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# Stability and fold bifurcation in a three-species model with mutual interference on parasitoids and hyperparasitoids

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## Abstract

This study establishes a novel three-species host–parasitoid–hyperparasitoid system with mutual interference effects on parasitoids and hyperparasitoids. We derive the asymptotic stability conditions for the equilibrium points and classify the impacts of hyperparasitoids on the dynamical behavior by comparing these stability conditions. Additionally, we demonstrate the presence of a fold bifurcation in the proposed three-dimensional model using a novel center manifold projection method. Finally, we verify our findings through numerical simulations.

**Keywords:** Host–parasitoid–hyperparasitoid system; Stability; Fold bifurcation; Center manifold projection

## 1 Introduction

The host–parasitoid models describe the interactions between insect species, where the organism being consumed is referred to as the host, while the organism benefiting from this consumption is identified as the parasitoid. Approximately 8–10% of all insect species are classified as parasitoids [1], with the majority being wasps; however, some flies, a few beetles, and moths have also evolved into parasitoids. Given that parasitoid species are specialists targeting specific hosts, they are frequently employed in biological control methods [2].

Most existing literature has primarily concentrated on the dynamics of two-species systems involving a single parasitoid species [3, 4]. Considering that the searching behavior of parasitoids may be altered in the presence of conspecifics or upon encountering a parasitized host, some researchers [5, 6] have improved their models by scaling the parasitoid's constant search efficiency to account for mutual interference effects. A general mutual interference host–parasitoid model was given by system (1.1) in [7],

$$\begin{cases} H_{t+1} = \lambda H_t e^{-aP_t^{1-m}}, \\ P_{t+1} = kH_t(1 - e^{-aP_t^{1-m}}), \end{cases} \quad (1.1)$$

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where  $H_t$  and  $P_t$  represent the host and parasitoid densities at generation  $t$ , respectively;  $m$  is the mutual interference constant, and  $a$  is the quest constant;  $\lambda$  stands for the mean number of eggs from a host that survive to be the subsequent generation, and  $k$  represents the mean number of eggs from a parasitoid on a host that survive to be the next generation.

In contrast, real insect ecosystems are characterized by the interaction of multiple species, resulting in complex interrelations. The challenges in linking theoretical models to practical applications arise from oversimplified assumptions regarding parasitism. Consequently, there are few significant findings on the changes in dynamical behavior induced by the presence of a third species. In 1977, Beddington and Hammand [8] proposed a discrete-time host–parasitoid–hyperparasitoid system, identifying several critical parameters related to its feasibility and stability. Subsequently, Zhang and Zhao [9] modified this model by incorporating the effects of prolonged diapause in the host, which led to the observation of various complex dynamic behaviors. Additionally, Broadley et al. [10] conducted field and laboratory biological control programs to assess the impact of hyperparasitoids on the efficiency of parasitoids as control agents.

Based on specific biological assumptions, we model a novel three-species host–parasitoid–hyperparasitoid system with mutual interference effects on both parasitoids and hyperparasitoids and investigate the stability and fold bifurcation of the system. We assume that hosts are initially parasitized by primary parasitoids, which subsequently become available for consumption by hyperparasitoids. Hyperparasitism occurs when the parasitoid is attacked by another hyperparasitoid. Uninfected insects produce the next generation, while successfully parasitized insects die. The eggs injected by the parasitic species survive and develop into their subsequent generation. Let  $H_t$ ,  $P_t$ , and  $Q_t$  denote the population densities of hosts, parasitoids, and hyperparasitoids in the  $t$ th generation, respectively. The number of encounters  $H_e$  (between hosts and parasitoids) and  $P_e$  (between parasitoids and hyperparasitoids) are quantified as follows [11]:

$$H_e := c_1 H_t P_t, \quad P_e := c_2 H_e Q_t,$$

where  $c_1$  and  $c_2$  represent the constant searching efficiencies of parasitoids and hyperparasitoids. Considering the host reproductive rate  $\lambda > 1$ , we derive the following:

$$\begin{cases} H_{t+1} = \lambda(H_t - H_e), \\ P_{t+1} = H_e - P_e, \\ Q_{t+1} = P_e. \end{cases} \tag{1.2}$$

Furthermore, by using the Poisson distribution for probabilities of encounters [12], we obtain the portion of insects without parasitism:

$$R_1(0) = e^{-c_1 P}, \quad R_2(0) = e^{-c_2 Q}.$$

Therefore,

$$\begin{aligned} H_{t+1} &= \lambda(H_t - H_e) = \lambda \left[ H_t - H_t(1 - e^{-c_1 P_t}) \right], \\ P_{t+1} &= H_e - P_e = H_e - H_e(1 - e^{-c_2 Q_t}) = H_t(1 - e^{-c_1 P_t})e^{-c_2 Q_t}, \\ Q_{t+1} &= P_e = H_e(1 - e^{-c_2 Q_t}) = H_t(1 - e^{-c_1 P_t})(1 - e^{-c_2 Q_t}). \end{aligned}$$

Considering the mutual interference effects within the parasitoids and hyperparasitoids, constant searching efficiencies can be modified to  $c_1 = aP_t^{-m}$  and  $c_2 = bQ_t^{-n}$ . System (1.2) is modified to

$$\begin{cases} H_{t+1} = \lambda H_t e^{-aP_t^{1-m}}, \\ P_{t+1} = H_t(1 - e^{-aP_t^{1-m}})e^{-bQ_t^{1-n}}, \\ Q_{t+1} = H_t(1 - e^{-aP_t^{1-m}})(1 - e^{-bQ_t^{1-n}}), \end{cases} \tag{1.3}$$

where  $m \in (0, 1)$  and  $n \in (0, 1)$  denote the mutual interference of parasitoids and hyperparasitoids, respectively;  $a > 0$  and  $b > 0$  are two quest constants.

### 2 Stability analysis

The positive equilibrium points are obtained by setting  $H_{t+1} = H_t = H^*$ ,  $P_{t+1} = P_t = P^*$ , and  $Q_{t+1} = Q_t = Q^*$  in system (1.3). Solving system (1.3), we get

$$\begin{aligned} P^* &= \left(\frac{\ln \lambda}{a}\right)^{\frac{1}{1-m}}, \\ Q^* &= P^*(e^{bQ^{*1-n}} - 1), \\ H^* &= \frac{\lambda \left(\frac{\ln \lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda - 1} e^{bQ^{*1-n}}. \end{aligned}$$

Due to the high nonlinearities, we can only illustrate that system (1.3) has positive equilibrium points  $(H^*, P^*, Q^*) \in \left(\frac{\lambda \left(\frac{\ln \lambda}{a}\right)^{\frac{1}{1-m}}}{\lambda - 1}, +\infty\right) \times \left\{\left(\frac{\ln \lambda}{a}\right)^{\frac{1}{1-m}}\right\} \times (0, +\infty)$ .

The Jacobian matrix of system (1.3) calculated at the positive equilibrium  $(H^*, P^*, Q^*)$  is given by

$$J_{(H^*, P^*, Q^*)} = \begin{pmatrix} 1 & -a(1-m)H^*P^{*-m} & 0 \\ P^*/H^* & a(1-m)P^{*-m}(H^*e^{-bQ^{*1-n}} - P^*) & -b(1-n)Q^{*-n}P^* \\ Q^*/H^* & a(1-m)P^{*-m}[H^*(1 - e^{-bQ^{*1-n}}) - Q^*] & b(1-n)Q^{*-n}P^* \end{pmatrix}.$$

The corresponding characteristic polynomial is

$$P_1(\gamma) = \gamma^3 + a_1\gamma^2 + a_2\gamma + a_3, \tag{2.1}$$

where  $a_1 = -\left[1 + \frac{M}{\lambda} + \frac{NP^*}{(1-m)H^*\ln \lambda}\right]$ ,  $a_2 = M + \frac{NP^*}{(1-m)H^*\ln \lambda} + \frac{N}{\lambda}$ ,  $a_3 = -N$ ,  $M = \frac{(1-m)\lambda \ln \lambda}{\lambda - 1}$ ,  $N = b(1-m)(1-n)H^*Q^{*-n} \ln \lambda$ , and  $\Theta = 1 + \frac{\lambda}{\lambda - N} \left[N(1-N) \left(1 - \frac{P^*}{(1-m)H^*\ln \lambda}\right)\right]$ .

**Lemma 1** ([12]) *The equilibrium point of a three-dimensional discrete system is locally asymptotically stable if all eigenvalues of its characteristic polynomial lie inside the unit*

disk if and only if

- (1)  $P_1(1) = 1 + a_1 + a_2 + a_3 > 0$ ,
- (2)  $P_1(-1) = -1 + a_1 - a_2 + a_3 < 0$ ,
- (3)  $D_2^+ = 1 + a_2 - a_3(a_1 + a_3) > 0$ ,
- (4)  $D_2^- = 1 - a_2 + a_3(a_1 - a_3) > 0$ .

**Theorem 1** *Suppose that  $N < 1$ ; then the positive equilibrium point  $(H^*, P^*, Q^*)$  of system (1.3) is locally asymptotically stable if and only if*

$$N < M < \Theta.$$

*Proof*  $P_1(1) = (1 - \frac{1}{\lambda})(M - N) > 0$  if and only if  $M > N$ ;  $P_1(-1) = -2 \left[ 1 + \frac{NP^*}{(1-m)H^* \ln \lambda} \right] - (1 + \frac{1}{\lambda})(M + N) < 0$  always holds.  $D_2^+ = M(1 - \frac{N}{\lambda}) + (1 - N) \left[ 1 + \frac{NP^*}{(1-m)H^* \ln \lambda} \right] + N(\frac{1}{\lambda} - N)$  and  $D_2^- = M(\frac{N}{\lambda} - 1) + 1 + N \left[ (1 - N) \left( 1 - \frac{P^*}{(1-m)H^* \ln \lambda} \right) - \frac{1}{\lambda} \right]$ .  $D_2^+ + D_2^- = 2(1 - N^2) \leq 0$  for  $N \geq 1$ , which is contradictory. Therefore, we assume that  $N < 1$ .  $D_2^+ > 0$  iff  $M > \frac{\lambda}{\lambda - N} \left[ N(N - \frac{1}{\lambda}) - (1 - N) \left( 1 + \frac{NP^*}{(1-m)H^* \ln \lambda} \right) \right]$ , which always holds for  $N < 1$ .  $D_2^- > 0$  iff  $M < \Theta$ . □

We compare the stability of the two-species host–parasitoid system (1.1) with the three-species host–parasitoid–hyperparasitoid system (1.3) to identify the effect of the hyperparasitoid  $Q$  on the dynamical behavior:

1. When  $0 < M < 1$ , the two-species equilibrium  $(H^*, P^*)$  is stable [7]. If  $N < 1$ , then stable coexistence of the host, parasitoid, and hyperparasitoid is possible for  $N < M < \min\{1, \Theta\}$ , where introducing the hyperparasitoid  $Q$  results in an increase in the host’s population level (if  $Q^* > 0$ ,  $H^* > \frac{\lambda(\frac{\ln \lambda}{a})^{\frac{1}{1-m}}}{\lambda - 1}$ ). Conversely, for  $M \leq N$ , the hyperparasitoid  $Q$  disrupts the stability. If  $N \geq 1$ , then the three-species equilibrium becomes unstable, indicating that  $Q$  destabilizes the interaction.
2. When  $M \geq 1$ , the two-species equilibrium  $(H^*, P^*)$  is consistently unstable. If  $N < 1$ , then a stable three-species equilibrium exists for  $M < \Theta$ , during which the hyperparasitoid stabilizes the interaction.

### 3 Fold bifurcation

The fold bifurcation serves as a biological switch that can create or destroy equilibrium points. It occurs when two equilibrium points—one stable and the other unstable—approach and annihilate each other as a bifurcation parameter is varied [13]. Fold bifurcation is associated with sudden population changes, such as sudden extinction events or rapid population booms. Therefore, recognizing and understanding the fold bifurcation is vital for effective population management and conservation strategies.

#### 3.1 Explicit criterion for the eigenvalue condition

The explicit criterion provides eigenvalue conditions for determining whether system (1.3) undergoes a fold bifurcation. The characteristic polynomial (2.1) has one real root equal

to 1 and all other roots are inside the unit circle if and only if [14]

$$P_1(1) = 0, \quad P_1(-1) < 0, \quad D_2^+ > 0, \quad D_2^- > 0.$$

**Proposition 2** *Assume  $N < 1$  and  $M < \Theta$ . If  $b = \frac{\lambda}{(1-n)(\lambda-1)H^*Q^{*-n}}$ , then system (1.3) has one eigenvalue  $\gamma_1 = 1$ , and all other eigenvalues are inside the open unit disk.*

*Proof* Similar to the proof of Theorem 1, if  $M = N$ , i.e.,  $b = \frac{\lambda}{(1-n)(\lambda-1)H^*Q^{*-n}}$ , we obtain  $P_1(1) = 0$ . When  $N < 1$  and  $M < \Theta$ , the conditions  $P_1(-1) < 0$ ,  $D_2^+ > 0$ , and  $D_2^- > 0$  are satisfied. □

### 3.2 Center manifold computation by the projection method

We rewrite system (1.3) in the following three-dimensional map:

$$X \mapsto f(X, b), \quad X \in \mathbb{R}^3, \quad b \in \mathbb{R}, \tag{3.1}$$

where  $X = (H, P, Q)$  and  $b$  is the bifurcation parameter. We assume that system (1.3) undergoes a fold bifurcation at  $(X^*, b_0)$ . Under the coordinate transformation [15],  $h = H - H^*$ ,  $v = P - P^*$ ,  $w = Q - Q^*$ , and  $\mu = b - b_0$ , the fold bifurcation point becomes  $(x, \mu) = (0, 0, 0, 0)$ , where  $x = (h, v, w) \in \mathbb{R}^3$ . The map (3.1) becomes

$$x \mapsto Jx + F(x, \mu), \quad x \in \mathbb{R}^3, \quad \mu \in \mathbb{R}, \tag{3.2}$$

where  $J = D_x f(X^*, b_0)$  and  $F(x, \mu) = f - Jx$ . The Jacobian matrix  $J$  has one eigenvalue  $\gamma_1 = 1$ , and the magnitudes of all other eigenvalues are less than one. The critical eigenspace  $T^c$  is one-dimensional and spanned by an eigenvector  $q \in \mathbb{R}^3$  such that  $Jq = \gamma_1 q$ . Let  $p \in \mathbb{R}^3$  denote the adjoint eigenvector such that  $J^T p = \gamma_1 p$ .  $p$  and  $q$  satisfy  $\langle p, q \rangle = 1$ . The 2-dimensional linear eigenspace  $T^{su}$  corresponds to the other two eigenvalues.

**Lemma 2** ([16]) *The vector  $y \in T^{su}$  if and only if  $\langle p, y \rangle = 0$ .*

For any vector  $x \in \mathbb{R}^3$ , it can be decomposed as follows:

$$x = uq + y, \tag{3.3}$$

where  $uq \in T^c$  and  $y \in T^{su}$ . Moreover,

$$\begin{cases} u = \langle p, x \rangle, \\ y = x - \langle p, x \rangle q, \end{cases} \tag{3.4}$$

where  $u \in \mathbb{R}$  and  $y \in \mathbb{R}^3$ . Upon designating the parameter  $\mu$  as a new dependent variable, the map (3.2) can be represented as

$$\begin{pmatrix} u \\ y \\ \mu \end{pmatrix} \mapsto \begin{pmatrix} \gamma_1 u + \langle p, F(uq + y, \mu) \rangle \\ Jy + F(uq + y, \mu) - \langle p, F(uq + y, \mu) \rangle q \\ \mu \end{pmatrix}. \tag{3.5}$$

Next, we give some functions:

$$D_{\mu,j} = \frac{\partial F_j(0, \mu)}{\partial \mu} \Big|_{\mu=0}, D_{\mu\mu,j} = \frac{\partial^2 F_j(0, \mu)}{\partial \mu^2} \Big|_{\mu=0}, D_{x\mu,j}(x) = \sum_{k=1}^n \frac{\partial^2 F_j(\xi, \mu)}{\partial \mu \partial \xi_k} \Big|_{\xi=0, \mu=0} \cdot x_k,$$

$$B_i(x, y) = \sum_{j,k=1}^n \frac{\partial^2 F_i(\xi, 0)}{\partial \xi_j \partial \xi_k} \Big|_{\xi=0} \cdot x_j y_k, C_i(x, y, z) = \sum_{j,k,l=1}^n \frac{\partial^3 F_i(\xi, 0)}{\partial \xi_j \partial \xi_k \partial \xi_l} \Big|_{\xi=0} \cdot x_j y_k z_l.$$

It becomes feasible to re-express system (3.5) as

$$\begin{pmatrix} u \\ y \\ \mu \end{pmatrix} \mapsto \begin{pmatrix} u + r_1\mu + \frac{1}{2}r_2u^2 + r_3\mu u + \frac{1}{2}r_4\mu^2 + \frac{1}{6}r_5u^3 + \langle p, B(q, y) \rangle u \\ + \langle p, D_{x\mu}(y) \rangle \mu + \frac{1}{2} \langle p, B(y, y) \rangle + \dots \\ Jy + r_6\mu + \frac{1}{2}r_7u^2 + r_8\mu u + r_9\mu^2 + (B(q, y) - \langle p, B(q, y) \rangle q)u \\ + (D_{x\mu}(y) - \langle p, D_{x\mu}(y) \rangle) \mu + \frac{1}{2}(B(y, y) - \langle p, B(y, y) \rangle q) + \dots \\ \mu \end{pmatrix}, \tag{3.6}$$

where  $r_1 = \langle p, D_{\mu} \rangle$ ,  $r_2 = \langle p, B(q, q) \rangle$ ,  $r_3 = \langle p, D_{x\mu}(q) \rangle$ ,  $r_4 = \langle p, D_{\mu\mu} \rangle$ ,  $r_5 = \langle p, C(q, q, q) \rangle$ ,  $r_6 = D_{\mu} - \langle p, D_{\mu} \rangle q$ ,  $r_7 = B(q, q) - \langle p, B(q, q) \rangle q$ ,  $r_8 = D_{x\mu}(q) - \langle p, D_{x\mu}(q) \rangle q$ , and  $r_9 = D_{\mu\mu} - \langle p, D_{\mu\mu} \rangle q$ . Assume that the center manifold has the following form:

$$y = W(u, \mu) = A_1u + A_2\mu + O(2), \tag{3.7}$$

where  $A_1, A_2 \in T^{su} \subset \mathbb{R}^3$ . Substituting (3.7) into (3.6) and comparing the coefficients, we can obtain  $A_1 = 0$  and  $A_2 = -(J - I)^{INV} r_6$ .

*Remark 1* The matrix  $J$  has an eigenvalue  $\gamma_1 = 1$ , so the notation ‘INV’ cannot be the inverse of a matrix.  $r_6 \in T^{su}$  since  $\langle p, r_6 \rangle = 0$ . The restriction of the linear transformation corresponding to  $(J - I)$  to its invariant subspace  $T^{su}$  is invertible, so equation  $(J - I)A_2 = -r_6$  has a unique solution  $A_2 \in T^{su}$ .

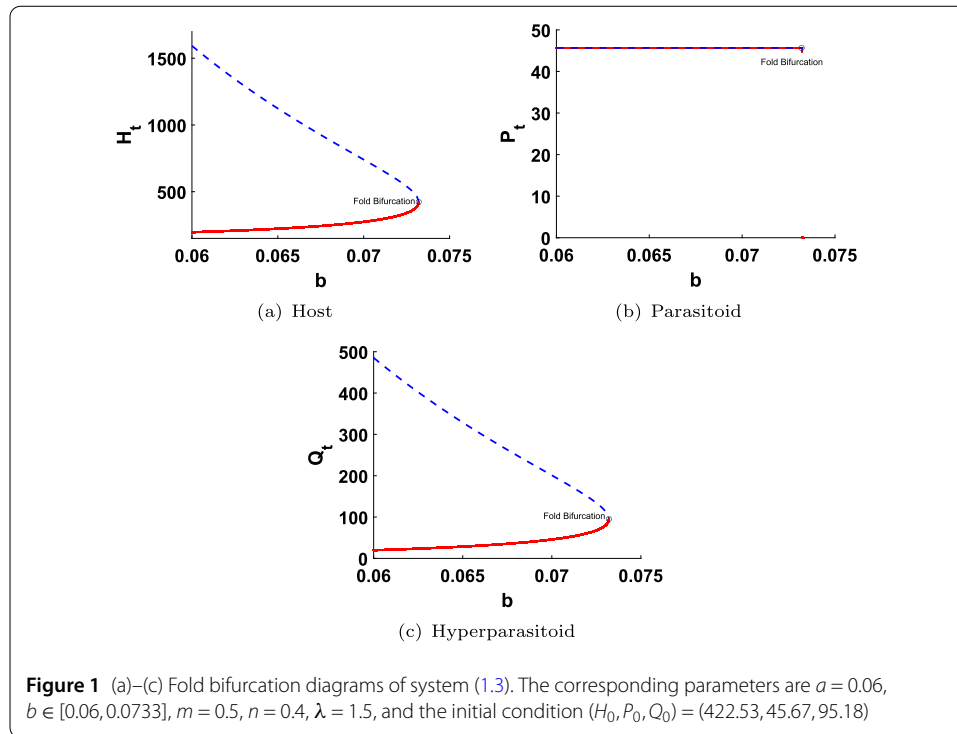
Substituting (3.7) into the first equation of (3.6), we obtain

$$\begin{pmatrix} u \\ \mu \end{pmatrix} \mapsto \begin{pmatrix} u + s_1\mu + \frac{1}{2}s_2u^2 + s_3\mu u + \frac{1}{2}s_4\mu^2 + \dots \\ \mu \end{pmatrix}, \tag{3.8}$$

where the coefficients are  $s_1 = r_1$ ,  $s_2 = r_2$ ,  $s_3 = r_3 + \langle p, B(q, A_2) \rangle$ , and  $s_4 = r_4 + 2\langle p, D_{x\mu}(A_2) \rangle + \langle p, B(A_2, A_2) \rangle$ . Finally, system (3.8) can be reduced to a one-dimensional map  $\varphi(u, \mu)$  at  $(0, 0)$  with  $\varphi_u(0, 0) = 1$ . It takes the following form:

$$\varphi(u, \mu) = u + \varphi_{\mu}(0, 0)\mu + \frac{1}{2}\varphi_{uu}(0, 0)u^2 + \varphi_{u\mu}(0, 0)u\mu + \frac{1}{2}\varphi_{\mu\mu}(0, 0)\mu^2 + \dots$$

Based on the fold bifurcation theory [16], we can establish the following fold bifurcation theorem.



**Theorem 3** System (1.3) undergoes a fold bifurcation at the positive equilibrium point  $(H^*, P^*, Q^*)$  when the bifurcation parameter  $b$  changes in the small range of  $b_0 = \frac{\lambda}{(1-n)(\lambda-1)H^*Q^{*n}}$  if and only if the following conditions hold:

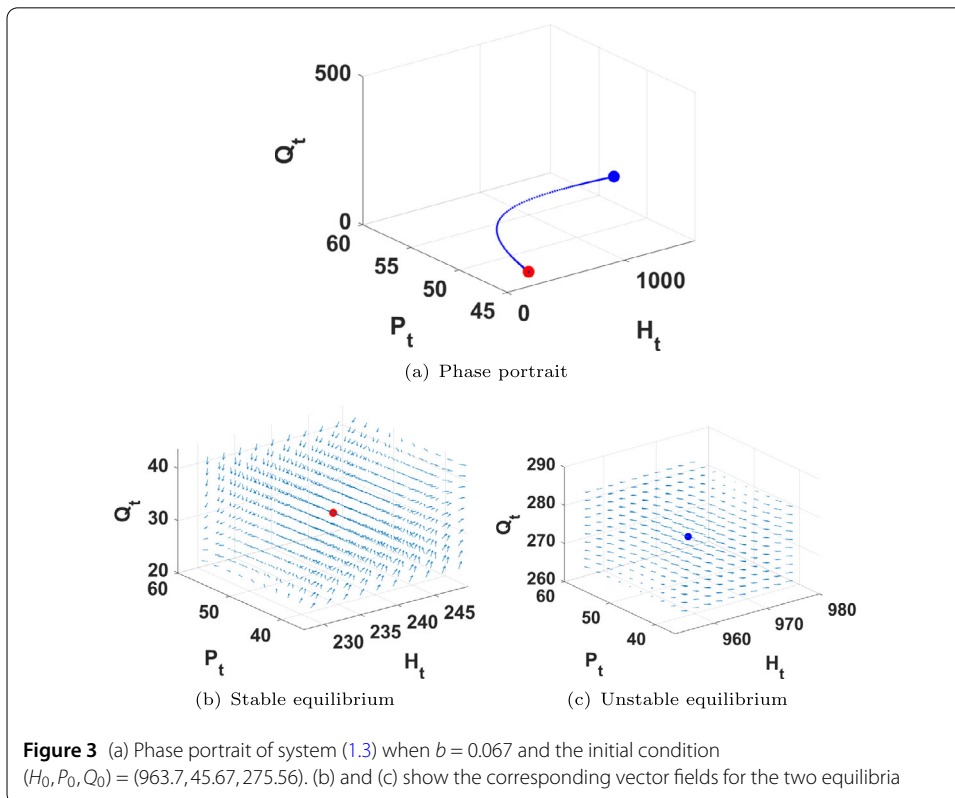
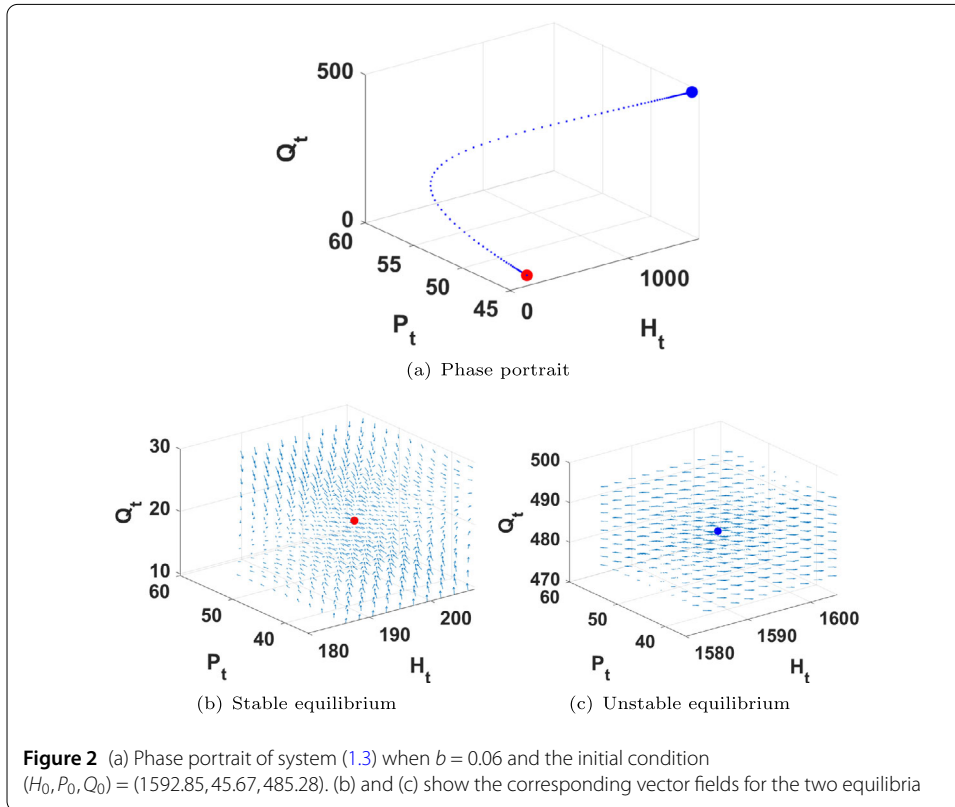
1. Eigenvalue assignment: Proposition 2;
2. Nondegenerance condition:  $s_1 \neq 0$ ;
3. Transversality condition:  $s_2 \neq 0$ .

Furthermore, two equilibrium points bifurcate for  $b < b_0$ , coalesce at  $b = b_0$ , and disappear for  $b > b_0$ .

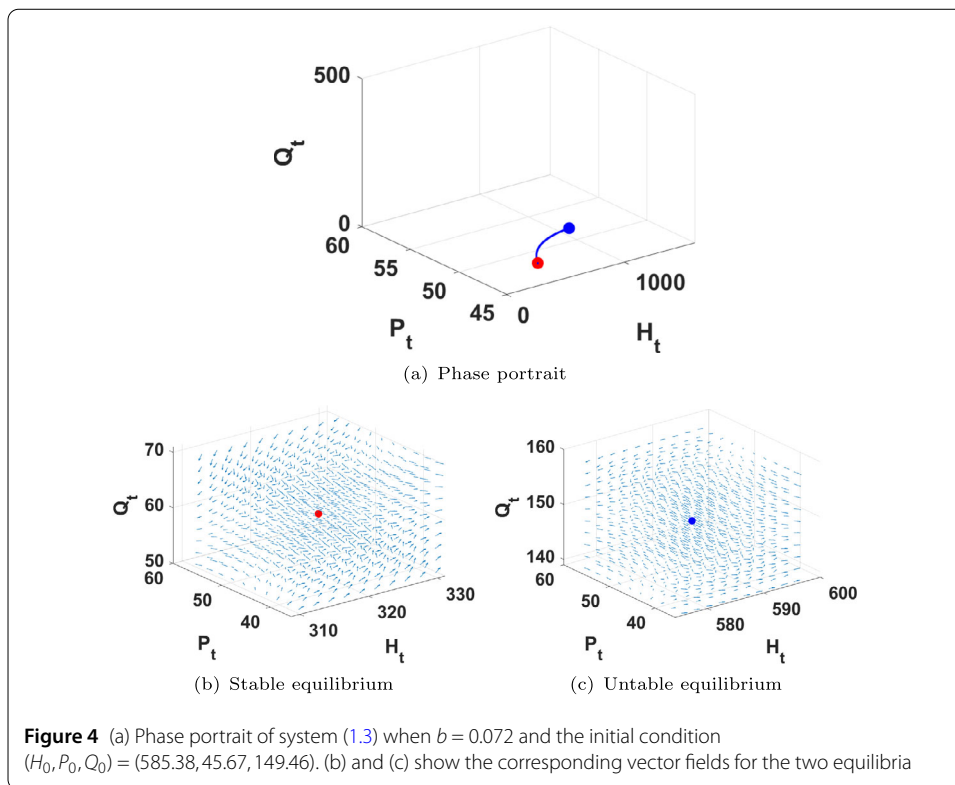
### 3.3 Numerical simulation

If  $a = 0.06$ ,  $b \in [0.06, 0.0733]$ ,  $m = 0.5$ ,  $n = 0.4$ , and  $\lambda = 1.5$ , then system (1.3) will undergo a fold bifurcation. Figure 1 gives the bifurcation diagrams for the host, parasitoid, and hyperparasitoid. From this figure, we observe that a stable equilibrium (red solid lines) and an unstable equilibrium (blue dashed lines) coalesce at  $b_0 \approx 0.0732023$ ; for  $b > b_0$ , there is no positive equilibrium. It indicates that the system undergoes a fold bifurcation when  $b = b_0$ . Figures 2, 3, and 4 present some phase portraits for various values of  $b$  and the corresponding vector fields for both stable and unstable equilibria:

1. Fig. 2(a) shows the phase portrait when  $b = 0.06$ . The blue solid dot represents a positive unstable equilibrium  $(1592.85, 45.67, 485.28)$ , which converges to the red stable equilibrium point  $(196.2, 45.67, 19.73)$  along the blue dashed trajectory. The vector fields for both stable and unstable positive equilibria are depicted in Figs. 2(b) and (c), respectively.
2. For  $b = 0.067$ , the phase portrait is illustrated in Fig. 3(a), where the stable and unstable equilibria are  $(238.32, 45.67, 33.77)$  and  $(963.7, 45.67, 275.56)$ , respectively. Figures 3(b) and (c) show their vector fields.







3. As  $b$  increases to 0.072, the phase portrait is shown in Fig. 4(a). Figures 4(b) and (c) display the vector fields for the stable equilibrium  $(319.8, 45.67, 60.93)$  and the unstable equilibrium  $(585.38, 45.67, 149.46)$ , respectively.

As  $b$  increases, the stable and unstable equilibrium points gradually approach each other and coalesce until they ultimately disappear. Next, we take the bifurcation parameter  $b_0 = 0.0732023$  and the bifurcation point  $(H^*, P^*, Q^*) = (422.52728872, 45.66720941, 95.17522016)$  to compute the coefficients of the fold bifurcation. The eigenvalues are  $\gamma_1 = 0.99999996 \approx 1$ ,  $\gamma_2 = 0.36485424 + 0.68925973i$ , and  $\gamma_3 = 0.36485424 - 0.68925973i$ . According to the results of the analysis in Sect. 3.2, we can take the normalized vectors  $q = (-0.94868329, -0.000000019024275, -0.31622778)$  and  $p = (-0.81083532, 1.5209207, -0.72977179)$ . We then compute the following coefficients:

$$s_1 = -1581.3754 \neq 0, \quad s_2 = -0.00021144108 \neq 0.$$

#### 4 Conclusion

This study models a three-species host–parasitoid–hyperparasitoid system based on specific biological assumptions. The parametric conditions for ensuring the stability of the positive equilibrium points are derived. Furthermore, we compare the stabilities of two-species and three-species systems, illustrating that hyperparasitoids can either stabilize interactions, destabilize the system, or increase the host population level. The projection method for center manifold computation effectively reduces the three-dimensional map to a one-dimensional map, enabling us to establish the conditions under which the system experiences a fold bifurcation. A numerical simulation example demonstrates the fold bi-

furcation, characterized by the destruction of equilibria, where one stable equilibrium and one unstable equilibrium coalesce and subsequently disappear as  $b$  passes through  $b_0$ .

#### Author contributions

All authors contributed equally and significantly in writing this paper. All authors read and approved the final manuscript.

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#### Availability of data and materials

Not applicable.

## Declarations

#### Competing interests

The authors declare that they have no conflict of interest.

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