

An analysis of the coexistence of two host species with a shared pathogen

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Abstract Population dynamics of two-host species under direct transmission of an infectious disease or a pathogen is studied based on the Holt–Pickering mathematical model, which accounts for the influence of the pathogen on the population of the two-host species. Through rigorous analysis and a numerical scheme of study, circumstances are specified under which the shared pathogen leads to the coexistence of the two-host species in either a persistent or periodic form. This study shows the importance of intrinsic growth rates or the differences between birth rates and death rates of the two host susceptibles in controlling these circumstances. It is also demonstrated that the periodicity may arise when the positive intrinsic growth rates are very small, but the periodicity is very weak which may not be observed in an empirical investigation.

Keywords Holt–Pickering model · Host population dynamics · Host–host–pathogen interactions · Stability and instability analysis

Mathematics Subject Classification (2000) 92D25 · 37C10 · 37C27

1 Introduction

In the study of community ecology, species coexistence and the structure of biological communities are essentially regulated by competitive interaction [21], predation [8, 12] and infectious disease caused by a microparasite or pathogen [18]. However, extensive investigations highlight the importance of pathogens in constraining the population of some host species [1, 2, 6, 18]. Although pathogens are often difficult

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to detect and quantify in an empirical study, host–pathogen interaction can be characterized by mathematical models derived from population dynamics and epidemiology [1–3, 14, 17].

In this investigation, we focus on the theoretical study of the mathematical model discussed by Holt and Pickering [14] showing population dynamics of two host species transmitted by a single pathogen. This model was developed from a single host model described by Anderson and May [2] in the form

$$\left. \begin{aligned} \frac{dS_1}{dt} &= (a_1 - b_1)S_1 + (\delta_1 + \gamma_1)I_1 - \beta_{11}S_1I_1, \\ \frac{dI_1}{dt} &= -(b_1 + \alpha_1 + \gamma_1)I_1 + \beta_{11}S_1I_1. \end{aligned} \right\}$$

Here S_1 represents the densities of individuals in host species 1 which are susceptible to the disease, whereas I_1 denotes the densities of those that are infected by the disease. The parameters a_1 and δ_1 are, respectively, the per capita birth rates of the susceptible and infected individuals; b_1 and α_1 are the per capita death rates of the S_1 and I_1 individuals, respectively; γ_1 is the per capita recovery rate from an infected to a susceptible state; β_{11} is the rate characterizing the transmission between susceptibles and infectives. This model admits a unique stable equilibrium

$$(S_1, I_1) = \left(\frac{b_1 + \alpha_1 + \gamma_1}{\beta_{11}}, \frac{(a_1 - b_1)(b_1 + \alpha_1 + \gamma_1)}{\beta_{11}(b_1 + \alpha_1 - \delta_1)} \right)$$

showing that the infectious disease can regulate the host species population which otherwise would grow exponentially.

Based on this single-host model, Holt and Pickering [14] examined the dynamical interactions of two species and a single infectious disease to deduce a two-host shared pathogen model. Similarly, by defining the unknown densities S_2 and I_2 and the parameters $a_2, \delta_2, b_2, \alpha_2$ and γ_2 for the second species, Holt and Pickering (1985) described this two-host model by the set of coupled equations

$$\left. \begin{aligned} \frac{dS_1}{dt} &= r_1S_1 + e_1I_1 - \beta_{11}S_1I_1 - \beta_{12}S_1I_2, \\ \frac{dI_1}{dt} &= -d_1I_1 + \beta_{11}S_1I_1 + \beta_{12}S_1I_2, \\ \frac{dS_2}{dt} &= r_2S_2 + e_2I_2 - \beta_{22}S_2I_2 - \beta_{21}S_2I_1, \\ \frac{dI_2}{dt} &= -d_2I_2 + \beta_{22}S_2I_2 + \beta_{21}S_2I_1. \end{aligned} \right\} \quad (1)$$

Here β_{ij} denotes the transmission rate of the susceptible individuals of species i and the infected individuals of species j , $r_i = a_i - b_i$ represents the intrinsic rate of growth of host species i ($= 1, 2$), $d_i = \alpha_i + b_i + \gamma_i$ expresses the rate of depletion of the infected fraction of population, $e_i = \delta_i + \gamma_i$ denotes the rate of entry of new susceptibles stemming from the infected portion of the population. This model assumes

the absence of vertical transmission. Moreover there is no acquired immunity in this model. This property applies to invertebrate species as discussed by Anderson and May [2].

The investigations of Holt and Pickering [14] and Greenman and Hudson [10] display three crucial equilibria of (1). That is, the infected one-host equilibria E_1 and E_2 and infected coexistence equilibrium E_3 , expressed as

$$\begin{aligned} E_1 &= (S_1, I_1, S_2, I_2) = \left(\frac{d_1}{\beta_{11}}, \frac{r_1 d_1}{\beta_{11}(d_1 - e_1)}, 0, 0 \right), \\ E_2 &= (S_1, I_1, S_2, I_2) = \left(0, 0, \frac{d_2}{\beta_{22}}, \frac{r_2 d_2}{\beta_{22}(d_2 - e_2)} \right), \\ E_3 &= (S_1, I_1, S_2, I_2) \\ &= \left(\frac{\frac{d_1 - e_1}{r_1} \left(\frac{\beta_{22} d_1 r_1}{d_1 - e_1} - \frac{\beta_{12} d_2 r_2}{d_2 - e_2} \right)}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}}, \frac{\frac{\beta_{22} d_1 r_1}{d_1 - e_1} - \frac{\beta_{12} d_2 r_2}{d_2 - e_2}}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}}, \frac{\frac{d_2 - e_2}{r_2} \left(\frac{\beta_{11} d_2 r_2}{d_2 - e_2} - \frac{\beta_{21} d_1 r_1}{d_1 - e_1} \right)}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}}, \right. \\ &\quad \left. \frac{\frac{\beta_{11} d_2 r_2}{d_2 - e_2} - \frac{\beta_{21} d_1 r_1}{d_1 - e_1}}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}} \right). \end{aligned}$$

We note that E_1 and E_2 are biologically relevant, or the population densities S_i and I_i of E_1 and E_2 are nonnegative, if $d_1 > e_1$ and $d_2 > e_2$. Moreover, E_3 is biologically relevant if

$$d_1 > e_1, \quad d_2 > e_2, \quad \frac{\frac{\beta_{22} d_1 r_1}{d_1 - e_1} - \frac{\beta_{12} d_2 r_2}{d_2 - e_2}}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}} \geq 0, \quad \frac{\frac{\beta_{11} d_2 r_2}{d_2 - e_2} - \frac{\beta_{21} d_1 r_1}{d_1 - e_1}}{\beta_{22} \beta_{11} - \beta_{12} \beta_{21}} \geq 0 \quad (2)$$

hold true.

It is easy to see that the shared pathogen does not lead to the extinction of both host species due to the instability of the trivial equilibrium $E_0 = (0, 0, 0, 0)$ whenever $d_i > 0$ and $r_i > 0$. However, the stability of E_1 implies the persistence of host species 1 and the extinction of host species 2, whereas the stability of E_2 indicates the persistence of host species 2 and the extinction of host species 1. Moreover, the stability of E_3 means the persistence of both host species under the transmission of the pathogen. The stability of E_1 and E_2 was derived by Holt and Pickering [14] and Greenman and Hudson [10]. However, the stability of the infected coexistence equilibrium E_3 remains unknown, and it is of interest to understand the population dynamics when E_3 is unstable. For example, it remains biologically important to understand the circumstances under which the shared pathogen leads to equilibrium or periodic coexistence. These biological phenomena depend on understanding the mechanisms of stability and instability of the equilibria, the existence of limit cycles and the inter-relation between the equilibria and limit cycles.

The present study is motivated by the conjecture [14] that for infected equilibria E_1 , E_2 and E_3 being biologically relevant, the coexistence equilibrium E_3 is stable if and only if both the one-host equilibria E_1 and E_2 are unstable. Greenman and Hudson [10] argued that this conjecture is not universally valid and three unstable equilibria

may coexist involving limit cycles. This is an important and interesting argument, since it provides another possibility of how interspecific interactions can generate unstable dynamics in the community.

The main objective of this paper is to provide rigorous analysis showing the validity of the conjecture of Holt and Pickering [14] in the case of large intrinsic growth rates r_1 and r_2 and providing a sufficient condition which ensures the existence of limit cycles. More precisely, it is shown that the infected coexistence equilibrium E_3 is stable if and only if both the infected one-host equilibria E_1 and E_2 are unstable when intrinsic growth rates r_1 and r_2 are large. However, when the intrinsic growth rates r_1 and r_2 decrease, this assertion becomes incorrect and the infected coexistence equilibrium E_3 may lose stability and bifurcates into a stable periodic trajectory or a limit cycle, which finally disappears when r_1 and r_2 decrease to zero or when the uninfected birth rates decrease to the uninfected death rates. This gives an analytical change of the populations of the infected two-host species from persistent coexisting to periodical coexisting due to the transmission of the single pathogen.

A famous insight in mathematical ecology, stemming back to Rosenzweig and MacArthur [20], was that predator–prey dynamics tend to destabilise by increasing prey productivity. This effect was christened *the paradox of enrichment* [19]. However, the results of the present paper show that in multispecies host–pathogen systems, there is a kind of *inverse paradox of enrichment* and increases in prey productivity (as measured by the intrinsic growth rates of the host species) can be stabilising.

An interest insight into the coexistence of ecology communities is known as *apparent competition* [11], which relates to indirect competition between two or more victim species sharing a natural enemy. As a result of the indirect competition, some victim species tend to be reduced significantly and even excluded from the community by other victim species because of their shared natural enemy [11–13]. Apparent competition arises in the coexistence of two preys sharing a predator [11] and in the coexistence of multiple insect host species coupled with a parasitoid [13]. The interaction of the pathogen and the two host species leads to the apparent competition between the two host species. This paper shows the mechanism underlying the coexistence of two host species is based on the their intrinsic growth rates. Due to the indirect competition, the two host species coexist either persistently (for high r_i values) or periodically (for low r_i values) when their intrinsic growth rates vary in a comparable level as described in the next section or by (19) in Sect. 5. The present investigation focuses on the study of dynamical behaviour around the coexistence equilibrium. One may consult Schreiber [22] for the close relation between the dynamical behaviour around a coexistence equilibrium and coexistence permanence [15] modulating apparent competition of two preys sharing a predator.

2 The two-host shared pathogen model under new scaled parameters

To understand the stability of (1), which is dominated by the three equilibria E_1 , E_2 and E_3 , it is necessary to adopt control parameters governing the dynamical behaviour of the system. From the expression of the infected host equilibria E_1 , E_2 and E_3 , it is convenient to introduce the following scaled parameters:

$$\lambda = \frac{r_1}{d_1 - e_1}, \quad \mu = \frac{r_2(d_1 - e_1)}{r_1(d_2 - e_2)}.$$

Thus, system (1) becomes

$$\left. \begin{aligned} \frac{dS_1}{dt} &= \lambda(d_1 - e_1)S_1 + e_1I_1 - \beta_{11}S_1I_1 - \beta_{12}S_1I_2, \\ \frac{dI_1}{dt} &= -d_1I_1 + \beta_{11}S_1I_1 + \beta_{12}S_1I_2, \\ \frac{dS_2}{dt} &= \lambda\mu(d_2 - e_2)S_2 + e_2I_2 - \beta_{22}S_2I_2 - \beta_{21}S_2I_1, \\ \frac{dI_2}{dt} &= -d_2I_2 + \beta_{22}S_2I_2 + \beta_{21}S_2I_1, \end{aligned} \right\} \quad (3)$$

and the expressions describing the equilibria are of the forms

$$E_1 = \left(\frac{d_1}{\beta_{11}}, \frac{\lambda d_1}{\beta_{11}}, 0, 0 \right), \quad (4)$$

$$E_2 = \left(0, 0, \frac{d_2}{\beta_{22}}, \frac{\lambda\mu d_2}{\beta_{22}} \right), \quad (5)$$

$$E_3 = \frac{\left(\beta_{22}d_1 - \beta_{12}d_2\mu, \lambda(\beta_{22}d_1 - \beta_{12}d_2\mu), \frac{\beta_{11}d_2\mu - \beta_{21}d_1}{\mu}, \lambda(\beta_{11}d_2\mu - \beta_{21}d_1) \right)}{\beta_{22}\beta_{11} - \beta_{12}\beta_{21}}. \quad (6)$$

In addition to the assumptions $d_1 > e_1$ and $d_2 > e_2$, the biologically relevant condition (2) of E_3 can be written as

$$\frac{\beta_{21}d_1}{\beta_{11}d_2} \geq \mu \geq \frac{\beta_{22}d_1}{\beta_{12}d_2} \quad \text{whenever } \beta_{11}\beta_{22} - \beta_{12}\beta_{21} < 0, \quad (7)$$

$$\frac{\beta_{21}d_1}{\beta_{11}d_2} \leq \mu \leq \frac{\beta_{22}d_1}{\beta_{12}d_2} \quad \text{whenever } \beta_{11}\beta_{22} - \beta_{12}\beta_{21} > 0. \quad (8)$$

From expressions (4)–(6) we see that the parameter μ valued between the limit values $\frac{\beta_{21}d_1}{\beta_{11}d_2}$ and $\frac{\beta_{22}d_1}{\beta_{12}d_2}$ given in (7), (8) treats E_3 as a bridge between E_1 and E_2 , or

$$\begin{aligned} E_1 &= E_3 \quad \text{if } \mu = \frac{\beta_{21}d_1}{\beta_{11}d_2}, \\ E_2 &= E_3 \quad \text{if } \mu = \frac{\beta_{22}d_1}{\beta_{12}d_2}. \end{aligned}$$

In the terminology of this paper, the result given by Holt and Pickering [14] and Greenman and Hudson [10] is expressed as

$$\left. \begin{aligned} E_1 \text{ and } E_2 \text{ are stable} & \quad \text{if } \beta_{11}\beta_{22} - \beta_{21}\beta_{12} < 0, \\ E_1 \text{ and } E_2 \text{ are unstable} & \quad \text{if } \beta_{11}\beta_{22} - \beta_{21}\beta_{12} > 0, \end{aligned} \right\}$$

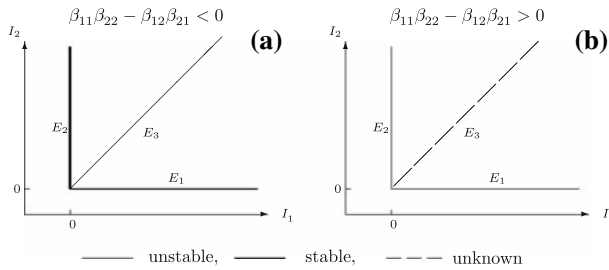


Fig. 1 The known profile in earlier works of the three biologically relevant equilibria projected on the (I_1, I_2) plane for a value of the parameter μ in between the numbers $\frac{\beta_{21}d_1}{\beta_{11}d_2}$ and $\frac{\beta_{22}d_1}{\beta_{12}d_2}$ and for the parameter λ running from zero to the infinite

under the Assumption (2), the biologically relevant assumption of E_3 , and the assumption that μ does not reach the limit values $\frac{\beta_{21}d_1}{\beta_{11}d_2}$ and $\frac{\beta_{22}d_1}{\beta_{12}d_2}$. This phenomenon is displayed in Fig. 1 with respect to λ running from zero to infinity. Figure 1a also illustrates the instability of E_3 under the condition

$$\beta_{11}\beta_{22} - \beta_{21}\beta_{12} < 0 \quad \text{and} \quad \frac{\beta_{21}d_1}{\beta_{11}d_2} > \mu > \frac{\beta_{22}d_1}{\beta_{12}d_2}, \quad (9)$$

a result obtained by Greenman and Hudson [10]. The instability of E_3 and stability of E_1 and E_2 illustrated in Fig. 1a show that either host species 1 or host species 2 eventually go extinct under transmission assumption $\beta_{11}\beta_{22} - \beta_{12}\beta_{21} < 0$. For completeness, a derivation of these known stability and instability results with respect to new parameters μ and λ is given in the Appendix.

However, as displayed in Fig 1b, in the previous investigations, it was unknown whether E_3 is stable or unstable under the condition

$$\beta_{11}\beta_{22} - \beta_{21}\beta_{12} > 0 \quad \text{and} \quad \frac{\beta_{21}d_1}{\beta_{11}d_2} < \mu < \frac{\beta_{22}d_1}{\beta_{12}d_2}. \quad (10)$$

As discussed herein, it is the purpose of this investigation to derive local dynamical behaviour (3) around the coexistence equilibrium E_3 . Furthermore, it is noted from the Appendix and Corollary A.1 that E_1 and E_3 are neutral (neither stable nor unstable) when μ equals the limit value $\frac{\beta_{21}d_1}{\beta_{11}d_2}$, whereas E_2 and E_3 are neutral when μ equals the other limit value $\frac{\beta_{22}d_1}{\beta_{12}d_2}$. In fact, E_1 and E_3 exchange their stability and instability at the value $\mu = \frac{\beta_{21}d_1}{\beta_{11}d_2}$, whereas E_2 and E_3 exchange their stability and instability at the value $\mu = \frac{\beta_{22}d_1}{\beta_{12}d_2}$. Thus, these two values are transcritical bifurcation values of these three equilibria. From Fig. 1 or by the definition of the equilibria in (4)–(6), we see that infected population densities I_1 and I_2 of the equilibria E_1 , E_2 and E_3 reduce to zero at $\lambda = 0$. That is, E_1 , E_2 and E_3 become uninfected and are in a state of neutral equilibria when the intrinsic rates $r_1 = 0$ and $r_2 = 0$.

3 Critical value λ_c and bifurcating periodic trajectories from E_3

Based on the analysis presented in the Appendix, we now discuss criterion for the existence of a critical value λ_c and the existence of bifurcating periodic trajectories of (3) with respect to the coexistence equilibrium E_3 assuming the validity of the condition (10).

The finding of this rigorous analysis are expressed as follows.

Theorem 3.1 (i) *For given positive values of the parameters d_i and β_{ij} , let μ satisfy condition (10) or the condition*

$$\frac{\beta_{21}d_1}{\beta_{11}d_2} < \mu < \frac{\beta_{22}d_1}{\beta_{12}d_2}. \quad (11)$$

Then E_3 is stable when λ is sufficiently large.

(ii) *In addition to assumption (11), we assume that $e_1 = \mu e_2$. Then there exists a unique critical value $\lambda_c \geq 0$ such that the coexistence host equilibrium E_3 is stable whenever $\lambda > \lambda_c$. If $\lambda_c \neq 0$, then E_3 is unstable whenever $0 < \lambda < \lambda_c$, and E_3 bifurcates into a branch of periodic trajectories when λ varies across λ_c .*

Proof In the derivation of this result, the parameters $\beta_{i,j}$, d_i , e_i and μ are constants, whereas the parameter λ varies from zero to infinity. The proof is based on the criterion of Routh and Hurwitz (see, for example, [7,9]) on the roots of characteristic polynomials and the Hopf bifurcation criterion of Liu [16].

(i) It follows from (11, A.10, A.11) that c_i , the coefficients of the characteristic polynomial of E_3

$$\det(J(E_3) - \rho) = \rho^4 + c_1\rho^3 + c_2\rho^2 + c_3\rho + c_4,$$

are positive and can be written as

$$c_1 = c_{1,1}\lambda + c_{1,2}, \quad c_2 = \lambda(c_{2,1}\lambda + c_{2,2}), \quad c_3 = \lambda(c_{3,1}\lambda + c_{3,2}), \quad c_4 = c_{4,1}\lambda^2, \quad (12)$$

where constants $c_{i,j}$ are positive and independent of λ .

It follows from the Routh–Hurwitz criterion that E_3 is linearly stable if and only if

$$\begin{aligned} D_3 &\equiv c_1c_2c_3 - c_3^2 - c_1^2c_4 \\ &= \lambda^2 \left[(c_{1,1}\lambda + c_{1,2})(c_{2,1}\lambda + c_{2,2})(c_{3,1}\lambda + c_{3,2}) - (c_{3,1}\lambda + c_{3,2})^2 \right. \\ &\quad \left. - (c_{2,1}\lambda + c_{2,2})^2c_{4,1} \right] > 0, \end{aligned}$$

which holds true for sufficiently large λ , because $c_1c_2c_3$ is a five degree positive polynomial of λ and $c_3^2 + c_1^2c_4$ is a four degree polynomial of λ .

This gives the validity of Assertion (i).

(ii) The validity of this assertion essentially lies in the observation that D_3 is a strictly increasing function of λ . To do so, we consider the derivative of D_3/λ^2 :

$$\begin{aligned} \frac{d}{d\lambda} \left(\frac{D_3}{\lambda^2} \right) &= c_{1,1}(c_{2,1}\lambda + c_{2,2})(c_{3,1}\lambda + c_{3,2}) + (c_{1,1}\lambda + c_{1,2})c_{2,1}(c_{3,1}\lambda + c_{3,2}) \\ &\quad + (c_{1,1}\lambda + c_{1,2})(c_{2,1}\lambda + c_{2,2})c_{3,1} - 2(c_{3,1}\lambda + c_{3,2})c_{3,1} \\ &\quad - 2(c_{1,1}\lambda + c_{1,2})c_{1,1}c_{4,1} \\ &> (c_{3,1}\lambda + c_{3,2})[c_{1,1}(c_{2,1}\lambda + c_{2,2}) - 2c_{3,1}] + (c_{1,1}\lambda + c_{1,2}) \\ &\quad \times [(c_{2,1}\lambda + c_{2,2})c_{3,1} - 2c_{1,1}c_{4,1}] \\ &> (c_{3,1}\lambda + c_{3,2})(c_{1,1}c_{2,2} - 2c_{3,1}) + (c_{1,1}\lambda + c_{1,2})(c_{2,2}c_{3,1} - 2c_{1,1}c_{4,1}). \end{aligned}$$

Therefore, $(d/d\lambda)(D_3/\lambda^2) > 0$, if

$$c_{1,1}c_{2,2} - 2c_{3,1} > 0 \quad \text{and} \quad c_{2,2}c_{3,1} - 2c_{1,1}c_{4,1} > 0 \quad (13)$$

hold true. To verify the validity of (13), we see from (12, A.9, A.10) that the constants $c_{i,j}$ can be expressed in the form

$$\begin{aligned} c_{1,1} &= e_1 + \mu e_2, \\ c_{2,2} &= (d_1 - e_1)\beta_{11}S_1 + e_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}e_2\mu^2S_2 + (d_2 - e_2)\beta_{22}\mu S_2, \\ c_{3,1} &= (d_1 - e_1)\beta_{11}S_1\mu e_2 + e_1(d_2 - e_2)\beta_{22}\mu S_2, \\ c_{4,1} &= \mu S_2S_1(\beta_{11}\beta_{22} - \beta_{12}\beta_{21})(d_1 - e_1)(d_2 - e_2), \end{aligned}$$

where S_1 and S_2 are the exponents of equilibrium $E_3 = (S_1, I_1, S_2, I_2)$ defined in (6). Thus, we have

$$\begin{aligned} &c_{1,1}c_{2,2} - 2c_{3,1} \\ &= (e_1 + \mu e_2) \left[(d_1 - e_1)\beta_{11}S_1 + e_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}e_2\mu^2S_2 + (d_2 - e_2)\beta_{22}\mu S_2 \right] \\ &\quad - 2[(d_1 - e_1)\beta_{11}S_1\mu e_2 + e_1(d_2 - e_2)\beta_{22}\mu S_2] \\ &> (e_1 + \mu e_2)[(d_1 - e_1)\beta_{11}S_1 + (d_2 - e_2)\beta_{22}\mu S_2] \\ &\quad - 2[(d_1 - e_1)\beta_{11}S_1\mu e_2 + e_1(d_2 - e_2)\beta_{22}\mu S_2] \\ &= (e_1 - \mu e_2)(d_1 - e_1)\beta_{11}S_1 + (\mu e_2 - e_1)(d_2 - e_2)\beta_{22}\mu S_2 = 0, \\ &\quad \text{whenever } e_1 = \mu e_2, \end{aligned}$$

and

$$\begin{aligned}
 & c_{2,2}c_{3,1} - 2c_{1,1}c_{4,1} \\
 &= \left[(d_1 - e_1)\beta_{11}S_1 + e_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}e_2\mu^2 S_2 + (d_2 - e_2)\beta_{22}\mu S_2 \right] \\
 &\quad \times [(d_1 - e_1)\beta_{11}\mu e_2 S_1 + e_1(d_2 - e_2)\beta_{22}\mu S_2] \\
 &\quad - 2(e_1 + \mu e_2)\mu S_2 S_1 (\beta_{11}\beta_{22} - \beta_{12}\beta_{21})(d_1 - e_1)(d_2 - e_2) \\
 &> [(d_1 - e_1)\beta_{11}S_1 + (d_2 - e_2)\beta_{22}\mu S_2] [(d_1 - e_1)\beta_{11}\mu e_2 S_1 + e_1(d_2 - e_2)\beta_{22}\mu S_2] \\
 &\quad - 2(e_1 + \mu e_2)\mu S_2 S_1 (\beta_{11}\beta_{22} - \beta_{12}\beta_{21})(d_1 - e_1)(d_2 - e_2) \\
 &> \mu e_2 [(d_1 - e_1)\beta_{11}S_1]^2 + e_1 [(d_2 - e_2)\beta_{22}\mu S_2]^2 \\
 &\quad - (e_1 + \mu e_2)\mu S_2 S_1 \beta_{11}\beta_{22}(d_1 - e_1)(d_2 - e_2) \\
 &= e_1 [(d_1 - e_1)\beta_{11}S_1 - (d_2 - e_2)\beta_{22}\mu S_2]^2 \geq 0, \quad \text{whenever } e_1 = \mu e_2.
 \end{aligned}$$

Combining these results, we have the strictly monotone increasing property of D_3/λ^2 . That is,

$$\frac{d}{d\lambda} \left(\frac{D_3}{\lambda^2} \right) > 0, \quad \text{whenever } e_1 = \mu e_2 \text{ and } \lambda > 0. \quad (14)$$

If there is a value $\lambda_c > 0$ such that $D_3 = 0$ at $\lambda = \lambda_c$, we have

$$\frac{dD_3}{d\lambda} = 2 \frac{D_3}{\lambda} + \lambda^2 \frac{d}{d\lambda} \left(\frac{D_3}{\lambda^2} \right) = \lambda^2 \frac{d}{d\lambda} \left(\frac{D_3}{\lambda^2} \right) > 0, \quad \text{at } \lambda = \lambda_c. \quad (15)$$

This together with the smoothness of D_3 with respect to the variable λ implies the uniqueness of such a value λ_c and the desired property

$$\begin{cases} D_3 = 0 & \text{when } \lambda = \lambda_c, \\ D_3 > 0 & \text{when } \lambda > \lambda_c, \\ D_3 < 0 & \text{when } 0 < \lambda < \lambda_c. \end{cases}$$

Moreover, the Hopf bifurcation criterion of Liu [16] shows that there is a branch of periodic trajectories $(S_{1,\lambda}(t), I_{1,\lambda}(t), S_{2,\lambda}(t), I_{2,\lambda}(t))$ of (3) when λ varies across λ_c , if

$$D_3 = 0 \quad \text{and} \quad \frac{dD_3}{d\lambda} = 0 \quad \text{at } \lambda = \lambda_c,$$

which is valid due the Assumption of λ_c and (15).

Finally, if $D_3 > 0$ for any $\lambda > 0$, we take $\lambda_c = 0$ since $D_3 = 0$ at $\lambda = 0$ is always true.

We thus obtain Assertion (ii) and hence complete the proof of Theorem 3.1.

To conclude this section, we give a necessary and sufficient condition for value $\lambda_c > 0$ or the coexistence equilibrium E_3 being unstable for some $\lambda > 0$ sufficiently

small. From (14), we see that $\lambda_c > 0$ if and only if

$$\lim_{\lambda \rightarrow 0} \frac{D_3}{\lambda^2} = c_{1,2}c_{2,2}c_{3,2} - c_{3,2}^2 - c_{1,2}^2c_{4,1} < 0.$$

or

$$\begin{aligned} 0 &> \left(\beta_{12}\mu S_2 + \frac{\beta_{21}S_1}{\mu} \right) \left((d_1 - e_1)\beta_{11}S_1 + e_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}\mu^2 S_2 e_2 + (d_2 - e_2)\beta_{22}\mu S_2 \right) \\ &\quad \times \left(e_1(d_2 - e_2)\beta_{22}\mu S_2 + (d_1 - e_1)d_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}\mu^2 S_2(d_2 - e_2)d_2 \right) \\ &\quad - \left(e_1(d_2 - e_2)\beta_{22}\mu S_2 + (d_1 - e_1)d_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}\mu^2 S_2(d_2 - e_2)d_2 \right)^2 \\ &\quad - \left(\beta_{12}\mu S_2 + \frac{\beta_{21}S_1}{\mu} \right)^2 (\beta_{11}\beta_{22} - \beta_{12}\beta_{21})\mu S_2 S_1 (d_1 - e_1)(d_2 - e_2) \end{aligned}$$

for

$$S_1 = \frac{\beta_{22}d_1 - \beta_{12}\mu d_2}{\beta_{11}\beta_{22} - \beta_{12}\beta_{21}}, \quad S_2 = \frac{\beta_{11}\mu d_2 - \beta_{21}d_1}{\mu(\beta_{11}\beta_{22} - \beta_{12}\beta_{21})}.$$

4 Numerical results

The rigorous analysis presented in the Appendix and previous section now classify the dynamical behaviour of (3) subject to condition (10). In order to simplify the proof of the existence of periodical trajectories, we impose the assumption $e_1 = \mu e_2$ in the assertion (ii) of Theorem 3.1. In fact, this assumption may not be necessary. For example, we illustrate the behavioural characteristics of E_3 by taking the data set

$$\begin{aligned} \lambda > 0, \quad \mu = 11.1609, \quad d_1 = 6.205, \quad e_1 = 1.933, \quad d_2 = 4.73, \quad e_2 = 0.151, \\ \beta_{11} = \beta_{22} = 1, \quad \beta_{12} = 0.11, \quad \beta_{21} = 8.156 \end{aligned} \quad (16)$$

with the varying parameter $\lambda < \infty$. We see that $e_1 > \mu e_2$ and

$$\begin{aligned} \beta_{11}\beta_{22} - \beta_{21}\beta_{12} &= 0.10384 > 0, \\ 10.6994 &= \frac{\beta_{21}d_1}{\beta_{11}d_2} < \mu = 11.1609 < \frac{\beta_{22}d_1}{\beta_{12}d_2} = 11.9258, \end{aligned} \quad (17)$$

which shows the validity of (10).

To examine the stability of E_3 under the data set (17), we consider the Jacobian matrix $J(E_3)$ and the characteristic polynomial

$$\det(J(E_3) - \rho) = \rho^4 + c_1\rho^3 + c_2\rho^2 + c_3\rho + c_4 \quad (18)$$

defined in (A.8, A.10, A.11). It is obvious that E_3 is stable if and only if the real parts of the four roots of this polynomial are negative. From (A.10) we see that all the coefficients c_i are positive under the condition (10). Thus, it follows from the Routh–Hurwitz criterion (see, for example, [7, 9]) that E_3 is stable or the real parts of the four roots are positive if and only if

$$c_1 c_2 c_3 - c_3^2 - c_1^2 c_4 > 0.$$

Since the coefficients c_i of the polynomial (A.10) or (A.11) are functions of λ , it is readily verified that $\lambda_c = 0.01736$ is a critical value in the following sense:

$$c_1 c_2 c_3 - c_3^2 - c_1^2 c_4 \begin{cases} < 0 & \text{for } 0 < \lambda < 0.01736, \\ = 0 & \text{for } \lambda = 0.01736, \\ > 0 & \text{for } \lambda > 0.01736. \end{cases}$$

That is, under the criterion of Routh and Hurwitz,

$$\begin{cases} E_3 \text{ is unstable} & \text{for } 0 < \lambda < 0.01736, \\ E_3 \text{ is neutral} & \text{for } \lambda = 0.01736, \\ E_3 \text{ is stable} & \text{for } \lambda > 0.01736. \end{cases}$$

Under the choice of (16), it was shown by numerical experiments adopting the classical fourth order Runge–Kutta method (see, for example, [5]) that when λ decreases through λ_c , a limit cycle arises and exists for $0 < \lambda < \lambda_c$, and finally disappears at $\lambda = 0$. This implies that when λ decreases across λ_c , the two host species coexist persistently becoming coexisting periodically under the transmission of the pathogen.

For demonstration purposes, we now display numerical results for selected values $\lambda = 0.012$, and $\lambda = 0.0012$ in the interval $(0, \lambda_c)$ together with (16).

Let us begin with the value $\lambda = 0.012$ or

$$r_1 = \lambda(d_1 - e_1) = 0.0513, \quad r_2 = \lambda\mu(d_2 - e_2) = 0.6133.$$

The Newton method shows the non-real eigenvalues

$$\rho = 0.00028 \pm 1.21637i \quad \text{for } \lambda = 0.012$$

of $J(E_3)$. This indicates a weakness of the instability of the equilibrium E_3 . Applying the fourth order Runge–Kutta method with the initial value $Y_0 = E_3 + (0, 0, 0, 1.5)$, an iteration step length $h = 0.005$ and ending at the maximum time $T = 1, 500$, we obtain a numerical trajectory (Fig. 2a) slowly attracted by a limit cycle as displayed respectively in the (S_1, I_1) plane (Fig. 2b) and the (S_2, I_2) plane (Fig. 2e).

Moreover, by choosing the value $\lambda = 0.0012$ or

$$r_1 = \lambda(d_1 - e_1) = 0.0051, \quad r_2 = \lambda\mu(d_2 - e_2) = 0.0613,$$

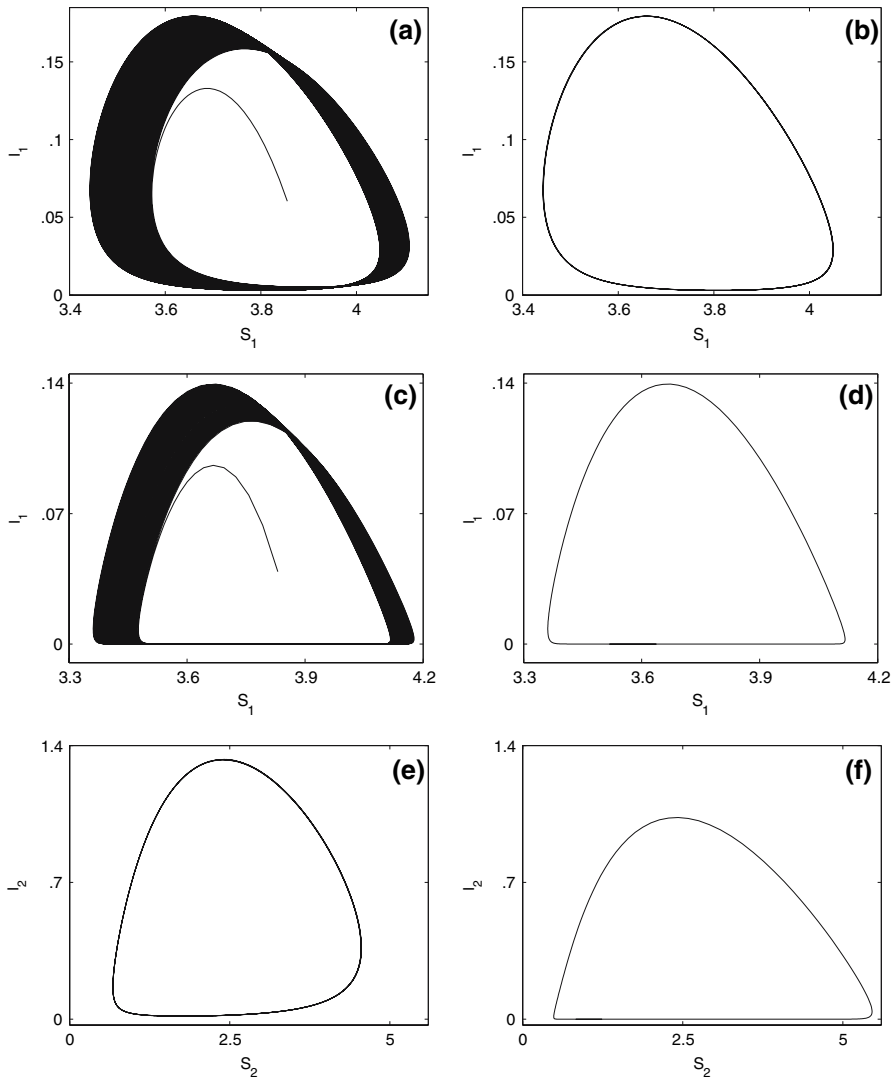


Fig. 2 The complete trajectories **a** for $\lambda = 0.012$ and **c** for $\lambda = 0.0012$ of the system (3, 16) stemming from the initial data $E_3 + (0, 0, 0, 1.5)$. The trajectory (a) converges to the limit cycle (b, e) projected on (S_1, I_1) and (S_2, I_2) planes. The trajectory (c) converges to the limit cycle (d, f) projected on (S_1, I_1) and (S_2, I_2) planes

the Newton method shows the non-real eigenvalues

$$\rho = 0.00009 \pm 0.38542i \quad \text{for } \lambda = 0.0012$$

of $J(E_3)$. This also indicates a weakness of the instability of the equilibrium E_3 . Applying the Runge–Kutta method with initial value $Y_0 = E_3 + (0, 0, 0, 1.5)$, an iteration step length $h = 0.005$ and ending at the maximum time $T = 6,000$, we obtain

a numerical trajectory (Fig. 2c) slowly attracted by a limit cycle as displayed respectively in the (S_1, I_1) plane (Fig. 2d) and the (S_2, I_2) plane (Fig. 2f). From Fig. 2c, d, f we see that either a small value of λ or small values of intrinsic growth rates r_1 and r_2 gives rise to a limit cycle such that the two host species coexist periodically.

If $\lambda = 0$, the limit cycle disappears and there arises an equilibrium plane $\{(S_1, 0, S_2, 0); S_1 \geq 0, S_2 \geq 0\}$. This plane contains the uninfected equilibria E_1, E_2 and E_3 for $\lambda = 0$, and any equilibrium in this plane is neither stable nor unstable (see Appendix).

5 Concluding remarks

Based on numerical experiments, it was conjectured by Holt and Pickering [14] that *the infected coexistence equilibrium E_3 is unstable whenever both infected one-host equilibria E_1 and E_2 are stable, and E_3 is stable whenever both E_1 and E_2 are unstable*. It was derived by Greenman and Hudson [10] that the stability of E_1 and E_2 leads to instability of E_3 . However, Greenman and Hudson [10] argued the coexistence of three equilibria involving limit cycles and the instability of E_1 and E_2 does not necessarily lead to the stability of E_3 .

To understand the population dynamics of the Holt–Pickering model describing the coexistence of two-host species with a shared pathogen, it is beneficial to specify the two scaled control parameters

$$r_1 = \lambda(d_1 - e_1) \quad \text{and} \quad r_2 = \lambda\mu(d_2 - e_2) \quad (19)$$

from amongst the large set of parameters appearing in system (1). These describe intrinsic growth rate r_i , the rate d_i of depletion of the infected fraction of population and the rate e_i of entry of new susceptibles stemming from the infected portion of population for host species i ($i = 1, 2$). The parameter μ controls the stability of the one-host equilibria E_1 and E_2 or determines whether the shared pathogen leads to extinction of one host species whilst the other exists persistently. Moreover, whether the infected coexistence two-host equilibrium E_3 is biologically relevant is also controlled by μ , whereas, parameter λ controls the stability of E_3 .

The purpose of this study is to understand more clearly the situation in which both the one-host equilibria E_1 and E_2 are unstable, and therefore, the coexistence behaviour of the two host species characterized by the coexistence infected equilibrium E_3 under the influence of the shared pathogen.

When the single host equilibria E_1 and E_2 are unstable or

$$\frac{\beta_{21}d_1}{\beta_{11}d_2} < \mu < \frac{\beta_{22}d_1}{\beta_{12}d_2},$$

it is proved through rigorous analysis that the coexistence equilibrium E_3 is stable if λ is sufficiently large. That is, the transmission of the single pathogen leads to the persistent coexistence of the two host infected species if the intrinsic rates r_1 and r_2 are sufficiently large. This also implies that the conjecture of Holt and Pickering [14]

is correct, if the intrinsic rates r_1 and r_2 are sufficiently large. Moreover, in relation to the paradox of enrichment by increases in prey productivity destabilising predator-prey dynamics [19], this result shows a kind of inverse paradox of enrichment in the multispecies host-pathogen system, so that the increases in the two host species productivity lead to the persistence of the coexistence of the two host species and the pathogen in the community.

However, the dynamic behaviour around E_3 is not completely clear when E_1 and E_2 are unstable. Fortunately, this situation is rectified if we add the condition $e_1 = \mu e_2$ by using the scaled parameters defined in (19). More precisely, when the single host equilibria E_1 and E_2 are unstable, it is proved through rigorous analysis that a critical value $\lambda_c \geq 0$ exists uniquely, such that

$$\begin{aligned} E_3 & \text{ is stable when } \lambda > \lambda_c, \\ E_3 & \text{ is neutral when } \lambda = \lambda_c, \\ E_3 & \text{ is unstable when } 0 < \lambda < \lambda_c \text{ if } \lambda_c > 0 \end{aligned}$$

provided that $e_1 = \mu e_2$. Periodic trajectories branching off this neutral equilibrium E_3 at the critical value λ_c occur whenever $\lambda_c > 0$.

Although it is difficult to elucidate in detail the stability of a periodic trajectory rigorously, we conclude that the presented bifurcating periodic trajectories are limit cycles and appear at values $0 < \lambda < \lambda_c$. That is, under the assumption $e_1 = \mu e_2$, the host infected species coexist persistently for $\lambda > \lambda_c$ and become coexisting periodically for λ decreasing across $\lambda_c > 0$, under the free transmission of the shared single pathogen.

It should be noted that the condition $e_1 = \mu e_2$ is not necessary for the occurrence of the instability of E_3 and limit cycles. An example given by numerical computation shows the existence of a critical value λ_c for a data set with $e_1 \neq \mu e_2$ and E_3 bifurcating into a limit cycle when λ decreases across λ_c . This limit cycle exists for $0 < \lambda < \lambda_c$ and disappears as $\lambda \rightarrow 0$ since, when $\lambda = 0$, system (3) admits a neutral equilibria plane $\{(S_1, 0, S_2, 0); \text{ for any } S_1, S_2\}$.

This numerical result also indicates that instability of the coexistence equilibrium E_3 and stability of the limit cycle are very weak. This limit cycle exists mathematically, but it may be difficult to observe this nontrivial dynamics physically because of the weakness character, although Briggs et al. [4], in their empirical study, concluded that the appearance of the pathogen did not necessarily lead to a limit cycle fluctuation.

Appendix A: Jacobian matrices and characteristic polynomials of the equilibria

To simplify the analysis in Sects. 2, 3 and 4, in this appendix, we display Jacobian matrices and characteristic polynomials of the equilibria E_1 , E_2 and E_3 under the scaled parameters λ and μ . As a by-product, we display the stability analysis results of these equilibria derived by Holt and Pickering [14] and Greenman and Hudson [10]. Moreover, the analysis on the equilibria $(S_1, 0, S_2, 0)$ of (3) for $\lambda = 0$ is discussed.

Let $E = (S_1, I_1, S_2, I_2)$ be an equilibrium of (3), i.e., $dS_i/dt = 0$ and $dI_i/dt = 0$ for $i = 1, 2$. The linearization of (3) around the equilibrium E allows the Jacobian matrix of the system of equations at E to be expressed as

$$J(E) = \begin{pmatrix} \lambda(d_1 - e_1) - \beta_{11}I_1 - \beta_{12}I_2 & e_1 - \beta_{11}S_1 & 0 & -\beta_{12}S_1 \\ \beta_{11}I_1 + \beta_{12}I_2 & \beta_{11}S_1 - d_1 & 0 & \beta_{12}S_1 \\ 0 & -\beta_{21}S_2 & \lambda\mu(d_2 - e_2) - \beta_{22}I_2 - \beta_{21}I_1 & e_2 - \beta_{22}S_2 \\ 0 & \beta_{21}S_2 & \beta_{22}I_2 + \beta_{21}I_1 & \beta_{22}S_2 - d_2 \end{pmatrix}. \quad (\text{A.1})$$

Thus, for the single host equilibria E_1 and E_2 described in (4, 5), we have the characteristic polynomials

$$\begin{aligned} \det(J(E_1) - \rho) &= [\rho^2 + \lambda e_1 \rho + \lambda d_1(d_1 - e_1)] \\ &\times \left[\rho^2 - \left(\lambda\mu(d_2 - e_2) - \frac{\lambda\beta_{21}d_1}{\beta_{11}} - d_2 \right) \rho - \lambda(d_2 - e_2) \left(\mu d_2 - \frac{\beta_{21}d_1}{\beta_{11}} \right) \right], \end{aligned} \quad (\text{A.2})$$

$$\begin{aligned} \det(J(E_2) - \rho) &= [\rho^2 + \lambda\mu e_2 \rho + \lambda\mu d_2(d_2 - e_2)] \\ &\times \left[\rho^2 - \left(\lambda(d_1 - e_1) - \frac{\lambda\mu\beta_{12}d_2}{\beta_{22}} - d_1 \right) \rho - \lambda(d_1 - e_1) \left(d_1 - \frac{\mu\beta_{12}d_2}{\beta_{22}} \right) \right]. \end{aligned} \quad (\text{A.3})$$

For an uninfected equilibrium $(S_1, 0, S_2, 0)$ with $\lambda = 0$, we have

$$\det(J((S_1, 0, S_2, 0)) - \rho) = \rho^2(-d_1 + \beta_{11}S_1 - \rho)(-d_2 + \beta_{22}S_2 - \rho). \quad (\text{A.4})$$

The uninfected equilibria plane is neutral since each of them has at least two zero eigenvalues.

Finally, we consider the coexistence equilibrium E_3 defined in (6). The addition of the first equation of (3) to the second one, and that of the third to the fourth give

$$\begin{aligned} I_1 &= \lambda S_1, \quad (-\lambda d_1 + \beta_{11}I_1 + \beta_{12}I_2) S_1 = 0, \\ I_2 &= \lambda\mu S_2, \quad (-\lambda\mu d_2 + \beta_{21}I_1 + \beta_{22}I_2) S_2 = 0 \end{aligned}$$

with respect to the equilibrium $E_3 = (S_1, I_1, S_2, I_2)$. Since $S_1 > 0$ and $S_2 > 0$, we have

$$d_1\lambda = \beta_{11}I_1 + \beta_{12}I_2, \quad d_2\lambda\mu = \beta_{21}I_1 + \beta_{22}I_2, \quad (\text{A.5})$$

$$d_1 = \frac{1}{\lambda}(\beta_{11}I_1 + \beta_{12}I_2) = \beta_{11}S_1 + \beta_{12}\mu S_2, \quad (\text{A.6})$$

$$d_2 = \frac{1}{\lambda\mu}(\beta_{21}I_1 + \beta_{22}I_2) = \beta_{21}\frac{S_1}{\mu} + \beta_{22}S_2. \quad (\text{A.7})$$

Applying (A.5)–(A.7) in (A.1), we obtain the Jacobian matrix of E_3 in the following form:

$$J(E_3) = \begin{pmatrix} -\lambda e_1 & e_1 - \beta_{11}S_1 & 0 & -\beta_{12}S_1 \\ \lambda d_1 & -\beta_{12}\mu S_2 & 0 & \beta_{12}S_1 \\ 0 & -\beta_{21}S_2 & -\lambda\mu e_2 & e_2 - \beta_{22}S_2 \\ 0 & \beta_{21}S_2 & \lambda\mu d_2 & -\frac{\beta_{21}S_1}{\mu} \end{pmatrix}. \quad (\text{A.8})$$

Therefore, by (A.6), (A.7), we have the characteristic polynomial of E_3 expressed as

$$\begin{aligned} \det(J(E_3) - \rho) &= [(\lambda e_1 + \rho)(\beta_{12}\mu S_2 + \rho) - \lambda d_1(e_1 - \beta_{11}S_1)] \\ &\quad \times \left[(\lambda\mu e_2 + \rho) \left(\frac{\beta_{21}S_1}{\mu} + \rho \right) - (e_2 - \beta_{22}S_2)\lambda\mu d_2 \right] \\ &\quad + [\lambda d_1\beta_{12}S_1 - (\lambda e_1 + \rho)\beta_{12}S_1][-\beta_{21}S_2\lambda\mu d_2 + (\lambda\mu e_2 + \rho)\beta_{21}S_2] \\ &= [\rho^2 + (\lambda e_1 + \beta_{12}\mu S_2)\rho + \lambda e_1\beta_{12}\mu S_2 - \lambda d_1e_1 + \lambda d_1\beta_{11}S_1] \\ &\quad \times \left[\rho^2 + \left(\frac{\beta_{21}S_1}{\mu} + \lambda\mu e_2 \right) \rho + \lambda e_2\beta_{21}S_1 - (e_2 - \beta_{22}S_2)\lambda\mu d_2 \right] \\ &\quad + \beta_{12}\beta_{21}S_2S_1 [-\rho^2 + (\lambda(d_1 - e_1) + \lambda\mu(d_2 - e_2))\rho - \lambda^2\mu(d_1 - e_1)(d_2 - e_2)] \\ &= [\rho^2 + (\lambda e_1 + \beta_{12}\mu S_2)\rho + \lambda(d_1 - e_1)\beta_{11}S_1] \\ &\quad \times \left[\rho^2 + \left(\frac{\beta_{21}S_1}{\mu} + \lambda\mu e_2 \right) \rho + \lambda\mu(d_2 - e_2)\beta_{22}S_2 \right] \\ &\quad + \beta_{12}\beta_{21}S_2S_1 [-\rho^2 + (\lambda(d_1 - e_1) + \lambda\mu(d_2 - e_2))\rho - \lambda^2\mu(d_1 - e_1)(d_2 - e_2)] \\ &= \rho^4 + (\lambda e_1 + \beta_{12}\mu S_2 + \frac{\beta_{21}S_1}{\mu} + \lambda\mu e_2)\rho^3 \\ &\quad + \left[\lambda(d_1 - e_1)\beta_{11}S_1 + (\lambda e_1 + \beta_{12}\mu S_2) \left(\frac{\beta_{21}S_1}{\mu} + \lambda\mu e_2 \right) \right. \\ &\quad \left. + \lambda\mu(d_2 - e_2)\beta_{22}S_2 - \beta_{12}\beta_{21}S_2S_1 \right] \rho^2 \\ &\quad + \left[\lambda(d_1 - e_1)\beta_{11}S_1 \left(\frac{\beta_{21}S_1}{\mu} + \lambda\mu e_2 \right) + (\lambda e_1 + \beta_{12}\mu S_2)\lambda\mu(d_2 - e_2)\beta_{22}S_2 \right] \rho \\ &\quad + \beta_{12}\beta_{21}S_2S_1((\lambda(d_1 - e_1) + \lambda\mu(d_2 - e_2)))\rho \\ &\quad + (\beta_{11}\beta_{22} - \beta_{12}\beta_{21})S_2S_1\lambda^2\mu(d_1 - e_1)(d_2 - e_2), \end{aligned}$$

which together with expressions

$$S_1 = \beta_{22}d_1 - \beta_{12}d_2\mu \quad \text{and} \quad S_2 = \frac{\beta_{11}d_2\mu - \beta_{21}d_1}{\mu}$$

of the equilibrium $E_3 = (S_1, I_1, S_2, I_2)$ described in (6) implies that

$$\begin{aligned}
 & \det(J(E_3) - \rho) \\
 &= \rho^4 + \left[(e_1 + \mu e_2)\lambda + \beta_{12}\mu S_2 + \frac{\beta_{21}S_1}{\mu} \right] \rho^3 \\
 &+ \lambda \left[\lambda e_1 \mu e_2 + (d_1 - e_1)\beta_{11}S_1 + e_1 \frac{\beta_{21}S_1}{\mu} + \beta_{12}\mu^2 S_2 e_2 + (d_2 - e_2)\beta_{22}\mu S_2 \right] \rho^2 \\
 &+ \lambda \left[\lambda [(d_1 - e_1)\beta_{11}S_1 \mu e_2 + e_1(d_2 - e_2)\beta_{22}\mu S_2] + (d_1 - e_1)d_1 \frac{\beta_{21}S_1}{\mu} \right. \\
 &\quad \left. + \beta_{12}\mu^2 S_2(d_2 - e_2)d_2 \right] \rho + \lambda^2 (\beta_{11}\beta_{22} - \beta_{12}\beta_{21})\mu S_2 S_1 (d_1 - e_1)(d_2 - e_2) \quad (\text{A.9}) \\
 &= \rho^4 + \left(\lambda(e_1 + \mu e_2) + \frac{\beta_{12}(\beta_{11}\mu d_2 - \beta_{21}d_1) + \beta_{21}(\beta_{22}d_1 - \beta_{12}\mu d_2)/\mu}{\beta_{11}\beta_{22} - \beta_{21}\beta_{12}} \right) \rho^3 + \lambda^2 \mu e_1 e_2 \rho^2 \\
 &+ \lambda \frac{\left[(d_1 - e_1)\beta_{11} + \frac{e_1 \beta_{21}}{\mu} \right] (\beta_{22}d_1 - \beta_{12}\mu d_2) + [\beta_{12}\mu e_2 + (d_2 - e_2)\beta_{22}] (\beta_{11}\mu d_2 - \beta_{21}d_1)}{\beta_{11}\beta_{22} - \beta_{21}\beta_{12}} \rho^2 \\
 &+ \lambda^2 \frac{\mu \beta_{11} e_2 (d_1 - e_1) (\beta_{22}d_1 - \beta_{12}\mu d_2) + e_1 \beta_{22} (d_2 - e_2) (\beta_{11}\mu d_2 - \beta_{21}d_1)}{\beta_{11}\beta_{22} - \beta_{21}\beta_{12}} \rho \\
 &+ \lambda \frac{\frac{d_1 \beta_{21}}{\mu} (d_1 - e_1) (\beta_{22}d_1 - \beta_{12}\mu d_2) + \beta_{12} \mu d_2 (d_2 - e_2) (\beta_{11}\mu d_2 - \beta_{21}d_1)}{\beta_{11}\beta_{22} - \beta_{21}\beta_{12}} \rho \\
 &+ \lambda^2 \frac{(\beta_{22}d_1 - \beta_{12}\mu d_2) (\beta_{11}\mu d_2 - \beta_{21}d_1) (d_1 - e_1) (d_2 - e_2)}{\beta_{11}\beta_{22} - \beta_{21}\beta_{12}}, \quad (\text{A.10})
 \end{aligned}$$

or

$$\det(J(E_3) - \rho) = \rho^4 + c_1 \rho^3 + c_2 \rho^2 + c_3 \rho + c_4, \quad (\text{A.11})$$

where expressions for the coefficients c_i are given in the characteristic polynomial of E_3 .

As an immediate consequence of the expressions defining the characteristic polynomials, the following assertions are true.

- Corollary A.1** (i) *The single host equilibrium E_1 is stable if and only if $\mu < \frac{\beta_{21}d_1}{\beta_{11}d_2}$.*
 (ii) *The single host equilibrium E_2 is stable if and only if $\mu > \frac{\beta_{22}d_1}{\beta_{12}d_2}$.*
 (iii) *Any uninfected equilibrium $(S_1, 0, S_2, 0)$ of (3) with $\lambda = 0$ is neutral.*
 (iv) *The coexistence equilibrium E_3 is unstable if $\frac{\beta_{22}d_1}{\beta_{12}d_2} < \mu < \frac{\beta_{21}d_1}{\beta_{11}d_2}$ or (9) is valid.*
 (v) *The equilibrium E_3 is neutral if either $\mu = \frac{\beta_{22}d_1}{\beta_{12}d_2}$ or $\mu = \frac{\beta_{21}d_1}{\beta_{11}d_2}$.*

We note that Assertion (i) is valid if and only if the real parts of the four roots of the characteristic polynomial $\det(J(E_1) - \rho) = 0$ are negative. Indeed, it follows from (A.2) that the four roots of this polynomial can be expressed as

$$\frac{-\lambda e_1 \pm \sqrt{\lambda^2 e_1^2 - 4\lambda d_1(d_1 - e_1)}}{2},$$

$$\frac{\lambda\mu(d_2 - e_2) - \frac{\lambda\beta_{21}d_1}{\beta_{11}} - d_2 \pm \sqrt{(\lambda\mu(d_2 - e_2) - \frac{\lambda\beta_{21}d_1}{\beta_{11}} - d_2)^2 + 4(d_2 - e_2)\lambda(\mu d_2 - \frac{\beta_{21}d_1}{\beta_{11}})}}{2}.$$

It is obvious that the first two roots have negative real parts for any value of μ and the last two roots have negative real parts if and only if

$$\mu < \frac{\beta_{21}d_1}{\beta_{11}d_2},$$

since this implies that

$$4(d_2 - e_2)\lambda \left(\mu d_2 - \frac{\beta_{21}d_1}{\beta_{11}} \right) < 0,$$

$$\lambda\mu(d_2 - e_2) - \frac{\lambda\beta_{21}d_1}{\beta_{11}} - d_2 < \lambda\mu(d_2 - e_2) - \lambda\mu d_2 - d_2 = -\lambda e_2 - d_2 < 0.$$

The validity of Assertion (ii) is verified in the same way due to the expression of the characteristic polynomial in (A.3).

The validity of Assertion (iii) is obvious since the corresponding characteristic polynomial (A.4) has the root zero.

For the validity of Assertion (iv), we see that the assumption of (iv) implies $S_1 > 0$, $S_2 > 0$ and $\beta_{11}\beta_{22} - \beta_{12}\beta_{21} < 0$ with S_1 and S_2 describing the uninfected population densities of the coexistence equilibrium E_3 . This gives that $\det(J(E_3)) = c_4 < 0$ due to (A.10, A.11). That is, the four roots ρ_1, ρ_2, ρ_3 and ρ_4 of polynomial $\det(J(E_3) - \rho) = 0$ satisfy

$$\rho_1\rho_2\rho_3\rho_4 = \det(J(E_3)) < 0.$$

This implies that there exists at least one root, which is positive, or E_3 is unstable.

Finally, when either $\mu = \frac{\beta_{22}d_1}{\beta_{12}d_2}$ or $\mu = \frac{\beta_{21}d_1}{\beta_{11}d_2}$, we see from (A.10, A.11) that $\det(J(E_3)) = c_4 = 0$. That is, there exists at least one zero eigenvalue of the Jacobian $J(E_3)$, or E_3 is neutral.

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