

## AN ECO–EPIDEMIOLOGICAL MODEL IN TWO COMPETING SPECIES

MATS GYLLENBERG, XIAOLI LIU AND PING YAN

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*Abstract.* The population sizes of species are affected not only by ecological interactions, such as predation and competition, but also by infectious diseases. In this paper, we propose a model combining disease and competition, and try to understand how the disease affects the two competing species. We assume that only one of the species is susceptible to an SI type disease with mass action incidence, and that infected individuals do not reproduce but suffer additional disease induced death. We further assume that infection does not reduce the competitive ability of infectives. We show that if species 1 is a superior competitor without disease, then infection of species 1 can enable an inferior competitor to coexist, either as a stable equilibrium or as a limit cycle. If in the absence of the disease, the two species coexist, then the introduction of the disease is partially determined by the basic reproduction number. If the basic reproduction number is larger than 1, then our system is uniformly persistent and the unique coexisting endemic disease equilibrium is globally stable under certain conditions. Meanwhile, if species 1 is an inferior competitor without disease, then infection of species 1 can not change the outcomes under certain conditions.

### 1. Introduction

Population sizes of species are affected not only by ecological factors, such as competition and predation, but also by infectious diseases. In this paper, we investigate how a disease affects two competing species. We assume that, in the absence of the disease, birth, death, as well as intra- and interspecific competition are modelled by the Lotka–Volterra equations:

$$\begin{aligned} N_1' &= N_1(r_1 - a_{11}N_1 - a_{12}N_2), \\ N_2' &= N_2(r_2 - a_{21}N_1 - a_{22}N_2), \end{aligned} \quad (1.1)$$

where  $N_i = N_i(t)$  is the number of individuals in species  $i$  and  $t \geq 0$ .  $b_i$  and  $d_i$  are the per capita birth and death rate of species  $i$ , respectively, and hence  $r_i = b_i - d_i$  is the per capita growth rate of species  $i$  at low densities.  $a_{ij}$  is the competition coefficient.  $a_{ij}/r_i$  is the inhibition coefficient of species  $j$  on the growth of species  $i$ .

We assume that only one of the species is susceptible to the disease and that the disease is of SI type. The disease is directly transmitted with mass action incidence

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and  $\lambda$  is the mass action coefficient (transmission rate). The birth rate is density independent. We also assume that infected individuals do not reproduce, but are subject to an additional disease induced death rate  $\nu$ . Moreover, the disease does not affect the competitive ability of infectives. Even though the model is based on these simplifying assumptions, it captures the essence of how certain diseases affect competing species.

Our model takes the following form:

$$\begin{aligned} S' &= S(r_1 - a_{11}S - a_{11}I - a_{12}N_2 - \lambda I), \\ I' &= I(\lambda S - a_{11}S - a_{11}I - a_{12}N_2 - u_I), \\ N_2' &= N_2(r_2 - a_{21}S - a_{21}I - a_{22}N_2), \end{aligned} \quad (1.2)$$

where  $S = S(t)$ ,  $I = I(t)$  is the number of susceptibles and infectives in species 1, respectively.  $S + I = N_1$ ,  $u_I = d_1 + \nu$  and all parameters are assumed to be strictly positive.

Van den Driessche and Zeeman [5] considered a similar model, in which they also assumed that only one of the species was susceptible to the disease, but they assumed that infectives could reproduce and that there was pure vertical transmission. In addition, they assumed that  $a_{11}$  was bigger than the horizontal transmission rate  $\lambda$ . Their assumptions led to a three dimensional competitive Lotka-Volterra system, which could be analyzed using the theory of Hirsch [9] and Zeeman [17]. Usually, the three dimensional dynamical systems combining disease and competition are not competitive Lotka-Volterra systems, such as system (1.2). The method used by Van den Driessche and Zeeman [5] cannot be used for our model. In this paper, we use a new method to analyze the dynamical behavior, in particular to prove global stability.

Host-host-pathogen models have been studied previously. Holt and Pickering [11] studied a model in which two hosts shared a directly transmitted disease while host populations could grow exponentially. Begon et al. [2] examined the situation in which two hosts were affected by the same pathogen but the two hosts were subject to self regulation (intra-specific competition). Both papers provided insights of predicting species coexistence and exclusion. Anderson and May [1] considered a two hosts model with intra- and interspecific competition for a limited resource but only one host was affected by a directly transmitted pathogen. Their model predicted the quite expected outcomes, eg, that disease caused stable coexistence, but it did not predict oscillatory phenomena. Venturino [16] considered a similar model of SIS type and found periodic solutions by numerical simulations when there was no recovery. Greenman and Hudson [6] studied the case in which two competing hosts shared a directly transmitted disease of SI type. They provided the possibility of both species coexistence and exclusion equilibria. Saenz and Hethcote [15] examined two host SIS, SIR and SIRS models with frequency dependent incidence. They found that SIS type model with birth rate density independent had the classical endemic dynamical behavior. Han and Pugliese [8] also considered a two host SIS model with mass action. They provided conditions for the persistence of either hosts or pathogens.

Most of those who have considered host-host-pathogen models used linearization techniques in their analysis. The purpose of this paper is to analyze qualitatively the dynamical behavior of system (1.2), in particular with respect to Hopf bifurcation, limit

cycles and global stability. To do this we need much more powerful methods than linearization.

The paper is organized as follows. In Section 2, we recall the dynamical behavior of the Lotka-Volterra system (1.1). Disregarding degenerate cases, there are four essentially different phase portraits of system (1.1). Later, in Section 5, we give a detailed account of the dynamics of the eco-epidemiological model (1.2) in each of these four cases. Before that we discuss the corresponding one-species eco-epidemiological model, that is, system (1.2) without species 2. In Sections 4 and 5 we treat the full model (1.2). In Section 4 we present some preliminaries, including existence of equilibria, local stability of boundary equilibria of system (1.2), and a framework for proving global stability of a unique interior equilibrium. The analysis can be found in Section 5. In Subsections 5.1 and 5.2, we prove that infection of a superior competitor can enable an inferior competitor to coexist, either as a stable steady state or as a limit cycle. In Subsection 5.3, in which two species coexist without disease, we introduce a basic reproduction number which is defined in the disease-free coexistence steady state. We show that under certain conditions, if the basic reproduction number is lower than 1, then the disease-free coexistence equilibrium of system (1.2) is globally stable. If the basic reproduction number is larger than 1, we show that system (1.2) is uniformly persistent, and if two inequalities are satisfied, then the unique interior equilibrium of system (1.2) is globally stable. In Subsection 5.4, where species 1 is an inferior competitor, we show that if a certain inequality holds, then infection of species 1 is unable to change the outcome. From a biological point of view it seems reasonable to conjecture that the inequality can be dropped from the assumptions. We also do numerical simulations in each case to support our analytical results. We close the paper by a brief discussion.

## 2. The Lotka-Volterra model without disease

A complete description of the dynamics of the Lotka-Volterra competition model (1.1) without disease can be found for instance in [10] and can be summarized as follows: System (1.1) has three boundary equilibrium points,  $E(0, 0)$ ,  $E_1(r_1/a_{11}, 0)$  and  $E_2(0, r_2/a_{22})$ . These boundary equilibria correspond to both species absent, or one species being absent while the other is at its carrying capacity. Solutions starting on a positive axis approach the carrying capacity equilibrium on that axis. We define the first and second zero-isoclines of system (1.1) as the straight lines on which  $N'_1 = 0$  and  $N'_2 = 0$ , respectively. In addition to the degenerate case in which the two zero-isoclines coincide, we have the following four possibilities:

- (A)  $r_2a_{11} < r_1a_{21}$  and  $r_2a_{12} < r_1a_{22}$ . The two zero-isoclines do not intersect and the first is above the second. Species 1 inhibits species 2 more than it inhibits itself and species 2 inhibits itself more than it inhibits species 1. Species 1 wins the competition and all paths with  $N_1(0) > 0$  approach the equilibrium  $E_1$ .
- (B)  $r_2a_{11} < r_1a_{21}$  and  $r_1a_{22} < r_2a_{12}$ . Each species inhibits the other more than it inhibits itself. The two zero-isoclines intersect at an unstable saddle equilibrium in

the interior of  $\mathbb{R}_+^2$ . There exists a separatrix through the interior equilibrium and the origin with solutions starting below the separatrix going to the equilibrium  $E_1$ , and solutions starting above it going to the boundary equilibrium  $E_2$ .

- (C)  $r_1 a_{21} < r_2 a_{11}$  and  $r_2 a_{12} < r_1 a_{22}$ . Each species inhibits itself more than it inhibits the other species. In this case, the two zero-isoclines intersect, but now the interior equilibrium is attractive, and all solutions starting with positive initial values approach this interior equilibrium. The two species coexist.
- (D)  $r_1 a_{21} < r_2 a_{11}$  and  $r_1 a_{22} < r_2 a_{12}$ . The two zero-isoclines do not intersect and the second lies entirely above the first. Species 2 inhibits species 1 more than it inhibits itself and species 1 inhibits itself more than it inhibits species 2. Species 2 wins the competition and the boundary equilibrium  $E_2$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^2$ .

In Section 5 we give a detailed analysis of how the introduction of a disease governed by (1.2) will affect the population dynamics in the four cases (A) – (D).

### 3. The one-species SI-model

In this section we investigate the following simple one-species eco-epidemiological model obtained by putting  $N_2 = 0$  in system (1.2):

$$\begin{aligned} S' &= S(r_1 - a_{11}S - a_{11}I - \lambda I), \\ I' &= I(\lambda S - a_{11}S - a_{11}I - u_I). \end{aligned} \quad (3.1)$$

The system (3.1) has two boundary equilibria. One is  $(S, I) = (0, 0)$ , which is attractive in the  $I$  direction and unstable in the  $S$  direction, and the other is  $(S, I) = (r_1/a_{11}, 0)$ , which is attractive in the  $S$  direction.

As is the case for all epidemiological models, the existence of an interior (*endemic*) equilibrium and the stability of the disease-free and endemic equilibria are determined by the basic reproduction number  $R_0$  [4]. There is a general procedure for calculating  $R_0$  as the spectral radius of the next generation operator [3], but for this simple model  $R_0$  can readily be written down directly from its verbal interpretation. The basic reproduction number is the expected number of secondary cases produced by one typical infected individual in an otherwise disease free population. The average infectious period of a typical infected individual is  $1/(r_1 + u_I)$ , and an infected individual will on average infect  $\lambda r_1/a_{11}$  individuals per unit of time when the population is fully susceptible. Hence

$$R_0 = \frac{\lambda S}{a_{11}S + u_I} = \frac{\lambda r_1/a_{11}}{r_1 + u_I}.$$

The following lemma shows that the intuitively expected result is indeed true. Analogous theorems hold true for a large variety of epidemiological models.

LEMMA 1. Consider the model (3.1). If  $R_0 < 1$ , there is no interior positive equilibrium and the disease-free equilibrium  $(S, I) = (r_1/a_{11}, 0)$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^2$ . If  $R_0 > 1$ , then there exists a unique positive (endemic) equilibrium  $(\bar{S}, \bar{I}) = (1/\lambda^2)(u_I\lambda + a_{11}(u_I + r_1), r_1\lambda - a_{11}(u_I + r_1))$  and it is a globally asymptotically stable focus in  $\text{int}\mathbb{R}_+^2$ .

*Proof.* By directly calculating the endemic equilibrium  $(\bar{S}, \bar{I})$  one finds that both components are positive, if and only if  $r_1\lambda - a_{11}(u_I + r_1) > 0$ , which is equivalent to  $R_0 > 1$ . We write  $F_1(S, I) = S(r_1 - a_{11}S - a_{11}I - \lambda I)$ ,  $F_2(S, I) = I(\lambda S - a_{11}S - a_{11}I - u_I)$  and  $F(S, I) = (F_1(S, I), F_2(S, I))^T$ . Define the scalar valued (Dulac) function  $\varphi$  by  $\varphi(S, I) = 1/(SI)$ . One easily verifies that  $\text{div}(\varphi F) < 0$ . Furthermore, all solutions of system (3.1) are bounded in a simply connected region. By the Poincaré-Dulac theorem (see [18], p.195), there is no periodic orbit for system (3.1), and  $(S, I)$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^2$  if  $R_0 < 1$  and  $(\bar{S}, \bar{I})$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^2$  if  $R_0 > 1$ .

#### 4. The two-species SI-model: Preliminaries

In this section we give some preliminaries on the full two-species model needed for the more detailed analysis of Section 5.

For system (1.2), solutions with nonnegative initial values remains nonnegative for all further time. It also eventually satisfy  $0 \leq \{S(t), I(t)\} \leq r_1/a_{11}$ ,  $0 \leq N_2(t) \leq r_2/a_{22}$ .

##### 4.1. Equilibria

System (1.2) has at most five equilibria on the boundary of  $\mathbb{R}_+^3$ . They are the origin  $O = (0, 0, 0)$ , the two axial equilibria

$$Q_S = (r_1/a_{11}, 0, 0), Q_{N_2} = (0, 0, r_2/a_{22}),$$

and possibly the two points

$$Q_{SI} = \frac{1}{\lambda^2}(u_I\lambda + a_{11}(u_I + r_1), r_1\lambda - a_{11}(u_I + r_1), 0),$$

$$Q_{SN_2} = \frac{1}{\Delta}(r_1a_{22} - r_2a_{12}, 0, r_2a_{11} - r_1a_{21}),$$

in the coordinate planes. Here

$$\Delta = a_{11}a_{22} - a_{12}a_{21}.$$

For later use, we write  $Q_{SN_2} = (\hat{S}, 0, \hat{N}_2)$ . From Section 3 we know that  $Q_{SI}$  exists and is globally asymptotically stable in the  $SI$  plane if and only if  $R_0 > 1$ . As explained in Section 2,  $Q_{SN_2}$  exists in and only in cases (B) and (C). Let

$$A = \begin{bmatrix} a_{11} & a_{11} + \lambda & a_{12} \\ \lambda - a_{11} & -a_{11} & -a_{12} \\ a_{21} & a_{21} & a_{21} \end{bmatrix}.$$

If  $\det(A) \neq 0$ , then system (1.2) has an equilibrium

$$Q_{SIN_2} = (S^*, I^*, N_2^*) = A^{-1}(r_1, u_I, r_2).$$

A straightforward calculation gives

$$\begin{aligned} S^* &= \frac{1}{a_{22}\lambda^2}(\Delta(r_1 + u_I) + \lambda(a_{22}u_I + a_{12}r_2)), \\ I^* &= \frac{1}{a_{22}\lambda^2}(-\Delta(r_1 + u_I) + \lambda(a_{22}r_1 - a_{12}r_2)), \\ N_2^* &= \frac{1}{a_{22}\lambda}(\lambda r_2 - a_{21}(r_1 + u_I)), \end{aligned} \tag{4.1}$$

and  $S^* + I^* = (r_1 + u_I)/\lambda$ .  $Q_{SIN_2}$  is biologically feasible and a coexistence endemic equilibrium if  $S^*, I^*, N_2^* > 0$ . Note that

$$\begin{aligned} S^* &= \frac{1}{a_{22}\lambda^2}[\Delta(r_1 + u_I) + \lambda(a_{22}u_I + a_{12}r_2)] \\ &= \frac{1}{a_{22}\lambda^2}[a_{11}a_{22}(r_1 + u_I) + \lambda a_{22}u_I + a_{12}(\lambda r_2 - a_{21}(r_1 + u_I))]. \end{aligned}$$

So, if  $N_2^* > 0$ , then we have  $S^* > 0$ .

### 4.2. Local stability of boundary equilibria

In order to study global behavior of system (1.2), it is helpful to know the local stability of each boundary equilibrium.

At equilibrium  $(S, I, N_2)$  of system (1.2), the Jacobian matrix is given by

$$J = \begin{bmatrix} S'/S - a_{11}S & -(a_{11} + \lambda)S & -a_{12}S \\ (\lambda - a_{11})I & I'/I - a_{11}I & -a_{12}I \\ -a_{21}N_2 & -a_{21}N_2 & N_2'/N_2 - a_{22}N_2 \end{bmatrix}.$$

For  $O = (0, 0, 0)$ , we have

$$J_0 = \begin{bmatrix} r_1 & 0 & 0 \\ 0 & -u_I & 0 \\ 0 & 0 & r_2 \end{bmatrix}.$$

So equilibrium  $O$  is locally unstable. It is attractive in the  $I$  direction and unstable in the  $S$  and  $N_2$  directions.

For  $Q_S = (r_1/a_{11}, 0, 0)$ , we have

$$J_S = \begin{bmatrix} -r_1 & -(a_{11} + \lambda)r_1/a_{11} & -a_{12}r_1/a_{11} \\ 0 & (r_1 + u_I)(R_0 - 1) & 0 \\ 0 & 0 & r_2 - a_{21}r_1/a_{11} \end{bmatrix}.$$

Hence, the Jacobian matrix at  $Q_S$  has eigenvalues  $-r_1$ ,  $(r_1 + u_I)(R_0 - 1)$  and  $r_2 - a_{21}r_1/a_{11}$ . It is locally stable if and only if  $R_0 < 1$ , and  $r_1 a_{21} > r_2 a_{11}$ , which is true in cases (A) and (B).

For  $Q_{N_2} = (0, 0, r_2/a_{22})$ , we have

$$J_{N_2} = \begin{bmatrix} -r_1 - a_{12}r_2/a_{22} & 0 & 0 \\ 0 & -a_{12}r_2/a_{22} - u_I & 0 \\ -a_{21}r_2/a_{22} & -a_{21}r_2/a_{22} & -r_2 \end{bmatrix}.$$

Thus, the Jacobian matrix at  $Q_{N_2}$  has three eigenvalues  $r_1 - a_{12}r_2/a_{22}$ ,  $-a_{12}r_2/a_{22} - u_I$  and  $-r_2$ . It is locally stable if and only if  $r_2a_{12} > r_1a_{22}$ , which is true in cases (B) and (D).

For  $Q_{SN_2} = (\hat{S}, 0, \hat{N}_2)$ , we have

$$J_{SN_2} = \begin{bmatrix} -a_{11}\hat{S} & -(a_{11} + \lambda)\hat{S} & -a_{12}\hat{S} \\ 0 & (\lambda - a_{11})\hat{S} - a_{12}\hat{N}_2 - u_I & 0 \\ -a_{21}\hat{N}_2 & -a_{21}\hat{N}_2 & -a_{22}\hat{N}_2 \end{bmatrix}.$$

As we have already mentioned, the equilibrium  $Q_{SN_2}$  exists in and only in cases (B) and (C). It has eigenvalue  $(\lambda - a_{11})\hat{S} - a_{12}\hat{N}_2 - u_I$ , and two other eigenvalues which are determined by submatrix  $\hat{J}_{SN_2}$ , which is obtained by deleting the middle row and middle column of matrix  $J_{SN_2}$ . Matrix  $\hat{J}_{SN_2}$  can be regarded as the Jacobian for the case of the two competing species introduced in Section 2. So,  $Q_{SN_2}$  is locally stable if and only if in case (C) and  $(\lambda - a_{11})\hat{S} - a_{12}\hat{N}_2 - u_I < 0$ . The latter condition can be reformulated in terms of the inequality  $\hat{R}_0 > 1$  for another reproduction number  $\hat{R}_0$  (see Subsection 5.3).

For  $Q_{SI} = (\bar{S}, \bar{I}, 0)$ , we have

$$J_{SI} = \begin{bmatrix} -a_{11}\bar{S} & -(a_{11} + \lambda)\bar{S} & -a_{12}\bar{S} \\ (\lambda - a_{11})\bar{I} & -a_{11}\bar{I} & -a_{12}\bar{I} \\ 0 & 0 & r_2 - a_{21}(r_1 + u_I)/\lambda \end{bmatrix}.$$

We know that  $Q_{SI}$  exists if and only if  $R_0 > 1$ . Consider the upper left matrix  $\hat{J}_{SI}$  of  $J_{SI}$ . We know its eigenvalues have negative real part if  $R_0 > 1$ . Therefore, once the equilibrium exists it is locally stable if and only if  $r_2 - a_{21}(r_1 + u_I)/\lambda < 0$  or, equivalently, if and only if  $N_2^* < 0$ .

### 4.3. Mathematical framework

For two dimensional autonomous ODE systems, the Poincaré-Bendixson theory together with Bendixson's criterion can be used to prove global stability of the unique equilibrium. In this section we introduce a theorem for proving global stability of the unique equilibrium for higher dimensional autonomous ODE systems, which can be regarded as an extension of the two dimensional case and which was developed in the paper of Li and Muldowney [13]. It will be used for our model in Subsection 5.3.

Consider the ordinary differential equation

$$x' = f(x), \tag{4.2}$$

where  $f : D \rightarrow \mathbb{R}^n$  is a  $C^1$  function in an open set  $D \subset \mathbb{R}^n$ . We make the following assumptions:

(H<sub>1</sub>) There exists a compact absorbing set  $K \subset D$ ,

(H<sub>2</sub>) Equation (4.2) has a unique equilibrium  $\bar{x}$  in  $D$ .

A *Bendixson criterion* for (4.2) is a condition satisfied by  $f$  which precludes the existence of nonconstant periodic solutions of (4.2). A Bendixson criterion is said to be *robust under  $C^1$  local perturbations of  $f$  at  $x_1 \in D$* , if for sufficiently small  $\varepsilon > 0$  and sufficiently small neighborhoods  $U$  of  $x_1$ , it is also satisfied by all  $g \in C^1$  such that the support  $\text{supp}(f - g) \in U$  and  $|f - g|_{C^1} < \varepsilon$ , where

$$|f - g|_{C^1} = \sup\{|f(x) - g(x)| + \left| \frac{\partial f}{\partial x}(x) - \frac{\partial g}{\partial x}(x) \right| : x \in D\}.$$

Such  $g$  is called a local  $\varepsilon$ -perturbation of  $f$  at  $x_1$ .

The following global stability result was established by Li and Muldowney [13].

LEMMA 2. *Suppose that assumptions (H<sub>1</sub>) and (H<sub>2</sub>) hold. Assume that  $f$  satisfies a Bendixson criterion that is robust under  $C^1$  local perturbations of  $f$  at all nonequilibrium nonwandering points for (4.2). Then  $\bar{x}$  is globally stable in  $D$  provided it is stable.*

We now turn our attention to a convenient Bendixson criterion introduced and proved to be robust in the paper [13].

Let  $P(x)$  be an  $\binom{n}{2} \times \binom{n}{2}$  matrix valued function and  $C^1$  for  $x \in D$  and assume that  $P^{-1}(x)$  exists and is continuous for  $x \in K$ . Let  $P_f$  be the matrix obtained by replacing each entry of  $P$  by its derivative in the direction of  $f$ , and let  $\frac{\partial f^{[2]}}{\partial x}$  be the second additive compound matrix of  $\frac{\partial f}{\partial x}$ . For instance, for a  $3 \times 3$  matrix  $L = (l_{ij})$ , the second additive compound matrix is

$$L^{[2]} = \begin{bmatrix} l_{11} + l_{22} & l_{23} & -l_{13} \\ l_{32} & l_{11} + l_{33} & l_{12} \\ -l_{31} & l_{21} & l_{22} + l_{33} \end{bmatrix}.$$

We now define

$$B = P_f P^{-1} + P \frac{\partial f^{[2]}}{\partial x} P^{-1}. \tag{4.3}$$

Let  $\mu(B)$  be the Lozinskii measure of  $B$  with respect to a vector norm  $|\cdot|$  in  $\mathbb{R}^N$ ;  $N = \binom{n}{2}$ . It is defined by

$$\mu(B) = \lim_{h \rightarrow 0^+} \frac{|E + hB| - 1}{h}.$$

We can now define the quantity

$$\overline{q_2} = \limsup_{t \rightarrow \infty} \sup_{x_0 \in K} \frac{1}{t} \int_0^t \mu(B(x(s; f, x_0))) ds, \tag{4.4}$$



where  $x(s; f, x_0)$  is the solution of (4.2) subject to the initial condition  $x(0; f, x_0) = x_0$ . The robust Bendixson criterion of Li and Muldowney [13] now takes the form

$$\overline{q_2} < 0.$$

## 5. Analysis of the two-species SI-model

In this section we systematically investigate the dynamics of the system (1.2) in four different cases. These cases correspond to the cases (A) – (D) of the classical Lotka-Volterra competition model without the disease as discussed in Section 2.

### 5.1. Case A

We assume that species 1 is a superior competitor in absence of the disease. As explained in Section 2, this is modeled by assuming

$$r_2 a_{11} < r_1 a_{21} \quad \text{and} \quad r_2 a_{12} < r_1 a_{22}. \quad (5.1)$$

Throughout this section, we assume that (5.1) holds.

**THEOREM 1.** *If  $R_0 \leq 1$ , then the disease-free equilibrium  $Q_S$  of system (1.2) is globally asymptotically stable in  $\text{int } \mathbb{R}_+^3$ .*

*Proof.* It follows from the first equation of (1.2) that

$$S' \leq S(r_1 - a_{11}S).$$

If  $S(0) > r_1/a_{11}$ , the density  $S(t)$  of susceptibles will therefore decrease until it hits the value  $r_1/a_{11}$  at a time  $t_0$ . By uniqueness of solutions, one cannot have  $I(t_0) = N_2(t_0) = 0$ . Therefore, every solution starting in  $\text{int } \mathbb{R}_+^3$  will eventually enter the region  $S \leq r_1/a_{11}$  and stay there thereafter. It now follows from the second equation of system (1.2) that

$$I' \leq I(\lambda(r_1/a_{11}) - (r_1 + u_I)) = I(R_0 - 1)/(r_1 + u_I).$$

Because  $R_0 \leq 1$ , we have  $I' \leq 0$ . Hence  $I(t)$  is decreasing and bounded below and therefore has a limit as  $t \rightarrow \infty$ . Because  $I' = 0$  if and only if  $I = 0$  this limit must be equal to 0. The limiting case of system (1.2) is the two dimensional competitive Lotka-Volterra system (1.1). With inequalities (5.1),  $(r_1/a_{11}, 0)$  is a globally asymptotically stable equilibrium of system (1.1) in  $\text{int } \mathbb{R}_+^2$ . Thus,  $Q_S$  is a globally asymptotically stable equilibrium of system (1.2) in  $\text{int } \mathbb{R}_+^3$ .

**THEOREM 2.** *If  $1 < R_0 < r_1 a_{21}/r_2 a_{11}$ , then  $Q_{SI}$  exists in the positive quadrant of the SI-plane and is a locally stable equilibrium of system (1.2). It is the only equilibrium in addition to the origin and the two axial equilibria.*

*Proof.*  $Q_{SN_2}$  does not exist under condition (5.1).  $O$ ,  $Q_S$  and  $Q_{N_2}$  are locally unstable.  $Q_{SI}$  exists in the positive quadrant of the SI-plane when  $R_0 > 1$  and is locally stable if  $R_0 < r_1 a_{21} / r_2 a_{11}$  as shown in Subsection 4.2. The condition  $R_0 < r_1 a_{21} / r_2 a_{11}$  is equivalent to  $N_2^* < 0$ . Thus,  $Q_{SN_2}$  does not exist in  $\mathbb{R}_+^3$ .

When  $R_0 = r_1 a_{21} / r_2 a_{11}$ , it is the degenerate case for Theorem 2. it is difficult to see  $Q_{SI}$  is local stable or not.  $Q_{SIN_2}$  does not exist as  $N_2^* = 0$  when  $R_0 = r_1 a_{21} / r_2 a_{11}$ .

**THEOREM 3.**  *$Q_{SI}$  is an unstable equilibrium of system (1.2) and  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  if and only if  $R_0 > r_1 a_{21} / r_2 a_{11}$ . If  $Q_{SIN_2}$  exists, system (1.2) is uniformly persistent.*

*Proof.* As shown in Subsection 4.2, the Jacobian  $J_{SI}$  has a positive eigenvalue if and only if  $N_2^* > 0$  or, equivalently, if and only if  $R_0 > r_1 a_{21} / r_2 a_{11}$ . Now, we only need to show that if  $N_2^* > 0$ , then  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$ . We already remarked that if  $N_2^* > 0$ , then  $S^* > 0$ . So we only need to show that  $I^* > 0$ . If  $\Delta < 0$ , then  $I^* > 0$  by the inequality  $r_2 a_{12} < r_1 a_{22}$ . If  $\Delta > 0$ , then  $I^* > 0$  is equivalent to

$$\frac{\lambda}{r_1 + u_I} \frac{a_{22}r_1 - a_{12}r_2}{\Delta} > 1.$$

Using the inequality  $r_2 a_{11} < r_1 a_{21}$  and  $N_2^* > 0$ , we get

$$\frac{\lambda}{r_1 + u_I} \frac{a_{22}r_1 - a_{12}r_2}{\Delta} > \frac{\lambda}{r_1 + u_I} \frac{r_1}{a_{11}} > \frac{a_{21}r_1}{r_2 a_{11}} > 1.$$

Thus  $I^* > 0$ . The proof of uniform persistence is similar to the corresponding proof of Theorem 9. Therefore we omit the details.

**THEOREM 4.** *If  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  and  $\Delta > 0$ , then  $Q_{SIN_2}$  is a locally stable equilibrium of system (1.2).*

*Proof.* The characteristic equation of the Jacobian matrix  $J$  evaluated at  $Q_{SIN_2}$  is

$$z^3 + k_1 z^2 + k_2 z + k_3 = 0, \tag{5.2}$$

where  $k_1 = a_{11}(S^* + I^*) + a_{22}N_2^*$ ,  $k_2 = \Delta(S^* + I^*)N_2^* + \lambda^2 S^* I^*$  and  $k_3 = \lambda^2 a_{22} S^* I^* N_2^*$ .

$$k_1 k_2 - k_3 = a_{11}(S^* + I^*)[\Delta(S^* + I^*)N_2^* + \lambda^2 S^* I^*] + a_{22}(S^* + I^*)N_2^* \Delta N_2^*.$$

We have  $k_1 > 0$  and  $k_3 > 0$  independently on whether  $\Delta$  is larger or smaller than 0.  $k_2 > 0$  and  $k_1 k_2 - k_3 > 0$  when  $\Delta > 0$ . By the Routh-Hurwitz conditions [14], all roots have negative real parts and thus  $Q_{SIN_2}$  is a locally stable equilibrium of system (1.2).

Next we consider the possibility of  $Q_{SIN_2}$  losing its stability through a Hopf bifurcation. We use the transmission rate  $\lambda$  as bifurcation parameter.

A simple Hopf bifurcation occurs at  $\lambda = \lambda_1$ , if

- (a) the characteristic equation (5.2) has a pair  $\{z_1, z_2\}$  of conjugate purely imaginary roots and the third root (which is necessarily real) is negative when  $\lambda = \lambda_1$ ,
- (b)  $\frac{d}{d\lambda}(\operatorname{Re} z_1(\lambda))|_{\lambda=\lambda_1} \neq 0$ ,
- (c)  $l_1(\lambda_1) \neq 0$ , where  $l_1(\lambda)$  is the *first Lyapunov coefficient* (see below).

Consider a smooth system

$$X' = F(X, \alpha),$$

where  $X \in \mathbb{R}^n$  and  $\alpha \in \mathbb{R}^m$  is a vector of parameters.  $F(0, \alpha) = 0$  and  $\alpha = 0$  is the bifurcation point.

For all sufficiently small  $\|\alpha\|$ , there exists a local invariant center manifold  $W^c(\alpha)$  of dimension  $n_c$  that is locally attracting if  $n_u = 0$ , repelling if  $n_s = 0$ , and of saddle type if  $n_s n_u > 0$ . Here,  $n_c$ ,  $n_u$  and  $n_s$  are the dimension of center manifold, unstable manifold and stable manifold, respectively.

In this place, we only consider codimension 1 equilibrium bifurcation, which means  $\alpha \in R$ . Then

$$F(X, 0) = AX + \frac{1}{2}B(X, X) + \frac{1}{6}C(X, X, X) + O(4),$$

where  $O(4)$  is a function with order at least four in their variable  $X$ .

For the Hopf bifurcation we have  $z_{1,2} = \pm iw$ ,  $w > 0$  ( $n_c = 2$ ). We calculate the first focal value using the following formula (see, for example, Kuznetsov [12]):

$$l_1(0) = \frac{1}{2w}R[\langle p, C(q, q, \bar{q}) \rangle - 2\langle p, B(q, A^{-1}B(q, \bar{q})) \rangle + \langle p, B(\bar{q}, (2iwE_n - A)^{-1}B(q, q)) \rangle],$$

where  $Aq = iwq$ ,  $A^T p = -iw p$ ,  $\langle p, q \rangle = \langle q, q \rangle = 1$ .

If  $l_1(0) \neq 0$  then the restriction of  $X' = F(X, \alpha)$  to its center manifold  $W^c(\alpha)$  is locally topologically equivalent to

$$\begin{aligned} \rho' &= \rho(\beta(\alpha) + l_1 \rho^2), \\ \varphi &= 1. \end{aligned}$$

Moreover, if  $l_1(0)$  is negative then there is a stable limit cycle for  $\beta(\alpha) > 0$ . If  $l_1(0)$  is positive then there is an unstable limit cycle for  $\beta(\alpha) < 0$ .

For system (1.2), the bifurcation equilibrium is  $Q_{SN_2}$  and the bifurcation point is  $\lambda_1$ , we can do the simple transformation to transfer them to 0 when we calculate  $l_1(\lambda_1)$  by using the formula  $l_1(0)$  given above.

Now we show that conditions (a) and (b) are equivalent to the following conditions:

$$(a') \quad k_3(\lambda_1) - k_1(\lambda_1)k_2(\lambda_1) = 0,$$

(b')  $(k_3 - k_1k_2)'|_{\lambda=\lambda_1} \neq 0$ .

If  $k_1 > 0$ , then it can be easily shown that condition (a) is equivalent to condition (a'). For  $\lambda = \lambda_1$ , we have

$$(z^2 + k_2)(z + k_1) = 0,$$

which has three roots  $z_1 = +i\sqrt{k_2}$ ,  $z_2 = -i\sqrt{k_2}$ ,  $z_3 = -k_1 < 0$ . For values  $\lambda$  near  $\lambda_1$ , the roots are in general of the following forms:

$$z_1(\lambda) = \xi_1(\lambda) + i\xi_2(\lambda), \quad z_2(\lambda) = \xi_1(\lambda) - i\xi_2(\lambda), \quad z_3 = \xi_3(\lambda).$$

Substituting  $z_j(\lambda) = \xi_1(\lambda) \pm i\xi_2(\lambda)$  ( $j = 1, 2$ ) into equation (5.2) and calculating the derivative, we find that

$$\psi(\lambda)\xi_1'(\lambda) - \phi(\lambda)\xi_2'(\lambda) + \Theta(\lambda) = 0, \tag{5.3}$$

$$\psi(\lambda)\xi_2'(\lambda) + \gamma(\lambda) = 0, \tag{5.4}$$

where

$$\begin{aligned} \psi &= 3\xi_1^2(\lambda) + 2k_1(\lambda)\xi_1(\lambda) + k_2(\lambda) - 3\xi_2^2(\lambda), \\ \phi &= 6\xi_1(\lambda)\xi_2(\lambda) + 2k_1(\lambda)\xi_2(\lambda), \\ \Theta &= \xi_1^2(\lambda)k_1'(\lambda) + k_2'(\lambda)\xi_1(\lambda) + k_3'(\lambda) - k_1'(\lambda)\xi_2^2(\lambda), \\ \phi &= 2\xi_1(\lambda)\xi_2(\lambda)k_1'(\lambda) + k_2'(\lambda)\xi_2(\lambda). \end{aligned}$$

If one multiplies equation (5.3) by  $\psi$  and multiplies equation (5.4) by  $\phi$ , and add the two equations, one obtains

$$\frac{d}{d\lambda}(\operatorname{Re} z(\lambda)) = -\frac{\phi\gamma + \psi\Theta}{\psi^2 + \phi^2}.$$

Note that  $\xi_1(\lambda_1) = 0$ ,  $\xi_2^2(\lambda_1) = k_2(\lambda_1)$ , and  $k_1(\lambda_1)k_2(\lambda_1) = k_3(\lambda_1)$ . Thus we have

$$\frac{d}{d\lambda}(\operatorname{Re} z(\lambda))|_{\lambda=\lambda_1} = -\frac{\phi\gamma + \psi\Theta}{\psi^2 + \phi^2}|_{\lambda=\lambda_1} = \frac{2k_2(k_3' - k_1'k_2 - k_1k_2')}{\psi^2 + \phi^2}|_{\lambda=\lambda_1}.$$

Therefore condition (b) is equivalent to condition (b').

Next we investigate under what circumstances the conditions (a') and (b') hold. A direct calculation shows that

$$\begin{aligned} k_3 - k_1k_2 &= \frac{-(r_1 + u_I)\Delta}{a_{22}\lambda^3} ((\lambda r_2 - c_1)(\lambda r_2 - c_2) - c_3(c_4\lambda + c_6)(c_5\lambda - c_6)) \\ &= \frac{-(r_1 + u_I)\Delta}{a_{22}\lambda^3} (A_1\lambda^2 + A_2\lambda + A_3), \end{aligned}$$

where

$$\begin{aligned} A_1 &= r_2^2 - c_3c_4c_5, \\ A_2 &= -r_2(c_1 + c_2) - c_3c_6(c_5 - c_4), \end{aligned}$$

$$\begin{aligned}
A_3 &= c_1c_2 + c_3c_6^2, \\
c_1 &= a_{21}(r_1 + u_I), \\
c_2 &= (a_{21} - a_{11})(r_1 + u_I), \\
c_3 &= -a_{11}/(a_{22}\Delta), \\
c_4 &= a_{22}r_1 - a_{12}r_2, \\
c_5 &= a_{22}u_I + a_{12}r_2, \\
c_6 &= -\Delta(r_1 + u_I).
\end{aligned}$$

Therefore condition (a') is equivalent to  $\lambda_1$  being a root of the quadratic equation

$$A_1\lambda^2 + A_2\lambda + A_3 = 0.$$

Consequently, condition (a') is satisfied by  $\lambda_1$  and  $\lambda_2$  given by

$$\lambda_{1,2} = \frac{-A_2 \pm \sqrt{A_2^2 - 4A_1A_3}}{2A_1}, \quad (5.5)$$

where  $\lambda_1$  is the expression with sign + and  $\lambda_2$  is the one with sign -.

Because  $\lambda$  is a positive parameter, the inequality

$$A_2^2 - 4A_1A_3 \geq 0,$$

is a necessary condition for a Hopf bifurcation at either  $\lambda_1$  or  $\lambda_2$ .

Next we consider condition (b'). Again a direct computation gives

$$\begin{aligned}
(k_3 - k_1k_2)'(\lambda) &= \frac{3(r_1 + u_I)\Delta}{a_{22}\lambda^4}(A_1\lambda^2 + A_2\lambda + A_3) - \frac{(r_1 + u_I)\Delta}{a_{22}\lambda^3}(2A_1\lambda + A_2) \\
&= -\frac{(r_1 + u_I)\Delta}{a_{22}\lambda^3}(2A_1\lambda + A_2).
\end{aligned}$$

Thus condition (b') holds at  $\lambda_1$  and  $\lambda_2$  if and only if

$$2A_1\lambda_{1,2} + A_2 \neq 0,$$

which means  $A_2^2 - 4A_1A_3 \neq 0$ . Combing with above inequality, we have

$$A_2^2 - 4A_1A_3 > 0. \quad (5.6)$$

We still have to check whether the equilibrium  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  for the parameter values  $\lambda_1$  and  $\lambda_2$ . A straightforward calculation shows that if

$$\frac{-A_2 + \sqrt{A_2^2 - 4A_1A_3}}{2A_1(r_1 + u_I)} > \frac{a_{21}}{r_2}, \quad (5.7)$$

then  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  for  $\lambda = \lambda_1$ , whereas the inequality

$$\frac{-A_2 - \sqrt{A_2^2 - 4A_1A_3}}{2A_1(r_1 + u_I)} > \frac{a_{21}}{r_2} \quad (5.8)$$

ensures the existence of  $Q_{SIN_2} \in \text{int}\mathbb{R}_+^3$  for  $\lambda = \lambda_2$ . If inequalities 5.7 and 5.8 hold, then  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  for both  $\lambda = \lambda_1$  and  $\lambda = \lambda_2$ .

We now collect our findings into a theorem.

**THEOREM 5.** *If  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$  and  $\Delta < 0$ , and if condition (5.6) and at least one of conditions (5.7) and (5.8) are satisfied, then system (1.2) undergoes Hopf bifurcation at  $Q_{SIN_2}$  if  $l_1 \neq 0$ . For conditions (5.7) and (5.8), if only inequality (5.7) holds, then system (1.2) undergoes Hopf bifurcation at  $\lambda = \lambda_1$ ; if only inequality (5.8) holds, then system (1.2) undergoes Hopf bifurcation at  $\lambda = \lambda_2$ ; if both inequalities hold, then system (1.2) undergoes Hopf bifurcation at  $\lambda = \lambda_i$ ,  $i = 1, 2$ . Moreover, if  $l_1(\lambda_i) < 0$ , then those periodic solutions are limit cycles, while if  $l_1(\lambda_i) > 0$ , then periodic solutions are repelling.*

**EXAMPLE 1.** We take

$$r_1 = 5, r_2 = 10, a_{11} = 1, a_{21} = 3, a_{12} = 2, a_{22} = 5 \quad \text{and} \quad u_i = 1.$$

Then

$$\Delta = -1 < 0, R_0 = 5\lambda/6, r_1 a_{21}/(r_2 a_{11}) = 3/2,$$

$$A_1 = 75, A_2 = -324, A_3 = 1116/5,$$

$$\lambda_1 = (54 + \sqrt{1056})/25 = 3.4598, \frac{d}{d\lambda}(\text{Re} z(\lambda))_{\lambda=\lambda_1} = 6\sqrt{1056}/(5\lambda_1^3) > 0,$$

and the first focal value  $l_1 = 0.0299399853$ . The equilibrium  $Q_{SIN_2}$ , evaluated for the parameter value  $\lambda = \lambda_1$ , is  $(1.3449, 0.3893, 0.9595)$ . The parameter  $\lambda$  is used to change the strength of the disease. We will show numerically how the dynamics of system (1.2) evolves as  $R_0$  is increased. Specifically, the dynamics for the parameter values  $\lambda = 1, 7/5, 2, 3.459, 3.5, 6$  are illustrated.

In Figure 1, if  $\lambda = 1$ , then  $R_0 < 1$ , and the disease-free equilibrium  $Q_S$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^3$ . The disease is not strong enough to affect the long-term demographics. When  $\lambda = 7/5$ ,  $1 < R_0 < 3/2$ ,  $Q_S$  is unstable, and  $Q_{SI}$  becomes biologically feasible and stable. The disease is strong enough to be endemic in species 1, and species 1 is still strong enough to drive species 2 to extinction. When  $\lambda = 2$ ,  $R_0 > 3/2$ ,  $Q_{SI}$  is unstable, and  $Q_{SIN_2}$  becomes biologically feasible and stable. The disease has weakened species 1 enough to let species 2 barely survive. In Figure 2,  $\lambda = 3.459$ , which is a little smaller than  $\lambda_1$ , we see that  $Q_{SIN_2}$  is locally stable, and there is one stable periodic orbit. When  $\lambda = \lambda_1$ , system (1.2) undergoes Hopf bifurcation, and from the signs of  $\frac{d}{d\lambda}(\text{Re} z(\lambda))_{\lambda=\lambda_1}$  and  $l_1$ , we know that there is an unstable limit cycle at  $\lambda = \lambda_1 - \varepsilon$ . Thus, when  $\lambda = 3.459$ , system (1.2) has at least two limit cycles, one is stable and the other is unstable. Figure 3 shows what happens when  $\lambda$  continues to increase and becomes larger than  $\lambda_1$ . In this situation,  $Q_{SIN_2}$  becomes unstable and there is stable periodic orbit. When  $\lambda = 3.5$ , the limit cycle looks like in the two dimensional case, but when  $\lambda$  increases more, the limit cycle does not look like in the two dimensional case. When  $\lambda$  attains larger values, the population size of species changes dramatically.

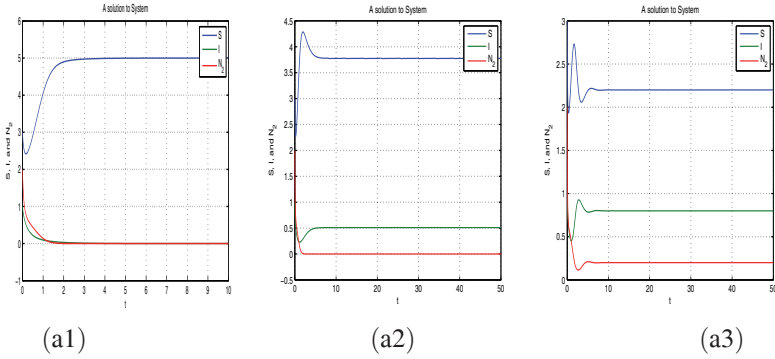


Figure 1: Dynamics of system (1.2) with  $\lambda = 1$  in (a1),  $\lambda = 7/5$  in (a2), and  $\lambda = 2$  in (a3).

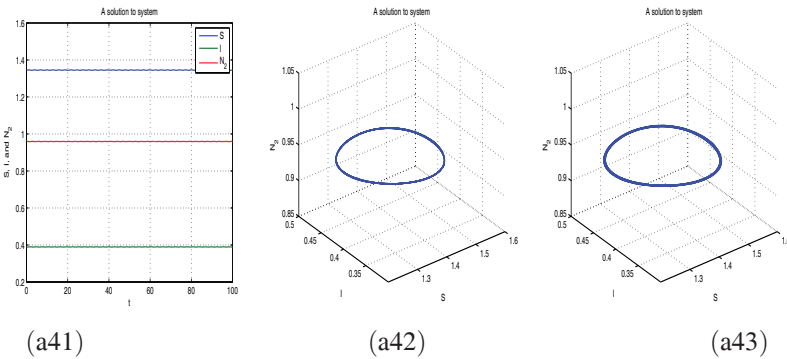


Figure 2: Dynamics of system (1.2) with  $\lambda = 3.459$ . The initial value is  $(1.344, 0.389, 0.959)$  in (a41),  $(1.3, 0.3, 0.9)$  in (a42), and  $(3, 2, 1)$  in (a43).

### 5.2. Case B

Throughout this section, we assume that

$$r_2 a_{11} < r_1 a_{21} \quad \text{and} \quad r_1 a_{22} < r_2 a_{12}. \tag{5.9}$$

It follows that  $\Delta < 0$  and that  $Q_{N_2}$  is locally stable.

**THEOREM 6.** *If  $R_0 \leq 1$ , then almost every trajectory of system (1.2) in  $\text{int}R_+^3$  is attracted to  $Q_S$  or  $Q_{N_2}$ .*

*Proof.* As in the poof of Theorem 1 one shows that if  $R_0 \leq 1$  all trajectories in  $\text{int}R^3$  are approaching a point in the  $SN_2$ -plane, where there is initial condition depen-

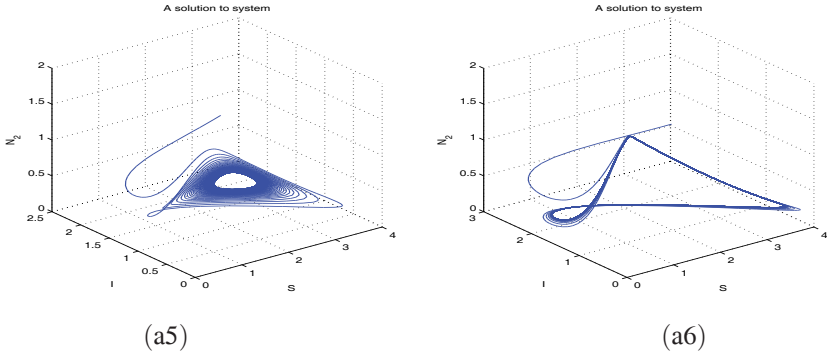


Figure 3: Dynamics of system (1.2) with  $\lambda = 3.5$  in (a5) and  $\lambda = 6$  in (a6).

dent competitive exclusion by inequalities (5.9). Thus, all trajectories except the two dimensional stable manifold of  $Q_{SN_2}$ , are attracted to  $Q_S$  or  $Q_{N_2}$  in  $\text{int } \mathbb{R}_+^3$ .

THEOREM 7.

- (i)  $Q_{SI}$  exists and it is locally stable if  $1 < R_0 < r_1 a_{21} / r_2 a_{11}$ .
- (ii)  $Q_{SIN_2}$  exists in  $\text{int } \mathbb{R}_+^3$  if  $r_1 a_{21} / r_2 a_{11} < R_0 < r_1 \Delta / (a_{11}(r_1 a_{22} - r_2 a_{12}))$ .
- (iii) If  $Q_{SIN_2}$  exists in  $\text{int } \mathbb{R}_+^3$ , and if condition (5.6) and at least one of conditions (5.7) and (5.8) are satisfied, then system (1.2) admits a Hopf bifurcation if  $l_1 \neq 0$ .

*Proof.* Statement (i) was proved in Theorem 2.  $N_2^* > 0$  is equivalent to  $R_0 > r_1 a_{21} / r_2 a_{11}$ , and  $I^* > 0$  is equivalent to  $R_0 < r_1 \Delta / (a_{11}(r_1 a_{22} - r_2 a_{12}))$ . The inequality  $r_1 a_{21} / r_2 a_{11} < r_1 \Delta / (a_{11}(r_1 a_{22} - r_2 a_{12}))$  follows from the first inequality of (5.9). Statement (iii) was proved in Theorem 5.

EXAMPLE 2. We take

$$r_1 = 20, r_2 = 18, a_{11} = 8, a_{21} = 10, a_{12} = 16, a_{22} = 10 \text{ and } u_I = 5.$$

Then

$$\begin{aligned} \Delta &= -80 < 0, R_0 = \lambda / 10, r_1 a_{21} / r_2 a_{11} = 25 / 18, \\ A_1 &= 621.44, A_2 = -13920, A_3 = 52500, \\ \lambda_1 &= 17.5993, \frac{d}{d\lambda}(\text{Re } z(\lambda))_{\lambda=\lambda_1} > 0, \end{aligned}$$

and the first focal value  $l_1 = -0.098445$ . The equilibrium  $Q_{SIN_2}$ , evaluated at  $\lambda = \lambda_1$ , is  $(1.2748, 0.1457, 0.3795)$ . From the signs of  $\frac{d}{d\lambda}(\text{Re } z(\lambda))_{\lambda=\lambda_1}$  and  $l_1$ , we know there is a stable limit cycle at  $\lambda = \lambda_1 + \varepsilon$ .



In Figure 4 (top left and bottom left),  $\lambda = 8$ , then  $R_0 < 1$ , and there is initial-condition-dependent exclusion between  $Q_S$  and  $Q_{N_2}$ . When  $\lambda = 12$  (top middle and bottom middle),  $1 < R_0 < 15/18$ ,  $Q_S$  loses its stability, but  $Q_{SI}$  is stable. Meanwhile,  $Q_{N_2}$  still keeps its stability. At  $\lambda = 15$  (top right and bottom right),  $25/18 < R_0 < 25/11$ ,  $Q_{SI}$  loses its stability, while  $Q_{SIN_2}$  becomes biologically feasible and stable.  $Q_{N_2}$  keeps on its stability. Increasing  $\lambda$  more,  $Q_{SIN_2}$  undergoes Hopf bifurcation. In Figure 5,  $\lambda = 18$ ,  $Q_{SIN_2}$  becomes unstable, and there is initial-condition-dependent oscillatory endemic coexistence or extinction of species 1.

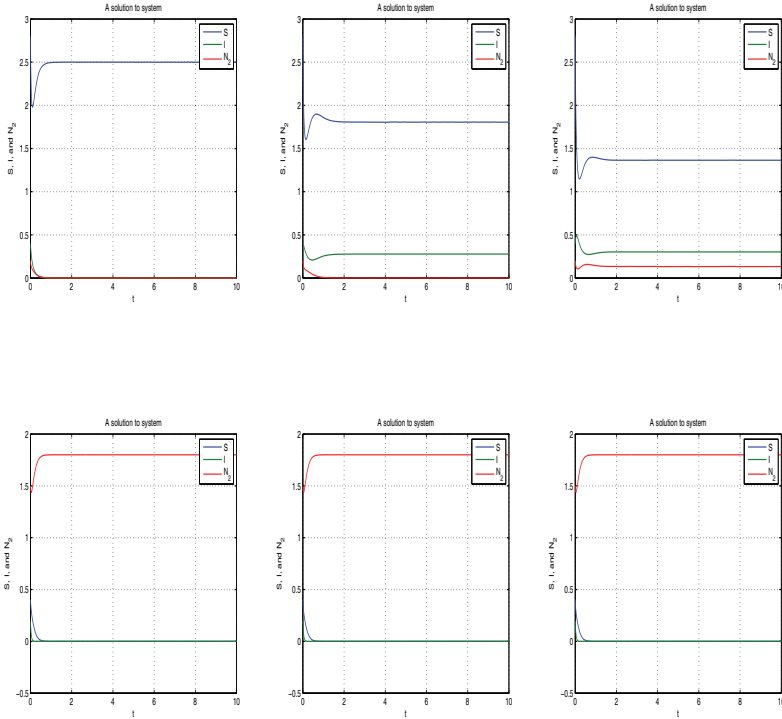


Figure 4: Dynamics of system (1.2) with different  $\lambda$ . Left:  $\lambda = 8$ . Middle:  $\lambda = 12$ . Right:  $\lambda = 15$ . On the top line the initial value is  $[2.8, 0.4, 0.2]$ . On the bottom line the initial value is  $[0.4, 0.2, 1.5]$ .

### 5.3. Case C

Throughout this section we assume that

$$r_1 a_{21} < r_2 a_{11} \quad \text{and} \quad r_2 a_{12} < r_1 a_{22}. \tag{5.10}$$

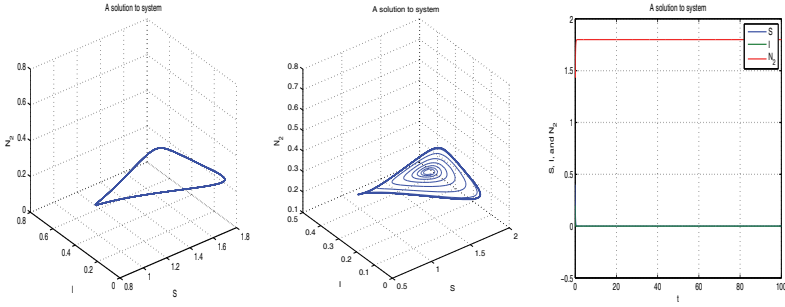


Figure 5: Dynamics of system (1.2) with  $\lambda = 18$ . Left: the initial value is  $[2.6, 0.1, 0.1]$ . Middle: the initial value is  $[1.26, 0.12, 0.4]$ . Right: the initial value is  $[0.4, 0.2, 1.5]$ .

Recall from Section 3 that the basic reproduction number for the one-species SI-model is

$$R_0 = \frac{r_1}{a_{11}} \frac{\lambda}{r_1 + u_I}.$$

We now define the basic reproduction number  $\hat{R}_0$  for the two-species model by

$$\hat{R}_0 = \frac{\lambda \hat{S}}{a_{11} \hat{S} + a_{12} \hat{N}_2 + u_I} = \frac{\lambda}{r_1 + u_I} \frac{r_1 a_{22} - r_2 a_{12}}{\Delta},$$

where, as before,  $\Delta = a_{11} a_{22} - a_{12} a_{21} > 0$ .  $\hat{R}_0$  is the expected number of secondary cases produced by one infected individual introduced into a population in the disease-free coexistence steady state  $Q_{SIN_2}$ . Note that it follows from the first inequality in (5.10) that

$$\hat{R}_0 = \frac{\lambda}{r_1 + u_I} \frac{r_1 a_{22} - r_2 a_{12}}{\Delta} < \frac{\lambda}{r_1 + u_I} \frac{r_1 a_{22} - r_1 \frac{a_{21}}{a_{11}} a_{12}}{\Delta} = R_0. \tag{5.11}$$

**THEOREM 8.**  $Q_{SIN_2}$  exists in  $\text{int} \mathbb{R}_+^3$  if and only if  $\hat{R}_0 > 1$ .

*Proof.* We start by writing the  $N$  and  $I$  components of  $Q_{SIN_2}$  in terms of  $R_0$  and  $\hat{R}_0$ . It follows from the expression (4.1) for  $N_2^*$  and the first inequality in (5.10) that

$$\begin{aligned} N_2^* &= \frac{1}{a_{22} \lambda} (\lambda r_2 - a_{21} (r_1 + u_I)) \\ &> \frac{1}{a_{22} \lambda} \left( \lambda \frac{r_1 a_{21}}{a_{11}} - a_{21} (r_1 + u_I) \right) \\ &= a_{21} \frac{r_1 + u_I}{a_{22} \lambda} (R_0 - 1). \end{aligned} \tag{5.12}$$

The expression (4.1) for  $I^*$  can be written as

$$I^* = \frac{\lambda(r_1 a_{22} - r_2 a_{12}) - (r_1 + u_I)\Delta}{a_{22}\lambda^2} = \frac{(r_1 + u_I)\Delta}{a_{22}\lambda^2}(\hat{R}_0 - 1). \quad (5.13)$$

Assume that  $Q_{SIN_2}$  exists in  $\text{int}\mathbb{R}_+^3$ . Then, in particular,  $I^* > 0$  and (5.13) shows that  $\hat{R}_0 > 1$ . Conversely, if  $\hat{R}_0 > 1$ , then by (5.11) also  $R_0 > 1$  and hence (5.12) implies that  $N_2^* > 0$  and (5.13) that  $I^* > 0$ . As shown in Subsection 4.1,  $N_2^* > 0$  implies that  $S^* > 0$  and so  $Q_{SIN_2} \in \text{int}\mathbb{R}_+^3$ .

**THEOREM 9.** *System (1.2) is uniformly persistent if  $\hat{R}_0 > 1$ .*

*Proof.* Define

$$\begin{aligned} X &= \{(S, I, N_2) : S \geq 0, I \geq 0, N_2 \geq 0\}, \\ X^0 &= \{(S, I, N_2) : S > 0, I > 0, N_2 > 0\}, \\ \partial X^0 &= X \setminus X^0, \end{aligned}$$

We see that  $X^0$  is open, dense in  $X$  and  $X^0 \subset X$ ,  $\partial X^0 \subset X$ ,  $\partial X^0 \cup X^0 = X$ ,  $\partial X^0 \cap X^0 = \emptyset$ . Also, we define  $T(t) : X \mapsto X$  by  $T(t)(x) = x(t, x)$ , where  $x(t, x)$  is the solution of system (1.2) at time  $t$  with initial value  $x$  at time 0. It is easy to see that  $T(t)$  is a  $C_0$  semigroup on  $X$ , compact and point dissipative in  $X$ . Both  $X^0$  and  $\partial X^0$  are positively invariant for system (1.2). Let

$$\bar{A}_\partial = \bigcup_{x \in A_\partial} \omega(x),$$

where  $A_\partial$  is the global attractor for  $T(t)$  on  $\partial X^0$ . It is easy to see that

$$\partial X^0 = M_1 \cup M_2 \cup M_3 \cup M_4 \cup M_5,$$

where:

$$\begin{aligned} M_1 &= \{(S, I, N_2) : S > 0, I > 0, N_2 = 0\}, \\ M_2 &= \{(S, I, N_2) : S > 0, I = 0, N_2 = 0\}, \\ M_3 &= \{(S, I, N_2) : S > 0, I = 0, N_2 > 0\}, \\ M_4 &= \{(S, I, N_2) : S = 0, I \geq 0, N_2 > 0\}, \\ M_5 &= \{(S, I, N_2) : S = 0, I = 0, N_2 \geq 0\}. \end{aligned}$$

$M_i$  is invariant. Analyzing the dynamics of system (1.2) in  $M_i$  respectively, one verifies the following assertions:  $Q_{SI}$  is a global attractor in  $M_1$ ;  $Q_S$  is a global attractor in  $M_2$ ;  $Q_{SN_2}$  is a global attractor in  $M_3$ ;  $Q_{N_2}$  is a global attractor in  $M_4$ ;  $O$  is a global attractor in  $M_5$ . It then follows that  $\{Q_{SI}, Q_S, Q_{SN_2}, Q_{N_2}, O\}$  is isolated and is an asyctic covering of  $\bar{A}_\partial$ . By the Theorem 4.1 of [7], we only need to show that  $W^s(Q_S) \cap X^0 = \emptyset$ ,  $W^s(Q_{SN_2}) \cap X^0 = \emptyset$ ,  $W^s(Q_{N_2}) \cap X^0 = \emptyset$ ,  $W^s(O) \cap X^0 = \emptyset$ .

Now we show that  $W^s(Q_S) \cap X^0 = \emptyset$ . As shown in Subsection 4.2, there are three eigenvalues of  $J_S$ . One of them is negative and the other two are positive under condition (5.10) and  $\hat{R}_0 > 1$ . The negative eigenvalue  $-r_1$  corresponds to an eigenvector of

the form  $[1, 0, 0]$ , and hence corresponds to solutions that remain in the boundary  $\partial X^0$ . Thus the stable set of this constant solution  $Q_S$  does not intersect  $X^0$ . Similar argument applies to  $Q_{SI}$ ,  $Q_{SN_2}$ ,  $Q_{N_2}$ , and  $O$ . By Theorem 4.1 of [7], we conclude that  $\partial X^0$  is a strong repeller for  $X^0$  and system (1.2) is uniformly persistent.

**THEOREM 10.** *If  $R_0 \leq 1$ , then the disease-free equilibrium  $Q_{SN_2}$  is globally asymptotically stable in  $\text{int } \mathbb{R}_+^3$ .*

*Proof.* Because  $R_0 \leq 1$ , we have  $I(t) \rightarrow 0$  as  $t \rightarrow +\infty$ . The limiting case of system (1.2) is the two dimensional competitive Lotka-Volterra system (1.1). For system (1.1) with inequalities (5.10), we know that  $(\hat{S}, \hat{N}_2)$  is globally asymptotically stable in  $\text{int } \mathbb{R}_+^2$ . Thus,  $Q_{SN_2}$  is globally asymptotically stable in  $\text{int } \mathbb{R}_+^3$ .

The assumption  $R_0 \leq 1$  of Theorem 10 seems too strong. It is formulated in terms of the basic reproduction number  $R_0$  for the single-species SI-model and not in terms of the basic reproduction number  $\hat{R}_0$  for the two-species model under consideration. Furthermore, one can easily check that if  $\hat{R}_0 < 1 < R_0$ , then  $Q_{SN_2}$  is the only stable equilibrium. Therefore, both our biological and mathematical intuition lead us to the following conjecture.

**CONJECTURE 1.** *If  $\hat{R}_0 \leq 1$ , then the disease-free equilibrium  $Q_{SN_2}$  is globally asymptotically stable in  $\text{int } \mathbb{R}_+^3$ .*

**THEOREM 11.** *If  $\hat{R}_0 > 1$  and if*

$$\left( \frac{a_{12}a_{21}}{a_{22}a_{11}}, \frac{a_{11}a_{22}}{a_{12}a_{21}} \right) \cap \left( \frac{\lambda + a_{11}}{a_{11}}, \frac{a_{11}}{\lambda - a_{11}} \right) \neq \emptyset, \tag{5.14}$$

*then the coexistence endemic disease equilibrium  $Q_{SIN_2}$  is globally asymptotically stable in  $\text{int } \mathbb{R}_+^3$ .*

*Proof.* The Jacobian matrix  $J$  associated with a general solution  $(S(t), I(t), N_2(t))$  to system (1.2) is

$$J = \begin{bmatrix} S'/S - a_{11}S - (a_{11} + \lambda)S & -a_{12}S & \\ (\lambda - a_{11})I & I'/I - a_{11}I & -a_{12}I \\ -a_{21}N_2 & -a_{21}N_2 & N_2'/N_2 - a_{22}N_2 \end{bmatrix},$$

and its second additive compound matrix  $J^{[2]}$  is

$$J^{[2]} = \begin{bmatrix} j_{11}^{[2]} & -a_{12}I & a_{12}S \\ -a_{21}N_2 & j_{22}^{[2]} & -(a_{11} + \lambda)S \\ a_{21}N_2 & (\lambda - a_{11})I & j_{33}^{[2]} \end{bmatrix},$$

where

$$j_{11}^{[2]} = S'/S + I'/I - a_{11}S - a_{11}I,$$

$$j_{22}^{[2]} = S'/S + N_2'/N_2 - a_{11}S - a_{22}N_2,$$

$$j_{33}^{[2]} = I'/I + N_2'/N_2 - a_{11}I - a_{22}N_2.$$

We introduce the function  $P(S, I, N_2) = \text{diag}(p_1, p_2, p_3)$ , where  $p_1, p_2, p_3$  are positive parameters. Then  $P_f P^{-1} = 0$  and matrix  $B = P_f P^{-1} + P J^{[2]} P^{-1}$  is

$$B = \begin{bmatrix} j_{11}^{[2]} & -k_1 a_{12} I / k_2 & k_1 a_{12} S / k_3 \\ -k_2 a_{21} N_2 / k_1 & j_{22}^{[2]} & -k_2 (a_{11} + \lambda) S / k_3 \\ k_3 a_{21} N_2 / k_1 & k_3 (\lambda - a_{11}) I / k_2 & j_{33}^{[2]} \end{bmatrix}.$$

Let  $(u, v, w)$  denote the vectors in  $\mathbb{R}^3 \cong \mathbb{R}^{\binom{3}{2}}$ , we select a norm in  $\mathbb{R}^3$  as  $|(u, v, w)| = \max\{|u|, |v|, |w|\}$ , then the Lozinskii measure  $\mu$  of  $B$  with respect to this  $l^\infty$  norm can be calculated by adding the absolute value of the off diagonal elements to the diagonal one in each column of  $B$ , and then take the maximum of the three sums, see [13]. We thus obtain

$$\mu(B) = \max \left( \begin{array}{l} S'/S + I'/I - q_1 S - q_2 I \\ S'/S + N_2'/N_2 - q_3 S - q_4 N_2 \\ I'/I + N_2'/N_2 - q_5 I - q_6 N_2 \end{array} \right),$$

where

$$q_1 = a_{11} - p_1 a_{12} / p_3,$$

$$q_2 = a_{11} - p_1 a_{12} / p_2,$$

$$q_3 = a_{11} - p_2 (a_{11} + \lambda) / p_3,$$

$$q_4 = a_{22} - p_2 a_{21} / p_1,$$

$$q_5 = a_{11} - p_3 (\lambda - a_{11}) / p_2, \text{ and}$$

$$q_6 = a_{22} - p_3 a_{21} / p_1.$$

Let  $q_i > 0$  for  $i = 1, 2, \dots, 6$ . We get

$$\frac{a_{12} a_{21}}{a_{11} a_{22}} < \frac{p_3}{p_2} < \frac{a_{11} a_{22}}{a_{12} a_{21}}, \frac{\lambda + a_{11}}{a_{11}} < \frac{p_3}{p_2} < \frac{a_{11}}{\lambda - a_{11}}.$$

So, if

$$\left( \frac{a_{12} a_{21}}{a_{22} a_{11}}, \frac{a_{11} a_{22}}{a_{12} a_{21}} \right) \cap \left( \frac{\lambda + a_{11}}{a_{11}}, \frac{a_{11}}{\lambda - a_{11}} \right) \neq \emptyset,$$

we can choose suitable values of  $p_i$  to ensure that  $q_i > 0$ . Since system (1.2) is uniform persistent when  $\hat{R}_0 > 1$ , there exists a constant  $c$  and  $T_0 > 0$  independent of  $(S(0), I(0), N_2(0)) \in K$ , the compact absorbing set, such that

$$S(t) > c, I(t) > c, \text{ and } N_2(t) > c \text{ for } t > T_0.$$

Thus, for each solution  $(S(t), I(t), N_2(t))$  of (1.2) with  $(S(0), I(0), N_2(0)) \in K$  and for  $t > T_0$ , we have

$$\frac{1}{t} \int_0^t \mu(B) ds < \frac{1}{t} \int_0^{T_0} \mu(B) ds + \frac{1}{t} \left( \log \frac{S(t)}{S(T_0)} + \log \frac{I(t)}{I(T_0)} \right) - q_1 c - q_2 c,$$

which implies  $\overline{q_2} < -(q_1 + q_2)c/2 < 0$ . This completes the proof.

EXAMPLE 3. We take

$$r_1 = 3.8, r_2 = 4, a_{11} = 2, a_{21} = 2, a_{12} = 1, a_{22} = 2.5 \quad \text{and} \quad u_I = 0.2.$$

Then  $\Delta = 3$ ,  $\hat{R}_0 = 11\lambda/24 < R_0 = 19\lambda/40$ . In Figure 6, when  $\lambda = 2$ ,  $R_0 < 1$ , the disease free equilibrium  $Q_{SN_2}$  is globally asymptotically stable. When  $\lambda = 2.15$ ,  $\hat{R}_0 < 1 < R_0$ ,  $Q_{SI}$  becomes biologically feasible, but unstable. The disease-free equilibrium  $Q_{SN_2}$  is locally stable. This supports our conjecture 1.

When  $\lambda = 2.5$ ,  $\hat{R}_0 > 1$  and condition (5.14) holds, the coexistence endemic equilibrium  $Q_{SIN_2}$  exists and is globally stable. When  $\lambda = 6$ ,  $\hat{R}_0 > 1$  and condition (5.14) does not hold, and from the bottom right of Figure 6, it seems that  $Q_{SIN_2}$  is still globally stable, but we have not been able to prove it.

The numerical simulations accounted for in Example 3 lead us to the following conjecture.

CONJECTURE 2.  $Q_{SIN_2}$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^3$  if  $\hat{R}_0 > 1$ .

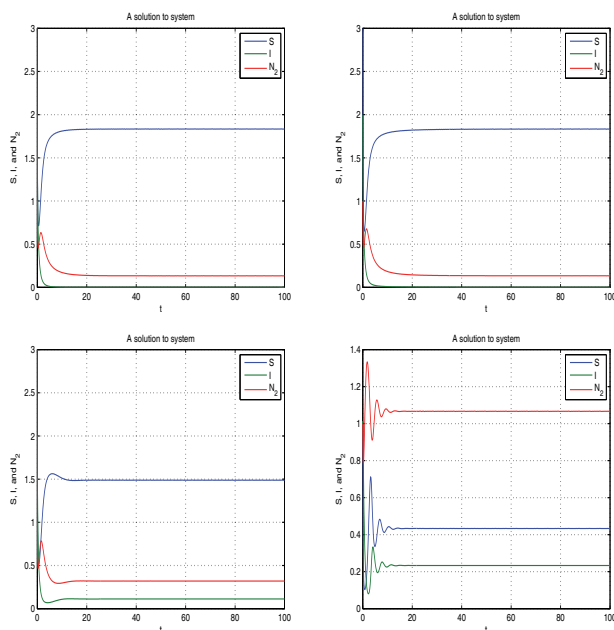


Figure 6: Dynamics of system (1.2) with  $\lambda = 2$ (top left),  $\lambda = 2.15$ (top right),  $\lambda = 2.5$ (bottom left) and  $\lambda = 5$ (bottom right).

#### 5.4. Case D

Throughout this section we assume that

$$r_1 a_{21} < r_2 a_{11} \quad \text{and} \quad r_1 a_{22} < r_2 a_{12}. \quad (5.15)$$

THEOREM 12. *If*

$$(a_{12} + a_{21})^2 < 4a_{22}a_{11}, \quad (5.16)$$

*then*  $Q_{N_2}$  *is a globally asymptotically stable equilibrium of system (1.2) in*  $\text{int}\mathbb{R}_+^3$ .

*Proof.* Let  $n_2^* = r_2/a_{22}$  and consider the Lyapunov function

$$V(S, I, N_2) = N_2 - n_2^* - n_2^* \log \frac{N_2}{n_2^*} + S + I$$

defined on the positive orthant. Note that  $V$  is nonnegative.

Its time derivative along the trajectories of system (1.2) is

$$\begin{aligned} V'(S, I, N_2) &= N_2' - n_2^* \frac{N_2'}{N_2} + S' + I' \\ &\leq (N_2 - n_2^*)(r_2 - a_{21}N_1 - a_{22}N_2) + N_1(r_1 - a_{11}N_1 - a_{12}N_2) \\ &= (N_2 - n_2^*)(r_2 - a_{21}N_1 - a_{22}N_2) + N_1(-a_{12}(N_2 - n_2^*) \\ &\quad - a_{11}N_1 + r_1 - a_{12}n_2^*) \\ &\leq -a_{22}(N_2 - n_2^*)^2 - (a_{21} + a_{12})N_1(N_2 - n_2^*) - a_{11}N_1^2 + (r_1 - a_{12}n_2^*)N_1. \end{aligned}$$

From the second inequality of (5.15), we know that  $r_1 - a_{12}n_2^* < 0$ . So we have

$$V'(S, I, N_2) \leq -a_{22}(N_2 - n_2^*)^2 - (a_{21} + a_{12})N_1(N_2 - n_2^*) - a_{11}N_1^2,$$

if  $(a_{21} + a_{12})^2 < 4a_{22}a_{11}$ , we have

$$V'(S, I, N_2) \leq 0 \quad \text{for all } \{(S, I, N_2) : S \geq 0, I \geq 0, N_2 > 0\}.$$

From the above analysis, we notice that only at  $Q_{N_2}$  one has  $V'(S, I, N_2) = 0$ . This proves the global stability of  $Q_{N_2}$  in  $\text{int}\mathbb{R}_+^3$ .

THEOREM 13.

- (i)  $Q_{N_2}$  is locally stable and it is globally asymptotically stable in  $\text{int}\mathbb{R}_+^3$  if  $R_0 \leq 1$ .
- (ii)  $Q_{SI}$  exists if  $R_0 > 1$ , and it is unstable.
- (iii) System (1.2) has no interior equilibrium  $Q_{SIN_2}$ .

*Proof.* Regarding statement (i), it is easy to check the global stability as we have done in former sections. The local stability, we get from the results of Section 4. As to statement (ii),  $Q_{SI}$  exists if  $R_0 > 1$ . We showed in Subsection 4.2 that once  $Q_{SI}$  existed it was locally stable if  $r_2 - a_{21}(r_1 + u_I)/\lambda < 0$ , which means that  $R_0 < r_1 a_{21}/(r_2 a_{11}) < 1$ . So if  $Q_{SI}$  exists, it is unstable. To prove statement (iii), assume that  $N_2^* > 0$ . If  $\Delta > 0$ , then  $I^* < 0$  by the second inequality of (5.15), if  $\Delta < 0$ , then  $I^* < 0$  by the first inequality of (5.15). Hence system (1.2) has no interior equilibrium.

By Theorem 13,  $Q_{N_2}$  is the only locally stable equilibrium. An increase of  $R_0$  gives rise to  $Q_{SI}$ , but it is unstable. Moreover, an increase of  $R_0$  does not give rise to an interior equilibrium. Furthermore, in the two-species model without disease, the boundary equilibrium without species 1 is globally asymptotically stable. The sufficient conditions in Theorem 13 are formulated in terms of the “wrong” basic reproduction number. Hence both mathematical and biological arguments make the following conjecture feasible.

CONJECTURE 3.  $Q_{N_2}$  is globally asymptotically stable in  $\text{int}\mathbb{R}_+^3$  whenever (5.15) holds.

## 6. Discussion

In this paper we have investigated a model for two competing species in which one species can be affected by an infectious disease that increase the mortality of infected individuals. We have proven results on global stability of steady states, permanence and Hopf bifurcation. As is usual in the theory of infectious diseases, we have formulated most of our results in terms of the basic reproduction number, that is, the expected number of secondary cases produced by one infected individual in an otherwise disease free population at equilibrium. As a matter of fact, we have had to deal with two different reproduction numbers evaluated at different disease free equilibria. Some of our results are what one would expect, for instance that the disease free steady state is globally asymptotically stable if the basic reproduction number is less than or equal to one. In other cases we have only been able to prove results that appear to be too weak because we have either formulated them in terms of the “wrong” reproduction number or added technical assumptions with no biological interpretation. In these case we have formulated precise conjectures of stronger results that we believe to be true.

In our analysis we have applied mathematical methods and results, e.g., the robust Bendixson criterion of Li and Muldowney [13], that as far as we know have not been used in mathematical epidemiology before.

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Mats Gyllenberg  
 Department of Mathematics and Statistics  
 P.O. Box 68, FI-00014 University of Helsinki  
 Helsinki  
 Finland  
 e-mail: mats.gyllenberg@helsinki.fi

Xioli Liu  
 Department of Mathematics and Statistics  
 P.O. Box 68, FI-00014 University of Helsinki  
 Helsinki  
 Finland  
 e-mail: xiaoli.liu@helsinki.fi

Ping Yan  
 Department of Mathematics and Statistics  
 P.O. Box 68, FI-00014 University of Helsinki  
 Helsinki  
 Finland  
 e-mail: ping.yan@helsinki.fi