第39卷第6期 中国科学技术大学学报 Vol. 39, No. 6
2009年6月 JOURNAL OF UNIVERSITY OF SCIENCE AND TECHNOLOGY OF CHINA Jun. 2009

Article ID: 0253-2778(2009)06-0570-13

Competitive exclusion and coexistence of a class of sexually-transmitted disease models

CHAI Cai-chun[1], JIANG Ji-fa[2,3]

(1. *School of Statistics and Applied Mathematics, Anhui University of Finance and Economics*, *Bengbu* 233030, *China*;
2. *Department of Mathematics, University of Science and Technology of China*, *Hefei* 230026, *China*;
3. *Department of Applied Mathematics, Tongji University*, *Shanghai* 200092, *China*)

Abstract: The dynamics of sexually transmitted pathogens in a heterosexually active population was studied, where females were divided into $N-1$ different groups based on their susceptibility to two distinct pathogenic strains. The coexistence and stability of that boundary equilibria was investigated, and the sufficient and necessary conditions for the existence and stability of these equilibria were obtained. It was verified that there is a strong connection between the stability of boundary equilibria and the existence of the coexistence equilibrium, that is, there exists at least one coexistence equilibrium if and only if the boundary equilibria both exist and have the same stability.

Key words: sexually transmitted disease; pathogen strains; coexistence

CLC number: O19 **Document code**: A

AMS Subject Classification (2000): 92A15

一类STD模型的竞争熄灭与共存

柴彩春[1],蒋继发[2,3]

(1.安徽财经大学统计与应用数学学院,安徽蚌埠 233030;
2.中国科学技术大学数学系,安徽合肥 230026;3.同济大学应用数学系,上海 200092)

摘要:研究了一种存在于异性活动人群中的,通过性活动进行传播的病菌所构成的系统.在这个系统中,女性被分成 $N-1$ 个不同的群体,而根据传播能力的不同,病原体菌株被分成两类.对这种系统,讨论了其地方病平衡点以及边界平衡点的稳定性,得到了这些平衡点存在及稳定的充分必要条件.结果确认,在边界平衡点的稳定性和地方病平衡点的存在性之间存在强烈的联系,即地方病平衡点存在当且仅当地方病平衡点同时存在并且具有相同的稳定性.

关键词:性传播疾病;病原体菌株;共存

Received: 2007-03-22; **Revised**: 2008-07-10

Foundation item: Supported by the NSF of the Educational Bureau of Anhui Province (KJ2009B103Z) and the Youth Foundation of Anhui University of Finance and Economics (ACKYQ0927).

Biography: CHAI Cai-chun, female, born in 1981, master. Research field: dynamical systems and biomathematics. E-mail: ccspring@ustc.edu

Corresponding author: JIANG Ji-fa, Prof. E-mail: jiangjf@mail.tongji.edu.cn

0 Introduction

Theoretical biologists and bio-mathematicians have long been concerned with evolutionary interactions that result from changing host and pathogen populations. Advances in evolutionary biology, behavior, and social dynamics have brought to the forefront of research the importance of a multitude of factors that not only influence disease dynamics, but also play a role in the evolution of virulence[1,3,4,7,8,11,12,13,15]. STDs, such as gonorrhea, have incredibly high incidences throughout the world, providing the necessary environment and opportunities for the evolution of new strains[14]. Understanding the mechanisms that lead to coexistence or competitive exclusion is a matter of urgency to the development of disease management strategies, to our understanding of STD dynamics and to stimulating additional research on those factors that may facilitate pathogens' survival and diversity.

In Refs. [5, 6, 7, 10, 17, 22], the authors formulated and analyzed two-sex SIS STD models with multiple competing strains in an exclusively heterosexually active population, where it was assumed that a host cannot be invaded simultaneously by more than one strain, and that symptoms appeared--a function of the pathogen, strain, virulence, and an individual's degree of susceptibility--then individuals could be treated and/or would recover. In a behaviorally and genetically homogeneous population they established that coexistence was not possible[5,10]. However, in a heterosexually active population where two "genetically" different female groups interact with a homogeneous (genetically uniform) male population in the presence of two competing strains of a venereal disease, the outcome was different as both competitive exclusion and coexistence were possible[6,7,22]. They obtained the sufficient and necessary conditions for the existence and the global stability of the boundary equilibria and the positive coexistence equilibrium.

As a continuation of their work, in this paper, we consider general $2N$-group models ($N \geqslant 4$) with two strains, where N denotes the total number of the subpopulation of the infective with each subpopulation divided into classes with strains x and y, respectively.

This paper is organized as follows: we introduce the model in Section 1. Section 2 presents some preliminaries. The necessary thresholds are computed and the stability of the infection-free state is studied in Section 3. A principle of competitive exclusion for SIS STD models with homogeneous mixing is established in Section 4. Section 5 presents our coexistence results. Some special results for $N=4$ will be given in Section 6. In Section 7, we discuss the biological meaning of our results.

1 Model description

In this paper, we consider a two-sex heterosexually active population. The population includes a single group of males and $N-1$ groups of females, based on their susceptibility, which is determined by their sexual behavior, genetics, or other factors. We assume that the infective are divided into two classes based on the pathogen strains in their bodies, and that the susceptible are infected by infectives with a certain pathogen strain will carry the same pathogen strain.

We use superscripts $f_2, f_3, \cdots, f_N$ to denote the $N-1$ female groups and the superscript m to denote the male group. We think of susceptible hosts as patches that are invaded or colonized by a pathogen. The assumption here is that once a patch has been infected (colonized), it cannot be invaded again. However, it is also assumed that if patches recover by getting rid of the pathogen and become equally susceptible to infection again, that is, the patches' immune systems do not remember previous infections. Let S^k, $k=m, f_2, \cdots, f_N$, denote the susceptible males, susceptible females in $N-1$ different groups, and let I_i^k, $k=m, f_2, \cdots, f_N$, $i=1,2$, denote the infectives with strains i, respectively. The model that describes the dynamics of the disease spread then takes the form

$$\left.\begin{aligned}&\dot{S}^k=\Lambda^k-B^k-\mu^k S^k+\sum_{i=1}^{2}\gamma_i^k I_i^k,\\&\dot{I}_i^k=B_i^k-(\mu^k+\gamma_i^k)I_i^k,\\&k=m,f_2,\cdots,f_N,\ i=1,2,\end{aligned}\right\}\qquad(1)$$

where

$$B_i^m=r^m(T^m,T^{f_2},\cdots,T^{f_N})S^m\sum_{j=2}^{N}\beta_i^{f_j}\frac{I_i^{f_j}}{T^{f_j}},$$

$$B_i^l=r^l(T^m,T^{f_2},\cdots,T^{f_N})S^l\beta_i^m\frac{I_i^m}{T^m},\ l=f_2,\cdots,f_N,$$

$$B^k=\sum_{i=1}^{2}B_i^k,\ k=m,f_2,\cdots,f_N,$$

with the constraint

$$r^m(T^m,T^{f_2},\cdots,T^{f_N})T^m=\sum_{j=2}^{N}r^{f_j}(T^m,T^{f_2},\cdots,T^{f_N})T^{f_j}.$$

Here Λ^k denotes the input flow (recruitment) entering the sexually active subpopulations; $\frac{1}{\mu^k}$ is the average sexual life span for people in group k; $\gamma_i{}^k$ is the rate of recovery; $T^k=S^k+\sum_{i=1}^{2}I_i^k$ is the total number of males and females in group $f_2,\cdots,f_N$, respectively; r^k, as a function of $T^m,T^{f_2},\cdots,T^{f_N}$ is the number of partners per individual per unit of time; and β_i^k is the rate of infection. The constraint indicates that the total number of female sexual partners of males per unit of time and the total number of male partners of females per unit of time given the current availability of partners must be balanced.

The principle of system (1) can be shown in Fig. 1.

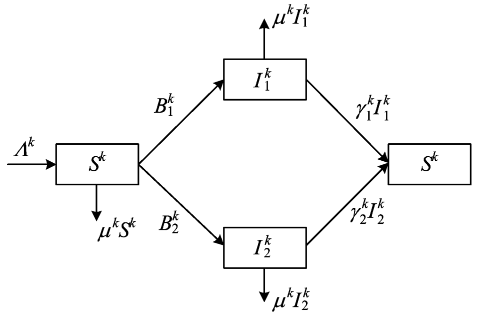

Fig. 1 Principle of system (1)

The limiting system of (1) is given by

$$\left.\begin{aligned}&\dot{I}_i^m=-\sigma_i^m I_i^m+(p^m-\sum_{n=1}^{2}I_n^m)\sum_{i=2}^{N}a_i^{mf_j}I_i^{f_j},\\&\dot{I}_i^{f_j}=-\sigma_i^{f_j}I_i^{f_j}+(p^{f_j}-\sum_{n=1}^{2}I_n^{f_j})a_i^{f_jm}I_i^m,\\&j=2,3,\cdots,N,\end{aligned}\right\}\qquad(2)$$

where we define

$$b^k:=r^k\left(\frac{\Lambda^m}{\mu^m},\frac{\Lambda^{f_2}}{\mu^{f_2}},\cdots,\frac{\Lambda^{f_N}}{\mu^{f_N}}\right)$$

and write

$$\sigma_i^k:=\mu^k+\gamma_i^k,\ p^k:=\frac{\Lambda^k}{\mu^k},$$

$$a_i^{mf_j}:=\frac{b^m\beta_i^{f_j}}{p^{f_j}},\ a_i^{f_jm}:=\frac{b^{f_j}\beta_i^m}{p^m},$$

$$j=2,3,\cdots,N.$$

2 Preliminaries

To facilitate our analysis, let

$$x_1:=I_1^m,\ x_2:=I_1^{f_2},\cdots,\ x_N:=I_1^{f_N},$$

$$y_1:=I_2^m,\ y_2:=I_2^{f_2},\cdots,\ y_N:=I_2^{f_N},$$

$$\gamma_1^x:=\sigma_1^m,\gamma_2^x:=\sigma_1^{f_2},\cdots,\ \gamma_N^x:=\sigma_1^{f_N},$$

$$\gamma_1^y:=\sigma_2^m,\gamma_2^y:=\sigma_2^{f_2},\cdots,\ \gamma_N^y:=\sigma_2^{f_N},$$

$$\alpha_{12}:=\frac{a_1^{mf_2}\alpha_1}{\sigma_1^m},\ \alpha_{13}:=\frac{a_1^{mf_3}}{\sigma_1^m},\cdots,\ \alpha_{1N}:=\frac{a_1^{mf_N}}{\sigma_1^m},$$

$$\beta_{12}:=\frac{a_2^{mf_2}\alpha_2}{\sigma_2^m},\ \beta_{13}:=\frac{a_2^{mf_3}}{\sigma_2^m},\cdots,\ \beta_{1N}:=\frac{a_2^{mf_N}}{\sigma_2^m},$$

$$\alpha_{21}:=\frac{a_1^{f_2m}}{\sigma_1^{f_2}},\ \alpha_{31}:=\frac{a_1^{f_3m}}{\sigma_1^{f_3}},\cdots,\ \alpha_{N1}:=\frac{a_1^{f_Nm}}{\sigma_1^{f_N}},$$

$$\beta_{21}:=\frac{a_2^{f_2m}}{\sigma_2^{f_2}},\ \beta_{31}:=\frac{a_2^{f_3m}}{\sigma_2^{f_3}},\cdots,\ \beta_{N1}:=\frac{a_2^{f_Nm}}{\sigma_2^{f_N}},$$

$$p_1:=p^m,p_2:=p^{f_2},\cdots,\ p_N:=p^{f_N},$$

$$\alpha_{11}=\alpha_{22}=\cdots=\alpha_{2N}=\alpha_{32}=\cdots=\alpha_{3N}=\alpha_{42}=\cdots=\alpha_{4N}=\cdots=\alpha_{N2}=\cdots=\alpha_{NN}=0,$$

$$\beta_{11}=\beta_{22}=\cdots=\beta_{2N}=\beta_{32}=\cdots=\beta_{3N}=\beta_{42}=\cdots=\beta_{4N}=\beta_{N2}=\cdots=\beta_{NN}=0.$$

With these notations, system (2) can then be written into the following compact form:

$$\left.\begin{aligned}&\dot{x}_i=\gamma_i^x[-x_i+(p_i-x_i-y_i)\sum_{j=1}^{N}\alpha_{ij}x_j]=:X_i(x,y),\\&\dot{y}_i=\gamma_i^y[-y_i+(p_i-x_i-y_i)\sum_{j=1}^{N}\beta_{ij}y_j]=:Y_i(x,y),\\&i=1,2,\cdots,N.\end{aligned}\right\}\qquad(3)$$

Note that p_i is the total population of group i, $i=$

$1,2,\cdots,N$. Here we consider only the dynamics (3) in $\subset R_+^{2N}$, where

$\Omega=\{(x,y)\in R_+^{2N}: x_i+y_i\leqslant p_i,\ i=1,2,\cdots,N\}$,

and

$$x=(x_1,x_2,\cdots,x_N)\in R^N,$$
$$y=(y_1,y_2,\cdots,y_N)\in R^N,$$
$$R_+^{2N}=\{(x_1,x_2,\cdots,x_N,y_1,y_2,\cdots,y_N):\ x_i\geqslant 0,\ y_i\geqslant 0,\ i=1,2,\cdots,N\}.$$

We can observe that the flow generated by (3) is positively invariant in Ω. Furthermore, the flow is monotone under the special order given below Refs. [5, 6].

Definition 2.1 Let $K=\{x=(x_1,x_2,\cdots,x_{2N})\in R^{2N}: x_i\geqslant 0,\ i=1,2,\cdots,N;\ x_j\leqslant 0,\ j=N+1,\cdots,2N\}$. A type K order, denoted by "$\leqslant_K$", is defined in such a way that

$$x\leqslant_K y \text{ if and only if } y-x\in K. \tag{4}$$

With this order, it is easy to see that the flow generated by Eq. (3) is monotone.

Theorem 2.2 Let $(x,y)=(x_1,x_2,\cdots,x_N,y_1,y_2,\cdots,y_N)$ and let $(x(t),y(t)):=\varphi_t(x_0,y_0)$ be a solution of (3) with initial value (x_0,y_0). Then

$$\varphi_t^a(x_0,y_0)\leqslant_K\varphi_t^b(x_0,y_0),\ t\geqslant 0,$$

if

$$\varphi_0^a(x_0,y_0),\varphi_0^b(x_0,y_0)\in\Omega$$

and

$$\varphi_0^a(x_0,y_0)\leqslant_K\varphi_0^b(x_0,y_0).$$

Proof Let $Q=\mathrm{diag}(q_i)$ with $q_1=q_2=\cdots=q_N=1$, $q_{N+1}=q_{N+2}=\cdots=q_{2N}=-1$. Then the matrix $QJ(x,y)Q$ has nonnegative off-diagonal elements for every $(x,y)\in\Omega$, where $J(x,y)$ is the Jacobian of Eq. (3) evaluated at (x,y). It follows from Lemma 2.1 in Ref. [16] that the flow $\varphi_t(x_0,y_0)$ preserves a type K order on Ω; that is, the flow is monotone under this type K order. □

3 Thresholds

Considering the linearization about the infection-free equilibrium of system (3):

$$\dot{x}:=\boldsymbol{X}x,\ \dot{y}:=\boldsymbol{Y}y.$$

We notice that the diagonal elements of $-\boldsymbol{X}$ and $-\boldsymbol{Y}$ are positive and their off-diagonal elements are nonpositive. Hence, $-\boldsymbol{X}$ and $-\boldsymbol{Y}$ are M-matrices. Let

$$\boldsymbol{A}_{NN}=\begin{pmatrix}1 & -p_1\alpha_{12} & -p_1\alpha_{13} & \cdots & -p_1\alpha_{1N}\\ -p_2\alpha_{21} & 1 & 0 & \cdots & 0\\ \cdots & \cdots & \cdots & \cdots & \cdots\\ -p_N\alpha_{N1} & 0 & 0 & \cdots & 1\end{pmatrix},$$

$$\boldsymbol{B}_{NN}=\begin{pmatrix}1 & -p_1\beta_{12} & -p_1\beta_{13} & \cdots & -p_1\beta_{1N}\\ -p_2\beta_{21} & 1 & 0 & \cdots & 0\\ \cdots & \cdots & \cdots & \cdots & \cdots\\ -p_N\beta_{N1} & 0 & 0 & \cdots & 1\end{pmatrix}.$$

Then

$$\boldsymbol{X}=\mathrm{diag}(\gamma_1^x,\gamma_2^x,\cdots,\gamma_N^x)\boldsymbol{A},$$
$$\boldsymbol{Y}=\mathrm{diag}(\gamma_1^y,\gamma_2^y,\cdots,\gamma_N^y)\boldsymbol{B},$$
$$\det\boldsymbol{A}_{NN}=1-\sum_{j=2}^{N}p_1p_j\alpha_{1j}\alpha_{j1},$$
$$\det\boldsymbol{B}_{NN}=1-\sum_{j=2}^{N}p_1p_j\beta_{1j}\beta_{j1}.$$

Hence, if $\sum_{j=2}^{N}p_1p_j\beta_{1j}\beta_{j1}<1$ and $\sum_{j=2}^{N}p_1p_j\alpha_{1j}\alpha_{j1}<1$, the leading principal minors of A_{NN} and B_{NN} are positive, meanwhile $\det A_{NN}$ and $\det B_{NN}$ are positive, it follows from M-matrix theory[2] that the infection-free equilibrium is locally stable. If $\sum_{j=2}^{N}p_1p_j\beta_{1j}\beta_{j1}>1$ or $\sum_{j=2}^{N}p_1p_j\alpha_{1j}\alpha_{j1}>1$, the infection-free equilibrium is unstable.

Define the reproductive number $R_i,i=1,2$ as follows:

$$\left.\begin{aligned}R_1&=p_1p_2\alpha_{12}\alpha_{21}+p_1p_3\alpha_{13}\alpha_{31}+\cdots+p_1p_N\alpha_{1N}\alpha_{N1},\\ R_2&=p_1p_2\beta_{12}\beta_{21}+p_1p_2\beta_{13}\beta_{31}+\cdots+p_1p_N\beta_{1N}\beta_{N1}.\end{aligned}\right\} \tag{5}$$

We can make the following observations. If $R_i<1$, $i=1,2$, $\varphi_t(x_0,y_0)\rightarrow(0,0)$. If $R_i<1$, for both $i=1$ and 2, then the infection-free equilibrium is stable, that is, $R_i<1$, for both $i=1$ and 2, leads to the extinction of the disease in the population. If there exists at least one strain such that $R_i>1$, then $\varphi_t(x_0,y_0)\nrightarrow(0,0)$, that is, the disease will spread in the population.

Following from the work in Ref. [5], we can get:

Lemma 3.1 Let $E_1=(x,0)$ and $E_2=(0,y)$ be equilibria of Eq. (3), where $x>0$, if $R_1>1$; $x=0$, if $R_1\leqslant 1$ and $y>0$, if $R_2>1$; $y=0$, if $R_2\leqslant 1$.

Let $\xi_1=(p_1,p_2,\cdots,p_N,0,\cdots,0)$ and $\xi_2=(0,\cdots,0,p_1,p_2,\cdots,p_N)$. Then

$$\lim_{t\to\infty}\varphi_t(\xi_i)=E_i, i=1,2.$$

Theorem 3.2 Let the reproductive number R_i be defined in Eq. (5). If $R_i\leqslant 1$ for both $i=1$ and 2, then the epidemic goes to extinction regardless of the initial level of infection. If, on the other hand, $R_i>1$ for $i=1$ or $i=2$, then the epidemic spreads in the population.

4 Competitive exclusion

4.1 Existence of boundary equilibria

The boundary equilibrium always exists whenever the epidemic spreads in the population. We have the result as follows.

Theorem 4.1 Boundary equilibrium $E_x=(x,0)$ exists if and only if $R_1>1$, and boundary equilibrium $E_y=(0,y)$ exists if and only if $R_2>1$.

Proof Without loss of generality, we prove only the existence of E_x. From

$$\left.\begin{aligned} &-x_1+(p_1-x_1)(\alpha_{12}x_2+\cdots+\alpha_{1N}x_N)=0,\\ &-x_2+(p_2-x_2)\alpha_{21}x_1=0,\\ &\qquad\vdots\\ &-x_N+(p_N-x_N)\alpha_{N1}x_1=0,\end{aligned}\right\}\tag{6}$$

it follows that

$$x_2=\frac{p_2\alpha_{21}x_1}{1+\alpha_{21}x_1},x_3=\frac{p_3\alpha_{31}x_1}{1+\alpha_{31}x_1},\cdots,x_N=\frac{p_N\alpha_{N1}x_1}{1+\alpha_{N1}x_1}.\tag{7}$$

Substituting Eq. (7) into the first equation of Eq. (6) yields

$$\frac{1}{p_1-x_1}-\left(\frac{p_2\alpha_{12}\alpha_{21}}{1+\alpha_{21}x_1}+\cdots+\frac{p_N\alpha_{1N}\alpha_{N1}}{1+\alpha_{N1}x_1}\right)=0.\tag{8}$$

Define

$$f(x_1):=\frac{1}{p_1-x_1}-\left(\frac{p_2\alpha_{12}\alpha_{21}}{1+\alpha_{21}x_1}+\cdots+\frac{p_N\alpha_{1N}\alpha_{N1}}{1+\alpha_{N1}x_1}\right).$$

It is easy to check

$$f'(x_1)>0,\ \lim_{x_1\to p_1}f(x_1)=+\infty,$$

there exists a unique positive solution x_1 of Eq. (8) if and only if $f(0)<0$.

However,

$$f(0)=\frac{1}{p_1}(1-\sum_{j=2}^{N}p_1p_j\alpha_{1j}\alpha_{j1})=\frac{1}{p_1}(1-R_1)<0$$

if and only if $R_1>1$. This unique positive x_1 uniquely determines positive x_j, $j=2,3,\cdots,N$, via Eq. (7). The proof is complete. □

4.2 Stability of the boundary equilibria

Now we establish stability criterion for the boundary equilibrium. The Jacobian of Eq. (3) at the equilibrium E_x has the form

$$\boldsymbol{J}=\begin{pmatrix}J_{11} & 0\\ J_{21} & J_{22}\end{pmatrix}.$$

Consider

$$\dot{x}_i=\gamma_i^x[-x_i+(p_i-x_i)\sum_{j=1}^{N}\alpha_{ij}x_j].\tag{9}$$

Let $\Phi:R_+^N\to R^N$ be defined by the right hand side of Eq. (9). Clearly, Φ is cooperative and $D\Phi(x)$ is irreducible for every $x\in R_+^N$. For any $\alpha\in(0,1)$ and $x=(x_1,x_2,\cdots,x_N)\in\mathrm{int}(R_+^N)$, there holds

$$\gamma_i^x(-\alpha x_i+(p_i-\alpha x_i)\sum_{j=1}^{N}\alpha_{ij}\alpha x_j)>$$

$$\alpha\gamma_i^x(-x_i+(p_i-x_i)\sum_{j=1}^{N}\alpha_{ij}x_j),\ i=1,2,\cdots,N.$$

Thus Φ is strongly sublinear on R_+^N (see Refs. [19, 24]), it then follows that for any $x_0\in R_+^N$, the unique solution $\varphi_t(x_0)$ of Eq. (9) exists globally on $[0,\infty)$, $\varphi_t(x_0)\geqslant 0$, $\forall t\geqslant 0$ and Eq. (9) has a unique positive equilibrium $\bar{x}=(\bar{x}_1,\cdots,\bar{x}_N)$ and $\bar{x}$ is globally asymptotically stable for $x\in R_+^N\setminus\{0\}$.

So the stability of the nontrivial equilibrium $(x,0)$ is determined by the stability of matrix $\boldsymbol{J}_{22}$, where

$$\boldsymbol{J}_{22}=\mathrm{diag}(\gamma_1^y,\gamma_2^y,\cdots,\gamma_N^y)\cdot\begin{pmatrix}-1 & (p_1-x_1)\beta_{12} & \cdots & (p_1-x_1)\beta_{1N}\\ (p_2-x_2)\beta_{21} & -1 & \cdots & 0\\ \cdots & \cdots & \cdots & \cdots\\ (p_N-x_N)\beta_{N1} & 0 & \cdots & -1\end{pmatrix}.$$

Let

$$\boldsymbol{M}_{NN}=\begin{pmatrix}1 & -(p_1-x_1)\beta_{12} & \cdots & -(p_1-x_1)\beta_{1N}\\ -(p_2-x_2)\beta_{21} & 1 & \cdots & 0\\ \cdots & \cdots & \cdots & \cdots\\ -(p_N-x_N)\beta_{N1} & 0 & \cdots & 1\end{pmatrix}.$$

Then the diagonal elements of $\boldsymbol{M}_{NN}$ are positive and its off-diagonal elements are nonpositive. Hence, $\boldsymbol{M}_{NN}$ is an M-matrix.

After simple algebraic manipulations, we have

$$\det M_{NN} = \frac{p_1 - x_1}{x_1}\Big(\frac{(\alpha_{12}\alpha_{21} - \beta_{12}\beta_{21})x_2}{\alpha_{21}} + \cdots + \frac{(\alpha_{1N}\alpha_{N1} - \beta_{1N}\beta_{N1})x_N}{\alpha_{N1}}\Big). \quad (10)$$

Denote $\Delta_j := \alpha_{1j}\alpha_{j1} - \beta_{1j}\beta_{j1}$, $j = 2, 3, \cdots, N$.

Then if $\Delta_j \geqslant 0$ and $\sum_{j=2}^{N}\Delta_j^2 \neq 0$, the leading principal minors of matrix $\boldsymbol{M}_{NN}$ and $\det\boldsymbol{M}_{NN}$ are positive. Hence, it follows from M-matrix theory that the equilibrium E_x is locally stable. On the other hand, if $\Delta_j \leqslant 0$ and $\sum_{j=2}^{N}\Delta_j^2 \neq 0$, the equilibrium E_x is unstable. It follows from Lemma 3.1 that if a boundary equilibrium is locally stable, it is globally stable.

Summing up the discussions above we obtain the following result:

Theorem 4.2 If $R_1 > 1$ ($R_2 > 1$) and $R_2 \leqslant 1$ ($R_1 \leqslant 1$), then boundary equilibrium E_y (E_x) does not exist and boundary equilibrium E_x (E_y) is globally asymptotically stable. Suppose both $R_1 > 1$ and $R_2 > 1$. Then if $\Delta_j \geqslant (\leqslant) 0, j = 2, 3, \cdots, N$ and $\sum_{j=2}^{N}\Delta_j^2 \neq 0$, the boundary equilibrium E_x is globally asymptotically stable (unstable) and the boundary equilibrium E_y is unstable (globally asymptotically stable).

Biologically, Theorem 4.2 implies that if E_x(E_y) is globally asymptotically stable and E_y(E_x) is unstable, strain 1(2) persists in the population globally and strain 2(1) goes extinct. Note that whenever one boundary equilibrium is stable, the other one is unstable. Then, the competitive exclusion holds under the assumptions in Theorem 4.2.

5 Coexistence

The existence and stability of a positive coexistence endemic equilibrium $E^* := (x^*, y^*)$, characterize the coexistence of the two competing pathogen strains in the population. We investigate the dynamics of the coexistence endemic equilibrium below.

Theorem 5.1 Coexistence is not possible if $\Delta_j \geqslant 0$, $j = 2, 3, \cdots, N$ and $\sum_{j=2}^{N}\Delta_j^2 \neq 0$ or $\Delta_j \leqslant 0$, $j = 2, 3, \cdots, N$ and $\sum_{j=2}^{N}\Delta_j^2 \neq 0$.

Proof If the coexistence equilibrium exists, then there exists (x, y) such that the following equations are true

$$\left.\begin{aligned} -x_i + ((p_i - x_i - y_i)\sum_{j=1}^{N}\alpha_{ij}x_j) = 0, \\ -y_i + ((p_i - x_i - y_i)\sum_{j=1}^{N}\beta_{ij}y_j) = 0. \end{aligned}\right\} \quad (11)$$

Let $q_i = p_i - x_i - y_i$, $i = 1, 2, \cdots, N$. Then

$$\left.\begin{aligned} x_2 = q_2\alpha_{21}x_1, x_3 = q_3\alpha_{31}x_1, \cdots, x_N = q_N\alpha_{N1}x_1, \\ y_2 = q_2\beta_{21}y_1, y_3 = q_3\beta_{31}y_1, \cdots, y_N = q_N\beta_{N1}y_1. \end{aligned}\right\} \quad (12)$$

Substituting Eq. (12) into Eq. (11) yields

$$x_1(1 - q_1(q_2\alpha_{12}\alpha_{21} + q_3\alpha_{13}\alpha_{31} + \cdots + q_N\alpha_{1N}\alpha_{N1})) = 0,$$
$$y_1(1 - q_1(q_2\beta_{12}\beta_{21} + q_3\beta_{13}\beta_{31} + \cdots + q_N\beta_{1N}\beta_{N1})) = 0.$$

Then

$$\sum_{j=2}^{N} q_j\Delta_j = 0. \quad (13)$$

If Eq. (11) has a positive solution then Eq. (13) holds. While Eq. (13) is true only if $\Delta_j, j = 2, 3, \cdots, N$ have different signs or $\Delta_2 = \Delta_3 = \cdots = \Delta_N = 0$. That is, if $\Delta_j \geqslant 0$, $j = 2, 3, \cdots, N$, $\sum_{j=2}^{N}\Delta_j^2 \neq 0$ or $\Delta_j \leqslant 0$, $j = 2, 3, \cdots, N$, $\sum_{j=2}^{N}\Delta_j^2 \neq 0$, Eq. (11) does not have a positive solution. □

Proposition 5.2 System (3) has at least one positive equilibrium, if the boundary equilibria both exist and have the same stability.

Proof Let $J(x, y)$ denote the Jacobian of system (3) at (x, y), which has the form

$$J(x, y) = DF(x, y) = D(X(x, y), Y(x, y)) = \begin{pmatrix} \frac{\partial X(x, y)}{\partial x} & \frac{\partial X(x, y)}{\partial y} \\ \frac{\partial Y(x, y)}{\partial x} & \frac{\partial Y(x, y)}{\partial y} \end{pmatrix}.$$

Then $\frac{\partial X}{\partial x}$ and $\frac{\partial Y}{\partial y}$ have nonnegative off-diagonal elements, $\frac{\partial X}{\partial y}\leqslant 0$, $\frac{\partial Y}{\partial x}\leqslant 0$, $\frac{\partial X}{\partial x}$ and $\frac{\partial Y}{\partial y}$ have negative diagonal elements. Let $z=(x,y)$, thus $\frac{\partial F}{\partial z}\geqslant_K 0$. Hence, there exists (x^*,y^*) such that $F(x^*,y^*)\geqslant_K 0$. It follows from Ref. [21] that the solution $\varphi_t(x_0,y_0)$ of system (3) tends to an equilibrium as $t\to\infty$. Then, if the boundary equilibria are unstable, there exists at least one globally stable positive equilibrium; if both boundary equilibria are stable, it follows from theorem 2.6 in Ref. [22] and Refs. [16, 18, 21, 23] that there exists a positive equilibrium and that is unstable. □

Theorem 5.3 Dynamics (3) has at least one positive equilibrium if the boundary equilibria have the same stability. Furthermore, if system (3) has a unique positive equilibrium, then the coexistence is globally stable (unstable) if the boundary equilibria are unstable (stable)[20, 21].

The result is one of results in Theorem 3.2 in Chapter 4 in Ref. [20], so the theorem can be proved in the same way.

Hence, we can summarize our results as follows.

System (3) (and hence (1)) has a positive coexistence equilibrium if the two nontrivial boundary equilibria have the same stability (both are stable or unstable). If the positive coexistence equilibrium is unique. Then the positive coexistence is stable if the boundary equilibria are both unstable. In this case the positive equilibrium is a global attractor. The positive coexistence equilibrium is unstable if the boundary equilibria are both stable. Furthermore, if there is no coexistence equilibrium, then the locally stable boundary equilibrium, if it exists, is also globally stable (See Refs. [20, 21]).

Referring to the foregoing discussion, in the case where either $R_1\leqslant 1$ or $R_2\leqslant 1$, the global behavior for Eq. (3) is clear. But in the case where both $R_1>1$ and $R_2>1$, we can't give a clearly answer. So in the next section we focus on the study for $R_1>1$, $R_2>1$ and $N=4$.

6 The dynamics of system (3) for N=4

Consider the following system

$$\left.\begin{aligned}&\dot{x}_i=\gamma_i^x\Big[-x_i+(p_i-x_i-y_i)\sum_{j=1}^4\alpha_{ij}x_j\Big],\\&\dot{y}_i=\gamma_i^y\Big[-y_i+(p_i-x_i-y_i)\sum_{j=1}^4\beta_{ij}y_j\Big],\\&i=1,2,3,4.\end{aligned}\right\}\tag{14}$$

In the case where both $R_1>1$ and $R_2>1$, as shown in Section 6, there exists no positive coexistence equilibrium if $\Delta_j\geqslant 0$ and $\sum_{j=2}^4\Delta_j^2\neq 0$ or $\Delta_j\leqslant 0$, $j=2,3,4$ and $\sum_{j=2}^4\Delta_j^2\neq 0$. If $\Delta_2=\Delta_3=\Delta_4=0$, then we can prove that there is a continuum of equilibria. However, this is a very special and unrealistic situation.

Without loss of generality, we assume that $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$. If $\Delta_2>0$, $\Delta_3<0$, $\Delta_4<0$, all our results in the following remain true. Furthermore, we assume $\alpha_{31}=\alpha_{41}$ and $\beta_{31}=\beta_{41}$ in the section.

Remark 6.1 ① If $\Delta_2>(<)0$, $\Delta_3<(>)0$, $\Delta_4>(<)0$, our results in Sections 6.1 and 6.2 remain true with α_{12}, α_{21}, β_{12}, β_{21}, p_2 exchanged for α_{13}, α_{31}, β_{13}, β_{31}, p_3.

② If $\Delta_2>(<)0$, $\Delta_3>(<)0$, $\Delta_4<(>)0$, our results in Sections 6.1 and 6.2 remain true with α_{12}, α_{21}, β_{12}, β_{21}, p_2 exchanged for α_{14}, α_{41}, β_{14}, β_{41}, p_4.

6.1 Boundary equilibria of system (14)

Next, we discuss the computation for $\bar{x}_1$, $\bar{x}_2$, $\bar{x}_3$, $\bar{x}_4$ in the case $R_1>1$ and $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$. Make the transformation

$$\left.\begin{aligned}&\bar{x}_1=u>0,\ \bar{x}_2=\Big(\frac{\tilde{\theta}_1}{\tilde{\omega}_1}+\frac{\tilde{\theta}_2}{\tilde{\omega}_2}\Big)\alpha_{21}u,\\&\bar{x}_3=\frac{\alpha_{31}u}{\tilde{\omega}_1},\ \bar{x}_4=\frac{\alpha_{41}u}{\tilde{\omega}_2},\ \tilde{\theta}_2=\frac{\Delta_4}{\Delta_3}\tilde{\theta}_1.\end{aligned}\right\}\tag{15}$$

Then u, $\tilde{\theta}_1$, $\tilde{\omega}_1$, $\tilde{\omega}_2$ satisfy the equations

$$\left.\begin{aligned}&-\tilde{\omega}_1\tilde{\omega}_2+(p_1-u)(h_1(\tilde{\theta}_1)\tilde{\omega}_2+h_2(\tilde{\theta}_2)\tilde{\omega}_1)=0,\\&p_2\tilde{\omega}_1\tilde{\omega}_2-(\tilde{\theta}_1\tilde{\omega}_2+\tilde{\theta}_2\tilde{\omega}_1)(1+\alpha_{21}u)=0,\\&p_3\tilde{\omega}_1-(1+\alpha_{31}u)=0,\\&p_4\tilde{\omega}_2-(1+\alpha_{41}u)=0,\end{aligned}\right\}\tag{16}$$

where

$$h_1(\tilde{\theta}_1)=\tilde{\theta}_1\alpha_{12}\alpha_{21}+\alpha_{13}\alpha_{31},$$
$$h_2(\tilde{\theta}_2)=\tilde{\theta}_2\alpha_{12}\alpha_{21}+\alpha_{14}\alpha_{41}.$$

Hence, by the last two equations in Eq. (16)

$$\tilde{\omega}_1=\frac{1}{p_3}(1+\alpha_{31}u),\ \tilde{\omega}_2=\frac{1}{p_4}(1+\alpha_{41}u). \quad (17)$$

Substituting Eq. (17) into Eq. (16), we have the following system of u and $\tilde{\theta}_1$:

$$\left.\begin{aligned}&(1+\alpha_{31}u)(1-2p_1p_4h_2(\tilde{\theta}_1)+\\&\quad(\alpha_{41}+2p_4h_2(\tilde{\theta}_2))u)+\\&\quad(1+\alpha_{41}u)(1-2p_1p_3h_1(\tilde{\theta}_1)+\\&\quad(\alpha_{31}+2p_3h_1(\tilde{\theta}_1))u)=0,\\&(1+\alpha_{31}u)(p_4\tilde{\theta}_2-p_1p_2p_4h_2(\tilde{\theta}_2+\\&\quad(p_2p_4h_2(\tilde{\theta}_2)+p_4\tilde{\theta}_2\alpha_{21})u)+\\&\quad(1+\alpha_{41}u)(p_3\tilde{\theta}_1-p_1p_2p_3h_1(\tilde{\theta}_1)+\\&\quad(p_2p_3h_1(\tilde{\theta}_1)+p_3\tilde{\theta}_1\alpha_{21})u)=0.\end{aligned}\right\}$$

Noticing the assumption that $\alpha_{31}=\alpha_{41}$, we obtain

$$\left.\begin{aligned}&1-p_1p_4h_2(\tilde{\theta}_2)-p_1p_3h_1(\tilde{\theta}_1)+\\&\quad(\alpha_{31}+p_4h_2(\tilde{\theta}_2)+p_3h_1(\tilde{\theta}_1))u=0,\\&p_4\tilde{\theta}_2+p_3\tilde{\theta}_1-p_1p_2p_4h_2(\tilde{\theta}_2)-p_1p_2p_3h_1(\tilde{\theta}_1)+\\&\quad(p_2p_4h_2(\tilde{\theta}_2)+p_4\tilde{\theta}_2\alpha_{21}+\\&\quad p_2p_3h_1(\tilde{\theta}_1)+p_3\tilde{\theta}_1\alpha_{21})u=0.\end{aligned}\right\} \quad (18)$$

From Eq. (18), we have

$$\frac{p_1p_4h_2(\tilde{\theta}_2)+p_1p_3h_1(\tilde{\theta}_1)-1}{\alpha_{31}+p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2)}=u=\frac{p_1p_2(p_4h_2(\tilde{\theta}_2)+p_3h_1(\tilde{\theta}_1))-(p_4\tilde{\theta}_2+p_3\tilde{\theta}_1)}{p_2p_4h_2(\tilde{\theta}_2)+p_2p_3h_1(\tilde{\theta}_1)+p_4\tilde{\theta}_2\alpha_{21}+p_3\tilde{\theta}_1\alpha_{21}},$$

which implies that $\tilde{\theta}_1$ must be a positive root of

$$G(\tilde{\theta}_1)=\frac{p_1p_4h_2(\tilde{\theta}_2)+p_1p_3h_1(\tilde{\theta}_1)-1}{\alpha_{31}+p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2)}-\frac{p_1p_2(p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2))-(p_4\tilde{\theta}_2+p_3\tilde{\theta}_1)}{p_2p_4h_2(\tilde{\theta}_2)+p_2p_3h_1(\tilde{\theta}_1)+p_4\tilde{\theta}_2\alpha_{21}+p_3\tilde{\theta}_1\alpha_{21}},$$
$$\tilde{\theta}_1\geqslant 0.$$

We can rewrite

$$G(\tilde{\theta}_1)=\frac{1}{(\alpha_{31}+p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2))(p_2p_4h_2(\tilde{\theta}_2)+p_2p_3h_1(\tilde{\theta}_1)+p_4\tilde{\theta}_2\alpha_{21}+p_3\tilde{\theta}_1\alpha_{21})}g(\tilde{\theta}_1),$$

where

$$\begin{aligned}g(\tilde{\theta}_1)=&(p_1p_4h_2(\tilde{\theta}_2)+p_1p_3h_1(\tilde{\theta}_1)-1)\cdot\\&(p_2p_4h_2(\tilde{\theta}_2)+p_2p_3h_1(\tilde{\theta}_1)+p_4\tilde{\theta}_2\alpha_{21}+p_3\tilde{\theta}_1\alpha_{21})-\\&(p_1p_2(p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2))-\\&(p_4\tilde{\theta}_2+p_3\tilde{\theta}_1))(\alpha_{31}+p_3h_1(\tilde{\theta}_1)+p_4h_2(\tilde{\theta}_2)).\end{aligned}$$

From the definition of $h_1(\tilde{\theta}_1)$ and $h_2(\tilde{\theta}_2)$, $g(\tilde{\theta}_1)$ is a quadratic function where the coefficient of $\tilde{\theta}_1{}^2$ is positive. Moreover,

$$g(0)=-p_2(p_4h_2(0)+p_3h_1(0))(1+p_1\alpha_{31})<0.$$

Hence, there exists a unique $\theta_1'>0$, such that $g(\theta_1')=0$, and

$$g(\theta_1)>0,\theta_1>\theta_1';\ g(\theta_1)<0,\ 0\leqslant\theta_1<\theta_1',$$

that is,

$$\left.\begin{aligned}&G(\theta_1')=0,\\&G(\theta_1)>0,\theta_1>\theta_1';\\&G(\theta_1)<0,\ 0\leqslant\theta_1<\theta_1'.\end{aligned}\right\} \quad (19)$$

From now on, we discuss the stability of the boundary equilibrium E_x. The Jacobian $\boldsymbol{J}(E_x)$ of Eq. (14) at E_x takes the form

$$\boldsymbol{J}(E_x)=\begin{pmatrix}\boldsymbol{C}_{11} & \boldsymbol{C}_{12}\\ 0 & \boldsymbol{C}_{22}\end{pmatrix},$$

where $\boldsymbol{C}_{11}$ is a stable matrix by Section 4 and

$$\boldsymbol{C}_{22}=\begin{pmatrix}-\gamma_1^y & \gamma_1^y(p_1-\bar{x}_1)\beta_{12} & \gamma_1^y(p_1-\bar{x}_1)\beta_{13} & \gamma_1^y(p_1-\bar{x}_1)\beta_{14}\\ \gamma_2^y(p_2-\bar{x}_2)\beta_{21} & -\gamma_2^y & 0 & 0\\ \gamma_3^y(p_3-\bar{x}_3)\beta_{31} & 0 & -\gamma_3^y & 0\\ \gamma_4^y(p_4-\bar{x}_4)\beta_{41} & 0 & 0 & -\gamma_4^y\end{pmatrix}.$$

We consider the following matrix

$$\tilde{\boldsymbol{C}}_{22}=\begin{pmatrix}-\gamma_4^y & 0 & 0 & \gamma_4^y(p_4-\bar{x}_4)\beta_{41}\\ 0 & -\gamma_3^y & 0 & \gamma_3^y(p_3-\bar{x}_3)\beta_{31}\\ 0 & 0 & -\gamma_2^y & \gamma_2^y(p_2-\bar{x}_2)\beta_{21}\\ \gamma_1^y(p_1-\bar{x}_1)\beta_{14} & \gamma_1^y(p_1-\bar{x}_1)\beta_{13} & \gamma_1^y(p_1-\bar{x}_1)\beta_{12} & -\gamma_1^y\end{pmatrix},$$

which is similar to $\boldsymbol{C}_{22}$. Note that the off-diagonal entries of $-\widetilde{\boldsymbol{C}}_{22}$ are nonpositive, diagonal entries of $-\widetilde{\boldsymbol{C}}_{22}$ are positive and that the first three leading principal minors of $-\widetilde{\boldsymbol{C}}_{22}$ are positive, if

$$\det(-\widetilde{\boldsymbol{C}}_{22}) = \det \boldsymbol{C}_{22} > 0.$$

Then, it follows from Ref. [2] that all eigenvalues of $-\widetilde{\boldsymbol{C}}_{22}$ have positive real parts. Hence, $\widetilde{\boldsymbol{C}}_{22}$ is stable and, equivalently, $\boldsymbol{C}_{22}$ is stable. Furthermore, from Eq. (16) we obtain

$$\theta'_1\tilde{\omega}_2 + \theta'_2\tilde{\omega}_1 = \tilde{\theta}_1\tilde{\omega}_2 + \tilde{\theta}_2\tilde{\omega}_1 = \frac{p_2 - \bar{x}_2}{(p_3 - \bar{x}_3)(p_4 - \bar{x}_4)}. \tag{20}$$

Now Eq. (20) and a straightforward calculation yield

$$\det \boldsymbol{C}_{22} = \gamma_1^y\gamma_2^y\gamma_3^y\gamma_4^y(p_1 - \bar{x}_1)(p_3 - \bar{x}_3)\cdot (p_4 - \bar{x}_4)(\Delta_3 + \Delta_2\tilde{\theta}_1)\left(\tilde{\omega}_2 + \frac{\Delta_4}{\Delta_3}\tilde{\omega}_1\right).$$

From this expression and the assumption that $\Delta_2 < 0$, $\Delta_3 > 0$, and $\Delta_4 > 0$, it is easy to check that E_x is linearly stable (unstable) if and only if

$$\Delta_3 + \Delta_2\tilde{\theta}_1 > 0 (< 0).$$

Hence, we have the results in the following theorem.

Theorem 6.2 Let $\theta_1^* = -\dfrac{\Delta_3}{\Delta_2}$, $\theta_2^* = -\dfrac{\Delta_4}{\Delta_3}\theta^*$, $h_1^* = h_1(\theta_1^*)$ and $h_2^* = h_2(\theta_2^*)$. Then E_x is stable (unstable) if and only if

$$\frac{p_1p_4h_2^* + p_1p_3h_1^* - 1}{\alpha_{31} + p_3h_1^* + p_4h_2^*} > \frac{p_1p_2(p_3h_1^* + p_4h_2^*) - (p_4\theta_2^* + p_3\theta_1^*)}{p_2p_4h_2^* + p_2p_3h_1^* + p_4\theta_2^*\alpha_{21} + p_3\theta_1^*\alpha_{21}}$$

$$\left(\frac{p_1p_4h_2^* + p_1p_3h_1^* - 1}{\alpha_{31} + p_3h_1^* + p_4h_2^*} < \frac{p_1p_2(p_3h_1^* + p_4h_2^*) - (p_4\theta_2^* + p_3\theta_1^*)}{p_2p_4h_2^* + p_2p_3h_1^* + p_4\theta_2^*\alpha_{21} + p_3\theta_1^*\alpha_{21}}\right)$$

and E_y is stable (unstable) if and only if

$$\frac{p_1p_4h_2^* + p_1p_3h_1^* - 1}{\beta_{31} + p_3h_1^* + p_4h_2^*} < \frac{p_1p_2(p_3h_1^* + p_4h_2^*) - (p_4\theta_2^* + p_3\theta_1^*)}{p_2p_4h_2^* + p_2p_3h_1^* + p_4\theta_2^*\beta_{21} + p_3\theta_1^*\beta_{21}}$$

$$\left(\frac{p_1p_4h_2^* + p_1p_3h_1^* - 1}{\beta_{31} + p_3h_1^* + p_4h_2^*} > \frac{p_1p_2(p_3h_1^* + p_4h_2^*) - (p_4\theta_2^* + p_3\theta_1^*)}{p_2p_4h_2^* + p_2p_3h_1^* + p_4\theta_2^*\beta_{21} + p_3\theta_1^*\beta_{21}}\right).$$

6.2 The positive endemic equilibrium of (14)

We first establish conditions for the existence of a positive coexistence equilibrium. Any equilibrium must satisfy the system

$$\left.\begin{aligned} & -x_i + (p_i - x_i - y_i)\sum_{j=1}^{4}\alpha_{ij}x_j = 0, \\ & -y_i + (p_i - x_i - y_i)\sum_{j=1}^{4}\beta_{ij}y_j = 0, \\ & i = 1,2,3,4. \end{aligned}\right\} \tag{21}$$

Let $q_i = p_i - x_i - y_i$, $i = 1,2,3,4$. Then

$$\left.\begin{aligned} & x_2 = q_2\alpha_{12}x_1,\ x_3 = q_3\alpha_{31}x_1,\ x_4 = q_4\alpha_{41}x_1, \\ & y_2 = q_2\beta_{21}y_1,\ y_3 = q_3\beta_{31}y_1,\ y_4 = q_4\beta_{41}y_1. \end{aligned}\right\} \tag{22}$$

Substituting Eq. (22) into Eq. (21), we have

$$x_1(1 - q_1(q_2\alpha_{12}\alpha_{21} + q_3\alpha_{13}\alpha_{31} + q_4\alpha_{14}\alpha_{41})) = 0,$$
$$y_1(1 - q_1(q_2\beta_{12}\beta_{21} + q_3\beta_{13}\beta_{31} + q_4\beta_{14}\beta_{41})) = 0.$$

Hence

$$q_2\alpha_{12}\alpha_{21} + q_3\alpha_{13}\alpha_{31} + q_4\alpha_{14}\alpha_{41} = q_2\beta_{12}\beta_{21} + q_3\beta_{13}\beta_{31} + q_4\beta_{14}\beta_{41}.$$

Denote

$$\theta_1^* := -\frac{\Delta_3}{\Delta_2} = \frac{\alpha_{13}\alpha_{31} - \beta_{13}\beta_{31}}{\beta_{12}\beta_{21} - \alpha_{12}\alpha_{21}},$$
$$h_1^* := \theta_1^*\alpha_{12}\alpha_{21} + \alpha_{13}\alpha_{31},$$
$$\theta_2^* := -\frac{\Delta_4}{\Delta_2} = \frac{\alpha_{14}\alpha_{41} - \beta_{14}\beta_{41}}{\beta_{12}\beta_{21} - \alpha_{12}\alpha_{21}},$$
$$h_2^* := \theta_2^*\alpha_{12}\alpha_{21} + \alpha_{14}\alpha_{41}.$$

Then

$$\theta_2^* = \theta_1^*\frac{\Delta_4}{\Delta_3} := \theta_1^*\theta,$$

$$q_2 = \theta_1^* q_3 + \theta_2^* q_4 \tag{23}$$

and it follows from Eqs. (22) and (23) that a positive solution of Eq. (21) must have the form

$$\left.\begin{aligned} & x_1 = u,\ x_2 = \left(\frac{\theta_1^*}{\omega_1} + \frac{\theta_2^*}{\omega_2}\right)\alpha_{21}u, \\ & x_3 = \frac{\alpha_{31}u}{\omega_1}, x_4 = \frac{\alpha_{41}u}{\omega_2}, \\ & y_1 = v, y_2 = \left(\frac{\theta_1^*}{\omega_1} + \frac{\theta_2^*}{\omega_2}\right)\beta_{21}v, \\ & y_3 = \frac{\beta_{31}v}{\omega_1}, y_4 = \frac{\beta_{41}v}{\omega_2}, \end{aligned}\right\} \tag{24}$$

where

$$\omega_1 := \frac{1}{q_3},\ \omega_2 := \frac{1}{q_4}.$$

By substituting Eq. (24) into Eq. (21), we obtain equations for u, v, ω_1, ω_2 in the following form:

$$\left.\begin{aligned}
&\frac{u}{\omega_1\omega_2}[-\omega_1\omega_2+(p_1-u-v)(\theta_1^*\alpha_{12}\alpha_{21}+\alpha_{13}\alpha_{31})\omega_2+\\
&\qquad(\theta_2^*\alpha_{12}\alpha_{21}+\alpha_{14}\alpha_{41})\omega_1]=0,\\
&\frac{\alpha_{21}u}{\omega_1\omega_2}[p_2\omega_1\omega_2-(\theta_1^*\omega_2+\theta_2^*\omega_1)(1+\alpha_{21}u+\beta_{21}v)]=0,\\
&\frac{\alpha_{31}u}{\omega_1}[p_3\omega_1-(1+\alpha_{31}u+\beta_{31}v)]=0,\\
&\frac{\alpha_{41}u}{\omega_2}[p_4\omega_2-(1+\alpha_{41}u+\beta_{41}v)]=0,\\
&\frac{v}{\omega_1\omega_2}[-\omega_1\omega_2+(p_1-u-v)(\theta_1^*\beta_{12}\beta_{21}+\beta_{13}\beta_{31})\omega_2+\\
&\qquad(\theta_2^*\beta_{12}\beta_{21}+\beta_{14}\beta_{41})\omega_1]=0,\\
&\frac{\beta_{21}v}{\omega_1\omega_2}[p_2\omega_1\omega_2-(\theta_1^*\omega_2+\theta_2^*\omega_1)(1+\alpha_{21}u+\beta_{21}v)]=0,\\
&\frac{\beta_{31}v}{\omega_1}[p_3\omega_1-(1+\alpha_{31}u+\beta_{31}v)]=0,\\
&\frac{\beta_{41}v}{\omega_2}[p_4\omega_2-(1+\alpha_{41}u+\beta_{41}v)]=0.
\end{aligned}\right\}\tag{25}$$

Notice that

$$\theta_1^*\alpha_{12}\alpha_{21}+\alpha_{13}\alpha_{31}=\theta_1^*\beta_{12}\beta_{21}+\beta_{13}\beta_{31}=h_1^*,$$
$$\theta_2^*\alpha_{12}\alpha_{21}+\alpha_{14}\alpha_{41}=\theta_2^*\beta_{12}\beta_{21}+\beta_{14}\beta_{41}=h_2^*.$$

Then, Eq. (25) is reduced to the system

$$\left.\begin{aligned}
&\omega_1\omega_2-(p_1-u-v)(h_1^*\omega_2+h_2^*\omega_1)=0,\\
&p_2\omega_1\omega_2-(\theta_1^*\omega_2+\theta_2^*\omega_1)(1+\alpha_{21}u+\beta_{21}v)=0,\\
&p_3\omega_1-(1+\alpha_{31}u+\beta_{31}v)=0,\\
&p_4\omega_2-(1+\alpha_{41}u+\beta_{41}v)=0,
\end{aligned}\right\}\tag{26}$$

and system (21) has a positive solution if and only if system (26) has a positive solution.

Hence, by the third equation and the fourth equation in Eq. (26)

$$\omega_1=\frac{1}{p_3}(1+\alpha_{31}u+\beta_{31}v),\ \omega_2=\frac{1}{p_4}(1+\alpha_{41}u+\beta_{41}v).\tag{27}$$

Substituting (27) into (26), we have the following system of u and v:

$$\begin{aligned}
&(1+\alpha_{31}u+\beta_{31}v)(1-2p_1p_4h_2^*+\\
&\quad(\alpha_{41}+2p_4h_2^*)u+(\beta_{41}+2p_4h_2^*)v)+\\
&\quad(1+\alpha_{41}u+\beta_{41}v)(1-2p_1p_3h_1^*+\\
&\quad(\alpha_{31}+2p_3h_1^*)u+(\beta_{31}+2p_3h_1^*)v)=0,\\
&(1+\alpha_{31}u+\beta_{31}v)(p_4\theta_2^*-p_1p_2p_4h_2^*+\\
&\quad(p_2p_4h_2^*+p_4\theta_2^*\alpha_{21})u+\\
&\quad(p_2p_4h_2^*+p_4\theta_2^*\beta_{21})v)+\\
&\quad(1+\alpha_{41}u+\beta_{41}v)(p_3\theta_1^*-p_1p_2p_3h_1^*+\\
&\quad(p_2p_3h_1^*+p_3\theta_1^*\alpha_{21})u+\\
&\quad(p_2p_3h_1+p_3\theta_1^*\beta_{21})v)=0.
\end{aligned}$$

Noticing the assumptions that $\alpha_{31}=\alpha_{41}$ and $\beta_{31}=\beta_{41}$, we have

$$\left.\begin{aligned}
&(1+\alpha_{31}u+\beta_{31}v)(2-2p_1p_4h_2^*-2p_1p_3h_1^*+\\
&\quad(\alpha_{41}+2p_4h_2^*+\alpha_{31}+2p_3h_1^*)u+\\
&\quad(\beta_{41}+2p_4h_2^*+\beta_{31}+2p_3h_1^*)v)=0,\\
&(1+\alpha_{31}u+\beta_{31}v)(p_4\theta_2^*+p_3\theta_1^*-p_1p_2p_4h_2^*-\\
&\quad p_1p_2p_3h_1^*+(p_2p_4h_2^*+p_4\theta_2^*\alpha_{21}+\\
&\quad p_2p_3h_1^*+p_3\theta_1^*\alpha_{21})u+(p_2p_4h_2^*+\\
&\quad p_4\theta_2^*\beta_{21}+p_2p_3h_1+p_3\theta_1^*\beta_{21})v)=0.
\end{aligned}\right\}\tag{28}$$

After simple algebraic manipulations, we arrive at the following results.

Theorem 6.3 System (14) has a unique positive equilibrium if and only if one of the following conditions is satisfied:

(H1) $p_1p_4h_2^*+p_1p_3h_1^*-1>0$, $p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)>0$, and

$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}>\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}>\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}.$$

(H2) $p_1p_4h_2^*+p_1p_3h_1^*-1>0$, $p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)>0$, and

$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}<\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}<\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}.$$

Remark In Theorem 6.3, we exclude the very special case where

$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_2\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}=\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}=\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}.$$

In this case it is easy to see from Eq. (28) that system (14) has a continuum of interior equilibria.

As an immediate consequence of Theorems 6.2 and 6.3, the following results are obtained.

Corollary 6.4 Eq. (14) has a coexistence equilibrium if and only if the boundary equilibria both exist and have the same stability. Furthermore, the coexistence equilibrium is stable (unstable) if the boundary equilibria both are unstable (stable).

Example 6.5 We now use the following set of parameters:

$$\alpha_{12}=\beta_{31}=\alpha_{13}=\beta_{41}=p_1=p_2=p_3=p_4=1,$$
$$\alpha_{14}=\beta_{21}=\alpha_{21}=\beta_{13}=2,\ \alpha_{31}=\alpha_{41}=\beta_{12}=\beta_{14}=3.$$

Then

$$\Delta_2=-4, \Delta_3=1, \Delta_4=3,$$
$$\theta_1^*=\frac{1}{4}, \theta_2^*=\frac{3}{4}, h_1^*=\frac{7}{2}, h_2^*=\frac{15}{2},$$
$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}=\frac{14}{13}>$$
$$\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}=1>$$
$$\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}=\frac{12}{13}.$$

Hence, from Theorem 6.3 and Corollary 6.4, the coexistence equilibrium exists and it is stable.

Example 6.6 Let

$$p_1=p_2=p_3=p_4=\alpha_{12}=\alpha_{31}=\alpha_{41}=\beta_{13}=\beta_{14}=1,$$
$$\beta_{21}=2,\ \beta_{12}=\beta_{41}=\beta_{31}=3,$$
$$\alpha_{13}=\alpha_{14}=\alpha_{21}=4.$$

Then

$$\Delta_2=-2, \Delta_3=1, \Delta_4=1,$$
$$\theta_1^*=\frac{1}{2}, \theta_2^*=\frac{1}{2}, h_1^*=6, h_2^*=6,$$
$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}=\frac{13}{16}<$$
$$\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}=1<$$
$$\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}=\frac{15}{14}.$$

Hence, by Theorem 6.3 and Corollary 6.4, the coexistence equilibrium exists and it is unstable.

7 Conclusion

In this section we mainly summarize our results and give their biological meanings.

In this article, we have mainly studied the asymptotical behavior of general $2N$-groups STD, by the theory of type-K monotone dynamical system. Especially as $N=4$, under two limited conditions, we have given the complete results in Section 6. It is shown that, if there is no positive equilibrium, then one of the nontrivial boundary equilibria attracts all positive solutions; if there is only one positive equilibrium, then the unique positive equilibrium attracts all the positive solutions or the only two positives solutions tend to it and the others tend to boundary equilibrium; otherwise the system has a continuum of equilibria.

System (3) is not only an epidemic model but also a model incorporating competition among multiple strains. One of the most important subjects in epidemic models is to obtain a threshold or reproductive numbers that determine the persistence or extinction of the disease. Theorem 3.2 provides the reproductive numbers R_1, R_2 of the two strains in this model, which are the threshold parameters for the diseases to invade into the population. From Ref. [17], we learn that R_1, R_2 are the total numbers of secondary cases generated by infection of the disease. When the two strains are able to invade into the same population, they will compete for the same resource, i.e. the susceptibles. Because the model incorporates competition between two strains, we have studied the conditions for the coexistence as well as the competitive exclusion.

Theorem 4.2 is the principal mathematical results of boundary equilibria. Moreover, the conditions and results in this theorem reflect some simple causes and results in biology.

The case $\Delta_j\geqslant(\leqslant)0$, $j=2,3,\cdots,N$ and $\sum_{j=2}^{N}\neq 0$. Biologically, $\Delta_j>(<)0$, $j=2,3,\cdots,N$ can be understood to mean that the epidemic of the disease with strain 1 is better (worse) in the sexual activity, between colonizing males and females of the colonizing group f_j, $j=2,3,\cdots,N$. In fact, it follows from the expression of Δ_j that we have

$$p^m p^{f_j}\Delta_j=\frac{r^m\beta_1^m}{\sigma_1^m}\frac{r^{f_j}\beta_1{}^{f_j}}{\sigma_1{}^{f_j}}-\frac{r^m\beta_2^m}{\sigma_2^m}\frac{r^{f_j}\beta_2{}^{f_j}}{\sigma_2{}^{f_j}}.$$

The first and the second items of the above formula can be understood as the number of secondary cases in the males and females of group f_j generated by infection of strain 1 and strain 2, respectively. We can easily see that $\Delta_j>(<)0$, $j=2,3,\cdots,N$ imply the number of secondary cases in the males and females of group f_j generated by infection of strain 1 is greater (less) than generated by infection of strain 2, i. e. , strain 1 is better (worse) of colonizing the males and females of colonizing group f_j. These lead to the fact that strain 1 may persist in the population while strain 2 will go extinct. Then, the competitive exclusion will hold, i. e. , E_x is global asymptotically stable.

Theorem 6.2 and Theorem 6.3 are the mathematical results of system (14) under two limited conditions. Next, we will explain those biologically meanings of the conditions and results in Theorems 6.2 and 6.3. We pick up two typical cases to explain their biological meanings. The other cases can be explained in the same way. For clearer explanation, males are excluded from our consideration.

(Ⅰ) The case $R_1>1$, $R_2>1$, $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$,

$$\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{\alpha_{31}+p_3h_1^*+p_4h_2^*}>\frac{p_1p_2(p_3h_1^*+p_4h_2^*)-(p_4\theta_2^*+p_3\theta_1^*)}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}.$$

It follows from the above that $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$ means strain 1 is better at colonizing group 3 and group 4, but worse at colonizing group 2, and strain 2 has the opposite order to that of strain 1. While from

$$\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{\alpha_{31}+p_3h_1^*+p_4h_2^*}>\frac{p_1p_2(p_3h_1^*+p_4h_2^*)-(p_4\theta_2^*+p_3\theta_1^*)}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}.$$

we have

$$(\beta_{12}\beta_{21}-\alpha_{12}\alpha_{21})(p_2-\bar{x}_2)+[(\beta_{13}\beta_{31}-\alpha_{13}\alpha_{31})\bar{\omega}_2+(\beta_{14}\beta_{41}-\alpha_{14}\alpha_{41})\bar{\omega}_1](p_3-\bar{x}_3)(p_4-\bar{x}_4)<0.$$

And $\beta_{12}\beta_{21}(p_2-\bar{x}_2)$ is the number of secondary cases generated by infection of strain 2 in group 2 when the number of susceptibles in the females of group 2 is $p_2-\bar{x}_2$. Briefly $\sum_{j=2}^{4}\beta_{1j}\beta_{j1}(p_j-\bar{x}_j)$ denotes the total number of secondary cases generated by the infection of strain 2 when the system has strain 1 only and is in balance. While $\sum_{j=2}^{4}\alpha_{1j}\alpha_{j1}(p_j-\bar{x}_j)$ denotes the total number of secondary cases generated by the infection of strain 1 when the system has strain 1 only and is in balance. So

$$\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{\alpha_{31}+p_3h_1^*+p_4h_2^*}>\frac{p_1p_2(p_3h_1^*+p_4h_2^*)-(p_4\theta_2^*+p_3\theta_1^*)}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}$$

can almost be understood that the number of secondary cases generated by infection of strain 2 is always smaller than that of strain 1. Which implies that females cannot provide proper refuge for strain 2. Therefore, strain 1 may persist in females while strain 2 will go extinct, i. e. , E_x is stable.

(Ⅱ) The case $R_1>1$, $R_2>1$, $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$,

$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}>\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}>\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}.$$

We have learned that $\Delta_2<0$, $\Delta_3>0$, $\Delta_4>0$ means group 2 creates refuge for strain 2 and groups 3, 4 create refuge for strain 1. Meanwhile

$$\frac{\alpha_{31}+p_3h_1^*+p_4h_2^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\alpha_{21}+p_3\theta_1^*\alpha_{21}}>\frac{p_1p_4h_2^*+p_1p_3h_1^*-1}{p_1p_2(p_4h_2^*+p_3h_1^*)-(p_4\theta_2^*+p_3\theta_1^*)}>\frac{\beta_{31}+p_4h_2^*+p_3h_1^*}{p_2p_4h_2^*+p_2p_3h_1^*+p_4\theta_2^*\beta_{21}+p_3\theta_1^*\beta_{21}}.$$

can be approximately understood that the population may create proper refuge for stains 1 and 2. It is such proper refuges that make the coexistence of the two strains possible.

Furthermore, from the above discussion, the positive equilibrium E^* is globally asymptotically stable.

References

[1] Anderson R M, May R R. Infectious Diseases of Humans [M]. Oxford: Oxford Science Publications, 1991.

[2] Berman A, Neumann M, Stern R. Nonnegative Matrices in Dynamics Systems[M]. New York: John Wiley and Son, 1989.

[3] Blythe S P, Brauer F, Castillo-Chavez C, et al. Sexually transmitted diseases with recruitment [R]. NY: Corenll University, 1993: Biometrics Unit Technical Report BU-1193-M.

[4] Brauer F, Blythe S P, Castillo-Chavez C. Demographic recruitment in sexually transmitted disease models[R]. NY: Corenll University, 1992: Biometrics Unit Technical Report BU-1154-M.

[5] Castillo-Chavez C, Huang W, Li J. Competitive exclusion in gonorrhea models and other sexually transmitted diseases[J]. SIAM J Appl Math, 1996, 56: 494-508.

[6] Castillo-Chavez C, Huang W, Li J. The effects of female's susceptibility on coexistence of multiple pathogen strains of sexually transmitted diseases[J]. J Math Biol, 1996, 35: 503-522.

[7] Castillo-Chavez C, Huang W, Li J. Competitive exclusion and coexistence of multiple strains in an SIS STD model[J]. SIAM J Appl Math, 1999, 59: 1 790-1 811.

[8] Castillo-Chavez C, Hethcote H W, Andreasen V, et al. Cross-immunity in the dynamics of homogeneous and heterogeneous populations [C]// Mathematical Ecology. Singapore: World Scientific, 1988: 303-316.

[9] Castillo-Chavez C, Hethcote H W, Andreasen V, et al. Epidemiological models with age structure, proportionate mixing, and cross-immunity[J]. J Math Biol, 1989, 27: 233-258.

[10] Castillo-Chavez C, Thieme H R. Asymptotically autonomous epidemic models [C]// Mathematical Population Dynamics: Analysis of Heterogeneity, Volume One: Theory of Epidemics. Winnipeg: Wuerz Publishing, 1995: 33-50.

[11] Castillo-Chavez C, Huang W, Li J. Dynamics of multiple pathogen strains in heterosexual epidemiological models[C]// Differential Equations and Applications to Biology and Industry. Singapore: World Scientific,1995: 289-298.

[12] Ewald W P. The evolution of virulence[J]. Scientific American, 1993, 268: 86-93.

[13] Ewald W P. Evolution of Infectious Disease [M]. Oxford: Oxford University Press, 1994.

[14] Hadeler K P, Castillo-Chavez C. A core group model for disease transmission[R]. NY: Cornell University, Mathematical Science Institute, 1994: Technical Report 94-42.

[15] Hethcote H W, Yoke J A. Gonorrhea Transmission Dynamics and Control [M]. New York: Springer-Verlag, 1984.

[16] Hess P. Periodic Parabolic Boundary Value Problems and Positivity [M]. Harlow, Essex, England: Longman,1991.

[17] Li J, Ma Z, Blythe S P, et al. Coexistence of pathogens in sexually-transmitted disease models[J]. J Math Biol, 2003, 47: 547-568.

[18] Hsu Schmitz S F. Some theories, estimation methods and applications of marriage functions in demography and epidemiology[D]. NY: Cornell University, 1993.

[19] Smith H L. Cooperative systems of differential equations with concave nonlinearities [J]. Nonlinear Analysis, Theory Methods and Applications, 1986, 10:1 037-1 052.

[20] Smith H L. Monotone Dynamical Systems [M]. Providence, Rhode Island: American Mathematical Society, 1995.

[21] Smith H L. Systems of ordinary differential equations which generate an order preserving flow: A survey of results[J]. SIAM Rev, 1988, 30: 87-113.

[22] Thieme H R. Convergence results and a Poincare-Bendixson tricho-tomy for asymptotically autonomous differential equations [J]. J Math Biol, 1992, 30: 755-763.

[23] Thieme H R. Asymptotically autonomous differential equations in the plane[J]. Rocky Mountain J Math, 1994, 24: 351-380.

[24] Zhao X Q, Jing Z J. Global asymptotic behavior in some cooperative systems of functional differential equations [J]. Canad Appl Math Quar, 1996, 4: 421-444.