Nonlinear Analysis: Modelling and Control, Vol. 28, No. 2, 326–364
https://doi.org/10.15388/namc.2023.28.31549

An ecoepidemic model with healthy prey herding and infected prey drifting away

Md. Sabiar Rahman[a,1], **Subhash Pramanik**[a], **Ezio Venturino**[b,c]

[a]Department of Mathematics, Gobardanga Hindu College,
North 24 Parganas, 731235 West Bengal, India
sabiarrahman@gmail.com; subhashpramanik607@gmail.com

[b]Dipartimento di Matematica "Giuseppe Peano",
Università di Torino,
via Carlo Alberto 10, 10123 Torino, Italy
ezio.venturino@unito.it

[c]INdAM research group GNCS

Received: January 8, 2022 / **Revised:** February 1, 2023 / **Published online:** February 22, 2023

Abstract. We introduce here a predator–prey model where the prey are affected by a disease. The prey are assumed to gather in herds, while the predators are loose and act on an individualistic basis. Therefore their hunting affects mainly the prey individuals occupying the outermost positions in the herd, which is modeled via a square root functional response. The conditions of boundedness and uniform persistence are established. Stability and bifurcation analysis of all feasible equilibrium are carried out. Conditions on the model parameters for the possible existence of limit cycles are derived, global stability analysis is also shown in proper choice of suitable Lyapunov function. Numerical simulation of the various bifurcations validate the theoretical results. It is found that the system ultimate behavior depends mainly on two crucial parameters, the force of infection and predator average handling time. A discussion of the biological significance of the investigation concludes the paper.

Keywords: ecoepidemic model, herd behavior, disease in prey, bifurcations, limit cycle, uniform persistence, global stability.

1 Introduction

In recent times, herd behavior was introduced in interacting population systems of various nature, of symbiotic, competing and predator–prey type, by [2], via a square root functional response, which models the predator–prey interaction occurring mainly on the perimeter of the prey herd. The main result appears to be the possible onset of persistent

[1]Corresponding author.

oscillations, which are not originated by the Holling type II functional response. Thus a different mechanism, other than feeding saturation, entails as consequence the insurgence of limit cycles. It should be noted that in fact, the idea of a nonlinear response involving a power law for the prey dates back a few decades, appearing indeed already in the original work of Gause [8]. Anyway, after the appearance of [2], other researchers undertook similar investigations based on the same idea. In particular, [4] considers a simple predator–prey model with interactions on the boundary, but in which also feeding saturation through a Holling type II functional response appears. Note also that the shape of the herd does not remain circular at all times so that, in general, the square root term becomes inadequate. But [5] shows that the modification to account for this change via a generic exponent in place of the square root do not lead to substantial modifications in the results. Further, a minimal model combining ecoepidemics and group behavior is introduced in [22], while an ecoepidemic model with prey herd behavior and an infection in the predators appears in [3]. Ecoepidemic models with Holling type I and II responses but without the group effect are, for instance, found in [12, 19]. In [24], they introduce a pathogenic agent, which influences the force of infection. Also, a predator-only equilibrium exists, which not appear in our system. Biologically, this occurs due to the absence of other food sources except for prey.

In [23] the alternative cases of infection remaining harmless for predators, infected individuals being not predated and the infected prey being toxic for predators were considered. It is assumed that susceptible prey behave individually, while infected gather together. Occasional contacts among the solitary susceptibles S and the herd of infected lead to new contagions via interactions with the infected individuals I occupying the outermost positions in the group, this being modeled by the term $S\sqrt{I}$.

Our basic assumption here is to revisit the assumptions of [23], exchanging the roles of the two prey subpopulations. Thus susceptible prey group together, while infected abandon the herd and behave individually. Still, the susceptibles can be infected via interactions that occur on the herd boundary, modeled in this case via the term $I\sqrt{S}$.

The paper is organized as follows. In the next section, we formulate the model and then discuss the boundedness and the persistence of the species. Next, we analyze the different kinds of feasible equilibria and carry out their stability analysis as well as investigating the Hopf and other bifurcations. Using Bendixson's criterion, we show the conditions for nonexistence of limit cycles at E_*. Applying instead the center manifold theorem, we also investigate the onset and nature of the bifurcating limit cycles. By using the results on uniform persistence, the conditions for global stability are obtained, constructing the suitable Lyapunov function. The fourth section contains the numerical validation of the results as well as the bifurcation diagrams. A final comparison with the earlier model of [23] concludes the paper.

2 Mathematical model formulation

We consider the situation in which prey are affected by an unrecoverable disease so that their population X is partioned among susceptibles s and infected i, $X = s + i$. Infected are assumed to be too weak to reproduce and compete with susceptibles for resources. They also drift away from the herd of susceptible prey and therefore are hunted on a one-to-one basis by predators. Also, the disease is assumed not to spread to the latter. The predators furthermore hunt the susceptible prey herd by mainly capturing the individuals occupying the perimeter of the herd and are subject to feeding satiation. Thus hunting on susceptible prey obeys a law that is the combination of Holling type II and the square root functions:

$$F(s) = \frac{\alpha\sqrt{s}}{1 + T_h\alpha\sqrt{s}}, \tag{1}$$

where T_h represents the predator's prey handling time, and α is the predator's search efficiency. Finally, infected prey with occasional contacts with the susceptible's herd could transmit the disease. Again, we assume that this process occurs mainly on the boundary of the herd.

With these assumptions, the model reads:

$$\begin{aligned}
\frac{\mathrm{d}s}{\mathrm{d}t} &= rs\left(1 - \frac{s}{K}\right) - \frac{\alpha\sqrt{s}p}{1 + h\alpha\sqrt{s}} - \lambda i\sqrt{s},\\
\frac{\mathrm{d}i}{\mathrm{d}t} &= \lambda i\sqrt{s} - mip - \mu i,\\
\frac{\mathrm{d}p}{\mathrm{d}t} &= \frac{\theta_1\alpha\sqrt{s}p}{1 + h\alpha\sqrt{s}} + \theta_2 mip - \delta p.
\end{aligned}$$

The first equation models the susceptible prey dynamics: they reproduce logistically with reproduction rate r and carrying capacity K, are hunted on the perimeter of the herd by predators with the functional response (1) and become infected with transmission rate λ, again by contacts on the herd boundary.

The second equation describes the infected prey recruited by "successful" contacts with susceptibles, hunted at rate m by predators and subject to natural plus disease-related mortality μ.

Finally, the third equation contains the predators evolution. They are specialist on the modeled prey, hunt the susceptible ones by predating on the herd perimeter with conversion rate θ_1, while capture the infected ones on an individual basis and with possibly a different conversion rate θ_2 due to the fact that the latter might be less palatable or contain different, most likely less, nutrient than the susceptible ones. Their mortality rate is δ.

Note that this model differs from other similar ones already published. In particular, with respect to [16], here infected prey are also abandoned, but we assume that they occasionally can still interact with the susceptible ones on the boundary of the herd, while in [16], such contagion process is assumed to occur inside the herd, before the infected abandon the it. A different mechanism is instead modeled in [6], where infected stay in the herd and are subject to hunting as the susceptibles are, this predation occurring once more on the perimeter of the herd.

Letting $\sqrt{s} = S$, then the above system reduces to

$$\begin{aligned}\frac{\mathrm{d}S}{\mathrm{d}t} &= \frac{1}{2}\left[rS\left(1-\frac{S^2}{K}\right) - \frac{\alpha P}{1+h\alpha S} - \lambda I\right] = F_1,\\ \frac{\mathrm{d}I}{\mathrm{d}t} &= \lambda IS - mIP - \mu I = F_2,\\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \frac{\theta_1 \alpha SP}{1+h\alpha S} + \theta_2 mIP - \delta P = F_3,\end{aligned} \tag{2}$$

which is now the subject of our investigation.

3 Mathematical analysis

3.1 Persistence

A system is persistent if a compact set $\Psi \subset G = \{(S, I, P)\colon\ S > 0,\ I > 0,\ P > 0\}$ exists so that all the solution of system (2) eventually enter and remain in it.

Theorem 1. *System* (2) *is persistent if the following conditions hold*:

(i) $\alpha > \mu + \delta$,

(ii) $\alpha + h\alpha^2\sqrt{K} < \mu + \delta - \lambda\sqrt{K}$,

(iii) $\mu\,\theta_2 m\big(K\lambda^3 + \mu\, h\alpha\, K\lambda^2 - \mu^2\lambda - \mu^3 h\alpha\big)r > K\lambda^4(-\alpha\,\lambda + \delta\,\lambda + \delta\, h\alpha\,\mu)$,

(iv) $$\begin{aligned}&\theta_1\big(\delta^5\theta_1 h^4 + 6\,\delta^3\theta_1^3 h^2 - 4\,\delta^4\theta_1^2 h^3 + 10\,\alpha\,\theta_1^2 h^3\delta^3 - 5\,\alpha\,\theta_1 h^4\delta^4\\ &\qquad + 5\,\alpha\,\theta_1^4 h\delta - 10\,\alpha\,\theta_1^3 h^2\delta^2 + \delta\,\theta_1^5 - \alpha\,{\theta_1}^5 - 4\,\delta^2\theta_1^4 h + \alpha\, h^5\delta^5\big)\\ &\quad < \alpha^4 K\big(\lambda\,\delta\,\alpha^3 K\theta_1^3 - 6\,\mu\,\alpha^4 K\theta_1^2 h^2\delta^2\\ &\qquad + 4\,\mu\,\alpha^4 K\theta_1 h^3\delta^3 - \mu\,\alpha^4 K h^4\delta^4 + mr\delta^3\theta_1 - \mu\,\alpha^4 K\theta_1^4\\ &\qquad + 3\,\lambda\,\delta^3\alpha^3 K\theta_1 h^2 - \lambda\,\delta^4\alpha^3 K h^3 - mr\delta\,\theta_1^3 K\alpha^2 - 3\,\lambda\,\delta^2\alpha^3 K\theta_1^2 h\\ &\qquad + 2\, mr\delta^2\theta_1^2 K\alpha^2 h - mr\delta^3\theta_1 K\alpha^2 h^2 + 4\,\mu\,\alpha^4 K\theta_1^3 h\delta\big).\end{aligned}$$

Proof. The proof is given in Appendix C. □

3.2 Boundedness

Proposition 1. *The healthy prey population is uniformly bounded.*

Proof. From system (2) we have

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \frac{1}{2}\left[rS\left(1-\frac{S^2}{K}\right) - \frac{\alpha P}{1+h\alpha S} - \lambda I\right] < \frac{1}{2}\left[rS\left(1-\frac{S^2}{K}\right)\right] < \frac{rS}{2K}\big(K - S^2\big).$$

Therefore

$$\limsup_{t\to\infty} S(t) < \sqrt{K}.$$

Now there exist a $A_1 > 0$ such that for all $t > A_1$, we have $S(t) < K + \epsilon = D$. □

Proposition 2. *The second equation of* (2) *can be bounded from above as follows:*

$$\frac{\mathrm{d}I}{\mathrm{d}t} = \lambda IS - mIP - \mu I < I(\lambda\sqrt{K} - \mu) = I\mu(R_0 - 1), \quad R_0 \equiv \frac{\lambda\sqrt{K}}{\mu}.$$

Therefore when $R_0 > 1$, then epidemic will spread, and if $R_0 \leqslant 1$, then epidemics is eradicated.

Theorem 2. *All the solutions of system* (2)*, which initiate in $\mathbb{R}_3^+$, are uniformly bounded.*

Proof. Let us define the function

$$T = S + I + \frac{1}{\theta_1}P. \tag{3}$$

Differentiating with respect to time (3) and taking $q < \min\{\mu, \delta\}$, we obtain

$$\begin{aligned}\frac{\mathrm{d}T}{\mathrm{d}t} + qT &= \frac{1}{2}\left[rS\left(1 - \frac{S^2}{K}\right) - \frac{\alpha P}{1 + h\alpha S} - \lambda I\right] + \lambda IS - mIP - \mu I \\ &\quad + \frac{1}{\theta_1}\left[\frac{\theta_1\alpha SP}{1 + h\alpha S} + \theta_2 mIP - \delta P\right] + qS + qI + \frac{qP}{\theta_1} \\ &\leqslant \frac{1}{2}\left[rS\left(1 - \frac{S^2}{K}\right)\right] + qS - (\mu - q)I - \frac{P(\delta - q)}{\theta_1} < \sqrt{\frac{K(2q + r)}{3r}} \\ &= \phi.\end{aligned}$$

Applying the theory of differential inequalities [18], we obtain

$$0 < q(S, I, P) < \frac{\phi}{q}\left(1 - \mathrm{e}^{-qt}\right) + q(S_0, I_0, P_0)\mathrm{e}^{-qt},$$

and for $t \to \infty$, we have $0 < \sigma < \phi/q$, where, $\sigma = \{(S, I, P)\colon S > 0, I > 0, P > 0\}$. Hence for any $\epsilon > 0$, all solutions of the system are confined in the region $G = \{(S, I, P) \in \mathbb{R}_+^3\colon T \leqslant \phi/q + \epsilon\}$. □

3.3 Equilibria and their feasibility

The reduced system of equation has following equilibria: the trivial equilibrium $E_0(0, 0, 0)$, the susceptible prey-only point $E_1(\sqrt{K}, 0, 0)$, the predator-free equilibrium $E_2(\mu/\lambda, r\mu(K\lambda^2 - \mu^2)/K\lambda^4, 0)$, the infected prey-free equilibrium $E_3(S_3, 0, P_3)$, the coexistence endemic equilibrium $E_*(S_*, I_*, P_*)$. Here E_2 is feasible when $K\lambda^2 > \mu^2$, that is,

$$R_0 > 1. \tag{4}$$

Further,

$$S_3 = \frac{\delta}{\alpha(\theta_1 - h\delta)}, \qquad P_3 = \frac{r\delta\,\theta_1(K\alpha^2\theta_1^2 - 2\,K\alpha^2\theta_1\delta\,h + K\alpha^2\delta^2h^2 - \delta^2)}{\alpha^4(-\theta_1 + \delta\,h)^4K}.$$

E_3 is feasible if

$$h_0^{[3]} < h < h_1^{[3]} \quad \text{or} \quad \delta_0^{[3]} < \delta < \delta_1^{[3]}, \tag{5}$$

where

$$h_0^{[3]} = \frac{K\theta_1\alpha - \delta\sqrt{K}}{K\delta\alpha}, \quad h_1^{[3]} = \frac{\theta_1}{\delta} \quad \text{and} \quad \delta_0^{[3]} = \frac{K\theta_1\alpha}{hK\alpha + \sqrt{K}}, \quad \delta_1^{[3]} = \frac{\theta_1}{h}.$$

In the coexistence equilibrium,

$$P_* = \frac{\lambda S_* - \mu}{m}, \qquad I_* = \frac{\delta + \alpha S_*(\delta h - \theta_1)}{\theta_2 m(1 + h\alpha S_*)},$$

S_* is the real positive root of the equation

$$\sum_{i=0}^{4} A_i\tau^i = 0, \tag{6}$$

where

$$A_0 = -K(-\lambda\delta + \mu\alpha\theta_2) < 0, \qquad A_1 = (\lambda\alpha - rm)\theta_2 K + \lambda\alpha(\delta h - \theta_1)K,$$
$$A_2 = -rK\theta_2 mh\alpha < 0, \qquad A_3 = r\theta_2 m, \qquad A_4 = r\theta_2 mh\alpha,$$

When

$$\lambda_0^{[*]} < \lambda < \lambda_1^{[*]}, \qquad h > h_1^{[3]}, \tag{7}$$

where

$$\lambda_0^{[*]} = \frac{\mu}{S_*}, \qquad \lambda_1^{[*]} = \theta_2 \min\left\{\frac{\mu\alpha}{\delta}, \frac{rm}{\alpha(\theta_2 - \theta_1\delta h)}\right\}, \qquad h_1^{[3]} = \frac{\theta_1}{\delta},$$

then $A_1 < 0$ and $A_0 < 0$, which satisfy Descartes rule of sign to have a unique positive real root S_* of (6). Moreover, by the above condition (7), I_* and P_* also feasibles. Hence $E_*(S_*, I_*, P_*)$ is feasible when (7) is satisfied.

3.4 Stability analysis

The system Jacobian matrix $J_B \equiv DF$ of system (2) is given by

$$J_B = \begin{pmatrix} \frac{r}{2}(1 - \frac{S^2}{K}) - \frac{rS^2}{K} + \frac{\alpha^2 Ph}{2(1+h\alpha S)^2} & -\frac{\lambda}{2} & -\frac{\alpha}{2(1+h\alpha S)} \\ \lambda I & \lambda S - mp - \mu & -Im \\ \frac{\theta_1\alpha P}{(1+h\alpha S)^2} & \theta_2 mP & \frac{\theta_1\alpha S}{1+h\alpha S} + \theta_2 mI - \delta. \end{pmatrix}$$

3.4.1 The behavior near $E_0(0,0,0)$

The eigenvalues of the Jacobian matrix J_{E_0} are

$$\lambda_1^{[E_0]} = \frac{r}{2}, \qquad \lambda_2^{[E_0]} = -\mu, \qquad \lambda_3^{[E_0]} = -\delta,$$

which shows that E_0 is an unstable hyperbolic critical point, namely, a saddle with the instability in the orthogonal direction to the IP-plane.

3.4.2 The behavior near $E_1(\sqrt{K},0,0)$

3.4.2.1 Stability

At the equilibrium point E_1, the eigenvalues of the Jacobian J_1 are

$$\lambda_1^{[E_1]} = -r, \qquad \lambda_2^{[E_1]} = \lambda\sqrt{K} - \mu, \qquad \lambda_3^{[E_1]} = \frac{\theta_1\alpha\sqrt{K}}{1 + h\alpha\sqrt{K}} - \delta.$$

Thus E_1 will be asymptotically stable if

$$R_0 < 1, \qquad 0 < K < S_3^2. \tag{8}$$

3.4.2.2 Bifurcations

Here and in what follows, to investigate local bifurcations, we use Sotomayor's theorem [10, 13].

The Jacobian $J_1 = (J_1^{ij})$, $i,j = 1,2,3$, the eigenvalue $-r$, while the remaining ones vanish if and only if $\det J_1 = 0$, which gives

$$\lambda = \lambda^{[te_1]} = \frac{\mu}{\sqrt{K}}, \qquad \alpha = \alpha^{[te_1]} = \frac{\delta}{\sqrt{K}(\theta_1 - \delta h)}, \qquad \theta_1 = \theta_1^{[te_1]} = \frac{\delta(\sqrt{K} + Kh\alpha)}{K\alpha},$$

$$K = \{K^{[te_1]}, K^{[te_2]}\}, \qquad K^{[te_1]} = \frac{\mu^2}{\lambda^2}, \qquad K^{[te_2]} = \frac{\delta^2}{\alpha^2(\theta_1 - \delta h)},$$

$$\mu = \mu^{[te_1]} = \lambda\sqrt{K}, \qquad h = h^{[te_1]} = \frac{K\theta_1\alpha - \sqrt{K}\delta}{K\delta\alpha}.$$

(i) Let μ_1 and γ_1 be the eigenvectors corresponding to the eigenvalue 0 of the matrices J_1 and its transpose J_1^{T}, respectively. For $\lambda = \lambda^{[te_1]}$, we obtain $\gamma_1^{\mathrm{T}} = (0, g_1^{[2]}, 0)$ and $\mu_1^{\mathrm{T}} = (m_1^{[1]}, m_1^{[2]}, 0)$, where

$$m_1^{[1]} = -\frac{J_1^{[12]}}{J_1^{[11]}} m_1^{[2]},$$

and $g_1^{[2]}, m_1^{[2]}$ represent arbitrary nonzero real numbers. We find

$$\gamma_1^{\mathrm{T}}\bigl[F_\lambda\bigl(E_1, \lambda^{[te_1]}\bigr)\bigr] = 0, \qquad \gamma_1^{\mathrm{T}}\bigl[DF_\lambda\bigl(E_1, \lambda^{[te_1]}\bigr)(\mu_1)\bigr] = \sqrt{K} m_1^{[2]} g_1^{[2]} \neq 0,$$

$$\gamma_1^{\mathrm{T}}\bigl[D^2F\bigl(E_1, \lambda^{[te_1]}\bigr)(\mu_1, \mu_1)\bigr] = \bigl(0, g_1^{[2]}, 0\bigr)\left(-\frac{3rm_1^{[1]2}}{\sqrt{K}}, 0, 0\right)^{\mathrm{T}} = 0,$$

$$\gamma_1^{\mathrm{T}}\bigl[D^3F\bigl(E_1, \lambda^{[te_1]}\bigr)(\mu_4, \mu_4, \mu_4)\bigr] = \bigl(0, g_1^{[2]}, 0\bigr)\left(-\frac{3rm_1^{[1]3}}{K}, 0, 0\right)^{\mathrm{T}} = 0.$$

Hence the system will experience neither a saddle node nor a transcritical bifurcation at E_1 for $\lambda = \lambda^{[te_1]}$.

(ii) For $h = h^{[te_1]}$, let μ_2 and γ_2 be the eigenvectors of the eigenvalue 0 of the matrix J_1 and its transpose, respectively. Then $\gamma_2^{\mathrm{T}} = (0, 0, g_2^{[3]})$, $\mu_2^{\mathrm{T}} = (m_2^{[1]}, 0, m_2^{[3]})$, where

$$m_2^{[1]} = -\frac{J_1^{[13]}}{J_1^{[11]}} m_2^{[3]},$$

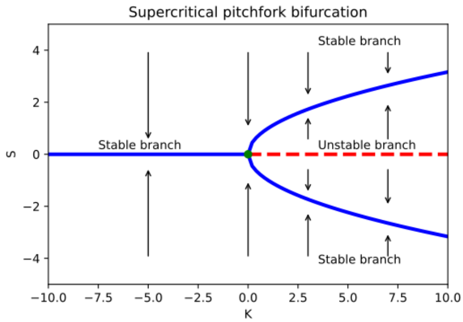


Figure 1. Choosing $K = r$, for $K < 0$, there is one stable equilibrium at $S = 0$. For $K > 0$, there is an unstable equilibrium at $S = 0$ and two stable equilibria at $S = \pm\sqrt{K}$ at E_1.

and $g_2^{[3]}$, $m_2^{[3]}$ represent any two nonzero real numbers. Since

$$\gamma_2^{\mathrm{T}}\big[F_h\big(E_1, \lambda^{[te_1]}\big)\big] = 0, \qquad \gamma_1^{\mathrm{T}}\big[DF_h\big(E_1, h^{[te_1]}\big)(\mu_2)\big] = -\frac{\delta^2 m_2^{[3]} g_2^{[3]}}{\theta_1} \neq 0,$$

$$\gamma_2^{\mathrm{T}}\big[D^2F\big(E_1, h^{[te_1]}\big)(\mu_2, \mu_2)\big] = \big(0, 0, g_1^{[3]}\big)\left(-\frac{3rm_2^{[1]2}}{\sqrt{K}}, 0, 0\right)^{\mathrm{T}} = 0,$$

$$\gamma_2^{\mathrm{T}}\big[D^3F\big(E_1, h^{[te_1]}\big)(\mu_2, \mu_2, \mu_2)\big] = \big(0, 0, g_2^{[3]}\big)\left(-\frac{3rm_2^{[1]3}}{K}, 0, 0\right)^{\mathrm{T}} = 0,$$

system (2) will experience neither a saddle node nor a transcritical bifurcation at E_1 for $h = h^{[te_1]}$.

(iii) For $K = K^{[te_1]}$, let γ_3 and μ_3 be the eigenvectors respectively corresponding to the 0 eigenvalues of the matrix J_1 and its transpose. We obtain $\mu_3^{\mathrm{T}} = (m_3^{[1]}, m_3^{[2]}, 0)$, $\gamma_3^{\mathrm{T}} = (0, g_3^{[2]}, 0)$ so that

$$m_3^{[1]} = -\frac{J_1^{12}}{J_1^{11}} m_3^{[2]},$$

where $g_3^{[2]}$, $m_3^{[2]}$ are two nonzero real numbers. Then

$$\gamma_3^{\mathrm{T}}\big[F_K\big(E_1, K^{[te_1]}\big)\big] = \big(0, g_3^{[2]}, 0\big)\left(\frac{r\lambda}{2\mu}, 0, 0\right)^{\mathrm{T}} = 0,$$

$$\gamma_3^{\mathrm{T}}\big[DF_K\big(E_1, K^{[te_1]}\big)(\mu_3)\big] = g_3^{[2]} m_3^{[2]} \frac{\lambda^2}{2}\mu \neq 0,$$

$$\gamma_3^{\mathrm{T}}\big[D^2F\big(E_1, K^{[te_1]}\big)(\mu_2, \mu_2)\big] = \big(0, g_3^{[2]}, 0\big)\left(-\frac{3rm_3^{[1]2}}{\sqrt{K}}, 0, 0\right)^{\mathrm{T}} = 0,$$

so that the system will experience neither a saddle node nor a transcritical bifurcation at E_1 for $K = K^{[te_1]}$.

For $K = K^{[te_2]}$, let μ_4, γ_4 respectively denote the eigenvectors corresponding to the eigenvalue 0 of the matrix J_1 and its transpose. Then we get $\mu_4^{\mathrm{T}} = (m_4^{[1]}, 0, m_4^{[3]})$,

$\gamma_5^{\mathrm{T}} = (0, 0, g_4^{[3]})$ so that

$$m_4^{[1]} = -\frac{J_1^{13}}{J_1^{11}} m_4^{[3]},$$

where $g_4^{[3]}$, $m_4^{[3]}$ are two arbitrary nonzero real numbers. Then

$$\gamma_4^{\mathrm{T}}\big[F_K\big(E_1, K^{[te_2]}\big)\big] = \big(0, g_4^{[2]}, 0\big)\left(\frac{r\sqrt{K}}{2}, 0, 0\right)^{\mathrm{T}} = 0,$$

$$\gamma_4^{\mathrm{T}}\big[DF_K\big(E_1, K^{[te_2]}\big)(\mu_4)\big] = \frac{(g_4^{[3]} m_4^{[3]} \theta_1 \alpha)}{\sqrt{K^{[te_2]}}(1 + h\alpha\sqrt{K^{[te_2]}})^2} \neq 0,$$

$$\gamma_4^{\mathrm{T}}\big[D^2F\big(E_1, K^{[te_2]}\big)(\mu_4, \mu_4)\big] = \big(0, 0, g_4^{[3]}\big)\left(-\frac{3r m_4^{[1]3}}{K}, 0, 0\right)^{\mathrm{T}} = 0$$

for which the system have neither a saddle node nor a transcritical bifurcation at E_1 for $K = K^{[te_2]}$.

3.4.2.3 Global stability analysis at E_1

Theorem 3. *The point $E_1(S_1, 0, 0)$ is globally asymptotically stable.*

We defer the proof to Appendix G.

3.4.3 The behavior near E_2

3.4.3.1 Stability

One eigenvalue of the Jacobian J_2 is

$$\lambda_1^{[E_2]} = \frac{\theta_1 \alpha\mu}{\lambda + h\alpha\mu} + \frac{\theta_2 m r\mu}{\lambda^2} - \frac{\theta_2 m r \mu^3}{K\lambda^4} - \delta,$$

and the other two are the roots of the equation $x^2 + a_1 x + a_2 = 0$, where

$$a_1 = \frac{1}{2}\left(r - \frac{3r\mu^2}{K\lambda^2}\right), \qquad a_2 = \frac{r\mu(K\lambda^2 - \mu^2)}{2K\lambda^2}.$$

E_2 will be locally asymptotically stable if the Routh–Hurwitz conditions are met, $a_1 > 0$ and $a_2 > 0$, which explicitly become

$$\frac{\mu^2}{\lambda^2} < K < \min\left\{\frac{3\mu^2}{\lambda^2}, \frac{\theta_2 m r \mu^3}{\tau'\lambda^4}\right\}, \qquad \tau' = \frac{\theta_1\alpha\mu}{\lambda + h\alpha\mu} + \frac{\theta_2 m r\mu}{\lambda^2} - \delta. \tag{9}$$

3.4.3.2 Bifurcations

The matrix $J_2 = (J_2^{ij})$, $i, j = 1, 2, 3$, has a zero eigenvalue if and only if $\det J_2 = 0$, which provides $\lambda = \{\lambda^{[te_2]}, \lambda^{[te_{2I}]}\}$, $K = \{K^{[te_2]}, K^{[te_{2I}]}\}$, $\mu = \{\mu^{[te_2]}, \mu^{[te_{2I}]}\}$, where

$$\lambda^{[te_2]} = \frac{\mu}{\sqrt{K}}, \qquad K^{[te_2]} = \frac{\mu^2}{\lambda^2}, \qquad \mu^{[te_2]} = \lambda\sqrt{K},$$

and the values of $K^{[te_{2I}]}$, $\lambda^{[te_{2I}]}$ and $\mu^{[te_{2I}]}$ are reported in Appendix E.

(i) For $\lambda = \lambda^{[te_2]}$, let μ_5, γ_5 respectively be the eigenvectors corresponding to the zero eigenvalue of the matrix J_2 and its transpose. We obtain $\gamma_5^{\mathrm{T}} = (0, g_5^{[2]}, 0)$, $\mu_5^{\mathrm{T}} = (m_5^{[1]}, m_5^{[2]}, 0)$ where

$$m_5^{[1]} = -\frac{J_2^{12}}{J_2^{11}} m_5^{[2]},$$

and $m_5^{[2]}$, $g_5^{[2]}$ are any two positive real numbers. Since

$$\begin{aligned}
\gamma_5^{\mathrm{T}}\big[F_\lambda\big(E_2, \lambda^{[te_2]}\big)\big] &= \frac{r\mu^2(K\lambda^2 - \mu^2)g_5^{[2]}}{\lambda^{[te_2]5}} = 0,\\
\gamma_5^{\mathrm{T}}\big[DF_\lambda\big(E_2, \lambda^{[te_2]}\big)(\mu_5)\big] &= \frac{2rKm_5^{[1]}g_5^{[2]}}{\mu} \neq 0,\\
\gamma_5^{\mathrm{T}}\big[D^2F\big(E_2, \lambda_i^{[te_2]}\big)(\mu_5, \mu_5)\big] &= -rm_5^{[1]^2} g_5^{[2]} \neq 0,
\end{aligned}$$

the system experiences a transcritical bifurcation at E_2 for $\lambda = \lambda_i^{[te_2]}$. Similarly, for $K = K^{[te_2]}$, $\mu = \mu^{[te_2]}$, there will be a transcritical bifurcation around E_2.

For $\lambda = \lambda^{[te_{2I}]}$, let μ_6, γ_6 respectively be the eigenvectors corresponding to the zero eigenvalue of the matrix J_2 and its transpose. We obtain $\gamma_6^{\mathrm{T}} = (0, 0, g_6^{[3]})$, $\mu_6^{\mathrm{T}} = (m_6^{[1]}, m_6^{[2]}, m_6^{[3]})$, where

$$m_6^{[1]} = -\frac{J_2^{33}}{J_2^{21}} m_6^{[3]} = -\frac{J_2^{13}}{J_2^{11}} m_6^{[3]}, \qquad m_6^{[2]} = -\frac{J_2^{13}}{J_2^{12}} m_6^{[3]},$$

and $m_6^{[3]}$, $g_6^{[3]}$ are any two positive real numbers. Since

$$\begin{aligned}
\gamma_6^{\mathrm{T}}\big[F_\lambda\big(E_2, \lambda^{[te_{2I}]}\big)\big] &= \big(0, 0, g_6^{[3]}\big)\left(-\frac{I_2}{2}, S_2I_2, 0\right)^{\mathrm{T}} = 0,\\
\gamma_6^{\mathrm{T}}\big[DF_\lambda\big(E_2, \lambda^{[te_{2I}]}\big)(\mu_5)\big] &= g_6^{[3]} m_6^{[3]} \frac{\partial J_2^{33}}{\partial \lambda}\bigg|_{\lambda = \lambda^{[te_{2I}]}} \neq 0,\\
\gamma_6^{\mathrm{T}}\big[D^2F\big(E_2, \lambda^{[te_{2I}]}\big)(\mu_6, \mu_6)\big] &= 0,
\end{aligned}$$

the system will experiences neither saddle-node nor a transcritical bifurcation at E_2 for $\lambda = \lambda^{[te_{2I}]}$.

(ii) If $\lambda_1^{[E_2]} = 0$ and the other eigenvalues of J_2 are nonzero, we will get $K = K^{[te_{2I}]}$ so that let μ_7, γ_7 respectively be the eigenvectors corresponding to the zero eigenvalue of J_2 and J_2^{T}. Then $\mu_7^{\mathrm{T}} = (m_7^{[1]}, m_7^{[2]}, m_7^{[3]})$, $\gamma_7^{\mathrm{T}} = (0, 0, g_7^{[3]})$ so that

$$m_7^{[1]} = -\frac{J_2^{33}}{J_2^{21}} m_7^{[3]} = -\frac{J_2^{13}}{J_2^{11}} m_7^{[3]}, \qquad m_7^{[2]} = -\frac{J_2^{13}}{J_2^{12}} m_7^{[3]},$$

where $m_7^{[3]}$, $g_7^{[3]}$ are two nonzero real numbers. Since

$$\gamma_7^{\mathrm{T}}\left[F_K\left(E_2, K^{[te_{2I}]}\right)\right] = \left(0, 0, g_7^{[3]}\right)\left(\frac{rS_2^2}{2K^{[te_{2I}]}}, 0, 0\right)^{\mathrm{T}} = 0,$$

$$\gamma_7^{\mathrm{T}}\left[DF_K\left(E_2, K^{[te_{2I}]}\right)(\mu_7, \mu_7)\right] = g_7^{[3]} m_7^{[3]} \frac{\partial J_2^{33}}{\partial \mu}\bigg|_{K=K^{[te_{2I}]}} \neq 0,$$

$$\gamma_7^{\mathrm{T}}\left[D^2F\left(E_2, K^{[te_{2I}]}\right)(\mu_7, \mu_7)\right] = \left(0, 0, g_7^{[3]}\right)\left(-\frac{3rS_2 {m_7^{[1]}}^2}{K^{[te_{2I}]}}, \lambda m_7^{[1]} m_7^{[2]}, 0\right)^{\mathrm{T}} = 0,$$

system (2) will experience neither a saddle-node nor a transcritical bifurcation at E_2 for $K = K^{[te_{2I}]}$. Similarly, there will be neither saddle-node nor transcritical bifurcations at $\mu = \mu^{[te_{2I}]}$.

3.4.3.3 Global stability analysis at E_2

Theorem 4. *The equilibrium point E_2 is globally asymptotically stable if*

$$k_0 r\sqrt{K} + \lambda \leqslant \frac{k_0 r L}{\sqrt{K}} + \frac{\lambda\sqrt{K} k_0}{2}, \qquad \frac{2}{\sqrt{K}} < k_0.$$

The proof is given in Appendix G.

3.4.4 The behavior near $E_3(S_3, 0, P_3)$

3.4.4.1 Stability

At E_3 the eigenvalues of the Jacobian $J_3 = (J_3^{ij})$, $i, j = 1, 2, 3$, are roots of the cubic equation $x^3 - (J_3^{11} + J_3^{22})x^2 + (J_3^{11}J_3^{22} - J_3^{31}J_3^{13})x + J_3^{31}J_3^{13}J_3^{22} = 0$, where the expressions of J_3^{11}, J_3^{22}, J_3^{31}, J_3^{13} are reported in Appendix A. By applying Routh–Hurwitz criterium, the equilibrium is asymptotically stable if

$$h < h_1^{[3]}, \qquad G_1 < K < G_2, \quad G_1 = \max\{l_1, l_2, l_3\}, \tag{10}$$

where $h_1^{[3]} = \theta_1/\delta$, and the values of l_i, $i = 1, \dots, 3$, and G_2 are given in Appendix A.

3.4.4.2 Bifurcations

The matrix $J_3 = (J_3^{ij})$, $i, j = 1, 2, 3$, has a zero eigenvalue if $\det J_2 = 0$, which gives $K = \{K^{[te_3]}, K^{[te_{3I}]}\}$, $h = \{h^{[te_3]}, h^{[te_{3I}]}\}$. The eigenvalues of J_3 are

$$\lambda_1^{[E_3]} = J_3^{22}, \quad \lambda_{2,3}^{[E_3]} = \frac{1}{2}\left[J_3^{11} \pm \sqrt{{J_3^{11}}^2 + 4J_3^{31}J_3^{13}}\right].$$

When $\lambda_1^{[E_3]} = 0$, we will get $K = K^{[te_3]}$, $h = h^{[te_3]}$, and $h_{2,3}^{[E_3]} = 0$ gives $K = K^{[te_{3I}]}$, $h = h^{[te_{3I}]}$. Here

$$K = K^{[te_{3I}]} = \frac{\delta^2}{(\theta_1^2 - 2\theta_1\delta h + \delta^2 h^2)\alpha^2},$$

and $h^{[te_{3I}]}$ is the positive value of

$$\frac{K\theta_1\alpha \pm \delta\sqrt{K}}{K\delta\alpha}.$$

The values of $K = K^{[te_3]}$, $h = h^{[te_3]}$ are mentioned in Appendix E.

(i) For $K = K^{[te_3]}$, there exist eigenvectors μ_8, γ_8 corresponding to the vanishing eigenvalue of J_3 and its transpose, respectively. Then $\mu_8^{\mathrm{T}} = (m_8^{[1]}, m_8^{[2]}, m_8^{[3]})$, $\gamma_8^{\mathrm{T}} = (0, g_8^{[2]}, g_8^{[3]})$ so that

$$m_8^{[1]} = -\frac{J_3^{32}}{J_3^{31}} m_8^{[2]}, \qquad m_8^{[3]} = \frac{J_3^{11}J_3^{32} - J_3^{31}J_3^{12}}{J_3^{31}J_3^{13}} m_8^{[2]},$$

where $m_8^{[2]}$, $g_8^{[2]}$ are nonzero real numbers. Since

$$\gamma_8^{\mathrm{T}}\bigl[F_K\bigl(E_3, K^{[te_3]}\bigr)\bigr] = \bigl(0, g_8^{[2]}, 0\bigr)\biggl(\frac{rS_3^3}{2K^{[te_3]}}, 0, 0\biggr)^{\mathrm{T}} = 0,$$
$$\gamma_8^{\mathrm{T}}\bigl[DF_K\bigl(E_3, K^{[te_3]}\bigr)(\mu_8)\bigr] = 0,$$

the system will experiences neither saddle-node nor transcritical bifurcations at E_3 for $K = K^{[te_3]}$.

For $K = K^{[te_{3I}]}$, there exist eigenvectors μ_9, γ_9 corresponding to the vanishing eigenvalue of J_3 and its transpose, respectively. Then $\mu_9^{\mathrm{T}} = (m_9^{[1]}, 0, m_9^{[3]})$, $\gamma_9^{\mathrm{T}} = (0, 0, g_9^{[3]})$ so that

$$m_9^{[1]} = -\frac{J_3^{13}}{J_3^{11}} m_9^{[3]},$$

where $m_9^{[3]}$, $g_9^{[3]}$ are nonzero real numbers. Since

$$\gamma_9^{\mathrm{T}}\bigl[F_K\bigl(E_3, K^{[te_{3I}]}\bigr)\bigr] = \bigl(0, g_9^{[2]}, 0\bigr)\biggl(\frac{rS_3^3}{2K^{[te_{3I}]}}, 0, 0\biggr)^{\mathrm{T}} = 0,$$
$$\gamma_9^{\mathrm{T}}\bigl[DF_K\bigl(E_3, K^{[te_{3I}]}\bigr)(\mu_9)\bigr] = \frac{\alpha}{\delta} r(\theta_1 - \delta h)^2 g_9^{[3]} m_9^{[1]} \neq 0,$$
$$\gamma_9^{\mathrm{T}}\bigl[D^2F\bigl(E_3, K^{[te_{3I}]}\bigr)(\mu_9, \mu_9)\bigr] = \frac{1}{\theta_1} g_9^{[3]} m_9^{[1]} m_9^{[3]} (\theta_1 - \delta h)^2 \neq 0,$$

the system experiences a transcritical bifurcation at E_3 for $K = K^{[te_{3I}]}$.

(ii) For $h = h^{[te_3]}$, there exist eigenvectors μ_8, γ_8 corresponding to the vanishing eigenvalue of J_3 and its transpose, respectively. We find $\mu_{10}^{\mathrm{T}} = (m_{10}^{[1]}, m_{10}^{[2]}, m_{10}^{[3]})$, $\gamma_{10}^{\mathrm{T}} = (0, g_{10}^{[2]}, 0)$ so that

$$m_{10}^{[1]} = -\frac{J_3^{32}}{J_3^{31}} m_{10}^{[2]}, \qquad m_{10}^{[3]} = \frac{J_3^{11}J_3^{32} - J_3^{31}J_3^{12}}{J_3^{31}J_3^{13}} m_{10}^{[2]},$$

where $m_{10}^{[2]}$, $g_{10}^{[2]}$ are any nonzero real numbers. Since

$$\gamma_{10}^{\mathrm{T}}\big[F_h\big(E_3, h^{[te_3]}\big)\big] = 0,$$

$$\gamma_{10}^{\mathrm{T}}\big[DF_h\big(E_3, h^{[te_3]}\big)(\mu_{10})\big] = \big(0, g_8^{[2]}, 0\big)\left(\frac{\alpha^2 S_3 P_3}{2(1+h^{[te_3]}\alpha S_3)^2}, 0, \frac{-\theta_1\alpha^2 S_3^2 P_3}{(1+h^{[te_3]}\alpha S_3)^2}\right)^{\mathrm{T}} = 0,$$

$$\gamma_{10}^{\mathrm{T}}\big[D^2F\big(E_3, h^{[te_3]}\big)(\mu_{10}, \mu_{10})\big] = 0,$$

the system will experiences neither saddle-node nor transcritical bifurcations at E_3 for $h = h^{[te_3]}$.

For $h = h^{[te_{3I}]}$, there exist eigenvectors μ_{11}, γ_{11} corresponding to the vanishing eigenvalue of J_3 and its transpose, respectively. Then $\mu_{11}^{\mathrm{T}} = (m_{11}^{[1]}, 0, m_{11}^{[3]})$, $\gamma_8^{\mathrm{T}} = (0, 0, g_{11}^{[3]})$ so that

$$m_{11}^{[1]} = -\frac{J_3^{13}}{J_3^{11}} m_{11}^{[3]},$$

where $m_{11}^{[3]}$, $g_{11}^{[3]}$ are nonzero real numbers. The system will experiences transcritical bifurcation at E_3 for $h = h^{[te_{3I}]}$ in view of the following results:

$$\begin{aligned}
\gamma_{11}^{\mathrm{T}}\big[F_h\big(E_3, h^{[te_{3I}]}\big)\big] &= \big(0, 0, g_{11}^{[3]}\big)\left(\frac{\alpha^2 S_3 P_3}{2(1+h^{[te_{3I}]}\alpha S_3)^2}, 0, -\frac{\theta_1\alpha^2 S_3^2 P_3}{(1+h^{[te_{3I}]}\alpha S_3)^2}\right)^{\mathrm{T}} \\
&= -\frac{g_{11}\theta_1\alpha^2 S_3^2 P_3}{(1+h^{[te_{3I}]}\alpha S_3)} = 0, \\
\gamma_{11}^{\mathrm{T}}\big[DF_h\big(E_3, h^{[te_{3I}]}\big)(\mu_{11})\big] &= 2\delta r\sqrt{K} g_{11}^{[3]} m_{11}^{[1]} \neq 0, \\
\gamma_{11}^{\mathrm{T}}\big[D^2F\big(E_3, h^{[te_{3I}]}\big)(\mu_{11}, \mu_{11})\big] &= \frac{g_{11}^{[3]} m_{11}^{[1]} m_{11}^{[3]} \delta^2}{\theta_1\alpha K} \neq 0.
\end{aligned}$$

3.4.4.3 Global stability analysis at E_3

Theorem 5. *The equilibrium $E_3(S_3, 0, P_3)$ is globally asymptotically stable if the following conditions hold*:

$$r < \frac{1}{\sqrt{K}}\left(\frac{Nk_3}{\sqrt{K}} + \frac{\alpha k_3\sqrt{K}}{2} - \theta_1\alpha\right), \qquad k_3 > \frac{2\theta_1}{\sqrt{K}}.$$

The proof is contained in Appendix G.

3.4.5 The behavior near $E_*(S_*, I_*, P_*)$

3.4.5.1 Stability

Proposition 3. *The coexistence equilibrium is asymptotically stable if and only if $b_1 > 0$, $b_3 > 0$, $b_1 b_2 > b_3$ hold.*

The proof and the values b_i, $i = 1, 2, 3$, are given in Appendix B.

3.4.5.2 Hopf bifurcation

Proposition 4. *System* (2) *undergoes a Hopf bifurcation at coexistence* E_* *when the critical parameter* $\lambda = \lambda_{\rm cr} \in D_{HB} = \{\lambda_{\rm cr} \in \mathbb{R}^+\colon\ a_1(\lambda_{\rm cr})a_2(\lambda_{\rm cr}) = a_3(\lambda_{\rm cr})\}$ *with*

$$a_1(\lambda_{\rm cr}), a_2(\lambda_{\rm cr}), a_3(\lambda_{\rm cr}) > 0, \qquad \left[\frac{\rm d}{{\rm d}\lambda} {\rm Re}\{x_j(\lambda)\}\right]_{\lambda=\lambda_{\rm cr}} \neq 0.$$

The proof is once more written in Appendix D.

3.4.5.3 Other bifurcations

We rewrite system (2) as

$$\frac{{\rm d}X}{{\rm d}t} = F(X), \quad X = (S, I, P)^t, \quad F = (F_1, F_2, F_3)^t, \quad J \equiv DF(X), \tag{11}$$

where F is a C^1 function in some open subset of $\mathbb{R}^N$. One of the eigenvalues of $J_* = (J_*^{ij})$, $i, j = 1, 2, 3$, vanishes if and only if $\det J_* = 0$, i.e., $m = m_4$ with

$$m_4 = \frac{\lambda_1\alpha(\theta_2 q - \theta_1)}{2J_*^{11}\theta_2 t^2}, \qquad J_*^{11} = \frac{r(K - 3S_*^2)}{2K} + \frac{\alpha^2 P_* h}{2(1 + h\alpha S_*)^2},$$
$$q = 1 + h\alpha S_*.$$

Let $U = (\gamma_1', \gamma_2', \gamma_2')^{\rm T}$, $V = (\mu_1', \mu_2', \mu_3')^{\rm T}$ respectively denote the two eigenvectors corresponding to the zero eigenvalue of J and its transpose $J^{\rm T}$, then we have

$$-\frac{J_*^{23}\gamma_1'}{J_*^{21}} = \frac{J_*^{31}J_*^{23}\gamma_2'}{J_*^{21}J_*^{32}} = \gamma_3', \qquad -\frac{J_*^{32}\mu_1'}{J_*^{12}} = \frac{J_*^{13}J_*^{32}\mu_2'}{J_*^{12}J_*^{23}} = \mu_3'$$

with γ_1', γ_2', μ_1', μ_2' being arbitrary nonvanishing real numbers. Since $V^{\rm T}F_m(E_*, m_4) \neq 0$ and $V^{\rm T}DF_m(E_*, m_4)(U) \neq 0$, there are three cases:

Case 1. There exist a Turing-saddle node bifurcation node if the following conditions hold:
$$\frac{\alpha^2 P_* h}{2(1 + h\alpha S_*)} + r < \frac{3S_*^2}{K}, \qquad \lambda = \frac{2J_*^{11} m\theta_2 q^2}{\alpha(\theta_2 q - \theta_1)}. \tag{12}$$

Case 2. There is a Turing-transcritical bifurcation if conditions (12) hold along with
$$h = \frac{I_*(P_*\alpha + I_*\lambda)}{\lambda\,\alpha\, S_*}. \tag{13}$$

Case 3. There is a Turing-pitchfork bifurcation if conditions (12) and (13) hold together with the critical value of m and the variational matrices being reported in Appendix E.

3.4.5.4 Global stability at E_*

Theorem 6. *The coexistence equilibrium $E_*(S_*, I_*, P_*)$ is globally asymptotically stable if it satisfies conditions similar to the ones of* [12, 20] *and* [19], *i.e.,*

$$\frac{1}{\theta_2(2h\alpha+3)} \leqslant \min\left\{\frac{\alpha K-2r}{K\alpha(2h\theta_2 m+3\theta_1-3h\delta)}, \frac{\alpha+m}{3\theta_2 m+3\,\theta_1\alpha+2h\alpha\theta_2 m-3h\alpha\delta}\right\},$$
$$\delta < \min\left\{\frac{1}{3\alpha h}(3\theta_2 m+3\theta_1\alpha+2h\alpha\theta_2 m), \frac{1}{3h}(2h\theta_2 m+3\theta_1)\right\}, \tag{14}$$
$$K > \frac{2r}{\alpha}.$$

The proof is given in Appendix G.

3.4.5.5 Nonexistence of periodic solutions near $E_*(S_*, I_*, P_*)$

To show the nonexistence of periodic orbits of the system near $E_*(S_*, I_*, P_*)$, we apply the technique of Li and Muldowney mentioned in [19]. Recalling the notation in (11), we denote by $J_{[2]}$ the $\binom{N}{2} \times \binom{N}{2}$ second additive compound matrix associated with the Jacobian J [19]. Explicitly,

$$J_{[2]} = \begin{pmatrix} \vartheta_{11}+\vartheta_{22} & \vartheta_{23} & -\vartheta_{13} \\ \vartheta_{32} & \vartheta_{11}+\vartheta_{33} & \vartheta_{12} \\ -\vartheta_{31} & \vartheta_{21} & \vartheta_{22}+\vartheta_{33} \end{pmatrix}.$$

We now use the results of [17] on Bendixson's criterion in $\mathbb{R}^n$ to analyse closed orbits.

Theorem 7. *A simple closed rectifiable curve that is invariant with respect to system* (2) *cannot exist if the following condition holds* [12]:

$$\sup\left\{\frac{\partial F_r}{\partial x_r} + \frac{\partial F_s}{\partial x_s} + \sum_{q\neq r,s}\left(\left|\frac{\partial F_q}{\partial x_r}\right| + \left|\frac{\partial F_q}{\partial x_s}\right|\right)\colon\ 1 \leqslant r < s \leqslant n\right\} < 0. \tag{15}$$

Proof. Let us reduce the system dimension by setting

$$S'' = \frac{S}{K}, \quad I'' = \frac{I}{K}, \quad P'' = \frac{P}{K}, \quad t'' = rt, \quad m'' = \frac{m}{K}, \quad \mu'' = \frac{\mu}{K},$$
$$\lambda'' = \frac{\lambda}{K}, \quad \alpha'' = \frac{\alpha}{K}, \quad \delta'' = \delta K^2, \quad \theta_1'' = K\theta_1, \quad \theta_2'' = K^2\theta_2, \quad \zeta = \frac{P^*}{1+h\alpha S^*}$$

to obtain

$$\frac{\mathrm{d}S}{\mathrm{d}t} = \frac{1}{2}\left[S_*\left(1-S_*^2\right) - \alpha\zeta - \lambda I_*\right] = F_1',$$
$$\frac{\mathrm{d}I}{\mathrm{d}t} = \lambda I_* S_* - mI_*P_* - \mu I_* = F_2',$$
$$\frac{\mathrm{d}P}{\mathrm{d}t} = \theta_1 S_*\alpha\zeta + \theta_2 m I_* P_* - \delta P_* = F_3'.$$

Now (15) becomes

$$
\begin{aligned}
&m(-1+\theta_2)P_* + \frac{1}{2}\big[1-3S_*^2\big] + \lambda\, S_* - \mu + \theta_1\alpha(\zeta) < 0,\\
&(-P_* + \theta_2 I_*)m + \lambda S_* - \mu - \delta < 0,\\
&\big((-1+\theta_2)m + \lambda\big)I_* + \frac{1}{2}\big[1-3S_*^2\big] - \delta < 0.
\end{aligned}
\tag{16}
$$

Sufficient conditions to satisfy (16) are

$$
\begin{gathered}
\theta_2 < 1, \qquad \frac{1}{\sqrt{3}} < S_* < \frac{\mu - \theta_1\alpha\zeta}{\lambda},\\
\theta_2 < \frac{P_*}{I_*}, \qquad S_* < \frac{\mu+\delta}{\lambda},\\
\lambda < m(1-\theta_2), \qquad S_* > \sqrt{\frac{1-2\delta}{3}}.
\end{gathered}
$$

In these conditions, system (2) admits no periodic solutions. □

3.4.5.6 Stability of bifurcating limit cycle

We now establish the stability of the limit cycle arising from the Hopf bifurcation. To this end, we apply the center manifold theorem [15,20]. Since the Jacobian $J_*(S_*, I_*, P_*)$ has purely imaginary eigenvalues leading to the Hopf bifurcation, we can analyze the present system just on a two-dimensional manifold, where the flow is exponentially contracting.

We translate E_* to the origin by $\bar{S} = S - S_*, \bar{I} = I - I_*$ and $\bar{P} = P - P_*$. The original system becomes

$$
\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix}\bar{S}\\ \bar{I}\\ \bar{P}\end{pmatrix} = J_*\begin{pmatrix}\bar{S}\\ \bar{I}\\ \bar{P}\end{pmatrix} + \begin{pmatrix}\phi_1\\ \phi_2\\ \phi_3\end{pmatrix}, \tag{17}
$$

where the Jacobian J_* is

$$
J_* = \begin{pmatrix} G & -\frac{\lambda}{2} & \frac{T}{2}\\ \lambda I_* & 0 & -I_* m\\ \frac{\theta_1 P_* T^2}{\alpha} & \theta_2 m P_* & 0 \end{pmatrix}
$$

with

$$
G = \frac{r(K-3S_*^2)}{2K} + \frac{T^2 P_* h}{2}, \qquad T = \frac{\alpha}{1+h\alpha S_*},
$$

and

$$
\begin{aligned}
\phi_1 &= \frac{1}{2}hT^2\bar{S}\bar{P} - T_1\bar{S}^2,\\
\phi_2 &= \lambda\bar{S}\bar{I} - m\bar{I}\bar{P},\\
\phi_3 &= \big(\theta_1 T - \theta_1 T^2 h S_*\big)\bar{S}\bar{P} - \theta_2 m\bar{I}\bar{P}\\
&\quad + \big(2\theta_1 T^3 h^2 S_* P_* - 2\theta_1 T^2 h P_*\big)\bar{S}^2.
\end{aligned}
\tag{18}
$$

We neglect the higher-order term such as $\bar{S}^3$ and the ones containing

$$T_1 = \frac{1}{2}\left[\frac{3S_* r}{K} + \frac{\alpha^3 h^2 P_*}{(1 + h\alpha S_*)^3}\right].$$

At the Hopf bifurcation, the characteristic equation has the eigenvalues $\lambda_1 = -a_1 = \eta$ for some η, and $\lambda_{2,3} = \pm\imath\sqrt{a_2} = \pm\imath\omega$, where

$$\omega^2 = a_2 = I_*\theta_2 m^2 P_* + \frac{1}{2} I_*\lambda^2 + \frac{\theta_1\alpha^2 P_*}{2 + 2\,h\alpha\,S_*}.$$

Let the eigenvector of J_* associated with λ_1 be η_1, and the ones corresponding to $\lambda_{2,3}$ be $\eta_2 \pm \imath\eta_3$, where η_1, η_2, η_3 denote real vectors. Then it can be shown that the matrix $B = [U_{ij}] = [\eta_3\eta_2\eta_1]$ is nonsingular and

$$B^{-1}J_*B = \begin{pmatrix} 0 & -\omega & 0 \\ \omega & 0 & 0 \\ 0 & 0 & \eta \end{pmatrix}, \qquad B = \begin{pmatrix} -\frac{\omega T}{2} & \frac{\lambda m I_*}{2} & \frac{\lambda m I_*}{2} - \frac{\eta T}{2} \\ -\omega I_* m & (Gm - \frac{\lambda T}{2})I_* & (Gm - \frac{\lambda T}{2} - \eta m)I_* \\ -\omega G & -\omega^2 + \frac{\lambda^2 I_*}{2} & \eta^2 - \eta G + \frac{\lambda^2 I_*}{2} \end{pmatrix},$$

and $Q_{ij} = B^{-1} = (1/\Delta)[q_{ij}]$, where $\Delta = \det B$.

Next, letting $\bar{\bar{Y}} = (\bar{S}, \bar{I}, \bar{P})^{\mathrm{T}}$, we use the following linear transformation: $\bar{\bar{Y}} = BW$ with $W = B^{-1}\bar{\bar{Y}} = (I_1, I_2, I_3)^{\mathrm{T}}$. Explicitly,

$$\begin{pmatrix} \bar{S} \\ \bar{I} \\ \bar{P} \end{pmatrix} = B \begin{pmatrix} I_1 \\ I_2 \\ I_3 \end{pmatrix}. \tag{19}$$

Substituting (19) into (17), we get

$$\frac{\mathrm{d}}{\mathrm{d}t}(BW) = J_*UW + F_1(BW), \qquad \frac{\mathrm{d}w}{\mathrm{d}t} = \bigl(B^{-1}J_*B\bigr)W + B^{-1}F_1(BW). \tag{20}$$

Now (20) can be rewritten as

$$\dot{l} = Hl + F_1(l, z), \qquad \dot{z} = Nz + G_1(l, z), \tag{21}$$

where $l = (I_1, I_2)^{\mathrm{T}}$, $z = (I_3)$. H and N are the constant matrices

$$H = \begin{pmatrix} 0 & -\omega \\ \omega & 0 \end{pmatrix}, \qquad N = (\eta),$$

and F_1 and G_1 are C^2 functions. System (20) can now be written as

$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} I_1 \\ I_2 \\ I_3 \end{pmatrix} = \begin{pmatrix} 0 & -\omega & 0 \\ \omega & 0 & 0 \\ 0 & 0 & \eta \end{pmatrix}\begin{pmatrix} I_1 \\ I_2 \\ I_3 \end{pmatrix} + B^{-1}\begin{pmatrix} \phi_1 \\ \phi_2 \\ \phi_3 \end{pmatrix}. \tag{22}$$

Now system (22) has a local center manifold $z = f(l)$, $l < \epsilon$, where f is in C^2. The function $f(l)$ can be approximated arbitrarily closely by a Taylor series as shown in the next theorem.

Theorem 8. *Let $\phi : R^n \to R^m$ be C^1 in a neighborhood of the origin, $\phi(0) = 0$, $\phi'(0) = 0$ and $M\phi(l) = O(|l|^{\varkappa})$ as $l \to \infty$, where $M\phi(l) = \phi'(l)[Nl + G_1(l, \phi(l))] - H\phi(l) - F_1(l, \phi(l))$ and $\varkappa > 1$. Then $f(l) = \phi(l) + O(|l|^{\varkappa})$ as $l \to \infty$.*

Hence in the present case the center manifold up to a quadratic approximation is described by

$$I_3 = f(I_1, I_2) = \frac{1}{2}\bigl(b_{11}I_1^2 + 2b_{12}I_1I_2 + b_{22}I_2^2\bigr).$$

It follows

$$\frac{\mathrm{d}I_3}{\mathrm{d}t} = \left(\frac{\mathrm{d}f}{\mathrm{d}I_1}, \frac{\mathrm{d}f}{\mathrm{d}I_2}\right)\begin{pmatrix}\frac{\mathrm{d}I_1}{\mathrm{d}t}\\ \frac{\mathrm{d}I_2}{\mathrm{d}t}\end{pmatrix},$$

which leads to

$$\frac{\mathrm{d}I_3}{\mathrm{d}t} = \bigl(b_{11}I_1 + b_{12}I_2,\ b_{12}I_1 + b_{22}I_2\bigr)\begin{pmatrix}0 & -\omega\\ \omega & 0\end{pmatrix}\begin{pmatrix}I_1\\ I_2\end{pmatrix}. \tag{23}$$

Calculating ϕ_1, ϕ_2, ϕ_3 of (19), we have

$$\begin{aligned}\bar{S} &= U_{11}I_1 + U_{12}I_2 + U_{13}I_3,\\ \bar{I} &= U_{21}I_1 + U_{22}I_2 + U_{23}I_3,\\ \bar{P} &= U_{31}I_1 + U_{32}I_2 + U_{33}I_3.\end{aligned} \tag{24}$$

Now from (18) and (24) we get

$$\begin{aligned}\phi_1 &= T^2h\biggl[(U_{11}I_1 + U_{12}I_2)\biggl(U_{31}I_1 + U_{32}I_2 + U_{33}\frac{\varLambda}{2}\biggr) + U_{13}\frac{\varLambda}{2}(U_{31}I_1 + U_{32}I_2)\biggr]\\ &\quad - T_1\bigl[(U_{11}I_1 + U_{12}I_2)^2 + U_{13}\varLambda(U_{11}I_1 + U_{12}I_2)\bigr],\\ \phi_2 &= \lambda\biggl[(U_{11}I_1 + U_{12}I_2)\biggl(U_{21}I_1 + U_{22}I_2 + U_{23}\frac{\varLambda}{2}\biggr) + U_{13}\frac{\varLambda}{2}(U_{21}I_1 + U_{22}I_2)\biggr]\\ &\quad - m\biggl[(U_{31}I_1 + U_{32}I_2)\biggl(U_{21}I_1 + U_{22}I_2 + U_{23}\frac{\varLambda}{2}\biggr) + U_{33}\frac{\varLambda}{2}(U_{21}I_1 + U_{22}I_2)\biggr],\\ \phi_3 &= \bigl(2\theta_1T^3h^2S_*P_* - 2\theta_1T^2P_*h\bigr)\bigl[(U_{11}I_1 + U_{12}I_2)^2 + U_{13}\varLambda(U_{11}I_1 + U_{12}I_2)\bigr]\\ &\quad + \bigl(\theta_1T - \theta_1T^2hS_*\bigr)\biggl[(U_{11}I_1 + U_{12}I_2)\biggl(U_{31}I_1 + U_{32}I_2 + U_{33}\frac{\varLambda}{2}\biggr)\\ &\quad + U_{13}\frac{\varLambda}{2}(U_{31}I_1 + U_{32}I_2)\biggr]\\ &\quad - \theta_2m\biggl[(U_{31}I_1 + U_{32}I_2)\biggl(U_{21}I_1 + U_{22}I_2 + U_{23}\frac{\varLambda}{2}\biggr) + U_{33}\frac{\varLambda}{2}(U_{21}I_1 + U_{22}I_2)\biggr],\\ &\qquad \varLambda = 2I_3 = b_{11}I_1^2 + 2b_{12}I_1I_2 + b_{22}I_2^2.\end{aligned}$$

From (22) the left-hand side of (23) becomes

$$\begin{aligned}&\bigl(b_{11}I_1 + b_{12}I_2,\ b_{12}I_1 + b_{22}I_2\bigr)\begin{pmatrix}0 & -\omega\\ \omega & 0\end{pmatrix}\begin{pmatrix}I_1\\ I_2\end{pmatrix}\\ &\quad = \omega b_{12}I_1^2 + b_{22}I_1I_2\omega - \omega b_{11}I_1I_2 - \omega b_{12}I_2^2\end{aligned}$$

$$= \frac{\eta}{2}\left(b_{11}I_1^2 + 2b_{12}I_1I_2 + b_{22}I_2^2\right) + \frac{1}{\Delta}(q_{31}\phi_1 + q_{32}\phi_2 + q_{33}\phi_3)$$
$$= \frac{\eta}{2}\left(b_{11}I_1^2 + 2b_{12}I_1I_2 + b_{22}I_2^2\right) + \frac{1}{\Delta}(Q_{31}\phi_1 + Q_{32}\phi_2 + Q_{33}\phi_3),$$

which equals the right-hand side of (23). Comparing both sides, the coefficients of I_1^2, I_1I_2, I_2^2, we get

$$\begin{aligned}
\Gamma_1 \equiv \omega b_{12} - \frac{\eta}{2}b_{11} &= Q_{31}\left[T^2hU_{31}U_{11} - T_1U_{11}^2\right] + Q_{32}[\lambda U_{11}U_{21} - mU_{31}U_{21}] \\
&+ Q_{33}\left[\frac{\theta_1}{\alpha}T^2U_{11}U_{31} + \theta_2 mU_{31}U_{21} - \frac{\theta_1}{\alpha}P^*hT^3U_{11}^2\right], \\
\Gamma_2 \equiv \omega(b_{22} - b_{11}) - \eta b_{12} &= Q_{31}\left[T^2h(U_{11}U_{32} + U_{12}U_{31}) - 2T_1U_{11}U_{12}\right] \\
&+ Q_{32}\left[\lambda(U_{11}U_{22} + U_{12}U_{21}) - m(U_{31}U_{22} + U_{32}U_{21})\right] \\
&+ Q_{33}\left[\frac{\theta_1}{\alpha}T^2(U_{11}U_{32}+U_{12}U_{31}) + \theta_2 m(U_{31}U_{21}+U_{32}U_{21}) - \frac{2\theta_1}{\alpha}P_*hT^3U_{11}U_{12}\right], \\
\Gamma_3 \equiv -\frac{\eta}{2}b_{22} - \omega b_{12} &+ Q_{31}\left[T^2hU_{12}U_{32} - TU_{12}^2\right] + Q_{32}[\lambda U_{12}U_{22} - mU_{32}U_{22}] \\
&+ Q_{33}\left[\frac{\theta_1}{\alpha}T^2U_{12}U_{32} + \theta_2 mU_{32}U_{22} - \frac{\theta_1}{\alpha}P_*hT^3U_{12}^2\right].
\end{aligned}$$

Here $[Q_{ij}] = [(1/\Delta)q_{ij}]$, $i, j = 1, 2, 3$. It can be easily shown that

$$b_{11} = -\frac{1}{2}\,\frac{4\,\omega^2\Gamma_3 + 2\,\eta\,\omega\,\Gamma_2 + \eta^3 + 2\,\eta^2\Gamma_1 + 2\,\omega^2\eta + 4\,\omega^2\Gamma_1}{\omega^2\eta},$$
$$b_{12} = \frac{1}{2}\,\frac{\eta + 2\,\Gamma_1}{\omega}, \qquad b_{22} = -\frac{2\,\Gamma_3 + \eta + 2\,\Gamma_1}{\eta}.$$

Then the flow on the center manifold is governed by the two-dimensional system

$$\dot{R} = HR + F\big(R, f(R)\big). \tag{25}$$

The central manifold theorem tell us that (25) contains all the information needed to determine the asymptotic behavior of the solution of (21).

Theorem 9. *Suppose the zero solution of* (25) *is asymptotically stable* (*unstable*)*, then zero solution of* (21) *is asymptotically stable* (*unstable*).

In detailed form, (25) can be written as

$$\frac{\mathrm{d}}{\mathrm{d}t}\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} = \begin{pmatrix} 0 & -\omega \\ \omega & 0 \end{pmatrix}\begin{pmatrix} I_1 \\ I_2 \end{pmatrix} + \begin{pmatrix} \Pi \\ \Sigma \end{pmatrix},$$

where, letting h.o.t. standing for higher-order terms,

$$\Pi = \frac{1}{\Delta}[Q_{11}\phi_1 + Q_{12}\phi_2 + Q_{13}\phi_3 + h.o.t.],$$
$$\Sigma = \frac{1}{\Delta}[Q_{21}\phi_1 + Q_{22}\phi_2 + Q_{23}\phi_3 + h.o.t.].$$

The stability of the limit cycle arising from a Hopf bifurcation is determined by the sign of Ω:

$$\begin{aligned}\Omega &= \Pi_{111} + \Sigma_{112} + \Pi_{122} + \Sigma_{222} + \frac{1}{\omega}\big[\Pi_{12}(\Pi_{11} + \Pi_{22}) \\ &\quad - \Sigma_{12}(\Sigma_{11} + \Sigma_{22}) - \Pi_{11}\Sigma_{11} + \Pi_{22}\Sigma_{22}\big], \\ \Pi_{ij} &= \frac{\partial^2 \Pi(0,0)}{\partial I_i \partial I_j}, \qquad \Pi_{ijk} = \frac{\partial^3 \Pi(0,0)}{\partial I_i \partial I_j \partial I_k}.\end{aligned} \tag{26}$$

If $\Omega < 0$, the Hopf bifurcating limit cycle is stable, and the Hopf bifurcation is supercritical; if $\Omega > 0$, the bifurcating limit cycle is unstable, and the Hopf bifurcation is subcritical. The sign of Ω can be obtained by substituting into (26) the values of Π_{111}, Σ_{112}, Π_{122}, Σ_{222}, Π_{11}, Π_{12}, Π_{22}, Σ_{11}, Σ_{22}, Σ_{12} given in Appendix F.

4 Simulations

4.1 Numerical settings

For the convenience of the reader, all the conditions found and the numerical data used in the following are listed in Tables 1–6.

Table 1. Conditions of equilibrium global stability.

Equilibrium	Global stability condition
E_1	Unconditionally globally stable
E_2	$k_0 r\sqrt{K} + \lambda \leqslant \frac{k_0 r L}{\sqrt{K}} + \frac{\lambda\sqrt{K}k_0}{2}, \ \frac{2}{\sqrt{K}} < k_0$
E_3	$r < \frac{1}{\sqrt{K}}(\frac{Nk_3}{\sqrt{K}} + \frac{\alpha k_3\sqrt{K}}{2} - \theta_1\alpha), \quad k_3 > \frac{2\theta_1}{\sqrt{K}}$
E^*	$K > \frac{2r}{\alpha}$ $\delta < \min\{\frac{1}{3\alpha h}(3\theta_2 m + 3\theta_1\alpha + 2h\alpha\theta_2 m), \frac{1}{3h}(2h\theta_2 m + 3\theta_1)\}\frac{3}{\theta_2(2h\alpha+3)}$ $\leqslant \min\{\frac{3(-2r+\alpha K)}{K\alpha(2h\theta_2 m + 3\theta_1 - 3h\delta)}, \frac{3(\alpha+m)}{3\theta_2 m + 3\theta_1\alpha + 2h\alpha\theta_2 m - 3h\alpha\delta}\}$

Table 2. Changes of various parameters values in the different equilibrium points.

Equilibrium points	α	λ	μ	θ_1	θ_2	δ	r	K	h	m
E_1	0.7	0.2	2	0.6	0.4	2.1	0.6	50	0.1	0.5
E_2	0.7	0.24	2	0.19	0.39	0.4	0.8	80	1.5	0.2
E_3	0.9	0.2	0.899	0.998	0.89	2.8	2.4	100	0.2	3

Table 3. Analytic conditions for feasibility.

Equilibrium	Feasibility condition	Sufficient condition
E_0	–	–
E_1	–	$0 < K < \min\{\frac{\mu^2}{\lambda^2}, S_3^2\}$
E_2	$K\lambda^2 > \mu^2$	$\min\{\frac{3\mu^2}{\lambda^2}, \frac{\theta_2 m r \mu^3}{\tau'\lambda^4}\} > K > \frac{\mu^2}{\lambda^2}$
E_3	$\frac{K\theta_1\alpha - \delta\sqrt{K}}{K\delta\alpha} < h < \frac{\theta_1}{\delta}$	$\theta_1 > \delta h$, $G_1 < K < G_2$
E^*	$\lambda > \frac{\mu}{S_*}, \theta_1 < \delta h$	$K > \max\{y_1, y_2, y_3\}$

Table 4. Stability conditions (LAS := locally asymptoically stable, US := unstable saddle point, GAS := globally asymptotically stable).

Point	Local nature	Sufficient condition	Global nature
E_0	US		
E_1	LAS	–	–
E_2	LAS	$a_1^2 - 4a_2 < 0$	GAS
E_3	LAS	–	GAS
E^*	LAS	–	GAS

Table 5. Variables and parameters used during simulations.

	Definitions	Units	Value
S	Susceptible prey density	v	–
I	Infected prey density	v	–
P	Predator density	v	–
r	Prey growth rate	t^{-1}	3.1
K	Prey carrying capacity	v	120
α	Predator search efficiency	t^{-1}	0.9
h	Predator average handling time	$v^{-1}t^{-1}$	–
λ	Force of infection	t^{-1}	–
m	Predation rate on infected prey	t^{-1}	–
μ	Infected prey natural plus disease-related mortality rate	t^{-1}	–
θ_1	Susceptible prey conversion factor	–	0.9998
θ_2	Infected prey conversion factor	–	0.89
δ	Predator natural mortality rate	t^{-1}	2.8

Table 6. Summary of the equilibria numerical results of system (2) (LAS := locally asymptotically stable, US := unstable saddle point, HB := Hopf bifurcation, GAS := globally asymptotically stable).

	λ	θ_2	Solutions	Eigenvalues	Result
E_1	0.2	0.2	$(7.071067, 0, 0)$	$(-0.3, 0, -1.891304)$	LAS
E_2	0.24	0.39	$(8.33, 3.66, 0)$	$(-0.00044, -0.319 \pm \imath 0.058)$	GAS
E_3	0.2	0.9	$(7.1029, 0, 21.3839)$	$(-0.1413 \pm \imath 0.843, -63.63)$	GAS

The disease-free equilibrium $E_1 = (7.1, 0, 0)$ can be achieved with the parameters of Table 2, which satisfy the feasibility condition $K < \min\{100, 59.2\}$.

The equilibrium $E_2 = (8.33, 3.66, 0)$ is obtained with the values of Table 2 satisfying the global stability condition

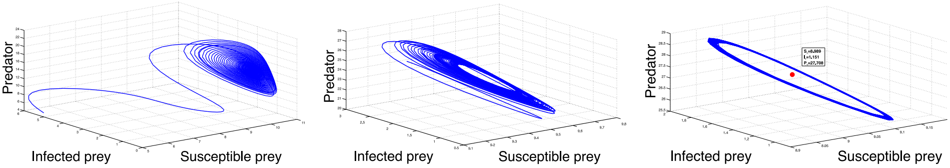
$$k_0 r\sqrt{K} + \lambda = 3.69 < \frac{k_0 r L}{\sqrt{K}} + \frac{\lambda\sqrt{K}k_0}{2} = 10.55.$$

See Appendix G with the eigenvalues in Table 6.

$E_3 = (7.1029, 0, 21.3839)$ arises by the parameter values from Table 2 satisfying the global stability condition

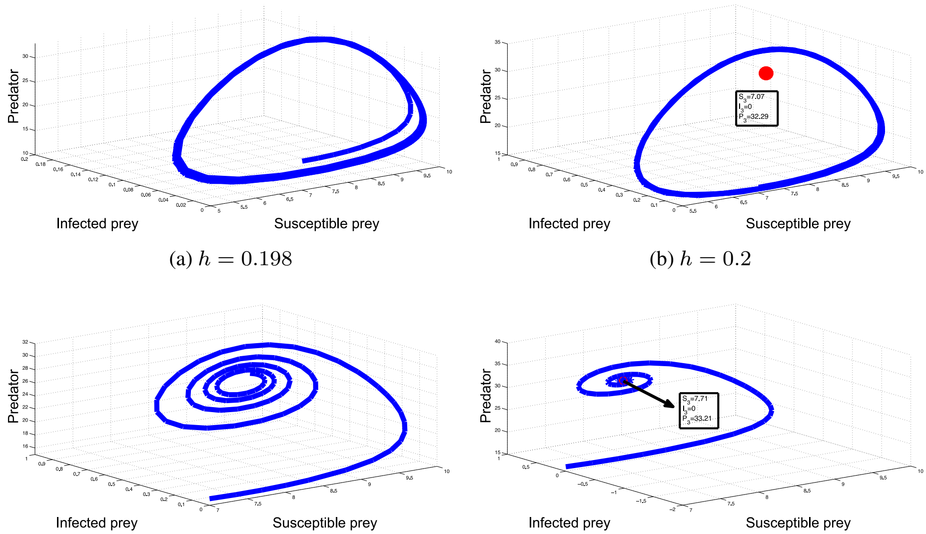
$$r < \frac{1}{\sqrt{K}}\left(\frac{Nk_3}{\sqrt{K}} + \frac{\alpha k_3\sqrt{K}}{2} - \theta_1\alpha\right) = 2.575.$$

See Appendix G with the eigenvalues provided in Table 6.



(a) (b) (c)

Figure 2. (a) Stable phase portrait for $\lambda_{\min} = 1.8 < \lambda_{\rm cr}$. (b) Phase portrait for $h = 0.513$, $m = 1.2$, $\mu = 0.01$ and other parameter values taken from Table 5. (c) Limit cycle for $\lambda = 3.7 > \lambda_{\rm cr}$ showing the Hopf bifurcation.



(a) $h = 0.198$ (b) $h = 0.2$

(c) $h = 0.207$ (d) $h = 0.213$

Figure 3. Sequence of changes in the stability of E_3 as function of the predator average handling time h for $h = 0.2$. There is a stable limit cycle arising from a Hopf bifurcation in frame (b). In frame (d), it becomes a stable spiral using the parameter values $\lambda = 1$, $\mu = 0.1$, $m = 3$, $K = 120$ and the other ones from Table 5.

$E_* = (10.06, 0.78, 16.77)$ is obtained by the choice $\lambda = 2$, $h = 0.4$, $m = 1.2$, $\mu = 0.01$ and the other parameters from Table 5 satisfying the global stability conditions in Section 3.4.5: $0.9061254081 < \min\{5.726564961, 1.352970737\}$, $\delta < \min\{6.178166667, 3.211500000\}$ and $K > 6.888888888$.

The Hopf bifurcation discussed in Section 3.4.5.1 is numerically validated by the parameters $h = 0.513$, $m = 1.2$, $\mu = 0.01$ and the other ones from Table 5. By varying the values of λ we obtain Figure 2. Increasing the value of λ to 1.8 while keeping the same values for the remaining parameters, all the feasibility conditions of the coexistence equilibrium are satisfied, giving $E_*(8.989, 1.151, 27.708)$. Here $\lambda_{\min} = 1.8$, $\lambda_{\rm cr} = 3$ and $\lambda_{\max} = 4.4$. E_* is asymptotically stable when $\lambda_{\min} = 1.8 < \lambda_{\rm cr}$. When λ lies between $\lambda_{\rm cr}$ and the maximum value of $\lambda_{\rm cr}$, a bifurcating limit cycle occurs from a Hopf bifurcation; Fig. 2. Here $\mathit{\Omega} = 10.49$; see Section 3.4.5.6. Therefore the Hopf bifurcation is subcritical. An extensive numerical simulation shows that when the value of λ is very close to λ_{cr}, the three populations S, I and P take long time to stabilize whereas when λ crosses the value λ_{cr} coming very close to $\lambda_{\max}$, the three populations become unstable. Thus in summary we have the following proposition.

Proposition 5. *The interval $[\lambda_{\min}, \lambda_{\max}]$ contains a critical value λ_{cr}, where a subcritical Hopf bifurcation occurs. For the Hopf bifurcation in the interval $[\lambda_{\min}, \lambda_{\max}]$, the interior equilibrium point is asymptotically stable between $\lambda_{\min}$ and λ_{cr}, and for λ lying between λ_{cr} and $\lambda_{\max}$, a limit cycle occurs. On the other hand, for $\lambda > \lambda_{\max}$, the equilibrium does not exist.*

The basic reproduction number depends on the ratio between infection and prey mortality multiplied by the square root of the system carrying capacity K. The disease will not die out if the prey mortality increases due just to infection rather than the natural predation rate.

4.2 Interpretation

Note that the trivial equilibrium is always unstable. This indicates that each subpopulation cannot disappear, thereby preserving the ecosystem.

The equilibrium E_1 is locally asymptotically stable if (8) holds, which biologically can be expressed by saying that the carrying capacity is bounded by a combination of the prey mortality rate and disease transmission. The bound is directly proportional to the former and inversely to the latter. In addition, it contains the equilibrium level of the predator-free point, which indicates the possibility of a transcritical bifurcation among the two equilibria.

Asymptotic stability of E_1 occurs for $R_0 < 1$; see (8). E_2 is feasible for $R_0 > 1$; see (4). These are opposite conditions so that a transcritical bifurcation occurs for which E_2 emanates from E_1 when the latter becomes unstable. Also, E_2 is stable for $\lambda_0^{[2]} < \lambda < \lambda_1^{[2]}$, which gives a condition for disease control.

The disease-free equilibrium E_3 is feasible when the predator search efficiency $h = (\alpha\sqrt{K})^{-1}$ lies in the interval $(h_0^{[3]}, h_1^{[3]})$; see (5). We find numerically the disease-free system experiences a Hopf bifurcation with bifurcation parameter h.

E_3 is stable for $h < h_1^{[3]}$ (see (10)), and the coexistence equilibrium is feasible for $h > h_1^{[3]}$ (see (7)) so that there exists a transcritical bifurcation for which the coexistence equilibrium E_* emanates from the disease-free equilibrium E_3 when the latter becomes unstable; recall Section 3.4.5.4. Also, for feasibility condition of the interior equilibrium, the force of infection must lie in the interval $(\lambda_0^{[*]}, \lambda_1^{[*]})$; see (7). This gives the condition for disease control. Based on these results, for all the equilibrium points, we underline the relevant role played by the parameter λ for the stability of points E_1 and E_2, while the parameter h is critical for achieving the disease-free equilibrium. The coexistence equilibrium evolution is regulated by the force of infection. Below a certain value of λ, the system may become extinct; Section 4.3.

In addition, the equilibria global stability conditions reported in Table 3 are obtained using Lyapunov and Lasalle theorem of Section 3.4.5.4.

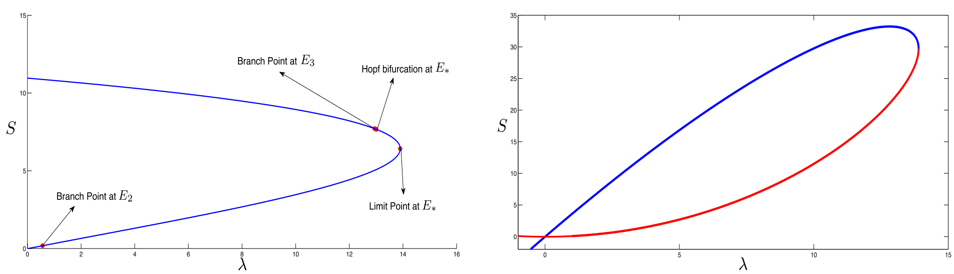
The crucial role of the parameters λ, μ, θ_2, δ, h and r in the control of the dynamical behavior of the system is therefore apparent. A future direction of the present work therefore can be well extended by introducing recovery of disease incorporating the prey refuge.

4.3 Bifurcations

We now investigate the bifurcations and corresponding limit point diagrams with respect to the disease transmission λ.

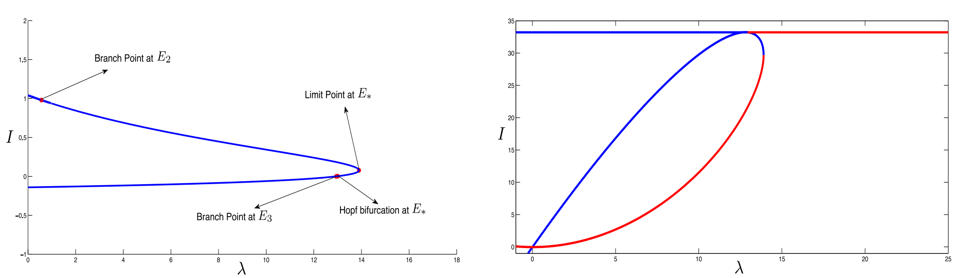
The parameter values are taken from Table 5 with initial conditions $S(0) = 7$, $I(0) = 0.7$, and $P(0) = 16$ and $\lambda = 1$, $h = 0.213$, $\mu = 0.1$, $m = 3$. Using MATCONT, we find the stable (blue) and unstable (red) branches of the bifurcations; see Figs. 4–5.

In each bifurcation diagram in the λS, λI, λP-planes, there exists a complete loop on the right half part. It has two branches, one of which is stable (blue), and the other is unstable (red) branch. The loop joins two different equilibria, thereby, it is a heteroclinic loop. This can be interpreted by saying that the heteroclinic point has different past and future. Also, the existence of a heteroclinic orbit for the critical parameter value related



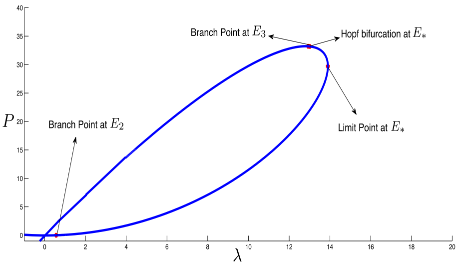
(a) (b)

Figure 4. (a) All bifurcation situations of (2) for susceptible prey S at all possible equilibria E_0, E_1, E_2, E_3 and E_* for the parameter values given in Table 5 and $\lambda = 1$, $h = 0.213$, $\mu = 0.1$, $m = 3$. (b) The bifurcation diagram with the stable (blue) and unstable (red) branches in the λS-plane.

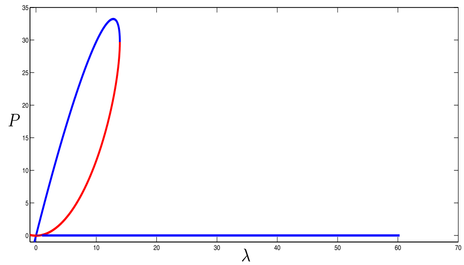


(a) (b)

Figure 5. (a) All bifurcation situations of (2) for the infected prey I at all equilibria E_0, E_1, E_2, E_3 and E_* for the parameter values in Table 5 and $\lambda = 1$, $h = 0.213$, $\mu = 0.1$, $m = 3$. (b) Bifurcation diagram with the stable (blue) and unstable (red) branches in the λI-plane.



(a)



(b)

Figure 6. (a) All bifurcation situations of (2) for the predators P at all equilibria E_0, E_1, E_2, E_3 and E_* for the parameter values in Table 5 and $\lambda = 1$, $h = 0.213$, $\mu = 0.1$, $m = 3$. (b) View of the bifurcation diagram with the stable (blue) and unstable (red) branches in the λP-plane.

to the force of infection implies biological overexploitation by the disease [21]. This shows that the force of infection affects the ultimate behavior of both system populations, determining their survival or extinction.

5 A comparison

The model presented here is closely related to the one of [23], where instead of the infected, it is the susceptible prey that behave individually. In both cases, the ecosystem cannot disappear, a result that from the biodiversity point of view is good. It is mainly due to the fact that environment has always means to support the prey, in particular healthy prey, by providing them enough feeding resources.

In [23] the predator-free point harbors always the disease endemically. In addition, we find the coexistence equilibrium in which also predators thrive, but where again the disease is not eradicated.

In this system, however, the disease can be eradicated, while the healthy prey is preserved at equilibrium E_1. Its feasibility and stability conditions provide the theoretical tools to achieve such goal if needed.

On the other hand, if the predators constitute a nuisance and should be eliminated, both here and [23] contain the predator-free point. The role of the relevant parameters in controlling the possible system outcomes have been elucidated and can be obtained from the tables provided in the previous sections.

The predator-free equilibrium becomes unstable for a very low predator mortality rate $\delta < \delta^{[1]}$, where $\delta^{[1]} = \theta_1 \alpha \sqrt{K}(1 + h\alpha\sqrt{K})^{-1}$; see (8). A similar result is found for the disease in predators [4, 9], where environmental carrying capacity K and the predation rate play an essential role. We find a supercritical pitchfork bifurcation around E_1 at K. In addition, the predator's average handling time h influences the threshold level. In [3], it is shown that the stability of the prey-only equilibrium in a predator–prey model with disease in predator changes when the predator mortality rate exceeds a threshold value. We have also similar results but for a large enough prey mortality rate, $\mu > \mu^{[1]}$, where λ influences the threshold value, which represents a different result from [3].

The predator-free point becomes unstable in the presence of the disease in [23]. But in this system the predator-free point is stable for $1 < R_0 < R_0^{[3]}$, where $R_0^{[3]} = \min\{\sqrt{3}, [\theta_2 mr\mu(\tau'\lambda^2)^{-1}]^{1/2}\}$; see (9).

In [2, 4, 9] the disease-free equilibrium is stable if the deaths of infected predator lie above a threshold value, where only susceptible predators thrive. A similar situation arises in [23], where the stability of the disease-free system required the predator mortality rate must fall below a threshold so that the predators invade the environment permanently. In this system, we find both upper and lower threshold value for predator mortality rate δ. For the feasibility of the equilibrium point, it must lie in the interval $(\delta_0^{[3]}, \delta_1^{[3]})$; see (5). The stability of E_3 holds for small enough predator's mortality rate, $\delta < \delta_1^{[3]}$; see (10). The predator average handling time h plays a role in both $\delta_0^{[3]}$ and $\delta_1^{[3]}$. A healthy predator–prey system becomes stable for predation rate above a threshold value in [3], but we get an opposite condition: the disease-free system is feasible for low prey search efficiency $\alpha < \alpha^{[3]}$, where $\alpha^{[3]} = \delta[\sqrt{K}(\theta_1 - \delta h)]^{-1}$.

Both prey-only and predator-free equilibria are unconditionally unstable in [24]. Instead, we get suitable stability conditions.

The different roles of the various parameters are shown in different equilibrium points. However, λ has the most crucial role for which a heteroclinic orbit in the coexistence equilibrium arises. It leads to extinction when the force of infection falls below the threshold $\lambda_0^{[*]}$; see (7). From the ecological point of view such a situation can arise due to overexploitation of force of infection discussed in Section 4.3. Both the theoretical and numerical analysis are found important to draw conclusions on a general level.

Acknowledgment. The authors are grateful to the reviewers for their beneficial comments and recommendations in the development of the manuscript.

Appendix A: The Jacobian J_B

A.1 Entries of $J_3 = (J_3^{ij}), i, j = 1, 2, 3$

$$
\begin{aligned}
J_3^{11} &= \frac{N_3^{11}}{2D_3^{11}}, \qquad J_3^{13} = (-\theta_1 + \delta h)\frac{\alpha}{\theta_1}, \qquad J_3^{22} = \frac{N_3^{22}}{D_3^{22}},\\
J_3^{31} &= \frac{r\delta K\alpha(-\theta_1+\delta h)^2}{K(-\theta_1+\delta h)^2\alpha^2 - \delta^2}, \qquad J_3^{32} = \frac{\theta_2 mr\delta\theta_1 K}{\alpha^2 K\theta_1^2 - 2\alpha^2 K\theta_1\delta h + \alpha^2 K\delta^2 h^2 - \delta^2},\\
N_3^{11} &= \bigl(\alpha^4K^2\theta_1^5 - 3\alpha^4K^2\theta_1^4\delta h + 2\alpha^4K^2\theta_1^3\delta^2h^2 - 4\alpha^2K\theta_1^3\delta^2 + 2\alpha^4K^2\theta_1^2\delta^3h^3\\
&\quad + 8\alpha^2K\theta_1^2\delta^3h\bigr)\bigl(-3\theta_1\alpha^4K^2\delta^4h^4 - 4\theta_1\alpha^2K\delta^4h^2 + 3\theta_1\delta^4 + \alpha^4\delta^5K^2h^5\bigr)r,\\
D_3^{11} &= \theta_1K(-\theta_1+\delta h)^2\alpha^2\bigl(\alpha^2K\theta_1^2 - 2\alpha^2K\theta_1\delta h\bigr) + \bigl(\alpha^2K\delta^2h^2 - \delta^2\bigr),\\
N_3^{22} &= -K\mu(-\theta_1+\delta h)^3\alpha^3 - K\delta\lambda(-\theta_1+\delta h)^2\alpha^2\\
&\quad - \delta(-\theta_1+\delta h)(-\mu\delta + mr\theta_1K)\alpha + \lambda\delta^3,\\
D_3^{22} &= \bigl(K(-\theta_1+\delta h)^2\alpha^2 - \delta^2\bigr)(-\theta_1+\delta h)\alpha.
\end{aligned}
$$

A.2 Values of l_1, l_2, l_3

$$l_1 = \frac{N^{l_1}}{D^{l_1}}, \qquad l_2 = \frac{\delta^2}{\theta_1^2\alpha^2 - 2\theta_1\alpha^2\delta h + \alpha^2\delta^2 h^2},$$
$$l_3 = \frac{\delta^2(3\theta_1 + \delta h)}{\alpha^2(\theta_1^3 - \theta_1^2\delta h - \theta_1\delta^2 h^2 + \delta^3 h^3)},$$
$$N^{l_1} = r\bigl(3\alpha^2\theta_1^3 - 5(2/5m + h\alpha^2)\delta\theta_1^2 + \theta_1\alpha^2\delta^2 h^2 + \delta^3 h^3\alpha^2\bigr)\delta^2,$$
$$D^{l_1} = \alpha^2(\delta h - \theta_1)^2\bigl(\alpha^2(r - 2\mu)\theta_1^3\bigr)\bigl(-\bigl(h(-4\mu + r)\alpha^2 - 2\lambda\alpha + 2rm\bigr)\delta\theta_1^2 - \bigl(h(2\mu + r)\alpha + 2\lambda\bigr)h\alpha\delta^2\theta_1 + r\alpha^2\delta^3 h^3\bigr),$$
$$G_2 = mr\delta^3\theta_1\bigl[\alpha^2\bigl(rm\delta\theta_1^3 - 2rm\delta^2\theta_1^2 h\bigr) + \bigl(rm\delta^3\theta_1 h^2 - \alpha\lambda\delta\theta_1^3 + 3\alpha\lambda\delta^2\theta_1^2 h - 3\alpha\lambda\delta^3\theta_1 h^2 + \lambda\delta^4\alpha h^3 + \theta_1^4\alpha^2\mu - 4\alpha^2\theta_1^3\mu\delta h + 6\theta_1^2\alpha^2\mu\delta^2 h^2\bigr) \times \bigl(-4\theta_1\alpha^2\mu\delta^3 h^3 + \alpha^2\mu\delta^4 h^4\bigr)\bigr]^{-1}.$$

Appendix B: Proof of Proposition 3

The Jacobian eigenvalues at E_* are the roots of the cubic equation $L^3 + b_1 L^2 + b_2 L + b_3 = 0$, where

$$b_1 = -\frac{1}{2}\frac{r(K - 3S_*^2)}{K} - \frac{1}{2}\frac{\alpha^2 P_* h}{(1 + h\alpha S_*)^2}, \quad b_2 = I_*\theta_2 m^2 P_* + \frac{1}{2}I_*\lambda^2 + \frac{\theta_1\alpha^2 P_*}{(2 + 2h\alpha S_*)^3},$$
$$b_3 = -\frac{I_*\theta_2 m^2 P_*}{2}\left[\frac{r(K - 3S_*^2)}{K} + \frac{\alpha^2 P_* h}{(1 + h\alpha S_*)^2}\right] - \frac{I_* m\theta_1\alpha P_*\lambda}{2(1 + h\alpha S_*)^2} - \frac{\alpha\lambda\theta_2 m I_* P_*}{2(1 + h\alpha S_*)}.$$

By the Routh–Hurwitz criteria asymptotic stability is achieved whenever $b_1 > 0$, $b_2 > 0$, $b_1 b_2 > b_3$, i.e., $K > \max\{y_1, y_2, y_3\}$, where

$$y_1 = \frac{1}{r}\bigl[3rS_*^2\bigl(1 + 2h\alpha S_* + h^2\alpha^2 S_*^2\bigr)\bigr] + 2rh\alpha S_* + rh^2\alpha^2 S_*^2 + \alpha^2 P_* h,$$
$$y_2 = \frac{1}{\theta_2 mr}\bigl(3\theta_2 mrS_*^2\bigl(1 + 2h\alpha S_* + h^2\alpha^2 S_*^2\bigr)\bigr) + 2\theta_2 mrh\alpha S_* + \theta_2 mrh^2\alpha^2 S_*^2 + \lambda\alpha\theta_1 + \lambda\alpha\theta_2 + \alpha^2\lambda\theta_2 hS_* + \theta_2 m\alpha^2 P_* h,$$
$$y_3 = \frac{z_1}{z_2},$$
$$z_1 = 3rS_*^2\bigl(\theta_1\alpha^2 P_* + 20I_*\lambda^2 h\alpha S_* + 40I_*\lambda^2 h^2\alpha^2 S_*^2\bigr) + 40I_*\lambda^2 h^3\alpha^3 S_*^3 + 20h^4\alpha^4 S_*^4 I_*\lambda^2 + 2h\alpha^3 S_*\theta_1 P_* + 4h^5\alpha^5 S_*^5 I_*\lambda^2 + h^2\alpha^4 S_*^2\theta_1 P_* + 4I_*\lambda^2,$$
$$z_2 = r\theta_1\alpha^2 P_* + 20rI_*\lambda^2 h\alpha S_* + 40rI_*\lambda^2 h^2\alpha^2 S_*^2 + 40rI_*\lambda^2 h^3\alpha^3 S_*^3 + 20rh^4\alpha^4 S_*^4 I_*\lambda^2 + 2rh\alpha^3 S_*\theta_1 P_* + 4rh^5\alpha^5 S_*^5 I_*\lambda^2 + rh^2\alpha^4 S_*^2\theta_1 P_* + 12\alpha^3 P_* h^2 I_*\lambda^2 S_* + 12\alpha^4 P_* h^3 I_*\lambda^2 S_*^2 + 4\alpha^5 P_* h^4 I_*\lambda^2 S_*^3 - 8I_* m\theta_1\alpha P_*\lambda - 8\alpha\lambda\theta_2 m I_* P_* + 4rI_*\lambda^2 + 4\alpha^2 P_* h I_*\lambda^2 + \alpha^4 P_* h\theta_1 P_* - 24\alpha^2\lambda m I_* P_*\theta_1 hS_*$$

$$
\begin{aligned}
&- 24\alpha^3\lambda m I_* P_* \theta_1 h^2 S_*^2 - 8\alpha^4\lambda m I_* P_* \theta_1 h^3 S_*^3 - 32\alpha^2\lambda m I_* P_* \theta_2 h S_* \\
&- 48\alpha^3\lambda m I_* P_* \theta_2 h^2 S_*^2 - 32\alpha^4\lambda m I_* P_* \theta_2 h^3 S_*^3 - 8\alpha^5\lambda m I_* P_* \theta_2 h^4 S_*^4.
\end{aligned}
$$

Appendix C: Proof of Theorem 1

We prove the persistence of system (2), applying average Lyapunov function method [7, 14]. Consider the Lyapunov function $V(S,I,P) = S^{j_0} I^{j_1} P^{j_2}$, where j_0, j_1 and j_2 are positive real numbers such that in the interior of $\mathbb{R}_+^3$,

$$
\begin{aligned}
\Theta(S,I,P) &= \frac{\dot V(S,I,P)}{V(S,I,P)} = j_0\frac{\dot S}{S} + j_1\frac{\dot I}{I} + j_2\frac{\dot P}{P} = \frac{N_\Theta}{D_\Theta},\\
N_\Theta &= j_0 rSK + j_0 rS^2Kh\alpha - j_0 rS^3 - j_0 rS^4 h\alpha - j_0\alpha PK - Ij_0\lambda K \\
&\quad + 2Ij_2K\theta_2 mh\alpha S + 2j_1K\lambda S + 2j_1K\lambda S^2 h\alpha - 2j_1KmP \\
&\quad - 2j_1KmPh\alpha S - 2j_1K\mu - 2j_1K\mu h\alpha S + 2j_2K\alpha + 2Ij_2K\theta_2 m \\
&\quad - Ij_0\lambda Kh\alpha S - 2j_2K\delta - 2j_2K\delta h\alpha S,\\
D_\Theta &= 2K(1 + h\alpha S).
\end{aligned}
$$

(i) At the trivial equilibrium point $E_0(0,0,0)$, $\Theta(0,0,0) = \alpha - \mu - \delta > 0$ if $\alpha > \mu + \delta$ when we choose $j_0 = j_1 = j_2$.

(ii) At the boundary equilibrium point,

$$
\Theta(\sqrt{K},0,0) = \frac{j_1\lambda\sqrt{K} + j_1\lambda Kh\alpha - j_1\mu - j_1\mu h\alpha\sqrt{K} + j_2\alpha - j_2\delta - j_2\delta h\alpha\sqrt{K}}{1 + h\alpha\sqrt{K}} > 0
$$

if $\alpha > (\mu + \delta - \lambda\sqrt{K})(1 + h\alpha\sqrt{K})$.

(iii) Similarly, at the predator-free equilibrium,

$$
\begin{aligned}
\Theta(S_2,I_2,0) = \frac{1}{K\lambda^4(\lambda + h\alpha\mu)} j_2\bigl(&K(\alpha-\delta)\lambda^5 - \delta h\alpha\mu K\lambda^4 + r\mu\theta_2 m\lambda^3 K \\
&+ r\mu^2\theta_2 mh\alpha K\lambda^2 - r\mu^3\theta_2 m\lambda - r\mu^4\theta_2 mh\alpha\bigr) > 0
\end{aligned}
$$

if

$$
\mu\theta_2 m\bigl(K\lambda^3 + \mu h\alpha K\lambda^2 - \mu^2\lambda - \mu^3 h\alpha\bigr) r > K\lambda^4(-\alpha\lambda + \delta\lambda + \delta h\alpha\mu),
$$

and the infected prey-free equilibrium is positive, that is,

$$
\begin{aligned}
\Theta(S_3,0,I_3) = \frac{1}{\theta_1\alpha^4(-\theta_1 + h\delta)^4 K}\bigl(&-K\alpha^4(-j_2\alpha + j_1\mu + j_2\delta)\theta_1^5 \\
&+ 4\bigl(-5/4 j_2 h\alpha^3 + h(j_1\mu + j_2\delta)\alpha^2 + 1/4 j_1\lambda\alpha - 1/4 j_1 mr\bigr)\delta\alpha^2 K\theta_1^4 \\
&- 6h\delta^2\alpha^2 K\bigl(-5/3 j_2 h\alpha^3 + h(j_1\mu + j_2\delta)\alpha^2 + 1/2 j_1\lambda\alpha - 1/3 j_1 mr\bigr)\theta_1^3 \\
&+ 4\delta^3\bigl(-5/2 j_2\alpha^5 Kh^3 + Kh^3(j_1\mu + j_2\delta)\alpha^4 \\
&+ 3/4 j_1\lambda\alpha^3 Kh^2 - 1/4 j_1 mrK\alpha^2 h^2 + 1/4 j_1 mr\bigr){\theta_1}^2 \\
&- h^3\delta^4\alpha^3 K\bigl(-5 j_2 h\alpha^2 + h(j_1\mu + j_2\delta)\alpha + j_1\lambda\bigr)\theta_1 - j_2\alpha^5 Kh^5\delta^5\bigr) > 0
\end{aligned}
$$

if we choose $j_0 = j_1 = j_2$ for all cases when

$$\begin{aligned}&\theta_1\big(\delta^5\theta_1 h^4 + 6\delta^3\theta_1^3 h^2 - 4\delta^4\theta_1^2 h^3 + 10\alpha\theta_1^2 h^3\delta^3 - 5\alpha\theta_1 h^4\delta^4 + 5\alpha\theta_1^4 h\delta \\ &\quad - 10\alpha\theta_1^3 h^2\delta^2 + \delta\theta_1^5 - \alpha\theta_1^5 - 4\delta^2\theta_1^4 h + \alpha h^5\delta^5\big) \\ &\quad < \alpha^4 K\big(\lambda\delta\alpha^3 K\theta_1^3 - 6\mu\alpha^4 K\theta_1^2 h^2\delta^2 + 4\mu\alpha^4 K\theta_1 h^3\delta^3 - \mu\alpha^4 K h^4\delta^4 \\ &\quad + mr\delta^3\theta_1 - \mu\alpha^4 K\theta_1^4 + 3\lambda\delta^3\alpha^3 K\theta_1 h^2 - \lambda\delta^4\alpha^3 K h^3 - mr\delta\theta_1^3 K\alpha^2 \\ &\quad - 3\lambda\delta^2\alpha^3 K\theta_1^2 h + 2mr\delta^2\theta_1^2 K\alpha^2 h - mr\delta^3\theta_1 K\alpha^2 h^2 + 4\mu\alpha^4 K\theta_1^3 h\delta\big).\end{aligned}$$

Since the value of $\Theta(S, I, P)$ is positive at all boundary points, system (2) is persistent.

Appendix D: Proof of Proposition 4

Bifurcation analysis deals with structurally unstable systems. The characteristic equation of (2) at E_* is

$$x^3 + a_1x^2 + a_2x + a_3 = 0, \tag{D.27}$$

where $a_1 = -\operatorname{tr}(J_*)$, $a_2 = M_{J_*}$, $a_3 = -\det(J_*)$. Now when $\lambda = \lambda_{\mathrm{cr}}$ so that $a_1a_2 = a_3$, the characteristic equation (D.27) factorizes as $(x^2 + a_2)(x + a_1) = 0$. Its roots are $x_1 = \imath\sqrt{a_2}$, $x_2 = -\imath\sqrt{a_2}$, $x_3 = -a_1$. In a neighborhood of λ_{cr}, the roots of the characteristic equation (D.27) for all λ are of the form $x_1 = \tau_1(\lambda) + \imath\tau_2(\lambda)$, $x_2 = \tau_1(\lambda) - \imath\tau_2(\lambda)$, $x_3 = -\tau_3(\lambda)$, where $\tau_1(\lambda)$, $\tau_2(\lambda)$, $\tau_3(\lambda)$ are real.

To verify the transversality condition, we substitute $x(\lambda) = \tau_1(\lambda) + \imath\tau_2(\lambda)$ into (D.27) to get

$$(\tau_1 + \imath\tau_2)^3 + a_1(\tau_1 + \imath\tau_2)^2 + a_2(\tau_1 + \imath\tau_2) + a_3 = 0.$$

Separating the real and imaginary parts, we find

$$\begin{aligned}&\tau_1^3 - 3\tau_1\tau_2^2 + a_1\big(\tau_1^2 - \tau_2^2\big) + a_2\tau_1 + a_3 = 0, \\ &3\tau_1^2\tau_2 - \tau_2^3 + 2a_1\tau_1\tau_2 + a_2\tau_2 = 0.\end{aligned} \tag{D.28}$$

From the second equation of (D.28), as $\tau_2 \neq 0$, we can set

$$f(\tau_1) = \tau_2^2 = 3\tau_1^2 + 2a_1\tau_1 + a_2, \tag{D.29}$$

and substituting the value of τ_2^2 into the first equation of (D.28), we get

$$\tau_1^3 - 3\tau_1 f(\tau_1) + a_1\big(\tau_1^2 - f(\tau_1)\big) + a_2\tau_1 + a_3 = 0. \tag{D.30}$$

Differentiating (D.30) with respect to λ, we get

$$\begin{aligned}&3\tau_1^2\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda} - 3\tau_1 f'(\tau_1)\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda} - 3f(\tau_1)\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda} + \frac{\mathrm{d}a_1}{\mathrm{d}\lambda}\big(\tau_1^2 - f(\tau_1)\big) \\ &\quad + a_1\big(2\tau_1 - f'(\tau_1)\big)\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda} + \tau_1\frac{\mathrm{d}a_2}{\mathrm{d}\lambda} + a_2\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda} + \frac{\mathrm{d}a_3}{\mathrm{d}\lambda} = 0.\end{aligned}$$

Since $\tau_1(\lambda_{\mathrm{cr}}) = 0$, from (D.29) we get $f(0) = a_2$ and $f'(0) = 2a_1$. Thus

$$\left[\frac{\mathrm{d}\tau_1}{\mathrm{d}\lambda}\right]_{\lambda=\lambda_{\mathrm{cr}}} = -\frac{1}{2(a_1^2 + a_2)}\left[\frac{\mathrm{d}a_3}{\mathrm{d}\lambda} - a_2\frac{\mathrm{d}a_1}{\mathrm{d}\lambda}\right] = \lambda_{\mathrm{cr}} \neq 0,$$
$$x_3(\lambda_{\mathrm{cr}}) = -\tau_3(\lambda_{\mathrm{cr}}).$$

Now $[\mathrm{d}\tau_1/\mathrm{d}\lambda]_{\lambda=\lambda_{\mathrm{cr}}} < 0$ when the condition of Proposition 3 is satisfied. Hence, E_* is unstable when $\lambda < \lambda_{\mathrm{cr}}$, and stable when $\lambda > \lambda_{\mathrm{cr}}$. Thus a Hopf bifurcation occurs at $\lambda = \lambda_{\mathrm{cr}}$.

Appendix E: Notations used in other bifurcations

The variational matrix is as follows:

$$\begin{aligned}
&D^2F(x,m)(U,U) \\
&\quad= \frac{\partial^2 F}{\partial x^2}u_1^2 + \frac{\partial^2 F}{\partial x\partial y}u_1u_2 + \frac{\partial^2 F}{\partial x\partial z}u_1u_3 + \frac{\partial^2 F}{\partial y\partial x}u_2u_1 + \frac{\partial F}{\partial y^2}u_2^2 \\
&\qquad+ \frac{\partial^2 F}{\partial y\partial z}u_2u_3 + \frac{\partial^2 F}{\partial z\partial x}u_3u_1 + \frac{\partial^2 F}{\partial z\partial y}u_3u_2 + \frac{\partial^2 F}{\partial z^2}u_3^2, \\
&D^3F(x,m)(U,U,U) \\
&\quad= \frac{\partial^3 F}{\partial x^3}u_1^3 + \frac{\partial^3 F}{\partial x^2\partial y}u_1^2u_2 + \frac{\partial^3 F}{\partial x^2\partial z}u_1^2u_3 + \frac{\partial^3 F}{\partial y\partial x^2}u_2u_1^2 + \frac{\partial^3 F}{\partial x\partial y^2}u_1u_2^2 \\
&\qquad+ \frac{\partial^3 F}{\partial x\partial y\partial z}u_1u_2u_3 + \frac{\partial^3 F}{\partial x\partial x^2}u_3u_1^2 + \frac{\partial^3 F}{\partial x\partial y\partial z}u_1u_3u_2 + \frac{\partial^3 F}{\partial x\partial z^2}u_1u_3^2 \\
&\qquad+ \frac{\partial^3 F}{\partial y\partial x^2}u_2u_1^2 + \frac{\partial^3 F}{\partial x\partial y^2}u_1u_2^2 + \frac{\partial^3 F}{\partial y\partial x\partial z}u_2u_1u_3 + \frac{\partial^3 F}{\partial y^2\partial x}u_2^2u_1 + \frac{\partial^3 F}{\partial y^3}u_2^3 \\
&\qquad+ \frac{\partial^3 F}{\partial y^2\partial z}u_2^2u_3 + \frac{\partial^3 F}{\partial y\partial z\partial x}u_2u_3u_1 + \frac{\partial^3 F}{\partial z\partial y^2}u_3u_2^2 + \frac{\partial^3 F}{\partial y\partial z^2}u_2u_3^2 + \frac{\partial^3 F}{\partial z\partial x^2}u_3u_1^2 \\
&\qquad+ \frac{\partial^3 F}{\partial z\partial x\partial y}u_3u_1u_2 + \frac{\partial^3 F}{\partial x\partial z^2}u_1u_3^2 + \frac{\partial^3 F}{\partial z\partial y\partial x}u_3u_2u_1 + \frac{\partial^3 F}{\partial z\partial y^2}u_3u_2^2 \\
&\qquad+ \frac{\partial^3 F}{\partial y\partial z^2}u_2u_3^2 + \frac{\partial^3 F}{\partial x^2\partial x}u_3^2u_1 + \frac{\partial^3 F}{\partial z^2\partial y}u_3^2u_2 + \frac{\partial^3 F}{\partial z^3}u_3^2,
\end{aligned}$$

where $F = (F_1, F_2, F_3)^{\mathrm{T}}$, and

$$V^{\mathrm{T}}F_m(E_*, m_4) = \frac{\theta_2 P_*(P_*\alpha + I_*\lambda + I_*\lambda h\alpha S_*)\mu_3'}{(1 + h\alpha S_*)\lambda},$$
$$V^{\mathrm{T}}DF(E_*, m_4)(U) = -\frac{\eta_1}{K(1 + h\alpha S)^2)\lambda},$$
$$V^{\mathrm{T}}D^2F(E_*, m_4)(U,U) = -\frac{\eta_2}{K(1 + h\alpha S_*)^3\lambda},$$
$$V^{\mathrm{T}}D^3F(E_*, m_4)(U,U,U) = \frac{\eta_3}{K(1 + h\alpha S_*)^4\lambda};$$

$$
\begin{aligned}
\eta_1 &= \mu_3'\bigl(-\theta_2 m P_*\gamma_1' r K + 3\theta_2 m P_*\gamma_1' r S_*^2 - K\lambda\theta_1\alpha P_*\gamma_1' - K\lambda\mu_3'\theta_1\alpha S_*\\
&\quad + \alpha\theta_2 P_* K\lambda\gamma_1' + K\lambda\mu_3'\delta - \theta_2 m P_*^2\gamma_1'\alpha^2 hK - K\lambda\mu_3'\theta_1\alpha^2 S_*^2 h + 2K\lambda\mu_3'\delta h\alpha S_*\\
&\quad + K\lambda\mu_3'\delta h^2\alpha^2 S_*^2 + I_*\alpha^2\theta_2 P_* K\mu_2'\mu h S_* + I_*\alpha^2\theta_2 P_*^2 K\mu_2' m h S_*\\
&\quad - I_*\alpha^2\theta_2 P_* K\mu_2'\lambda S_*^2 h + I_*\alpha\theta_2 P_* K\mu_2'\mu + I_*\alpha\theta_2 P_*^2 K\mu_2' m + \alpha^2\theta_2 P_* K\lambda\gamma_1' h S_*\\
&\quad + 6\theta_2 m P_*\gamma_1' r S_*^3 h\alpha - 2\theta_2 m P_*\gamma_1' r K h\alpha S_* - \theta_2 m P_*\gamma_1' r K h^2\alpha^2 S_*^2\\
&\quad - I_*\alpha\theta_2 P_* K\mu_2'\lambda S_* - I_* K\lambda\mu_3'\theta_2 m h^2\alpha^2 S_*^2 - 2I_* K\lambda\mu_3'\theta_2 m h\alpha S_*\\
&\quad - I_* K\lambda\mu_3'\theta_2 m + 3\theta_2 m P_*\gamma_1' r S_*^4 h^2\alpha^2\bigr),\\
\eta_2 &= \mu_3'(6\theta_2 m P_*{\gamma_1'}^2 r S_* + 18\theta_2 m P_*{\gamma_1'}^2 r S_*^2 h\alpha + 18\theta_2 m P_*{\gamma_1'}^2 r S_*^3 h^2\alpha^2\\
&\quad + 6\theta_2 m P_*{\gamma_1'}^2 r S_*^4 h^3\alpha^3 + 2\theta_2 m P_*^2{\gamma_1'}^2\alpha^3 h^2 K - \theta_2 m P_*\gamma_1'\alpha^2\mu_3' h K\\
&\quad - \theta_2 m P_*\gamma_1'\alpha^3\mu_3' h^2 K S_* + I_*\mu_2'\alpha^3\theta_2 P_* K m\mu_3' h^2 S_*^2 - I_*\gamma_1'\mu_2'\alpha\theta_2 P_* K\lambda\\
&\quad + I_*\mu_2'\alpha\theta_2 P_* K m\mu_3' - I_*\gamma_1'\mu_2'\alpha^3\theta_2 P_* K\lambda h^2 S_*^2 - 2I_*\gamma_1'\mu_2'\alpha^2\theta_2 P_* K\lambda h S_*\\
&\quad + 2I_*\mu_2'\alpha^2\theta_2 P_* K m\mu_3' h S_* + 2K\lambda\theta_1\alpha^2 P_* h{\gamma_1'}^2 - K\lambda\theta_2 m\mu_3'\mu_2'\\
&\quad - 3K\lambda\theta_2 m\mu_3'\mu_2' h\alpha S_* - 3K\lambda\theta_2 m\mu_3'\mu_2' h^2\alpha^2 S_*^2 - K\lambda\theta_2 m\mu_3'\mu_2' h^3\alpha^3 S_*^3\\
&\quad - K\lambda\theta_1\alpha\gamma_1'\mu_3' - K\lambda\theta_1\alpha^2\gamma_1'\mu_3' h S_*\bigr),\\
\eta_3 &= 2{\gamma_1'}^2\mu_3'\bigl(-3\theta_2 m P_*\gamma_1' r - 12\theta_2 m P_*\gamma_1' r h\alpha S_* - 18\theta_2 m P_*\gamma_1' r h^2\alpha^2 S_*^2\\
&\quad - 12\theta_2 m P_*\gamma_1' r h^3\alpha^3 S_*^3 - 3\theta_2 m P_*\gamma_1' r h^4\alpha^4 S_*^4 + 3\theta_2 m P_*^2\gamma_1'\alpha^4 h^3 K\\
&\quad - 2\theta_2 m P_*\alpha^3 h^2\mu_3' K - 2\theta_2 m P_*\alpha^4 h^3\mu_3' K S_* + 3\theta_1\alpha^3 h^2 K\lambda P_*\mu_1'\\
&\quad - 2\theta_1\alpha^2 h K\lambda\mu_3' - 2\theta_1\alpha^3 h^2 K\lambda\mu_3' S_*\bigr),\\
m &= \frac{N_m}{D_m},\\
N_m &= I_*\mu_1'\mu_2'\alpha\theta_2 P_* K\lambda + 2I_*\mu_1'\mu_2'\alpha^2\theta_2 P_* K\lambda h S_* + I_*\mu_1'\mu_2'\alpha^3\theta_2 P_* K\lambda h^2 S_*^2\\
&\quad - 2K\lambda\theta_1\alpha^2 P_* h{\mu_1'}^2 + K\lambda\theta_1\alpha\mu_1'\mu_3' + K\lambda\theta_1\alpha^2\mu_1'\mu_3' h S_*\\
D_m &= 18\theta_2 P_*{\mu_1'}^2 r S_*^2 h\alpha + 18\theta_2 P_*{\mu_1'}^2 r S_*^3 h^2\alpha^2 + 6\theta_2 P_*{\mu_1'}^2 r S^4 h^3\alpha^3\\
&\quad - \theta_2 P_*\mu_1'\alpha^2\mu_3' h K - \theta_2 P_*\mu_1'\alpha^3\mu_3' h^2 K S_* + I_*\mu_2'\alpha^3\theta_2 P_* K\mu_3' h^2 S_*^2\\
&\quad + I_*\mu_2'\alpha\theta_2 P_* K\mu_3' + 2I_*\mu_2'\alpha^2\theta_2 P_* K\mu_3' h S_* - 3K\lambda\theta_2\mu_3'\mu_2' h\alpha S_*\\
&\quad - 3K\lambda\theta_2\mu_3'\mu_2' h^2\alpha^2 {S_*}^2 - K\lambda\theta_2\mu_3'\mu_2' h^3\alpha^3 S_*^3 + 2\theta_2 P_*^2{\mu_1'}^2\alpha^3 h^2 K\\
&\quad + 6\theta_2 P_*{\mu_1'}^2 r S_* - K\lambda\theta_2\mu_3'\mu_2',
\end{aligned}
$$

$$
K^{[te_{2I}]} = \frac{\theta_2 m r\mu^3(\lambda + h\alpha\mu)}{\lambda^2(-\delta\lambda^3 + \lambda^2\theta_1\mu\alpha - \lambda^2\delta h\alpha\mu + \theta_2 m r\mu\lambda + \theta_2 m r\mu^2 h\alpha)},
$$

$$
\begin{aligned}
K^{[te_3]} &= \frac{m r\delta^3\theta_1}{\varXi},\\
\varXi &= \alpha^2\bigl(\mu\alpha^2\theta_1^4 - 4\mu\alpha^2\theta_1^3\delta h + 6\mu\alpha^2\theta_1^2\delta^2 h^2 - 4\mu\alpha^2\theta_1\delta^3 h^3 + \mu\alpha^2\delta^4 h^4 - \lambda\delta\alpha\theta_1^3\\
&\quad + 3\lambda\delta^2\alpha\theta_1^2 h - 3\lambda\delta^3\alpha\theta_1 h^2 + \lambda\delta^4\alpha h^3 + m r\delta\theta_1^3 - 2m r\delta^2\theta_1^2 h + m r\delta^3\theta_1 h^2\bigr).
\end{aligned}
$$

Now $\lambda^{[te_{2I}]}$ is the positive root of the equation $\sum_{i=0}^{5} b_i X^i = 0$, where

$$b_0 = \theta_2 mr\mu^4 h\alpha, \qquad b_1 = \theta_2 mr\mu^3, \qquad b_2 = -\theta_2 mr\mu^2 Kh\alpha,$$
$$b_3 = -\theta_2 mr\mu K, \qquad b_4 = K\alpha\mu(\delta h - \theta_1), \qquad b_5 = \delta K,$$

$\mu^{[te_{2I}]}$ is the positive root of the equation $\sum_{i=0}^{4} c_i Y^i = 0$, where

$$c_0 = \delta K\lambda, \qquad c_1 = -\lambda\theta_1\alpha K + \lambda\delta Kh\alpha - \theta_2 mrK,$$
$$c_2 = -\theta_2 mrKh\alpha, \qquad c_3 = \theta - 2mr, \qquad c_4 = \theta_2 mrh\alpha,$$

and $K^{[te_3]}$ is the positive root of the equation $\sum_{i=0}^{4} d_i Z^i/(\delta\alpha) = 0$, where

$$\begin{aligned}
d_0 &= \mu\alpha^4 K\theta_1^4 - \lambda\delta\alpha^3 K\theta_1^3 - mr\delta^3\theta_1 + mr\delta\theta_1^3 K\alpha^2,\\
d_1 &= 3\delta\lambda K\theta_1^2\alpha^2 - 2\delta mKr\theta_1^2\alpha - 4\mu K\theta_1^3\alpha^3,\\
d_2 &= -3\delta\lambda\theta_1\alpha + mKr\delta\theta_1 + 6\mu K\theta_1^2\alpha^2,\\
d_3 &= \lambda K\delta - 4\mu K\theta_1\alpha, \qquad d_4 = \mu K.
\end{aligned}$$

Appendix F: Notations used in Section 3.4.5.6

$$\begin{aligned}
\varPi = {}& Q_{11}\biggl[T^2 h\biggl\{(U_{11}I_1+U_{12}I_2)\biggl(U_{31}I_1+U_{32}I_2+U_{33}\frac{\varLambda}{2}\biggr) + U_{13}\frac{\varLambda}{2}(U_{31}I_1+U_{32}I_2)\biggr\}\\
& - T_1\bigl\{(U_{11}I_1+U_{12}I_2)^2 + U_{13}\varLambda(U_{11}I_1+U_{12}I_2)\bigr\}\biggr]\\
& + Q_{12}\biggl[\lambda\biggl\{(U_{11}I_1+U_{12}I_2)\biggl(U_{21}I_1+U_{22}I_2+U_{23}\frac{\varLambda}{2}\biggr) + U_{13}\frac{\varLambda}{2}(U_{21}I_1+U_{22}I_2)\biggr\}\\
& - m\biggl\{(U_{31}I_1+U_{32}I_2)\biggl(U_{21}I_1+U_{22}I_2+U_{23}\frac{\varLambda}{2}\biggr) + U_{33}\frac{\varLambda}{2}(U_{21}I_1+U_{22}I_2)\biggr\}\biggr]\\
& + Q_{13}\biggl[\bigl(\theta_1 T - \theta_1 T^2 hS_*\bigr)\biggl\{(U_{11}I_1+U_{12}I_2)\biggl(U_{31}I_1+U_{32}I_2+U_{33}\frac{\varLambda}{2}\biggr)\\
& + U_{13}\frac{\varLambda}{2}(U_{31}I_1+U_{32}I_2)\biggr\}\\
& - \theta_2 m\biggl\{(U_{31}I_1+U_{32}I_2)\biggl(U_{21}I_1+U_{22}I_2+U_{23}\frac{\varLambda}{2}\biggr) + U_{33}\frac{\varLambda}{2}(U_{21}I_1+U_{22}I_2)\biggr\}\\
& + \bigl(2\theta_1 T^3 h^2 S_* P_* - 2\theta_1 T^2 P_* h\bigr)\bigl\{(U_{11}I_1+U_{12}I_2)^2 + U_{13}\varLambda(U_{11}I_1+U_{12}I_2)\bigr\}\biggr],
\end{aligned}$$

$$\begin{aligned}
\varPi_{11} = {}& Q_{11}\bigl[T^2 h\{2U_{11}U_{31}\} - T_1\bigl\{2U_{11}^2\bigr\}\bigr] + Q_{12}\bigl[\lambda\{2U_{11}U_{21}\} - m\{2U_{31}U_{21}\}\bigr]\\
& + Q_{13}\bigl[\bigl(\theta_1 T - \theta_1 T^2 hS^*\bigr)\{2U_{11}U_{31}\} - \theta_2 m\{2U_{31}U_{21}\}\\
& + \bigl(2\theta_1 T^3 h^2 S_* P_* - 2\theta_1 T^2 hP_*\bigr)\{2U_{11}^2\}\bigr],
\end{aligned}$$

$$
\begin{aligned}
\varPi_{22} = {} & U_{11}\bigl[T^2h\{2U_{12}U_{32}\} - T_1\bigl\{2U_{12}^2\bigr\}\bigr] + Q_{12}\bigl[\lambda\{2U_{12}U_{22}\} - m\{2U_{32}U_{22}\}\bigr] \\
& + Q_{13}\bigl[\bigl(\theta_1 T - \theta_1 T^2 hS_*\bigr)\{2U_{12}U_{32}\} - \theta_2 m\{2U_{32}U_{22}\} \\
& + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\bigl\{2{U_{12}}^2\bigr\}\bigr], \\
\varPi_{12} = {} & U_{11}\bigl[T^2h\{U_{11}U_{32} + U_{12}U_{31}\} - T_1\{2U_{12}U_{11}\}\bigr] + Q_{12}\bigl[\lambda\{U_{11}U_{22} + U_{12}U_{21}\} \\
& - m\{U_{31}U_{22} + U_{32}U_{21}\}\bigr] + Q_{13}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{U_{11}U_{32} + U_{12}U_{31}\} \\
& - \theta_2 m\{U_{31}U_{22} + U_{32}U_{21}\} + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\{2U_{12}U_{11}\}\bigr], \\
\varSigma_{11} = {} & Q_{21}\bigl[T^2h\{2U_{11}U_{31}\} - T_1\bigl\{2{U_{11}}^2\bigr\}\bigr] + Q_{22}\bigl[\lambda\{2U_{11}U_{21}\} - m\{2U_{31}U_{21}\}\bigr] \\
& + Q_{23}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{2U_{11}U_{31}\} - \theta_2 m\{2U_{31}U_{21}\} \\
& + (2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*)\bigl\{2{U_{11}}^2\bigr\}\bigr], \\
\varSigma_{22} = {} & Q_{21}\bigl[T^2h\{2U_{12}U_{32}\} - T_1\bigl\{2{U_{12}}^2\bigr\}\bigr] + Q_{22}\bigl[\lambda\{2U_{12}U_{22}\} - m\{2U_{32}U_{22}\}\bigr] \\
& + Q_{23}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{2U_{12}U_{32}\} - \theta_2 m\{2U_{32}U_{22}\} \\
& + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\bigl\{2{U_{12}}^2\bigr\}\bigr], \\
\varSigma_{12} = {} & Q_{21}\bigl[T^2h\{U_{11}U_{32} + U_{12}U_{31}\} - T_1\{2U_{12}U_{11}\}\bigr] + Q_{22}\bigl[\lambda\{U_{11}U_{22} + U_{12}U_{21}\} \\
& - m\{U_{31}U_{22} + U_{32}U_{21}\}\bigr] + Q_{23}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{U_{11}U_{32} + U_{12}U_{31}\} \\
& - \theta_2 m\{U_{31}U_{22} + U_{32}U_{21}\} + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\{2U_{12}U_{11}\}\bigr], \\
\varSigma_{222} = {} & Q_{21}\bigl[T^2h\{3U_{12}U_{33}b_{22} + 3U_{13}U_{32}b_{22}\}\bigr] \\
& + Q_{22}\bigl[\lambda\{3U_{12}U_{23}b_{22} + 3U_{13}U_{22}b_{22}\} - m\{3U_{32}U_{23}b_{22} + 3U_{33}U_{22}b_{22}\}\bigr] \\
& + Q_{23}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{3U_{12}U_{33}b_{22} + 3U_{13}U_{32}b_{22}\} \\
& - \theta_2 m\{3U_{32}U_{23}b_{22} + 3U_{33}U_{22}b_{22}\} \\
& + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\{6b_{22}U_{13}U_{12}\}\bigr], \\
\varSigma_{112} = {} & Q_{21}\bigl[T^2h\{2U_{11}U_{33}b_{12} + U_{12}U_{33}b_{11} + 2U_{13}U_{31}b_{12} + U_{13}U_{32}b_{11}\}\bigr] \\
& + Q_{22}[\lambda\{2U_{11}U_{23}b_{12} + U_{12}U_{23}b_{11} + 2U_{13}U_{21}b_{12} + U_{13}U_{22}b_{11}\} \\
& - m\{2U_{31}U_{23}b_{12} + U_{32}U_{23}b_{11} + 2U_{33}U_{21}b_{12} + U_{33}U_{22}b_{11}\}] \\
& + Q_{23}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr) \\
& \times \{2U_{11}U_{33}b_{12} + U_{12}U_{33}b_{11} + 2U_{13}U_{31}b_{12} + U_{13}U_{32}b_{11}\} \\
& - \theta_2 m\{2U_{31}U_{23}b_{12} + U_{32}U_{23}b_{11} + 2U_{33}U_{21}b_{12} + U_{33}U_{22}b_{11}\} \\
& + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\{2b_{11}U_{13}U_{12} + 4b_{12}U_{13}U_{11}\}\bigr], \\
\varPi_{111} = {} & Q_{11}\bigl[T^2h\{3U_{11}U_{33}b_{11} + 3U_{13}U_{31}b_{11}\}\bigr] \\
& + Q_{12}\bigl[\lambda\{3U_{11}U_{23}b_{11} + 3U_{13}U_{21}b_{11}\} - m\{3U_{31}U_{23}b_{11} + 3U_{33}U_{21}b_{11}\}\bigr] \\
& + Q_{13}\bigl[\bigl(\theta_1 T - \theta_1 T^2hS_*\bigr)\{3U_{11}U_{33}b_{11} + 3U_{13}U_{31}b_{11}\} \\
& - \theta_2 m\{3U_{31}U_{23}b_{11} + 3U_{33}U_{21}b_{11}\} \\
& + \bigl(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2hP_*\bigr)\{6b_{11}U_{13}U_{11}\}\bigr],
\end{aligned}
$$

$$\begin{aligned}
\Pi_{122} &= Q_{11}\big[T^2h\{U_{11}U_{33}b_{22} + 2U_{12}U_{33}b_{12} + U_{13}U_{31}b_{22} + 2U_{13}U_{32}b_{12}\}\big] \\
&\quad + Q_{12}\big[\lambda\{U_{11}U_{23}b_{22} + 2U_{12}U_{23}b_{12} + U_{13}U_{21}b_{22} + 2U_{13}U_{22}b_{12}\} \\
&\quad - m\{U_{31}U_{23}b_{22} + 2U_{32}U_{23}b_{12} + U_{33}U_{21}b_{22} + 2U_{33}U_{22}b_{12}\}\big] \\
&\quad + Q_{13}\big[(\theta_1 T - \theta_1 T^2 hS_*)\{U_{11}U_{33}b_{22} + 2U_{12}U_{33}b_{12} + U_{13}U_{31}b_{22} + 2U_{13}U_{32}b_{12}\} \\
&\quad - \theta_2 m\{U_{31}U_{23}b_{22} + 2U_{32}U_{23}b_{12} + U_{33}U_{21}b_{22} + 2U_{33}U_{22}b_{12}\} \\
&\quad + \big(2\theta_1 T^3h^2S_*P_* - 2\theta_1 T^2 hP_*\big)\{4b_{12}U_{13}U_{12} + 2b_{22}U_{13}U_{11}\}\big].
\end{aligned}$$

Appendix G: Proof of global stability

G.1 At E_1

Let $\mathbb{R}^3 = [(S, I, P) \in \mathbb{R}^3\colon\ S > 0,\ I \geqslant 0,\ P \geqslant 0]$ and consider the scalar function defined in [1, 11]

$$Z_1 = \left(S - S_1 - S_1 \ln\frac{S}{S_1}\right) + I + P. \tag{G.31}$$

The derivative of (G.31) along the solution trajectories of (2) is

$$\frac{\mathrm{d}Z_1}{\mathrm{d}t} = \left(1 - \frac{s_1}{S}\right)\frac{\mathrm{d}S}{\mathrm{d}t} + \frac{\mathrm{d}I}{\mathrm{d}t} + \frac{\mathrm{d}P}{\mathrm{d}t} = \left(1 - \frac{S_1}{S}\right)\left(\frac{1}{2}rS\left(1 - \frac{S^2}{K}\right)\right). \tag{G.32}$$

At the equilibrium point E_1 of system (2), we have $K = S_1^2$, and using it in (G.32), we obtain

$$\frac{\mathrm{d}Z_1}{\mathrm{d}t} = \frac{1}{2}r(S - S_1)\left(1 - \frac{S^2}{S_1^2}\right) = -\frac{r}{2S_1^2}(S - S_1)^2(S + S_1) \leqslant 0 \tag{G.33}$$

with the derivative vanishing when $(S, I, P) = (S_1, 0, 0)$. The proof follows from (G.33) and Lyapunov–Lasalle's invariance principle [11].

G.2 At E_2

Let $\mathbb{R}^3_+ = [(S, I, P) \in \mathbb{R}^3_+\colon\ S > 0,\ I > 0,\ P \geqslant 0]$ and consider the scalar function $Z_2 : \mathbb{R}^3_+ \to \mathbb{R}$ defined by

$$Z_2 = k_0\left(S - S_2' - S_2' \ln\frac{S}{S_2'}\right) + \left(I - I_2' - I_2' \ln\frac{I}{I_2'}\right). \tag{G.34}$$

The derivative of equation (G.34) along the solution of system (2) is given by

$$\begin{aligned}
\frac{\mathrm{d}Z_2}{\mathrm{d}t} &= k_2\left(1 - \frac{S_2'}{S}\right)\frac{\mathrm{d}S}{\mathrm{d}t} + \left(1 - \frac{I^*}{I}\right)\frac{\mathrm{d}I}{\mathrm{d}t} \\
&= \frac{k_0}{2}\left(1 - \frac{S_2'}{S}\right)\left(rS - \frac{rS^3}{K} - \lambda I\right) + (I - I_2')(\lambda S - \mu).
\end{aligned} \tag{G.35}$$

At the equilibrium point E_2 of system (2), we have

$$rS_2' - \frac{rS_2'^3}{K} - \lambda I_2' = 0, \qquad \mu = \lambda S_2'. \tag{G.36}$$

Then equations (G.36) reduce (G.35) to

$$\begin{aligned}
\frac{\mathrm{d}Z_2}{\mathrm{d}t} &= \frac{k_0}{2}\frac{S-S_2'}{S}\left[rS - \frac{rS^3}{K} - \lambda I - \left(rS_2' - \frac{rS_2'^3}{K} - \lambda I_2'\right)\right] + \lambda(I-I_2')(S-S_2') \\
&= \frac{k_0}{2S}(S-S_2')\left[r(S-S_2') - \frac{r}{K}\left(S^3 - S_2'^3\right) - \lambda(I-I_2')\right] + \lambda(I-I_2')(S-S_2') \\
&= \frac{k_0 r}{2S}(S-S_2')^2 - \frac{rk_0}{2KS}(S-S_2')^2\left(S^2 + SS - 2 + S_2'^2\right) \\
&\quad - \frac{\lambda k_0}{2S}(S-S_2')(I-I_2') + \lambda(S-S_2')(I-I_2') \\
&\leqslant \left[\frac{k_0 r}{2S} - \frac{k_0 r}{2KS}\left(S^2 + SS_2' + S_2'^2\right) - \frac{\lambda k_0}{4S} + \frac{\lambda}{2}\right](S-S_2')^2 + \left[\frac{\lambda}{2} - \frac{\lambda k_0}{4S}\right](I-I_2')^2 \\
&< \left[\frac{k_0 r\sqrt{K}}{2} - \frac{k_0 rL}{2\sqrt{K}} - \frac{\lambda k_0\sqrt{K}}{4} + \frac{\lambda}{2}\right](S-S_2')^2 + \left[\frac{\lambda}{2} - \frac{\lambda k_0\sqrt{K}}{4}\right](I-I_2')^2
\end{aligned} \tag{G.37}$$

so that the above derivative is nonpositive if

$$k_0 r\sqrt{K} + \lambda \leqslant \frac{k_0 rL}{\sqrt{K}} + \frac{\lambda\sqrt{K}k_0}{2}, \qquad \frac{2}{\sqrt{K}} < k_0,$$

and it vanishes when $(S, I, P) = (S_2', I_2', 0)$, where

$$L = K + \frac{\sqrt{K}\mu}{\lambda} + \frac{\mu^2}{\lambda^2},$$

and $S_2' = \mu/\lambda$, $I_2' = r\mu(K\lambda^2 - \mu^2)/K\lambda^4$. The proof follows from equation (G.37) and Lyapunov–Lasalle's invariance principle [11].

G.3 At E_3

Let $\mathbb{R}_+^3 = [(S, I, P) \in \mathbb{R}_+^3\colon\ S > 0,\ I \geqslant 0,\ P > 0]$ and consider the scalar function $Z_3 : \mathbb{R}_+^3 \to \mathbb{R}$ defined by

$$Z_3 = k_3\left(S - S_3 - S_3\ln\frac{S}{S_3}\right) + \left(P - P_3 - P_3\ln\frac{P}{P_3}\right). \tag{G.38}$$

At the equilibrium point E_3, we have

$$rS_3 - \frac{rS_3^3}{K} - \frac{\alpha P_3}{1 + h\alpha S_3} = 0, \qquad \delta = \frac{\theta_1\alpha S_3}{1 + h\alpha S_3}. \tag{G.39}$$

Equations (G.39) reduce (G.38) to

$$
\begin{aligned}
\frac{\mathrm{d}Z_3}{\mathrm{d}t} &= \frac{1}{2}k_3\left(1-\frac{S_3}{S}\right)\left(rS-\frac{rS^3}{K}-\frac{\alpha P}{1+h\alpha S}-rS_3+\frac{rS_3^3}{K}+\frac{\alpha P_3}{1+h\alpha S_3}\right)\\
&\quad+(P-P_3)\left[\frac{\theta_1\alpha S}{1+h\alpha S}-\frac{\theta_1\alpha S_3}{1+h\alpha S_3}\right]\\
&\leqslant \frac{k_3}{2S}(S-S_3)\left[r(S-S_3)-\frac{r}{K}\left(S^3-S_3^3\right)-\alpha(P-P_3)\right]\\
&\quad+\theta_1\alpha(S-S_3)(I-I_3)\\
&= \frac{rk_3}{2S}(S-S_3)^2-\frac{rk_3}{2KS}(S-S_3)^2\left(S^2+SS_3+S_3^2\right)\\
&\quad-\frac{rk_3}{2S}(S-S_3)(P-P_3)+\theta_1\alpha(S-S_3)(I-I_3)\\
&\leqslant \left[\frac{rk_3}{2S}-\frac{rk_3(S^2+SS_3+S_3^2)}{2KS}+\frac{\alpha k_3}{4S}+\frac{\theta_1\alpha}{2}\right](S-S_3)^2\\
&\quad+\left[\frac{\theta_1\alpha}{2}-\frac{\alpha k_3}{4S}\right](P-P_3)^2\\
&< \left[\frac{rk_3\sqrt{K}}{2}-\frac{rk_3N}{2\sqrt{K}}-\frac{\alpha k_3\sqrt{K}}{4}+\frac{\theta_1\alpha}{2}\right](S-S_3)^2\\
&\quad+\left[\frac{\theta_1\alpha}{2}-\frac{\alpha k_3\sqrt{K}}{4}\right](P-P_3)^2.
\end{aligned}
\tag{G.40}
$$

Again, the above derivative is nonpositive if

$$
r<\frac{1}{\sqrt{K}}\left(\frac{Nk_3}{\sqrt{K}}+\frac{\alpha k_3\sqrt{K}}{2}-\theta_1\alpha\right),\qquad k_3>\frac{2\theta_1}{\sqrt{K}},
$$

and it vanishes when $(S,I,P)=(S_3,0,P_3)$, where $N=K+\sqrt{K}S_3+S_3^2$. The proof follows from (G.40) and Lyapunov-Lasalle's invariance principle.

G.4 At E_*

Let $\mathbb{R}^3=\{(S,I,P)\in\mathbb{R}^+\colon\ S>0,\ I>0,\ P>0\}$ and consider the scalar function $Z:\mathbb{R}^3\to\mathbb{R}$ defined by

$$
Z(t)=k_1\int\limits_{S_*}^{S}\frac{S-S_*}{S}\,\mathrm{d}S+\int\limits_{I_*}^{I}\frac{I-I_*}{I}\,\mathrm{d}I+k_2\int\limits_{P_*}^{P}\frac{P-P_*}{P}\,\mathrm{d}P.
\tag{G.41}
$$

The derivative of equation (G.41) along the solution trajectories of (2) is

$$
\frac{\mathrm{d}Z(t)(S,I,P)}{\mathrm{d}t}=\frac{\mathrm{d}Z_1(t)(S,I,P)}{\mathrm{d}t}+\frac{\mathrm{d}Z_2(t)(S,I,P)}{\mathrm{d}t}+\frac{\mathrm{d}Z_3(t)(S,I,P)}{\mathrm{d}t}.
$$

Now

$$\begin{aligned}\frac{\mathrm{d}Z_1(t)}{\mathrm{d}t}(S,I,P) &= k_1\left(1-\frac{S_*}{S}\right)\left(r(S-S_*)\left(1-\frac{(S-S_*)^2}{K}\right)\right.\\&\quad\left.-\frac{\alpha(P-P_*)}{1+h\alpha(S-S_*)}-\lambda(I-I_*)\right),\\\frac{\mathrm{d}Z_2(t)}{\mathrm{d}t}(S,I,P) &= \left(1-\frac{I_*}{I}\right)\big(\lambda(S-S_*)-m(P-P_*)-\mu\big),\\\frac{\mathrm{d}Z_3(t)}{\mathrm{d}t}(S,I,P) &= k_2\left(1-\frac{P_*}{P}\right)\left(\frac{\theta_1\alpha(S-S_*)}{1+h\alpha(S-S_*)}+\theta_2 m(I-I_*)-\delta\right).\end{aligned}$$

Therefore, letting $S-S_*=x$, $I-I_*=y$, $P-P_*=z$, we get

$$\begin{aligned}&\frac{\mathrm{d}Z(t)}{\mathrm{d}t}(S,I,T)\\&\quad=\frac{k_1x}{KS}\big[rx(K-x^2)-K\alpha z-K\lambda y(1+h\alpha x)\big]+y(\lambda x-mz-\mu)\\&\qquad+\frac{k_2z}{P(1+h\alpha x)}\big[\theta_1\alpha x+(1+h\alpha x)(\theta_2my-\delta)\big]\\&\quad\leqslant -k_1rx^4+k_1rx^2-k_1Kh\alpha\lambda x^2y+k_2h\alpha\theta_2mxyz+\lambda(1-k_1K)xy\\&\qquad+m(k_2\theta_2-1)yz+(k_2\theta_1\alpha-k_1K\alpha-k_2h\alpha\delta)zx-\mu y-\delta k_2z\\&\quad<\left[k_1r+\frac{1}{3}h\alpha m+\frac{1}{2}\lambda(1-k_1K)+\frac{1}{2}K_2\theta_1\alpha-\frac{1}{2}k_1K\alpha-\frac{1}{2}\frac{h\alpha\delta}{\theta_2}\right]x^2\\&\qquad+\left[\frac{1}{3}h\alpha m+\frac{1}{2}\lambda(1-k_1K)\right]y^2+\left[\frac{1}{3}h\alpha m+\frac{1}{2}K_2\theta_1\alpha-\frac{1}{2}k_1K\alpha-\frac{1}{2}\frac{h\alpha\delta}{\theta_2}\right]z^2,\end{aligned}$$

having taken

$$k_1=\frac{1}{K},\qquad k_2=\frac{3}{\theta_2(2h\alpha+3)},$$

$$k_1\leqslant\frac{3(-2r+\alpha K)}{K\alpha(2h\theta_2m+3\theta_1-3h\delta)},\qquad k_2\leqslant\frac{3(\alpha+m)}{3\theta_2m+3\theta_1\alpha+2h\alpha\theta_2m-3h\alpha\delta},$$

which correspond to assumptions (14). Also, the derivative vanishes only at the equilibrium E_*. Thus $Z(t)$ is a Lyapunov function and by Lasalle's theorem global stability follows.

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