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Asymptotic profiles of the steady states for an SIS epidemic patch model with asymmetric connectivity matrix

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Abstract

The dynamics of an SIS epidemic patch model with asymmetric connectivity matrix is analyzed. It is shown that the basic reproduction number R_0 is strictly decreasing with respect to the dispersal rate of the infected individuals. When $R_0 > 1$, the model admits a unique endemic equilibrium, and its asymptotic profiles are characterized for small dispersal rates. Specifically, the endemic equilibrium converges to a limiting disease-free equilibrium as the dispersal rate of susceptible individuals tends to zero, and the limiting disease-free equilibrium has a positive number of susceptible individuals on each low-risk patch. Furthermore, a sufficient and necessary condition is provided to characterize that the limiting disease-free equilibrium has no positive number of susceptible individuals on each high-risk patch. Our results extend earlier results for symmetric connectivity matrix, providing a positive answer to an open problem in Allen et al. (SIAM J Appl Math 67(5):1283–1309, 2007).

Keywords SIS epidemic patch model · Asymmetric connectivity matrix · Asymptotic profile

Mathematics Subject Classification 92D30 · 37N25 · 92D40

1 Introduction

Various mathematical models have been proposed to describe and simulate the transmissions of infectious diseases, and the predictions provided by those models may help to prevent and control the outbreak of the diseases (Anderson and May 1991;

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Brauer et al. 2008; Diekmann and Heesterbeek 2000). The spreading of the infectious diseases in populations depends on the spatial structure of the environment and the dispersal pattern of the populations. The impact of the spatial heterogeneity of the environment and the dispersal rate of the populations on the transmission of the diseases can be modeled in discrete-space settings by ordinary differential equation patch models (Allen et al. 2007; Arino and van den Driessche 2003; Lloyd and May 1996; Wang and Zhao 2004) or in continuous-space settings by reaction-diffusion equation models (Allen et al. 2008; Fitzgibbon and Langlais 2008; Wang and Zhao 2012).

In a discrete-space setting, Allen et al. (2007) proposed the following susceptible-infected-susceptible (SIS) epidemic patch model:

$$\begin{cases} \dfrac{d\overline{S}_j}{dt} = d_S \displaystyle\sum_{k\in\Omega}(\overline{L}_{jk}\overline{S}_k - \overline{L}_{kj}\overline{S}_j) - \dfrac{\beta_j \overline{S}_j \overline{I}_j}{\overline{S}_j + \overline{I}_j} + \gamma_j \overline{I}_j, & j \in \Omega, \\ \dfrac{d\overline{I}_j}{dt} = d_I \displaystyle\sum_{k\in\Omega}(\overline{L}_{jk}\overline{I}_k - \overline{L}_{kj}\overline{I}_j) + \dfrac{\beta_j \overline{S}_j \overline{I}_j}{\overline{S}_j + \overline{I}_j} - \gamma_j \overline{I}_j, & j \in \Omega, \end{cases} \tag{1.1}$$

where $\Omega = \{1, 2, \ldots, n\}$ with $n \geq 2$. Here $\overline{S}_j(t)$ and $\overline{I}_j(t)$ denote the number of the susceptible and infected individuals in patch j at time t, respectively; β_j denotes the rate of disease transmission and γ_j represents the rate of disease recovery in patch j; d_S, d_I are the dispersal rates of the susceptible and infected populations, respectively; and $\overline{L}_{jk} \geq 0$ describes the degree of the movement of the individuals from patch k to patch j for $j, k \in \Omega$. A major assumption in Allen et al. (2007) is that the matrix $(\overline{L}_{jk})$ is symmetric. In Allen et al. (2007), the authors defined the basic reproduction number R_0 of the model (1.1); they showed that if $R_0 < 1$ the disease-free equilibrium is globally asymptotically stable, and if $R_0 > 1$ the model has a unique positive endemic equilibrium. Moreover, the asymptotic profile of the endemic equilibrium as $d_S \to 0$ is characterized in Allen et al. (2007), and the case $d_I \to 0$ is studied in Li and Peng (2019) recently. We remark that there are extensive studies on patch epidemic models, see Almarashi and McCluskey (2019), Eisenberg et al. (2013), Gao and Ruan (2011), Gao et al. (2019), Jin and Wang (2005), Li and Shuai (2009, 2010), Salmani and van den Driessche (2006), Tien et al. (2015), Wang and Zhao (2004, 2005) and the references therein. The corresponding reaction-diffusion model of (1.1) was studied in Allen et al. (2008) where the dispersal of the population is modeled by diffusion. A similar model with diffusive and advective movement of the population is studied in Cui et al. (2017), Cui and Lou (2016), and more studies on diffusive SIS models can be found in Deng and Wu (2016), Jiang et al. (2018), Kuto et al. (2017), Li and Peng (2019), Li et al. (2018), Magal et al. (2018), Peng (2009), Peng and Liu (2009), Peng and Yi (2013), Tuncer and Martcheva (2012), Wu et al. (2017), Wu and Zou (2016) and the references therein.

The assumption that the matrix $(\overline{L}_{jk})$ is symmetric in Allen et al. (2007), Li and Peng (2019) is similar to the assumption of diffusive dispersal in reaction-diffusion models. However, asymmetric (e.g. advective) movements of the populations in space are common, and so in this paper we consider (1.1) with $(\overline{L}_{jk})$ being asymmetric and establish the corresponding results in Allen et al. (2007), Li and Peng (2019).

Moreover, we will provide solutions to some of the open problems in Allen et al. (2007) without assuming $(\overline{L}_{jk})$ is symmetric: (1) we prove that the basic reproduction number R_0 is strictly decreasing in d_I; (2) we partially characterize the asymptotic profile of the S-component of the endemic equilibrium as $d_S \to 0$. The monotonicity of R_0 has also been proven recently in [11], Gao (2019), Gao and Dong (2020) with $\beta_i, \gamma_i > 0$ for all $i \in \Omega$, while this assumption will be dropped in our result. We also establish the asymptotic profile of the endemic equilibrium as $d_I \to 0$ when L is asymmetric, which extends the results of Li and Peng (2019) in which L is assumed to be symmetric.

Denote

$$L_{jk} = \begin{cases} \overline{L}_{jk}, & j \neq k, \\ -\sum\limits_{k\in\Omega, k\neq j} \overline{L}_{kj}, & j = k, \end{cases}$$

where L_{jj} is the total degree of movement out from patch $j \in \Omega$. We rewrite (1.1) as:

$$\begin{cases} \dfrac{d\overline{S}_j}{dt} = d_S \sum\limits_{k\in\Omega} L_{jk}\overline{S}_k - \dfrac{\beta_j \overline{S}_j \overline{I}_j}{\overline{S}_j + \overline{I}_j} + \gamma_j \overline{I}_j, & j \in \Omega, \\ \dfrac{d\overline{I}_j}{dt} = d_I \sum\limits_{k\in\Omega} L_{jk}\overline{I}_k + \dfrac{\beta_j \overline{S}_j \overline{I}_j}{\overline{S}_j + \overline{I}_j} - \gamma_j \overline{I}_j, & j \in \Omega. \end{cases} \tag{1.2}$$

Let H^- and H^+ denote the sets of low-risk and high-risk patches, respectively; that is,

$$H^- = \{j \in \Omega : \beta_j < \gamma_j\} \text{ and } H^+ = \{j \in \Omega : \beta_j > \gamma_j\}.$$

Define the patch reproduction number $R_{0j} = \beta_j/\gamma_j$. Hence a high-risk patch is one where the patch reproduction number $R_{0j} > 1$, while a low-risk patch is one where $R_{0j} < 1$. We impose the following four assumptions:

- (A_0) $\beta_j \geq 0$ and $\gamma_j \geq 0$ for all $j \in \Omega$; $d_S, d_I > 0$;
- (A_1) The connectivity matrix $L := (L_{jk})$ is irreducible and quasi-positive (meaning that off-diagonal entries are nonnegative);
- (A_2) $\overline{S}_j(0) \geq 0$, $\overline{I}_j(0) \geq 0$, and

$$N := \sum_{j\in\Omega} [\overline{S}_j(0) + \overline{I}_j(0)] > 0; \tag{1.3}$$

- (A_3) H^- and H^+ are nonempty, and $\Omega = H^- \cup H^+$.

By adding the $2n$ equations in (1.2), we see that the total population is conserved in the sense that

$$N = \sum_{j\in\Omega} \left[\overline{S}_j(t) + \overline{I}_j(t)\right] \text{ for any } t \geq 0. \tag{1.4}$$

We remark that (A_0)–(A_3) are assumed in Allen et al. (2007) with L being symmetric in addition.

Throughout the paper, we use the following notations. For $n \geq 2$,

$$\begin{aligned} \mathbb{R}^n &= \{\boldsymbol{u} = (u_1, \ldots, u_n)^T : u_i \in \mathbb{R} \text{ for any } i = 1, \ldots, n\}, \\ \mathbb{R}^n_+ &= \{\boldsymbol{u} = (u_1, \ldots, u_n)^T : u_i \geq 0 \text{ for any } i = 1, \ldots, n\}. \end{aligned} \tag{1.5}$$

For an $n \times n$ real-valued matrix A, we denote the spectral bound of A by

$$s(A) := \max\{\mathcal{R}e(\lambda) : \lambda \text{ is an eigenvalue of } A\},$$

and the spectral radius of A by

$$\rho(A) := \max\{|\lambda| : \lambda \text{ is an eigenvalue of } A\}.$$

The matrix A is *nonnegative* if all the entries of A are nonnegative. The matrix A is zero if all the entries of A are zero. The matrix A is *positive* if A is nonnegative and not zero. The matrix A is *quasi-positive* (or cooperative) if all off-diagonal entries of A are nonnegative.

Let $\boldsymbol{u} = (u_1, \ldots, u_n)^T$ and $\boldsymbol{v} = (v_1, \ldots, v_n)^T$ be two vectors. We write $\boldsymbol{u} \geq \boldsymbol{v}$ if $u_i \geq v_i$ for all $i = 1, \ldots, n$. We write $\boldsymbol{u} > \boldsymbol{v}$ if $u_i \geq v_i$ for all $i = 1, \ldots, n$, and there exists i_0 such that $u_{i_0} > v_{i_0}$. We write $\boldsymbol{u} \gg \boldsymbol{v}$ if $u_i > v_i$ for all $i = 1, \ldots, n$. We say $\boldsymbol{u}$ is strongly positive if $\boldsymbol{u} \gg \mathbf{0}$.

The rest of the paper is organized as follows. In Sect. 2, we prove that model (1.2)–(1.3) admits a unique endemic equilibrium if $R_0 > 1$ and that R_0 is strictly decreasing in d_I. In Sect. 3, the asymptotic profile of the endemic equilibrium is studied in two cases, $d_S \to 0$ and $d_I \to 0$. In Sect. 4, we consider a toy example where the connectivity matrix corresponds to a star graph.

2 The basic reproduction number

In this section, we study the properties of the basic reproduction number R_0 of model (1.2). The following result on the spectral bound of the connectivity matrix L follows directly from the Perron-Frobenius theorem.

Lemma 2.1 *Suppose that* (A_1) *holds. Then* $s(L) = 0$ *is a simple eigenvalue of* L *with a strongly positive eigenvector* $\boldsymbol{\alpha}$*, where*

$$\boldsymbol{\alpha} = (\alpha_1, \ldots, \alpha_n)^T, \quad \alpha_j > 0 \textit{ for any } j \in \Omega, \textit{ and } \sum_{i=1}^{n} \alpha_i = 1. \tag{2.1}$$

Moreover, there exists no other eigenvalue of L *corresponding with a nonnegative eigenvector.*

In the rest of the paper, we denote $\boldsymbol{\alpha}$ the positive eigenvector of L as specified in Lemma 2.1.

Then we observe that model (1.2)–(1.3) admits a unique disease-free equilibrium.

Lemma 2.2 *Suppose that* (A_0)–(A_2) *hold. Then model* (1.2)–(1.3) *has a unique disease-free equilibrium* $(\hat{S}_1, \ldots, \hat{S}_n, 0, \ldots, 0)^T$ *with* $\hat{S}_j = \alpha_j N$.

Proof At the disease-free equilibrium $(\hat{S}_1, \ldots, \hat{S}_n, 0, \ldots, 0)^T$, $L(\hat{S}_1, \ldots, \hat{S}_n)^T = 0$. It follows from Lemma 2.1 that there exists $\hat{k} \in \mathbb{R}$ such that $\hat{S}_j = \alpha_j \hat{k}$ for any $j \in \Omega$. Since $\sum_{j\in\Omega} S_j = \hat{k} \sum_{j\in\Omega} \alpha_j = N$, we have $\hat{k} = N$. This completes the proof. □

We follow the next generation matrix approach Diekmann and Heesterbeek (2000), van den Driessche and Watmough (2002) to compute the basic reproduction number. Specifically, the two matrices representing new infections and transfer are determined respectively:

$$F = diag(\beta_j), \quad V = diag(\gamma_j) - d_I L, \tag{2.2}$$

and the basic reproduction number R_0 is thus defined as

$$R_0 = \rho(FV^{-1}).$$

We recall the following well-known result [see, e.g., Berman and Plemmons (1994), Corollary 2.1.5]:

Lemma 2.3 *Suppose that* P *and* Q *are* $n \times n$ *real-valued matrices,* P *is quasi-positive,* Q *is nonnegative and nonzero, and* $P + Q$ *is irreducible. Then,* $s(P + aQ)$ *is strictly increasing for* $a \in (0, \infty)$.

By Lemma 2.3, if γ_j $(j \in \Omega)$ are not all zero, then V is invertible and therefore an M-matrix. Then, we have the following result.

Proposition 2.4 *Suppose that* (A_0)–(A_1) *hold and* γ_j $(j \in \Omega)$ *are not all zero. Then the following statements hold:*

(i) $R_0 - 1$ *has the same sign as* $s(F - V) = s\left(d_I L + diag(\beta_j - \gamma_j)\right)$.
(ii) *If* $R_0 < 1$, *the disease-free equilibrium* $(\hat{S}_1, \ldots, \hat{S}_n, 0, \ldots, 0)^T$ *of* (1.2)–(1.3) *is globally asymptotically stable; if* $R_0 > 1$, *the disease-free equilibrium is unstable.*

Proof Result in (i) and the local stability result in (ii) follow immediately from (van den Driessche and Watmough 2002, Theorem 2). If $R_0 < 1$, the global attractivity of the disease free equilibrium can be established similarly as the one in Allen et al. (2007, Lemma 2.3). □

The following result on the monotonicity of the spectral bound was proved in [11, Theorem 3.3 and 4.4], which is related to Karlin's theorem on the reduction principle in evolution biology (Altenberg 2012; Altenberg et al. 2017; Karlin 1982).

Lemma 2.5 *Suppose that* (A_1) *holds. Let* $f_j \in \mathbb{R}$ *for* $j \in \Omega$. *Then the following two statements hold:*

(i) *If* $(f_1, \ldots, f_n)$ *is a multiple of* $(1, \ldots, 1)$, *then* $s\left(d_I L + diag(f_j)\right) \equiv f_1$.
(ii) *If* $(f_1, \ldots, f_n)$ *is not a multiple of* $(1, \ldots, 1)$, *then* $s\left(d_I L + diag(f_j)\right)$ *is strictly decreasing for* $d_I \in (0, \infty)$.

Moreover,

$$\lim_{d_I \to 0} s\left(d_I L + diag(f_j)\right) = \max_{j\in\Omega} f_j,$$

and

$$\lim_{d_I \to \infty} s\left(d_I L + diag(f_j)\right) = \sum_{j\in\Omega} f_j \alpha_j.$$

Now we prove the monotonicity of the basic reproduction number R_0 with respect to d_I. Note that this result was also proved in Gao (2019), Gao and Dong (2020) with an additional assumption $\beta_j, \gamma_j > 0$ for all $j \in \Omega$. If $\gamma_j = 0$, we set $\beta_j/\gamma_j = \infty$ when $\beta_j > 0$ and $\beta_j/\gamma_j = 0$ when $\beta_j = 0$.

Theorem 2.6 *Suppose that (A_0)–(A_1) hold and γ_j ($j \in \Omega$) are not all zero. Then R_0 is strictly decreasing for $d_I \in (0, \infty)$ if $(\beta_1, \beta_2, \ldots, \beta_n)$ is not a multiple of $(\gamma_1, \gamma_2, \ldots, \gamma_n)$.*

Proof Clearly, $R_0 = R_0(d_I) > 0$ for $d_I \in (0, \infty)$. We claim that

$$\min_{j\in\Omega} \frac{\beta_j}{\gamma_j} \le R_0 \le \max_{j\in\Omega} \frac{\beta_j}{\gamma_j}. \tag{2.3}$$

To see this, we first assume $\gamma_j > 0$ for all $j \in \Omega$. Then, we have $F_1 \le F \le F_2$, where

$$F_1 = \left(\min_{j\in\Omega} \frac{\beta_j}{\gamma_j}\right) diag(\gamma_j), \quad F_2 = \left(\max_{j\in\Omega} \frac{\beta_j}{\gamma_j}\right) diag(\gamma_j).$$

Therefore,

$$\rho(F_1 V^{-1}) \le \rho(F V^{-1}) \le \rho(F_2 V^{-1}), \tag{2.4}$$

where F and V are defined by (2.2). Since

$$(1, \ldots, 1)V = (\gamma_1, \ldots, \gamma_n), \quad (1, \ldots, 1)F_1 = \left(\min_{j\in\Omega} \frac{\beta_j}{\gamma_j}\right)(\gamma_1, \ldots, \gamma_n),$$
$$(1, \ldots, 1)F_2 = \left(\max_{j\in\Omega} \frac{\beta_j}{\gamma_j}\right)(\gamma_1, \ldots, \gamma_n), \tag{2.5}$$

we have

$$\rho(F_1 V^{-1}) = \min_{j\in\Omega} \frac{\beta_j}{\gamma_j}, \quad \rho(F_2 V^{-1}) = \max_{j\in\Omega} \frac{\beta_j}{\gamma_j}.$$

This, together with (2.4), implies (2.3). It is not hard to check that (2.3) still holds when $\gamma_j \ge 0$. Indeed, if $\gamma_{j_0} = \beta_{j_0} = 0$ for some $j_0 \in \Omega$, the arguments above still hold as $\beta_{j_0}/\gamma_{j_0} = 0$. If $\gamma_{j_0} = 0$ and $\beta_{j_0} > 0$ for some $j_0 \in \Omega$, then $\beta_{j_0}/\gamma_{j_0} = \infty$. We can replace the j_0-th entry of F_1 by 0 to obtain the first inequality of (2.3), and the second inequality of (2.3) is trivial.

Let

$$\mu_0(d_I) = \frac{1}{R_0(d_I)}, \tag{2.6}$$

and

$$\lambda_1(d_I, a) := s(-V + aF) = s\left(d_I L + aF - diag(\gamma_j)\right).$$

The following discussion is divided into two cases.

Case 1 For any $a \in (0, \infty)$, $(a\beta_1 - \gamma_1, \dots, a\beta_n - \gamma_n)$ is not a multiple of $(1, \dots, 1)$. Then we see from Lemma 2.5 that for any fixed $a > 0$, $\lambda_1(d_I, a)$ is strictly decreasing for $d_I \in (0, \infty)$. Let $\phi > 0$ be the corresponding eigenvector of $V^{-1}F$ with respect to $\rho(V^{-1}F)$. Then

$$d_I L\phi - diag(\gamma_j)\phi + \mu_0(d_I)F\phi = 0.$$

Since L is irreducible, it follows that $\phi \gg 0$ and $\lambda_1(d_I, \mu_0(d_I)) = 0$ for any $d_I > 0$. Let $d_I^1 > d_I^2$. Then, by Lemma 2.5,

$$\begin{aligned}&\lambda_1\left(d_I^2, \mu_0\left(d_I^1\right)\right) - \lambda_1\left(d_I^2, \mu_0\left(d_I^2\right)\right)\\&\quad = \lambda_1\left(d_I^2, \mu_0\left(d_I^1\right)\right) - \lambda_1\left(d_I^1, \mu_0\left(d_I^1\right)\right) > 0,\end{aligned} \tag{2.7}$$

which implies that

$$\mu_0\left(d_I^1\right) > \mu_0\left(d_I^2\right).$$

As a consequence, $\mu_0(d_I)$ is strictly increasing for $d_I \in (0, \infty)$.

Case 2 There exists $\tilde{a} > 0$ such that $(\tilde{a}\beta_1 - \gamma_1, \dots, \tilde{a}\beta_n - \gamma_n)$ is a multiple of $(1, \dots, 1)$. That is, there exists $k \in \mathbb{R}$ such that

$$(\tilde{a}\beta_1 - \gamma_1, \dots, \tilde{a}\beta_n - \gamma_n) = k(1, \dots, 1).$$

Clearly, $\tilde{a}$ is unique and $k \neq 0$ if $(\beta_1, \beta_2, \dots, \beta_n)$ is not a multiple of $(\gamma_1, \gamma_2, \dots, \gamma_n)$.

If $k > 0$, then $\beta_j > 0$ for all $j \in \Omega$ and

$$R_0 \geq \min_{j\in\Omega} \frac{\beta_j}{\gamma_j} > \frac{1}{\tilde{a}},$$

which implies that $\mu_0(d_I) < \tilde{a}$ for any $d_I > 0$. It follows from Lemma 2.5 that $\lambda_1(d_I, a)$ is strictly decreasing for $d_I \in (0, \infty)$ for any fixed $a < \tilde{a}$. Similarly to Case 1, let $d_I^1 > d_I^2$, and then $\lambda_1\left(d_I, \mu_0\left(d_I^1\right)\right)$ is strictly decreasing for d_I since $\mu_0(d_I^1) < \tilde{a}$. Therefore, (2.7) holds, and $\mu_0(d_I)$ is strictly increasing for $d_I \in (0, \infty)$.

If $k < 0$, then $\gamma_j > 0$ for all $j \in \Omega$ and

$$R_0 \leq \max_{j\in\Omega} \frac{\beta_j}{\gamma_j} < \frac{1}{\tilde{a}},$$

which implies that $\mu_0(d_I) > \tilde{a}$ for any $d_I > 0$. The rest of the proof is similar to the case of $k > 0$. □

The limiting behaviors of R_0 as $d \to 0$ or $d \to \infty$ can be established as follows.

Theorem 2.7 *Suppose that* (A_0)*–*(A_1) *hold and* γ_j *(*$j \in \Omega$*) are not all zero. Then the basic reproduction number* $R_0 = R(d_I)$ *satisfies the following:*

$$\lim_{d_I \to 0} R_0(d_I) = \max_{j\in\Omega} \frac{\beta_j}{\gamma_j} \quad \textit{and} \quad \lim_{d_I\to\infty} R_0(d_I) = \frac{\sum_{j\in\Omega} \alpha_j \beta_j}{\sum_{j\in\Omega} \alpha_j \gamma_j}.$$

Remark 2.8 If L is symmetric, then $\alpha_j \equiv 1/n$ and thus

$$\lim_{d_I\to\infty} R_0(d_I) = \frac{\sum_{j\in\Omega} \beta_j}{\sum_{j\in\Omega} \gamma_j},$$

agreeing with the result for symmetric connectivity matrix in Allen et al. (2007, Lemma 3.4).

Proof Let $\mu_0(d_I)$ and $\lambda_1(d_I, a)$ be defined as in the proof of Theorem 2.6. Noticing that $\mu_0(d_I)$ is increasing in d_I, let

$$\mu_1 = \lim_{d_I\to 0} \mu_0(d_I) \ \text{ and } \ \mu_2 = \lim_{d_I\to\infty} \mu_0(d_I),$$

where $\mu_1 \in [0, \infty)$ and $\mu_2 \in (0, \infty]$. By Lemma 2.5, for any $a > 0$,

$$\lim_{d_I\to 0} \lambda_1(d_I, a) = \max_{j\in\Omega}\{a\beta_j - \gamma_j\} \ \text{ and } \ \lim_{d_I\to\infty} \lambda_1(d_I, a) = \sum_{j\in\Omega}(a\beta_j - \gamma_j)\alpha_j. \quad (2.8)$$

Since $\lambda_1(d_I, \mu_0(d_I)) = 0$, we have

$$\max_{j\in\Omega}\{\mu_1\beta_j - \gamma_j\} = 0 \ \text{ and } \ \sum_{j\in\Omega}(\mu_2\beta_j - \gamma_j)\alpha_j = 0. \quad (2.9)$$

Indeed, to see the first equality, for given $\epsilon > 0$ there exists $\hat{d}_I > 0$ such that $\mu_1 - \epsilon < \mu_0(d_I) < \mu_1 + \epsilon$ for all $d_I < \hat{d}_I$. By Lemma 2.3, we have

$$\lambda_1(d_I, \mu_1 - \epsilon) < \lambda_1(d_I, \mu_0(d_I)) = 0 < \lambda_1(d_I, \mu_1 + \epsilon) \ \text{ for all } d_I < \hat{d}_I.$$

By (2.8), we have

$$\max_{j\in\Omega}\{(\mu_1 - \epsilon)\beta_j - \gamma_j\} \le 0 \le \max_{j\in\Omega}\{(\mu_1 + \epsilon)\beta_j - \gamma_j\}.$$

Since $\epsilon > 0$ is arbitrary, we obtain the first equality. The other equality in (2.9) can be proved similarly.

It follows from (2.9) that

$$\lim_{d_I \to 0} R_0(d_I) \geq \max_{j \in \Omega} \frac{\beta_j}{\gamma_j} \quad \text{and} \quad \lim_{d_I \to \infty} R_0(d_I) = \frac{\sum_{j \in \Omega} \alpha_j \beta_j}{\sum_{j \in \Omega} \alpha_j \gamma_j},$$

where the equality holds for $d_I \to 0$ if there exists no $j \in \Omega$ such that $\beta_j = \gamma_j = 0$. Noticing (2.3), the proof is complete. □

3 The endemic equilibrium

In this section, we consider the endemic equilibrium of model (1.2)–(1.3). Let $d = d_I/d_S$ throughout this section. The equilibria of (1.2)–(1.3) satisfy

$$\begin{cases} d_S \sum_{k \in \Omega} L_{jk} S_k - \frac{\beta_j S_j I_j}{S_j + I_j} + \gamma_j I_j = 0, & j \in \Omega, \\ d_I \sum_{k \in \Omega} L_{jk} I_k + \frac{\beta_j S_j I_j}{S_j + I_j} - \gamma_j I_j = 0, & j \in \Omega, \\ \sum_{j \in \Omega} (S_j + I_j) = N. \end{cases} \tag{3.1}$$

Firstly, we study the existence and uniqueness of the endemic equilibrium. Then, we investigate the asymptotic profile of the endemic equilibrium as $d_S \to 0$ and/or $d_I \to 0$, while the ratio $d = d_I/d_S$ may approach 0, ∞, or a positive constant.

3.1 The existence and uniqueness

In this section, we show that (1.2)–(1.3) has a unique endemic equilibrium if $R_0 > 1$. Motivated by Allen et al. (2007), we first introduce an equivalent problem of (3.1).

Lemma 3.1 *Suppose that* (A_0)–(A_3) *hold. Then* $(S_1, \ldots, S_n, I_1, \ldots, I_n)^T$ *is a nonnegative solution of* (3.1) *if and only if*

$$(S_1, \ldots, S_n, I_1, \ldots, I_n) = \left(\kappa \check{S}_1, \ldots, \kappa \check{S}_n, \frac{\kappa}{d_I} \check{I}_1, \ldots, \frac{\kappa}{d_I} \check{I}_n \right),$$

where $(\check{S}_1, \ldots, \check{S}_n, \check{I}_1, \ldots, \check{I}_n)$ *satisfies*

$$\begin{cases} d_S \check{S}_j + \check{I}_j = \alpha_j, & j \in \Omega, \\ d_I \sum_{k \in \Omega} L_{jk} \check{I}_k + \check{I}_j \left(\beta_j - \gamma_j - \frac{d_S \beta_j \check{I}_j}{d_I(\alpha_j - \check{I}_j) + d_S \check{I}_j} \right) = 0, & j \in \Omega, \end{cases} \tag{3.2}$$

and

$$\kappa = \frac{d_I N}{\sum_{j \in \Omega} (d_I \check{S}_j + \check{I}_j)}. \tag{3.3}$$

Proof Clearly, from (3.1), we have $\sum_{k\in\Omega} L_{jk}(d_S S_k + d_I I_k) = 0$ for any $j \in \Omega$. Then it follows from Lemma 2.1 that there exists $\kappa > 0$ such that

$$d_S S_j + d_I I_j = \kappa\alpha_j \quad \text{for any} \quad j \in \Omega. \tag{3.4}$$

Let

$$\check{S}_j = \frac{S_j}{\kappa}, \quad \check{I}_j = \frac{d_I I_j}{\kappa}. \tag{3.5}$$

Then $d_S\check{S}_j + \check{I}_j = \alpha_j$ for any $j \in \Omega$. Plugging (3.4)–(3.5) into the second equation of (3.1), we see that $\check{I}_j$ satisfies the second equation of (3.2). Since

$$N = \sum_{j\in\Omega}(S_j + I_j) = \kappa\sum_{j\in\Omega}\left(\check{S}_j + \frac{\check{I}_j}{d_I}\right),$$

(3.3) holds. This completes the proof. □

From Lemma 3.1, to analyze the solutions of (3.2), we only need to consider the equations of $\check{I}_j$ in (3.2). We consider an auxiliary problem of (3.2).

Lemma 3.2 *Suppose that* (A_0)–(A_3) *hold and* $R_0 > 1$*. Then, for any* $d > 0$*, the following equation*

$$\begin{cases} d_I\sum_{k\in\Omega} L_{jk}\check{I}_k + \check{I}_j\left(\beta_j - \gamma_j - \dfrac{\beta_j\check{I}_j}{d(\alpha_j - \check{I}_j) + \check{I}_j}\right) = 0, & j \in \Omega, \\ 0 \le \check{I}_j \le \alpha_j, & j \in \Omega, \end{cases} \tag{3.6}$$

admits exactly one non-trivial solution $\check{\boldsymbol{I}} = (\check{I}_1, \ldots, \check{I}_n)^T$*, where* $0 < \check{I}_j < \alpha_j$ *for any* $j \in \Omega$*. Moreover,* $\check{I}_j$ *is monotone increasing in* $d \in (0, \infty)$ *for any* $j \in \Omega$*.*

Proof Since $R_0 > 1$, $s\left(d_I L + diag(\beta_j - \gamma_j)\right) > 0$. Let

$$f_j(\check{I}_j) = \check{I}_j\left(\beta_j - \gamma_j - \frac{\beta_j\check{I}_j}{d(\alpha_j - \check{I}_j) + \check{I}_j}\right), \tag{3.7}$$

and consider the following problem

$$\frac{d\bar{I}_j}{dt} = d_I\sum_{k\in\Omega} L_{jk}\bar{I}_k + f_j(\bar{I}_j), \quad j \in \Omega, \quad t > 0. \tag{3.8}$$

Let $\boldsymbol{g}(\check{\boldsymbol{I}}) = \left(g_1(\check{\boldsymbol{I}}), \ldots, g_n(\check{\boldsymbol{I}})\right)^T$ be the vector field corresponding to the right hand side of (3.8), and let

$$U = \{\check{\boldsymbol{I}} = \left(\check{I}_1, \ldots, \check{I}_n\right)^T \in \mathbb{R}^n : 0 \le \check{I}_j \le \alpha_j, \ j \in \Omega\}.$$

Then U is positive invariant with respect to (3.8), and for any $\check{\boldsymbol{I}} \in U$,

$$D_{\check{\boldsymbol{I}}}\boldsymbol{g}(\check{\boldsymbol{I}}) = d_I L + diag(f_j'(\check{I}_j)),$$

which is irreducible and quasi-positive. Let Ψ_t be the semiflow induced by (3.8). By Smith and Waltman (1995, Theorem B.3), Ψ_t is strongly positive and monotone.

For any $\lambda \in (0, 1)$ and $\check{I}_j \in (0, \alpha_j]$, we have

$$\begin{aligned} f_j(\lambda \check{I}_j) - \lambda f(\check{I}_j) &= -\frac{\lambda^2 \beta_j \check{I}_j^2}{d(\alpha_j - \lambda \check{I}_j) + \lambda \check{I}_j} + \frac{\lambda \beta_j \check{I}_j^2}{d(\alpha_j - \check{I}_j) + \check{I}_j} \\ &= \frac{d\lambda \alpha_j \beta_j \check{I}_j^2 (1-\lambda)}{[d(\alpha_j - \lambda \check{I}_j) + \lambda \check{I}_j][d(\alpha_j - \check{I}_j) + \check{I}_j]} \geq 0, \end{aligned} \tag{3.9}$$

and the strict inequality holds for at least one j. This implies that $\boldsymbol{g}(\check{\boldsymbol{I}})$ is strictly sublinear on U [see Zhao and Jing (1996) for the definition of strictly sublinear functions]. Noticing $s\left(d_I L + diag(\beta_j - \gamma_j)\right) > 0$, it follows from Zhao (2017, Theorem 2.3.4) [or (Zhao and Jing 1996, Corollary 3.2)] that there exists a unique $\check{\boldsymbol{I}} \gg \boldsymbol{0}$ in U such that every solution in $U \backslash \{\boldsymbol{0}\}$ converges to $\check{\boldsymbol{I}}$. Moreover, if $\check{I}_j = \alpha_j$ for some $j \in \Omega$, then $\check{I}_j' \leq -\gamma_j < 0$, which implies that $\check{I}_j \in (0, \alpha_j)$ for any $j \in \Omega$.

Suppose $d_1 > d_2$. Let $\check{\boldsymbol{I}}^{(i)} = (\check{I}_1^{(i)}, \ldots, \check{I}_n^{(i)})^T$ be the unique strongly positive solution of (3.6) with $d = d_i$ for $i = 1, 2$, and let $\bar{\boldsymbol{I}}^{(i)}(t) = (\bar{I}_1^{(i)}(t), \ldots, \bar{I}_n^{(i)}(t))^T$ be the solution of (3.8) with $d = d_i$ for $i = 1, 2$, and $\bar{\boldsymbol{I}}^{(1)}(0) = \bar{\boldsymbol{I}}^{(2)}(0) \in U \backslash \{\boldsymbol{0}\}$. Then for any $j \in \Omega$,

$$\begin{aligned} \frac{d\bar{I}_j^{(1)}}{dt} &= d_I \sum_{k \in \Omega} L_{jk} \bar{I}_k^{(1)} + \bar{I}_j^{(1)} \left(\beta_j - \gamma_j - \frac{\beta_j \bar{I}_j^{(1)}}{d_1(\alpha_j - \bar{I}_j^{(1)}) + \bar{I}_j^{(1)}} \right) \\ &\geq d_I \sum_{k \in \Omega} L_{jk} \bar{I}_k^{(1)} + \bar{I}_j^{(1)} \left(\beta_j - \gamma_j - \frac{\beta_j \bar{I}_j^{(1)}}{d_2(\alpha_j - \bar{I}_j^{(1)}) + \bar{I}_j^{(1)}} \right). \end{aligned} \tag{3.10}$$

It follows from the comparison principle that $\bar{I}_j^{(1)}(t) \geq \bar{I}_j^{(2)}(t)$ for any $t \geq 0$ and $j \in \Omega$. Therefore, $\check{I}_j^{(1)} = \lim_{t \to \infty} \bar{I}_j^{(1)}(t) \geq \check{I}_j^{(2)} = \lim_{t \to \infty} \bar{I}_j^{(2)}(t)$ for any $j \in \Omega$. □

Lemma 3.2 was proved in Allen et al. (2007) when L is symmetric by virtue of the upper and lower solution method. Here we prove it without assuming the symmetry of L by the monotone dynamical system method.

By Lemmas 3.1–3.2, we can show that model (1.2)–(1.3) has a unique endemic equilibrium if $R_0 > 1$.

Theorem 3.3 *Suppose that* (A_0)–(A_3) *hold and* $R_0 > 1$. *Then* (1.2)–(1.3) *has exactly two non-negative equilibria: the disease-free equilibrium and the endemic equilibrium*

$$(S_1, \ldots, S_n, I_1, \ldots, I_n) = \left(\kappa \check{S}_1, \ldots, \kappa \check{S}_n, \frac{\kappa \check{I}_1}{d_I}, \ldots, \frac{\kappa \check{I}_n}{d_I}\right), \tag{3.11}$$

where

$$\check{S}_j = \frac{\alpha_j - \check{I}_j}{d_S}, \quad \kappa = \frac{d_I N}{\sum_{j \in \Omega}(d_I \check{S}_j + \check{I}_j)}, \tag{3.12}$$

and $(\check{I}_1, \ldots, \check{I}_n)^T$ *is the unique strongly positive solution of* (3.6) *with* $d = d_I/d_S$.

Proof This result follows from Lemmas 3.1–3.2. □

3.2 Asymptotic profile with respect to d_S

In this subsection, we study the asymptotic profile of the endemic equilibrium of (1.2)–(1.3) as $d_S \to 0$. We suppose that (A_0)–(A_3) hold throughout this subsection. Moreover, we observe that R_0 is independent of d_S. Therefore, we assume $R_0 > 1$ throughout this subsection so that the endemic equilibrium exists for all $d_S > 0$.

We first study the asymptotic profile of κ and I_j, where κ and I_j are defined in Theorem 3.3.

Lemma 3.4 *If* $d_S \to 0$, *then* $\kappa \to 0$ *and* $I_j \to 0$ *for any* $j \in \Omega$.

Proof For any sequence $\{d_S^{(m)}\}_{m=1}^{\infty}$ such that $\lim_{m\to\infty} d_S^{(m)} = 0$, we denote the corresponding endemic equilibrium by $(S_1^{(m)}, \ldots, S_n^{(m)}, I_1^{(m)}, \ldots, I_n^{(m)})$. Since $I_j^{(m)} \in (0, N]$, there exists a subsequence $\{d_S^{(m_l)}\}_{l=1}^{\infty}$ such that $\lim_{l\to\infty} I_j^{(m_l)} = I_j^*$ for some $I_j^* \in [0, N]$. For $j \in H^-$,

$$d_S^{(m_l)} \sum_{k \in \Omega} L_{jk} S_k^{(m_l)} \le I_j^{(m_l)}(\beta_j - \gamma_j) \le 0.$$

Since $S_k^{(m_l)} \in (0, N]$ for any $l \ge 1$ and $k \in \Omega$, we have

$$\lim_{l\to\infty} d_S^{(m_l)} \sum_{k \in \Omega} L_{jk} S_k^{(m_l)} = 0,$$

which implies $I_j^* = 0$. Therefore $I_j \to 0$ as $d_S \to 0$ for $j \in H^-$.

Since $d_S S_j + d_I I_j = \kappa \alpha_j$ for any $j \in \Omega$, and $H^- \neq \emptyset$ by (A_3), we have $\kappa \to 0$ as $d_S \to 0$. This in turn implies that for $j \in H^+$, $I_j = \dfrac{\kappa \alpha_j - d_S S_j}{d_I} \to 0$ as $d_S \to 0$. □

Lemma 3.5 *For each* $j \in \Omega$, $\check{I}_j$ *is monotone decreasing in* $d_S \in (0, \infty)$ *and* $\lim_{d_S \to 0} \check{I}_j = \check{I}_j^* \in (0, \alpha_j]$.

Proof We notice that $(\check{I}_j)$ is the positive solution of (3.6) with $d = d_I/d_S$. By Lemma 3.2, $\check{I}_j$ is monotone increasing in d, which implies that $\check{I}_j$ is monotone decreasing in d_S for each $j \in \Omega$. Since $\check{I}_j \in (0, \alpha_j)$ from Lemma 3.1, we have $\lim_{d_S \to 0} \check{I}_j = \check{I}_j^* \in (0, \alpha_j]$. □

From Lemma 3.5, we denote

$$J^- = \{j \in \Omega : 0 < \check{I}_j^* < \alpha_j\}, \quad \text{and} \quad J^+ = \{j \in \Omega : \check{I}_j^* = \alpha_j\}. \tag{3.13}$$

Clearly $\Omega = J^- \cup J^+$. We show that J^- is nonempty.

Lemma 3.6 *The set J^- is nonempty, and $H^- \subset J^-$.*

Proof Suppose that there exists $j \in \Omega$ such that $\beta_j - \gamma_j < 0$ and $\check{I}_j^* = \alpha_j$. By (3.6), we have

$$d_I \sum_{k \in \Omega} L_{jk} \check{I}_k + \check{I}_j(\beta_j - \gamma_j) \geq 0.$$

Taking $d_S \to 0$ on both sides, we have

$$d_I \sum_{k \neq j, k \in \Omega} L_{jk} \check{I}_k^* + d_I L_{jj} \alpha_j \geq \alpha_j(\gamma_j - \beta_j) > 0. \tag{3.14}$$

Since

$$d_I \sum_{k \neq j, k \in \Omega} L_{jk} \alpha_k + d_I L_{jj} \alpha_j = 0,$$

and $\check{I}_j^* \in (0, \alpha_j]$ for any $j \in \Omega$, we have

$$d_I \sum_{k \neq j, k \in \Omega} L_{jk} \check{I}_k^* + d_I L_{jj} \alpha_j \leq 0,$$

which contradicts with (3.14). Therefore, $H^- \subset J^-$. □

By virtue of the above lemma, we can prove the following result about the asymptotic profile of S_j. The proof is similar to Allen et al. (2007, Lemma 4.4), and we omit it here.

Lemma 3.7 *Let J^- be defined as above. Then*

(i) $\lim_{d_S \to 0} \dfrac{\kappa}{d_S} = \dfrac{N}{\sum_{k \in J^-}(\alpha_k - \check{I}_k^*)}$;

(ii) *For any $j \in \Omega$,* $\lim_{d_S \to 0} S_j = \dfrac{N}{\sum_{k \in J^-}(\alpha_k - \check{I}_k^*)}(\alpha_j - \check{I}_j^*)$.

Similar to Allen et al. (2007, Lemma 4.5), we can prove that J^+ is nonempty.

Lemma 3.8 *The set J^+ is nonempty.*

For some further analysis of J^+ with respect to d_I, we define

$$M = \left(M_{jk}\right)_{j,k\in H^-}, \quad \text{where} \quad M_{jk} = \begin{cases} -d_I L_{jk}, & j,k \in H^-,\ j \neq k, \\ -d_I L_{jj} - (\beta_j - \gamma_j), & j,k \in H^-,\ j = k, \end{cases} \tag{3.15}$$

Then M is an M-matrix, and M^{-1} is positive. Therefore, the following system

$$-d_I \sum_{k\in H^-} L_{jk} I_k - (\beta_j - \gamma_j) I_j = d_I \sum_{k\in H^+} L_{jk}\alpha_k, \quad j \in H^-, \tag{3.16}$$

has a unique solution $(I_j)_{j\in H^-} = \left(\alpha_j^*\right)_{j\in H^-}$.

Define

$$\check{I}_j^{(0)} = \begin{cases} \alpha_j^*, & j \in H^-, \\ \alpha_j, & j \in H^+, \end{cases} \tag{3.17}$$

and denote

$$h_j(d_I) = d_I \sum_{k\in\Omega} L_{jk} \check{I}_k^{(0)} + (\beta_j - \gamma_j)\alpha_j, \quad j \in H^+. \tag{3.18}$$

The following result describes the asymptotic profile of the endemic equilibrium as $d_S \to 0$.

Theorem 3.9 *Suppose that (A_0)–(A_3) hold and $R_0 > 1$. Let $(S_1, \cdots, S_n, I_1, \cdots, I_n)^T$ be the unique endemic equilibrium of (1.2)–(1.3) and $\check{\boldsymbol{I}} = (\check{I}_1, \ldots, \check{I}_n)^T$ be the unique strongly positive solution of (3.6) with $d = d_I/d_S$. Then the following statements hold:*

(i) $\lim_{d_S\to 0}(S_1, \ldots, S_n, I_1, \ldots, I_n) = (S_1^*, \ldots, S_n^*, 0, \ldots, 0)$.

(ii) *If $h_j(d_I) > 0$ for all $j \in H^+$, then $J^+ = H^+$ and $J^- = H^-$. Moreover,*

$$S_j^* = \begin{cases} \dfrac{\alpha_j - \alpha_j^*}{\sum_{k\in H^-}(\alpha_k - \alpha_k^*)} N, & \text{for} \ \ j \in H^-, \\ 0, & \text{for} \ \ j \in H^+. \end{cases} \tag{3.19}$$

(iii) *If $h_{j_0}(d_I) < 0$ for some $j_0 \in H^+$ and $h_j(d_I) \neq 0$ for any $j \in H^+$, then $H^- \subsetneq J^-$ and $J^+ \subsetneq H^+$. Moreover, there exists $j_1 \in H^+$ such that $S_{j_1}^* > 0$ and $S_j^* > 0$ for any $j \in H^-$.*

Proof (i) follows from Lemma 3.4. Without loss of generality, we assume $H^- = \{1, 2, \ldots, p\}$ and $H^+ = \{p+1, \ldots, n\}$ for some $p > 0$. Then

$$\check{I}_j^{(0)} = \begin{cases} \alpha_j^*, & 1 \le j \le p, \\ \alpha_j, & p+1 \le j \le n, \end{cases}$$

and $M = \left(M_{jk}\right)_{1\le j,k\le p}$ is defined as in (3.15). Since

$$
\begin{aligned}
&-\left[d_I\sum_{k=1}^{p} L_{jk}\alpha_k + (\beta_j-\gamma_j)\alpha_j\right] > d_I\sum_{k=p+1}^{n} L_{jk}\alpha_k \ \text{ for } \ 1\le j\le p,\\
&-\left[d_I\sum_{k=1}^{p} L_{jk}\alpha_k^* + (\beta_j-\gamma_j)\alpha_j^*\right] = d_I\sum_{k=p+1}^{n} L_{jk}\alpha_k \ \text{ for } \ 1\le j\le p,
\end{aligned}
\tag{3.20}
$$

and M^{-1} is positive, we have $\alpha_j^* \in [0,\alpha_j)$ for any $1\le j\le p$. Since L is irreducible, it is not hard to show that $\alpha_j^* > 0$ for any $1\le j\le p$.

Define

$$
\boldsymbol{G}(d_S,\tilde{\boldsymbol{I}}) = \begin{pmatrix}
\left[d_I\sum_{k\in\Omega} L_{1k}\tilde{I}_k + (\beta_1-\gamma_1)\tilde{I}_1\right]\left[d_S\tilde{I}_1 + d_I(\alpha_1-\tilde{I}_1)\right] - d_S\beta_1\tilde{I}_1^2\\
\left[d_I\sum_{k\in\Omega} L_{2k}\tilde{I}_k + (\beta_2-\gamma_2)\tilde{I}_2\right]\left[d_S\tilde{I}_2 + d_I(\alpha_2-\tilde{I}_2)\right] - d_S\beta_2\tilde{I}_2^2\\
\vdots\\
\left[d_I\sum_{k\in\Omega} L_{nk}\tilde{I}_k + (\beta_n-\gamma_n)\tilde{I}_n\right]\left[d_S\tilde{I}_n + d_I(\alpha_n-\tilde{I}_n)\right] - d_S\beta_n\tilde{I}_n^2
\end{pmatrix},
$$

where $\tilde{\boldsymbol{I}} = (\tilde{I}_1,\dots,\tilde{I}_n)^T$. Let $\check{\boldsymbol{I}}^{(0)} = (\check{I}_1^{(0)},\dots,\check{I}_n^{(0)})$. Then $\boldsymbol{G}(0,\check{\boldsymbol{I}}^{(0)}) = \boldsymbol{0}$. Moreover, if (3.6) has a solution $\check{\boldsymbol{I}}$ with $d = d_I/d_S$, then $\boldsymbol{G}(d_S,\check{\boldsymbol{I}}) = \boldsymbol{0}$; if $\boldsymbol{G}(d_S,\check{\boldsymbol{I}}) = \boldsymbol{0}$ with $\check{\boldsymbol{I}} = (\check{I}_1,\dots,\check{I}_n)^T$ satisfying $0 < \check{I}_j < \alpha_j$, then $\check{\boldsymbol{I}}$ is a nontrivial solution of (3.6) with $d = d_I/d_S$.

A direct computation shows that

$$
D_{\tilde{\boldsymbol{I}}}G\left(0,\check{\boldsymbol{I}}^{(0)}\right) = (V_{jk})_{j,k\in\Omega},
$$

where

$$
V_{jk} = \begin{cases}
d_I^2(\alpha_j-\alpha_j^*)L_{jk}, & 1\le j\le p,\ k\ne j,\\
d_I(\alpha_j-\alpha_j^*)\left(d_I L_{jj} + (\beta_j-\gamma_j)\right), & 1\le j\le p,\ k=j,\\
0, & p+1\le j\le n,\ k\ne j,\\
-d_I\left[d_I\sum_{k\in\Omega} L_{jk}\check{I}_k^{(0)} + (\beta_j-\gamma_j)\alpha_j\right], & p+1\le j\le n,\ k=j.
\end{cases}
$$

Therefore, we have

$$
D_{\tilde{\boldsymbol{I}}}G\left(0,\check{\boldsymbol{I}}^{(0)}\right) = d_I\begin{pmatrix} V_1 & * \\ \boldsymbol{0} & V_2\end{pmatrix}
$$

where V_1 is a $p \times p$ matrix

$$V_1 = \begin{pmatrix} (\alpha_1 - \alpha_1^*)(d_I L_{11} + \beta_1 - \gamma_1) & d_I(\alpha_1 - \alpha_1^*)L_{12} & \cdots & d_I(\alpha_1 - \alpha_1^*)L_{1p} \\ \cdots & \cdots & \cdots & \cdots \\ d_I(\alpha_p - \alpha_p^*)L_{p1} & d_I(\alpha_p - \alpha_p^*)L_{p2} & \cdots & (\alpha_p - \alpha_p^*)(d_I L_{1p} + \beta_p - \gamma_p) \end{pmatrix}$$

and $V_2 = \text{diag}(-h_j(d_I))$ is a diagonal matrix. It is not hard to check that V_1 is non-singular. Indeed, V_1 has negative diagonal entries and nonnegative off-diagonal entries. Moreover, the sum of the j-th row of V_1 is

$$\begin{aligned} & d_I \sum_{k=1}^{p} L_{jk}\alpha_j + (\beta_j - \gamma_j)\alpha_j - d_I \sum_{k=1}^{p} L_{jk}\alpha_j^* - (\beta_j - \gamma_j)\alpha_j^* \\ & = d_I \sum_{k=1}^{n} L_{jk}\alpha_j + (\beta_j - \gamma_j)\alpha_j = (\beta_j - \gamma_j)\alpha_j < 0, \end{aligned}$$

where we use (3.16) and Lemma 2.1. Therefore, V_1 is strictly diagonally dominant and invertible ($-V_1$ is an M-matrix). Hence if $h_j(d_I) \neq 0$ for all $j \in H^+$, (V_{jk}) is invertible. It follows from the implicit function theorem that there exist a constant $\delta > 0$, a neighborhood $N(\check{\boldsymbol{I}}^{(0)})$ of $\check{\boldsymbol{I}}^{(0)}$ and a continuously differentiable function

$$\tilde{\boldsymbol{I}}(d_S) = (\tilde{I}_1(d_S), \ldots, \tilde{I}_n(d_S))^T : [0, \delta] \to N(\check{\boldsymbol{I}}^{(0)})$$

such that for any $d_S \in [0, \delta]$, the unique solution of $\boldsymbol{G}(d_S, \tilde{\boldsymbol{I}}) = \boldsymbol{0}$ in the neighborhood $N(\check{\boldsymbol{I}}^{(0)})$ is $\tilde{\boldsymbol{I}}(d_S)$ and $\tilde{\boldsymbol{I}}(0) = \check{\boldsymbol{I}}^{(0)}$.

Differentiating $\boldsymbol{G}(d_S, \tilde{\boldsymbol{I}}(d_S)) = \boldsymbol{0}$ with respect to d_S at $d_S = 0$, and using the definition of $\check{I}_j^{(0)}$, we have

$$\begin{cases} d_I(\alpha_j - \alpha_j^*)\left[d_I \sum_{k\in\Omega} L_{jk}\tilde{I}_k'(0) + (\beta_j - \gamma_j)\tilde{I}_j'(0)\right] - \beta_j(\alpha_j^*)^2 = 0, & 1 \le j \le p, \\ -d_I\left[d_I \sum_{k\in\Omega} L_{jk}\check{I}_k^{(0)} + (\beta_j - \gamma_j)\alpha_j\right]\tilde{I}_j'(0) & \\ = -d_I\alpha_j \sum_{k\in\Omega} L_{jk}\check{I}_k^{(0)} + \gamma_j\alpha_j^2 > 0, & p+1 \le j \le n. \end{cases}$$

If $h_j(d_I) > 0$ for all $j \in H^+$, then $\tilde{I}_j'(0) < 0$ for every $j \in H^+$. This implies that $\tilde{I}_j(d_S) \approx \alpha_j + \tilde{I}_j'(0)d_S < \alpha_j$ for $j \in H^+$ if $d_S > 0$ is sufficiently small. Moreover for $j \in H^-$, $\tilde{I}_j(d_S) \approx \alpha_j^* < \alpha_j$ for small $d_S > 0$. Therefore, $\tilde{\boldsymbol{I}}$ is a nontrivial solution of (3.6), and $\tilde{\boldsymbol{I}} = \check{\boldsymbol{I}}$ by the uniqueness of the positive solution of (3.6). Since $\lim_{d_S\to 0} \check{\boldsymbol{I}} = \check{\boldsymbol{I}}^{(0)}$, we have $J^+ = H^+$ and $J^- = H^-$. By Lemma 3.7, we have

$$S_j^* = \lim_{d_S\to 0} S_j = \frac{\alpha_j - \alpha_j^*}{\sum_{k\in H^-}(\alpha_k - \alpha_k^*)} N \quad \text{for} \quad j \in H^-,$$

and $S_j^* = \lim_{d_S\to 0} S_j = 0$ for $j \in H^+$.

On the other hand, if there exists $j_0 \in H^+$ such that $h_{j_0}(d_I) < 0$, then $\tilde{I}'_{j_0}(0) > 0$, which implies that $\tilde{I}_{j_0}(d_S) \approx \alpha_{j_0} + \tilde{I}'_{j_0}(0)d_S > \alpha_{j_0}$, so $\tilde{\boldsymbol{I}}$ is not a solution of (3.6) with $d = d_I/d_S$. Therefore, $\lim_{d_S\to 0} \check{\boldsymbol{I}} \neq \check{\boldsymbol{I}}^{(0)}$, which yields $H^- \subsetneqq J^-$ and $J^+ \subsetneqq H^+$. Then there exists $j_1 \in H^+$ such that $S_{j_1}^* > 0$. This completes the proof. □

The function $h_j(d_I)$ in Theorem 3.9 is critical in determining the asymptotic profile of the endemic equilibrium as $d_S \to 0$. The next result explores further properties of the function $h_j(d_I)$.

Proposition 3.10 *Suppose that* (A_0)–(A_3) *hold, and* $H^- = \{1, 2, \ldots, p\}$ *and* $H^+ = \{p+1, \ldots, n\}$ *for some* $p > 0$. *Then for any* $p+1 \le j \le n$, $h_j(d_I)$ *is either constant or strictly decreasing in* d_I. *Moreover,*

$$\lim_{d_I\to\infty} \begin{pmatrix} h_{p+1}(d_I) \\ \vdots \\ h_n(d_I) \end{pmatrix} = -\tilde{N}\tilde{M}^{-1} \begin{pmatrix} (\gamma_1 - \beta_1)\alpha_1 \\ \vdots \\ (\gamma_p - \beta_p)\alpha_p \end{pmatrix} + \begin{pmatrix} (\beta_{p+1} - \gamma_{p+1})\alpha_{p+1} \\ \vdots \\ (\beta_n - \gamma_n)\alpha_n \end{pmatrix},$$

and

$$\lim_{d_I\to 0} \begin{pmatrix} h_{p+1}(d_I) \\ \vdots \\ h_n(d_I) \end{pmatrix} = \begin{pmatrix} (\beta_{p+1} - \gamma_{p+1})\alpha_{p+1} \\ \vdots \\ (\beta_n - \gamma_n)\alpha_n \end{pmatrix},$$

where $\tilde{M} = (\tilde{m}_{ij})$ *is a* $p \times p$ *matrix with* $\tilde{m}_{ij} = -L_{ij}$ *for* $1 \le i, j \le p$ *and* $\tilde{N} = (\tilde{n}_{ij})$ *is an* $(n-p) \times p$ *matrix with* $\tilde{n}_{ij} = L_{(i+p)j}$ *for* $1 \le i \le n-p$ *and* $1 \le j \le p$, *i.e.*

$$L = \begin{pmatrix} -\tilde{M} & * \\ \tilde{N} & * \end{pmatrix}.$$

Proof First we claim that α_j^* is strictly increasing in d_I for each $1 \le j \le p$. To see this, we differentiate both sides of (3.16) with respect to d_I to get

$$-d_I \sum_{k=1}^{p} L_{jk}(\alpha_k^*)' - (\beta_j - \gamma_j)(\alpha_j^*)' - \sum_{k=1}^{p} L_{jk}\alpha_k^* = \sum_{k=p+1}^{n} L_{jk}\alpha_k, \quad 1 \le j \le p. \tag{3.21}$$

Combining (3.16) and (3.21), we have

$$-d_I \sum_{k=1}^{p} L_{jk}(\alpha_k^*)' - (\beta_j - \gamma_j)(\alpha_j^*)' = d_I^{-1}(\gamma_j - \beta_j)\alpha_j^* > 0, \quad 1 \le j \le p.$$

Since M is an M-matrix and $\beta_j < \gamma_j$ for $1 \le j \le p$, $(\alpha_j^*)'$ is strictly positive. This proves the claim.

By the fact that $\alpha_j^* \in (0, \alpha_j)$ and the monotonicity of α_j^* for $d_I \in (0, \infty)$, the limits $\lim_{d_I\to 0} \alpha_j^*$ and $\lim_{d_I\to\infty} \alpha_j^*$ exist for $1 \le j \le p$. It follows that $\lim_{d_I\to 0} \alpha_j^* = 0$.

Dividing both sides of (3.16) by d_I and taking $d_I \to \infty$, we have

$$-\sum_{k=1}^{p} L_{jk} \lim_{d_I \to \infty} \alpha_k^* = \sum_{k=p+1}^{n} L_{jk}\alpha_k, \quad 1 \le j \le p.$$

Therefore,

$$\lim_{d_I \to \infty} \alpha_j^* = \alpha_j, \quad 1 \le j \le p. \tag{3.22}$$

Next we claim that $\alpha_j^* + d_I(\alpha_j^*)' < \alpha_j$ for all $1 \le j \le p$ and $d_I > 0$. To see this, by (3.21), we have

$$-\sum_{k=1}^{p} L_{jk}(\alpha_k^* + d_I(\alpha_k^*)') < \sum_{k=p+1}^{n} L_{jk}\alpha_k, \quad 1 \le j \le p.$$

By the definition of α_j,

$$-\sum_{k=1}^{p} L_{jk}\alpha_k = \sum_{k=p+1}^{n} L_{jk}\alpha_k, \quad 1 \le j \le p. \tag{3.23}$$

Then, it follows that

$$-\sum_{k=1}^{p} L_{jk}(\alpha_k^* + d_I(\alpha_k^*)' - \alpha_k) < 0.$$

Then the claim follows from the fact that $\tilde{M}$ is an M-matrix.

Differentiating $h_j(d_I)$ with respect to d_I, we find

$$h_j'(d_I) = \sum_{k=1}^{p} L_{jk}(\alpha_k^* + d_I(\alpha_k^*)') + \sum_{k=p+1}^{n} L_{jk}\alpha_k, \quad p+1 \le j \le n.$$

It follows from (3.23) that

$$h_j'(d_I) = \sum_{k=1}^{p} L_{jk}(\alpha_k^* + d_I(\alpha_k^*)' - \alpha_k), \quad p+1 \le j \le n.$$

Since $\alpha_j^* + d_I(\alpha_j^*)' < \alpha_j$ for all $1 \le j \le p$, either $h_j'(d_I) < 0$ or $h_j'(d_I) = 0$ for all $d_I > 0$ and $p+1 \le j \le n$ ($h_j'(d_I) = 0$ for all $d_I > 0$ if $L_{jk} = 0$ for all $1 \le k \le p$; otherwise $h_j'(d_I) < 0$ for all $d_I > 0$). Therefore, $h_j(d_I)$ is either strictly decreasing or constant for all $d_I > 0$ and $p+1 \le j \le n$.

Finally, we compute the limit of $h_j(d_I)$. By (3.16) and $L\boldsymbol{\alpha} = 0$, we have

$$-d_I \sum_{k=1}^{p} L_{jk}(\alpha_k - \alpha_k^*) - (\beta_j - \gamma_j)(\alpha_j - \alpha_j^*) = -(\beta_j - \gamma_j)\alpha_j, \quad 1 \le j \le p.$$

Let $u_j = d_I(\alpha_j - \alpha_j^*)$, $1 \le j \le p$. Then,

$$-\sum_{k=1}^{p} L_{jk}u_k - \frac{(\beta_j - \gamma_j)}{d_I}u_j = -(\beta_j - \gamma_j)\alpha_j, \quad 1 \le j \le p.$$

Taking $d_I \to \infty$, we find

$$-\sum_{k=1}^{p} L_{jk} \lim_{d_I \to \infty} u_k = -(\beta_j - \gamma_j)\alpha_j, \quad 1 \le j \le p.$$

So, we have

$$\lim_{d_I \to \infty} \begin{pmatrix} u_1 \\ u_2 \\ \vdots \\ u_p \end{pmatrix} = \tilde{M}^{-1} \begin{pmatrix} (\gamma_1 - \beta_1)\alpha_1 \\ (\gamma_2 - \beta_2)\alpha_2 \\ \vdots \\ (\gamma_p - \beta_p)\alpha_p \end{pmatrix}.$$

Since

$$\begin{aligned} h_j(d_I) &= d_I \sum_{k=1}^{n} L_{jk}\alpha_k + d_I \sum_{k=1}^{p} L_{jk}(\alpha_k^* - \alpha_k) + (\beta_j - \gamma_j)\alpha_j \\ &= -\sum_{k=1}^{p} L_{jk}u_k + (\beta_j - \gamma_j)\alpha_j, \quad p+1 \le j \le n, \end{aligned}$$

we have

$$\begin{aligned} \lim_{d_I \to \infty} \begin{pmatrix} h_{p+1}(d_I) \\ h_{p+2}(d_I) \\ \vdots \\ h_n(d_I) \end{pmatrix} &= -\tilde{N} \lim_{d_I \to \infty} \begin{pmatrix} u_1 \\ u_2 \\ \vdots \\ u_p \end{pmatrix} + \begin{pmatrix} (\beta_{p+1} - \gamma_{p+1})\alpha_{p+1} \\ (\beta_{p+2} - \gamma_{p+2})\alpha_{p+2} \\ \vdots \\ (\beta_n - \gamma_n)\alpha_n \end{pmatrix} \\ &= -\tilde{N}\tilde{M}^{-1} \begin{pmatrix} (\gamma_1 - \beta_1)\alpha_1 \\ (\gamma_2 - \beta_2)\alpha_2 \\ \vdots \\ (\gamma_p - \beta_p)\alpha_p \end{pmatrix} + \begin{pmatrix} (\beta_{p+1} - \gamma_{p+1})\alpha_{p+1} \\ (\beta_{p+2} - \gamma_{p+2})\alpha_{p+2} \\ \vdots \\ (\beta_n - \gamma_n)\alpha_n \end{pmatrix}. \end{aligned}$$

The limit of $h_j(d_I)$ as $d_I \to 0$ follows from (3.22) and the definition of $h_j(d_I)$. □

Now we have the following results summarizing the dynamics of (1.2)–(1.3) when the diffusion rate of the infectious population d_I varies and the diffusion rate of the susceptible population d_S tends to 0.

Corollary 3.11 *Suppose that* (A_0)–(A_3) *hold. Let* $(S_1^*, \cdots, S_n^*, 0, \cdots, 0)^T$ *be the limiting disease-free equilibrium as* $d_S \to 0$ *defined as in Theorem 3.9. Then there exists* $d_I^* \in (0, \infty]$ *and* $d_I^{**} \in (0, d_I^*]$ *such that*

1. *when* $0 < d_I < d_I^*$, $R_0(d_I) > 1$ *and there exists a unique endemic equilibrium* $(S_1, \cdots, S_n, I_1, \cdots, I_n)^T$ *of* (1.2)–(1.3)*; and when* $d_I > d_I^*$, $R_0(d_I) < 1$ *and the disease-free equilibrium is globally asymptotically stable.*
2. *When* $0 < d_I < d_I^{**}$, $H^+ = J^+$ *and* $H^- = J^-$*; and* $S_j^* > 0$ *for* $j \in H^- = J^-$, $S_j^* = 0$ *for* $j \in H^+ = J^+$ *as defined in* (3.19).
3. *When* $d_I^{**} < d_I < d^*$ *and except a finite number of* d_I*'s,* $H^+ = J^+ \cup J_1^-$, $H^- = J_2^-$, *where* $J^- = J_1^- \cup J_2^-$ *such that* $J_1^- \neq \emptyset$*; and* $S_j^* > 0$ *for* $j \in J^-$, $S_j^* = 0$ *for* $j \in J^+$.

Proof From the condition (A_3) and Theorem 2.7, $R_0 > 1$ for small $d_I > 0$. From the monotonicity of R_0 shown in Theorem 2.6, either (i) there exists a unique $d_I^* > 0$ such that $R_0(d_I) = 1$ and when $R_0 > 1$ when $d_I > d_I^*$, or (ii) $R_0 > 1$ for all $d_I > 0$. We denote $d_I^* = \infty$ in the case (ii). The uniqueness of endemic equilibrium is shown in Theorem 3.3, and the global stability of the disease-free equilibrium when $R_0 < 1$ can be established similarly as in Allen et al. (2007, Lemma 2.3).

For $0 < d_I < d_I^*$, $h_j(d_I) > 0$ for all $j \in H^+$ and small $d_I > 0$ from Proposition 3.10. Then from part (ii) of Theorem 3.9, for $d_I > 0$ small, $H^+ = J^+$ and $H^- = J^-$; and $S_j^* > 0$ for $j \in H^- = J^-$, $S_j^* = 0$ for $j \in H^+ = J^+$ as defined in (3.19). From the monotonicity of $h_j(d_I)$ shown in Proposition 3.10, either (i) there exists a unique $d_I^{**} \in (0, d_I^*)$ such that $h_j(d_I) > 0$ for all $j \in H^+$ and $d \in (0, d_I^{**})$ and $h_{j_0}(d_I^{**}) = 0$ for some $j_0 \in H^+$, or (ii) $h_j(d_I) > 0$ for all $j \in H^+$ and $d \in (0, d_I^*)$. We let $d_I^{**} = d_I^*$ in case (ii). In case (i), the monotonicity of $h_{j_0}(d_I)$ implies that $h_{j_0}(d_I) < 0$ for all $d_I \in (d_I^{**}, d_I^*)$, and except a finite number of d_I's, $h_j(d_I) \neq 0$ for $d_I \in (d_I^{**}, d_I^*)$. Thus results in part (iii) of Theorem 3.9 hold for all $d_I \in (d_I^{**}, d_I^*)$ except a finite number of d_I's. □

We show that the condition on the function $h_j(d_I)$ is comparable to the conditions on d_I given in Allen et al. (2007).

Proposition 3.12 *Suppose that* (A_0)–(A_3) *hold and* L *is symmetric. Define*

$$L_k^- = \sum_{j \in H^-,\ j \neq k} L_{kj}, \quad L_k^+ = \sum_{j \in H^+,\ j \neq k} L_{kj}. \tag{3.24}$$

If

$$\frac{1}{d_I} > \max_{k \in H^+} \frac{L_k^-}{\beta_k - \gamma_k} + \max_{k \in H^-} \frac{L_k^+}{\beta_k - \gamma_k}, \tag{3.25}$$

then $h_j(d_I) > 0$ *for all* $j \in H^+$.

Proof Assume on the contrary that $h_j(d_I) \le 0$ for some $j \in H^+$. Let $\alpha_m^* = \min\{\alpha_k^* : k \in H^-\}$. Since L is symmetric, $\alpha_j = 1/n$ for all $j \in \Omega$. Then, we have

$$h_j(d_I) = d_I \sum_{k\in H^-} L_{jk}\alpha_k^* + \frac{1}{n}\left[d_I \sum_{k\in H^+} L_{jk} + \beta_j - \gamma_j\right] \le 0. \tag{3.26}$$

Since $j \in H^+$ and $L_{jj} = -L_j^+ - L_j^-$, we have $\sum_{k\in H^+} L_{jk} = -L_j^-$. Therefore, by (3.26) and the definition of α_m^*, we have $d_I L_j^- \alpha_m^* + \frac{1}{n}\left[-d_I L_j^- + \beta_j - \gamma_j\right] \le 0$, which implies

$$n\alpha_m^* \le \frac{\gamma_j - \beta_j + d_I L_j^-}{d_I L_j^-}. \tag{3.27}$$

By $m \in H^-$ and (3.16), we have

$$d_I \sum_{k\in H^-} L_{mk}\alpha_k^* + d_I \sum_{k\in H^+} L_{mk}\alpha_k + (\beta_m - \gamma_m)\alpha_m^* = 0,$$

which impiles

$$d_I \sum_{k\in H^-, k\ne m} L_{mk}(\alpha_k^* - \alpha_m^*) - d_I L_m^+\alpha_m^* + d_I \frac{L_m^+}{n} + (\beta_m - \gamma_m)\alpha_m^* = 0.$$

By the definition of α_m^*, we have $-d_I L_m^+\alpha_m^* + d_I \frac{L_m^+}{n} + (\beta_m - \gamma_m)\alpha_m^* \le 0$. Therefore,

$$\frac{d_I L_m^+}{-\beta_m + \gamma_m + d_I L_m^+} \le n\alpha_m^*.$$

It then follows from (3.27) that

$$\frac{d_I L_m^+}{-\beta_m + \gamma_m + d_I L_m^+} \le \frac{\gamma_j - \beta_j + d_I L_j^-}{d_I L_j^-},$$

which can be simplified as

$$(\gamma_m - \beta_m)(\gamma_j - \beta_j) + (\gamma_j - \beta_j)d_I L_m^+ + (\gamma_m - \beta_m)d_I L_j^- \ge 0.$$

Dividing both sides by $d_I(\gamma_m - \beta_m)(\gamma_j - \beta_j)$ (which is negative), we obtain

$$\frac{1}{d_I} \le \frac{L_m^+}{\beta_m - \gamma_m} + \frac{L_j^-}{\beta_j - \gamma_j} \le \max_{j\in H^-} \frac{L_j^+}{\beta_j - \gamma_j} + \max_{j\in H^+} \frac{L_j^-}{\beta_j - \gamma_j},$$

which is a contradiction. Therefore, $h_j(d_I) > 0$ for all $j \in H^+$. □

Remark 3.13 1. By Theorem 3.9, the unique endemic equilibrium converges to a limiting disease-free equilibrium as $d_S \to 0$. Moreover, the limiting disease-free equilibrium has a positive number of susceptible individuals on each low-risk patch. This is in agreement of the results in Allen et al. (2007) which assumes L is symmetric.

2. In Allen et al. (2007), the distribution of susceptible individuals as $d_S \to 0$ on high-risk patches is left as an open problem. In Theorem 3.9, we show that the distribution of susceptible individuals on high-risk patches depends on the function $h_j(d_I)$: $S_j^* = 0$ on each high-risk patch if $h_j(d_I) > 0$ for all j. In Proposition 3.10, we have shown that $h_j(d_I)$ is monotone in d_I. As a consequence, there exists $d_I^{**} > 0$ such that $S_j^* = 0$ on each high-risk patch when $0 < d_I < d_I^{**}$. This partially solves an open problem in Allen et al. (2007).
3. The sharp threshold diffusion rate d_I^{**} is characterized by the smallest zero of function $h_j(d_I)$ on any high-risk patch j. When L is symmetric, a lower bound of d_I^{**} is shown in Proposition 3.12 and also Allen et al. (2007, Theorem 2):

$$d_I^{**} \geq \left[\max_{k \in H^+} \frac{L_k^-}{\beta_k - \gamma_k} + \max_{k \in H^-} \frac{L_k^+}{\beta_k - \gamma_k} \right]^{-1} := \widetilde{d_I^{**}}. \tag{3.28}$$

It is an interesting question to have a more explicit expression or estimate of d_I^{**} when L is not symmetric.

3.3 Asymptotic profile with respect to d_I and d_S

We suppose that (A_0)–(A_3) hold throughout this subsection, and we consider the asymptotic profile of the endemic equilibrium of (1.2)–(1.3) as $d_I \to 0$. The case that L is symmetric was studied in Li and Peng (2019) recently, and we consider the asymmetric case here. For simplicity, we assume $\gamma_j > 0$ for any $j \in \Omega$. Since $\lim_{d_I \to 0} R_0 = \max_{j \in \Omega} \beta_j / \gamma_j > 1$, we have $R_0 > 1$ ($s\left(d_I L + diag(\beta_j - \gamma_j)\right) > 0$) and the existence and uniqueness of the endemic equilibrium for sufficiently small d_I.

Firstly, we consider the asymptotic profile of positive solution of (3.6) as $d_I \to 0$. The proof is similar to that of Theorem 3.9, and we put it in the Appendix. We denote $(x)_+ = 0$ if $x \leq 0$ and $(x)_+ = x$ if $x > 0$.

Lemma 3.14 *Suppose that* (A_0)–(A_3) *hold and* $\gamma_j > 0$ *for all* $j \in \Omega$. *Let* $\check{\boldsymbol{I}} = (\check{I}_1, \ldots, \check{I}_n)^T$ *be the unique strongly positive solution of* (3.6). *Then the following two statements hold:*

(i) *For any* $d > 0$, *but* $d_I \to 0$,

$$\check{I}_j \to \frac{d\alpha_j \left(\beta_j - \gamma_j\right)_+}{d(\beta_j - \gamma_j)_+ + \gamma_j}, \quad j \in \Omega. \tag{3.29}$$

(ii) *As* $(d_I, d) \to (0, \infty)$ *(or equivalently,* $(d_I, 1/d) \to (0, 0)$*),*

$$\check{I}_j \to 0 \;\; for \;\; j \in H^- \;\; and \;\; \check{I}_j \to \alpha_j \;\; for \;\; j \in H^+.$$

We also have the following result on an auxiliary problem. The proof is similar to that of Lemma 3.2, and we also put it in the Appendix. We note that $\check{\boldsymbol{U}} = \check{\boldsymbol{I}}/d$, where $\check{\boldsymbol{I}}$ is defined in Lemma 3.2.

Lemma 3.15 *Suppose that* (A_0)–(A_3) *hold and* $R_0 > 1$. *Then for any* $d \in [0, 1)$, *the following equation*

$$\begin{cases} d_I \sum_{k\in\Omega} L_{jk}U_k + U_j\left(\beta_j - \gamma_j - \dfrac{\beta_j U_j}{\alpha_j + (1-d)U_j}\right) = 0, & j \in \Omega, \\ U_j \geq 0 & j \in \Omega, \end{cases} \tag{3.30}$$

has a unique strongly positive solution $\check{\boldsymbol{U}} = (\check{U}_1, \ldots, \check{U}_n)^T$. *Moreover,* $\check{U}_j$ *is monotone decreasing in* $d \in [0, 1)$, *and*

$$\lim_{d_I\to 0} \check{U}_j = \frac{\alpha_j\left(\beta_j - \gamma_j\right)_+}{d\beta_j + (1-d)\gamma_j}, \quad j \in \Omega. \tag{3.31}$$

By virtue of Lemmas 3.14 and 3.15, we have the following results.

Theorem 3.16 *Suppose that* (A_0)–(A_3) *hold and* $\gamma_j > 0$ *for all* $j \in \Omega$. *Let* $(S_1, \cdots, S_n, I_1, \cdots, I_n)^T$ *be the unique endemic equilibrium of* (1.2)–(1.3). *Let* $d_I \to 0$ *and* $d := d_I/d_S \to d_0 \in [0, \infty]$. *Then the following statements hold:*

(i) *If* $d_0 = 0$, *then*

$$S_j \to \frac{N\alpha_j}{\sum_{k\in\Omega}\left[\alpha_k + \frac{\alpha_k(\beta_k-\gamma_k)_+}{\gamma_k}\right]}, \quad I_j \to \frac{N\dfrac{\alpha_j\left(\beta_j-\gamma_j\right)_+}{\gamma_j}}{\sum_{k\in\Omega}\left[\alpha_k + \frac{\alpha_k(\beta_k-\gamma_k)_+}{\gamma_k}\right]}, \quad j \in \Omega. \tag{3.32}$$

(ii) *If* $d_0 \in (0, \infty)$, *then*

$$S_j \to \frac{N\left(\alpha_j - \dfrac{d_0\alpha_j\left(\beta_j-\gamma_j\right)_+}{d_0(\beta_j-\gamma_j)_+ + \gamma_j}\right)}{\sum_{k\in\Omega}\left[\alpha_k + (1-d_0)\frac{\alpha_k(\beta_k-\gamma_k)_+}{d_0(\beta_k-\gamma_k)_+ + \gamma_k}\right]}, \quad j \in \Omega,$$

$$I_j \to \frac{N\dfrac{\alpha_j(\beta_j-\gamma_j)_+}{d_0(\beta_j-\gamma_j)_+ + \gamma_j}}{\sum_{k\in\Omega}\left[\alpha_k + (1-d_0)\frac{\alpha_k(\beta_k-\gamma_k)_+}{d_0(\beta_k-\gamma_k)_+ + \gamma_k}\right]}, \quad j \in \Omega. \tag{3.33}$$

(iii) If $d_0 = \infty$, *then*

$$S_j \to \begin{cases} \dfrac{N\alpha_j}{\sum_{k\in H^-}\alpha_k}, & j \in H^-, \\ 0, & j \in H^+, \end{cases} \quad I_j \to 0, \quad j \in \Omega. \tag{3.34}$$

Proof Let

$$\check{\boldsymbol{U}} = (\check{U}_1, \ldots, \check{U}_n)^T = \check{\boldsymbol{I}}/d = (\check{I}_1/d, \ldots, \check{I}_n/d)^T,$$

where $\check{\boldsymbol{I}}$ is the unique strongly positive solution of (3.6) with $d = d_I/d_S$. Then $\check{\boldsymbol{U}}$ is the unique strongly positive solution of (3.30). It follows from Theorem 3.3 that

$$S_j = \frac{dN(\alpha_j - \check{I}_j)}{\sum_{k\in\Omega}\left[d(\alpha_k - \check{I}_k) + \check{I}_k\right]}, \quad I_j = \frac{N\check{I}_j}{\sum_{k\in\Omega}\left[d(\alpha_k - \check{I}_k) + \check{I}_k\right]}, \tag{3.35}$$

or equivalently,

$$S_j = \frac{N(\alpha_j - d\check{U}_j)}{\sum_{k\in\Omega}\left[(\alpha_k - d\check{U}_k) + \check{U}_k\right]}, \quad I_j = \frac{N\check{U}_j}{\sum_{k\in\Omega}\left[(\alpha_k - d\check{U}_k) + \check{U}_k\right]}. \tag{3.36}$$

(i) Let $\check{\boldsymbol{U}}^{(i)} = (\check{U}_1^{(i)}, \ldots, \check{U}_n^{(i)})$ be the unique strongly positive solution of (3.30) with $d = d_i$ for $i = 1, 2$, where $d_1 = 0$ and $d_2 = 1/2$. Then by Lemma 3.15, for $d \in (0, 1/2)$ we have

$$\check{U}_j^{(2)} \le \check{U}_j \le \check{U}_j^{(1)}. \tag{3.37}$$

Therefore, if $j \in H^-$, then

$$\lim_{(d_I,d)\to(0,0)} \check{U}_j \le \lim_{d_I\to 0} \check{U}_j^{(1)} = 0.$$

Next we consider the case $j \in H^+$. Notice that $\{\check{U}_j\}$ is bounded when d_I and d are small. Then for any sequences $d_I^{(m)} \to 0$ and $d^{(m)} \to 0$, there are subsequences $\{d_I^{(m_l)}\}_{l=1}^{\infty}$ and $\{d^{(m_l)}\}_{l=1}^{\infty}$ such that the corresponding solution $\check{U}_j^{(l)}$ of (3.30) with $d_I = d_I^{(m_l)}$ and $d = d^{(m_l)}$ satisfies $\lim_{l\to\infty} \check{U}_j^{(l)} = \check{U}_j^*$. It follows from (3.37) that $\check{U}_j^* \ge \lim_{d_I\to 0} \check{U}_j^{(2)} > 0$. Substituting $U_j = \check{U}_j^{(l)}$, $d = d^{(m_l)}$ and $d_I = d_I^{(m_l)}$ into (3.30) and taking $l \to \infty$ on both sides, we see that

$$\check{U}_j^* \left(\beta_j - \gamma_j - \frac{\beta_j \check{U}_j^*}{\alpha_j + \check{U}_j^*}\right) = 0,$$

which implies that

$$\lim_{(d_I,d)\to(0,0)} \check{U}_j^* = \frac{\alpha_j\left(\beta_j - \gamma_j\right)_+}{\gamma_j}, \quad j \in \Omega. \tag{3.38}$$

This, combined with (3.36), implies (3.32).

(ii) Let $\check{\boldsymbol{I}}^{(i)} = (\check{I}_1^{(i)}, \dots, \check{I}_n^{(i)})^T$ be the unique strongly positive solution of (3.2) with $d = d_i$ for $i = 1, 2$, where $d_1 = d_0/2$ and $d_2 = 2d_0$. We see from Lemma 3.2 that, for $d \in [d_0/2, 2d_0]$, $\check{I}_j^{(1)} \le \check{I}_j \le \check{I}_j^{(2)}$ for any $i \in \Omega$. Therefore, if $j \in H^-$, then

$$\lim_{(d_I,d)\to(0,d_0)} \check{I}_j \le \lim_{d_I\to 0} \check{I}_j^{(2)} = 0.$$

Next we consider the case $j \in H^+$. Note that $\{\check{I}_j\}$ is bounded. Then for any sequences $d_I^{(m)} \to 0$ and $d^{(m)} \to d_0$, there are subsequences $\{d_I^{(m_l)}\}_{l=1}^{\infty}$ and $\{d^{(m_l)}\}_{l=1}^{\infty}$ such that the corresponding solution $\check{I}_j^{(l)}$ of (3.6) with $d_I = d_I^{(m_l)}$ and $d = d^{(m_l)}$ satisfies $\lim_{l\to\infty} \check{I}_j^{(l)} = \check{I}_j^*$. It follows from (3.29) that $\check{I}_j^* \ge \lim_{d_I\to 0} \check{I}_j^{(1)} > 0$. Substituting $I_j = \check{I}_j^{(l)}$, $d = d^{(m_l)}$ and $d_I = d_I^{(m_l)}$ into (3.6) and taking $l \to \infty$ on both sides, we see that

$$\check{I}_j^* \left(\beta_j - \gamma_j - \frac{\beta_j \check{I}_j^*}{d_0(\alpha_j - \check{I}_j^*) + \check{I}_j^*} \right) = 0,$$

which implies that

$$\lim_{(d_I,d)\to(0,\infty)} \check{I}_j^* = \frac{d_0\alpha_j \left(\beta_j - \gamma_j\right)_+}{d_0(\beta_j - \gamma_j)_+ + \gamma_j}, \quad j \in \Omega. \tag{3.39}$$

This, combined with (3.35), implies (3.33).

(iii) By Lemma 3.14, we have

$$\lim_{(d_I,d)\to(0,\infty)} \check{I}_j = \begin{cases} 0, & j \in H^-, \\ \alpha_j, & j \in H^+. \end{cases} \tag{3.40}$$

This, together with (3.35), implies (3.34). ◻

Remark 3.17 Above we consider the asymptotic profile of the endemic equilibrium $(S_1, \cdots, S_n, I_1, \cdots, I_n)^T$ as $d_I \to 0$. If d_S is fixed or tends to a positive number, then the limits of S_j and I_j satisfy (3.32). If d_S also tends to zero, we have the following results:

1. if d_I and d_S are infinitesimals of the same order, then the limits of S_j and I_j satisfy (3.33).
2. if d_S is an infinitesimal of higher order than d_I, then the limits of S_j and I_j satisfy (3.34).

4 An example

In this section, we illustrate the results in Sections 2-3 to a heterogeneous landscape of a star graph; see Fig. 1. Specifically, the graph consists of a hub, labelled as 1,

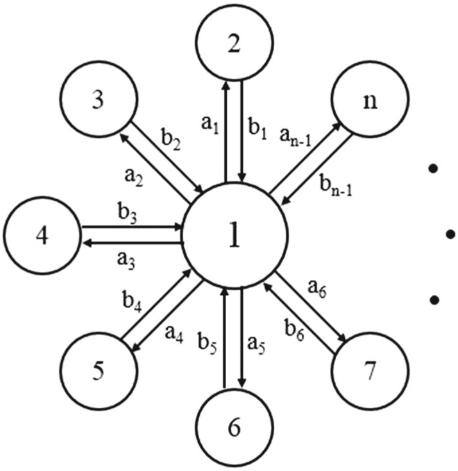


Fig. 1 The star migration graph

and $n-1$ leaves, labelled as $2, 3, \ldots, n$, respectively; the migration rate from the hub to each leaf i $(2 \le i \le n)$ is a_{i-1} while from leaf i to the hub is b_{i-1}. This kind of heterogeneous landscapes have previously been applied to study the disease outbreak around a metropolitan area or water source, such as measles (Bjørnstad et al. 2002), leptospirosis (Saldaña and Barradas 2018), and cholera (Shuai and Van den Driessche 2015). Also the hub and leaves can be explained as a central deme and the corresponding colonies, respectively; see, for example Karlin (1982).

The connectivity matrix L corresponding to the star graph can be rewritten as:

$$L = \begin{pmatrix} -\sum_{i=1}^{n-1} a_i & b_1 & b_2 & b_3 & \cdots & b_{n-1} \\ a_1 & -b_1 & 0 & 0 & \cdots & 0 \\ a_2 & 0 & -b_2 & 0 & \cdots & 0 \\ a_3 & 0 & 0 & -b_3 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ a_{n-1} & 0 & 0 & 0 & \cdots & -b_{n-1} \end{pmatrix}. \tag{4.1}$$

Denote $r_i = a_i/b_i$ for $i = 1, \ldots, n-1$. A direct computation of the positive eigenvector of L gives

$$\boldsymbol{\alpha} = \left(\frac{1}{1+s}, \frac{r_1}{1+s}, \ldots, \frac{r_{n-1}}{1+s} \right),$$

where $s = \sum_{i=1}^{n-1} r_i$. In order to investigate the joint effect of asymmetric connectivity and high-/low-risk patches, we assume that the hub (patch 1) and one leaf (say, patch 2) are of high-risk, and all other leafs are of low-risk. That is,

(A) $H^+ = \{1, 2\}$ and $H^- = \{3, \ldots, n\}$.

For this situation, straightforward computations yield

$$\check{I}_j^{(0)} = \begin{cases} \alpha_j, & j = 1, 2, \\ \dfrac{d_I a_{j-1}\alpha_1}{d_I b_{j-1} + \gamma_j - \beta_j}, & j = 3, \dots, n, \end{cases}$$

and

$$\begin{aligned} h_1(d_I) =& d_I \left[\left(-\sum_{k=1}^{n-1} a_k \right) \alpha_1 + b_1\alpha_2 + \sum_{k=3}^{n} \frac{d_I \alpha_1 a_{k-1} b_{k-1}}{d_I b_{k-1} + \gamma_k - \beta_k} \right] + \alpha_1(\beta_1 - \gamma_1), \\ h_2(d_I) =& \alpha_2(\beta_2 - \gamma_2) > 0. \end{aligned}$$

It follows from Proposition 3.10 that $h_1(d_I)$ is strictly decreasing and satisfies

$$\lim_{d_I \to 0} h_1(d_I) = \alpha_1(\beta_1 - \gamma_1) > 0, \quad \text{and} \quad \lim_{d_I \to \infty} h_1(d_I) = \alpha_1(\beta_1 - \gamma_1) + \sum_{k=3}^{n} \alpha_k(\beta_k - \gamma_k). \tag{4.2}$$

By Lemma 2.5, we obtain

$$\begin{aligned} \lim_{d_I \to 0} s\left(d_I L + diag(\beta_j - \gamma_j)\right) &= \max_{1 \le k = \le n} (\beta_k - \gamma_k) > 0, \\ \lim_{d_I \to 0} s\left(d_I L + diag(\beta_j - \gamma_j)\right) &= \sum_{k=1}^{n} \alpha_k(\beta_k - \gamma_k). \end{aligned}$$

Since $s\left(d_I L + diag(\beta_j - \gamma_j)\right)$ has the same sign as $R_0 - 1$ and is strictly decreasing for d_I, we have the following result.

Proposition 4.1 *Suppose $a_k, b_k > 0$ for $k = 1, \dots, n-1$ and (A) holds. Then the following statements hold:*

(i) If $\sum_{k=1}^{n} \alpha_k(\beta_k - \gamma_k) > 0$, then $R_0 > 1$ for any $d_I > 0$. Moreover,

(i_1) if $\alpha_1(\beta_1 - \gamma_1) + \sum_{k=3}^{n} \alpha_k(\beta_k - \gamma_k) \ge 0$, then $J^+ = H^+$ and $J^- = H^-$ for any $d_I > 0$;

(i_2) if $\alpha_1(\beta_1 - \gamma_1) + \sum_{k=3}^{n} \alpha_k(\beta_k - \gamma_k) < 0$, then there exists a unique d_I^{**} such that $h_1(\tilde{d}_I) = 0$, and $J^+ = H^+$ and $J^- = H^-$ for $0 < d_I < d_I^{**}$, and $J^+ = \{1\}$ and $J^- = \{2, \dots, n\}$, or $J^+ = \{2\}$ and $J^- = \{1, 3, \dots, n\}$ for $d_I > d_I^{**}$.

(ii) If $\sum_{k=1}^{n} \alpha_k(\beta_k - \gamma_k) < 0$, then $\alpha_1(\beta_1 - \gamma_1) + \sum_{k=3}^{n} \alpha_k(\beta_k - \gamma_k) < 0$, and there exists $d_I^* > 0$ such that $R_0 > 1$ for $d_I < d_I^*$ and $R_0 < 1$ for $d_I > d_I^*$. Moreover,

(ii_1) if $d_I^{**} \ge d_I^*$, where d_I^{**} is defined as in (i_2), then $J^+ = H^+$ and $J^- = H^-$ for $d_I < d_I^*$;

(ii_2) if $d_I^{**} < d_I^*$, then $J^+ = H^+$ and $J^- = H^-$ for $d_I < d_I^{**}$; and $J^+ = \{1\}$ and $J^- = \{2, \dots, n\}$, or $J^+ = \{2\}$ and $J^- = \{1, 3, \dots, n\}$ for $d_I \in (d_I^{**}, d_I^*)$.

Remark 4.2 From Proposition 4.1, we see that case (i_1) could hold when $\beta_1 - \gamma_1$ is sufficiently large; case (i_2) could hold when $\beta_1 - \gamma_1$ is sufficiently small but $\beta_2 - \gamma_2$ is sufficiently large; and if both $\beta_1 - \gamma_1$ and $\beta_2 - \gamma_2$ are sufficiently small, case (ii_1) or (ii_2) could occur.

The asymptotic profile of the endemic equilibrium as $d_I \to 0$ can also be obtained from Theorem 3.16. To further illustrate our results, we compare some numerical examples of star graph with $n = 4$. Let

$$L_A = \begin{pmatrix} -6 & 1 & 1 & 1 \\ 1 & -1 & 0 & 0 \\ 2 & 0 & -1 & 0 \\ 3 & 0 & 0 & -1 \end{pmatrix}, \ L_B = \begin{pmatrix} -3 & 1 & 1 & 1 \\ 1 & -1 & 0 & 0 \\ 1 & 0 & -1 & 0 \\ 1 & 0 & 0 & -1 \end{pmatrix}, \ L_C = \begin{pmatrix} -3 & 1 & 2 & 3 \\ 1 & -1 & 0 & 0 \\ 1 & 0 & -2 & 0 \\ 1 & 0 & 0 & -3 \end{pmatrix}.$$

We choose $\beta_1 = 3, \beta_2 = 4, \beta_3 = 1, \beta_4 = 1, \gamma_1 = 1, \gamma_2 = 1, \gamma_3 = 2, \gamma_4 = 3$ such that $H^+ = \{1, 2\}$ and $H^- = \{3, 4\}$, and $N = 100$. The principal eigenvectors of L_p ($p = A, B, C$) are $\alpha_A = (1/7, 1/7, 2/7, 3/7)$, $\alpha_B = (1/4, 1/4, 1/4, 1/4)$, and $\alpha_C = (6/17, 6/17, 3/17, 2/17)$ respectively. For the Laplacian matrices L_p defined above, Theorem 2.6 states that R_0 is strictly deceasing in d_I with

$$\lim_{d_I \to 0} R_0 = \max\left\{\frac{\beta_j}{\gamma_j} : j \in \Omega\right\} = 4 \quad \text{and} \quad \lim_{d_I \to \infty} R_0 = \frac{\sum_{j \in \Omega} \alpha_j \beta_j}{\sum_{j \in \Omega} \alpha_j \gamma_j} = R_{0p},$$

where R_{0p} ($p = A, B, C$) are $R_{0A} = 4/5$, $R_{0B} = 9/7$ and $R_{0C} = 47/24$ respectively. In Fig. 2, we plot R_0 as a function of d_I for the three cases, which confirms Theorem 2.6. Here, only for L_A, $R_0 - 1$ changes sign at $d_I^* \approx 8.478$.

The sign of the function $h_j(d_I)$ at the high-risk patches defined in (3.18) plays an important role in the asymptotic profile of the endemic equilibrium. For the above example, the graphs of function $h_j(d_I)$ for $j = 1, 2$ are plotted in Fig. 2 for L_A, L_B and L_C. By Proposition 3.10, $h_j(d_I)$ is constant or strictly decreasing in d_I. For L_A, from (4.2), we have

$$\lim_{d_I \to 0} h_1(d_I) = \frac{2}{7} \quad \text{and} \quad \lim_{d_I \to \infty} h_1(d_I) = -\frac{6}{7},$$

$h_2(d_I) = 3/7$ for all $d_I > 0$, and $h_1(0.549) \approx 0$. Since $\sum_{j \in \Omega} \alpha_j(\beta_j - \gamma_j) = -3/7 < 0$ and Proposition 4.1(ii), the profile of the endemic equilibrium changes at $d_I^{**} \approx 0.549$. Similarly for L_B, $d_I^{**} \approx 3.21$ but for L_C, $h_1(d_I) > 0$ for all $d_I > 0$.

In Fig. 3, we plot the S component of the endemic equilibrium with $L = L_A$ as $d_S \to 0$, where $S_j^*(d_I) = \lim_{d_S \to 0} S_j(d_S, d_I)$ for $j = \{1, 2, 3, 4\}$. We see that a transition occurs at $d = d_I^{**} \approx 0.549$: $J^+ = \{1, 2\}$ and $J^- = \{3, 4\}$ for $d_I \in (0, d_I^{**})$, and $J^+ = \{2\}$ and $J^- = \{1, 3, 4\}$ for $d_I \in (d_I^{**}, d_I^*)$. A similar transition also occurs for $L = L_B$ with $d_I^{**} \approx 3.21$, but $J^+ = \{1, 2\}$ for all $d_I > 0$ for L_C.

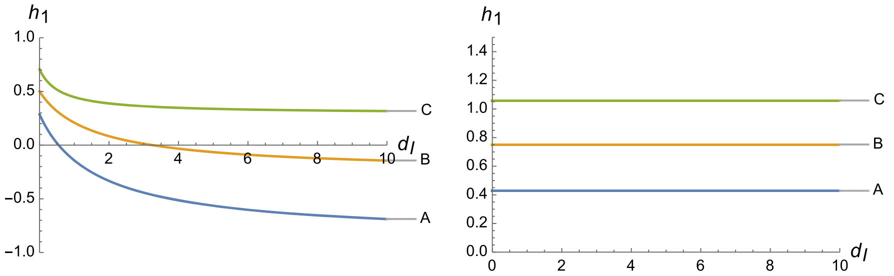


Fig. 2 The graph of $h(d_I)$ for $L = L_A, L_B, L_C$ and $\beta_1 = 3, \beta_2 = 4, \beta_3 = 1, \beta_4 = 1, \gamma_1 = 1, \gamma_2 = 1, \gamma_3 = 2, \gamma_4 = 3$

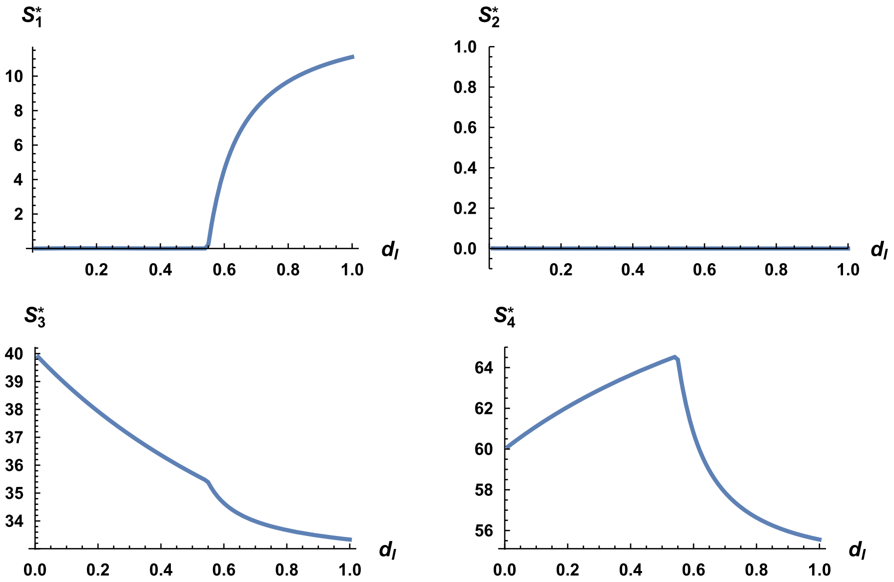
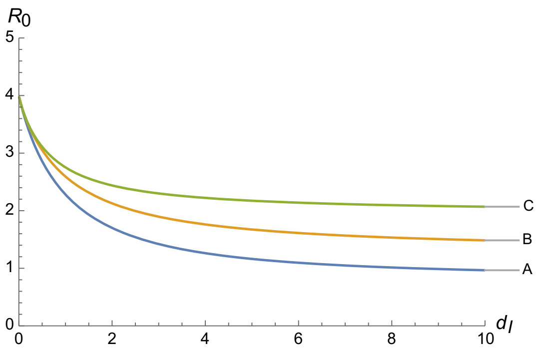


Fig. 3 The limit S_j^* (the S component of the endemic equilibrium as $d_S \to 0$) as a function of d_I for $L = L_A$ and $\beta_1 = 3, \beta_2 = 4, \beta_3 = 1, \beta_4 = 1, \gamma_1 = 1, \gamma_2 = 1, \gamma_3 = 2, \gamma_4 = 3$

Fig. 4 The basic reproduction number R_0 as a function of d_I for $L = L_A, L_B, L_C$ and $\beta_1 = 3, \beta_2 = 4, \beta_3 = 1, \beta_4 = 1, \gamma_1 = 1, \gamma_2 = 1, \gamma_3 = 2, \gamma_4 = 3$



The above numerical example verifies all theoretical results proved in previous sections. It also partially shows the effect of dispersal patterns between patches on the epidemic dynamics. Here L_B describes a symmetric dispersal between the hub and leafs in which outflux equals to influx, L_A depicts a pattern that the outflux $(1, 2, 3)$ from the hub is larger than the influx $(1, 1, 1)$, and L_C describes the opposite situation that the outflux $(1, 1, 1)$ from the hub is smaller than the influx $(1, 2, 3)$. From Fig. 4, we find that in addition to the declining of R_0 in d_I, it also holds that $R_0(L_C) > R_0(L_B) > R_0(L_A)$ for the same $d_I > 0$. This can be interpreted as that the disease transmission rate is higher when people from satellite cities (leafs) come to work in the city center (hub) during morning rush hours than the one when people return to their suburb home after work in afternoon/evening rush hours. Such situation has also been studied in Bjørnstad et al. (2002) for measles transmission but with a totally different approach. Detailed studies on these would involve non-autonomous differential equations, which could be a research project in the future.

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5 Appendix

Proof of Lemma 3.14: (i) Define

$$\boldsymbol{F}(d_I, \tilde{\boldsymbol{I}}) = \begin{pmatrix} d_I \sum_{k\in\Omega} L_{1k}\tilde{I}_k + \tilde{I}_1 \left(\beta_1 - \gamma_1 - \dfrac{\beta_1 \tilde{I}_1}{d(\alpha_1 - \tilde{I}_1) + \tilde{I}_1}\right) \\ d_I \sum_{k\in\Omega} L_{2k}\tilde{I}_k + \tilde{I}_2 \left(\beta_2 - \gamma_2 - \dfrac{\beta_2 \tilde{I}_2}{d(\alpha_2 - \tilde{I}_2) + \tilde{I}_2}\right) \\ \vdots \\ d_I \sum_{k\in\Omega} L_{nk}\tilde{I}_k + \tilde{I}_n \left(\beta_n - \gamma_n - \dfrac{\beta_n \tilde{I}_n}{d(\alpha_n - \tilde{I}_n) + \tilde{I}_n}\right) \end{pmatrix}, \tag{5.1}$$

and denote $\check{\boldsymbol{I}}^{(1)} = \left(\check{I}_1^{(1)}, \ldots, \check{I}_n^{(1)}\right)^T$, where

$$\check{I}_j^{(1)} = \frac{d\alpha_j \left(\beta_j - \gamma_j\right)_+}{d(\beta_j - \gamma_j)_+ + \gamma_j} \quad \text{for} \quad j \in \Omega.$$

Clearly, $\boldsymbol{F}(0, \check{\boldsymbol{I}}^{(1)}) = \boldsymbol{0}$, and $D_{\tilde{\boldsymbol{I}}}\boldsymbol{F}(0, \check{\boldsymbol{I}}^{(1)}) = diag(\delta_j^{(1)})$, where

$$\delta_j^{(1)} = \begin{cases} \beta_j - \gamma_j < 0, & j \in H^-, \\ -\dfrac{d\alpha_j \beta_j \check{I}_j^{(1)}}{\left[d\left(\alpha_j - \check{I}_j^{(1)}\right) + \check{I}_j^{(1)}\right]^2} < 0, & j \in H^+. \end{cases} \tag{5.2}$$

Therefore, $D_{\tilde{\boldsymbol{I}}}\boldsymbol{F}(0, \check{\boldsymbol{I}}^{(1)})$ is invertible. It follows from the implicit function theorem that there exist $d_1 > 0$ and a continuously differentiable mapping

$$d_I \in [0, d_1] \mapsto \tilde{\boldsymbol{I}}(d_I) = (\tilde{I}_1(d_I), \ldots, \tilde{I}_n(d_I))^T \in \mathbb{R}^n$$

such that $\boldsymbol{F}(d_I, \tilde{\boldsymbol{I}}(d_I)) = \boldsymbol{0}$ and $\tilde{\boldsymbol{I}}(0) = \check{\boldsymbol{I}}^{(1)}$.

Taking the derivative of $\boldsymbol{F}(d_I, \tilde{\boldsymbol{I}}(d_I)) = \boldsymbol{0}$ with respect to d_I at $d_I = 0$, we have

$$-diag(\delta_j^{(1)}) \begin{pmatrix} \tilde{I}_1'(0) \\ \tilde{I}_2'(0) \\ \vdots \\ \tilde{I}_n'(0) \end{pmatrix} = L \begin{pmatrix} \tilde{I}_1(0) \\ \tilde{I}_2(0) \\ \vdots \\ \tilde{I}_n(0) \end{pmatrix}.$$

Then

$$\begin{pmatrix} \tilde{I}_1'(0) \\ \tilde{I}_2'(0) \\ \vdots \\ \tilde{I}_n'(0) \end{pmatrix} = -diag(1/\delta_j^{(1)}) L \begin{pmatrix} \tilde{I}_1(0) \\ \tilde{I}_2(0) \\ \vdots \\ \tilde{I}_n(0) \end{pmatrix}.$$

Since $\tilde{\boldsymbol{I}}(0) = \check{\boldsymbol{I}}^{(1)} > \boldsymbol{0}$, we see that $\tilde{I}_j'(0) \geq 0$ for $j \in H^-$, which implies that $\tilde{\boldsymbol{I}} = \check{\boldsymbol{I}}$, and consequently, (3.29) holds.

(ii) Let $\eta = 1/d$. Define

$$\boldsymbol{H}(d_I, \eta, \tilde{\boldsymbol{I}}) = \begin{pmatrix} \left[d_I \sum_{k\in\Omega} L_{1k}\tilde{I}_k + (\beta_1 - \gamma_1)\tilde{I}_1\right]\left[\alpha_1 - \tilde{I}_1 + \eta\tilde{I}_1\right] - \eta\beta_1\tilde{I}_1^2 \\ \left[d_I \sum_{k\in\Omega} L_{2k}\tilde{I}_k + (\beta_2 - \gamma_2)\tilde{I}_2\right]\left[\alpha_2 - \tilde{I}_2 + \eta\tilde{I}_2\right] - \eta\beta_2\tilde{I}_2^2 \\ \vdots \\ \left[d_I \sum_{k\in\Omega} L_{nk}\tilde{I}_k + (\beta_n - \gamma_n)\tilde{I}_n\right]\left[\alpha_n - \tilde{I}_n + \eta\tilde{I}_n\right] - \eta\beta_n\tilde{I}_n^2 \end{pmatrix},$$

and denote $\check{\boldsymbol{I}}^{(2)} = (\check{I}_1^{(2)}, \ldots, \check{I}_n^{(2)})^T$, where

$$\check{I}_j^{(2)} = \begin{cases} 0, & j \in H^-, \\ \alpha_j, & j \in H^+. \end{cases}$$

Clearly, $\boldsymbol{H}(0, 0, \check{\boldsymbol{I}}^{(2)}) = \boldsymbol{0}$, and $D_{\tilde{\boldsymbol{I}}}\boldsymbol{H}(0, 0, \check{\boldsymbol{I}}^{(2)}) = diag(\delta_j^{(2)})$, where

$$\delta_j^{(2)} = \begin{cases} \alpha_j(\beta_j - \gamma_j), & j \in H^-, \\ -\alpha_j(\beta_j - \gamma_j), & j \in H^+. \end{cases} \tag{5.3}$$

Therefore, $D_{\tilde{\boldsymbol{I}}}\boldsymbol{H}(0,0,\check{\boldsymbol{I}}^{(2)})$ is invertible. It follows from the implicit function theorem that there exist $d_2, \eta_2 > 0$ and a continuously differentiable mapping

$$(d_I,\eta)\in[0,d_2]\times[0,\eta_2]\mapsto \tilde{\boldsymbol{I}}(d_I,\eta)=(\tilde{I}_1(d_I,\eta),\ldots,\tilde{I}_n(d_I,\eta))^T\in\mathbb{R}^n$$

such that $\boldsymbol{H}(d_I,\eta,\tilde{\boldsymbol{I}}(d_I,\eta))=\boldsymbol{0}$ and $\tilde{\boldsymbol{I}}(0,0)=\check{\boldsymbol{I}}^{(2)}$.

Taking the derivative of $\boldsymbol{H}(d_I,\eta,\tilde{\boldsymbol{I}}(d_I,\eta))=\boldsymbol{0}$ with respect to (d_I,η) at $(d_I,\eta)=(0,0)$, we have

$$\begin{cases}\dfrac{\partial \tilde{I}_j}{\partial d_I}(0,0)=\dfrac{\sum_{k\in\Omega}L_{jk}\check{I}_k^{(2)}}{\gamma_j-\beta_j}>0, & j=H^-,\\ \dfrac{\partial \tilde{I}_j}{\partial d_I}(0,0)=0, & j=H^+.\end{cases}$$

Similarly, we have

$$\begin{cases}\dfrac{\partial \tilde{I}_j}{\partial \eta}(0,0)=0, & j=H^-,\\ \dfrac{\partial \tilde{I}_j}{\partial \eta}(0,0)=-\dfrac{\gamma_j\alpha_j^2}{(\beta_j-\gamma_j)\alpha_j}<0, & j=H^+.\end{cases}$$

Therefore, $\tilde{\boldsymbol{I}}=\check{\boldsymbol{I}}$. This completes the proof of (ii). □

Proof of Lemma 3.15: We only need to consider the existence and uniqueness of the solution for the case $d=0$, and the other cases can be proved similar to Lemma 3.2. Consider the following problem

$$\frac{d\bar{U}_j(t)}{dt}=d_I\sum_{k\in\Omega}L_{jk}\bar{U}_k+\bar{U}_j\left(\beta_j-\gamma_j-\frac{\beta_j\bar{U}_j}{\alpha_j+\bar{U}_j}\right),\quad j\in\Omega. \tag{5.4}$$

Let $\boldsymbol{g}(\bar{\boldsymbol{U}})=\left(g_1(\bar{\boldsymbol{U}}),\ldots,g_n(\bar{\boldsymbol{U}})\right)^T$ be the vector field corresponding to the right hand side of (5.4), and let Ψ_t be the semiflow induced by (5.4). As in the proof of Lemma 3.2, $\mathbb{R}_+^n$ is positive invariant with respect to (5.4), Ψ_t is strongly positive and monotone, and $\boldsymbol{g}(\bar{\boldsymbol{U}})$ is strongly sublinear on $\mathbb{R}_+^n$. Since $R_0>1$, we have $s\left(d_IL+diag(\beta_j-\gamma_j)\right)>0$. Therefore, by Zhao and Jing (1996, Corollary 3.2), we have either

(i) for any initial value $\bar{\boldsymbol{U}}(0)\in\mathbb{R}_+^n\backslash\{\boldsymbol{0}\}$, the corresponding solution $\bar{\boldsymbol{U}}(t)$ of (5.4) satisfies $\lim_{t\to\infty}|\bar{\boldsymbol{U}}(t)|=\infty$,

or alternatively,

(ii) there exists a unique $\check{\boldsymbol{U}}\gg 0$ such that every solution of (5.4) in $\mathbb{R}_+^n\backslash\{\boldsymbol{0}\}$ converges to $\check{\boldsymbol{U}}$.

A direct computation implies that, for sufficiently large M,

$$\mathcal{V}=\left\{\boldsymbol{U}=(U_1,\ldots,U_n)^T\in\mathbb{R}^n: 0\le U_j\le M\alpha_j,\ j\in\Omega\right\}$$

is positive invariant with respect to (5.4). Therefore, (i) does not hold and (ii) must hold. The monotonicity of $\check{U}$ and (3.31) can be proved similarly as in the proof of Lemmas 3.2 and 3.14, respectively. This completes the proof. □

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