

Epidemics in Two Competing Species

Litao Han¹

School of Information, Renmin University of China, Beijing, 100872 P. R. China

Andrea Pugliese²

Department of Mathematics, University of Trento, Trento, 38050 Italy

Abstract

An SIS epidemic model in two competing species with the mass action incidence is formulated and analyzed. Thresholds for the existence of boundary equilibria are identified and conditions for their local asymptotic stability or instability are found. By persistence theory, conditions for the persistence of either hosts or pathogens are proved. Using Hopf bifurcation theory and numerical simulations, some aspects of the complicated dynamical behaviors of the model are shown: the system may have zero up to three internal equilibria, may have a stable limit cycle, may have three stable attractors. Through the results on persistence and stability of the boundary equilibria, some important interactions between infection and competition are revealed: (1) a species that would get extinct without the infection, may persist in presence of the infection; (2) a species that would coexist with its competitor without the infection, is driven to extinction by the infection; (3) an infection that would die out in either species without the inter-infection of disease, may persist in both species in presence of this factor.

Key words: Epidemic model, Multi-host infection, Species extinction, Uniform persistence, Hopf bifurcation, Periodic solutions

1 Introduction

Models for ecological interactions, and models for host-pathogen interactions were initially developed separately. However, it has been recognized that a strong interaction may arise between these factors: a pathogen may tilt the balance between competing species, or may provoke a negative influence between the densities of two species that are not otherwise interacting (“apparent competition”), even causing the extinction of one of them; a pathogen may be able to persist in a community of 2 (or more) competing species, but not in any of them in isolation.

The problem, however, is that the models become quickly very difficult to analyse. Even the simplest possible model with an SI epidemics spreading in two not interacting species [1] gives rise to a 4-dimensional ODE model that may have multiple stable attractors often in the form of limit cycles [2].

It must be however remarked that the behavior of the model becomes much simpler [3] if one assumes that infection incidence is proportional to the infected fractions in each species and not to the densities of infectives. Which is the most appropriate form for the infection rate has been debated in sev-

Email addresses: `hanlitao@ruc.edu.cn` (Litao Han),

`pugliese@science.unitn.it` (Andrea Pugliese).

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eral papers, and the conclusion should clearly depend on the actual transmission routes on the pathogen. Considering a generic infection that is indirectly (through air-borne propagules or through the soil) transmitted among competing species, we believe that the standard bilinear form (mass action incidence) used in [1] is quite reasonable, and we will use it in our model.

Some empirical investigations on epidemics in competing species have been performed, with the help of epidemic models, by Begon *et al.* [4] on the cowpox virus in coexisting populations of bank voles and wood mice, and by Tompkins *et al.* [5] on a pathogen in competing squirrel species. Begon *et al.* [6] suggest that the data on the presence of the pathogen in islands are not compatible with the mass action incidence, but we believe that several different interpretation of these data are possible.

Models for two species which share a disease without competition have been discussed in some papers. In their works, Holt and Pickering [7], Begon and Bowers [1,8] conjectured that the models have the classic endemic model behavior: the infected coexistence equilibrium is relevant and stable if and only if no other stable equilibrium exists in the nonnegative orthant. But this conjecture was soon denied by some counterexamples given by Greenman and Hudson [2]. On the other hand, Hethcote *et al.* [9] later found that the models have the behavior of a classic endemic model if the frequency-dependent incidence is used.

Epidemic models in competing species have also been studied previously. Anderson and May [10] considered a host-competitor-pathogen model which involves two direct competitors, one subject to a pathogen. They examined the effect of a pathogen on conventional competition. Bowers and Turner [11]

introduced a proto-typical model of two hosts sharing a pathogen and competing directly. They studied the interplay between infection and competition. In their model, the death rates are density-independent. Venturino [12] analyzed the dynamics of two competing species when one of them is subject to a disease. In his model with mass action incidence, he obtained limit cycles. Han *et al.* [13] studied an SIRS epidemic model of two competitive species without disease-related deaths. They analyzed the effect of inter-infection of disease on the dynamical behaviors of the model. Saenz and Hethcote [3] considered some models of SIS, SIR and SIRS type with frequency-dependent incidence. They found that the models have the classic endemic model behavior. In their paper, a key result is that the disease must either die out in both species or remain endemic in both species.

Our model is different from the previous models, because it uses the mass action incidence, both density-dependent and disease-related death rates, and both species can be infected. Because of the complicated behaviors of the system, shown by [2], we do not aim at a complete analysis. Rather, instead of considering the global stabilities of the equilibria, we focus on the concept of persistence, and present conditions that guarantee the persistence (or the non-persistence) of either hosts or pathogens, following ideas by Thieme [14]. Together with the discussion on the local stabilities of the equilibria, by the analysis of persistence, we investigate the interactions between infection and competition. Moreover, by Hopf bifurcation theory and numerical simulations, some complex behaviors of the model are shown.

The organization of this paper is as follows. In the next section, we introduce the model and some preliminary results. In section 3, the existences and stabilities of the equilibria are discussed. In section 4, we analyze the persistence

of either hosts or pathogens. In section 5, we study the bifurcation phenomena and analyze the periodic orbits and the number of the internal equilibria. Finally, in section 6, the detailed discussion and conclusions are given.

2 Formulation of the Model

We consider two competing species, whose densities are denoted by N_1 and N_2 , whose dynamics follow a standard Lotka-Volterra system. K_i are the carrying capacity of each species in isolation, $r_i = b_i - d_i$ the intrinsic growth rates, α_{12} and α_{21} the competition coefficients. When considering the spread of an infectious disease in a species that grows logistically, it becomes necessary to specify explicitly the birth and the death rate; we follow Gao and Hethcote [15], assuming that $b_i - \frac{a_i r_i N_i}{K_i}$ is the birth rate and $[d_i + (1 - a_i) \frac{r_i N_i}{K_i}]$ the death rate of species i in isolation, where $0 \leq a_i \leq 1$ is a parameter that subdivides the density-dependence between births and deaths (note that for $a_i > 0$ the birth rates become negative at very high densities, which may be disturbing; however, such densities are outside the compact attracting set in which the analysis is relevant). Competition will be assumed to act only on death rates, so that the death rate of species i when its own density is N_i and that of the competitor is N_j are $d_i + (1 - a_i) \frac{r_i N_i}{K_i} + \alpha_{ij} \frac{r_i N_j}{K_i}$.

We now assume that both species can be infected by a common pathogen, whose cycle follow an *SIS* scheme, i.e. following recovery an individual become susceptible and can be infected again. Each species will then be divided in a susceptible part S_i and an infected class Y_i . We let β_{ii} be the intra-infection rate of disease in species i , and β_{ij} ($i \neq j$) the inter-infection rate of disease between the two species, both following the mass action incidence

rule. Moreover, γ_i is the recovery rate and δ_i is the disease-related death rate. We assume $\delta_i > 0$ (otherwise, the system's behavior would be much simpler), but neglect any effect of the infection on the birth rates.

From these assumptions, we obtain the following system:

$$\left\{ \begin{array}{l}
 \frac{dS_1}{dt} = (b_1 - \frac{a_1 r_1 N_1}{K_1}) N_1 - [d_1 + r_1 \left(\frac{(1-a_1)N_1 + \alpha_{12}N_2}{K_1} \right)] S_1 \\
 \quad - S_1(\beta_{11}Y_1 + \beta_{12}Y_2) + \gamma_1 Y_1 \\
 \frac{dY_1}{dt} = S_1(\beta_{11}Y_1 + \beta_{12}Y_2) - \gamma_1 Y_1 - [d_1 + r_1 \left(\frac{(1-a_1)N_1 + \alpha_{12}N_2}{K_1} + \delta_1 \right)] Y_1 \\
 \frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12}N_2}{K_1} \right) N_1 - \delta_1 Y_1 \\
 \frac{dS_2}{dt} = (b_2 - \frac{a_2 r_2 N_2}{K_2}) N_2 - [d_2 + r_2 \left(\frac{(1-a_2)N_2 + \alpha_{21}N_1}{K_2} \right)] S_2 \\
 \quad - S_2(\beta_{21}Y_1 + \beta_{22}Y_2) + \gamma_2 Y_2 \\
 \frac{dY_2}{dt} = S_2(\beta_{21}Y_1 + \beta_{22}Y_2) - \gamma_2 Y_2 - [d_2 + r_2 \left(\frac{(1-a_2)N_2 + \alpha_{21}N_1}{K_2} + \delta_2 \right)] Y_2 \\
 \frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2}{K_2} - \frac{\alpha_{21}N_1}{K_2} \right) N_2 - \delta_2 Y_2
 \end{array} \right. \quad (2.1)$$

System (2.1) comprises 6 equations, but only 4 are necessary, since $N_i = S_i + Y_i$. We choose to use as variables N_i and $I_i = \frac{Y_i}{N_i}$ for $i = 1, 2$, obtaining the

following 4 dimensional system:

$$\left\{ \begin{array}{l} \frac{dI_1}{dt} = [\beta_{11}(1 - I_1)N_1 - (b_1 - \frac{a_1 r_1 N_1}{K_1}) - (\gamma_1 + \delta_1) + \delta_1 I_1]I_1 \\ \quad + \beta_{12}(1 - I_1)I_2 N_2 \\ \frac{dN_1}{dt} = [r_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1}\right) - \delta_1 I_1]N_1 \\ \frac{dI_2}{dt} = [\beta_{22}(1 - I_2)N_2 - (b_2 - \frac{a_2 r_2 N_2}{K_2}) - (\gamma_2 + \delta_2) + \delta_2 I_2]I_2 \\ \quad + \beta_{21}(1 - I_2)I_1 N_1 \\ \frac{dN_2}{dt} = [r_2 \left(1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2}\right) - \delta_2 I_2]N_2 \\ 0 \leq I_i \leq 1, \quad 0 \leq N_i \quad i = 1, 2 \end{array} \right. \quad (2.2)$$

It is easy to see that system (2.2) is mathematically well posed in the positive invariant region $D = \{(I_1, N_1, I_2, N_2) | 0 \leq I_i \leq 1, 0 \leq N_i \leq K_i, i = 1, 2\}$ and solutions in D exist for all positive time. In the remainder of the paper, system (2.2) is always analyzed in the region D .

Before proceeding, we briefly summarize known results on the two ingredients of system (2.2), the Lotka-Volterra competition model, and the host-pathogen model.

2.1 Basic results on Lotka-Volterra competition model

Consider first the classic Lotka-Volterra competition model

$$\left\{ \begin{array}{l} \frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1}\right) N_1 \\ \frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2}{K_2} - \frac{\alpha_{21} N_1}{K_2}\right) N_2 \end{array} \right. \quad (2.3)$$

The following result can be found in all books on theoretical ecology.

Lemma 2.1 *System (2.3) always has the equilibria $E_0 = (0, 0)$, $E_1 = (K_1, 0)$ and $E_2 = (0, K_2)$. Assuming that all parameters are positive, E_0 is always unstable. As for the existence of an internal equilibrium and the stability of them all, there are 4 generic cases:*

- (1) *If $\alpha_{12}K_2 < K_1$ and $\alpha_{21}K_1 < K_2$, there exists also a unique internal equilibrium $E_{12} = (N_{1E}, N_{2E})$. E_{12} is globally asymptotically stable in $\Omega = \{(N_1, N_2) | 0 < N_i \leq K_i, i = 1, 2\}$.*
- (2) *If $\alpha_{12}K_2 > K_1$ and $\alpha_{21}K_1 > K_2$, there exists a unique internal equilibrium E_{12} , which is a saddle point. Both E_1 and E_2 are locally asymptotically stable.*
- (3) *If $\alpha_{12}K_2 < K_1$ and $\alpha_{21}K_1 > K_2$, there is no internal equilibrium, and E_1 is globally asymptotically stable in Ω .*
- (4) *If $\alpha_{12}K_2 > K_1$ and $\alpha_{21}K_1 < K_2$, there is no internal equilibrium, and E_2 is globally asymptotically stable in Ω .*

The coordinates of E_{12} are:

$$N_{1E} = \frac{K_1 - \alpha_{12}K_2}{1 - \alpha_{12}\alpha_{21}}, \quad N_{2E} = \frac{K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}}.$$

2.2 SIS host-pathogen system

Restricting system (2.2) to a single host species, one obtains the following SIS model, already considered in [16]

$$\begin{cases} \frac{dI}{dt} = [\beta(1 - I)N - (b - \frac{arN}{K}) - (\gamma + \delta) + \delta I]I \\ \frac{dN}{dt} = [r(1 - \frac{N}{K}) - \delta I]N \end{cases} \quad (2.4)$$

The state space for the variables is $0 \leq I \leq 1$, $0 \leq N$, and we assume $r = b - d > 0$, $0 \leq a \leq 1$.

The behavior of system (2.4) can be obtained on the basis of the reproduction number

$$R = \frac{\beta K}{b + \gamma + \delta - ar} \quad (2.5)$$

of the infection [17]; note that the denominator can be written as $d + r(1 - a) + \gamma + \delta$; hence, it is positive, and represents the average length of the infectious period.

Precisely, one has

Lemma 2.2 ([16,18]) *For system (2.4), if $R \leq 1$, the disease-free equilibrium $E_1 = (0, K)$ is globally asymptotically stable in the region $\{(I, N) | 0 \leq I \leq 1, 0 < N\}$.*

If $R > 1$, there exists a unique internal equilibrium $P = (I^, N^*)$ which is globally asymptotically stable in the region $\{(I, N) | 0 < I \leq 1, 0 < N\}$. Any solution starting from the I axis goes to $E_0 = (0, 0)$, while those starting from the N axis go to E_1 .*

Remark 2.3 *Setting the RHS of (2.4) equal to 0, one sees that (I^*, N^*) can be found as follows:*

$$N^* = K \left(1 - \frac{\delta}{r} I^* \right) \quad F(I^*) = 0 \quad (2.6)$$

where

$$F(x) = \frac{\delta}{r} x^2 - Ax + \frac{R-1}{R} \quad \text{with } A = 1 + \frac{\delta}{r} - \frac{\delta(1-a)}{\beta K}$$

It is immediate to see that, since $R > 1$, $F(0) > 0$, while

$$F(1) = \frac{\delta(1-a)}{\beta K} - \frac{1}{R} = -\frac{a\delta + b + \gamma - ar}{\beta K} = -\frac{a\delta + d + \gamma + r(1-a)}{\beta K} < 0.$$

Hence from (2.6) one finds a unique I^* in the feasible interval $(0, 1)$, that can be written as

$$I^* = \frac{r}{\delta} \frac{A - \sqrt{A^2 - 4\frac{\delta}{r}\frac{R-1}{R}}}{2}.$$

Moreover one can see that $\frac{\delta}{r}I^* < 1$ since

$$F\left(\frac{r}{\delta}\right) = \frac{r(1-a)}{\beta K} - \frac{1}{R} = -\frac{\delta + d + \gamma}{\beta K} < 0.$$

Hence, expression (2.6) shows that $N^* > 0$.

3 Equilibria

3.1 Existence of the equilibria

System (2.2) always has the following 3 boundary equilibria:

$$E_0 = (0, 0, 0, 0), \quad E_1 = (0, K_1, 0, 0), \quad E_2 = (0, 0, 0, K_2).$$

Let now

$$R_1 = \frac{\beta_{11}K_1}{b_1 + \gamma_1 + \delta_1 - a_1r_1}, \quad R_2 = \frac{\beta_{22}K_2}{b_2 + \gamma_2 + \delta_2 - a_2r_2}$$

be the reproductive ratios of the infection, analogously to (2.5).

If $R_1 > 1$ [or $R_2 > 1$], the following boundary equilibrium exists:

$$B_1 = (I_1^*, N_1^*, J_2^*, 0) \quad [\text{or } B_2 = (J_1^*, 0, I_2^*, N_2^*)].$$

With the same procedure of Remark 2.3, one sees that I_i^* and N_i^* satisfy

$$N_i^* = K_i \left(1 - \frac{\delta_i}{r_i} I_i^* \right) \quad F_i(I_i^*) = 0 \quad (3.1)$$

where

$$F_i(x) = \frac{\delta_i}{r_i} x^2 - A_i x + \frac{R_i - 1}{R_i} \quad \text{with } A_i = 1 + \frac{\delta_i}{r_i} - \frac{\delta_i(1 - a_i)}{\beta_{ii} K_i}$$

Finally, J_i^* can be found as the smaller solution of $G_i(x) = 0$, where

$$G_i(x) = \delta_i x^2 - (b_i + \gamma_i + \delta_i + \beta_{ij} I_j^* N_j^*) x + \beta_{ij} I_j^* N_j^* \quad (3.2)$$

and j indicates the index different from i . It is in fact immediate to see that $G_i(x) = 0$ has a unique solution in $(0, 1)$ given by

$$J_i^* = \frac{b_i + \gamma_i + \delta_i + \beta_{ij} I_j^* N_j^* - \sqrt{(b_i + \gamma_i + \delta_i + \beta_{ij} I_j^* N_j^*)^2 - 4\delta_i \beta_{ij} I_j^* N_j^*}}{2\delta_i}.$$

From Section 2.1 we see that there may exist an infection-free coexistence equilibrium E_{12} :

$$E_{12} = (0, N_{1E}, 0, N_{2E})$$

under two different conditions:

$$\text{a) } \alpha_{12} K_2 < K_1 \text{ and } \alpha_{21} K_1 < K_2; \quad \text{b) } \alpha_{12} K_2 > K_1 \text{ and } \alpha_{21} K_1 > K_2.$$

In case a), the equilibrium is stable relatively to infection-free perturbations; in case b), it is unstable and the equilibria E_1 and E_2 are stable relatively to infection-free perturbations.

There may exist an internal equilibrium P^* . Its coordinates must satisfy the equations:

$$I_1 = \frac{r_1}{\delta_1} \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12} N_2}{K_1} \right), \quad I_2 = \frac{r_2}{\delta_2} \left(1 - \frac{\alpha_{21} N_1}{K_2} - \frac{N_2}{K_2} \right)$$

while N_1 and N_2 can be found as solution of a system of 2 algebraic equations.

As shown in [1,2] (in the case without competition), there are not simple conditions that guarantee the existence of an internal equilibrium. Moreover, there exist cases in which there are several internal equilibria [2]. Hence, we do not attempt to characterize conditions for their existence, and we will limit ourselves to show some computer-assisted bifurcation diagrams, and to give sufficient conditions for their existence, based on persistence theory.

3.2 Local stabilities of the equilibria

In the following, we study the local stabilities of boundary equilibria. The Jacobian is

$$A = \begin{bmatrix} a_{11} & \beta_{11}I_1(1-I_1) + \frac{a_1r_1}{K_1}I_1 & \beta_{12}(1-I_1)N_2 & \beta_{12}(1-I_1)I_2 \\ -\delta_1N_1 & r_1\left(1 - \frac{2N_1 + \alpha_{12}N_2}{K_1}\right) - \delta_1I_1 & 0 & -\frac{r_1\alpha_{12}}{K_1}N_1 \\ \beta_{21}(1-I_2)N_1 & \beta_{21}(1-I_2)I_1 & a_{33} & \beta_{22}(1-I_2)I_2 + \frac{a_2r_2}{K_2}I_2 \\ 0 & -\frac{r_2\alpha_{21}}{K_2}N_2 & -\delta_2N_2 & r_2\left(1 - \frac{\alpha_{21}N_1 + 2N_2}{K_2}\right) - \delta_2I_2 \end{bmatrix}$$

where

$$a_{11} = \beta_{11}N_1 - 2\beta_{11}I_1N_1 - (b_1 + \gamma_1 + \delta_1) + \frac{a_1r_1}{K_1}N_1 + 2\delta_1I_1 - \beta_{12}I_2N_2,$$

$$a_{33} = \beta_{22}N_2 - 2\beta_{22}I_2N_2 - (b_2 + \gamma_2 + \delta_2) + \frac{a_2r_2}{K_2}N_2 + 2\delta_2I_2 - \beta_{21}I_1N_1.$$

For $E_0 = (0, 0, 0, 0)$, we have

$$A_0 = \begin{bmatrix} -(b_1 + \gamma_1 + \delta_1) & 0 & 0 & 0 \\ 0 & r_1 & 0 & 0 \\ 0 & 0 & -(b_2 + \gamma_2 + \delta_2) & 0 \\ 0 & 0 & 0 & r_2 \end{bmatrix}$$

So E_0 is unstable.

For $E_1 = (0, K_1, 0, 0)$, we have

$$A_1 = \begin{bmatrix} \beta_{11}K_1 - (b_1 + \gamma_1 + \delta_1) + a_1r_1 & 0 & 0 & 0 \\ -\delta_1K_1 & -r_1 & 0 & -r_1\alpha_{12} \\ \beta_{21}K_1 & 0 & -(b_2 + \gamma_2 + \delta_2) & 0 \\ 0 & 0 & 0 & r_2\left(1 - \frac{\alpha_{21}K_1}{K_2}\right) \end{bmatrix}$$

Its eigenvalues are

$$\lambda_1 = \beta_{11}K_1 - (b_1 + \gamma_1 + \delta_1) + a_1r_1, \lambda_2 = -r_1, \lambda_3 = -(b_2 + \gamma_2 + \delta_2), \lambda_4 = r_2\left(1 - \frac{\alpha_{21}K_1}{K_2}\right).$$

So E_1 is stable if $\alpha_{21}K_1 > K_2$ and $R_1 < 1$; it is unstable if either inequality is reversed.

Analogously, one finds that $E_2 = (0, 0, 0, K_2)$ is stable if $\alpha_{12}K_2 > K_1$ and $R_2 < 1$; it is unstable if either inequality is reversed.

For $B_2 = (J_1^*, 0, I_2^*, N_2^*)$, we have

$$A_{B_2} = \begin{bmatrix} b_{11} & \beta_{11}J_1^*(1 - J_1^*) + \frac{a_1r_1}{K_1}J_1^* & \beta_{12}(1 - J_1^*)N_2^* & \beta_{12}(1 - J_1^*)I_2^* \\ 0 & r_1\left(1 - \alpha_{12}\frac{N_2^*}{K_1}\right) - \delta_1J_1^* & 0 & 0 \\ 0 & \beta_{21}(1 - I_2^*)J_1^* & -(\beta_{22}N_2^* - \delta_2)I_2^* & \beta_{22}(1 - I_2^*)I_2^* + \frac{a_2r_2}{K_2}I_2^* \\ 0 & -\alpha_{21}\frac{r_2}{K_2}N_2^* & -\delta_2N_2^* & r_2 - 2\frac{r_2}{K_2}N_2^* - \delta_2I_2^* \end{bmatrix}$$

where

$$b_{11} = -(b_1 + \gamma_1 + \delta_1) + 2\delta_1J_1^* - \beta_{12}I_2^*N_2^*.$$

It is immediate to see that the eigenvalues of A_{B_2} are

$\lambda_1 = b_{11}$, $\lambda_2 = r_1\left(1 - \alpha_{12}\frac{N_2^*}{K_1}\right) - \delta_1J_1^*$, while λ_3 and λ_4 the two eigenvalues of the bottom-right submatrix

$$BR = \begin{bmatrix} -(\beta_{22}N_2^* - \delta_2)I_2^* & \beta_{22}(1 - I_2^*)I_2^* + \frac{a_2r_2}{K_2}I_2^* \\ -\delta_2N_2^* & r_2 - 2\frac{r_2}{K_2}N_2^* - \delta_2I_2^* \end{bmatrix}.$$

Both eigenvalues of BR have negative real parts, as known from the analysis

of SIS models in a single population (see Section 2.2) and confirmed by the sign of its trace and determinant.

Moreover, we have

$$\lambda_1 = b_{11} = \frac{1}{J_1^*}(\delta_1 J_1^{*2} - \beta_{12} I_2^* N_2^*) < 0$$

using the fact that J_1^* is the smaller root of (3.2).

Hence B_2 is stable if $\pi_1 = r_1 \left(1 - \alpha_{12} \frac{N_2^*}{K_1}\right) - \delta_1 J_1^* < 0$, and unstable if the inequality is reversed.

Analogously, B_1 is stable if $\pi_2 = r_2 \left(1 - \alpha_{21} \frac{N_1^*}{K_2}\right) - \delta_2 J_2^* < 0$, unstable otherwise.

For studying the eigenvalues of the Jacobian at E_{12} , it is more convenient to change the order of coordinates to (I_1, I_2, N_1, N_2) ; hence, the equilibrium will be $(0, 0, N_{1E}, N_{2E})$. Then, its Jacobian is

$$C_{12} = \begin{bmatrix} c_{11} & \beta_{12} N_{2E} & 0 & 0 \\ \beta_{21} N_{1E} & c_{22} & 0 & 0 \\ -\delta_1 N_{1E} & 0 & r_1 \left(1 - \frac{2N_{1E} + \alpha_{12} N_{2E}}{K_1}\right) & -\frac{r_1 \alpha_{12}}{K_1} N_{1E} \\ 0 & -\delta_2 N_{2E} & -\frac{r_2 \alpha_{21}}{K_2} N_{2E} & r_2 \left(1 - \frac{\alpha_{21} N_{1E} + 2N_{2E}}{K_2}\right) \end{bmatrix} \quad (3.3)$$

with

$$c_{11} = \beta_{11} N_{1E} - (b_1 + \gamma_1 + \delta_1) + \frac{a_1 r_1}{K_1} N_{1E}, \quad c_{22} = \beta_{22} N_{2E} - (b_2 + \gamma_2 + \delta_2) + \frac{a_2 r_2}{K_2} N_{2E}$$

Since C_{12} is block triangular, its eigenvalues are those of the top-left and of the bottom-right submatrices. The top-left matrix TL can be written as

$$TL = K - D \quad \text{with}$$

$$K = \begin{bmatrix} \beta_{11} N_{1E} & \beta_{12} N_{2E} \\ \beta_{21} N_{1E} & \beta_{22} N_{2E} \end{bmatrix} \quad \text{and} \quad D = \text{diag} \begin{bmatrix} d_1 + \gamma_1 + \delta_1 + r_1 \left(1 - a_1 \frac{N_{1E}}{K_1}\right) \\ d_2 + \gamma_2 + \delta_2 + r_2 \left(1 - a_2 \frac{N_{2E}}{K_2}\right) \end{bmatrix}.$$

In conclusion, the eigenvalues of TL have all negative real parts if and only if all eigenvalues of KD^{-1} are in the interior of the unit ball [19,20]. One can then define R_{12} as the largest eigenvalue of KD^{-1} , in formula

$$R_{12} = \rho \left(\begin{bmatrix} \frac{\beta_{11}N_{1E}}{d_1+\gamma_1+\delta_1+r_1(1-a_1\frac{N_{1E}}{K_1})} & \frac{\beta_{12}N_{2E}}{d_2+\gamma_2+\delta_2+r_2(1-a_2\frac{N_{2E}}{K_2})} \\ \frac{\beta_{21}N_{1E}}{d_1+\gamma_1+\delta_1+r_1(1-a_1\frac{N_{1E}}{K_1})} & \frac{\beta_{22}N_{2E}}{d_2+\gamma_2+\delta_2+r_2(1-a_2\frac{N_{2E}}{K_2})} \end{bmatrix} \right). \quad (3.4)$$

The bottom-right submatrix

$$\begin{bmatrix} r_1 \left(1 - \frac{2N_{1E}+\alpha_{12}N_{2E}}{K_1} \right) & -\frac{r_1\alpha_{12}}{K_1} N_{1E} \\ -\frac{r_2\alpha_{21}}{K_2} N_{2E} & r_2 \left(1 - \frac{\alpha_{21}N_{1E}+2N_{2E}}{K_2} \right) \end{bmatrix}$$

is the Jacobian of the infection-free competition system. Its eigenvalues are negative when E_{12} is stable relatively to infection-free perturbations, i.e. when $\alpha_{12}K_2 < K_1$ and $\alpha_{21}K_1 < K_2$. If the inequalities are reversed, one eigenvalue is positive.

Hence, E_{12} is stable if $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 < K_2$ and $R_{12} < 1$. It is unstable if any of these inequalities is reversed.

Remark 3.1 *It is useful to distinguish between two subcases when $R_{12} > 1$: in the first, both eigenvalues of TL have positive real parts; in the other, the eigenvalues are real and opposite in sign. In the first subcase, necessarily we have $R_1 > 1$ and $R_2 > 1$. In fact, both eigenvalues have positive real parts if and only if $\text{tr}(TL) > 0$ and $\text{det}(TL) > 0$; these two conditions together imply*

$$\beta_{ii}N_{iE} - \left(b_i + \gamma_i + \delta_i - \frac{a_i r_i}{K_i} N_{iE} \right) > 0 \quad (i = 1, 2)$$

i.e.

$$Q_i(N_{iE}) := \frac{\beta_{ii}N_{iE}}{b_i + \gamma_i + \delta_i - \frac{a_i r_i}{K_i}N_{iE}} > 1. \quad (3.5)$$

Since $N_{iE} < K_i$ and $Q_i(\cdot)$ are increasing functions, we obtain $1 < Q_i(K_i) = R_i$.

The results of this section are summarized in the table below.

Equilibrium	Existence?	Stable?
$E_0 = (0, 0, 0, 0)$	Yes	No
$E_1 = (0, K_1, 0, 0)$	Yes	$\alpha_{21}K_1 > K_2$ and $R_1 < 1$
$E_2 = (0, 0, 0, K_2)$	Yes	$\alpha_{12}K_2 > K_1$ and $R_2 < 1$
$B_1 = (I_1^*, N_1^*, J_2^*, 0)$	$R_1 > 1$	$\pi_2 = r_2 \left(1 - \frac{\alpha_{21}N_1^*}{K_2}\right) - \delta_2 J_2^* < 0$
$B_2 = (J_1^*, 0, I_2^*, N_2^*)$	$R_2 > 1$	$\pi_1 = r_1 \left(1 - \frac{\alpha_{12}N_2^*}{K_1}\right) - \delta_1 J_1^* < 0$
$E_{12} = (0, N_{1E}, 0, N_{2E})$	$\alpha_{ij}K_j < K_i$ (or both reversed)	$\alpha_{ij}K_j < K_i$ and $R_{12} < 1$

Table 1

Conditions for existence and stability of boundary equilibria

4 Persistence

We start by recalling some basic definition and results about persistence, following the presentation by Thieme [14].

Let X be a metric space with metric d and the union of two disjoint subsets X_1 , X_2 , and Φ a continuous semiflow on X_1 , i.e., a continuous mapping $\Phi :$

$[0, \infty) \times X_1 \longrightarrow X_1$ with the following properties:

$$\Phi_t \circ \Phi_s = \Phi_{t+s}, \quad t, s \geq 0; \quad \Phi_0(x) = x, \quad x \in X_1$$

Let Y_2 be a subset of X_2 , and recall that the distance $d(x, Y)$ of a point $x \in X$ from a subset Y of X is defined by $d(x, Y) = \inf_{y \in Y} d(x, y)$. Then

Y_2 is called a weak repeller for X_1 if

$$\limsup_{t \rightarrow \infty} d(\Phi_t(x_1), Y_2) > 0 \quad \forall x_1 \in X_1.$$

Y_2 is called a strong repeller for X_1 if

$$\liminf_{t \rightarrow \infty} d(\Phi_t(x_1), Y_2) > 0 \quad \forall x_1 \in X_1.$$

Y_2 is called a uniform weak repeller for X_1 if there is some $\epsilon > 0$ such that

$$\limsup_{t \rightarrow \infty} d(\Phi_t(x_1), Y_2) > \epsilon \quad \forall x_1 \in X_1.$$

Y_2 is called a uniform strong repeller for X_1 if there is some $\epsilon > 0$ such that

$$\liminf_{t \rightarrow \infty} d(\Phi_t(x_1), Y_2) > \epsilon \quad \forall x_1 \in X_1.$$

Let M be a subset of X , M is called forward invariant if and only if $\Phi_t(M) \subset M$, $t > 0$, and invariant if and only if $\Phi_t(M) = M$, $t > 0$. A compact invariant subset M of $Y \subseteq X$ is called an isolated compact invariant set in Y if there is an open subset U of X such that there is no invariant set \tilde{M} with $M \subsetneq \tilde{M} \subseteq U \cap Y$ except M . A finite covering $M = \bigcup_{k=1}^m M_k$ in X_2 is called isolated if the sets M_k are pairwise disjoint subsets of X_2 , which are isolated compact invariant sets in X .

A set $M \subset X_2$ is said to be chained (in X_2) to another (not necessarily different) set $N \subset X_2$, symbolically $M \mapsto N$, if there is some $y \in X_2$, $y \notin M \cup N$, and a full orbit through y in X_2 whose α -limit set is contained in M and whose ω -limit set is contained in N . We recall that an element $y \in X$ has a full orbit, if there is a function $x(t)$, $-\infty < t < \infty$, such that $x(0) = y$ and $x(t + s) = \Phi_t(x(s))$ for all $t \geq 0$, $s \in \mathbb{R}$. Moreover, the ω -limit set of a point y is defined as usual:

$$\omega(y) = \bigcap_{t \geq 0} \overline{\Phi([t, \infty) \times \{y\})}$$

A finite covering $M = \bigcup_{k=1}^m M_k$ is called cyclic if, after possible renumbering, $M_1 \mapsto M_1$ or $M_1 \mapsto M_2 \mapsto \dots \mapsto M_k \mapsto M_1$ for some $k \in \{2, 3, \dots, m\}$. M is called an acyclic covering otherwise.

We now state two useful results of Thieme [14] on how to obtain persistence through the acyclicity of the flow on X_2 .

Lemma 4.1 ([14, Theorem 4.5]) *Let X be locally compact, and let X_2 be compact in X and X_1 be forward invariant under the continuous semiflow Φ on X . Assume that*

$$\Omega_2 = \bigcup_{y \in Y_2} \omega(y), \quad Y_2 = \{x \in X_2; \Phi_t(x) \in X_2, \forall t > 0\}. \quad (4.1)$$

has an acyclic isolated covering $M = \bigcup_{k=1}^m M_k$. If each part M_k of M is a weak repeller for X_1 , then X_2 is a uniform strong repeller for X_1 .

Lemma 4.2 ([14, Proposition 4.3]) *Let X be locally compact, and let X_2 be compact in X and X_1 be forward invariant under the continuous semiflow*

Φ on X . Let x_n be a sequence of elements in X_1 satisfying

$$\limsup_{t \rightarrow \infty} d(\Phi_t(x_n), X_2) \rightarrow 0, \quad n \rightarrow \infty$$

Let $M = \bigcup_{k=1}^m M_k$ be an isolated covering of Ω_2 such that $\omega(x_n) \not\subset M_k$ for all n, k . Then M is cyclic.

We will use these concepts with Φ_t denoting the mapping given by $\Phi_t(x) = \Phi(t, x)$, the solution of system (2.2) with initial condition $x \in X = D = \{(I_1, N_1, I_2, N_2) | 0 \leq I_i \leq 1, 0 \leq N_i \leq K_i, i = 1, 2\}$. We analyze the persistence of system (2.2), meaning that a given set $D_2 \subset X$ is a repeller for $D_1 = X \setminus D_2$ or some $\tilde{D}_1 \subset D_1$. D_2 will represent (part of) the boundary of the compact set D . For ease of notation, we will let $x(t) = (I_1(t), N_1(t), I_2(t), N_2(t)) = \Phi_t(x^0)$ with $x^0 = (I_1(0), N_1(0), I_2(0), N_2(0))$.

At first, we consider persistence of the populations.

Theorem 4.3 *For system (2.2), we have the following result: there exists an $\epsilon > 0$ such that, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$,*

$$\liminf_{t \rightarrow \infty} \max\{N_1(t), N_2(t)\} > \epsilon.$$

Proof. Define

$$D_2 = \{(I_1, N_1, I_2, N_2) | 0 \leq I_i \leq 1, N_i = 0, i = 1, 2\}, \quad D_1 = D \setminus D_2$$

D_2 is clearly compact (in D), D_1 and D_2 are forward invariant.

Let $\Omega_2 = \bigcup_{y \in D_2} \omega(y)$.

It is easy to see that $\Omega_2 = \{E_0\} = \{(0, 0, 0, 0)\}$ and $\{E_0\}$ is an acyclic covering for Ω_2 . Looking at system (2.2) we see that this covering is isolated and a weak repeller for D_1 . So by Lemma 4.1, D_2 is a uniform strong repeller for D_1 , i.e.

the thesis. □

The previous result shows that always at least one population does not get extinct. Let now consider assumptions that guarantee strong persistence of one specific host, say host population 1.

Theorem 4.4 *Let $\alpha_{12}K_2 < K_1$ and either*

a) $R_2 \leq 1$,

or

b) $R_2 > 1$ and $\pi_1 > 0$.

Then there exists an $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} N_1(t) > \epsilon$, for any solution $x(t)$ with $N_1(0) > 0$.

Proof. Define

$$D_2 = \{(I_1, N_1, I_2, N_2) | 0 \leq I_i \leq 1, N_1 = 0, 0 \leq N_2 \leq K_2\}, \quad D_1 = D \setminus D_2.$$

The proof of case a) is analogous (but simpler) to that of case b). Hence we restrict the analysis to case b).

D_2 is compact in D , D_1 and D_2 are forward invariant. Let $\Omega_2 = \bigcup_{y \in D_2} \omega(y)$.

In order to study Ω_2 , we analyze the semiflow induced by (2.2) on the forward invariant set D_2 , i.e., for $N_1 \equiv 0$:

$$\begin{cases} \frac{dI_1}{dt} = [-(b_1 + \gamma_1 + \delta_1) + \delta_1 I_1] I_1 + \beta_{12}(1 - I_1) I_2 N_2 \\ \frac{dI_2}{dt} = [\beta_{22}(1 - I_2) N_2 - (b_2 - \frac{\alpha_2 r_2 N_2}{K_2}) - (\gamma_2 + \delta_2) + \delta_2 I_2] I_2 \\ \frac{dN_2}{dt} = [r_2(1 - \frac{N_2}{K_2}) - \delta_2 I_2] N_2 \end{cases} \quad (4.2)$$

It is easy to see that there are three equilibria $E_0 = (0, 0, 0, 0)$, $E_2 = (0, 0, 0, K_2)$ and $B_2 = (J_1^*, 0, I_2^*, N_2^*)$ for system (4.2). By Section 2.2 and the first equation of system (4.2), we have: (1) any solution $(I_1(t), 0, I_2(t), N_2(t)) \in D_2$ with $N_2(0) = 0$ tends to E_0 as $t \rightarrow \infty$; (2) any solution $(I_1(t), 0, I_2(t), N_2(t)) \in D_2$ with $I_2(0) = 0$, $N_2(0) > 0$ tends to E_2 as $t \rightarrow \infty$; (3) any solution $(I_1(t), 0, I_2(t), N_2(t)) \in D_2$ with $I_2(0) > 0$, $N_2(0) > 0$ tends to B_2 as $t \rightarrow \infty$. So Ω_2 consists of the three equilibria. And it is easy to see that these equilibria cannot be chained to themselves in D_2 . Furthermore, they cannot be chained to each other in a cyclic way in D_2 .

Let $M_1 = \{E_0\}$, $M_2 = \{E_2\}$, $M_3 = \{B_2\}$, then $M = \bigcup_{i=1}^3 M_i$ represents an acyclic covering for Ω_2 . To show that this covering is isolated in D and a weak repeller for D_1 , we analyze the behavior of

$$\frac{dN_1}{dt} = [r_1 \left(1 - \frac{N_1}{K_1} - \frac{\alpha_{12}N_2}{K_1}\right) - \delta_1 I_1] N_1, \quad N_1(0) > 0 \quad (4.3)$$

when a solution $x(t)$ stays close to E_0 , E_2 or B_2 respectively. If $x(t)$ stays close to E_0 , by (4.3) N_1 increases exponentially. Similarly, if $x(t)$ stays close to E_2 or B_2 , by (4.3), and the conditions $\alpha_{12}K_2 < K_1$ or $\pi_1 = r_1 \left(1 - \frac{\alpha_{12}N_2^*}{K_1}\right) - \delta_1 J_1^* > 0$, N_1 increases exponentially too. So the covering M is isolated and each part M_i is a weak repeller for D_1 .

Hence by Lemma 4.1, D_2 is a uniform strong repeller for D_1 . Namely there exists an $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} N_1(t) > \epsilon$, for any solution $x(t)$ with $N_1(0) > 0$.
□

Theorem 4.4 assumes that the equilibrium E_2 is unstable for the pure competition system (2.3). Without that assumption, we may still prove weak persistence of population 1.

Theorem 4.5 For system (2.2), if $\alpha_{12}K_2 > K_1$, $R_2 > 1$ and $\pi_1 > 0$, then we have:

- (1) there exists a solution $x(t) = (0, N_1(t), 0, N_2(t))$ with $N_1(0) > 0$, such that $\lim_{t \rightarrow \infty} N_1(t) = 0$;
- (2) there exists an $\epsilon > 0$ such that $\limsup_{t \rightarrow \infty} N_1(t) > \epsilon$, for any solution $x(t)$ with $I_1(0) > 0$, $N_1(0) > 0$, $I_2(0) > 0$, $N_2(0) > 0$.

Proof. 1. When $\alpha_{12}K_2 > K_1$, by Section 2.1 $(0, K_2)$ is stable for system (2.3). So we can find a solution $(0, N_1(t), 0, N_2(t))$ with $N_1(0) > 0$, such that $\lim_{t \rightarrow \infty} N_1(t) = 0$.

2. Define

$$D_2 = \{(I_1, N_1, I_2, N_2) | 0 \leq I_i \leq 1, N_1 = 0, 0 \leq N_2 \leq K_2\}, \quad D_1 = D \setminus D_2,$$

$$\tilde{D}_1 = \{(I_1, N_1, I_2, N_2) | 0 < I_i \leq 1, 0 < N_i \leq K_i, i = 1, 2\}$$

It is easy to see that D_1 , \tilde{D}_1 and D_2 are forward invariant.

$$\text{Let } \Omega_2 = \bigcup_{y \in D_2} \omega(y).$$

In order to study Ω_2 , we must analyze the semiflow on D_2 , i.e. (4.2). As above, Ω_2 consists of three equilibria E_0 , E_2 and B_2 . And it is easy to see that these equilibria cannot be chained to themselves or to each other in a cyclic way in D_2 .

Letting again $M_1 = \{E_0\}$, $M_2 = \{E_2\}$, $M_3 = \{B_2\}$, then $M = \bigcup_{i=1}^3 M_i$ represents an acyclic covering for Ω_2 , and it is easy to see that this covering is isolated in D and each part M_i is a weak repeller for \tilde{D}_1 .

We cannot apply Lemma 4.1, since it is not true that each part is a weak

repeller for D_1 . However, we will show, using Lemma 4.2, that D_2 is a uniform weak repeller for \tilde{D}_1 .

If D_2 is not a uniform weak repeller for \tilde{D}_1 , then we find a sequence $x_n = (I_{1n}, N_{1n}, I_{2n}, N_{2n}) \in \tilde{D}_1 \subset D_1$ satisfying

$$\limsup_{t \rightarrow \infty} d(\Phi_t(x_n), D_2) \rightarrow 0, \quad n \rightarrow \infty$$

As each part M_i is a weak repeller for \tilde{D}_1 , we have $\omega(x_n) \not\subset M_i$ for all n, i . Hence the assumptions of Lemma 4.2 are satisfied (indeed D_2 is compact) and the covering M has to be cyclic, in contradiction to the acyclic property of M . So D_2 is a uniform weak repeller for \tilde{D}_1 , which is the thesis. \square

The previous Theorem shows that a species that would get extinct without the infection, may (weakly) persist in presence of the infection.

Remark 4.6 *The results on the stability of the boundary equilibria yield conditions for the non-persistence of N_1 . Precisely, if $\alpha_{12}K_2 > K_1$ and $R_2 < 1$, or if $R_2 > 1$ and $\pi_1 < 0$, then N_1 is not persistent. In fact, in the first case, E_2 is asymptotically stable; in the second, B_2 is asymptotically stable.*

Clearly, similar results would hold for species 2, exchanging all indices.

We now consider persistence of the infection.

Theorem 4.7 *If $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 < K_2$ and $R_2 > 1$, there exists an $\epsilon > 0$ such that, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_2(0) > 0$ or $I_1(0) > 0$, $\liminf_{t \rightarrow \infty} \min\{I_1(t), I_2(t)\} > \epsilon$.*

Proof. Define

$$D_2 = \{(I_1, N_1, I_2, N_2) | I_1 = 0 \text{ or } I_2 = 0, 0 \leq N_i \leq K_i\}, \quad D_1 = D \setminus D_2,$$

$$\tilde{D}_1 = \{(I_1, N_1, I_2, N_2) | 0 < I_i \leq 1, 0 < N_i \leq K_i, i = 1, 2\}$$

It is easy to see that D_1 and \tilde{D}_1 are forward invariant.

From the assumption $N_1(0) > 0$, $N_2(0) > 0$, and $I_2(0) > 0$ or $I_1(0) > 0$, it follows that $\Phi_t(x^0) \in \tilde{D}_1$ for all $t > 0$. We can then assume $x_0 \in \tilde{D}_1$.

Let

$$\Omega_2 = \bigcup_{y \in Y_2} \omega(y), \quad Y_2 = \{x = (I_1, N_1, I_2, N_2) \in D_2; \Phi_t(x) \in D_2, \forall t > 0\}$$

By analyzing the semiflow induced by (2.2), we find that Ω_2 consists of three equilibria, $E_0 = (0, 0, 0, 0)$, $E_1 = (0, K_1, 0, 0)$ and $E_2 = (0, 0, 0, K_2)$. Furthermore, they cannot be chained to themselves, or to each other in a cyclic way in D_2 .

Setting $M_1 = \{E_0\}$, $M_2 = \{E_1\}$, $M_3 = \{E_2\}$, $M = \bigcup_{i=1}^3 M_i$ represents an acyclic covering for Ω_2 . By analysing the flow in the neighbourhood of each equilibrium, it is easy to see that this covering is isolated in D and each part M_i is a weak repeller for \tilde{D}_1 . As in the Proof of Theorem 4.5, we can use this to prove that D_2 is a uniform weak repeller for \tilde{D}_1 , i.e. there exists an $0 < \tilde{\epsilon} < \min\{J_1^*, J_2^*, I_1^*, I_2^*\}$ such that

$$\limsup_{t \rightarrow \infty} \min\{I_1(t), I_2(t)\} > \tilde{\epsilon} \tag{4.4}$$

for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$, $I_1(0) > 0$ and $I_2(0) > 0$.

Now, we prove that D_2 is a uniform strong repeller for \tilde{D}_1 . Suppose that D_2 is not a uniform strong repeller for \tilde{D}_1 . Then there exist sequences $x_j^0 =$

$(I_1^j(0), N_1^j(0), I_2^j(0), N_2^j(0)) \in \tilde{D}_1$ and $0 < \epsilon_j < \tilde{\epsilon}$ such that

$$\liminf_{t \rightarrow \infty} \min\{I_1^j(t), I_2^j(t)\} < \epsilon_j \quad \text{for } j = 1, 2, \dots \quad (4.5)$$

Here $\lim_{t \rightarrow \infty} \epsilon_j = 0$ and $(I_1^j(t), N_1^j(t), I_2^j(t), N_2^j(t))$ are the solutions of system (2.2) with initial values $x_j^0 \in \tilde{D}_1$.

From (4.5) and (4.4), we can find sequences $0 < r_j < s_j < t_j$ with $\lim_{j \rightarrow \infty} r_j = \infty$ such that

$$\lim_{j \rightarrow \infty} \min\{I_1^j(s_j), I_2^j(s_j)\} = 0, \quad (4.6)$$

$$\min\{I_1^j(r_j), I_2^j(r_j)\} = \min\{I_1^j(t_j), I_2^j(t_j)\} = \tilde{\epsilon}, \quad (4.7)$$

$$\min\{I_1^j(t), I_2^j(t)\} \leq \tilde{\epsilon} \quad \text{for } r_j \leq t \leq t_j. \quad (4.8)$$

Moreover, r_j may be chosen large enough such that: (1) when $R_1 \leq 1$, $N_2^j(t) > \epsilon^*$ for $t \geq r_j$, where $\epsilon^* > 0$ is a positive constant (this follows from Theorem 4.4, reversing the indices); (2) when $R_1 > 1$, $\max\{N_1^j(t), N_2^j(t)\} > \epsilon^*$ for $t \geq r_j$ (this follows from Theorem 4.3).

After choosing a subsequence, the sequence $(I_1^j(r_j), N_1^j(r_j), I_2^j(r_j), N_2^j(r_j))$ is convergent in D , and let

$$\lim_{j \rightarrow \infty} (I_1^j(r_j), N_1^j(r_j), I_2^j(r_j), N_2^j(r_j)) = (I_1^{**}(0), N_1^{**}(0), I_2^{**}(0), N_2^{**}(0)) = x^{**}(0).$$

Then by (4.7) we have $\min\{I_1^{**}(0), I_2^{**}(0)\} = \tilde{\epsilon}$, so that $x^{**}(0) \in D_1$.

In the following, we prove the thesis in two steps.

First, we prove by contradiction that $t_j - r_j$ is unbounded. Suppose in fact that $t_j - r_j$ is bounded; then, after taking a subsequence, $s_j - r_j$ is convergent

and let $\lim_{j \rightarrow \infty} (s_j - r_j) = s^*$. By the basic properties of flow we have

$$\lim_{j \rightarrow \infty} (I_1^j(r_j + s^*), N_1^j(r_j + s^*), I_2^j(r_j + s^*), N_2^j(r_j + s^*)) = x^{**}(s^*) \quad (4.9)$$

where $x^{**}(t)$ is the solution of system (2.2) with initial value $x^{**}(0)$. Since $x^{**}(0) \in D_1$ and D_1 is invariant, we have $x^{**}(s^*) \in D_1$. At the same time, by the basic properties of flow we also have

$$\lim_{j \rightarrow \infty} (I_1^j(s_j), N_1^j(s_j), I_2^j(s_j), N_2^j(s_j)) = x^{**}(s^*).$$

Moreover we have $x^{**}(s^*) \in D_2$ by (4.6) and the compactness of D_2 . A contradiction occurs, so $t_j - r_j$ is unbounded.

Next, we prove a contradiction under the assumption of non-uniform strong repeller. If $x^{**}(0) \in \tilde{D}_1$, then, by (4.4), we have

$$\limsup_{t \rightarrow \infty} \min\{I_1^{**}(t), I_2^{**}(t)\} > \tilde{\epsilon} \quad (4.10)$$

We show that (4.10) always holds. If $x^{**}(0) \in D_1 \setminus \tilde{D}_1$, then we have two cases:

- (1) when $R_1 \leq 1$, we have seen above that $N_2^j(t) > \epsilon^*$ for $t \geq r_j$ so that $N_2^{**}(0) \geq \epsilon^*$; then, from (4.7), we have $\min\{I_1^{**}(0), I_2^{**}(0)\} = \tilde{\epsilon}$, so that it must be $N_1^{**}(0) = 0$. Then $N_1^{**}(t) \equiv 0$ and from Lemma 2.2 and the first equation of system (2.2) we have

$$\lim_{t \rightarrow \infty} I_1^{**}(t) = J_1^* \text{ and } \lim_{t \rightarrow \infty} I_2^{**}(t) = I_2^*$$

which means that (4.10) holds.

- (2) when $R_1 > 1$, we obtain by $\max\{N_1^j(t), N_2^j(t)\} > \epsilon^*$ for $t \geq r_j$ that either $N_1^{**}(0) = 0$ and $N_2^{**}(0) \geq \epsilon^*$ or vice versa. Analogously to the previous case, we can then prove that (4.10) holds.

Now, since $t_j - r_j$ is unbounded, after choosing a subsequence, we may assume

that $t_j - r_j$ is increasing monotonically and $\lim_{j \rightarrow \infty} t_j - r_j = \infty$. Then by (4.8) we have, for $k > j$,

$$\min\{I_1^k(r_k + r), I_2^k(r_k + r)\} \leq \tilde{\epsilon} \text{ for } 0 \leq r \leq t_j - r_j.$$

Fixing r and j , and letting k tend to infinity, we obtain, for $0 \leq r \leq t_j - r_j$,

$$\min\{I_1^{**}(r), I_2^{**}(r)\} = \lim_{k \rightarrow \infty} \min\{I_1^k(r_k + r), I_2^k(r_k + r)\} \leq \tilde{\epsilon}. \quad (4.11)$$

We now let $j \rightarrow \infty$ and, as $\lim_{j \rightarrow \infty} t_j - r_j = \infty$, (4.11) holds for all $r \geq 0$, contradicting (4.10). This means that D_2 is a uniform strong repeller for \tilde{D}_1 , i.e. the thesis. \square

A similar result holds exchanging hosts 1 and 2.

For the cases where the competition model has an internal equilibrium, we have the following:

Theorem 4.8 *For system (2.2), if $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 < K_2$ and $R_{12} > 1$, there exists an $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} \min\{I_1(t), I_2(t)\} > \epsilon$, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_2(0) > 0$ or $I_1(0) > 0$.*

Proof. Define

$$D_2 = \{(I_1, N_1, I_2, N_2) | I_1 = 0 \text{ or } I_2 = 0, 0 \leq N_i \leq K_i\}, \quad D_1 = D \setminus D_2,$$

$$\tilde{D}_1 = \{(I_1, N_1, I_2, N_2) | 0 < I_i \leq 1, 0 < N_i \leq K_i, i = 1, 2\}$$

D_1 and \tilde{D}_1 are forward invariant. Let

$$\Omega_2 = \bigcup_{y \in Y_2} \omega(y), \quad Y_2 = \{x = (I_1, N_1, I_2, N_2) \in D_2; \Phi_t(x) \in D_2, \forall t > 0\}$$

By analyzing the semiflow induced by (2.2), we find that Ω_2 consists of four equilibria, $E_0 = (0, 0, 0, 0)$, $E_1 = (0, K_1, 0, 0)$, $E_2 = (0, 0, 0, K_2)$ and $E_{12} =$

$(0, N_{1E}, 0, N_{2E})$. These equilibria cannot be chained to themselves in D_2 or to each other in a cyclic way in D_2 .

Let $M_1 = \{E_0\}$, $M_2 = \{E_1\}$, $M_3 = \{E_2\}$, $M_4 = \{E_{12}\}$; then $M = \bigcup_{i=1}^4 M_i$ represents an acyclic covering for Ω_2 . To show that this covering is isolated in D , we analyze the behavior of system (2.2) when any solution $x(t)$ stays close to E_0 , E_1 , E_2 or E_{12} respectively.

If $x(t)$ stays close to E_0 , we have two cases: (1) if $N_1(0) = N_2(0) = 0$, then $N_1(t) = N_2(t) \equiv 0$. In this case, I_1 and I_2 decrease exponentially; (2) if $N_1(0) > 0$ or $N_2(0) > 0$, then $N_1(t) > 0$ or $N_2(t) > 0$. By (2.2) N_1 or N_2 increases exponentially. So by the two cases, M_1 is isolated in D .

If $x(t)$ stays in a small neighbourhood of E_2 , we have three cases:

- (1) if $N_1(0) = I_2(0) = 0$, then $N_1(t) = I_2(t) \equiv 0$. By (2.2), $K_2 - N_2(t)$ decreases exponentially, so $x(t)$ has to exit the neighbourhood as $t \rightarrow -\infty$;
- (2) if $N_1(0) > 0$, then $N_1(t) > 0$ and

$$\frac{dN_1}{dt} \geq \left[r_1 \left(1 - \frac{\eta}{K_1} - \frac{\alpha_{12}K_2}{K_1} \right) - \delta_1\eta \right] N_1$$

where η is the size of the neighbourhood. Since $\alpha_{12}K_2 < K_1$, choosing $\eta > 0$ small enough, we see that N_1 increases exponentially as $t \rightarrow +\infty$;

- (3) if $N_1(0) = 0$ and $I_2(0) > 0$, then $N_1(t) \equiv 0$ and $I_2(t) > 0$ for all $t > 0$. In this case, $(I_2(t), N_2(t))$ satisfy system (2.4) that has no invariant subset other than E_2 in its neighbourhood; in fact, if $R_2 \leq 1$, $I_2(t)$ is monotonically decreasing; otherwise $I_2(t)$ increases to I_2^* .

So by all cases, M_3 is isolated in D .

Similarly, we can prove that M_2 is isolated in D .

If $x(t)$ stays close to E_{12} , we have two cases:

- (1) if $I_1(0) = I_2(0) = 0$, then $I_1(t) = I_2(t) \equiv 0$. Then (2.3) with $\alpha_{12}K_2 < K_1$ and $\alpha_{21}K_1 < K_2$ shows that $(N_1(t), N_2(t))$ goes far away from E_{12} as $t \rightarrow -\infty$.
- (2) if $I_1(0) > 0$ or $I_2(0) > 0$, then $I_1(t) > 0$ and $I_2(t) > 0$ for all $t > 0$. When $x(t)$ stays very close to E_{12} , by (2.2) there exists some $\delta > 0$ (related to the size of the neighbourhood of E_{12}) such that

$$\begin{cases} \frac{dI_1}{dt} > \tilde{c}_{11}I_1 + \tilde{c}_{12}I_2 \\ \frac{dI_2}{dt} > \tilde{c}_{21}I_1 + \tilde{c}_{22}I_2 \end{cases} \quad (4.12)$$

where $\tilde{c}_{ij} = c_{ij} - \delta$ and c_{ij} are the entries of the top-left matrix TL of the matrix C_{12} in (3.3). By choosing δ small enough, the matrix \tilde{C} in (4.12) has positive non-diagonal elements and its largest eigenvalue is positive, since $R_{12} > 1$ [17]. Hence the solution of the linear quasi-monotonic system

$$\begin{cases} \frac{dx_1}{dt} = \tilde{c}_{11}x_1 + \tilde{c}_{12}x_2 \\ \frac{dx_2}{dt} = \tilde{c}_{21}x_1 + \tilde{c}_{22}x_2 \end{cases}$$

with $x_1(0) > 0$, $x_2(0) > 0$ are exponentially increasing as $t \rightarrow \infty$. By the comparison principle, $(I_1(t), I_2(t))$ goes away from $(0, 0)$.

Hence, by the two cases M_4 is isolated in D , so that M is isolated in D .

The arguments used in these proofs (cases 2.) show also that each part M_i is a weak repeller for \tilde{D}_1 .

Using Lemma 4.2 as in the proof of Theorem 4.5, we can prove that D_2 is a uniform weak repeller for \tilde{D}_1 ; and then as in the proof of Theorem 4.7, we can prove that D_2 is a uniform strong repeller for \tilde{D}_1 , i.e. the thesis. \square

The previous Theorem shows that it is possible that an infection that would die out in either species without the inter-infection of disease, may persist in both species in presence of this factor.

By the strong uniform persistence of infection, in several cases, the weak uniform persistence of populations (Theorem 4.5) can be strengthened to the strong uniform persistence.

Theorem 4.9 *Let $\alpha_{12}K_2 > K_1$, $R_2 > 1$, $\pi_1 > 0$ and either*

a) $\alpha_{21}K_1 < K_2$

or

b) $\alpha_{21}K_1 > K_2$, $R_1 > 1$ and $R_{12} > 1$.

Then there exists an $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} N_1(t) > \epsilon$, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_1(0) > 0$ or $I_2(0) > 0$.

Proof. The idea and method of the proof are similar to those of the previous Theorem and the proof is, therefore, omitted. \square

A similar result holds exchanging hosts 1 and 2.

Finally, by the strong uniform persistence of populations and infection, we can obtain the strong uniform persistence of (2.2) relatively to all components.

Theorem 4.10 *For system (2.2), if $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 < K_2$, $R_2 > 1$,*

$\pi_1 > 0$, and either (1) $R_1 < 1$, or (2) $R_1 > 1$ and $\pi_2 > 0$, then there exists an $\epsilon > 0$ such that, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_1(0) > 0$ or $I_2(0) > 0$, $\liminf_{t \rightarrow \infty} \min\{I_1(t), N_1(t), I_2(t), N_2(t)\} > \epsilon$.

A similar result holds exchanging hosts 1 and 2.

For the cases where the competition model has an internal equilibrium, we have the following:

Theorem 4.11 For system (2.2), if $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 < K_2$, $R_{12} > 1$, and any one of the following conditions holds:

- (1) $R_1 < 1$, $R_2 < 1$;
- (2) $R_1 > 1$, $R_2 < 1$, $\pi_2 > 0$;
- (3) $R_1 < 1$, $R_2 > 1$, $\pi_1 > 0$;
- (4) $R_1 > 1$, $R_2 > 1$, $\pi_1 > 0$, $\pi_2 > 0$,

conditions				conclusion		
$R_j < 1$ ($j \neq i, j = 1, 2$)	$\alpha_{ij}K_j > K_i$			NP, E_j stable		
	$\alpha_{ij}K_j < K_i$			SUP		
$R_j > 1$	$\pi_i < 0$			NP, B_j stable		
	$\pi_i > 0$	$\alpha_{ij}K_j < K_i$			SUP	
		$\alpha_{ij}K_j > K_i$	$\alpha_{ji}K_i < K_j$		SUP	
			$\alpha_{ji}K_i > K_j$	$R_i < 1$		WUP
				$R_i > 1$	$R_{12} < 1$	WUP
					$R_{12} > 1$	SUP

Table 2

Persistence of either population N_i ($i = 1, 2$), where, NP stands for non-persistence, SUP stands for strong uniform persistence, WUP stands for weak uniform persistence

then there exists an $\epsilon > 0$ such that $\liminf_{t \rightarrow \infty} \min\{I_1(t), N_1(t), I_2(t), N_2(t)\} > \epsilon$, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_1(0) > 0$ or $I_2(0) > 0$.

Remark 4.12 Note that, by Remark 3.1, if both eigenvalues of the top-left matrix TL of (3.3) have positive real parts, then $R_1 > 1$ and $R_2 > 1$, so that only case 4) may occur, and one needs only check $\pi_1 > 0$ and $\pi_2 > 0$.

Theorem 4.13 For system (2.2), if $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 > K_2$, $R_{12} > 1$, $R_1 > 1$, $R_2 > 1$, $\pi_1 > 0$, $\pi_2 > 0$, then there exists an $\epsilon > 0$ such that, for any solution $x(t)$ with $N_1(0) > 0$, $N_2(0) > 0$ and $I_1(0) > 0$ or $I_2(0) > 0$, $\liminf_{t \rightarrow \infty} \min\{I_1(t), N_1(t), I_2(t), N_2(t)\} > \epsilon$.

conditions		conclusion		
$\alpha_{12}K_2 > K_1, \alpha_{21}K_1 < K_2$	$R_2 < 1$	NP, E_2 stable		
	$R_2 > 1$	SUP		
$\alpha_{12}K_2 < K_1, \alpha_{21}K_1 > K_2$	$R_1 < 1$	NP, E_1 stable		
	$R_1 > 1$	SUP		
$\alpha_{12}K_2 < K_1, \alpha_{21}K_1 < K_2$	$R_{12} < 1$	NP, E_{12} stable		
	$R_{12} > 1$	SUP		
$\alpha_{12}K_2 > K_1, \alpha_{21}K_1 > K_2$	$R_2 < 1$	NP, E_2 stable		
	$R_2 > 1$	$R_1 < 1$	NP, E_1 stable	
		$R_1 > 1$	$R_{12} < 1$	NP, 3d-SM at E_{12}
		$R_{12} > 1$	SUP	

Table 3

Persistence of both of I_i ($i = 1, 2$) where, 3d-SM stands for a 3-dimensional stable manifold

Remark 4.14 If $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 < K_2$ and $R_{12} < 1$, then the equilibrium E_{12} is stable; hence system (2.2) is not persistent.

On the other hand, if $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 > K_2$ and $R_{12} < 1$, the equilibrium E_{12} has a 3-dimensional stable manifold V^s and a 1-dimensional unstable manifold V^u lying on the plane (N_1, N_2) . Letting

$$D_1 = \{(N_1, N_2, I_1, I_2) : I_1 > 0, I_2 > 0\}$$

it is clear that $D_2 = D \setminus D_1$ is not a repeller for D_1 , since points lying in $D_1 \cap V^s$ are attracted to E_{12} . The question of what happens if $x(0) \in D_1 \setminus V^s$ remains open.

We summarize the results on persistence, together with the stability results of the previous Section, in Tables 2, 3 and 4. In reading Table 4, remember that in case III when $R_{12} > 1$ and both eigenvalues of the top-left matrix TL of the matrix C_{12} in (3.3) have positive real parts, necessarily $R_1 > 1$ and $R_2 > 1$.

.

Corollary 4.15 *In all conditions listed in Table 4 that guaranteed strong uniform persistence, there exists at least one internal equilibrium of (2.2).*

Proof. It follows from a general result from persistence theory [21, Remark 3.10 and Theorem 4.7], [22, pp. 160–166]. \square

5 Bifurcation Phenomena

In this section, we present, with the help of numerical software, some bifurcation diagrams of system (2.2) in order to explore the possible behaviors of the solutions.

First, we recall the conditions for Hopf bifurcation, following the presentation

conditions					conclusion	
I	$R_2 < 1$				NP, E_2 stable	
	$R_2 > 1$	$\pi_1 < 0$			NP, B_2 stable	
		$\pi_1 > 0$	$R_1 < 1$		SUP	
			$R_1 > 1$	$\pi_2 < 0$	NP, B_1 stable	
				$\pi_2 > 0$	SUP	
II	$R_1 < 1$				NP, E_1 stable	
	$R_1 > 1$	$\pi_2 < 0$			NP, B_1 stable	
		$\pi_2 > 0$	$R_2 < 1$		SUP	
			$R_2 > 1$	$\pi_1 < 0$	NP, B_2 stable	
				$\pi_1 > 0$	SUP	
III	$R_{12} < 1$				NP, E_{12} stable	
	$R_{12} > 1$	$R_2 < 1$	$R_1 < 1$		SUP	
			$R_1 > 1$	$\pi_2 < 0$	NP, B_1 stable	
				$\pi_2 > 0$	SUP	
		$R_2 > 1$	$\pi_1 < 0$			NP, B_2 stable
			$\pi_1 > 0$	$R_1 < 1$		SUP
	$R_1 > 1$			$\pi_2 < 0$	NP, B_1 stable	
				$\pi_2 > 0$	SUP	
	IV	$R_2 < 1$				NP, E_2 stable
$R_2 > 1$		$R_1 < 1$			NP, E_1 stable	
		$R_1 > 1$	$\pi_1 < 0$			NP, B_2 stable
			$\pi_1 > 0$	$\pi_2 < 0$		NP, B_1 stable
				$\pi_2 > 0$	$R_{12} < 1$	NP, 3d-SM at E_{12}
					$R_{12} > 1$	SUP

Table 4

Persistence of all of I_1 , N_1 , I_2 and N_2 . I stands for $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 < K_2$, II stands for $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 > K_2$, III stands for $\alpha_{12}K_2 < K_1$, $\alpha_{21}K_1 < K_2$, IV stands for $\alpha_{12}K_2 > K_1$, $\alpha_{21}K_1 > K_2$. 34

by Shen and Jing [23].

Consider the following differential system

$$\frac{dx}{dt} = f(x, \mu), \quad x \in R^n, \quad \mu \in R \quad (5.1)$$

with an equilibrium point $x = x_0(\mu)$. If the Jacobian matrix

$$A(\mu) = D_x f(x_0(\mu), \mu)$$

has a pair of complex conjugate eigenvalues

$$\lambda_1(\mu) \pm i\lambda_2(\mu) \quad (5.2)$$

and for some value $\mu = \mu_0$,

$$\lambda_1(\mu_0) = 0, \quad \lambda_2(\mu_0) > 0, \quad \frac{d\lambda_1(\mu_0)}{d\mu} \neq 0 \quad (5.3)$$

and the remaining eigenvalues of $A(\mu_0)$ have nonzero real parts, then the crucial hypotheses of Hopf bifurcation theorem are satisfied, and the equilibrium x_0 bifurcates into a “small amplitude” periodic solution as μ passes through μ_0 .

For system (5.1), the characteristic equation at the equilibrium $x = x_0$ can be written as

$$P(\lambda) = \lambda^n + c_{n-1}(\mu)\lambda^{n-1} + \cdots + c_0(\mu) = 0 \quad (5.4)$$

Conditions (5.2) and (5.3) can be written in terms of the coefficients of (5.4), as stated in the following lemma:

Lemma 5.1 ([23, Theorem 3]) *Conditions (5.2) and (5.3) for the existence of the Hopf bifurcation are satisfied for system (5.4), if the following conditions are satisfied: 1) $\mu = \mu_0$ is a zero of $H_{n-1}(\mu) = 0$; 2) $H_{n-2}(\mu_0) \neq 0$*

0, $H_{n-3}(\mu_0) \neq 0$, $c_j(\mu_0) > 0$, $j = 0, 1, 2, \dots, n-1$; 3) $\frac{dH_{n-1}(\mu_0)}{d\mu} \neq 0$, where $H_j(\mu)$, $j = 1, 2, \dots, n$, are the Hurwitz determinants.

To use this theorem for system (2.2), we need to discuss Hopf bifurcation at an internal equilibrium. However, for system (2.2) there are no explicit formulae for an internal equilibrium and, in general, not even its existence can be proved. Hence we will study the bifurcation in the very special case, where all the analogous parameters are same for species 1 and 2. Although it is a very particular case, it displays several interesting behaviors that can shed light also outside of this special structure.

Namely, we let

$$\begin{aligned} r_1 = r_2 = r, \quad b_1 = b_2 = b, \quad d_1 = d_2 = d, \quad a_1 = a_2 = a, \quad K_1 = K_2 = K, \\ \alpha_{12} = \alpha_{21} = \alpha, \quad \gamma_1 = \gamma_2 = \gamma, \quad \delta_1 = \delta_2 = \delta, \quad \beta_{11} = \beta_{22} = \beta_1, \quad \beta_{12} = \beta_{21} = \beta_2. \end{aligned}$$

Then system (2.2) becomes a symmetric (with respect to the exchange of 1 and 2) system.

When $R^* > 1$, there exists a unique internal equilibrium $P^* = (I^*, N^*, I^*, N^*)$ where

$$R^* = \frac{(\beta_1 + \beta_2 + \frac{ar}{K})\frac{r}{K(1+\alpha)}}{b + \gamma + \delta}, \quad I^* = \frac{r}{\delta} - \frac{r}{\delta K}(1 + \alpha)N^*$$

and N^* is the larger solution of the equation

$$(\beta_1 + \beta_2)\frac{r}{\delta K}(1 + \alpha)x^2 + [(\beta_1 + \beta_2)(1 - \frac{r}{\delta}) - \frac{(1 + \alpha - a)r}{K}]x - (d + \gamma + \delta) = 0$$

For this equilibrium, the Jacobian matrix is

$$A^* = \begin{bmatrix} a_1 & b_1 & c_1 & d_1 \\ a_2 & b_2 & 0 & d_2 \\ c_1 & d_1 & a_1 & b_1 \\ 0 & d_2 & a_2 & b_2 \end{bmatrix}$$

where

$$a_1 = -\beta_1 I^* N^* - \beta_2 N^* + \delta I^*, \quad b_1 = \beta_1 I^* (1 - I^*) + \frac{ar}{K} I^*, \quad c_1 = \beta_2 (1 - I^*) N^*,$$

$$d_1 = \beta_2 (1 - I^*) I^*, \quad a_2 = -\delta N^*, \quad b_2 = -\frac{r}{K} N^*, \quad d_2 = -\frac{r\alpha}{K} N^*.$$

Through long computations, one finds that its characteristic equation is

$$A_0 + A_1 \lambda + A_2 \lambda^2 + A_3 \lambda^3 + \lambda^4 = 0$$

where

$$A_0 = (a_1 b_2 - a_2 b_1)^2 - (a_2 d_1 - a_1 d_2)^2 + 2a_2 b_2 c_1 d_1 - 2a_2 b_1 c_1 d_2 - b_2^2 c_1^2 + c_1^2 d_2^2,$$

$$A_1 = -2(a_1 + b_2)(a_1 b_2 - a_2 b_1) - 2d_2(a_2 d_1 - a_1 d_2) - 2a_2 c_1 d_1 + 2b_2 c_1^2,$$

$$A_2 = (a_1 + b_2)^2 - d_2^2 - c_1^2 + 2(a_1 b_2 - a_2 b_1), \quad A_3 = -2(a_1 + b_2),$$

and its Hurwitz determinants are

$$H_1 = A_3, \quad H_2 = A_2 A_3 - A_1, \quad H_3 = A_1 A_2 A_3 - A_0 A_3^2 - A_1^2, \quad H_4 = A_0 H_3.$$

Clearly $A_0, A_1, A_2, A_3, H_1, H_2, H_3$ and H_4 are the functions of all the parameters of the system. In the following, we choose β_2 as the bifurcation parameter, and fix the other parameters. Because of the complexity of the characteristic equation, we present only numerical results, shown in Fig. 1, where β_2 varies from 0.14 to 0.18 .

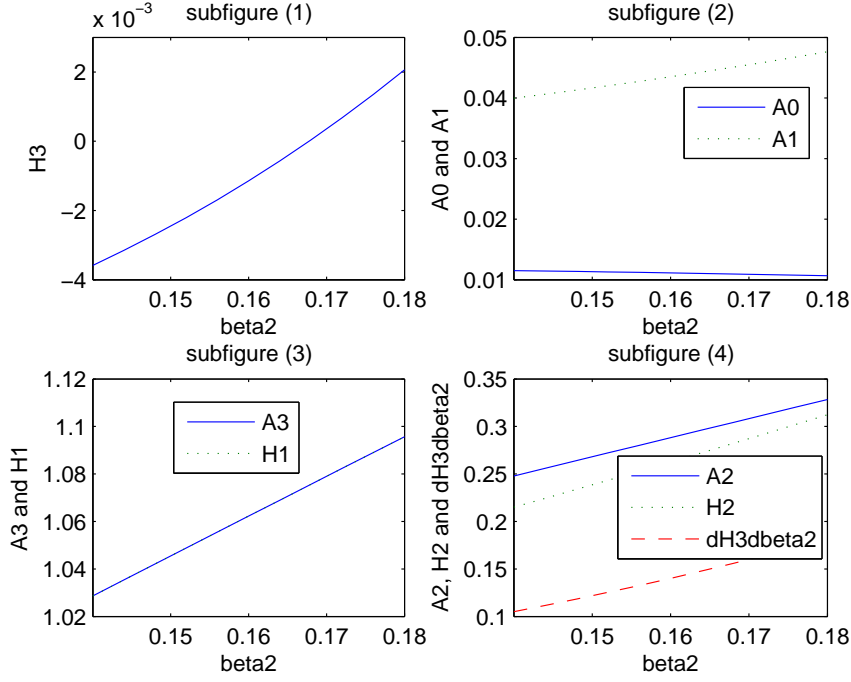


Fig. 1. the curves of A_0 , A_1 , A_2 , A_3 , H_1 , H_2 , H_3 and $\frac{dH_3}{d\beta_2}$ as functions of β_2 . Parameter values are $r = 1$, $b = 2$, $a = 0.5$, $K = 2$, $d = 1$, $\alpha = 2$, $\delta = 1$, $\gamma = 1$ and $\beta_1 = 6$.

From Fig. 1, we see that, as β_2 changes from 0.14 to 0.18, the values of A_0 , A_1 , A_2 , A_3 , H_1 , H_2 , $\frac{dH_3}{d\beta_2}$ always remain positive, but the value of H_3 changes from negative to positive. Hence, there exists some $\tilde{\beta}_2 \in [0.14, 0.18]$ such that $H_3(\tilde{\beta}_2) = 0$ and A_0 , A_1 , A_2 , A_3 , H_1 , H_2 , $\frac{dH_3}{d\beta_2}$ are all positive. The conditions of Lemma 5.1 are satisfied and Hopf bifurcation occurs. So, the internal equilibrium P^* bifurcates into a “small amplitude” periodic solution as β_2 passes through $\tilde{\beta}_2$.

Precisely, we find that, when $\beta_2 = 0.1677$ (in fact, this is just the value of $\tilde{\beta}_2$ in Fig. 1), Hopf bifurcation occurs at the internal equilibrium $P^* = (0.038509, 0.640994, 0.038509, 0.640994)$ and the corresponding Lyapunov coefficient $l = -23.93361$ is negative, which means that the periodic orbits are born stable (namely, stable limit cycles). In other words, as β_2 decreases

through $\tilde{\beta}_2 = 0.1677$, the stability of the internal equilibrium changes from stable to unstable and a stable limit cycle arises. In Fig. 2, we show the stable limit cycle for $\beta_2 = 0.1$ (plotting, for simplicity, only the coordinates I_1 and N_1 of the limit cycle).

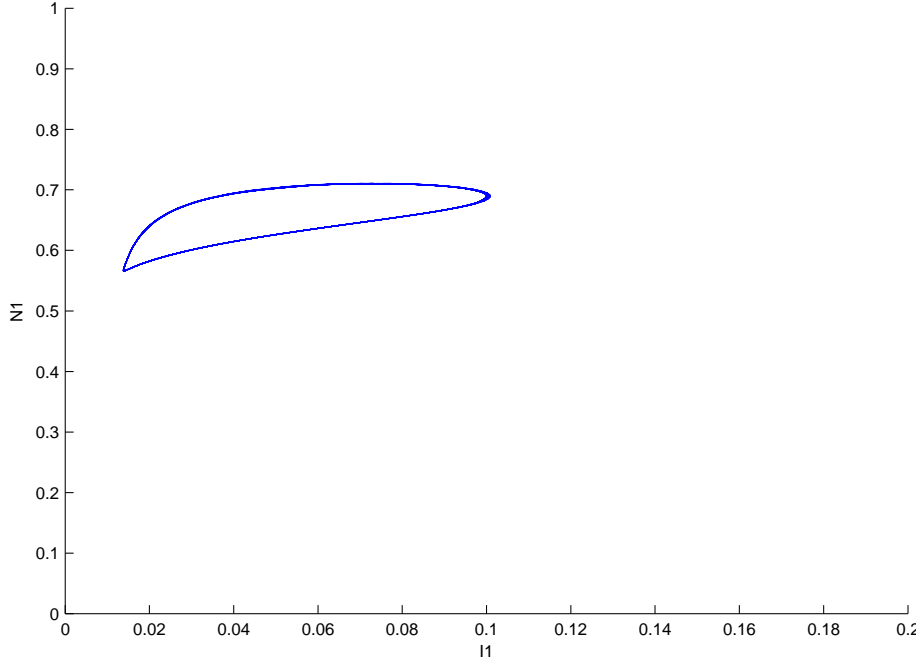


Fig. 2. The stable limit cycle for $\beta_2 = 0.1$

Let us moreover consider the stabilities of the boundary equilibria in this case. By numerical computations, we find that, for β_2 near $\tilde{\beta}_2 = 0.1677$, the equilibria E_0 , E_1 , E_2 , E_{12} are always unstable, but B_1 and B_2 are always stable. So we have the results as follows: (1) When $\beta_2 > \tilde{\beta}_2 = 0.1677$, there exist three stable equilibria B_1 , B_2 and P^* ; (2) When $\beta_2 < \tilde{\beta}_2 = 0.1677$, there exist two stable equilibria B_1 , B_2 and a stable limit cycle.

Note that, with these parameter values, the pure competition model has both boundary equilibria E_1 and E_2 stable, and an internal unstable equilibrium E_{12} ; i.e., the competition model is “bi-stable”. Adding the infection, the sys-

tem moves to a “tri-stable” situation: depending on the initial conditions, the solutions may settle to a state with either species alone with the endemic infection, or to a state with both species present and the infection either at an equilibrium, or, depending on the value of β_2 , fluctuating in a limit cycle.

One can look at how the Hopf bifurcation depends on the other parameters. For instance in Fig. 3, we let β_2 and the inter-specific competition coefficient α vary; the points on the curve shown in that figure are all Hopf bifurcation points.

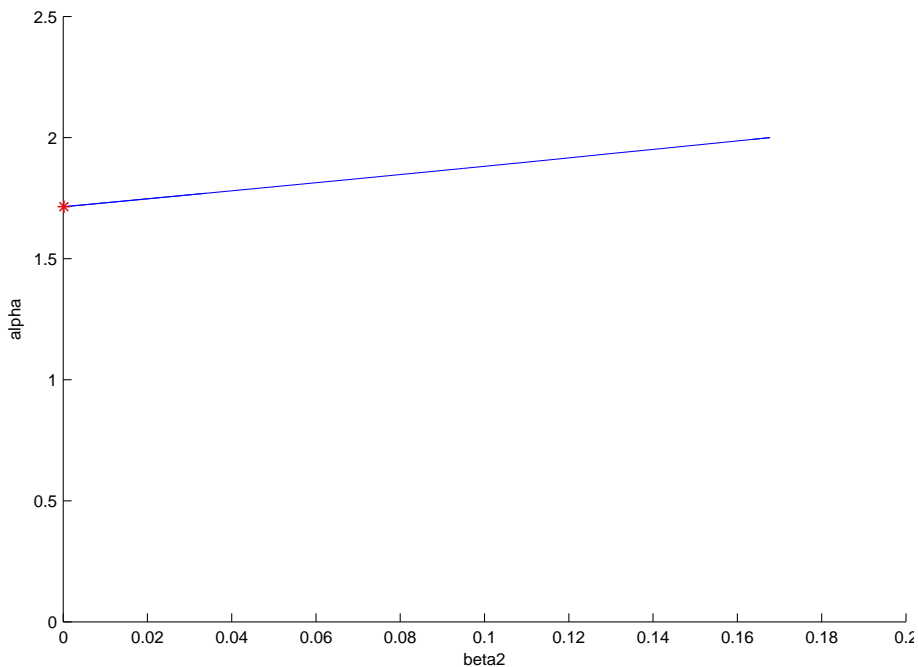


Fig. 3. the continuation curve of Hopf bifurcation points

This means that, for each point $(\tilde{\beta}_2, \tilde{\alpha})$ on the curve, and $\alpha = \tilde{\alpha}$ is fixed, as β_2 decreases through $\tilde{\beta}_2$, the stability of the internal equilibrium P^* changes from stable to unstable and a stable limit cycle occurs; similarly, if $\beta_2 = \tilde{\beta}_2$ is fixed and α increases through $\tilde{\alpha}$.

One can also check that, for values of $(\tilde{\beta}_2, \tilde{\alpha})$ on the curve, the boundary equilibria E_0, E_1, E_2, E_{12} are always unstable, while the equilibria B_1 and B_2 can be stable or unstable. This brings us important information, in agreement with [2]: (1) when all the boundary equilibria are unstable, the internal equilibrium may be stable or unstable; (2) when there exists a stable boundary equilibrium, the internal equilibrium may be stable or unstable; (3) the system may have three stable attractors and one of which is a limit cycle.

Finally, we present the bifurcation diagram in a special asymmetric case, in which all parameters

$$r_1 = r_2 = r, \quad b_1 = b_2 = b, \quad d_1 = d_2 = d, \quad a_1 = a_2 = a, \quad K_1 = K_2 = K,$$

$$\gamma_1 = \gamma_2 = \gamma, \quad \delta_1 = \delta_2 = \delta, \quad \beta_{11} = \beta_{22} = \beta_1, \quad \beta_{12} = \beta_{21} = \beta_2$$

are the same, except for the competition coefficients α_{12} and α_{21} that may be different.

We choose α_{21} as the bifurcation parameter, and fix the other parameters. With the help of MatCont numerical software [24], we obtain Fig. 4.

Fig. 4 shows (for simplicity, only the coordinate N_2) the bifurcation diagram of the internal equilibria and of the boundary equilibrium B_1 when α_{21} varies between 1.6 and 2.4. The stability is shown with the letters 's' (=stable) or 'u' (=unstable), and the bifurcation points are shown as 'H' (Hopf bifurcation point), 'LP' (saddle-node bifurcation point) and 'BP' (branching point, or transcritical bifurcation point). From Fig. 4, one sees that: (1) when $\alpha_{21} < 1.7932$, there is no internal equilibria; (2) when $1.7932 < \alpha_{21} < 1.8946$, there exist two internal equilibria, one is stable, the other is unstable; (3) when $1.8946 < \alpha_{21} < 1.9512$, there exist three internal equilibria, one is stable,

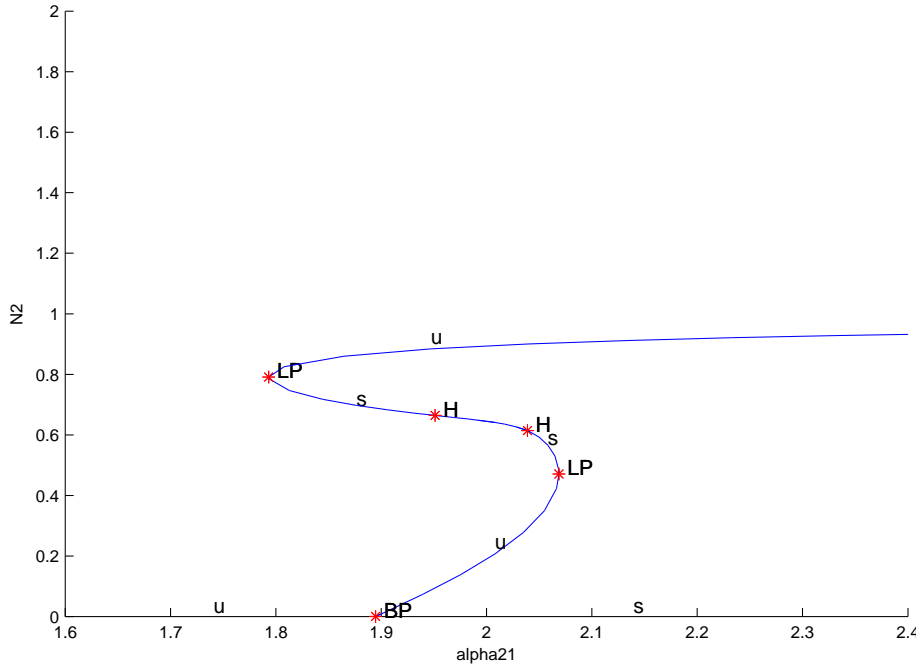


Fig. 4. the continuation curve of the internal equilibria. Parameter values are $r = 1$, $b = 2$, $a = 0.5$, $K = 2$, $d = 1$, $\alpha_{12} = 2$, $\delta = 1$, $\gamma = 1$, $\beta_1 = 6$ and $\beta_2 = 0.1$.

the other two are unstable; (4) when $1.9512 < \alpha_{21} < 2.0388$, there exist a stable limit cycle and three internal equilibria which are all unstable; (5) when $2.0388 < \alpha_{21} < 2.0688$, there exist three internal equilibria, one is stable, the other two are unstable; (6) when $\alpha_{21} > 2.0688$, there exists an internal equilibrium which is unstable. In cases (1) and (2), the equilibrium B_1 is unstable, while it is stable in the other cases. Finally, it is possible to check that, independently of the value of α_{21} , the equilibrium B_2 is always stable.

We have obtained the important information: (1) the system may have between zero and three internal equilibria; (2) with two stable boundary equilibrium, the system may have three internal equilibria, one of which may be stable. It is also possible that the system has three stable attractors, one of

which is a limit cycle.

6 Discussion

In this paper, we considered an SIS epidemic model of two competitive species and obtained some results that show the biological significance and complicated behaviors of the model.

In general, one species does not exist alone in the natural world. It always interacts with other species for food, space and so on. Therefore, it is valuable to consider the effect of interacting species when we study the dynamical behaviors of epidemiological models. From this an interesting question occurs: how do infection and ecological interactions among species affect each other? In this competition model we found, by a careful analysis, important interactions between infection and competition as follows: (1) a species that would get extinct without the infection, may persist in presence of the infection; (2) a species that would coexist with its competitor without the infection, but is driven to extinction by the infection; (3) an infection that would die out in either species without the inter-infection of disease, may persist in both species in presence of this factor.

By mathematical analysis and numerical investigation, Holt and Pickering [7], Begon and Bowers [1,8] conjectured that their models have the classic endemic model behavior with a unique attracting equilibrium, below and above the threshold. But Greenman and Hudson [2] did extensive analysis of these models and found counterexamples to this conjecture, showing that the two host epidemic models can have complicated behaviors.

In our model, using Hopf bifurcation theory and numerical simulations, we have extended the analysis by Greenman and Hudson, revealing the following complicated behaviors: (1) when all the boundary equilibria are unstable, the internal equilibrium may be stable or unstable; (2) when there exists a stable boundary equilibrium, the internal equilibrium may exist or not, and be stable or unstable; (3) the system may have three stable attractors and one of which may be a limit cycle; (4) the system may have zero up to three internal equilibria; (5) when there exists a stable boundary equilibrium, the system may have three internal equilibria: sometimes all of them are unstable, but sometimes one of them is stable. Probably, several other interesting behaviors may be ascertained through a more extensive numerical investigation.

We have also analysed the system from the point of view of persistence. A much clearer picture emerges from this, and it is almost always possible to decide whether the system is persistent or not on the basis of a few quantities, related to the stability of the boundary equilibria (Table 4). A few cases remain partially undecided from this analysis. From Table 2 we find that host population i ($i = 1, 2$) is weakly uniform persistent when $R_j > 1$, $\pi_i > 0$, $\alpha_{ij}K_j > K_i$, $\alpha_{ji}K_i > K_j$ ($i \neq j$) and $R_i < 1$ or $R_i > 1$, $R_{12} < 1$. For this case, we can not prove the strong uniform persistence; but we conjecture that there may exist some oscillating trajectory which destroys the strong uniform persistence.

Finally, we compare our model with the model by Saenz and Hethcote [3] who use the frequency-dependent incidence. In their model, there exists an extinction equilibrium $E^* = (I_1^c, 0, I_2^c, 0)$ stable under some conditions; this means that the infectious disease may drive both species to extinction. But in our model, there does not exist such an equilibrium, thus total extinction

can not occur. It is in fact known that an infection may cause population extinction only with the frequency-dependent incidence, and not with the standard bilinear form, or other laws increasing with population density [25].

Another difference is that their model never has periodic solutions, nor multiple attractors, contrary to what we found in model (2.2). Hence, the different forms of the incidence can lead to rather different dynamical behaviors of the models.

At last, in their model, a key result is that the disease must either die out or remain endemic synchronously in both species. Which still occurs in our model, since the equilibrium value I_1 is zero if and only if I_2 is also zero. So, the occurrence of this behavior is independent of the form of the incidence.

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