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The effect of population dispersal on the spread of a disease ☆

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Abstract

The effect of population dispersal among n patches on the spread of a disease is investigated. Population dispersal does not destroy the uniqueness of a disease free equilibrium and its attractivity when the basic reproduction number of a disease $R_0 < 1$. When $R_0 > 1$, the uniqueness and global attractivity of the endemic equilibrium can be obtained if dispersal rates of susceptible individuals and infective individuals are the same or very close in each patch. However, numerical calculations show that population dispersal may result in multiple endemic equilibria and even multi-stable equilibria among patches, and also may result in the extinction of a disease, even though it cannot be eradicated in each isolated patch, provided the basic reproduction numbers of isolated patches are not very large.

Keywords: Epidemic model; Population dispersal; Threshold; Multiple endemic equilibria

1. Introduction

Population dispersal, as a common phenomenon in nature and in human society, is a major mechanism for the generation and support of species diversity, which can affect

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population's life in many other aspects as well, such as the spread of a disease in a population. In common life, a disease can be easily transmitted from one place to other places when population frequently travel from one place to another. Moreover, population dispersal can sometimes help eradicate a disease or intensify a disease spread or even cause a disease which can die out if patches are isolated to be endemic [1,2,6,7,9,10,15–18]. In human history there were many incidences which were related to population dispersal [6,9]. Early in medieval times, plague was spread from Asia into Europe by the packages in many travelling ships which were infested by rats [1]. In 2003, SARS began in Guangdong province of China, but at last broke out in almost all parts of China and some other cities in the world, just because of people's dispersal [17]. Thus investigating the effect of population dispersal on the spread of a disease is very important for effectively controlling and eradicating the disease.

Hethcote [7] proposed an epidemic model with population dispersal between two patches. Brauer and van den Driessche [2] proposed a model with immigration of infective individuals. Ruxton [10] proposed a model with density-dependent migration.

In paper [18], Wang and Zhao proposed an n-patch model with population dispersal. They considered disease transmission of an *SIS* type for populations in n patches which are distinguished by subscripts i, $i = 1, \ldots, n$, and assumed that population in each patch is divided into two classes: susceptible individuals and infective individuals, the numbers of which at time t are denoted by $S_i(t)$ and $I_i(t)$, respectively; the total number of the ith patch is $N_i(t) = S_i(t) + I_i(t)$; susceptible individuals become infective after contacting with infective individuals and infective individuals return to susceptible class when they are recovered. The dynamics of individuals is governed by the following model:

$$\begin{aligned} S_i' &= B_i(N_i)N_i - \mu_i S_i - \beta_i S_i I_i + \gamma_i I_i + \sum_{j=1}^{n} a_{ij} S_j, \quad 1 \leqslant i \leqslant n, \\ I_i' &= \beta_i S_i I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} b_{ij} I_j, \quad 1 \leqslant i \leqslant n, \end{aligned} \tag{1.1}$$

where

$B_i(N_i)$ is the birth function of population in patch i;
μ_i is the death rate of the population in the ith patch;
β_i is the contact rate of the population in the ith patch;
γ_i is the recovery rate of infective individuals in the ith patch;
$a_{ij} \geqslant 0$, $j \neq i$, is the immigration rate of susceptible individuals from the jth patch to the ith patch;
$b_{ij} \geqslant 0$, $j \neq i$, is the immigration rate of infective individuals from the jth patch to the ith patch;
$a_{ii} \leqslant 0$ is the emigration rate of susceptible individuals in the ith patch;
$b_{ii} \leqslant 0$ is the emigration rate of infective individuals in the ith patch.

Death rates and birth rates of the individuals during the dispersal process are neglected. And there also holds the assumption that the n patches cannot be separated into two groups such that there is no immigration of susceptible and infective individuals from

one group to the other group, which indicates that two $n \times n$ matrix (a_{ij}) and (b_{ij}) are irreducible.

For (1.1), paper [18] has established a threshold above which a disease is persistent and below which the disease free equilibrium is globally attractive when both susceptible and infective individuals in each patch have the same dispersal rate. By means of the threshold, for $n = 2$, two examples by numerical calculations showed that population dispersal can intensify or reduce the spread of a disease.

In this paper, we continue to investigate the effect of population dispersal among n patches on transmission and control of the disease of model (1.1), by means of R_0 which was established in [18]. By comparing isolated environment (patches are isolated) with connected environment (population dispersal exists among n patches), we find that population dispersal does not destroy the uniqueness of the disease free equilibrium and its attractivity when $R_0 < 1$, and the uniqueness and global attractivity of the endemic equilibrium in isolated environment can be preserved in connected environment when $R_0 > 1$ if dispersal rates of susceptible individuals and infective ones are the same in each patch. If only two patches are considered, the endemic equilibrium is even globally asymptotically stable when $R_0 > 1$ if these two rates in either patch are the same and is globally attractive if they are very close to each other. For fixed birth functions in two patches, by numerical calculations, we find that population dispersal may result in co-existence of multiple endemic equilibria or even multi-stable endemic equilibria if $R_0 > 1$. Numerical calculations also show that, if a disease can be extinct in two patches when they are isolated, it can be still extinct within two patches when dispersal rates of individuals are in some range, otherwise it will be endemic. A simulation shows a very interesting phenomenon that population dispersal may help eradicate a disease which can be endemic in either patch when they are isolated, provided the basic reproduction numbers of isolated patches are not very large and the contact rates in two patches are not very large too. Some simulations also show that, if a disease can be eradicated in either patch in isolated environment, reducing the ratios of dispersal rates of infective individuals to those of susceptible ones may cause the range of dispersal rates of susceptible individuals, which implies that the disease will be endemic, to be larger, but if the disease is endemic in two isolated patches, this may reduce the total number of infective individuals within two patches.

Following [3], we assume that $B_i(N_i)$ satisfies the following three basic assumptions for $N_i \in (0, \infty)$:

(A1) $B_i(N_i) > 0,\ i = 1, 2;$
(A2) $B_i(N_i)$ is continuously differentiable with $B_i'(N_i) < 0,\ i = 1, 2;$
(A3) $\mu_i > B_i(\infty),\ i = 1, 2.$

We also consider the following three types of birth functions $B_i(N_i)$ which were presented in [3] and can be found in the biological literature:

(B1) $B_i(N_i) = \frac{p_i}{N_i^n + q_i}$, with $p_i > 0$, $q_i > 0$, $n > 0$, and $\frac{p_i}{q_i} > \mu_i$;
(B2) $B_i(N_i) = p_i e^{-q_i N_i}$, with $p_i > 0$, $q_i > 0$, and $p_i > \mu_i$;
(B3) $B_i(N_i) = \frac{A_i}{N_i} + C_i$, with $A_i > 0$, $C_i > 0$, $\mu_i > c_i$.

Functions (B1) with $n = 1$ and (B2) are used in fisheries and known as the Beverton–Holt function and the Ricker function, respectively. (B3) represents a constant immigration rate A_i together with a linear birth term $C_i N_i$. Mackey and Glass [8] considered a model with birth function as (B1). Birth function as (B2) was used by Velasco-Hernandez [14] for vector population equation in a model for Chagas disease. In this paper, we mainly use birth functions (B1) with $n = 2$.

This paper is organized as follows: in Section 2, we introduce some preliminaries established in [18]. In Section 3, we compare the existence and stability of equilibria including disease free equilibrium and endemic equilibria in isolated environment with those in connected environment. In Section 4, by simulations, we analyze the effect of population dispersal on extinction and persistence of a disease.

2. Preliminaries

Let $s(M)$ denote the stability modulus of an $n \times n$ matrix M, which is defined by

$$s(M) = \max\{\operatorname{Re}\lambda\colon\ \lambda \text{ is an eigenvalue of M}\}.$$

Suppose (1.1) admits a disease free equilibrium $E_0 = (S_1^0, \ldots, S_n^0, 0, \ldots, 0)$. Set

$$M_1 = \begin{pmatrix} \beta_1 S_1^0 - \mu_1 + b_{11} - \gamma_1 & b_{12} & \cdots & b_{1n} \\ b_{21} & \beta_2 S_2^0 - \mu_2 + b_{22} - \gamma_2 & \cdots & b_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ b_{n1} & b_{n2} & \cdots & \beta_n S_n^0 - \mu_n + b_{nn} - \gamma_n \end{pmatrix}.$$

Clearly M_1 is irreducible and has nonnegative off-diagonal elements. Then $s(M_1)$ is a simple eigenvalue of M_1 with a positive eigenvector. We adopt the definition of R_0 in [18, Section 2]. Define $\mathcal{F} = \operatorname{diag}(\beta_1 S_1^0, \beta_2 S_2^0, \ldots, \beta_n S_n^0)$ and

$$\mathcal{V} = -\begin{bmatrix} -\mu_1 + b_{11} - \gamma_1 & b_{12} & \cdots & b_{1n} \\ b_{21} & -\mu_2 + b_{22} - \gamma_2 & \cdots & b_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ b_{n1} & b_{n2} & \cdots & -\mu_n + b_{nn} - \gamma_n \end{bmatrix}.$$

Set $R_0 = \rho(\mathcal{F}\mathcal{V}^{-1})$ [4,13], where ρ represents the spectral radius of a matrix. R_0 is called the basic reproduction number for (1.1). It is epidemiologically defined as the average number of secondary infections produced when one infected individual is introduced into a host population where everyone is susceptible. It is a threshold to determine the persistence and extinction of a disease for (1.1). For (1.1), paper [18] has proved that a disease will be persistent when $R_0 > 1$ and the disease free equilibrium is locally attractive when $R_0 < 1$ and globally attractive when $R_0 < 1$ if both susceptible and infective individuals have the same dispersal rate in each patch. For completeness we list results in [18] as follows:

Set $S(t) = (S_1(t), \ldots, S_n(t))$, $I(t) = (I_1(t), \ldots, I_n(t))$, $t \geqslant 0$, and

$$M_0 = \begin{bmatrix} B_1(0) - \mu_1 + a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & B_2(0) - \mu_2 + a_{22} & \cdots & a_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ a_{n1} & a_{n2} & \cdots & B_n(0) - \mu_n + a_{nn} \end{bmatrix}.$$

Assume

(A4) $s(M_0) > 0$.

Let $S^0 = (S_1^0, \ldots, S_n^0)$ and G be the positively invariant set of (1.1), the existence of which has been verified in [18].

Lemma 2.1. *There hold two equivalences*: $R_0 > 1 \Leftrightarrow s(M_1) > 0$ *and* $R_0 < 1 \Leftrightarrow s(M_1) < 0$.

Theorem 2.1. *Let* (A1)–(A4) *hold and* $R_0 < 1$. *If* $a_{ij} = b_{ij}$ *for* $i = 1, \ldots, n$, $j = 1, \ldots, n$, *then* E_0 *is globally attractive for* $(S(0), I(0)) \in R_+^n \setminus \{0\} \times R_+^n$.

Theorem 2.2. *Let* (A1)–(A4) *hold and* $R_0 < 1$. *Then there exists* $\delta > 0$ *such that for every* $(S(0), I(0)) \in G$ *with* $I_i(0) < \delta$, $i = 1, 2, \ldots, n$, *the solution* $(S(t), I(t))$ *of* (1.1) *satisfies*

$$\lim_{t\to\infty} \big(S(t), I(t)\big) = \big(S^0, \mathbf{0}\big).$$

Theorem 2.3. *Let* (A1)–(A4) *hold and* $R_0 > 1$. *Then* (1.1) *admits at least one positive equilibrium, and there is a positive constant* ε *such that every solution* $(S(t), I(t))$ *of* (1.1) *with* $(S(0), I(0)) \in R_+^n \times \operatorname{int}(R_+^n)$ *satisfies* $\liminf_{t\to\infty} I_i(t) \geqslant \varepsilon$, $i = 1, 2, \ldots, n$.

3. The effect on existence and stability of equilibria

In this section, we analyze the existence and stability of equilibria including disease free equilibrium and endemic equilibria, both in isolated environment (n patches are isolated) and in connected environment (population dispersal exists among n patches). From such comparison we can see the effect of population dispersal on the existence and stability of equilibria within n patches.

3.1. Equilibria in isolated environment

When n patches are isolated, (1.1) can be divided into n isolated systems and the system in the ith ($1 \leqslant i \leqslant n$) patch is

$$\begin{aligned} S_i' &= B_i(N_i)N_i - \mu_i S_i - \beta_i S_i I_i + \gamma_i I_i, \\ I_i' &= \beta_i S_i I_i - (\mu_i + \gamma_i) I_i. \end{aligned} \tag{3.1}$$

Let $(S_i^0, 0)$ be the disease free equilibrium of (3.1). Then S_i^0 is the positive solution of $B_i(S_i) - \mu_i = 0$. By (A1)–(A3), (3.1) admits a unique disease free equilibrium if $B_i(0) > \mu_i$ and no disease free equilibrium if $B_i(0) < \mu_i$. Moreover, $(S_i^0, 0)$ is locally asymptotically stable if $S_i^0 < (\mu_i + \gamma_i)/\beta_i$, which by (A2) is equivalent to $B_i((\mu_i + \gamma_i)/\beta_i) < \mu_i$, and unstable if $S_i^0 > (\mu_i + \gamma_i)/\beta_i$.

Let (S_i^*, I_i^*) be the endemic equilibrium of (3.1). Then $S_i^* = (\mu_i + \gamma_i)/\beta_i$, and I_i^* satisfies $B_i((\mu_i + \gamma_i)/\beta_i + I_i^*) = \mu_i$. Thus if $B_i((\mu_i + \gamma_i)/\beta_i) > \mu_i$, (3.1) admits a unique

endemic equilibrium, while if $B_i((\mu_i+\gamma_i)/\beta_i) < \mu_i$, there is no endemic equilibrium of (3.1).

Let (f_1^i, f_2^i) be the vector field of (3.1). For Dulac function $D = 1/S_i I_i$,

$$\frac{\partial(Df_1^i)}{\partial S_i} + \frac{\partial(Df_2^i)}{\partial I_i} = -\frac{r_i}{S_i^2} + \frac{B_i'(N_i)}{I_i} - \frac{B_i(N_i)}{S_i^2} + \frac{B_i'(N_i)}{S_i} < 0.$$

Thus (3.1) does not have a limit cycle. It is not difficult to see that the forward orbits of (3.1) are bounded, by Poincaré–Bendixson theorem, under assumptions of (A1)–(A3), if $B_i(0) > \mu_i$, (3.1) admits a disease free equilibrium which is globally asymptotically stable when $B_i((\mu_i+\gamma_i)/\beta_i) < \mu_i$, and when $B_i((\mu_i+\gamma_i)/\beta_i) > \mu_i$, (3.1) admits a unique endemic equilibrium which is globally asymptotically stable.

In fact, we can define a reproduction number R_{0i} for (3.1). For example, if birth functions are chosen as (B1), let $R_{0i} = \beta_i\sqrt{p_i\mu_i - \mu_i^2 q_i}/\mu_i(\mu_i+\gamma_i)$, $i = 1, \ldots, n$. Then when $R_{0i} < 1$, the disease free equilibrium is globally asymptotically stable and when $R_{0i} > 1$ the unique endemic equilibrium exists and is globally asymptotically stable.

In a word, when patches are isolated, in each patch there is at most one disease free equilibrium and one endemic equilibrium, and one of them is globally asymptotically stable.

3.2. Equilibria in connected environment

(1) *Disease free equilibrium*

It has been proved in [18, Section 2] that under the assumptions of (A1)–(A4), there is a unique disease free equilibrium $E_0 = (S_1^0, \ldots, S_n^0, 0, \ldots, 0)$ of (1.1). Therefore, when population dispersal exists among n patches, the uniqueness of the disease free equilibrium is preserved. It is locally attractive when $R_0 < 1$ and globally attractive when both susceptible and infective individuals have the same dispersal rate in each patch and $R_0 < 1$ (see Theorems 2.1 and 2.2).

(2) *Endemic equilibria*

By Theorem 2.3, we have known that the disease is persistent among n patches when $s(M_1) > 0$, and endemic equilibria exist when $s(M_1) > 0$.

In the situation where susceptible individuals and infective individuals have the same dispersal rate in each patch, the uniqueness and global attractivity of the endemic equilibrium are preserved.

Theorem 3.1. *Let* (A1)–(A4) *hold and* $R_0 > 1$. *If* $a_{ij} = b_{ij}$ *for* $i = 1, \ldots, n$, $j = 1, \ldots, n$, *then* (1.1) *admits a unique endemic equilibrium* $E^* = (S_1^*, \ldots, S_n^*, I_1^*, \ldots, I_n^*)$ *which is globally attractive for* $(S(0), I(0)) \in (R_+^n \setminus \{\mathbf{0}\}) \times R_+^n$.

Proof. By (1.1), when $a_{ij} = b_{ij}$ we have

$$S_i' = B_i(N_i)N_i - \mu_i S_i - \beta_i S_i I_i + \gamma_i I_i + \sum_{j=1}^{n} a_{ij} S_j, \quad 1 \leqslant i \leqslant n,$$

$$I_i' = \beta_i S_i I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j, \quad 1 \leqslant i \leqslant n. \tag{3.2}$$

Since $N_i = S_i + I_i$, we obtain

$$N_i' = B_i(N_i) N_i - \mu_i N_i + \sum_{j=1}^{n} a_{ij} N_j, \quad 1 \leqslant i \leqslant n. \tag{3.3}$$

By the conclusion about disease free equilibrium in [18, Section 2], (3.3) admits a unique positive equilibrium $N^* = (N_1^*, \ldots, N_n^*)$ which is globally asymptotically stable for $N \in R_+^n \setminus \{\mathbf{0}\}$. Then the total number of population in each patch will tend to a constant when t tends to infinity. Then (3.2) is equivalent to the following system:

$$\begin{aligned} N_i' &= B_i(N_i) N_i - \mu_i N_i + \sum_{j=1}^{n} a_{ij} N_j, \quad 1 \leqslant i \leqslant n, \\ I_i' &= \beta_i (N_i - I_i) I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j, \quad 1 \leqslant i \leqslant n. \end{aligned} \tag{3.4}$$

Clearly, the first n equations are independent of the last n equations and $N_i(t)$, $i = 1, \ldots, n$, can be decided by the first n equations. Then (3.4) can be transformed into a nonautonomous system:

$$I_i' = \beta_i \big(N_i(t) - I_i\big) I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j, \quad 1 \leqslant i \leqslant n. \tag{3.5}$$

Since $N_i(t) \to N_i^*$, $i = 1, \ldots, n$, as $t \to +\infty$, (3.5) has the following limiting system:

$$I_i' = \beta_i \big(N_i^* - I_i\big) I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j, \quad 1 \leqslant i \leqslant n. \tag{3.6}$$

Now let us consider (3.6). Let $F : R_+^n \to R^n$ be defined by the right-hand side of (3.6), $F = (F_1, \ldots, F_n)$. Clearly F is continuously differentiable, $F(0) = 0$, $F_i(I) \geqslant 0$, $\forall I \in R_+^n$, $I_i = 0$, $i = 1, \ldots, n$. $\partial F_i / \partial I_j = a_{ij} \geqslant 0$, $i \neq j$, so F is cooperative. Clearly $DF(I)$ is irreducible for every $I \in R_+^n$. For every $\alpha \in (0, 1)$ and $I \in \operatorname{int}(R_+^n)$,

$$\begin{aligned} &\beta_i \big(N_i^* - \alpha I_i\big) \alpha I_i - (\mu_i + \gamma_i) \alpha I_i + \sum_{j=1}^{n} a_{ij} \alpha I_j \\ &\quad > \alpha \left(\beta_i \big(N_i^* - I_i\big) I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j \right), \quad i = 1, \ldots, n, \end{aligned}$$

i.e., $F(\alpha I) > \alpha F(I)$. Thus F is strongly sublinear on R_+^n. It then follows that for any $I(0) \in R_+^n$, the unique solution $I(t, I(0))$ of (3.6) satisfying $I(0, I(0)) = I(0)$ exists globally on $[0, \infty)$ and $I(t, I(0)) \geqslant 0$, $\forall t \geqslant 0$. We further claim that (3.6) admits a bounded positive solution. Set

$$M(Z) = \begin{pmatrix} \beta_1(N_1^* - Z) - \mu_1 + a_{11} - \gamma_1 & a_{12} & \cdots & a_{1n} \\ a_{21} & \beta_2(N_2^* - Z) - \mu_2 + a_{22} - \gamma_2 & \cdots & a_{2n} \\ \cdots & \cdots & \cdots & \cdots \\ a_{n1} & a_{n2} & \cdots & \beta_n(N_n^* - Z) - \mu_n + a_{nn} - \gamma_n \end{pmatrix}.$$

Clearly $M(Z)$ is irreducible and has nonnegative off-diagonal elements. Thus $s(M(Z))$ is a simple eigenvalue and has a positive eigenvector. We choose a sufficiently large real number $K > 0$ such that $0 < \beta_i(N_i^* - K) < \mu_i + \gamma_i$, $i = 1, \ldots, n$. Let $\bar{v} = (\bar{v}_1, \ldots, \bar{v}_n)$ be a positive eigenvector associated with $s(M(K))$. Then $v(t) = (v_1(t), \ldots, v_n(t)) = \bar{v}e^{s(M(K))t}$ is a positive solution of the linear ordinary differential system $v' = M(K)v$. Let

$$\sum(t) = \sum_{i=1}^{n} v_i(t) = e^{s(M(K))t} \sum_{i=1}^{n} \bar{v}_i.$$

Then

$$\sum{}'(t) = e^{s(M(K))t} s\big(M(K)\big) \sum_{i=1}^{n} \bar{v}_i.$$

Since $M\bar{v} = s(M(K))\bar{v}$, we may have $\sum'(t) \leqslant a \sum(t)$, where $a = \max\{\beta_i(N_i^* - K) - (\mu_i + \gamma_i),\ i = 1, \ldots, n\} < 0$. Thus $\lim_{t\to\infty} \sum(t) = 0$ and hence $s(M(K)) < 0$. Choose $l > 0$ large enough such that $l\bar{v}_i > K$, $i = 1, \ldots, n$. Set $x(t) \equiv l\bar{v}$. If we rewrite (3.6) as $I' = FI$, it is easy to see that

$$x'(t) \equiv 0 > s\big(M(K)\big)x(t) = M(K)x(t) > F\big(x(t)\big).$$

By the standard comparison theorem, it follows that

$$0 < I(t, l\bar{v}) \leqslant x(t) = l\bar{v}.$$

Consequently, $I(t, l\bar{v})$ is a bounded positive solution of (3.6).

Then if $s(M(0)) > 0$, by [20, Corollary 3.2], (3.6) admits a unique equilibrium $(I_1^*, \ldots, I_n^*)$ in $R_+^n \setminus \{0\}$, which is positive and globally asymptotically stable, and hence (3.2) admits a unique equilibrium $(N_1^* - I_1^*, \ldots, N_n^* - I_n^*, I_1^*, \ldots, I_n^*)$ in $R_+^{2n} \setminus \{0\}$, which is positive. Let $S_i^* = N_i^* - I_i^*$, $i = 1, \ldots, n$. Notice that $M(0) = M_1$. As a consequence, if $R_0 > 1$, (3.2) admits a unique positive equilibrium $(S_1^*, \ldots, S_n^*, I_1^*, \ldots, I_n^*)$ in $R_+^{2n} \setminus \{0\}$.

Let $\Phi(t): R_+^n \to R_+^n$ be the solution semi-flow of (3.4), that is, $\Phi(t)(N_0, I_0) = (N(t), I(t))$ is the solution of (3.4) with $(N(0), I(0)) = (N_0, I_0)$. It easily follows that $N_i(t) \geqslant 0$, $I_i(t) \geqslant 0$, $\forall t \geqslant 0$, when $N_i(0) \geqslant 0$ and $I_i(0) \geqslant 0$. Let $\omega = \omega(N_0, I_0)$ be the omega limit set of $\Phi(t)(N_0, I_0)$. Since $N_i(t) \to N_i^*$, $i = 1, \ldots, n$, as $t \to +\infty$, there holds $\omega = \{N^*\} \times \tilde{\omega}$, $\tilde{\omega} \in R_+^n$. Restricting $\Phi(t)$ on ω, we have $\Phi(t)|_\omega : \omega \to \omega$, that is, $\Phi(t)|_\omega(N_1^*, \ldots, N_n^*, I_1, \ldots, I_n) = (N_1^*, \ldots, N_n^*, \Phi_1(I_1, \ldots, I_n))$, where $\Phi_1(t)$ is the solution semi-flow of system (3.6). By [19, Lemma 1.2.1'], ω is an internal chain transitive set for $\Phi(t)$. Thus by the relationship between ω and $\tilde{\omega}$, it easily follows that $\tilde{\omega}$ is an internal chain transitive set for $\Phi_1(t)$. Since for (3.6) there are only two equilibria $\mathbf{0}$ and I^*, when $R_0 > 1$ and I^* is globally asymptotically stable for (3.6) in $R_+^n \setminus \{\mathbf{0}\}$, by the continuous time version of [19, Theorem 1.2.2], $\tilde{\omega}$ should be $\mathbf{0}$ or I^*.

We claim that $\tilde{\omega} \neq \{\mathbf{0}\}$. Assume that, by contradiction, $\tilde{\omega} = \{\mathbf{0}\}$. Then $\omega = (N_1^*, \ldots, N_n^*, 0, \ldots, 0)$, that is $N_i(t) \to N_i^*$, $I_i(t) \to 0$, $i = 1, \ldots, n$, as $t \to +\infty$. Since $s(M_1) > 0$, we can choose a small $\eta > 0$ such that $s(M_1 - \eta E) > 0$, where $E = \operatorname{diag}(1, \ldots, 1)$. It follows

that there exists a $\bar{t}$ such that $\beta_i(N_i(t) - I_i(t)) > \beta_i N_i^* - \eta$, $\forall t \geqslant \bar{t}$, $i = 1, \ldots, n$. Then $I(t) = (I_1(t), \ldots, I_n(t))$ satisfies

$$I_i'(t) > \big(\beta_i N_i^* - \eta\big) I_i - (\mu_i + \gamma_i) I_i + \sum_{j=1}^{n} a_{ij} I_j, \quad \forall t \geqslant \bar{t},\ i = 1, \ldots, n.$$

Let $\mathbf{v} = (v_1, \ldots, v_n)$ be a positive eigenvector of $M_1 - \eta E$ associated with $s(M_1 - \eta E)$. Choose an small number α such that $I(\bar{t}) \geqslant \alpha \mathbf{v}$. Then by the comparison theorem,

$$I(t) \geqslant \alpha e^{s(M_1 - \eta E)(t - \bar{t})}, \quad \forall t \geqslant \bar{t},$$

and hence $I_i(t) \to +\infty$, $i = 1, \ldots, n$, which contradicts $\tilde{\omega} = \{\mathbf{0}\}$.

Thus $\tilde{\omega} = I^*$ and $\omega = (N_1^*, \ldots, N_n^*, I_1^*, \ldots, I_n^*)$. Consequently the unique endemic equilibrium $(S_1^*, \ldots, S_n^*, I_1^*, \ldots, I_n^*)$ is globally attractive. □

For simplicity, we only consider two patches in the remaining part of this paper. When population dispersal exists only within two patches, the dynamics of those individuals is governed by the following model:

$$\begin{aligned}
S_1' &= B_1(N_1)N_1 - (\mu_1 + a_1)S_1 - \beta_1 S_1 I_1 + \gamma_1 I_1 + a_2 S_2,\\
S_2' &= B_2(N_2)N_2 - (\mu_2 + a_2)S_2 - \beta_2 S_2 I_2 + \gamma_2 I_2 + a_1 S_1,\\
I_1' &= \beta_1 S_1 I_1 - (\mu_1 + \gamma_1 + b_1)I_1 + b_2 I_2,\\
I_2' &= \beta_2 S_2 I_2 - (\mu_2 + \gamma_2 + b_2)I_2 + b_1 I_1,
\end{aligned} \tag{3.7}$$

where $a_i \geqslant 0$ is the emigration rate of susceptible individuals in the ith patch; $b_i \geqslant 0$ is the emigration rate of infective individuals in the ith patch. Here we suppose that population just disperse between two patches, population emigrating from one patch must immigrate into the other patch. For (3.7), we will analyze the stability of endemic equilibria.

Theorem 3.2. *Assume* (A1)–(A4) *and* $R_0 > 1$. *If* $a_i = b_i$, *then the unique endemic equilibrium of* (3.7) *is local asymptotically stable.*

Proof. It is equivalent to consider the following model:

$$\begin{aligned}
N_1' &= B_1(N_1)N_1 - (\mu_1 + a_1)N_1 + a_2 N_2,\\
N_2' &= B_2(N_2)N_2 - (\mu_2 + a_2)N_2 + a_1 N_1,\\
I_1' &= \beta_1(N_1 - I_1)I_1 - (\mu_1 + \gamma_1 + a_1)I_1 + a_2 I_2,\\
I_2' &= \beta_2(N_2 - I_2)I_2 - (\mu_2 + \gamma_2 + a_2)I_2 + a_1 I_1.
\end{aligned} \tag{3.8}$$

By Theorem 3.1, let $(N_1^*, N_2^*, I_1^*, I_2^*)$ be the unique endemic equilibrium of (3.8). The Jacobian matrix at this point is

$$A = \begin{pmatrix} a_{11} & a_2 & 0 & 0\\ a_1 & a_{22} & 0 & 0\\ \beta_1 I_1^* & 0 & a_{33} & a_2\\ 0 & \beta_2 I_2^* & a_1 & a_{44} \end{pmatrix},$$

where

$$a_{11} = B_1'(N_1^*)N_1^* + B_1(N_1^*) - (\mu_1 + a_1),$$
$$a_{22} = B_2'(N_2^*)N_2^* + B_2(N_2^*) - (\mu_2 + a_2),$$
$$a_{33} = \beta_1 N_1^* - 2\beta_1 I_1^* - (\mu_1 + \gamma_1 + a_1),$$
$$a_{44} = \beta_2 N_2^* - 2\beta_2 I_2^* - (\mu_2 + \gamma_2 + a_2).$$

The characteristic equation of A is: $|\lambda E - A| = \lambda^4 + e_1\lambda^3 + e_2\lambda^2 + e_3\lambda + e_4 = 0$ where

$$e_1 = -a_{11} - a_{22} - a_{33} - a_{44},$$
$$e_2 = a_{33}a_{44} + a_{11}a_{22} - 2a_1a_2 + a_{22}a_{33} + a_{22}a_{44} + a_{11}a_{44} + a_{11}a_{33},$$
$$e_3 = a_1a_2(a_{11} + a_{22} + a_{33} + a_{44}) - a_{11}a_{22}a_{33} - a_{11}a_{22}a_{44} - a_{22}a_{33}a_{44} - a_{11}a_{33}a_{44},$$
$$e_4 = (-a_1a_2 + a_{33}a_{44})(-a_1a_2 + a_{11}a_{22}).$$

By the definition of $(N_1^*, N_2^*, I_1^*, I_2^*)$, we have

$$a_{11} = B_1'(N_1^*)N_1^* - a_2N_2^*/N_1^*, \qquad a_{22} = B_2'(N_2^*)N_2^* - a_1N_1^*/N_2^*,$$
$$a_{33} = -a_2I_2^*/I_1^* - \beta_1 I_1^*, \qquad a_{44} = -a_1I_1^*/I_2^* - \beta_2 I_2^*. \tag{3.9}$$

Since $B_i(N_i)$ is a decreasing function of N_i, it is obvious that $a_{11} < 0$, $a_{22} < 0$, $a_{33} < 0$, $a_{44} < 0$, thus $e_1 > 0$. By (3.9), we have

$$e_4 = \frac{(a_2I_2^{*3}\beta_2 + a_1I_1^{*3}\beta_1 + I_2^{*2}\beta_2I_1^{*2}\beta_1)(B_1'(N_1^*)N_1^{*2}B_2'(N_2^*)N_2^{*2} - B_1'(N_1^*)N_1^{*3}a_1 - B_2'(N_2^*)N_2^{*3}a_2)}{I_1^*I_2^*N_1^*N_2^*},$$

thus $e_4 > 0$. Let

$$\Delta_2 = \begin{vmatrix} e_1 & 1 \\ e_3 & e_2 \end{vmatrix}, \qquad \Delta_3 = \begin{vmatrix} e_1 & 1 & 0 \\ e_3 & e_2 & e_1 \\ 0 & e_4 & e_3 \end{vmatrix}.$$

Similarly by (3.9) it is not difficult to see $\Delta_2 > 0$, $\Delta_3 > 0$. Then by Routh–Rouwitz criteria, all eigenvalues of A have negative real parts. Thus $(N_1^*, N_2^*, I_1^*, I_2^*)$ is locally asymptotically stable. □

Then by Theorems 3.1 and 3.2 it is easy to obtain the globally asymptotic stability of the unique endemic equilibrium when $n = 2$:

Theorem 3.3. *Assume* (A1)–(A4) *hold and* $R_0 > 1$. *If* $a_i = b_i$ *for* $i = 1, 2$, *then* (3.7) *admits a unique endemic equilibrium* $E^* = (S_1^*, S_2^*, I_1^*, I_2^*)$, *which is globally asymptotically stable.*

By using a similar method used in paper [21], we can also obtain the uniqueness of the endemic equilibrium and its global attractivity under a small perturbation of (3.8).

Define

$$X = \{(S_1, S_2, I_1, I_2)\colon\ S_i \geqslant 0,\ I_i \geqslant 0,\ i = 1, 2\},$$
$$X_0 = \{(S_1, S_2, I_1, I_2)\colon\ I_i > 0,\ i = 1, 2\},$$
$$\partial X_0 = X \setminus X_0.$$

Clearly, X_0 is an open set related to X and both X and X_0 are positively invariant for (3.7).

Theorem 3.4. *Assume* (A1)–(A4) *hold. Let* $\mathbf{a} = (a_1, a_2)$, $\mathbf{b} = (b_1, b_2)$. *For any fixed* $\mathbf{a}$ *with* $a_i \geqslant 0$, $i = 1, 2$, $\mathbf{b}_0 \equiv \mathbf{a}$. *If* $R_0 > 1$, *then there exists an* $\bar{\varepsilon} > 0$ *such that for any* $\mathbf{b}$ *with* $|\mathbf{b} - \mathbf{b}_0| \leqslant \bar{\varepsilon}$, *and* $b_i \neq 0$, $i = 1, 2$, (3.7) *admits a unique endemic equilibrium* $E^*(\mathbf{b}) = (S_1^*(\mathbf{b}), S_2^*(\mathbf{b}), I_1^*(\mathbf{b}), I_2^*(\mathbf{b}))$, *which is globally attractive for* $(S(0), I(0)) \in X_0$.

Proof. By the definition of R_0, there exists an $\varepsilon_0 > 0$ such that $R_0 > 1$ when $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$.

By [18, Lemma 2.2], solutions of (3.7) in R_+^4 are uniformly bounded and ultimately bounded uniformly for $\mathbf{a}, \mathbf{b} \in R_+^2$. It follows that there exists a bounded and closed set G in R_+^4, which is independent of $\mathbf{b}$ if $\mathbf{a}$ is fixed, such that for any $\phi \in X$ and $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$, there exists $t_0 = t_0(\phi, \mathbf{b}) > 0$ such that $\Phi(\mathbf{b}, t) \in G$ for all $t \geqslant t_0$. Then every forward orbit in R_+^4 of (3.7) eventually enters into G.

Let $\Phi(\mathbf{b}, t)$ be the solution semi-flow generated by (3.7).

It is easy to see that when $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$ and $t > 0$, $\Phi(\mathbf{b}, t) : X \to X$ is compact. It follows that for any fixed $t > 0$, $\Phi(., t)_\phi : \bigcup(\mathbf{b}_0, \varepsilon_0) \to X$ is continuous uniformly for ϕ in any bounded subset B of X, and hence $\overline{\bigcup_{\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0)} \Phi(\mathbf{b}, t)B}$ is compact in X (see, e.g., the Claim in the proof of Smith and Zhao [12, Theorem 3.1]). Since G is closed and $\forall \phi \in X$, $\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0)$, there exists $t_0 = t_0(\phi, \mathbf{b}) > 0$ such that $\Phi(\mathbf{b}, t)_\phi \in G$ for all $t \geqslant t_0$. Let $\omega_{\mathbf{b}}(\phi)$ be the omega limit set of $\phi \in X$ for $\Phi(\mathbf{b}, t) : X \to X$. Clearly $\omega_{\mathbf{b}}(\phi)$ is invariant for $\Phi(\mathbf{b}, t)$ and $\omega_{\mathbf{b}}(\phi) \in G$. Then

$$\overline{\bigcup_{\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0), \phi \in X} \omega_{\mathbf{b}}(\phi)} \subset \overline{\bigcup_{\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0), \phi \in X} \Phi(\mathbf{b}, t)\omega_{\mathbf{b}}(\phi)} \subset \overline{\bigcup_{\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0)} \Phi(\mathbf{b}, t)G}$$

and hence $\overline{\bigcup_{\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0), \phi \in X} \omega_{\mathbf{b}}(\phi)}$ is compact in X.

By Theorem 2.3, for each $\mathbf{b} \in \bigcup(\mathbf{b}_0, \varepsilon_0)$, $\Phi(\mathbf{b}, t)$ is uniformly persistent with respect to $(X_0, \partial X_0)$ and hence by Hale and Waltman [5, Theorem 3.2], there is a global attractor $A_{\mathbf{b}}^0$ for $\Phi(\mathbf{b}, t) : X_0 \to X_0$.

In the case that $b_i \neq 0$, $i = 1, 2$, and $R_0 > 1$, there are only two equilibria $W_1 = (0, 0)$ and $W_2 = (S_{\mathbf{b}}^0, 0)$ in ∂X_0. By the analysis of disease free equilibrium in [18], we have $\widetilde{A_{\mathbf{b}\partial}} = \bigcup_{\phi \in \partial X_0} \omega_{\mathbf{b}}(\phi) = \{W_1, W_2\}$, where $\omega_{\mathbf{b}}(\phi)$ is the omega limit set of ϕ for the solution semi-flow $\Phi(\mathbf{b}, t)$. Clearly $\widetilde{A_{\mathbf{b}\partial}}$ is the maximal compact set of $\Phi(\mathbf{b}, t)$ in ∂X_0 and W_1 and W_2 are disjoint compact and isolated invariant sets for semi-flow $\Phi(\mathbf{b}, t)|_{\partial X_0}$ and no subset of $\{W_1, W_2\}$ forms a cycle in ∂X_0. Thus $\{W_1, W_2\}$ is an acyclic covering of $\widetilde{A_{\mathbf{b}\partial}}$.

We claim there exists $\delta = \delta(\varepsilon_0) > 0$ such that for any $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$, there hold $R_0 > 1$ and $\limsup_{t \to +\infty} \|\Phi(\mathbf{b}, t)_\phi\| \geqslant \delta$, $\forall \phi \in X_0$.

Assume that, by contradiction, $\forall \delta > 0$, there exist $\phi \in X_0$, and $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$ such that $s(M_1) > 0$ and $\limsup_{t \to +\infty} \|\Phi(\mathbf{b}, t)_\phi\| < \delta$. Then we can choose an small $\eta > 0$ such that $s(M_1 - \eta M_2) > 0$, where $M_2 = \operatorname{diag}(\beta_1, \beta_2)$. By the form of (3.7), $\Phi \geqslant 0$ if $\phi \geqslant 0$. Then under the above assumption there hold $I_i(t) < \delta$, $i = 1, 2$, and

$$\begin{aligned} S_1'(t) &\geqslant B_1(S_1 + \delta)S_1 - (\mu_1 + \beta_1\delta)S_1 - a_1S_1 + a_2S_2, \\ S_2'(t) &\geqslant B_2(S_2 + \delta)S_2 - (\mu_2 + \beta_2\delta)S_2 - a_2S_2 + a_1S_1. \end{aligned} \tag{3.10}$$

By the analysis of disease free equilibrium in [18], we can restrict δ very small such that

$$\begin{aligned} S_1'(t) &= B_1(S_1+\delta)S_1 - (\mu_1+\beta_1\delta)S_1 - a_1S_1 + a_2S_2, \\ S_2'(t) &= B_2(S_2+\delta)S_2 - (\mu_2+\beta_2\delta)S_2 - a_2S_2 + a_1S_1 \end{aligned} \tag{3.11}$$

admits a unique positive equilibrium $S^*(\delta)$ which is globally asymptotically stable for $S^0 \in R_+^2 \setminus \{\mathbf{0}\}$. By the implicit function theorem, it follows that $S^*(\delta)$ is continuous in δ. Thus we can further restrict δ small enough such that $S^*(\delta) > S^* - \eta$. Then there exists a $T > 0$ such that $S(t) > S^* - \eta$, $\forall t \geqslant T$. As a consequence, for all $t \geqslant T$,

$$\begin{aligned} I_1' &\geqslant \beta_1\big(S_1^* - \eta\big)I_1 - (\mu_1+\gamma_1)I_1 - b_1I_1 + b_2I_2, \\ I_2' &\geqslant \beta_2\big(S_2^* - \eta\big)I_2 - (\mu_2+\gamma_2)I_2 - b_2I_2 + b_1I_1. \end{aligned} \tag{3.12}$$

Since $M_1 - \eta M_2$ has a positive eigenvalues $s(M_1 - \eta M_2)$ with a positive eigenvector, by comparison theorem, it is easy to see that $I_i(t) \to \infty$, $i = 1, 2$, which contradicts to the assumption. Thus for the above ε_0, there exists $\delta = \delta(\varepsilon_0) > 0$ such that for any $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$, there holds $\limsup_{t\to+\infty} \|\Phi(\mathbf{b}, t)_\phi\| \geqslant \delta$, $\forall \phi \in X_0$.

Similarly we can also prove that there exists a $\delta_1 = \delta_1(\varepsilon_0) > 0$ such that for any $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_0$, there holds $\limsup_{t\to+\infty} \|\Phi(\mathbf{b}, t)_\phi - (S^0, 0)\| \geqslant \delta_1$, $\forall \phi \in X_0$.

Then by the theorem on the uniform persistence uniform in parameters (see Smith and Zhao [12, Theorem 4.3 and Remark 4.2]), it follows that there exists $\varepsilon_1 \in (0, \varepsilon_0]$, $\beta_1 > 0$ such that $\liminf_{t\to+\infty} d(\Phi(\mathbf{b}, t)_\phi, \partial X_0) \geqslant \beta_1$ for all $\phi \in X_0$ and $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_1$, $b_i \neq 0$, $i = 1, 2$. Thus there exists a bounded and closed subset B_0^* of X_0 such that $A_{\mathbf{b}}^0 \subset B_0^*$ for all $|\mathbf{b} - \mathbf{b}_0| \leqslant \varepsilon_1$. For all $t > 0$,

$$\overline{\bigcup_{\mathbf{b}\in\bigcup(\mathbf{b}_0,\varepsilon_1)} \Phi(\mathbf{b}, t)A_{\mathbf{b}}^0} \subset \overline{\bigcup_{\mathbf{b}\in\bigcup(\mathbf{b}_0,\varepsilon_1)} \Phi(\mathbf{b}, t)B_0^*} \quad \text{and}$$

$$\overline{\bigcup_{\mathbf{b}\in\bigcup(\mathbf{b}_0,\varepsilon_1)} \Phi(\mathbf{b}, t)A_{\mathbf{b}}^0} = \overline{\bigcup_{\mathbf{b}\in\bigcup(\mathbf{b}_0,\varepsilon_1)} A_{\mathbf{b}}^0} \subset \overline{B_0^*} = B_0^* \subset X_0.$$

Thus $\overline{\bigcup_{\mathbf{b}\in\bigcup(\mathbf{b}_0,\varepsilon_1)} \Phi(\mathbf{b}, t)A_{\mathbf{b}}^0}$ is compact in X_0.

When $\mathbf{b} = \mathbf{b}_0$, system (3.7) admits a unique positive equilibrium $(S_1^*, S_2^*, I_1^*, I_2^*)$ which is globally asymptotically stable in X_0 (Theorem 3.1). Let $U = X_0$ and $B_{\mathbf{b}} = A_{\mathbf{b}}^0$. By Smith and Waltman [11, Theorem 2.2] there exists an $\bar{\varepsilon} \in (0, \varepsilon_1]$ such that for any $\mathbf{b}$ with $|\mathbf{b} - \mathbf{b}_0| \leqslant \bar{\varepsilon}$, (3.7) admits a positive equilibrium $(S_1^*(\mathbf{b}), S_2^*(\mathbf{b}), I_1^*(\mathbf{b}), I_2^*(\mathbf{b}))$ which is globally attractive in X_0. □

From above results we see that the uniqueness, global attractivity and even globally asymptotic stability of the endemic equilibrium in connected environment can be preserved from isolated environment, if dispersal rates of susceptible individuals and infective ones are the same or very close in each patch. However, this may not be true, when dispersal rates of two group individuals are not very close to each other in each patch. In fact, some numerical examples show that multi-endemic equilibria may emerge from (3.7) in some cases. We show this by fixing birth functions as (B1) in (3.7):

$$
\begin{aligned}
S_1' &= \frac{p_1}{N_1^2+q_1}N_1 - (\mu_1+a_1)S_1 - \beta_1 S_1 I_1 + \gamma_1 I_1 + a_2 S_2,\\
S_2' &= \frac{p_2}{N_2^2+q_2}N_2 - (\mu_2+a_2)S_2 - \beta_2 S_2 I_2 + \gamma_2 I_2 + a_1 S_1,\\
I_1' &= \beta_1 S_1 I_1 - (\mu_1+\gamma_1+b_1)I_1 + b_2 I_2,\\
I_2' &= \beta_2 S_2 I_2 - (\mu_2+\gamma_2+b_2)I_2 + b_1 I_1.
\end{aligned} \tag{3.13}
$$

In the case that $b_i = 0$, $i = 1, 2$, i.e., infective individuals in two patches are prevented from dispersal, (3.13) is reduced to

$$
\begin{aligned}
S_1' &= \frac{p_1}{(S_1+I_1)^2+q_1}(S_1+I_1) - (\mu_1+a_1)S_1 - \beta_1 S_1 I_1 + \gamma_1 I_1 + a_2 S_2,\\
S_2' &= \frac{p_2}{(S_2+I_2)^2+q_2}(S_2+I_2) - (\mu_2+a_2)S_2 - \beta_2 S_2 I_2 + \gamma_2 I_2 + a_1 S_1,\\
I_1' &= \beta_1 S_1 I_1 - (\mu_1+\gamma_1)I_1,\\
I_2' &= \beta_2 S_2 I_2 - (\mu_2+\gamma_2)I_2.
\end{aligned} \tag{3.14}
$$

To find the endemic equilibrium $(S_1^*, S_2^*, I_1^*, I_2^*)$, set the right side of above system equal to zero, we can obtain $S_1^* = (\mu_1+\gamma_1)/\beta_1$, $S_2^* = (\mu_2+\gamma_2)/\beta_2$, and I_1^* and I_2^* satisfy the two equations below:

$$
\begin{aligned}
&\frac{p_1}{\left(\frac{\mu_1+\gamma_1}{\beta_1}+I_1\right)^2+q_1}\left(\frac{\mu_1+\gamma_1}{\beta_1}+I_1\right) - (\mu_1+a_1)\frac{\mu_1+\gamma_1}{\beta_1}\\
&\quad + a_2\frac{\mu_2+\gamma_2}{\beta_2} - \mu_1 I_1 = 0,
\end{aligned} \tag{3.15}
$$

$$
\begin{aligned}
&\frac{p_2}{\left(\frac{\mu_2+\gamma_2}{\beta_2}+I_2\right)^2+q_2}\left(\frac{\mu_2+\gamma_2}{\beta_2}+I_2\right) - (\mu_2+a_2)\frac{\mu_2+\gamma_2}{\beta_1}\\
&\quad + a_1\frac{\mu_1+\gamma_1}{\beta_1} - \mu_2 I_2 = 0.
\end{aligned} \tag{3.16}
$$

Suppose $a_1 > 0$, $a_2 > 0$. We find by numerical calculations that for sufficiently large β_1 and β_2 there may exist two positive solutions to (3.15) or (3.16) when a_1 and a_2 are in some range, if other parameter values are fixed, which indicates that if infective individuals do not disperse, then when contact rates are sufficiently large there may exist two different endemic equilibria within the two patches. This phenomenon can be seen in an example, for which we choose $b_i = 0$, $i = 1, 2$, $\beta_1 = 8$, $\beta_2 = 6$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $a_1 = 4$ and the relationships between I_1^*, I_2^* and a_2 are shown in Fig. 1. As a detailed example, when $a_2 = 8$, we may obtain two endemic equilibria: $(0.1, 1/6, 4.36746, 1.7941)$ and $(0.1, 1/6, 4.36746, 0.545307)$. Moreover, by using XPPAUT, we can project the phrase portrait of (3.14) with these special parameter values onto I_1–I_2 plane and obtain the stability of endemic equilibria by Sing which is embedded in XPPAUT. Then it is shown that, of these two endemic equilibria, $(0.1, 1/6, 4.36746, 1.7941)$ is a stable node, and $(0.1, 1/6, 4.36746, 0.545307)$ is a saddle with 1-dimension stable manifold and 3-dimension unstable manifold (see Fig. 2). In fact, in this case, there is an equilibrium on the boundary of $R_+^4 \setminus \{0\}$:

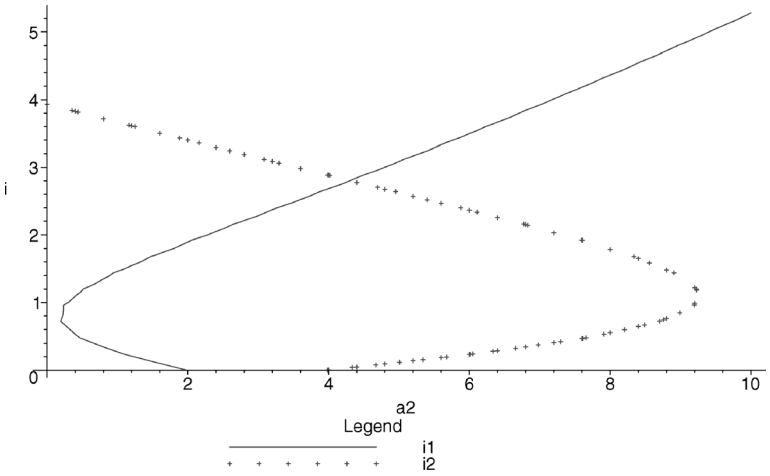

Fig. 1. Relationships between I_1^*, I_2^* and a_2 for (3.13) when $b_i = 0$, $i = 1, 2$, $\beta_1 = 8$, $\beta_2 = 6$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $a_1 = 4$.

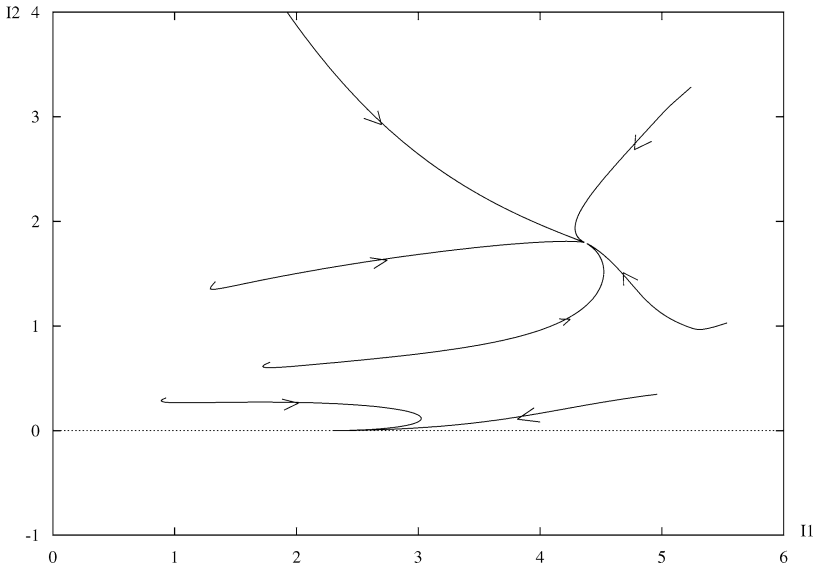

Fig. 2. For (3.13), a projection of solution graphs of (3.13) onto I_1–I_2 plane when $b_1 = b_2 = 0$, $\beta_1 = 8$, $\beta_2 = 6$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $u_1 = 0.3$, $u_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $a_1 = 4$, $a_2 = 8$. Endemic equilibria are $(0.1, 1/6, 4.36746, 1.7941)$, a stable node; $(0.1, 1/6, 4.36746, 0.545307)$, a saddle. Besides $(0, 0)$, there are two equilibria on the boundary of $R_+^4 \setminus \{0\}$: $(0.395356, 0.1666667, 0, 3.69008)$, a saddle; $(0.1, 0.0624746, 2.29613, 0)$, a stable node.

$(0.1, 0.624746, 2.29613, 0)$, which is also a stable node. Thus multi-stable steady states may emerge and if $I_2(0)$ is very small, the system will settle into the stable steady state on the boundary of $R_+^4 \setminus \{0\}$, otherwise into the stable endemic steady state.

Next we consider the case where the ratios of dispersal rates of infective individuals to those of susceptible ones are less than 1. We will see multi-stable endemic equilibria from numerical examples.

Let $b_1 = ka_1$, $b_2 = ka_2$, $k \in [0, 1]$. Choosing the same parameter values except b_1 and b_2 for (3.13) as above example, we find that the number of endemic equilibria may change from 2 to 3 then to 2 again and finally to 1 when k varies from 0 to 1, i.e., there may exist two or three endemic equilibria in the two patches when the ratio of dispersal rates of infective individuals to those of susceptible ones in two patches is sufficiently small, and there is only one endemic steady state when the ratio is large enough (this agrees with Theorems 3.3 and 3.4). We have seen the two endemic equilibria when $k = 0$. Moreover, when k increases to for example 0.004, i.e., $b_i = 0.004a_i$, $i = 1, 2$, (3.13) admits three endemic equilibria $(0.101866, 0.0924322, 2.746, 0.0920306)$, $(0.101656, 0.14095, 3.68417, 0.316411)$ and $(0.1003, 0.165725, 4.31626, 1.83436)$; when $k = 1$, i.e., $b_i = a_i$, $i = 1, 2$, there is only one endemic equilibrium $(0.102039, 0.161207, 4.0536, 2.01853)$. Also by XPPAUT we see: for this example, if there exists a unique endemic equilibrium, it is asymptotically stable (Fig. 3); if there are two endemic equilibria, one is a stable node, the other is a saddle with 1-dimension stable manifold and 3-dimension unstable manifold and the projection of phase portrait is the same as Fig. 2; if there are three endemic equilibria in (3.13), two are stable nodes, the other one is a saddle with 1-dimension stable manifold and 3-dimension unstable manifold. The last case is illustrated in Fig. 4, where $k = 0.004$ and the stable equilibria are $(0.101866, 0.0924322, 2.746, 0.0920306)$ and $(0.1003, 0.165725, 4.31626, 1.83436)$, the unstable equilibrium is $(0.101656, 0.14095, 3.68417, 0.316411)$. If $I_2(0)$ is very small and

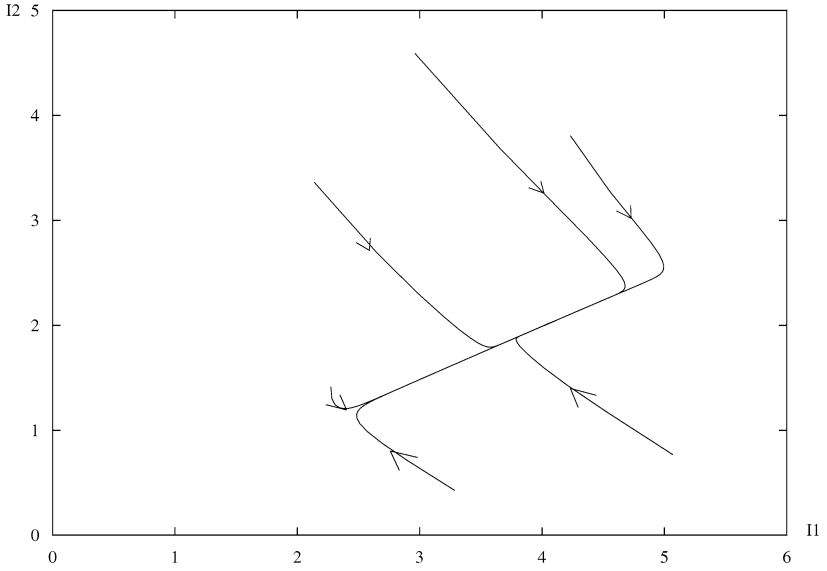

Fig. 3. For (3.13), a projection of solution graphs of (3.13) onto I_1–I_2 plane when $b_i = 0.8a_i$, $i = 1, 2$, $\beta_1 = 8$, $\beta_2 = 6$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $u_1 = 0.3$, $u_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $a_1 = 4$, $a_2 = 8$. The endemic equilibrium is $(0.101595, 0.162238, 4.11605, 1.97599)$, which is a stable node.

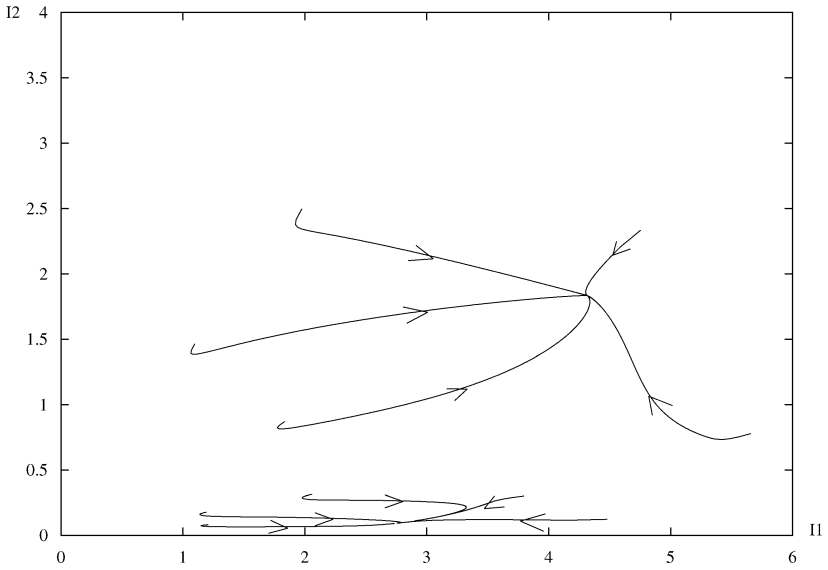

Fig. 4. For (3.13), a projection of solution graphs of (3.13) onto I_1–I_2 plane when $b_i = 0.004a_i$, $i = 1, 2$, $\beta_1 = 8$, $\beta_2 = 6$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $a_1 = 4$, $a_2 = 8$. Endemic equilibria are $(0.101866, 0.0924322, 2.746, 0.0920306)$, a stable node; $(0.101656, 0.14095, 3.68417, 0.316411)$, a saddle; $(0.1003, 0.165725, 4.31626, 1.83436)$, a stable node.

$I_1(0)$ is not large, $I(t)$ converges to the stable endemic equilibrium with smaller values, otherwise to the other stable endemic equilibrium.

In fact, for (3.13), for above parameters, when $a_i = 0$, $b_i = 0$, $i = 1, 2$, it is easy to obtain that $R_{01} = 21.60246899 \gg 1$, $R_{02} = 20.78460969 \gg 1$ and the unique endemic equilibrium which is globally asymptotically stable is $(0.1, 0.166667, 2.06025, 3.29743)$. Then above analysis shows that when k increases from 0 to 1, population dispersal will result in an increase of the number of infective individuals in patch one and a decrease of the number of infective individuals in patch two. If the numbers of infective individuals in two patches are small initially, to permit a few infective individuals to disperse will result in a stable steady state with much less total number of infective individuals within two patches than that when they are isolated. However, if the numbers of initial infective individuals in two patches are large, population dispersal will increase the total number of infective individuals when stable steady state is achieved. Actually, in this case, the more the infective individuals are prevented from dispersal, the larger the total number of infective individuals will be in the stable endemic steady state.

Remark 3.1. If there are two endemic equilibria when $b_i = 0$, $i = 1, 2$, then when the ratio between b_i and a_i, $i = 1, 2$ are different, i.e., $b_1 = k_1 a_1$, $b_2 = k_2 a_2$, $k_1, k_2 \in [0, 1]$, and k_1 is not necessarily equal to k_2, we can also find multi-endemic equilibria. Let k_1 be fixed. If k_1 is not very large, the total number of endemic equilibria may also change from 2 to 3 then to 2 again and finally to 1 when k_2 varies from 0 to 1, while if k_1 is sufficiently large the number will always be 1. The results are similar if we fix k_2.

Thus, when population dispersal exists among patches, although the uniqueness of the disease free equilibrium can be preserved from isolated environment, the uniqueness of the endemic equilibrium cannot always be obtained. When the ratios of dispersal rates of infective individuals to those of susceptible ones are sufficiently small, multiple endemic equilibria or even multi-stable equilibria may emerge.

4. Extinction and persistence of a disease in connected environment

In this section we analyze the extinction and persistence of a disease in connected environment, mainly by studying the two-patch model (3.13) in which the birth functions are chosen as (B1).

4.1. The condition for a disease to be extinct

By Theorems 2.1 and 2.2, in order to eradicate a disease, we should require $R_0 < 1$. For (3.13), basing on the expression of $s(M_1)$ we will give a specific condition for $s(M_1) < 0$, which, by the equivalence of $s(M_1) < 0$ and $R_0 < 1$, will lead the disease free equilibrium to be stable.

To find the disease free equilibrium of (3.13), we consider the following system:

$$\begin{aligned} S_1' &= \frac{p_1}{S_1^2 + q_1} S_1 - (\mu_1 + a_1) S_1 + a_2 S_2, \\ S_2' &= \frac{p_2}{S_2^2 + q_2} S_2 - (\mu_2 + a_2) S_2 + a_1 S_1. \end{aligned} \tag{4.1}$$

By the assumption of (B1), (4.1) has a positive equilibrium (S_1^0, S_2^0). Let

$$S_1 = m_1 \sqrt{p_1\mu_1 - \mu_1^2 q_1}/\mu_1, \qquad S_2 = m_2 \sqrt{p_2\mu_2 - \mu_2^2 q_2}/\mu_2.$$

Setting the right side of (4.1) equal to zero, we have

$$\begin{aligned} &\frac{p_1 \mu_1^2 m_1}{m_1^2(p_1\mu_1 - \mu_1^2 q_1) + \mu_1^2 q_1} - (\mu_1 + a_1) m_1 + a_2 m_2 k = 0, \\ &\frac{p_2 \mu_2^2 m_2}{m_2^2(p_2\mu_2 - \mu_2^2 q_2) + \mu_2^2 q_2} - (\mu_2 + a_2) m_2 + \frac{a_1 m_1}{k} = 0, \end{aligned} \tag{4.2}$$

where $k = \sqrt{p_2\mu_2 - \mu_2^2 q_2}\mu_1/(\sqrt{p_1\mu_1 - \mu_1^2 q_1}\mu_2)$. Suppose (m_1^0, m_2^0) is a positive solution to (4.2). Clearly

$$\big(S_1^0, S_2^0\big) = \big(m_1^0 \sqrt{p_1 u_1 - u_1^2 q_1}/u_1, m_2^0 \sqrt{p_2 u_2 - u_2^2 q_2}/u_2\big).$$

It is not difficult to see $s(M_1) = (h_1 + \sqrt{h_1^2 - 4h_2})/2$, where

$$\begin{aligned} h_1 &= \beta_1 S_1^0 + \beta_2 S_2^0 - b_1 - b_2 - \gamma_1 - \gamma_2 - \mu_1 - \mu_2, \\ h_2 &= \big(-\beta_1 S_1^0 + b_1 + \gamma_1 + \mu_1\big)\big(-\beta_2 S_2^0 + b_2 + \gamma_2 + \mu_2\big) - b_1 b_2. \end{aligned}$$

To make $s(M_1) < 0$ it suffices to make $h_1 < 0$ and $h_2 > 0$. Note the relationship between (S_1^0, S_2^0) and (m_1^0, m_2^0), we obtain the following theorem:

Theorem 4.1. *For* (3.13), $s(M_1) < 0$ *if and only if* a_i *and* b_i, $i = 1, 2$, *are suitable to ensure that the positive solution* (m_1^0, m_2^0) *of* (4.2) *satisfies one of the following three conditions*:

(1) $m_1^0 < \dfrac{1}{R_{01}}, \qquad m_2^0 < \dfrac{1}{R_{02}};$

(2) $\dfrac{1}{R_{01}} < m_1^0 < \dfrac{1}{R_{01}}\left(1 + \dfrac{b_1}{\mu_1 + \gamma_1}\right), \qquad m_2^0 < \dfrac{1}{R_{02}},$

$$\left(-m_1^0 R_{01} + 1 + \frac{b_1}{\mu_1 + \gamma_1}\right)\left(-m_2^0 R_{02} + 1 + \frac{b_2}{\mu_2 + \gamma_2}\right) - \frac{b_1 b_2}{(\gamma_1 + \mu_1)(\gamma_2 + \mu_2)} > 0;$$

(3) $m_1^0 < \dfrac{1}{R_{01}}, \qquad \dfrac{1}{R_{02}} < m_2^0 < \dfrac{1}{R_{02}}\left(1 + \dfrac{b_2}{\mu_2 + \gamma_2}\right),$

$$\left(-m_1^0 R_{01} + 1 + \frac{b_1}{\mu_1 + \gamma_1}\right)\left(-m_2^0 R_{02} + 1 + \frac{b_2}{\mu_2 + \gamma_2}\right) - \frac{b_1 b_2}{(\gamma_1 + \mu_1)(\gamma_2 + \mu_2)} > 0.$$

4.2. Simulations

Now let us investigate the range of population dispersal rates for the extinction of a disease by numerical calculations by Maple.

Suppose that the disease will be extinct when two patches are isolated. Obviously it is expected not to be endemic when population dispersal exists between these two patches. However, elementary calculations show that this is the case only when a_i and b_i satisfy some relationship, otherwise the disease will be endemic. For (3.13), let $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $\beta_1 = 0.3$, $\beta_2 = 0.2$. Then $R_{01} = 0.8100925871 < 1$, $R_{02} = 0.6928203230 < 1$. First we assume susceptible individuals and infective individuals disperse at the same rate in either patch, i.e., $a_1 = b_1$, $a_2 = b_2$. Calculus shows that in a region U which is surrounded by two curves in the first quadrant of a_1–a_2 plane there holds $s(M_1) > 0$ (Fig. 5). Thus when values of dispersal rates of two patches lie in this region, the disease will keep spreading although it will disappear when the two patches are isolated. In other words, to eradicate the disease, population dispersal rates should be controlled out of this region.

By using the parameters used in previous paragraph except a_i and b_i, $i = 1, 2$, for (3.13), we see another phenomenon by simulations: in some cases, reducing the ratios of dispersal rates of infective individuals to those of susceptible ones may cause the range of dispersal rates of susceptible individuals, which implies that the disease will be endemic, to be larger, if the disease will be extinct when two patches are isolated. This can be seen from Fig. 6 where the region (U_1) in the first quadrant of a_1–a_2 plane for $s(M_1) > 0$ when $b_i = 0$, $i = 1, 2$, is larger than that (U_3) when $b_i = a_i$, $i = 1, 2$, which implies that, in this case, the disease may extinct if both susceptible individuals and infective individuals in either patch disperse at some same rate, but it will spread if only susceptible individuals disperse at that rate and infective ones are barred to disperse. Moreover, let $b_i = ka_i$, $i = 1, 2$, $k \in [0, 1]$. Calculations show that the larger the ratio k is the smaller the region in the first quadrant

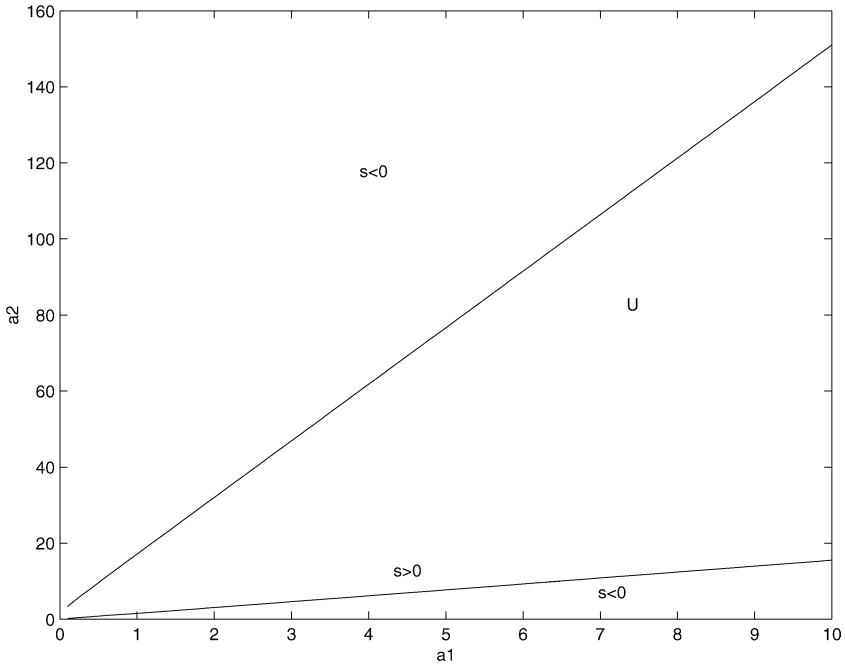

Fig. 5. For (3.13), a region U for $s(M_1) > 0$, when $R_{01} < 1$, $R_{02} < 1$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $\beta_1 = 0.3$, $\beta_2 = 0.2$, $a_1 = b_1$, $a_2 = b_2$.

of a_1–a_2 plane for $s(M_1) > 0$ is. Thus, if the disease can be extinct when two patches are isolated, on some occasions, only reducing the ratios of dispersal rates of infective individuals to those of susceptible ones may not surely help guarantee the disease to be extinct within two patches.

Now suppose that the disease will be endemic in two patches when they are isolated. Numerical calculations show a very interesting type of behavior of (3.13): if R_{01} and R_{02} are greater than 1 but very near 1, the disease may be eradicated in two patches when population dispersal exists between two patches, in some cases where contact rates are very small and dispersal rates of infective individuals are some small values. We can see this in an example. Let $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $u_1 = 0.3$, $u_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$. When $a_1, a_2, b_1, b_2, \beta_1$ and β_2 vary, $R_{01} > 1$, $R_{02} > 1$ and $s(M_1) < 0$ can be obtained at the same time only when $\beta_1 > 0.3703280400$ and is less than some value between 0.5 and 0.6, $\beta_2 > 0.2886751346$ and is less than some value between 0.4 and 0.5, and b_1 and b_2 are chosen as 0.1, 0.2, 0.9 or 1 according to values of a_1 and a_2. We may fix $b_1 = 0.1$, $b_2 = 1$, $\beta_1 = 0.5$, $\beta_2 = 0.4$ and obtain a region in the first quadrant of a_1–a_2 plane which leads to $s(M_1) < 0$ (Fig. 7).

Therefore although the disease can spread in two patches when they are isolated, if it is not very serious and contact rates in two patches are very small, population dispersal at some special rates may help eradicate it within the two patches.

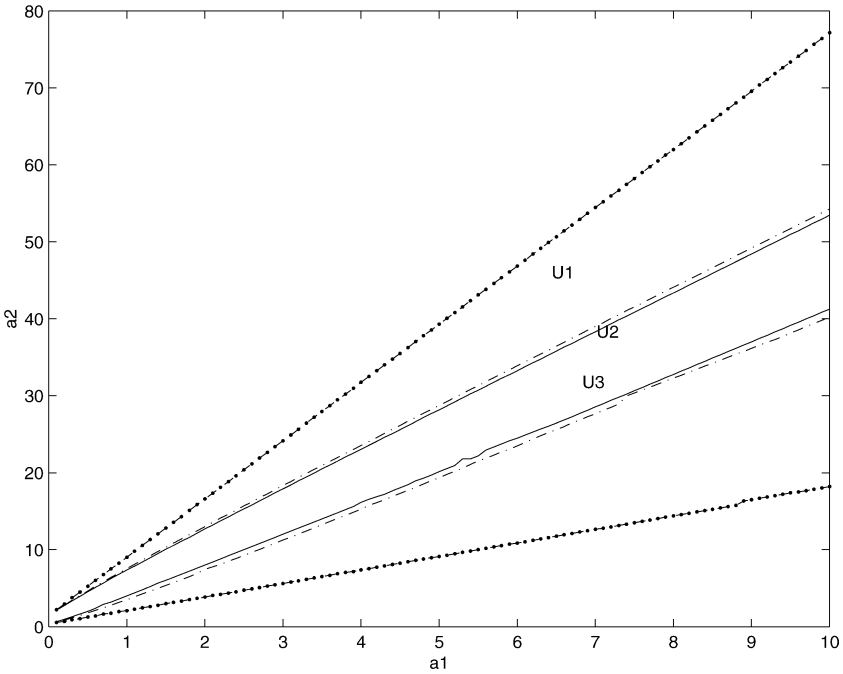

Fig. 6. For (3.13), a comparison of three regions for $s(M_1) > 0$ as k increases from 0 to 1. $R_{01} < 1$, $R_{02} < 1$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $\mu_1 = 0.3$, $\mu_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$, $\beta_1 = 0.2$, $\beta_2 = 0.1$. U_1 corresponds to $b_i = 0$; U_2 corresponds to $b_i = 0.5a_i$; U_3 corresponds to $b_i = a_i$. $U_1 \supset U_2 \supset U_3$.

Remark 4.1. If we choose birth functions as (B2), all simulations in Sections 3 and 4 can be similarly obtained, but if we choose birth functions as (B3), we cannot find co-existence of multiple endemic equilibria.

5. Discussion

In this paper, we have studied the epidemic model proposed in [18] in which population dispersal among n patches are considered, and suggested that population dispersal has important effect on the persistence and extinction of a disease. By comparing isolated environment with connected environment, we find that when population dispersal exists among n patches, the uniqueness of the disease free equilibrium in isolated environment can be preserved in connected environment. Recalling relative results in [18], we see the attractivity of the disease free equilibrium can be preserved if $R_0 < 1$. For endemic equilibria, the uniqueness and global attractivity when $R_0 > 1$ can be preserved from isolated environment if dispersal rates of susceptible individuals and infective ones are the same in each patch. For 2-patch model, we can even obtain globally asymptotic stability of the unique endemic equilibrium when $R_0 > 1$ and dispersal rates of susceptible individuals and infective ones are the same in either patch and global attractivity of the unique endemic equilibrium when $R_0 > 1$, if dispersal rates of susceptible individuals and infective

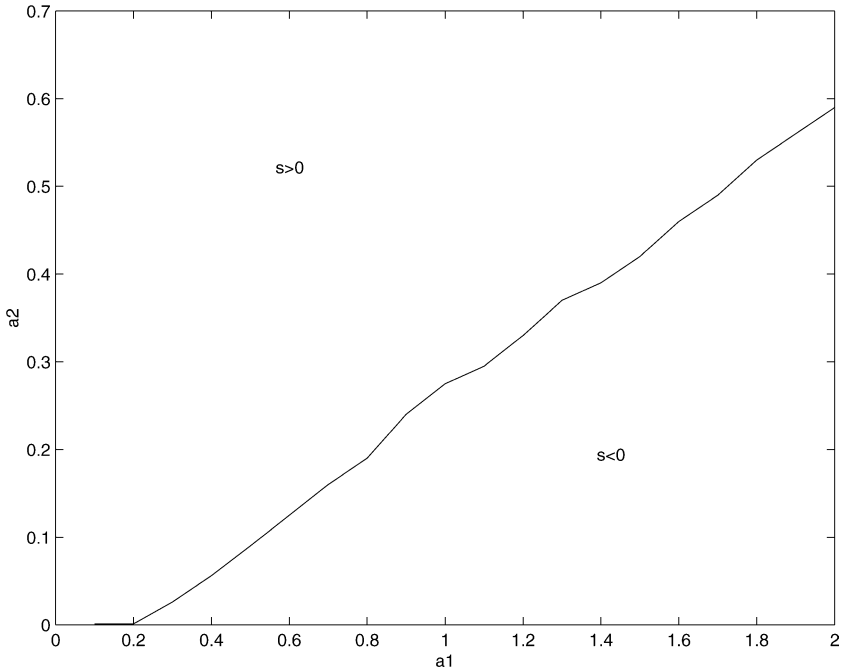

Fig. 7. For (3.13), a region for $s(M_1) < 0$ when $R_{01} = 1.350154312 > 1$, $R_{02} = 1.385640646 > 1$, $b_1 = 0.1$, $b_2 = 1$, $\beta_1 = 0.5$, $\beta_2 = 0.4$, $p_1 = 2$, $p_2 = 6$, $q_1 = 2$, $q_2 = 3$, $u_1 = 0.3$, $u_2 = 0.4$, $\gamma_1 = 0.5$, $\gamma_2 = 0.6$.

ones are very close. However, if dispersal rates of susceptible individuals and infective ones are not very close to each other in either patch, by fixing the birth functions as (B1) in (3.7), we see, by numerical calculations, the behavior of multiple endemic equilibria and even multi-stable endemic equilibria when $R_0 > 1$. For (3.13) with those special parameter values we choose, by using XPPAUT, we see that, if there are two endemic equilibria, one is stable and the other is unstable; if there are three endemic equilibria, one is unstable, and the other two are stable, in which case the actual state the system settles into depends on the initial conditions. In the simulations of Section 4, for $n = 2$, we fix the birth function as (B1) and find that if a disease can be extinct in two patches when they are isolated, then when dispersal rates lie in a subset of nonnegative orthant in the 4-dimensional space, it will still be extinct, otherwise it will be endemic. Detailed simulations also show that if a disease can be eradicated in either patch in isolated environment, only preventing infective individuals from dispersal will not reduce the possibility of the disease to be endemic. An interesting qualitative phenomenon arising in simulations shows that even if the disease will spread in either isolated patch, it can be extinct when population dispersal exists if reproduction numbers and contact rates in either patch are small enough and dispersal rates of infective individuals in two patches are chosen to be some special small values.

There is still much work to do in this field. An improvement worth looking into would be to add an exposed stage in the model. To consider a variable dispersal rate in the model is also an interesting work to do.

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