \tilde{I}), \tag{3.1d}$$

where κ is some positive constant that is independent of $x \in \Omega$.

Proof.

(a) Suppose first that $(\tilde{S}, \tilde{I})$ is a solution of (1.4). Eqs. (1.4a)–(1.4c) imply that

$$\Delta\big(d_S \tilde{S} + d_I \tilde{I}\big) = 0 \ \text{ for } \ x \in \Omega \quad \text{and} \quad \frac{\partial}{\partial n}\big(d_S \tilde{S} + d_I \tilde{I}\big) = 0 \ \text{ for } \ x \in \partial\Omega.$$

By the maximum principle, $d_S \tilde{S} + d_I \tilde{I} = \kappa$ on Ω for some constant κ. Since $\tilde{S}$, $\tilde{I} \geq 0$ on Ω and $N > 0$, it must be that $d_S \tilde{S} + d_I \tilde{I} > 0$ for some $x \in \Omega$. Therefore, $\kappa > 0$. The fact that $(\tilde{S}, \tilde{I})$ satisfies (3.1b)–(3.1d) is clear by inspection.

(b) Suppose now that $(\tilde{S}, \tilde{I})$ is a solution of (3.1) for some $\kappa > 0$. To see that $(\tilde{S}, \tilde{I})$ satisfies (1.4a), observe from (3.1a) and (3.1b) that if $x \in \Omega$ then

$$d_S \Delta \tilde{S} = -d_I \Delta \tilde{I} = \tilde{I}\left(\beta - \gamma - \frac{\beta \tilde{I}}{\tilde{S} + \tilde{I}}\right) = \frac{\beta \tilde{S} \tilde{I}}{\tilde{S} + \tilde{I}} - \gamma \tilde{I}.$$

Thus, (1.4a) is satisfied. The fact that $(\tilde{S}, \tilde{I})$ satisfies (1.4b)–(1.4d) is clear by inspection. □

For our second equivalent formulation, let

$$S(x) \stackrel{\text{def}}{=} \frac{\tilde{S}(x)}{\kappa} \quad \text{and} \quad I(x) \stackrel{\text{def}}{=} \frac{d_I \tilde{I}(x)}{\kappa}, \tag{3.2}$$

where κ is as in Lemma 3.1, and let

$$f(x,u) \stackrel{\text{def}}{=} \beta(x)\left(1 - \frac{d_S u}{d_I + (d_S - d_I)u}\right) - \gamma(x), \quad x \in \Omega \text{ and } u \in [0,1]. \tag{3.3}$$

Observe that f strictly decreases from $\beta(x) - \gamma(x)$ to $-\gamma(x)$ as u increases from 0 to 1. The next result follows from a direct calculation.

Lemma 3.2. *The pair $(\tilde{S}, \tilde{I})$ is a solution of (3.1) if and only if (S, I) is a solution of*

$$1 = d_S S + I, \qquad x \in \Omega, \tag{3.4a}$$

$$0 = d_I \Delta I + I f(x, I), \quad x \in \Omega, \tag{3.4b}$$

$$0 = \frac{\partial I}{\partial n}, \qquad x \in \partial\Omega, \tag{3.4c}$$

$$\kappa = \frac{d_I N}{\int_\Omega \left(d_I S + I\right)}. \tag{3.4d}$$

3.2 Existence and uniqueness of the EE

Lemma 3.3. *Suppose that $\mathcal{R}_0 > 1$. Then (3.4) has a nonnegative solution (S, I) which satisfies $S(x), I(x) \in C^2(\overline{\Omega})$ and $I \not\equiv 0$ on Ω. Furthermore, this solution with $I \not\equiv 0$ is unique, $S(x) > 0$, and $0 < I(x) < 1$ for $x \in \Omega$.*

Proof. In view of (3.4b) and (3.4c), consider the boundary value problem

$$G(I) \stackrel{\text{def}}{=} d_I \Delta I + I f(x, I) = 0 \text{ for } x \in \Omega \quad \text{and} \quad \frac{\partial I}{\partial n} = 0 \text{ for } x \in \partial\Omega. \tag{3.5}$$

If $\underline{I}$ and $\overline{I}$ is a sub-solution and super-solution of (3.5), respectively, i.e., $G(\underline{I}) \geq 0 \geq G(\overline{I})$ on Ω and $\partial \underline{I}/\partial n = \partial \overline{I}/\partial n = 0$ on $\partial\Omega$, and they are ordered, i.e., $\underline{I} \leq \overline{I}$ on Ω, then there must exist some $I \in [\underline{I}, \overline{I}]$ satisfying (3.5), where $[\underline{I}, \overline{I}] \stackrel{\text{def}}{=} \{I \in C^2(\overline{\Omega}) : \underline{I}(x) \leq I(x) \leq \overline{I}(x) \text{ for } x \in \Omega\}$ (Smoller 1983).

Recall that (λ^*, ψ^*) satisfies (2.2) and that $\psi^* > 0$ on Ω. We now show that $\underline{I} = \epsilon\psi^*$ and $\overline{I} \equiv 1$ are sub- and super-solutions for (3.5) if ϵ is chosen to be positive and sufficiently small. Lemma 2.3(d) implies that $\lambda^* < 0$. In view of (3.3), define

$$g(u) = \frac{d_S u}{d_I + (d_S - d_I)u}, \quad u \in [0,1].$$

We remark that g increases from 0 to 1 as u increases from 0 to 1. Observe from (3.3) and (2.2) that

$$\begin{aligned} G(\underline{I}) &= d_I \Delta(\epsilon\psi^*) + \epsilon\psi^* f(x, \epsilon\psi^*) \\ &= \epsilon\left[d_I \Delta\psi^* + \psi^*(\beta - \gamma) - \beta\psi^* g(\epsilon\psi^*)\right] \\ &= \epsilon\psi^*\left[-\lambda^* - \beta g(\epsilon\psi^*)\right] \end{aligned}$$

is positive for $x \in \Omega$ when $0 < \epsilon \ll 1$. Also, $\partial \underline{I}/\partial n = 0$ on $\partial\Omega$ by (2.2). Therefore, $\underline{I}$ is a sub-solution of (3.5) for ϵ positive and sufficiently small. Next, since $G(\overline{I}) = f(x,1) = -\gamma(x)$ is negative on Ω, and $\partial \overline{I}/\partial n = 0$ on $\partial\Omega$, it follows that $\overline{I}$ is a super-solution of (3.5). Also, it is obvious that $\underline{I} \le \overline{I}$ on Ω if ϵ is chosen sufficiently small. We conclude from the remarks above that there must be an $I \in [\underline{I}, \overline{I}]$ satisfying (3.5). That is, there exists some $I(x) \in C^2(\overline{\Omega})$ satisfying (3.4b) and (3.4c) with $0 < I(x) \le 1$ for $x \in \Omega$. We argue by contradiction to show that I is strictly less than 1 on Ω. Suppose that $I(x) = 1$ for some $x \in \Omega$. As I achieves its maximum on Ω at x, it must be that $\Delta I(x) \le 0$. But then $G(I(x)) = d_I \Delta I(x) - \gamma(x) < 0$, a contradiction. We conclude that $0 < I(x) < 1$ for every $x \in \Omega$. In view of (3.4a), let us define S by $1 = d_S S + I$. Then $S(x) \in C^2(\overline{\Omega})$ and $S > 0$ on Ω. Thus, (S, I) is a positive solution of (3.4) with $I(x), S(x) \in C^2(\overline{\Omega})$ and $I(x) < 1$ for $x \in \Omega$.

To show uniqueness, we argue by contradiction. Suppose that (3.4) has two nonnegative solutions (S_1, I_1) and (S_2, I_2) with $I_1, I_2 \not\equiv 0$ and $I_1 \not\equiv I_2$ on Ω. It follows from (3.4a) that $0 \le I_1, I_2 \le 1$ on Ω. From the maximum principle, we obtain that $0 < I_1, I_2 \le 1$ on $\overline{\Omega}$. Therefore, we may choose ϵ small enough so that $\underline{I} \le I_1, I_2 \le \overline{I}$ on $\overline{\Omega}$. Let $I_{\rm m}$ and $I^{\rm m}$ denote the minimal and maximal solutions of (3.4b) and (3.4c), respectively, within the set $[\underline{I}, \overline{I}]$. Since $I_1 \not\equiv I_2$, we have $I_{\rm m} \le I^{\rm m}$ and $I_{\rm m} \not\equiv I^{\rm m}$. The maximum principle now implies that $I_{\rm m} < I^{\rm m}$ on $\overline{\Omega}$. Multiplying (3.4b) with $I = I_{\rm m}$ by $I^{\rm m}$ and (3.4b) with $I = I^{\rm m}$ by $I_{\rm m}$, subtracting the resulting equations, and then integrating by parts over Ω gives

$$\int_\Omega I_{\rm m} I^{\rm m} \big[f(x, I_{\rm m}) - f(x, I^{\rm m}) \big] \, dx = 0. \tag{3.6}$$

The fact that $\partial f/\partial u < 0$ for $x \in \Omega$ and $u \in [0,1]$ implies that $f(x, I_{\rm m}) - f(x, I^{\rm m}) > 0$ on Ω. But this result contradicts (3.6) because $I_{\rm m}$ and $I^{\rm m}$ are both positive functions. We conclude that (3.4) has a unique nonnegative solution (S, I) with $I \not\equiv 0$ on Ω. □

The next result follows from Lemmas 3.1–3.3 and (3.2).

Lemma 3.4. *Suppose that $\mathcal{R}_0 > 1$. Then* (1.4) *has a nonnegative solution $(\tilde{S}, \tilde{I})$ which satisfies $\tilde{S}(x), \tilde{I}(x) \in C^2(\overline{\Omega})$ and $\tilde{I} \not\equiv 0$ on Ω. Furthermore, this solution is unique, it is given by $(\tilde{S}, \tilde{I}) = (\kappa S, \kappa I/d_I)$ where κ is as in* (3.4d)*, and both $\tilde{S}$ and $\tilde{I}$ are positive on Ω.*

We have shown that a unique EE exists when $\mathcal{R}_0 > 1$ and that both $\tilde{S}$ and $\tilde{I}$ are positive. In the next section, we consider the asymptotic behavior of the EE as $d_S \to 0$.

4 Asymptotic Behavior of the Endemic Equilibrium

Throughout this section, we still assume that (A1) and (A2) hold and that N is fixed. We also assume that $\mathcal{R}_0 > 1$, so that Lemma 3.3 for (S, I) and Lemma 3.4 for $(\tilde{S}, \tilde{I})$ always apply. Theorem 4 is a combination of Lemmas 4.2–4.7 and Lemma 4.9.

4.1 The limiting DFE

Observe that $\tilde{S}$, $\tilde{I}$, and κ are all functions of d_S in (1.4) and (3.1). To determine their behavior as $d_S \to 0$, we must first establish some asymptotic properties of I in (3.2).

Lemma 4.1. *I is a monotone decreasing function of d_S.*

Proof. Suppose that $0 < d_{S_1} < d_{S_2}$ and let I_1 and I_2 be corresponding solutions to (3.4b) and (3.4c) with $0 < I_1, I_2 < 1$ on Ω. Then

$$d_I \Delta I_1 + I_1 f(x, I_1, d_{S_1}) = 0 \text{ for } x \in \Omega \quad \text{and} \quad \frac{\partial I_1}{\partial n} = 0 \text{ for } x \in \partial\Omega, \tag{4.1a}$$

$$d_I \Delta I_2 + I_2 f(x, I_2, d_{S_2}) = 0 \text{ for } x \in \Omega \quad \text{and} \quad \frac{\partial I_2}{\partial n} = 0 \text{ for } x \in \partial\Omega, \tag{4.1b}$$

where

$$f(x, u, d_S) = \beta(x)\left(1 - \frac{d_S u}{d_S u + d_I(1-u)}\right) - \gamma(x), \quad x \in \Omega \text{ and } u \in [0,1].$$

It is easy to see that $\partial f/\partial d_S \leq 0$. It follows from this fact and (4.1b) with d_{S_1} in place of d_{S_2} that

$$d_I \Delta I_2 + I_2 f(x, I_2, d_{S_1}) \geq 0 \text{ for } x \in \Omega \quad \text{and} \quad \frac{\partial I_2}{\partial n} = 0 \text{ for } x \in \partial\Omega.$$

Thus, I_2 is a sub-solution of (4.1a). Again, $\overline{I} \equiv 1$ on Ω is a super-solution of (4.1a). Also, $I_2 < \overline{I}$ on Ω. By the sub-solution and super-solution method, (4.1a) has a unique solution $I_1 \in [I_2, \overline{I}]$. We conclude that $I_1 \geq I_2$ on Ω. □

Lemma 4.2. *$I \to I^*$ in $C^1(\overline{\Omega})$ as $d_S \to 0$ for some $I^*(x) \in C^1(\overline{\Omega})$ with $0 < I^*(x) \leq 1$ on $\overline{\Omega}$ and $\partial I^*/\partial n = 0$ on $\partial\Omega$.*

Proof. Recall from Lemma 3.3 that $0 < I(x) < 1$ for $x \in \Omega$. It follows from Lemma 4.1 that

$$I^*(x) \stackrel{\text{def}}{=} \lim_{d_S \to 0} I(x) \tag{4.2}$$

exists for every $x \in \overline{\Omega}$ and that $0 < I^*(x) \leq 1$ for $x \in \overline{\Omega}$. Since I and $f(x, I)$ are uniformly bounded for all $d_S > 0$, it follows from (3.4b) and L^p-estimates that $\|I\|_{W^{2,p}(\Omega)}$ is bounded for every $d_S > 0$ and $p > 1$ (Gilbarg and Trudinger 1983). Consequently, $\|I\|_{C^{1,\alpha}(\Omega)}$ is bounded for every $d_S > 0$ and $\alpha \in (0,1)$ by the Sobolev embedding theorem (Gilbarg and Trudinger 1983). Passing to a subsequence if necessary, we obtain that $I \to I^*$ in $C^1(\overline{\Omega})$ as $d_S \to 0$. We see from (4.2) that this property holds for the whole sequence. The fact that $\partial I^*/\partial n = 0$ on $\partial\Omega$ follows from $\partial I/\partial n = 0$ on $\partial\Omega$ for every $d_S > 0$ and $I \to I^*$ in $C^1(\overline{\Omega})$ as $d_S \to 0$. □

It remains to determine where $0 < I^* < 1$ and where $I^* = 1$ on Ω. Let

$$J^- = \{x \in \overline{\Omega} : 0 < I^*(x) < 1\} \quad \text{and} \quad J^+ = \{x \in \overline{\Omega} : I^*(x) = 1\}. \tag{4.3}$$

Observe that $J^- \cup J^+ = \overline{\Omega}$. It turns out that J^- and J^+ are both nonempty. We first show this for J^- by demonstrating that it contains H^- and therefore has positive measure.

Lemma 4.3. *$H^- \subseteq J^-$.*

Proof. We argue by contradiction. Suppose that there exists some $x_0 \in H^-$ such that $x_0 \notin J^-$, i.e., $I^*(x_0) = 1$. We see from (3.4b) and the properties of f that $\Delta I(x) > 0$ for all $x \in H^-$. Hence, there exists some $\tau > 0$ such that $\overline{B(x_0, \tau)} \subset H^-$ and

$$I(x_0) \leq \frac{1}{|B|} \int_B I(x)\, dx,$$

where $B = B(x_0, \tau)$. We let $d_S \to 0$ and apply Lemma 4.2 to get

$$I^*(x_0) \leq \frac{1}{|B|} \int_B I^*(x)\, dx.$$

Since $I^*(x_0) = 1$ and $I^*(x) \leq 1$ on B, it follows that $I^* \equiv 1$ on B. We now choose some $\varphi \in C_0^\infty(B)$ such that $\varphi \geq 0$ on B, $\partial\varphi/\partial n = 0$ on ∂B, and $\varphi(x) > 0$ for some $x \in B$. Multiplying (3.4b) by φ, integrating over B, and making use of the properties of f, we obtain

$$d_I \int_B (\Delta I)\varphi + \int_B I(\beta - \gamma)\varphi \geq 0.$$

We integrate by parts to get

$$d_I \int_B I(\Delta\varphi) + \int_B I(\beta - \gamma)\varphi \geq 0.$$

Since $I \to I^* \equiv 1$ on B as $d_S \to 0$, and $\int_B \Delta\varphi = 0$, we must have that

$$\int_B (\beta - \gamma)\varphi \geq 0.$$

But this is a contradiction because $\beta - \gamma < 0$ on B, $\varphi \geq 0$ on B, and $\varphi(x) > 0$ for some $x \in B$. □

We now determine the asymptotic behavior of κ and $\tilde{I}$.

Lemma 4.4. *As $d_S \to 0$, $\kappa \to 0$ and $\tilde{I} \to 0$.*

Proof. We first show that $\kappa \to 0$ as $d_S \to 0$. By (1.4d), the positivity of $\tilde{I}$ on Ω, (3.1a), and (3.2) we have

$$N = \int_\Omega (\tilde{S} + \tilde{I}) > \int_\Omega \tilde{S} = \frac{\kappa}{d_S} \int_\Omega \big(1 - I\big).$$

It follows from Lemmas 4.2 and 4.3 that

$$\int_\Omega (1 - I^*) \geq \int_{H^-} (1 - I^*) > 0.$$

This inequality and Lemma 4.2 again implies that if d_S is sufficiently small then

$$\int_\Omega (1 - I) \geq \frac{1}{2} \int_\Omega (1 - I^*).$$

Hence,

$$0 < \frac{\kappa}{d_S} < \frac{N}{\int_\Omega (1 - I)} \leq \frac{2N}{\int_\Omega (1 - I^*)}.$$

As the right-hand side is constant, we conclude that $\kappa \to 0$ as $d_S \to 0$. It now follows from (3.1a) and the positivity of $\tilde{S}$ and $\tilde{I}$ on Ω that $\tilde{I} \to 0$ as $d_S \to 0$. □

We are now in a position to determine the asymptotic behavior of $\tilde{S}$.

Lemma 4.5. *The following statements hold:*

(a) $\kappa/d_S \to N^* \stackrel{\text{def}}{=} N/\int_\Omega (1 - I^*)$ *as* $d_S \to 0$;

(b) $\tilde{S} \to S^* \stackrel{\text{def}}{=} (1 - I^*)N^*$ *in* $C^1(\overline{\Omega})$ *as* $d_S \to 0$*;*

(c) $S^* \geq 0$ *on* Ω*,* $\partial S^*/\partial n = 0$ *on* $\partial\Omega$*, and* $\int_\Omega S^* = N$*.*

Proof.

(a) Eqs. (3.1a), (3.1d), and (3.2) imply that

$$N = \int_\Omega \left(\frac{\kappa - d_I \tilde{I}}{d_S} \right) + \int_\Omega \tilde{I} = \frac{\kappa}{d_S} \int_\Omega (1 - I) + \int_\Omega \tilde{I}.$$

Lemmas 4.2 and 4.4 imply that

$$\frac{\kappa}{d_S} \to \frac{N}{\int_\Omega (1 - I^*)} \quad \text{as} \quad d_S \to 0.$$

This limit is well-defined because J^- has positive measure.

(b) Again, (3.1a) and (3.2) imply that

$$\tilde{S} = \frac{\kappa - d_I \tilde{I}}{d_S} = (1 - I)\frac{\kappa}{d_S}.$$

Lemma 4.2 and part (a) imply that $\tilde{S} \to (1 - I^*)N^*$ in $C^1(\overline{\Omega})$ as $d_S \to 0$.

(c) This part follows immediately from parts (a) and (b), the positivity of N, and Lemma 4.2. □

4.2 Properties of the set J^+

Observe from (4.3) and Lemma 4.5 (b) that $S^* = 0$ on J^+.

Lemma 4.6. *The set* J^+ *is nonempty and has positive measure.*

Proof. We argue by contradiction. Suppose that J^+ is empty or has measure zero, i.e., $0 < I^*(x) < 1$ a.e. on Ω. We multiply both sides of (3.1b) by d_I/κ and make use of (3.2) to get

$$d_I \Delta I + I \left(\beta - \gamma - \frac{\beta \tilde{I}}{\tilde{S} + \tilde{I}} \right) = 0, \quad x \in \Omega. \tag{4.4}$$

Since $I \to I^*$ on Ω as $d_S \to 0$, and $I^* \in (0, 1)$ a.e. on Ω, we have from (3.4a) that

$$S = \frac{1 - I}{d_S} \xrightarrow{\text{a.e.}} \infty \quad \text{as} \quad d_S \to 0.$$

Hence, by (3.2),

$$\frac{\beta \tilde{I}}{\tilde{S} + \tilde{I}} = \frac{\beta I}{d_I S + I} \xrightarrow{\text{a.e.}} 0 \quad \text{as} \quad d_S \to 0.$$

Letting $d_S \to 0$ in (4.4), we see from Lemma 4.2 that I^* is an H^1 weak solution of

$$d_I \Delta I^* + I^*(\beta - \gamma) = 0 \ \text{ for } \ x \in \Omega \quad \text{and} \quad \frac{\partial I^*}{\partial n} = 0 \ \text{ for } \ x \in \partial\Omega.$$

By elliptic regularity, the weak solution I^* is a classical solution, that is, $I^* \in C^2(\overline{\Omega})$. We conclude that $(\lambda, \phi) = (0, I^*)$ is a solution of (2.1b). Since $I^* > 0$ on Ω, it must be that $\lambda^* = 0$. But this contradicts Lemma 2.3 (d) with $\mathcal{R}_0 > 1$. Hence, J^+ is nonempty and has positive measure. □

4.3 Properties of the set J^-

Lemma 4.7. *Suppose that* (A3) *holds. Then the following statements hold:*

(a) $\overline{H^-} \subseteq J^-$;

(b) $J^- \setminus \overline{H^-}$ *is nonempty, open, and has positive measure;*

(c) $I^*(x) \in C^2(J^-)$ *and* $d_I \Delta I^* + I^*(\beta - \gamma) = 0$ *for* $x \in J^-$.

Proof.

(a) We argue by contradiction. Suppose that J^- does not contain $\overline{H^-}$. By Lemma 4.3, it must be that J^- does not contain ∂H^-. Thus, there exists some $x_0 \in \partial H^-$ such that $x_0 \notin J^-$, i.e., $I^*(x_0) = 1$. Observe that I^* attains its maximum on $\overline{\Omega}$ at x_0. If $x_0 \in \partial\Omega$ then the Hopf Boundary Lemma implies that

$$\frac{\partial I^*}{\partial n}(x_0) > 0,$$

with n being the outward unit normal vector on $\partial\Omega$. But this inequality contradicts Lemma 4.2. We conclude that $x_0 \notin \partial\Omega$, and that instead $x_0 \in \Omega$. As Ω is open, it must be that $\nabla I^*(x_0) = 0$. Since $H^- \subseteq J^-$, it follows from an argument similar to the one given in the proof of Lemma 4.6 that $I^*(x) \in C^2(H^-)$ and that $d_I \Delta I^* + I^*(\beta - \gamma) = 0$ for $x \in H^-$. Lemma 4.3 implies that $I^*(x) \in (0, 1)$ for every $x \in H^-$, and therefore that $\Delta I^* > 0$ on H^-. With n now as the outward unit normal vector on ∂H^-, the Hopf Boundary Lemma implies that

$$\frac{\partial I^*}{\partial n}(x_0) > 0,$$

which is again a contradiction. We conclude that $\overline{H^-} \subseteq J^-$.

(b) Since J^- is an open set (it is the inverse image of an open interval) and $\overline{H^-}$ is closed, we see that $J^- \setminus H^-$ is nonempty, open, and has positive measure.

(c) By an argument similar to the one in Lemma 4.6, we see that I^* is an H^1 weak solution of $d_I \Delta I^* + I^*(\beta - \gamma) = 0$ for $x \in J^-$. By elliptic regularity, the weak solution I^* is a classical solution, that is, $I^* \in C^2(J^-)$. This completes the proof. □

For $\delta > 0$, let $H_\delta^+ \stackrel{\text{def}}{=} \{x \in H^+ : \beta(x) - \gamma(x) > \delta\}$, let K_δ denote any connected component of the open set $H_\delta^+ \cap J^-$, and let λ_δ^* denote the smallest eigenvalue of $-\Delta$ with zero Dirichlet boundary condition on K_δ.

Lemma 4.8. *Suppose that* (A3) *holds. Then* $\lambda_\delta^* \geq \delta/d_I$ *for every* $\delta > 0$.

Proof. We argue by contradiction. Suppose that $\lambda_\delta^* < \delta/d_I$ for some $\delta > 0$. Let I_δ be an eigenfunction of λ_δ^* chosen in such a way that $0 < I_\delta(x) \leq I^*(x)$ for every $x \in \Omega$. Then $-\Delta I_\delta = \lambda_\delta^* I_\delta < (\delta/d_I) I_\delta$ for $x \in K_\delta$ and $I_\delta = 0$ for $x \in \partial K_\delta$. Lemma 4.7 (c) implies that $-d_I \Delta I^* = (\beta - \gamma) I^* \geq \delta I^*$ for $x \in K_\delta$ and $I^* \geq 0$ for $x \in \partial K_\delta$. Therefore, I_δ and I^* are sub- and super-solutions, respectively, of the boundary value problem

$$-\Delta\varphi = \frac{\delta}{d_I}\varphi \ \text{ for } \ x \in K_\delta \quad \text{and} \quad \varphi = 0 \ \text{ for } \ x \in \partial K_\delta. \tag{4.5}$$

Also, $I_\delta \leq I^*$ on K_δ. By the sub-solution and super-solution method we see that (4.5) has a solution φ satisfying $0 < I_\delta \leq \varphi \leq I^*$ on K_δ. This implies that $\lambda_\delta^* = \delta/d_I$, which contradicts our assumption that $\lambda_\delta^* < \delta/d_I$. We conclude that $\lambda_\delta^* \geq \delta/d_I$ for every $\delta > 0$. □

Lemma 4.9. *Suppose that* (A3) *holds and* $m = 1$. *Then* $|J^- \setminus H^-| \to 0$ *as* $d_I \to 0$.

Proof. Let $\epsilon > 0$. By assumption (A3), the set H° is a union of finitely many points. Hence, there exists $\delta^* > 0$ such that the set $M_\delta \stackrel{\text{def}}{=} H^\circ \cup (H^+ \setminus H^+_\delta) = \{x \in \Omega : 0 \le \beta(x) - \gamma(x) \le \delta\}$ satisfies $|M_\delta| < \epsilon$ whenever $0 < \delta \le \delta^*$. Also, (A3) implies that the open set H^- is a union of finitely many disjoint open intervals, i.e, $H^- = \bigcup_{j=1}^r (\alpha_j, \beta_j)$, where r denotes the total number of intervals.

We now show that J^- is also a union of at most r disjoint open intervals. Since J^- is open, it is a union of countably many disjoint open intervals, i.e, $J^- = \bigcup_{k=1}^\infty (a_k, b_k)$. Recall from Lemma 4.7 (a) that J^- contains $\overline{H^-} = \bigcup_{j=1}^r [\alpha_j, \beta_j]$. Since an interval is connected, every $[\alpha_j, \beta_j]$ is contained in some (a_k, b_k). We claim that every (a_k, b_k) contains some $[\alpha_j, \beta_j]$. For suppose otherwise. Then there exists some (a_l, b_l) which does not contain any $[\alpha_j, \beta_j]$. Since every $[\alpha_j, \beta_j]$ is contained in some (a_k, b_k), it must be that (a_l, b_l) lies entirely outside of $\overline{H^-}$, i.e., $(a_l, b_l) \subseteq H^+$. Integrating the equation for I^* in Lemma 4.7 (c) over (a_l, b_l), and using the fact that the derivative of I^* vanishes at a_l and b_l, we obtain $\int_{a_l}^{b_l} (\beta - \gamma) I^* = 0$. But this contradicts $\beta > \gamma$ and $I^* > 0$ on $(a_l, b_l) \subseteq H^+$. We conclude that every (a_k, b_k) contains some $[\alpha_j, \beta_j]$. Since there are only r intervals of the form $[\alpha_j, \beta_j]$, we conclude that there are at most r intervals of the form (a_k, b_k). That is, J^- is a union of at most r disjoint open intervals.

By (A3), there exists δ^{**} such that if $0 < \delta \le \delta^{**}$ then the open set $\Omega_\delta \stackrel{\text{def}}{=} H^+_\delta \cap J^-$ is also a union of finitely many disjoint open intervals, i.e., $\Omega_\delta = \bigcup_{k=1}^s (c_k, d_k)$, with $s \le 2r$. Let μ_k^* denotes the smallest eigenvalue of $-\Delta$ subject to zero Dirichlet boundary conditions on the interval (c_k, d_k). By the comparison principle for eigenvalues and Lemma 4.8, $\mu_k^* \ge \lambda_\delta^* \ge \delta/d_I$ for every k. Therefore,

$$|\Omega_\delta| = \sum_{k=1}^s (d_k - c_k) \le s\pi \sqrt{\frac{d_I}{\delta}} \le 2r\pi \sqrt{\frac{d_I}{\delta}}.$$

Since r is independent of d_I, we have $|\Omega_\delta| \le \epsilon$ for $0 < \delta \le \delta^{**}$ and $0 < d_I \ll 1$. Therefore, $|J^- \setminus H^-| = |J^- \cap H^+| = |J^- \cap (M_\delta \cup H^+_\delta)| \le |M_\delta| + |\Omega_\delta| \le 2\epsilon$ for $0 < \delta \le \min\{\delta^*, \delta^{**}\}$ and d_I sufficiently small. □

5 Discussion

5.1 Connections to a related patch model

Many of these results agree with those obtained in our paper on discrete patch SIS-model (Allen et al. 2006). The model studied here, with a continuous spatial habitat, can be viewed as consisting of infinitely many discrete patches. Theorems 1 to 4 are concerned mainly with the effect of the spatial heterogeneity of the environment and the difference in movement of susceptible and infected individuals on disease persistence and extinction. Similar questions are addressed in Allen et al. (2006) and most of the results in this paper have analogues in Allen at al. (2006), although the techniques are rather different. Furthermore, the two papers provide ideas and intuitions for each other. In particular, in both papers it is shown that when the disease-free equilibrium is stable ($\mathcal{R}_0 < 1$), then it is globally asymptotically stable; and when it is unstable ($\mathcal{R}_0 > 1$), then there exists a unique endemic equilibrium. A surprising result is also established in both papers: as $d_S \to 0$, the disease cannot persist (i.e., $\tilde{I} \to 0$) while $\tilde{S}$ converges to some S^* which must be positive at all low-risk sites. However, for high-risk sites, there is a big difference: for the patch model in Allen at al. (2006), S^* can be zero on all high-risk sites, while for the PDE model S^* must be positive at some high-risk sites. However, if d_I is sufficiently small, the two papers have

some similar results (again proved by completely different techniques): for the patch model, S^* is equal to zero on all high-risk patches if d_I is small; for the PDE model, as $d_I \to 0$, the measure of the set $J^- \setminus H^-$ (i.e., where S^* is positive on H^+) tends to 0.

5.2 Open Questions

We conjecture that for each fixed N, the unique EE from Theorem 3 is globally asymptotically stable among all initial data satisfying (1.2). While this result is difficult to prove, the following problems are more approachable.

(i) Local stability of EE when d_S is sufficiently small. The results in Theorem 4 provide the asymptotic profile of the EE and such information is likely to be useful in establishing the linear stability of the EE, but a much better understanding of the free boundary problem as described in the Introduction seems to be needed.

(ii) Clearly, the global attractivity of the unique EE and Theorem 4 will imply that for any $\epsilon > 0$, there exists $d_S^* > 0$ such that if $d_S < d_S^*$, then $\limsup_{t\to\infty} \bar{I}(x,t) \le \epsilon$ for every $x \in \Omega$. A direct proof of this result without invoking the global asymptotic stability of the unique EE would be very interesting.

Acknowledgements

We thank S. Ruan and H. Thieme for pointing out some of the references. This research was initiated during the visit of LJSA and BMB to the Mathematical Biosciences Institute, The Ohio State University. This material is based upon work supported by the National Science Foundation under Agreement No. 0112050. LJSA acknowledges support from NSF grant DMS-0201105, BMB acknowledges support from NSF Integrated Research Challenges in Environmental Biology grant IBN 9977063, and YL acknowledges support from NSF grant DMS-0615845.

References

[1] L.J.S. Allen, B.M. Bolker, Y. Lou, and A.L. Nevai: Asymptotic profile of the steady states for an SIS epidemic disease patch model. (2006) In review.

[2] I. Beardmore and R. Beardmore: The global structure of a spatial model of infections disease. Proc. Roy. Soc. Lond. A (2003) 459: 1427-1448.

[3] I. Beardmore and K.A.J. White: Spreading disease through social groupings in competition. Journal of Theoretical Biology (2001) 212: 253-269.

[4] R.S. Cantrell and C. Cosner: Spatial Ecology via Reaction-Diffusion Equations. John Wiley & Sons Ltd., Chichester, UK, 2003.

[5] O. Diekmann and J. A. P. Heesterbeek: Mathematical Epidemiology of Infectious Diseases. John Wiley and Sons Ltd, Chichester, New York, 2000.

[6] O. Diekmann, J.A.P. Heesterbeek, and J.A.J. Metz: On the definition and the computation of the basic reproduction ratio $\mathcal{R}_0$ in models for infectious diseases in heterogeneous populations. J. Math. Biol. (1990) 28: 365-382.

[7] W. Fitzgibbon and M. Langlais: Simple models for the transmission of microparasites between host populations living on non coincident domains. 50 pages, to appear in *Structured Population Models in Biology and Epidemiology* edited by Pierre Magal and Shigui Ruan.

[8] W.E. Fitzgibbon, M. Langlais, and J.J. Morgan: A mathematical model of the spread of Feline Leukemia Virus (FeLV) through a highly heterogeneous spatial domain. SIAM J. Math. Anal. (2001) 33: 570-588.

[9] W.E. Fitzgibbon, M. Langlais, and J.J. Morgan: A reaction-diffusion system modeling direct and indirect transmission of diseases. Discrete and Continuous Dynamical Systems, Series B, (2004) 4: 893-910.

[10] I. D. Gilbarg and N. S. Trudinger: Elliptic Partial Differential Equations of Second Order, 2nd ed. Springer, Berlin, 1983.

[11] I. Gudelj and K.A.J. White: Spatial heterogeneity, social structure and disease dynamics of animal populations. Theoretical Population Biology (2004) 66: 139-149.

[12] I. Gudelj, K.A.J. White, and N.F. Britton: The effects of spatial movement and group interactions on disease dynamics of social animals. Bulletin of Mathematical Biology (2004) 66: 91-108.

[13] D. Henry: Geometric Theory of Semilinear Parabolic Equations, Springer-Verlag, New York, 1981.

[14] M.G. Krein and M.A. Rutman: Linear operators leaving invariant a cone in Banach space. Amer. Math. Soc. Transl. (1962) 10: 199-325.

[15] Y. Lou and T. Nagylaki: Evolution of a semilinear parabolic system for migration and selection without dominance. J. Diff. Eqns. (2006) 225: 624-665.

[16] J.D. Murray: Mathematical Biology. Springer-Verlag, Heidelberg, 1990.

[17] M.H. Protter and H.F. Weinberger: Maximum Principles in Differential Equations, 2nd ed., Springer, Berlin, 1984.

[18] S. Ruan: Spatial-temporal dynamics in nonlocal epidemiological models. In: Mathematics for Life Science and Medicine, Vol. 2. Y. Takeuchi, K. Sato and Y. Iwasa (Eds.), Springer-Verlag, New York (to appear).

[19] J. Smoller: Shock Waves and Reaction-Diffusion Equations. Springer Verlag, New York, 1983.

[20] H. Thieme: Book review on *Spatial Deterministic Epidemics* by L. Rass and J. Radcliffe, AMS, 2003, Math. Biosci. (2006) 202: 218-225.

[21] P. van den Driessche and J. Watmough: Reproduction numbers and sub-threshold endemic equilibria for compartmental models of disease transmission, Math. Biosci. (2002) 180: 29-48.

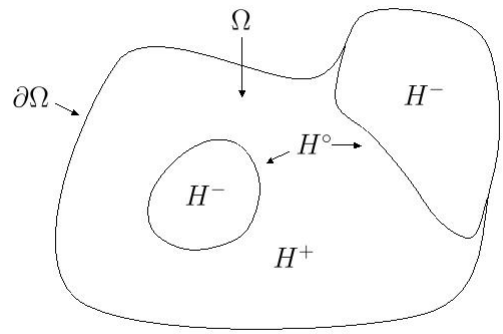

Figure 1: An illustration of how the set Ω can be partitioned into subsets H^-, H°, and H^+.

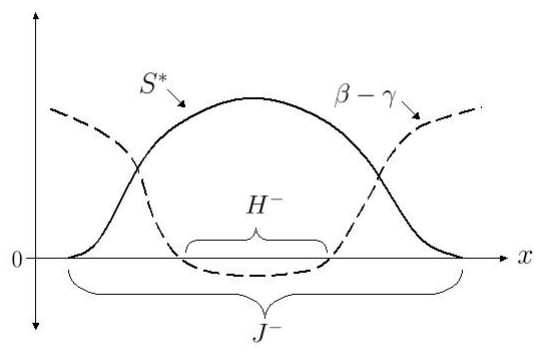

Figure 2: An illustration of Theorem 4 for $m = 1$.