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Competition of Two Host Species for a Single-Limited Resource Mediated by Parasites

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Abstract. In this paper we consider a mathematical model of two host species competing for a single -limited resource mediated by parasites. Each host population is divided into susceptible and infective populations. We assume that species 1 has the lowest break-even concentration with respect to nutrient, when there is no parasite. Thus species 1 is a superior competitor that outcompetes species 2. When parasites present, the competitive outcome is determined by the contact rate of the superior competitor. We analyze the model by finding the conditions for the existence of various equilibria and doing their stability analysis. Two bifurcation diagrams are presented. The first one is in $\beta_1\beta_2$ plane (See Figure 3) and the second one is in $R^{(0)}$-line (See Figure 4).

1 Introduction

Ecologists are interested in understanding how and to what extent interspecific interactions influence community structure, species coexistence and biodiversity. Host-parasite interactions occurr frequently in nature and has been shown that parasites could affect the growth and survival rate of a host thus influence its competitive ability. In the past two decades, people investigate the potential importance of parasites and pathogens in determining the outcome in trophic interactions and community process. In the paper ([1]) the authors reviewed the recent research on how parasites influence competitive and predatory interactions of the host species they infected. However, no theoretical model has been developed that consider the competitive outcome between two hosts who shared the same parasite. In this paper we shall investigate a mathematical model of competition of two host species for a single-limited resource mediated by parasites. Especially we focus on the question: Can infection produce coexistence of species? When there is no infection mediated by parasites, it is well-known that species with the smallest break-even

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concentration will survive ([2],[3],[4],[5],[6]). With the infection by parasites we show that it is possible that two species coexist if the contact rate of surviving species is large enough. We shall find conditions for the existence of various equilibria and their stability analysis. A bifurcation diagram is presented with contact rates β_1, β_2 as two bifurcation parameters. We also present a bifurcation diagram by using input concentration $R^{(0)}$ of the nutrient as a bifurcation parameter.

2 The Model

The model of two hosts competing for a single-limited resource mediated by parasites leads to the following system of differential equations

$$
\begin{aligned}
\frac{dR}{dt} &= (R^{(0)} - R)D - \frac{1}{y_1}\frac{m_1 R}{a_1 + R}(S_1 + I_1) - \frac{1}{y_2}\frac{m_2 R}{a_2 + R}(S_2 + I_2) \\
\frac{dS_1}{dt} &= \left(\frac{m_1 R}{a_1 + R} - d_1\right) S_1 - \beta_1 I_1 S_1 + \gamma_1 I_1 \\
\frac{dI_1}{dt} &= \beta_1 I_1 S_1 - (d_1 + \delta_1 + \gamma_1) I_1 \\
\frac{dS_2}{dt} &= \left(\frac{m_2 R}{a_2 + R} - d_2\right) S_2 - \beta_2 I_2 S_2 + \gamma_2 I_2 \\
\frac{dI_2}{dt} &= \beta_2 I_2 S_2 - (d_2 + \delta_2 + \gamma_2) I_2 \\
R^{(0)} &\geq 0, \quad S_1(0) > 0, \quad I_1(0) > 0, \quad S_2(0) > 0, \quad I_2(0) > 0.
\end{aligned}
\tag{2.1}
$$

Here we assume that each host population is divided into susceptible, infectious populations which are designated S, I. The parameter R is the concentration of resource. The rest of the model's parameters are defined in Table 1.

Table1 Definition of parameters used in the model

Parameter	Definition
$R^{(0)}$	input concentration of nutrient R
D	dilution rate
y_i	yield constant of i-th host
m_i	maximum growth rate of i-th host
a_i	half-saturation constant for i-th host
d_i	death rate of i-th host
δ_i	per capita additional mortality of i-th host when infected with parasite
γ_i	per capita rate of recovery of i-th host from infection

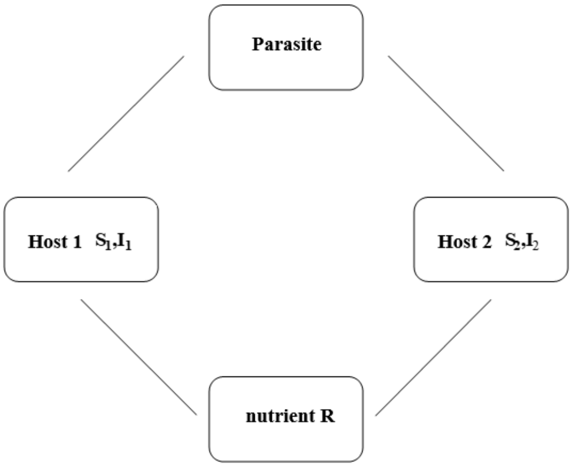

Figure 1:

When there is no parasites, the infective populations $I_1(t)$, $I_2(t)$ satisfy $I_1(t) \equiv 0$, $I_2(t) \equiv 0$. Then the system (2.1) becomes

$$\begin{aligned} R' &= (R^{(0)} - R)D - \frac{1}{y_1}\frac{m_1 R}{a_1 + R}S_1 - \frac{1}{y_2}\frac{m_2 R}{a_2 + R}S_2, \\ S_1' &= \left(\frac{m_1 R}{a_1 + R} - d_1\right) S_1, \\ S_2' &= \left(\frac{m_2 R}{a_2 + R} - d_2\right) S_2, \\ R^{(0)} &\geq 0, S_1(0) > 0, S_2(0) > 0. \end{aligned} \tag{2.2}$$

If the maximal growth rate m_i is less than or equal to the death rate d_i of the i-th host, then $S_i(t) \to 0$ as $t \to \infty$, i.e. the i-th host cannot survive. Consider the break-even concentration of the i-th host $\lambda_i = \frac{a_i}{(m_i/d_i)-1} > 0$.

If the break-even concentration λ_i is less than the input concentration $R^{(0)}$ then the i-th host species goes to extinction due to the input concentration $R^{(0)}$ is too small to support the survival of i-th host species S_i ([3],[6]).

Thereafter we assume that

$$0 < \lambda_1 < \lambda_2 < R^{(0)}. \tag{H1}$$

Under assumption (H1), we conclude that 1st host species S_1 outcompetes the 2nd host species S_2 ([3], [6]) and the solutions $R(t)$, $S_1(t)$, $S_2(t)$ satisfy

$$\lim_{t\to\infty} R(t) = \lambda_1,$$

$$\lim_{t\to\infty} S_1(t) = S_1^* = \frac{(R^{(0)} - \lambda_1)Dy_1}{d_1},$$
$$\lim_{t\to\infty} S_2(t) = 0.$$

3 Equilibria and Their Stability Analysis of the System (2.1):

In the following we study the existence of equilibria and their stability analysis. The equilibria take the forms :

$$\begin{aligned} E_1 &= (\lambda_1, S_1^*, 0, 0, 0), \\ E_{1I_1} &= (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0), \\ E_{1I_12} &= (\lambda_2, \tilde{S}_1, \tilde{I}_1, \tilde{S}_2, 0), \\ E_{1I_12I_2} &= (\bar{R}, \bar{S}_1, \bar{I}_1, \bar{S}_2, \bar{I}_2). \end{aligned}$$

The variational matrix of the system (2.1) at $E = (R, S_1, I_1, S_2, I_2)$ is

$$J(E) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} \\ a_{21} & a_{22} & a_{23} & 0 & 0 \\ 0 & a_{32} & a_{33} & 0 & 0 \\ a_{41} & 0 & 0 & a_{44} & a_{45} \\ 0 & 0 & 0 & a_{54} & a_{55} \end{bmatrix}$$

where

$$\begin{aligned} a_{11} &= -D - \frac{1}{y_1} f_1'(R)(S_1 + I_1) - \frac{1}{y_2} f_2'(R)(S_2 + I_2), \\ a_{12} &= -\frac{1}{y_1} f_1(R), \\ a_{13} &= -\frac{1}{y_1} f_1(R), \\ a_{14} &= -\frac{1}{y_2} f_2(R), \\ a_{15} &= -\frac{1}{y_2} f_2(R), \\ a_{21} &= f_1'(R) S_1, \\ a_{22} &= (f_1(R) - d_1) - \beta_1 I_1, \\ a_{23} &= -\beta_1 S_1 + \gamma_1, \\ a_{32} &= \beta_1 I_1, \\ a_{33} &= \beta_1 S_1 - (d_1 + \delta_1 + \gamma_1), \end{aligned}$$

$$
\begin{aligned}
a_{41} &= f_2'(R)S_2,\\
a_{44} &= (f_2(R)-d_2)-\beta_2 I_2,\\
a_{45} &= -\beta_2 S_2+\gamma_2,\\
a_{54} &= \beta_2 I_2,\\
a_{55} &= \beta_2 S_2-(d_2+\delta_2+\gamma_2),\\
f_1(R) &= \frac{m_1 R}{a_1+R},\\
f_2(R) &= \frac{m_2 R}{a_2+R}.
\end{aligned}
$$

Theorem 3.1. $E_1=(\lambda_1, S_1^*, 0, 0, 0)$ *always exists.*

(i) *If*

$$\beta_1 S_1^* - (d_1+\delta_1+\gamma_1) < 0 \tag{3.1}$$

then E_1 *is locally asymptotically stable.*

(ii) *If*

$$\beta_1 S_1^* - (d_1+\delta_1+\gamma_1) > 0 \tag{3.2}$$

then the equilibrium $E_{1I_1}=(\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ *exists, where* $\hat{R}_1, \hat{S}_1, \hat{I}_1$ *satisfy*

$$\hat{S}_1=\frac{d_1+\delta_1+\gamma_1}{\beta_1}>0, \tag{3.3}$$

$$\left(\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}-d_1\right)\hat{S}_1=(d_1+\delta_1)\hat{I}_1>0 \quad \Leftrightarrow \hat{R}_1>\lambda_1, \tag{3.4}$$

$$(R^{(0)}-\hat{R}_1)D=\frac{1}{y_1}\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}\left(\frac{\dfrac{m_1\hat{R}_1}{a_1+\hat{R}_1}+\delta_1}{d_1+\delta_1}\right)\hat{S}_1. \tag{3.5}$$

Proof. The variational matrix $J(E_1)$ of system (2.1) at equilibrium $E_1=(\lambda_1, S_1^*, 0, 0, 0)$ is

$$
J(E_1)=\begin{bmatrix}
\multicolumn{2}{c}{\multirow{2}{*}{M_1}} & -\frac{d_1}{y_1} & -\frac{1}{y_2}f_2(\lambda_1) & -\frac{1}{y_2}f_2(\lambda_1)\\
 & & -\beta_1 S_1^*+\gamma_1 & 0 & 0\\
0 & 0 & \beta_1 S_1^*-(d_1+\delta_1+\gamma_1) & 0 & 0\\
0 & 0 & 0 & f_2(\lambda_1)-d_2 & \gamma_2\\
0 & 0 & 0 & 0 & -(d_2+\delta_2+\gamma_2)
\end{bmatrix}
$$

The eigenvalues of $J(E_1)$ are

$$\mu_1 = -(d_2+\delta_2+\gamma_2) < 0,$$
$$\mu_2 = f_2(\lambda_1) - d_2 < 0, \qquad \text{(by(H1))}$$
$$\mu_3 = \beta_1 S_1^* - (d_1+\delta_1+\gamma_1),$$

and μ_4, μ_5 are the eigenvalues of

$$M_1 = \begin{bmatrix} -D - \frac{1}{y_1} f_1'(\lambda_1)S_1^* & -\frac{d_1}{y_1} \\ f_1'(\lambda_1)S_1^* & 0 \end{bmatrix}$$

which characteristic polynomial is $g(\mu) = \mu(\mu + (D + \frac{1}{y_1} f_1'(\lambda_1)S_1^*)) + \frac{d_1}{y_1} f_1'(\lambda_1)S_1^*$. Then Re $\lambda(M_1) < 0, i.e.,$ Re $\mu_4 < 0$ and, Re $\mu_5 < 0$. Thus E_1 is locally stable if $\mu_3 < 0$, i.e. $\beta_1 S_1^* < d_1+\delta_1+\gamma_1$ and E_1 is unstable if $\mu_3 > 0$, i.e. $\beta_1 S_1^* > d_1+\delta_1+\gamma_1$.

Next we shall show that if E_1 is unstable then the equilibrium $E_{1I_1} = (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ exists where $\hat{R}_1, \hat{S}_1, \hat{I}_1$ satisfy (3.3), (3.4), (3.5). From (3.4), (3.5) we have the following Figure 2.

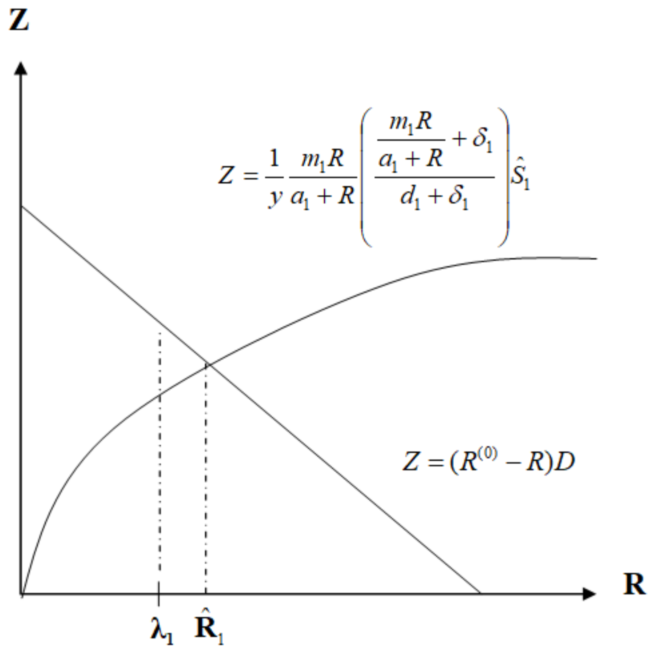

Figure 2

claim : $\lambda_1 < \hat{R}_1$

If not, $\lambda_1 \geq \hat{R}_1$ then

$$\begin{aligned}(R^{(0)} - \lambda_1)D &< (R^{(0)} - \hat{R}_1)D \\ &= \frac{1}{y_1}\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}\frac{\dfrac{m_1\hat{R}_1}{a_1+\hat{R}_1}+\delta_1}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1} \\ &\leq \frac{1}{y_1}\frac{m_1\lambda_1}{a_1+\lambda_1}\frac{\dfrac{m_1\lambda_1}{a_1+\lambda_1}+\delta_1}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1} \\ &= \frac{1}{y_1}d_1\frac{d_1+\delta_1}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1} = \frac{d_1}{y_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1},\end{aligned}$$

or equivalently

$$S_1^* = \frac{(R^{(0)} - \lambda_1)Dy_1}{d_1} \leq \frac{d_1+\delta_1+\gamma_1}{\beta_1}.$$

This is a contradiction to instability condition (3.2). Hence we complete the proof. □

The variational matrix of (2.1) at $E_{1I_1} = (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ is

$$J(E_{1I_1}) = \begin{bmatrix} & M_2 & & -\frac{1}{y_2}f_2(\hat{R}_1) & -\frac{1}{y_2}f_2(\hat{R}_1) \\ & & & 0 & 0 \\ & & & 0 & 0 \\ 0 & 0 & 0 & f_2(\hat{R}_1) - d_2 & \gamma_2 \\ 0 & 0 & 0 & 0 & -(d_2+\delta_2+\gamma_2) \end{bmatrix}.$$

The eigenvalues of $J(E_{1I_1})$ are

$$\begin{aligned}\mu_1 &= -(d_2+\delta_2+\gamma_2) < 0 \\ \mu_2 &= f_2(\hat{R}_1) - d_2\end{aligned}$$

and μ_3, μ_4, μ_5 eigenvalues of the 3×3 matrix

$$M_2 = \begin{bmatrix} -D - \frac{1}{y_1}f_1'(\hat{R}_1)(\hat{S}_1+\hat{I}_1) & -\frac{1}{y_1}f_1(\hat{R}_1) & -\frac{1}{y_1}f_1(\hat{R}_1) \\ f_1'(\hat{R}_1)\hat{S}_1 & -\frac{\gamma_1\hat{I}_1}{\hat{S}_1} & -\beta_1\hat{S}_1+\gamma_1 \\ 0 & \beta_1\hat{I}_1 & 0 \end{bmatrix}$$

which characteristic polynomial is $\mu^3 + a_1\mu^2 + a_2\mu + a_3$

where

$$a_1 = \frac{\gamma_1\hat{I}_1}{\hat{S}_1} + J_1 > 0, \quad J_1 = D + \frac{1}{y_1}f_1'(\hat{R}_1)(\hat{S}_1+\hat{I}_1),$$

$$a_2 = \frac{\gamma_1 \hat{I}_1}{\hat{S}_1} J_1 + f_1'(\hat{R}_1)\hat{S}_1 \frac{1}{y_1} f_1(\hat{R}_1) + \beta_1 \hat{I}_1(\delta_1 + d_1) > 0,$$
$$a_3 = \beta_1 \hat{I}_1(\delta_1 + d_1) J_1 + \beta_1 \hat{I}_1 \frac{1}{y_1} f_1(\hat{R}_1) f_1'(\hat{R}_1)\hat{S}_1 > 0.$$

From Routh-Hurwitz criteria, E_{1I_1} is locally asymptotically stable if $a_1 a_2 > a_3$. The routine computations show $a_1 a_2 > a_3$ as follows

$$\left(\frac{\gamma_1 \hat{I}_1}{\hat{S}_1} + J_1\right)\left(\frac{\gamma_1 \hat{I}_1}{\hat{S}_1} J_1 + f_1'(\hat{R}_1)\hat{S}_1 \frac{1}{y_1} f_1(\hat{R}_1) + \beta_1 \hat{I}_1(\delta_1 + d_1)\right)$$
$$> \beta_1 \hat{I}_1(\delta_1 + d_1) J_1 + \beta_1 \hat{I}_1 \frac{1}{y_1} f_1(\hat{R}_1) f_1'(\hat{R}_1)\hat{S}_1,$$

or

$$\begin{aligned} &\left(\frac{r_1 I_1}{\hat{S}_1}\right)^2 J_1 + \frac{r_1 \hat{I}_1}{\hat{S}_1}\left(f_1'(\hat{R}_1)\hat{S}_1 \frac{1}{y_1} f_1(\hat{R}_1) + \beta_1 \hat{I}_1(\delta_1 + d_1)\right) \\ &+ \frac{r_1 \hat{I}_1}{\hat{S}_1} J_1^2 + J_1\left(f_1'(\hat{R}_1)\hat{S}_1 \frac{1}{y_1} f_1(\hat{R}_1)\right) \\ &> \beta_1 \hat{I}_1 \frac{1}{y_1} f_1(\hat{R}_1) f_1'(\hat{R}_1)\hat{S}_1. \end{aligned} \tag{H2}$$

Theorem 3.2. *Let (3.4) and Re $\lambda(M_2) < 0$ (i.e. (H2) holds).*

(i) *If*

$$\hat{R}_1 < \lambda_2 \tag{3.6}$$

then E_{1I_1} is locally asymptotically stable.

(ii) *If*

$$\hat{R}_1 > \lambda_2 \tag{3.7}$$

then the equilibrium $E_{1I_12} = (\lambda_2, \tilde{S}_1, \tilde{I}_1, \tilde{S}_2, 0)$ exists, where

$$\tilde{S}_1 = \hat{S}_1 = \frac{d_1 + \delta_1 + \gamma_1}{\beta_1} \tag{3.8}$$

and $\tilde{S}_2$, $\tilde{I}_1$ satisfy

$$\tilde{I}_1 = \frac{1}{d_1 + \delta_1}\left(\frac{m_1 \lambda_2}{a_1 + \lambda_2} - d_1\right)\tilde{S}_1 > 0 \tag{3.9}$$

$$\tilde{S}_2 = \frac{y_2}{d_2}\left[(R^{(0)} - \lambda_2)D - \frac{1}{y_1}\left(\frac{m_1 \lambda_2}{a_1 + \lambda_2}\right)\tilde{S}_1\left(\frac{\frac{m_1 \lambda_2}{a_1 + \lambda_2} + \delta_1}{d_1 + \delta_1}\right)\right] > 0. \tag{3.10}$$

Proof. (i) $\mu_2 < 0$ if and only if $\hat{R}_1 < \lambda_2$. Since we assume Re $\lambda(M_2)$, i.e. (H2) holds then $E_{1I_1} = (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ is locally asymptotically stable.

(ii) Under the assumption (H2), we shall prove that the instability condition (3.7) implies the existence of equilibrium E_{1I_12}.

From (H1), $\tilde{I}_1 > 0$.

claim : $\tilde{S}_2 > 0$.

If not, $\tilde{S}_2 \leq 0$, then

$$(R^{(0)} - \lambda_2)D \leq \frac{1}{y_1}\left(\frac{m_1\lambda_2}{a_1+\lambda_2}\right)\frac{\left(\frac{m_1\lambda_2}{a_1+\lambda_2}+\delta_1\right)}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1}$$

The instability condition $\hat{R}_1 > \lambda_2$ implies

$$(R^{(0)} - \lambda_2)D > (R^{(0)} - \hat{R}_1)D = \frac{1}{y_1}\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}\left(\frac{\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}+\delta_1}{d_1+\delta_1}\right)\frac{d_1+\delta_1+\gamma_1}{\beta_1}$$

$$> \frac{1}{y_1}\frac{m_1\lambda_2}{a_1+\lambda_2}\frac{\frac{m_1\lambda_2}{a_1+\lambda_2}+\delta_1}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1}$$

We obtain a contradiction. Thus we have $\tilde{S}_2 > 0$. Hence we complete the proof. □

The variation matrix of (2.1) at $E_{1I_12} = (\lambda_2, \tilde{S}_1, \tilde{I}_1, \tilde{S}_2, 0)$ is

$$J(E_{1I_12}) = \begin{bmatrix} & & & & -\frac{1}{y_2}f_2(\lambda_2) \\ & & & & 0 \\ & M_3 & & & 0 \\ & & & & -\beta_2\tilde{S}_2+\gamma_2 \\ 0 & 0 & 0 & 0 & \beta_2\tilde{S}_2-(d_2+\delta_2+\gamma_2) \end{bmatrix}$$

The eigenvalues of $J(E_{1I_12})$ is

$$\mu_1 = \beta_2\tilde{S}_2 - (d_2+\delta_2+\gamma_2)$$

and μ_2, μ_3, μ_4, μ_5 which are eigenvalues of the 4×4 matrix

$$M_3 = \begin{bmatrix} -D-\frac{1}{y_1}f_1'(\lambda_2)(\tilde{S}_1+\tilde{I}_1)-\frac{1}{y_2}f_2'(\lambda_2)\tilde{S}_2 & -\frac{1}{y_1}f_1(\lambda_2) & -\frac{1}{y_1}f_1(\lambda_2) & -\frac{1}{y_2}f_2(\lambda_2) \\ f_1'(\lambda_2)\tilde{S}_1 & (f_1(\lambda_2)-d_1)-\beta_1\tilde{I}_1 & -\beta_1\tilde{S}_1+\gamma_1 & 0 \\ 0 & \beta_1\hat{I}_1 & 0 & 0 \\ f_2'(\lambda_2)\tilde{S}_2 & 0 & 0 & 0 \end{bmatrix}.$$

From routine computation the characteristic polynomial of M_3 is $\mu^4 + a_1\mu^3 + a_2\mu^2 + a_3\mu + a_4$

where

$$\begin{aligned}
a_1 &= J_2 - (f_1(\lambda_2) - d_2 - \beta_1 \tilde{I}_1), \qquad J_2 = D + \frac{1}{y_1} f_1'(\lambda_2)(\tilde{S}_1 + \tilde{I}_1) + \frac{1}{y_2} f_2'(\lambda_2)\tilde{S}_2, \\
a_2 &= \frac{1}{y_1} f_1(\lambda_2) f_1'(\lambda_2)\tilde{S}_1 + \beta_1 \tilde{I}_1(\beta_1 \tilde{S}_1 - \gamma_1) + f_2'(\lambda_2)\tilde{S}_2 \frac{1}{y_2} f_2(\lambda_2), \\
a_3 &= \beta_1 \tilde{I}_1 (\frac{1}{y_1} f_1(\lambda_2) f_1'(\lambda_2)\tilde{S}_1 + J_2(\beta_1 \tilde{S}_1 - \gamma_1)) \\
&\quad - f_2'(\lambda_2)\tilde{S}_2 \frac{1}{y_2} f_2(\lambda_2)(f_1(\lambda_2) - d_1 - \beta_1 \tilde{I}_1), \\
a_4 &= \beta_1 \tilde{I}_1(\beta_1 \tilde{S}_1 - \gamma_1)\frac{1}{y_2} f_2(\lambda_2).
\end{aligned}$$

We note that

$$\beta_1 \tilde{S}_1 - \gamma_1 = d_1 + \delta_1 > 0$$

and from (H1)

$$\begin{aligned}
f_1(\lambda_2) - d_1 - \beta_1 \tilde{I}_1 &= (f_1(\lambda_2) - d_1) - \beta_1 \frac{1}{d_1 + \delta_1}(f_1(\lambda_2) - d_1)\tilde{S}_1 \\
&= (f_1(\lambda_2) - d_1)(1 - \frac{S_1 + d_1 + \gamma_1}{d_1 + \delta_1}) < 0,
\end{aligned}$$

then it follows that $a_1 > 0, a_2 > 0, a_3 > 0, a_4 > 0$. From Routh-Hurwitz criteria, E_{1I_12} is locally asymptotically stable if and only if

$$a_3(a_1 a_2 - a_3) > a_1^2 a_4. \tag{H3}$$

We conjecture that (H3) holds if $\mu_1 < 0$.

Theorem 3.3. *Let (H3) and (3.7) hold.*

(i) *If*

$$\tilde{S}_2 < \hat{S}_2 = \frac{d_2 + \delta_2 + \gamma_2}{\beta_2} \tag{3.11}$$

then E_{1I_12} is locally asymptotically stable.

(ii) *If the instability condition*

$$\tilde{S}_2 > \hat{S}_2 \tag{3.12}$$

holds, then equilibrium $E_{1I_12I_2} = (\bar{R}, \bar{S}_1, \bar{I}_1, \bar{S}_2, \bar{I}_2)$ *exists where*

$$\bar{S}_1 = \hat{S}_1 = \frac{d_1 + \delta_1 + \gamma_1}{\beta_1}, \tag{3.13}$$

$$\bar{S}_2 = \hat{S}_2 = \frac{d_2 + \delta_2 + \gamma_2}{\beta_2}, \tag{3.14}$$

$$\bar{I}_1 = \frac{1}{d_1 + \delta_1}\left(\frac{m_1 \bar{R}}{a_1 + \bar{R}} - d_1\right)\bar{S}_1 > 0 \quad \Leftrightarrow \bar{R} > \lambda_1, \tag{3.15}$$

$$\bar{I}_2 = \frac{1}{d_2 + \delta_2}\left(\frac{m_2 \bar{R}}{a_2 + \bar{R}} - d_2\right)\bar{S}_2 > 0 \quad \Leftrightarrow \bar{R} > \lambda_2, \tag{3.16}$$

and $\bar{R}$ *satisfies*

$$\begin{aligned}(R^{(0)} - \bar{R})D =& \frac{1}{y_1}\frac{m_1 \bar{R}}{a_1 + \bar{R}}\bar{S}_1\left(\frac{\frac{m_1 \bar{R}}{a_1 + \bar{R}} + \delta_1}{d_1 + \delta_1}\right) + \\ & \frac{1}{y_2}\frac{m_2 \bar{R}}{a_2 + \bar{R}}\bar{S}_2\left(\frac{\frac{m_2 \bar{R}}{a_2 + \bar{R}} + \delta_2}{d_2 + \delta_2}\right)\end{aligned} \tag{3.17}$$

Proof. (i) Since Re $\lambda(M_3) < 0$ and from (3.11) $\mu_1 < 0$, E_{1I_12} is locally asymptotically stable.
(ii) From (H1), it suffice to show that (3.16) holds. If not, $\bar{R} \le \lambda_2$ then

$$\begin{aligned}(R^{(0)} - \lambda_2)D \le (R^{(0)} - \bar{R})D &= \frac{1}{y_1}\frac{m_1 \bar{R}}{a_1 + \bar{R}}\bar{S}_1\frac{\frac{m_1 \bar{R}}{a_1 + \bar{R}} + \delta_1}{d_1 + \delta_1} + \frac{1}{y_2}\frac{m_2 \bar{R}}{a_2 + \bar{R}}\bar{S}_2\frac{\frac{m_2 \bar{R}}{a_2 + \bar{R}} + \delta_2}{d_2 + \delta_2} \\ &\le \frac{1}{y_1}\frac{m_1 \lambda_2}{a_1 + \lambda_2}\bar{S}_1\frac{\frac{m_1 \lambda_2}{a_1 + \lambda_2} + \delta_1}{d_1 + \delta_1} + \frac{1}{y_2}\frac{m_2 \lambda_2}{a_2 + \lambda_2}\bar{S}_2\frac{\frac{m_2 \lambda_2}{a_2 + \lambda_2} + \delta_2}{d_2 + \delta_2} \\ &= \frac{1}{y_1}\frac{m_1 \lambda_2}{a_1 + \lambda_2}\bar{S}_1\frac{\frac{m_1 \lambda_2}{a_1 + \lambda_2} + \delta_1}{d_1 + \delta_1} + \frac{1}{y_2}d_2\bar{S}_2\end{aligned}$$

$$\begin{aligned}\tilde{S}_2 &= \frac{y_2}{d_2}\left[(R^{(0)} - \lambda_2)D - \frac{1}{y_2}\left(\frac{m_1 \lambda_2}{a_1 + \lambda_2}\right)\tilde{S}_1\left(\frac{\frac{m_1 \lambda_2}{a_1 + \lambda_2} + \delta_1}{d_1 + \delta_1}\right)\right] \\ &\le \frac{y_2}{d_2}\frac{1}{y_2}d_2\bar{S}_2 = \tilde{S}_2\end{aligned}$$

This contradiction to the instability (3.12). □

It is difficult to determine the local stability of $E_{1I_12I_2}$. We verify it by extensive numerical simulation. We conjecture that Hopf bifurcation may occurs and there exists periodic solutions in some parameter ranges.

4 Bifurcation Analysis

Let (H1) hold. The equilibrium $E_1 = (\lambda_1, S_1^*, 0, 0, 0)$ is locally stable if (3.1) holds. We rewrite (3.1) as

$$\beta_1 < \hat{\beta}_1 = \frac{(d_1+\delta_1+\gamma_1)d_1}{(R^{(0)}-\lambda_1)Dy_1}. \tag{4.1}$$

When $\beta_1 > \hat{\beta}_1$, the equilibrium E_1 becomes unstable and the equilibrium $E_{1I_1} = (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ exists. If (3.6) and (H2) hold then E_{1I} is locally stable. From (3.6) it follow that

$$(R^{(0)}-\lambda_2)D < (R^{(0)}-\hat{R}_1)D = \frac{1}{y_1}\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}\frac{\left(\frac{m_1\hat{R}_1}{a_1+\hat{R}_1}+\delta_1\right)}{d_1+\delta_1}\hat{S}_1$$
$$< \frac{1}{y_1}\frac{m_1\lambda_2}{a_1+\lambda_2}\frac{\left(\frac{m_1\lambda_2}{a_1+\lambda_2}+\delta_1\right)}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{\beta_1}$$

or

$$\beta_1 < \tilde{\beta}_1 = \frac{1}{y_1}\frac{m_1\lambda_2}{a_1+\lambda_2}\frac{\left(\frac{m_1\lambda_2}{a_1+\lambda_2}+\delta_1\right)}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{(R^{(0)}-\lambda_2)D} \tag{4.2}$$

and

$$\hat{\beta}_1 < \tilde{\beta}_1.$$

If $\beta_1 > \tilde{\beta}_1$ then the equilibrium E_{1I} is unstable and the equilibrium $E_{1I_12} = (\lambda_2, \tilde{S}_1, \tilde{I}_1, \tilde{S}_2, 0)$ exists. If (3.11) and (H3) hold then the equilibrium E_{1I_12} is locally stable. It can be shown that (3.11) can be rewritten as

$$\beta_2 < \frac{A_1}{\left(A_2 - \frac{A_3}{\beta_1}\right)} := f(\beta_1) \tag{4.3}$$

where

$$A_1 = \frac{d_2}{y_2}(d_2+\delta_2+\gamma_2),$$
$$A_2 = (R^{(0)}-\lambda_2)D,$$

$$A_3 = \frac{1}{y_1} \frac{m_1\lambda_2}{a_1+\lambda_2} \frac{d_1+\delta_1+\gamma_1}{\delta_1+d_1} \left(\frac{m_1\lambda_2}{a_1+\lambda_2} + \delta_1 \right).$$

We note that the vertical asymptote of the curve $\beta_2 = \frac{A_1}{\left(A_2 - \frac{A_3}{\beta_1}\right)}$ is $\beta_1 = \frac{A_3}{A_2} = \tilde{\beta}_1$.

If $\beta_2 > \frac{A_1}{\left(A_2 - \frac{A_3}{\beta_1}\right)}$ then the equilibrium E_{1I_12} becomes unstable and the equilibrium $E_{1I_12I_2} = (\bar{R}, \bar{S}_1, \bar{I}_1, \bar{S}_2, \bar{I}_2)$ exists. It is difficult to prove the local stability of $E_{1I_12I_2}$ analytically. In the Figure 3, using β_1, β_2 as bifurcation parameters, we plot a bifurcation diagram. It shows that the Hopf bifurcation occurs and there are periodic oscillation for some parameter ranges.

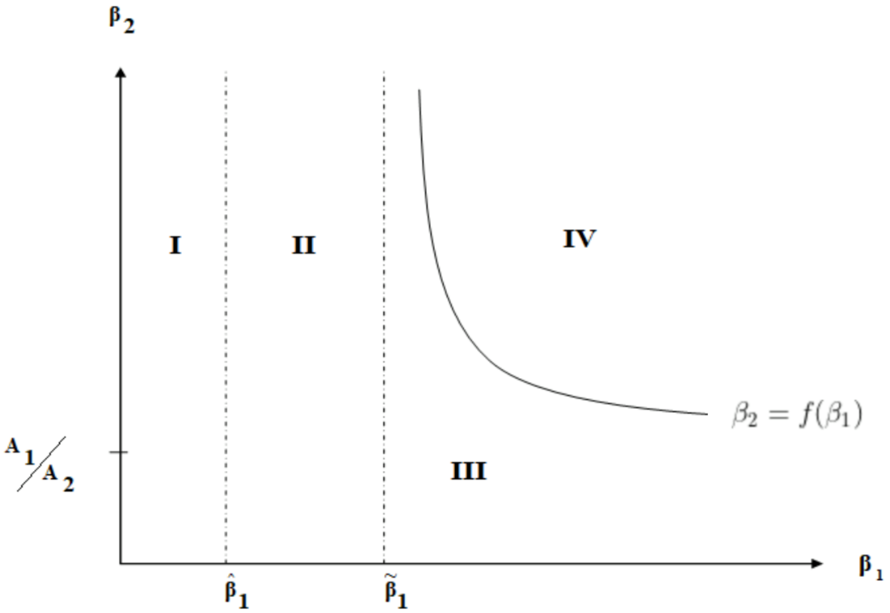

Figure 3

In region I , the equilibrium E_1 is locally stable.

In region II , the equilibrium E_{1I_1} is locally stable.

In region III , the equilibrium E_{1I_12} is locally stable.

In region IV , the equilibrium $E_{1I_12I_2}$ is locally stable or unstable.

Under the basic assumption (H1), species 1 outcompetes species 2 when there is no infection by the parasites. When the contact rate β_1 satisfies $0 < \beta_1 < \hat{\beta}_1$ regardless of magnitudes of the species 2's contact rate β_2, the species 1 still outcompetes the species 2 and there is no infection population of species 1. If we increase β_1 such that $\hat{\beta}_1 < \beta_1 < \tilde{\beta}_1$, then regardless of the magnitudes of β_2 species 1 still outcompetes species 2, but there is some infective population for the species 1 in this case. For $\beta_1 > \tilde{\beta}_1$, species 1 and species 2 coexist. If the point (β_1, β_2) is under the curve $\beta_2 = f(\beta_1) = \frac{A_1}{(A_2 - \frac{A_3}{\beta_1})}$ in the $\beta_1 - \beta_2$ plane, then species 1 which has both susceptible and infective population, coexists with species 2 which has only susceptible population. If the point (β_1, β_2) is above the curve $\beta_2 = f(\beta_1)$ in the $\beta_1 - \beta_2$ plane then species 1 and species 2 both with infective population coexists in the steady state or the form of periodic oscillation.

If we vary the input concentration $R^{(0)}$ and fix the other parameters then from (3.17), (4.1), (4.2) it follows that

$$\beta_1 < \hat{\beta}_1 \Leftrightarrow R^{(0)} < \lambda_1 + \frac{(d_1 + \delta_1 + \gamma_1)d_1}{Dy_1\beta_1} = \hat{R}^{(0)}$$

$$\beta_1 < \tilde{\beta}_1 \Leftrightarrow R^{(0)} < \lambda_2 + \frac{(d_1 + \delta_1 + \gamma_1)}{Dy_1\beta_1} \frac{m_1\lambda_2}{a_1 + \lambda_2} \frac{\left(\frac{m_1\lambda_2}{a_1 + \lambda_2} + \delta_1\right)}{d_1 + \delta_1} = \tilde{R}^{(0)}$$

$$\beta_2 < \frac{A_1}{\left(A_2 - \frac{A_3}{\beta_1}\right)} \Leftrightarrow R^{(0)} < \tilde{R}^{(0)} + \frac{d_2(d_2 + \delta_2 + \gamma_2)}{\beta_2 D y_1} = \bar{R}^{(0)}$$

From the hypothesis (H1), we have $\hat{R}^{(0)} < \tilde{R}^{(0)} < \bar{R}^{(0)}$.

The bifurcation diagram is the following **Figure 4:**

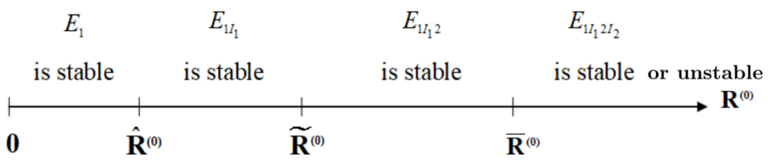

Figure 4

Thus in order to have coexistence of species 1 and species 2, we need to have large input concentration $R^{(0)}$ i.e. $R^{(0)} > \tilde{R}^{(0)}$.

5 Discussion and Numerical Simulations

By the following scalings:

$$R \to R/R^{(0)}, \quad S_1 \to S_1/R^{(0)}y_1, \quad I_1 \to I_1/R^{(0)}y_1$$

$$S_2 \to \frac{S_2}{R^{(0)}y_2}, \quad I_2 \to I_2/R^{(0)}y_2, \quad m_1 \to m_1/D, \quad m_2 \to m_2/D$$
$$d_1 \to d_1/D, \quad d_2 \to d_2/D, \quad a_1 \to a_1/R^{(0)}, \quad a_2 \to a_2/R^{(0)}$$
$$\beta_1 \to \beta_1 R^{(0)}y_1/D, \quad \delta_1 \to \delta_1/D, \quad \gamma_1 \to \gamma_1/D$$
$$\beta_2 \to \beta_2 R^{(0)}y_2/D, \quad \delta_2 \to \delta_2/D, \quad \gamma_2 \to \gamma_2/D$$
$$t \to tD$$

then the non-dimensional system for (2.1) is

$$\begin{aligned}
\frac{dR}{dt} &= (1-R)D - \frac{m_1R}{a_1+R}(S_1+I_1) - \frac{m_2R}{a_2+R}(S_2+I_2)\\
\frac{dS_1}{dt} &= \left(\frac{m_1R}{a_1+R} - d_1\right)S_1 - \beta_1I_1S_1 + \gamma_1I_1\\
\frac{dI_1}{dt} &= \beta_1I_1S_1 - (d_1+\delta_1+\gamma_1)I_1\\
\frac{dS_2}{dt} &= \left(\frac{m_2R}{a_2+R} - d_2\right)S_2 - \beta_2I_2S_2 + \gamma_2I_2\\
\frac{dI_2}{dt} &= \beta_2I_2S_2 - (d_2+\delta_2+\gamma_2)\,I_2\\
0 < R^{(0)} &< 1, \quad S_1(0)>0, \quad I_1(0)>0, \quad S_2(0)>0, \quad I_2(0)>0.
\end{aligned} \tag{5.1}$$

Hence we may assume $D = 1, \quad R^{(0)} = 1, \quad y_1 = 1, \quad y_2 = 1$ in (2.1).

Let $d_1 = 1, \quad m_1 = 2, \quad a_1 = 0.5, \quad d_2 = 1.2, \quad m_2 = 1.8, \quad a_2 = 0.35$, then

$$0 < \lambda_1 = \frac{a_1}{(\frac{m_1}{d_1}) - 1} = 0.5 < \lambda_2 = \frac{a_2}{(\frac{m_2}{d_2}) - 1} = 0.7 < R^{(0)} = 1.$$

Let $\delta_1 = 0.05, \quad \delta_2 = 0.03, \quad \gamma_1 = 0.1, \quad \gamma_2 = 0.2$, then

$$\hat{\beta}_1 = \frac{(d_1+\delta_1+\gamma_1)d_1}{(R^{(0)}-\lambda_1)Dy_1} = 2.3,$$
$$\tilde{\beta}_1 = \frac{1}{y_1}\frac{m_1\lambda_2}{a_1+\lambda_2}\frac{\frac{m_1\lambda_2}{a_1+\lambda_2}+\delta_1}{d_1+\delta_1}\frac{d_1+\delta_1+\gamma_1}{(R^{(0)}-\lambda_2)D} = 5.1821.$$

Let $R(0) = 0.8, \quad S_1(0) = 0.5, \quad I_1(0) = 0.1, \quad S_2(0) = 0.5, \quad I_2(0) = 0.1.$

(i) Let $\beta_1 = 1.5, \quad \beta_2 = 3$, we conject that $E_1 = (\lambda_1, S_1^*, 0, 0, 0)$ is globally stable where $\lambda_1 = 0.5, \quad S_1^* = \frac{(R^{(0)}-\lambda_1)Dy_1}{d_1} = 0.5.$

(ii) Let $\beta_1 = 3, \quad \beta_2 = 6$, we conject that $E_{1I_1} = (\hat{R}_1, \hat{S}_1, \hat{I}_1, 0, 0)$ is globally stable.

(iii) Choose a point (β_1, β_2) below the curve $\beta_2 = f(\beta_1), \quad \beta_1 = 10, \quad \beta_2 = 11 < f(\beta_1) = 11.8724$, we expect $E_{1I_12} = (\lambda_2, \tilde{S}_1, \tilde{I}_1, \tilde{S}_2, 0)$ is globally stable.

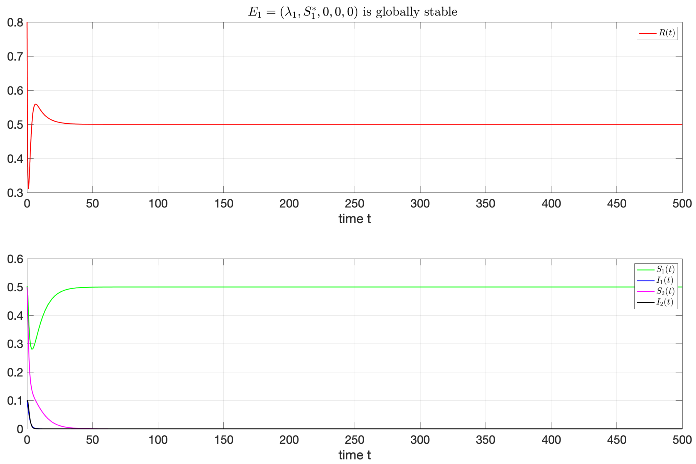

Figure 5(i) Let $\beta_1 = 1.5$ and $\beta_2 = 3$

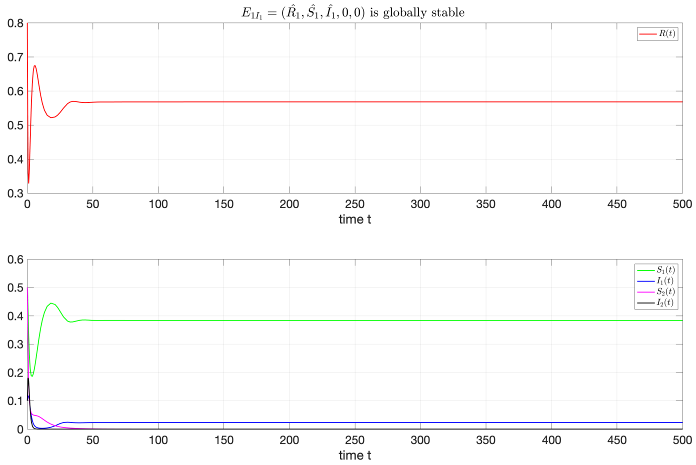

Figure 5(ii) Let $\beta_1 = 3$ and $\beta_2 = 6$

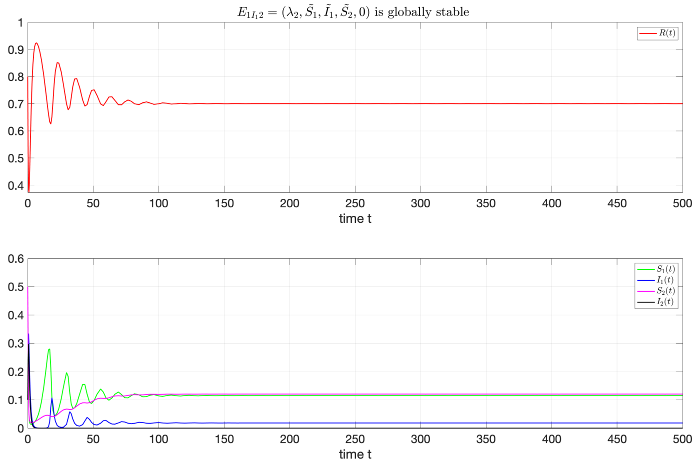

Figure 5(iii) Let $\beta_1 = 10$ and $\beta_2 = 11$

(iv) For point (β_1, β_2) above the curve $\beta_2 = f(\beta_1)$, choosing $\beta_1 = 10, \beta_2 = 12 > f(\beta_1) = 11.8724$, we predict $E_{1I_12I_2} = (\bar{R}, \bar{S}_1, \bar{I}_1, \bar{S}_2, \bar{I}_2)$ is globally stable.

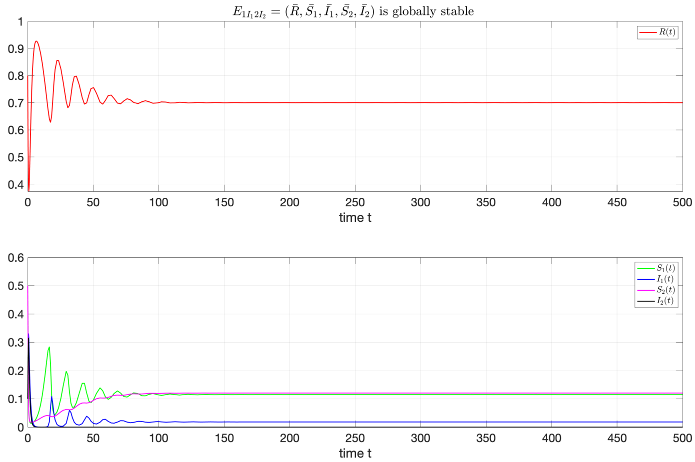

Figure 5(iv) Let $\beta_1 = 10$ and $\beta_2 = 12$

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