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Bifurcation Analysis of a Predator-Prey System with Density Dependent Disease Recovery

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Abstract. The center manifold is an invariant manifold that plays a crucial role in the bifurcation analysis of dynamical systems. The center manifold existence theorem assures the local existence of an invariant submanifold of the state space of a dynamical system around a non-hyperbolic equilibrium point. Center manifold theory is essential in the reduction of different bifurcation scenarios to their normal forms. Our study focuses on a predator-prey interactive system with density-dependent growth in predators subject to a contagious disease. The disease is assumed to be horizontally transmitted, and the rate of recovery of the infected predator is assumed to be density-dependent. At the trivial (zero) equilibrium, the center manifold is calculated whose dynamical behaviour is similar to that of the original system. Further, using the center manifolds, the normal form of a Hopf bifurcation point is determined from which the criticality of the system can be deduced. Finally, numerical simulations are performed with biologically plausible parameters to substantiate the analytical findings. Using numerical continuation methods we detect Generalized Hopf and Zero-Hopf bifurcation points. We discuss their normal form coefficients, compute their two-parameter unfoldings and relate these results to the mathematical theory of codimension two bifurcations.

1. Introduction

Equivalence relations play a significant role in the study of general (qualitative) properties of dynamical systems, especially in classifying possible types of behaviour and for comparing the behaviour of different dynamical systems. Two dynamical systems are said to be topologically equivalent if there exists a homeomorphism from one state space onto the other that maps orbits to orbits, preserving the direction ([17, Definition 2.1]). The concept of topological equivalence of dynamical systems was first introduced in the article by Andronov & Pontryagin 1937 [2] on structurally stable systems on the plane. Local topological equivalence of a nonlinear dynamical system to its linearization at a hyperbolic equilibrium was proved by Grobman 1959 [10] and Hartman in 1963 [13]. Interested readers can see [17] for more about the historical background.

Center manifold theory and the method of normal forms are two rigorous mathematical techniques for reducing the dimensionality of a dynamical system and handling nonlinearity. At a non-hyperbolic equilibrium point of a dynamical system the center subspace is the linear space T^c spanned by the eigenvectors

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and generalized eigenvectors of the eigenvalues with real part zero. According to the center manifold existence theorem there is locally an invariant center manifold $W^c_{loc}(0)$ tangential to T^c. The importance of center manifolds in dynamical systems is due to their ability to describe the dynamics of the corresponding system. The stability theorem of center manifold [6] says that for initial conditions of the full system sufficiently close to the bifurcation point, trajectories through them asymptotically approach a trajectory on the center manifold either in forward or backward time. In the local theory of dynamical systems, generally in bifurcation analysis, these techniques are the most important and applicable methods [24]. Because intriguing behaviour occurs on the center manifold, center manifolds play an essential role in bifurcation theory. Among the pioneers, Plissof Pliss in 1964 [20], Vanderbauwhede 1989 [22], and Kelley in 1967 [15] were the first to prove the center manifold theorem for finite dimensions. The study by Shoshitaishvili in 1975 [21] provides the foundation of the theory of topological normal forms in the context of multidimensional bifurcations of equilibria and isolated periodic orbits.

In this article, we introduce a new mathematical model on predator-prey epidemics. Pioneering work on modeling of epidemics was proposed by Kermack and Mc Kendrick in 1927 [16], after which various researchers implemented the framework of epidemiology in predator-prey modeling [1, 7, 11, 23]. Density-dependent recovery plays a significant role in the study of epidemics. Citing the examples of different diseases and their slow recovery due to different factors arising in aquaculture, Bhattacharjee et. al. [4] proposed a tri-trophic epidemiological model with density-dependent disease recovery, which exhibits chaotic dynamics. Using this density-dependent disease recovery framework, we propose a model where the predator species is classified into susceptible and infected. Our main aim in this article is to analyze the possible bifurcations using the center manifold theory and method of normal forms. Using the center manifold reduction technique, the center manifold of the dynamical system representing the epidemic model is obtained, which describes the dynamics of the system. Then using the center manifold, the normal form of a Hopf bifurcation point is obtained. The normal form, being topologically equivalent to the local center manifold of the original system, confirms the existence of a Hopf bifurcation point in the original system. The following is a breakdown of the article's framework:

In Section 2, the model is presented along with the basic assumptions. Section 3 contains a discussion on the boundedness of the solutions and existence of equilibrium points of the system. Section 4 deals with the stability analysis of different equilibrium states. Center manifold reduction and normal form reduction are described therein. In section 5 and 6 we recall the mathematical background of the parameter unfoldings of Generalized Hopf and zero-Hopf bifurcation points as far as they are useful to understand the numerical results in section 7. In section 7 numerical simulations and continuations are carried out to verify the analytical results, using a biologically plausible parameter set. Section 8 gives a brief summary of the results obtained in the paper.

2. Mathematical model

The basic assumptions of our proposed model are outlined in this section.

1. A prey-predator ecosystem is considered where the total prey and predator population densities are represented by S and N, respectively. We assume that predators are susceptible to some form of contagious disease (such as a virus) and that in the presence of the disease, predator populations are classified into two groups: (i) susceptible and (ii) infected. Let $P(t)$ and $Y(t)$ be, respectively, the concentrations of the biomass of susceptible predator and infected predator at time t. Suppose that the prey reproduces logistically with intrinsic growth rate $r_1 > 0$ and also the susceptible predator follows logistic growth with intrinsic growth rate $r_2 > 0$. The infected individuals do not reproduce; infection reduces the remaining capacity due to the inability to compete for resources [12]. Thus, we may assume that only susceptible species follow the logistic growth law, and the infected predators (Y) die before having the capability of reproducing [3, 8].

2. We assume that the predator species predates their prey following a Holling I (1959) [14] function response with catching rate α; β is the rate of energy transfer.

3. The disease transmission rate is assumed to be λ with a recovery rate b. The term $bY(1-\delta Y)$ represents density-dependent disease recovery [4].

4. Let d_1, d_2 and d_3 represent the natural mortality rate of prey, susceptible predator and infected predator, respectively.
With the above assumptions the model is,

$$\left.\begin{aligned}\frac{dS}{dt} &= r_1S(1-c_1S) - \alpha SP - d_1S,\\ \frac{dP}{dt} &= r_2P(1-c_2P) + \beta SP - \lambda PY + bY(1-\delta Y) - d_2P,\\ \frac{dY}{dt} &= \lambda PY - bY(1-\delta Y) - d_3Y,\end{aligned}\right\} \tag{1}$$

with initial conditions, $S(0) > 0$; $Y(0) > 0$; $P(0) > 0$.

3. Qualitative analysis of the system

This section deals with the the uniform boundedness of the solutions (*Theorem* 3.1) of the system (1) and the steady states of the system i.e. the equilibrium points together with their existence conditions.

Theorem 3.1. *The orbits of system* (1) *are uniformly bounded, i.e. there exists a bounded set $\mathcal{B}$ such that for every orbit $(S(t), P(t), Y(t))$ of* (1) *there is a time t_0 such that $(S(t), P(t), Y(t)) \in \mathcal{B}$ for all $t \geq t_0$.*

Proof. Let us define a function $U(t) = S(t) + \frac{\alpha}{\beta}P(t) + \frac{\alpha}{\beta}Y(t)$. Then

$$\frac{dU}{dt} = \frac{dS}{dt} + \frac{\alpha}{\beta}\frac{dP}{dt} + \frac{\alpha}{\beta}\frac{dY}{dt}.$$

Now choose any μ with $0 < \mu < d_3$. Then,

$$\begin{aligned}\frac{dU}{dt} + \mu U &\leq S(r_1+\mu) - r_1c_1S^2 + \frac{\alpha}{\beta}(r_2+\mu)P - \frac{\alpha r_2 c_2}{\beta}P^2 + \frac{\alpha}{\beta}(\mu - d_3)Y\\ &\leq -r_1c_1\left(S^2 - 2S\frac{(r_1+\mu)}{2r_1c_1} + \frac{(r_1+\mu)^2}{4(r_1c_1)^2} - \frac{(r_1+\mu)^2}{4(r_1c_1)^2}\right)\\ &\quad - \frac{\alpha r_2c_2}{\beta}\left(P^2 - 2P\frac{(r_2+\mu)}{2r_2c_2} + \frac{(r_2+\mu)^2}{4(r_2c_2)^2} - \frac{(r_2+\mu)^2}{4(r_2c_2)^2}\right) + \frac{\alpha}{\beta}(\mu - d_3)\\ &\leq -r_1c_1\left\{\left(S - \frac{(r_1+\mu)}{2r_1c_1}\right)^2 - \frac{(r_1+\mu)^2}{4(r_1c_1)^2}\right\} +\\ &\quad - \frac{\alpha r_2c_2}{\beta}\left\{\left(P - \frac{(r_2+\mu)}{2r_2c_2}\right)^2 - \frac{(r_2+\mu)^2}{4(r_2c_2)^2}\right\} + \frac{\alpha}{\beta}(\mu - d_3)\\ &\leq \frac{(r_1+\mu)^2}{4r_1c_1} + \frac{\alpha}{\beta}\frac{(r_2+\mu)^2}{4r_2c_2}\end{aligned}$$

Define $K = \frac{(r_1+\mu)^2}{4r_1c_1} + \frac{\alpha}{\beta}\frac{(r_2+\mu)^2}{4r_2c_2}$. Then the above differential inequality can be written in the form,

$$\frac{d}{dt}\left(U - \frac{K}{\mu}\right) \leq -\mu\left(U - \frac{K}{\mu}\right).$$

Now by applying Lemma 2 on page 27 in Birkhoff and Rota (1989) [5], we obtain

$$0 \leq U(t) \leq \frac{K}{\mu}\left(1 - e^{-\mu t}\right) + U(0)e^{-\mu t}.$$

For any $\epsilon > 0$ define

$$\mathcal{B} = \left\{ (S, P, Y) : S \geq 0, P \geq 0, Y \geq 0, S + \frac{\alpha}{\beta}P + \frac{\alpha}{\beta}Y \leq \frac{K}{\mu} + \epsilon \right\}.$$

Then for every orbit of (1) there is a time t_0 such that $(S(t), P(t), Y(t)) \in \mathcal{B}$ for all $t \geq t_0$. □

3.1. Equilibrium points

System (1) can have the following equilibrium points:

(a) The trivial equilibrium $E_0(0, 0, 0)$ which always exists.

(b) The axial or predator-free equilibrium $E_1(\hat{S} > 0, 0, 0)$ where $\hat{S} = \frac{r_1 - d_1}{c_1 r_1}$, which exists for $r_1 > d_1$.

(c) The disease-free equilibrium $E_2(\bar{S} > 0, \bar{P} > 0, 0)$ where,
$\bar{S} = \frac{\alpha d_2 - r_2(\alpha + c_2(d_1 - r_1))}{\alpha\beta + c_1 c_2 r_1 r_2}$ and $\bar{P} = \frac{r_1\left(\beta + c_1(r_2 - d_2)\right) - \beta d_1}{\alpha\beta + c_1 c_2 r_1 r_2}$. A disease-free equilibrium exists if and only if,

$$\alpha(d_2 - r_2) + r_2 c_2(d_1 - r_1) > 0,$$

and

$$r_1 c_1(d_2 - r_2) + \beta(d_1 - r_1) < 0.$$

As a consequence, no disease-free equilibrium exists if $d_1 - r_1$ and $d_2 - r_2$ are both positive or both negative.

(d) The prey and infection-free equilibrium $E_3(0, P_3 > 0, 0)$ where $P_3 = \frac{r_2 - d_2}{c_2 r_2}$, which exists for $r_2 > d_2$.

(e) The prey-free equilibrium $E_4(0, P_4 > 0, Y_4 > 0)$ where,

$$P_4 = \frac{-b\delta d_2 + b\delta r_2 + d_3\lambda - \mathcal{K}}{2bc_2\delta r_2},$$
$$Y_4 = \frac{2b^2c_2\delta r_2 + 2bc_2\delta d_3 r_2 + b\delta d_2\lambda - b\delta\lambda r_2 - d_3\lambda^2 + \lambda\mathcal{K}}{2b^2c_2\delta^2 r_2,}$$
$$\text{where,} \quad \mathcal{K} = \sqrt{(-b\delta d_2 + b\delta r_2 + d_3\lambda)^2 - 4bc_2\delta d_3 r_2(b + d_3)} > 0.$$

$\mathcal{K}$ exists and is positive if and only if $(-b\delta d_2 + b\delta r_2 + d_3\lambda)^2 > 4bc_2\delta d_3 r_2(b + d_3)$.
$P_4 > 0$ and $Y_4 > 0$ under any of the conditions (i) or (ii),

(i) $r_2 > d_2; 0 < \delta \leq \frac{d_3\lambda}{br_2 - bd_2}; 0 < c_2 < \frac{\lambda r_2 - d_2\lambda}{br_2 + d_3 r_2}$,

(ii) $r_2 > d_2; \delta > \frac{d_3\lambda}{br_2 - bd_2}; 0 < c_2 < \frac{b^2d_2^2\delta^2 - 2b^2d_2\delta^2 r_2 + b^2\delta^2 r_2^2 - 2bd_2d_3\delta\lambda + 2bd_3\delta\lambda r_2 + d_3^2\lambda^2}{4b^2\delta d_3 r_2 + 4b\delta d_3^2 r_2}$.

For the parameters in Table 1 with $\delta = 0.02$/day and $d_2 = 0.4$/day, the prey-free equilibrium E_4 exists because conditions (i) are satisfied.

(f) Coexistence equilibrium $E^*(S^* > 0, P^* > 0, Y^* > 0)$:
From the equation of the prey nullcline we obtain $P^* = \frac{r_1 - c_1 r_1 S^* - d_1}{\alpha}$. Substituting this in the equations of the predator nullclines we get,

$$\begin{aligned} \alpha^2 bY^*(1 - cY^*) - (r_1(c_1S^* - 1) + d_1)\,(r_2(\alpha + c_2(r_1(c_1S^* - 1) + d_1)) \\ + \alpha(-d_2 + \beta S^* - \lambda Y^*)) = 0, \\ Y^*(\alpha(-b) + \alpha b\delta Y^* - c_1\lambda r_1 S^* - \alpha d_3 - d_1\lambda + \lambda r_1) = 0. \end{aligned} \tag{2}$$

Since $Y^* \neq 0$, (otherwise we are in the case (c)) we can solve the second equation in (2) for Y^* and substitute this in the first equation of (2). So S^* is the solution of a quadratic equation

$$\mathcal{A}S^2 + \mathcal{B}S + C = 0, \tag{3}$$

where,

$$\mathcal{A} = bc_1\delta r_1 (\alpha\beta + c_1 c_2 r_1 r_2),$$
$$\mathcal{B} = r_1 (c_1 (b\delta r_2 (\alpha - 2c_2 r_1) + \alpha(-b)\delta d_2 + \alpha d_3 \lambda) - \alpha b \beta \delta) + b\delta d_1 (\alpha\beta + 2c_1 c_2 r_1 r_2),$$
$$C = b\delta r_2 (d_1 - r_1)(\alpha + c_2 (d_1 - r_1)) + \alpha (\alpha d_3 (b + d_3) + d_1 (d_3\lambda - b\delta d_2) + r_1 (b\delta d_2 - d_3\lambda)).$$

If S^* is a solution of (3), then the corresponding P^* and Y^* are defined uniquely. Hence (1) can have at most two coexistence equilibria. If $S^* \neq 0$ is a real positive solution of the quadratic equation (3), then P^* and Y^* are also real and positive if

$$\frac{\lambda r_1 - \alpha (b + d_3) - d_1\lambda}{c_1 \lambda r_1} < S^* < \frac{r_1 - d_1}{c_1 r_1}.$$

The coexistence equilibrium (S^*, P^*, Y^*) exists under the sufficient condition,

$$r_1 > d_1, \quad r_2 \geq d_2, \quad c_2 > \frac{\alpha (d_2 - r_2)}{r_2 (d_1 - r_1)} \quad \text{and} \quad \lambda > \frac{(b + d_3)(\alpha\beta + c_1 c_2 r_1 r_2)}{r_1 (\beta + c_1 (r_2 - d_2)) - \beta d_1}.$$

For the parameter set in Table 1 with $\delta = 0.02$/day we verified that $\mathcal{A}S^2 + \mathcal{B}S + C = 0$ has a unique non-zero and non-negative real root $S^* = 6.12077$. The corresponding P^*, Y^* are also real and positive with $P^* = 0.763768$ and $Y^* = 4.52902$.

4. Stability of equilibrium points

The six types of equilibria in §3.1 (a)-(f) all have a clear biological meaning. In the biological practice we cannot expect to find them if they are not mathematically stable. We therefore now study their stability in §4.1-6. The Jacobian matrix of the system (1) is given by,

$$J = \begin{pmatrix} r_1 (1 - 2c_1 S) - d_1 + \alpha(-P) & \alpha(-S) & 0 \\ \beta P & r_2 (1 - 2c_2 P) - d_2 + \beta S - \lambda Y & -2b\delta Y + b - \lambda P \\ 0 & \lambda Y & b(2\delta Y - 1) - d_3 + \lambda P \end{pmatrix} \tag{4}$$

4.1. *Stability of the trivial equilibrium* $E_0(0, 0, 0)$

The Jacobian of the system (1) at the trivial equilibrium E_0 is given by,

$$J_{E_0} = \begin{pmatrix} r_1 - d_1 & 0 & 0 \\ 0 & r_2 - d_2 & b \\ 0 & 0 & -b - d_3 \end{pmatrix}.$$

The eigenvalues of J_{E_0} are $r_1 - d_1, r_2 - d_2, -b - d_3$. Therefore the trivial equilibrium E_0 is locally asymptotically stable if $r_1 < d_1$ and $r_2 < d_2$. The equilibrium E_0 becomes non-hyperbolic if $r_1 = d_1$ or $r_2 = d_2$ or both $r_1 = d_1$ and $r_2 = d_2$. In the following cases, we discuss the stability of the non-hyperbolic equilibrium E_0 by using center manifold theory.

We will use the theory described in [24], §18.1. This requires that the system be written in the form (18.1.1) with (18.1.2) in [24]. We will achieve this by linear transformations of the coordinates based on the eigenvectors of the Jacobian in the equilibrium point.
Case 1: $r_1 - d_1 = 0$, $r_2 < d_2$. In this case the eigenvalues of the Jacobian are $0, r_2 - d_2, -b - d_3$. The stable

manifold is two-dimensional and the center manifold is one-dimensional. To investigate the stability we will study the dynamics in the center manifold. We will exclude the case with an algebraically double and geometrically simple eigenvalue $-b - d_3 = r_2 - d_2$ i.e. when $b + d_3 + r_2 - d_2 = 0$. Under this assumption, the eigenvectors corresponding to the three eigenvalues are the column vectors of the nonsingular matrix,

$$Q = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & -\frac{b}{b-d_2+d_3+r_2} \\ 0 & 0 & 1 \end{pmatrix},$$

with

$$Q^{-1} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & \frac{b}{b-d_2+d_3+r_2} \\ 0 & 0 & 1 \end{pmatrix}.$$

Next, we introduce the transformation $X = QV$ where $X = \begin{pmatrix} S \\ P \\ Y \end{pmatrix}$, $V = \begin{pmatrix} u \\ v \\ w \end{pmatrix}$ into system (1) and after some algebraic manipulations obtain the diagonal form,

$$\begin{pmatrix} \dot{u} \\ \dot{v} \\ \dot{w} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & r_2 - d_2 & 0 \\ 0 & 0 & -b - d_3 \end{pmatrix} \begin{pmatrix} u \\ v \\ w \end{pmatrix} + \begin{pmatrix} \mathcal{H}_1(u,v,w) \\ \mathcal{H}_2(u,v,w) \\ \mathcal{H}_3(u,v,w) \end{pmatrix}, \tag{5}$$

where,

$$\begin{aligned}
\mathcal{H}_1(u,v,w) &= \frac{\alpha buv}{b - d_2 + d_3 + r_2} - c_1 d_1 u^2 - \alpha uw, \\
\mathcal{H}_2(u,v,w) &= \frac{b^2 \delta v^2}{b - d_2 + d_3 + r_2} - \frac{b^2 c_2 r_2 v^2}{(b - d_2 + d_3 + r_2)^2} - \frac{b^2 \lambda v^2}{(b - d_2 + d_3 + r_2)^2} + \frac{2bc_2 r_2 vw}{b - d_2 + d_3 + r_2} \\
&\quad - \frac{b\beta uv}{b - d_2 + d_3 + r_2} + \frac{b\lambda v^2}{b - d_2 + d_3 + r_2} + \frac{b\lambda vw}{b - d_2 + d_3 + r_2} - b\delta v^2 - c_2 r_2 w^2 + \beta uw - \lambda vw, \\
\mathcal{H}_3(u,v,w) &= b\delta v^2 + \lambda vw - \frac{b\lambda v^2}{b - d_2 + d_3 + r_2}.
\end{aligned}$$

The functions $\mathcal{H}_1, \mathcal{H}_2, \mathcal{H}_3$ are quadratic in u, v, w, hence the system (5) has the form (18.1.1) with (18.1.2) in [24]. The center manifold can locally be represented as follows:

$$W^c(0) = \left\{(u,v,w) \in \mathbf{R}^3 | v = h_1(u), w = h_2(u), h_i(0) = 0, Dh_i(0) = 0, i = 1,2\right\},$$

for u sufficiently small. We now will compute the center manifold and derive the vector field on the center manifold. We assume,

$$h = \begin{pmatrix} h_1(u) \\ h_2(u) \end{pmatrix} = \begin{pmatrix} a_1 u^2 + a_2 u^3 + O(u^4) \\ b_1 u^2 + b_2 u^3 + O(u^4) \end{pmatrix}, \tag{6}$$

the center manifold must satisfy,

$$D_u h[Au + f(u, h_1(u), h_2(u))] - Bh - g(u, h_1(u), h_2(u)) = 0, \tag{7}$$

where (7) is a quasilinear partial differential equation, see equation 18.1.9 on page 248 in [24], that $h(u)$ must satisfy in order for its graph to be an invariant center manifold.

In (7), $A = 0$, $B = \begin{pmatrix} r_2 - d_2 & 0 \\ 0 & -b - d_3 \end{pmatrix}$, $f(u,v,w) = \mathcal{H}_1(u,v,w)$,
$g(u,v,w) = \begin{pmatrix} \mathcal{H}_2(u,v,w) \\ \mathcal{H}_3(u,v,w) \end{pmatrix}$. Substituting the above together with $v = h_1(u)$ and $w = h_2(u)$ in (7) and equating the coefficients of u^2, u^3, u^4 gives,

$$\begin{aligned} a_1 &= 0, \\ a_2 &= -\frac{3\beta c_1^2 d_1^2}{\alpha\,(b + d_3)\,(d_2 - r_2)}, \\ b_1 &= -\frac{3c_1^2 d_1^2}{\alpha\,(b + d_3)}, \\ b_2 &= -\frac{6c_1^3 d_1^3}{\alpha\,(b + d_3)^2}. \end{aligned}$$

Now, substituting a_1, a_2, b_1, b_2 in equation (6) gives,

$$\begin{aligned} h_1(u) &= -\frac{3\beta c_1^2 d_1^2 u^3}{\alpha\,(b + d_3)\,(d_2 - r_2)} + O(u^4), \\ h_2(u) &= -\frac{3c_1^2 d_1^2 u^2}{\alpha\,(b + d_3)} - \frac{6c_1^3 d_1^3 u^3}{\alpha\,(b + d_3)^2} + O(u^4). \end{aligned}$$

Using the formulae for $h_1(u)$ and $h_2(u)$ in (5) yields,

$$\begin{aligned} \dot{u} = -c_1 d_1 u^2 - \frac{3bc_1^2 d_1^2 u^3}{(b + d_3)\,(b - d_2 + d_3 + r_2)} \\ + u^4 \left(\frac{3\beta c_1^2 d_1^2}{(b + d_3)\,(d_2 - r_2)} - \frac{6bc_1^3 d_1^3}{(b + d_3)^2\,(b - d_2 + d_3 + r_2)} \right) + O(u^5), \end{aligned}$$

on the center manifold $W^c(0)$ near the origin. $u = 0$ is an unstable equilibrium of the equation since $c_1 d_1 > 0$ so that for small negative values of u the flow is in the negative direction, away from the equilibrium point. By Theorem 18.1.3 in [24] the origin is also an unstable equilibrium of (5).
Case 2: $r_2 - d_2 = 0$, $r_1 < d_1$. We proceed as in Case 1. In this case the eigenvalues of the Jacobian are $r_1 - d_1, 0, -b - d_3$. The stable manifold is two-dimensional and the center manifold is one-dimensional. The corresponding eigenvectors are the column vectors of,

$$Q = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & -\frac{b}{b+d_3} \\ 0 & 0 & 1 \end{pmatrix},$$

with

$$Q^{-1} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & \frac{b}{b+d_3} \\ 0 & 0 & 1 \end{pmatrix}.$$

Next, we introduce the transformation $X = QV$ where $X = \begin{pmatrix} S \\ P \\ Y \end{pmatrix}$, $V = \begin{pmatrix} u \\ v \\ w \end{pmatrix}$ into system (1) and after some algebraic manipulations get the diagonal form,

$$\begin{pmatrix} \dot{u} \\ \dot{v} \\ \dot{w} \end{pmatrix} = \begin{pmatrix} r_1 - d_1 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -b - d_3 \end{pmatrix} \begin{pmatrix} u \\ v \\ w \end{pmatrix} + \begin{pmatrix} \mathcal{H}_1(u,v,w) \\ \mathcal{H}_2(u,v,w) \\ \mathcal{H}_3(u,v,w) \end{pmatrix}, \tag{8}$$

where,

$$\begin{aligned}
\mathcal{H}_1(u,v,w) &= \frac{\alpha b u w}{b+d_3} - c_1 r_1 u^2 - \alpha u v, \\
\mathcal{H}_2(u,v,w) &= -\frac{b^3 c_2 d_2 w^2}{(b+d_3)^3} + \frac{2b^2 c_2 d_2 v w}{(b+d_3)^2} - \frac{b^2 c_2 d_2 d_3 w^2}{(b+d_3)^3} - \frac{\beta b^2 u w}{(b+d_3)^2} - \frac{b c_2 d_2 v^2}{b+d_3} \\
&\quad - \frac{c_2 d_2 d_3 v^2}{b+d_3} + \frac{2b c_2 d_2 d_3 v w}{(b+d_3)^2} + \frac{\beta b u v}{b+d_3} + \frac{\beta d_3 u v}{b+d_3} - \frac{\beta b d_3 u w}{(b+d_3)^2} - \frac{d_3 \lambda v w}{b+d_3} - \frac{b \delta d_3 w^2}{b+d_3} + \frac{b d_3 \lambda w^2}{(b+d_3)^2}, \\
\mathcal{H}_3(u,v,w) &= -\frac{b \lambda w^2}{b+d_3} + b \delta w^2 + \lambda v w.
\end{aligned}$$

The center manifold can locally be represented as follows:

$$W^c(0) = \left\{(u,v,w) \in \mathbf{R}^3 | u = h_1(v), w = h_2(v), h_i(0) = 0, Dh_i(0) = 0, i = 1,2\right\},$$

for v sufficiently small. We now will compute the center manifold and derive the vector field on the center manifold. We assume,

$$h = \begin{pmatrix} h_1(v) \\ h_2(v) \end{pmatrix} = \begin{pmatrix} a_1 v^2 + a_2 v^3 + O(v^4) \\ b_1 v^2 + b_2 v^3 + O(v^4) \end{pmatrix}. \tag{9}$$

The center manifold must satisfy,

$$D_v h[Av + f(h_1(v), v, h_2(v))] - Bh - g(h_1(v), v, h_2(v)) = 0, \tag{10}$$

where (10) is a quasilinear partial differential equation, see equation 18.1.9 on page 248 in [24], that $h(v)$ must satisfy in order for its graph to be an invariant center manifold.

In (10), $A = r_1 - d_1$, $B = \begin{pmatrix} 0 & 0 \\ 0 & -b - d_3 \end{pmatrix}$, $f(u,v,w) = \mathcal{H}_1(u,v,w)$,

$g(u,v,w) = \begin{pmatrix} \mathcal{H}_2(u,v,w) \\ \mathcal{H}_3(u,v,w) \end{pmatrix}$. Substituting the above together with $u = h_1(v)$ and $w = h_2(v)$ in equation (10) and equating the coefficients of v^3, v^4 gives,

$$a_1 = \frac{\lambda^2\,(2bc_2d_2 - d_3\lambda)}{(b+d_3)\,(b\beta(b\delta-\lambda) - 4\alpha bc_2d_2 + d_3(2\alpha\lambda + b\beta\delta))},$$

$$a_2 = \frac{2b^3\beta^2c_2\delta d_2\lambda^3 - 8\alpha b^2\beta c_2^2d_2^2\lambda^3 - 8\alpha b^2c_2^2d_2^2\lambda^4 - 3b^2\beta^2c_2d_2\lambda^4}{\beta\,(b+d_3)^2\,(\beta b^2\delta - \beta b\lambda - 4\alpha bc_2d_2 + \beta b\delta d_3 + 2\alpha d_3\lambda)^2} + \frac{2b^2\beta^2c_2\delta d_2d_3\lambda^3 + 8\alpha b\beta c_2d_2d_3\lambda^4 + 8\alpha bc_2d_2d_3\lambda^5 + b\beta^2d_3\lambda^5 - 2\alpha\beta d_3^2\lambda^5 - 2\alpha d_3^2\lambda^6}{\beta\,(b+d_3)^2\,(\beta b^2\delta - \beta b\lambda - 4\alpha bc_2d_2 + \beta b\delta d_3 + 2\alpha d_3\lambda)^2},$$

$$b_1 = \frac{\beta\lambda^2}{b\beta(\lambda - b\delta) + 4\alpha bc_2d_2 - d_3(2\alpha\lambda + b\beta\delta)},$$

$$b_2 = -\frac{\beta\lambda^3}{(b+d_3)\,(b\beta(b\delta-\lambda) - 4\alpha bc_2d_2 + d_3(2\alpha\lambda + b\beta\delta))}.$$

Now, substituting a_1, a_2, b_1, b_2 in equation (9) gives,

$$h_1(v) = \frac{\lambda^2v^2\,(2bc_2d_2 - d_3\lambda)}{(b+d_3)\,(b\beta(b\delta-\lambda) - 4\alpha bc_2d_2 + d_3(2\alpha\lambda + b\beta\delta))} + v^3\Bigg[\frac{2b^3\beta^2c_2\delta d_2\lambda^3 - 8\alpha b^2\beta c_2^2d_2^2\lambda^3 - 8\alpha b^2c_2^2d_2^2\lambda^4 - 3b^2\beta^2c_2d_2\lambda^4}{\beta\,(b+d_3)^2\,(\beta b^2\delta - \beta b\lambda - 4\alpha bc_2d_2 + \beta b\delta d_3 + 2\alpha d_3\lambda)^2} + \frac{2b^2\beta^2c_2\delta d_2d_3\lambda^3 + 8\alpha b\beta c_2d_2d_3\lambda^4 + 8\alpha bc_2d_2d_3\lambda^5 + b\beta^2d_3\lambda^5 - 2\alpha\beta d_3^2\lambda^5 - 2\alpha d_3^2\lambda^6}{\beta\,(b+d_3)^2\,(\beta b^2\delta - \beta b\lambda - 4\alpha bc_2d_2 + \beta b\delta d_3 + 2\alpha d_3\lambda)^2}\Bigg] + O(v^4),$$

$$h_2(v) = \frac{\beta\lambda^2v^2}{b\beta(\lambda - b\delta) + 4\alpha bc_2d_2 - d_3(2\alpha\lambda + b\beta\delta)} - \frac{\beta\lambda^3v^3}{(b+d_3)\,(b\beta(b\delta-\lambda) - 4\alpha bc_2d_2 + d_3(2\alpha\lambda + b\beta\delta))} + O(v^4).$$

Using the formulae for $h_1(v)$ and $h_2(v)$ in (8) yields,

$$\dot{v} = -c_2d_2v^2 - \frac{2v^4\left(4\alpha b^2c_2^2d_2^2\lambda^4 - 4\alpha bc_2d_2d_3\lambda^5 + \alpha d_3^2\lambda^6\right)}{(b+d_3)^2\,(\beta b^2\delta - \beta b\lambda - 4\alpha bc_2d_2 + \beta b\delta d_3 + 2\alpha d_3\lambda)^2} + O(v^5),$$

on the center manifold $W^c(0)$ near the origin. $v = 0$ is an unstable equilibrium of the equation since $c_2d_2 > 0$ so that for small negative values of v the flow is in the negative direction, away from the equilibrium point. By Theorem 18.1.3 in [24] the origin is also an unstable equilibrium of (8).

Case 3: When $r_1 - d_1 = 0$ and $r_2 - d_2 = 0$, two eigenvalues of the Jacobian (4) of the system (1) become zero. Since it is a non-hyperbolic equilibrium point, we cannot draw any conclusions about the stability or instability of the equilibrium point based on linearization. Therefore we determine the stability using the center manifold. The eigenvalues of the Jacobian of the system at E_0 are $0, 0, -b - d_3$ and hence the center manifold is two-dimensional and the stable subspace is one-dimensional. The corresponding eigenvectors are the column vectors of,

$$Q = \begin{pmatrix} 0 & 1 & 0 \\ 1 & 0 & -\frac{b}{b+d_3} \\ 0 & 0 & 1 \end{pmatrix},$$

with

$$Q^{-1} = \begin{pmatrix} 0 & 1 & \frac{b}{b+d_3} \\ 1 & 0 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

Next, we introduce the transformation $X = QV$ where $X = \begin{pmatrix} S \\ P \\ Y \end{pmatrix}$, $V = \begin{pmatrix} u \\ v \\ w \end{pmatrix}$ into system (1) and after some algebraic manipulations get the diagonal form,

$$\begin{pmatrix} \dot{u} \\ \dot{v} \\ \dot{w} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -b-d_3 \end{pmatrix} \begin{pmatrix} u \\ v \\ w \end{pmatrix} + \begin{pmatrix} \mathcal{H}_1(u,v,w) \\ \mathcal{H}_2(u,v,w) \\ \mathcal{H}_3(u,v,w) \end{pmatrix}, \tag{11}$$

where,

$$\begin{aligned} \mathcal{H}_1(u,v,w) &= -\frac{b^3c_2d_2w^2}{(b+d_3)^3} + \frac{2b^2c_2d_2uw}{(b+d_3)^2} - \frac{b^2c_2d_2d_3w^2}{(b+d_3)^3} - \frac{\beta b^2vw}{(b+d_3)^2} - \frac{bc_2d_2u^2}{b+d_3} - \frac{c_2d_2d_3u^2}{b+d_3} \\ &\quad + \frac{2bc_2d_2d_3uw}{(b+d_3)^2} + \frac{\beta buv}{b+d_3} + \frac{\beta d_3uv}{b+d_3} - \frac{d_3\lambda uw}{b+d_3} - \frac{\beta bd_3vw}{(b+d_3)^2} - \frac{b\delta d_3w^2}{b+d_3} + \frac{bd_3\lambda w^2}{(b+d_3)^2}, \\ \mathcal{H}_2(u,v,w) &= \frac{\alpha bvw}{b+d_3} - c_1d_1v^2 - \alpha uv, \\ \mathcal{H}_3(u,v,w) &= -\frac{b\lambda w^2}{b+d_3} + b\delta w^2 + \lambda uw. \end{aligned}$$

The center manifold can locally be represented as follows:

$$W^c(0) = \left\{(u,v,w) \in \mathbf{R}^3 | w = h(u,v), h(0,0) = 0, Dh(0,0) = 0\right\}, \tag{12}$$

for u, v, sufficiently small. We now will compute the center manifold and derive the vector field on the center manifold. We assume,

$$\begin{aligned} h(u,v) &= a_1u^2 + a_2uv + a_3v^2 + O((|u|,|v|)^3), \\ Dh(u,v) &= [2a_1u + a_2v, a_2u + 2a_3v] + O((|u|,|v|)^2). \end{aligned} \tag{13}$$

The equation for the center manifold is given by,

$$Dh(u,v)\left[A\begin{pmatrix} u \\ v \end{pmatrix} + f(u,v,h(u,v))\right] - Bh(u,v) - g(u,v,h(u,v)) = 0, \tag{14}$$

where equation (14) is a quasilinear partial differential equation, see equation 18.1.9 on page 248 in [24], that $h(u,v)$ must satisfy in order for its graph to be an invariant center manifold.
In (14),

$$A = \begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}, \quad B = -b - d_3$$

$$f(u,v,w) = \begin{pmatrix} \mathcal{H}_1(u,v,w) \\ \mathcal{H}_2(u,v,w) \end{pmatrix}, \quad g(u,v,w) = \mathcal{H}_3(u,v,w)$$

Substituting the above in (14) gives,

$$
\begin{aligned}
&(2a_1 u + a_2 v + O((|u|,|v|)^2))\Big\{\frac{bw\,(c_2 d_2\,(2bu - bw + 2d_3 u) - \beta v\,(b + d_3) + d_3\lambda w)}{(b + d_3)^{\,2}} \\
&+ \frac{bw(b\delta w + \lambda u)}{b + d_3} - b\delta w^2 - c_2 d_2 u^2 + \beta uv - \lambda uw\Big\} + \Big(a_2 u + 2a_3 v + O((|u|,|v|)^2)\Big) \\
&\left(\frac{\alpha bvw}{b + d_3} - c_1 d_1 v^2 - \alpha uv\right) + (b + d_3)\left(a_1 u^2 + a_2 uv + a_3 v^2 + O((|u|,|v|)^3)\right) - b\delta w^2 - \lambda uw + \frac{b\lambda w^2}{b + d_3} = 0.
\end{aligned}
$$

Putting $w = h(u, v)$ in above equation and equating coefficients of u^2v, uv^2 and uv^3 gives,

$$
\begin{aligned}
a_1 &= 1, \\
a_2 &= \frac{2\beta}{\alpha + c_2 d_2 + \lambda}, \\
a_3 &= \frac{2\beta\,(\beta - c_1 d_1)}{(2\alpha + \lambda)\,(\alpha + c_2 d_2 + \lambda)}.
\end{aligned}
$$

Thus,

$$
h(u, v) = u^2 + \frac{2\beta uv}{\alpha + c_2 d_2 + \lambda} + \frac{2\beta v^2\,(\beta - c_1 d_1)}{(2\alpha + \lambda)\,(\alpha + c_2 d_2 + \lambda)} + O\left((|u|,|v|)^3\right).
$$

Using (11) yields,

$$
\begin{aligned}
\dot{u} &= -c_2 d_2 u^2 + \beta uv + \frac{u^2 v\,(-\alpha b\beta - b\beta\lambda + 3b\beta c_2 d_2 - 2\beta d_3\lambda)}{(b + d_3)\,(\alpha + c_2 d_2 + \lambda)} \\
&\quad - \frac{2uv^2\left(2\alpha b\beta^2 + b\beta^2\lambda - 2b\beta^2 c_2 d_2 + 2b\beta c_1 c_2 d_1 d_2 - \beta c_1 d_1 d_3\lambda + \beta^2 d_3\lambda\right)}{(2\alpha + \lambda)\,(b + d_3)\,(\alpha + c_2 d_2 + \lambda)} + O((|u|,|v|)^4), \\
\dot{v} &= -\alpha uv - c_1 d_1 v^2 + \frac{\alpha b u^2 v}{b + d_3} + \frac{2\alpha b\beta uv^2}{(b + d_3)\,(\alpha + c_2 d_2 + \lambda)} + O((|u|,|v|)^4).
\end{aligned} \tag{15}
$$

on the center manifold $W^c(0)$ near the origin.

Clearly, $(0, 0)$ is an equilibrium point of the reduced system (15). We draw the phase portrait of (15) neglecting order terms $O((|u|,|v|)^4)$ with the parameters in Table 1 except for $r_1 = 0.2$/day and $\delta = 0.02$/day, see Figure 3. By Theorem 18.1.3 in [24] the equilibrium E_0 of (1) has the same stability properties as the equilibrium $(0, 0)$ of (15). So we have reduced a 3D problem to a 2D problem.

4.2. Stability of the axial equilibrium $E_1(\hat{S}, 0, 0)$

The Jacobian of the system (1) at the axial equilibrium E_1 has eigenvalues $\zeta_{11} = -b - d_3$, $\zeta_{12} = d_1 - r_1$, $\zeta_{13} = \frac{\beta(r_1 - d_1)}{c_1 r_1} - d_2 + r_2$. Therefore at E_1 the system is locally asymptotically stable if $d_1 < r_1$, $\frac{\beta(r_1 - d_1)}{c_1 r_1} < d_2 - r_2$.
As in section 4.1 there are non-hyperbolic cases which could be studied by using center manifold theory.

4.3. Stability of the disease-free equilibrium $E_2(\bar{S}, \bar{P}, 0)$

The Jacobian of the system (1) at the disease-free equilibrium E_2 has a pair of complex conjugate characteristic roots $\zeta_{21,22} = \theta \pm i\phi$ where,

$$\theta = \frac{c_1 r_1 \left(r_2 (\alpha + c_2 (d_1 + d_2 - r_1)) - c_2 r_2^2 - \alpha d_2\right) + \beta c_2 r_2 (d_1 - r_1)}{2(\alpha\beta + c_1 c_2 r_1 r_2)}, \quad \text{and} \quad \phi \neq 0,$$

and

$$\zeta_{23} = -\frac{\alpha b \beta + b c_1 c_2 r_1 r_2 + d_3(\alpha\beta + c_1 c_2 r_1 r_2) + c_1 d_2 \lambda r_1 - c_1 \lambda r_1 r_2 + \beta d_1 \lambda - \beta \lambda r_1}{\alpha\beta + c_1 c_2 r_1 r_2}.$$

Near the equilibrium state E_3, the system (1) is locally asymptotically stable if $\zeta_{23} < 0$ and $\theta < 0$, which implies,

$$r_2 > d_2, \quad 0 < d_1 < \frac{-c_1 d_2 r_1 + c_1 r_1^2 + c_1 r_2 r_1 + \beta r_1}{\beta + c_1 r_1},$$
$$c_2 > \frac{\alpha c_1 r_1 r_2 - \alpha c_1 d_2 r_1}{-c_1 d_1 r_2 r_1 - c_1 d_2 r_2 r_1 + c_1 r_2 r_1^2 + c_1 r_2^2 r_1 - \beta d_1 r_2 + \beta r_2 r_1},$$
$$0 < \lambda < \frac{\alpha b \beta + b c_1 c_2 r_1 r_2 + c_1 c_2 d_3 r_1 r_2 + \alpha \beta d_3}{-c_1 d_2 r_1 + c_1 r_1 r_2 - \beta d_1 + \beta r_1}.$$

4.4. Stability of the prey and infection free equilibrium $E_3(0, P_3 > 0, 0)$

The Jacobian of the system (1) at the prey and infection free equilibrium E_3 has eigenvalues,

$$\zeta_{31} = d_2 - r_2, \quad \zeta_{32} = -\frac{b c_2 r_2 + c_2 d_3 r_2 + d_2 \lambda - \lambda r_2}{c_2 r_2} \quad \text{and} \quad \zeta_{33} = -\frac{c_2 d_1 r_2 - c_2 r_1 r_2 - \alpha d_2 + \alpha r_2}{c_2 r_2}.$$

Therefore the equilibrium E_3 is locally asymptotically stable if $r_2 - d_2 > 0$, $\lambda(r_2 - d_2) - c_2 r_2 (b + d_3) < 0$ and $\alpha(r_2 - d_2) + c_2 r_2 (d_1 - r_1) > 0$.

4.5. Stability of the prey-free equilibrium $E_4(0, P_4 > 0, Y_4 > 0)$:

The Jacobian of the system (1) at the prey-free equilibrium E_4 has eigenvalues,

$$\zeta_{41} = \frac{\alpha \mathcal{K} - 2 b c_2 \delta d_1 r_2 + 2 b c_2 \delta r_1 r_2 + \alpha b \delta d_2 - \alpha b \delta r_2 - \alpha d_3 \lambda}{2 b c_2 \delta r_2},$$
$$Re(\zeta_{42,43}) = \frac{b \delta r_2 \left(2 c_2 \left(b^2 \delta + d_3 (b\delta - 2\lambda) - b\lambda + \mathcal{K}\right) + \lambda(\lambda - b\delta)\right) + \lambda (b\delta - \lambda)(b \delta d_2 - d_3 \lambda + \mathcal{K})}{4 b^2 c_2 \delta^2 r_2}.$$

Therefore the equilibrium E_4 is locally asymptotically stable if,

$$0 < \delta < \frac{b\lambda + d_3 \lambda}{b^2 + b(r_2 - d_2) + b d_3}, \quad 0 < \mathcal{K} < b\delta(r_2 - d_2) + d_3 \lambda,$$

$$0 < c_2 < \frac{\lambda (b\delta - \lambda)(b\delta(r_2 - d_2) + d_3 \lambda - \mathcal{K})}{2 b \delta r_2 (b^2 \delta + d_3 (b\delta - 2\lambda) - b\lambda + \mathcal{K})}, \quad \alpha > \frac{2 b c_2 \delta r_2 (r_1 - d_1)}{b\delta(r_2 - d_2) + d_3 \lambda - \mathcal{K}}.$$

For the parameter set in Table 1 (with $d_2 = 0.4$ and $\delta = 0.02$ such that $r_2 - d_2 > 0$) the equilibrium E_4 is not locally asymptotically stable as $0 < c_2 \not< \frac{\lambda(b\delta - \lambda)(b\delta(r_2 - d_2) + d_3\lambda - \mathcal{K})}{2 b \delta r_2 (b^2 \delta + d_3 (b\delta - 2\lambda) - b\lambda + \mathcal{K})}$.

4.6. Stability of a coexistence equilibrium state $E^* = (S^*, P^*, Y^*)$

The Jacobian of (1) at the coexistence equilibrium E^* is,

$$J_{E^*} = \begin{pmatrix} r_1(1-2c_1S^*) - d_1 + \alpha(-P^*) & \alpha(-S^*) & 0 \\ \beta P^* & r_2(1-2c_2P^*) - d_2 + \beta S^* - \lambda Y^* & -2b\delta Y^* + b - \lambda P^* \\ 0 & \lambda Y^* & b(2\delta Y^* - 1) - d_3 + \lambda P^* \end{pmatrix} \tag{16}$$

The characteristic equation of J_{E^*} has the form,

$$\chi^3 + D_1\chi^2 + D_2\chi + D_3 = 0. \tag{17}$$

By the Routh-Hurwitz criteria, the coexistence equilibrium E^* is locally asymptotically stable if $D_1, D_3 > 0$ and $\Delta = D_1D_2 - D_3 > 0$. If the coexistence equilibrium E^* depends on a parameter, say δ in this case, then it undergoes a Hopf bifurcation at the threshold value $\delta = \delta^H$ if $D_1(\delta^H) > 0, D_2(\delta^H) > 0, D_3(\delta^H) > 0$; $\Delta = D_1(\delta^H).D_2(\delta^H) - D_3(\delta^H) = 0$ and $\frac{\partial\Delta}{\partial\delta}(\delta^H) \neq 0$, see [18].

4.6.1. Normal form reduction of Hopf bifurcation using center manifold reduction

In this subsection we study theoretically the center manifold of (1) at a coexistence equilibrium point E^* which is also a Hopf bifurcation point (a numerical example will be given in section 5). We will obtain the normal form of this point by using center manifold theory. Poincaré's method will be used to convert the system into normal form. We introduce new variables $x_1 = S - S^*$, $x_2 = P - P^*$ and $x_3 = Y - Y^*$. Then (1) can be represented in matrix form as,

$$\dot{X} = \hat{A}X + \hat{B}, \tag{18}$$

where $\hat{A}$ denotes the Jacobian matrix of the converted system (18). $\hat{A}X$ and $\hat{B}$ denote the linear and nonlinear parts of the new system respectively, where

$$X = \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}, \qquad \hat{A} = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}, \qquad \hat{B} = \begin{pmatrix} B_1(x_1, x_2, x_3) \\ B_2(x_1, x_2, x_3) \\ B_3(x_1, x_2, x_3) \end{pmatrix},$$

$a_{ij}(i, j = 1, 2, 3)$, $B_i(x_1, x_2, x_3)(i = 1, 2, 3)$ are given in the Appendix. At the threshold parameter $\delta = \delta^H$, the system (1) has a pair of purely imaginary eigenvalues. We consider two conjugate imaginary eigenvalues $\rho_{1,2} = \pm i\sigma$, $\rho_3 = \nu$ where $\sigma > 0$ and $\rho_3 < 0$. Next, we find an invertible transformation matrix T which transforms the matrix $\hat{A}$ to the form,

$$T^{-1}\hat{A}T = \begin{pmatrix} 0 & -\sigma & 0 \\ \sigma & 0 & 0 \\ 0 & 0 & \nu \end{pmatrix},$$

where,

$$T = \begin{pmatrix} 1 & 0 & 1 \\ c_{21} & c_{22} & c_{23} \\ c_{31} & c_{32} & c_{33} \end{pmatrix},$$

where $c_{ij}(i = 2; 3, j = 1; 2; 3)$ are given in the Appendix. We perform a further transformation of the variables $X = TV$, where $V = (u, v, w)'$ to achieve the normal form of (18). Then the $V-$ form of corresponding to (18) is,

$$\frac{dV}{dt} = T^{-1}\hat{A}TV + F, \tag{19}$$

where

$$F = T^{-1}\hat{B} = \begin{pmatrix} F_1(u,v,w) \\ F_2(u,v,w) \\ F_3(u,v,w) \end{pmatrix}.$$

$F_i(u,v,w)(i = 1,2,3)$ (given in the Appendix) can be determined by converting B_i's using the new variables $x_1 = u + w$, $x_2 = c_{21}u + c_{22}v + c_{23}w$, $x_3 = c_{31}u + c_{32}v + c_{33}w$. Next, on the basis of the center manifold theorem, we determine the center manifold $W^c(0,0,0)$ of the system (19) at the origin, which can be described as follows:
Assume,

$$\begin{aligned} h(u,v) &= a_1u^2 + a_2uv + a_3v^2 + O((|u|,|v|)^3), \\ Dh(u,v) &= [2a_1u + a_2v, a_2u + 2a_3v] + O((|u|,|v|)^2). \end{aligned} \tag{20}$$

$h(u,v)$ must satisfy (14) with
$A = \begin{pmatrix} 0 & -\sigma \\ \sigma & 0 \end{pmatrix}$, $B = \nu$, $f(u,v,w) = \begin{pmatrix} F_1(u,v,w) \\ F_2(u,v,w) \end{pmatrix}$, $g(u,v,w) = F_3(u,v,w)$.
Substituting the above in (14) gives

$$\begin{aligned} &\Big(2a_1u + a_2v + O((|u|,|v|)^2)\Big)\Big\{ -\sigma v + F_1(u,v,w)\Big\} + (a_2u + 2a_3v + O((|u|,|v|)^2)) \\ &\qquad \Big\{\sigma u + F_2(u,v,w)\Big\} - Bh(u,v) - g(u,v,h(u,v)) = 0. \end{aligned} \tag{21}$$

Putting $w = h(u,v)$ in (21) and equating coefficients of u^2,uv and v^2 gives,

$$\begin{aligned} a_1 &= \frac{bc_{31}^2\delta(c_{22}+c_{32}) - \alpha c_{21}^2 c_{32} + c_{21}(c_{22}c_{31}(\alpha+\lambda) + c_{31}c_{32}\lambda + \beta(-c_{32}))}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))} \\ &\quad + \frac{c_2c_{21}^2c_{32}r_2 + c_1r_1(c_{22}c_{31} - c_{21}c_{32})}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))}, \\ a_2 &= 0, \\ a_3 &= \frac{c_{32}\left((c_{22}+c_{32})(bc_{32}\delta + c_{22}\lambda) + c_2c_{22}^2r_2\right)}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))}. \end{aligned}$$

Thus substituting a_1, a_2, a_3 in equation (20),

$$\begin{aligned} h(u,v) &= \frac{u^2\left(c_2c_{21}^2c_{32}r_2 + c_1r_1(c_{22}c_{31} - c_{21}c_{32})\right)}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))} + \frac{c_{32}v^2\left((c_{22}+c_{32})(bc_{32}\delta + c_{22}\lambda) + c_2c_{22}^2r_2\right)}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))} \\ &\quad + \frac{u^2\left(bc_{31}^2\delta(c_{22}+c_{32}) - \alpha c_{21}^2c_{32} + c_{21}(c_{22}c_{31}(\alpha+\lambda) + c_{31}c_{32}\lambda + \beta(-c_{32}))\right)}{\nu(c_{32}(c_{23}-c_{21}) + c_{22}(c_{31}-c_{33}))} + O\left((|u|,|v|)^3\right). \end{aligned} \tag{22}$$

Substituting (22) in (19) yields,

$$\begin{aligned} \dot{u} &= -\sigma v + \xi_{11}u^2 + \xi_{12}uv + \xi_{13}v^2 + \xi_{14}u^2v + \xi_{15}uv^2 + O\left((|u|,|v|)^4\right), \\ \dot{v} &= \sigma u + \xi_{21}u^2 + \xi_{22}uv + \xi_{23}v^2 + \xi_{24}u^2v + \xi_{25}uv^2 + O\left((|u|,|v|)^4\right), \end{aligned} \tag{23}$$

on the center manifold $W^c(0)$ near the origin where ξ_{ij} $(i = 1;2, j = 1;2;3;4;5)$ are given in the Appendix. Clearly, $(0,0)$ is an equilibrium point of the reduced system (23).

Now, we use the method of normal forms to simplify the new system (23). For this we follow the procedure mentioned in [19]. The Jacobian matrix of the system (23) near the origin has eigenvalues $\pm i\sigma$. The right and left eigenvectors of the matrix corresponding to the eigenvalue $i\sigma$ are $p = \begin{pmatrix} i \\ 1 \end{pmatrix}$ and $q = \frac{1}{2}\begin{pmatrix} -i \\ 1 \end{pmatrix}$.
Second, we introduce the transformation,

$$\begin{pmatrix} u \\ v \end{pmatrix} = px(t) + \bar{p}\bar{x}(t),$$

and obtain,
$u(t) = ix(t) - i\bar{x}(t)$, $v(t) = x(t) + \bar{x}(t)$. Using this transformation system (23) and multiplying the result from the left with q yields,

$$\begin{aligned} \dot{x} &= i\sigma x\frac{1}{2} + (i\xi_{11} + \xi_{12} - i\xi_{13} - \xi_{21} + i\xi_{22} + \xi_{23})\,x^2 + \frac{1}{2}\left((-i\xi_{14} + \xi_{15} + \xi_{24} + i\xi_{25})\,x^2\bar{x}\right) \\ &- (i\,(\xi_{11} + \xi_{13} + i\xi_{21} + i\xi_{23})\,xx\bar{x}) + \frac{1}{2}\left((-i\xi_{14} - \xi_{15} + \xi_{24} - i\xi_{25})\,x\bar{x}^2\right) \\ &+ \frac{1}{2}\,(i\xi_{11} - \xi_{12} - i\xi_{13} - \xi_{21} - i\xi_{22} + \xi_{23})\,\bar{x}^2 + \text{nonresonance cubic and higher-order terms.} \end{aligned} \tag{24}$$

Third, we introduce a near-identity transformation of the form,

$$z(t) = z(t) + \hat{q}_1 z(t)^2 + \hat{q}_2 z(t)\bar{z}(t) + \hat{q}_3\bar{z}(t)^2,$$

into system (24), approximate $\dot{\bar{z}} = -i\bar{z}$, and obtain

$$\begin{aligned} \dot{z} &= i\sigma z + z\bar{z}\,(-i\xi_{11} - i\xi_{13} + \xi_{21} + \xi_{23} + i\hat{q}_2) + \frac{1}{2}z^2(i\xi_{11} + \xi_{12} - i\xi_{13} - \xi_{21} + i\xi_{22} + \xi_{23} \\ &- 2i\hat{q}_1\sigma) + \frac{1}{2}i\bar{z}^2\,(\xi_{11} + i\xi_{12} - \xi_{13} + i\xi_{21} - \xi_{22} - i\xi_{23} + 2\hat{q}_3\sigma + 4\hat{q}_3) + \frac{1}{2}z^2\bar{z}(-i\xi_{14} + \xi_{15} + \xi_{24} \\ &+ i\xi_{25} - i\xi_{11}\hat{q}_2 + \xi_{12}\hat{q}_2 - 3i\xi_{13}\hat{q}_2 + \xi_{21}\hat{q}_2 + i\xi_{22}\hat{q}_2 + 3\xi_{23}\hat{q}_2 + 2i\xi_{11}\hat{q}_1 + 2i\xi_{11}\hat{q}_3 - 2\xi_{12}\hat{q}_3 \\ &+ 2i\xi_{13}\hat{q}_1 - 2i\xi_{13}\hat{q}_3 - 2\xi_{21}\hat{q}_1 - 2\xi_{21}\hat{q}_3 - 2i\xi_{22}\hat{q}_3 - 2\xi_{23}\hat{q}_1 + 2\xi_{23}\hat{q}_3 + 2i\hat{q}_1\hat{q}_2\sigma - 4i\hat{q}_1\hat{q}_2). \end{aligned} \tag{25}$$

Fourth, we choose the $\hat{q}_i$, $(i = 1, 2, 3)$ to eliminate the quadratic terms and obtain,

$$\begin{aligned} \hat{q}_1 &= \frac{\xi_{11} - \xi_{13} + \xi_{22} + i\,(-\xi_{12} + \xi_{21} - \xi_{23})}{2\sigma}, \\ \hat{q}_2 &= \xi_{11} + \xi_{13} + i\,(\xi_{21} + \xi_{23})\,, \\ \hat{q}_3 &= \frac{-\xi_{11} + \xi_{13} + \xi_{22} + i\,(-\xi_{12} - \xi_{21} + \xi_{23})}{2(\sigma + 2)}. \end{aligned} \tag{26}$$

Finally, we substitute the $\hat{q}_i$ in (25) and obtain the normal form

$$\dot{z} = i\sigma z - \kappa z^2\bar{z}, \tag{27}$$

where κ is given in the Appendix.

We note that for the system (27) the first Lyapunov coefficient l_1 (in the version implemented in MatCont [9]) is equal to $-2Re(\kappa)$. Hence the Hopf bifurcation is supercritical if $\kappa > 0$ and subcritical if $\kappa < 0$.

5. Unfolding of the Generalized Hopf bifurcation

In this section we briefly summarize the parts of [17], §8.3 which are relevant to our numerical computations in §7.1. At a generalized Hopf bifurcation (also called Bautin bifurcation) the Jacobian matrix of system (1) has a pair of simple purely imaginary eigenvalues $\zeta_{1,2} = \pm i\omega_0, \omega_0 > 0$, and the first Lyapunov coefficient vanishes: $l_1 = 0$. In this case, the restriction of the system to the center manifold of dimension 2 at the critical parameter values is locally smoothly orbitally equivalent to the one-dimensional complex normal form

$$\dot{z} = iz + l_2 z|z|^4 + O(|z|^6). \tag{28}$$

The second Lyapunov coefficient l_2 is given in [17], eq. (8.23). More precisely, there is a smooth invertible local coordinate transformation combined with a time reparametrization reducing the restriction of the system (1) to the center manifold at the generalized Hopf bifurcation point to the form (28). If $l_2 \neq 0$ then the reduced system on the parameter-dependent center manifold is orbitally topologically equivalent to

$$\dot{z} = (\beta_1 + i)z + \beta_2 z|z|^2 + sz|z|^4 + O(|z|^6), \tag{29}$$

with $s = sign(l_2)$ and two unfolding parameters β_1, β_2.

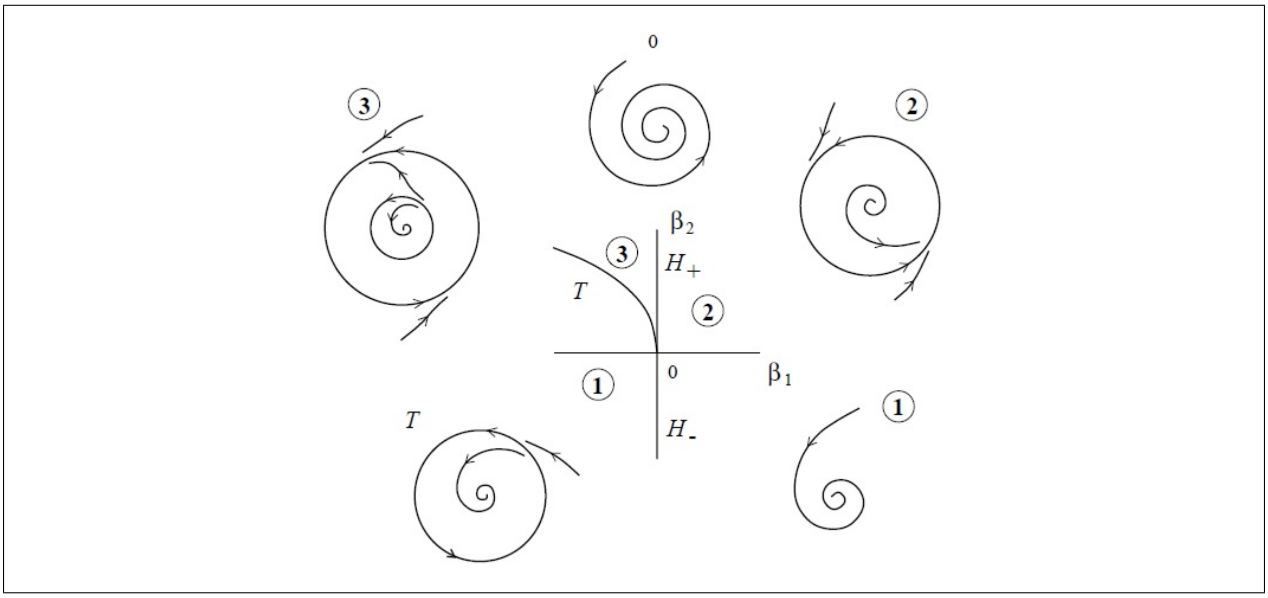


Figure 1: Unfolding of the truncated normal form of the Generalized Hopf bifurcation. Figure reproduced from [17], Fig. 8.7.

The truncated normal form of (29) is obtained by omitting the $O(|z|^6)$ terms. The unfolding of this truncated normal form in the case $l_2 < 0$ is displayed in [17], Fig. 8.7 and shown here in Figure 1. The β_2-axis is the Hopf bifurcation curve where H_+, respectively H_-, consists of subcritical, respectively, supercritical Hopf bifurcations. The GH point is at the origin. The β_1-axis is not a bifurcation curve. In region 1 the system has a single stable equilibrium and no cycles at all. In the region 2 the system has an unstable equilibrium and a stable limit cycle. In region 3 the system has a stable equilibrium, a stable cycle and an unstable limit cycle. The two limit cycles collide and disappear at the curve of folds of cycles (LPC) curve T.

In [17] it is proved that the unfolding of the truncated normal form is also the topological normal form of the Generalized Hopf bifurcation.

6. Unfolding of the fold-Hopf bifurcation

In this section we briefly summarize the parts of [17], §8.5 which are relevant to our numerical computations in §7.1. The fold-Hopf bifurcation is a codimension 2 bifurcation which is also called zero-Hopf (ZH) bifurcation, saddle-node Hopf bifurcation or Gavrilov-Guckenheimer bifurcation. At a fold-Hopf bifurcation the Jacobian matrix of system (1) has one zero eigenvalue $\zeta_1 = 0$ and a pair of simple purely imaginary eigenvalues $\zeta_{2,3} = \pm i\omega_0, \omega_0 > 0$. In this case, the system is locally orbitally smoothly equivalent near the origin to the complex normal form

$$\begin{aligned} \dot{\xi} &= \beta_1 + \xi^2 + s|\zeta|^2 + O(\|\xi, \zeta, \bar{\zeta}\|^4), \\ \dot{\zeta} &= (\beta_2 + i\omega_1)\zeta + (\theta + i\nu)\xi\zeta + \xi^2\zeta + O(\|\xi, \zeta, \bar{\zeta}\|^4), \end{aligned} \tag{30}$$

$\xi \in \mathbb{R}^1, \zeta \in \mathbb{C}^1$ are new variables; β_1 and β_2 are new parameters; θ, ν, ω_1 are smooth real-valued functions of $\beta = (\beta_1, \beta_2)$. The normal form coefficients of the ZH bifurcation are s, $\theta 0 = \theta(0,0)$ and $E0$. $E0$ does not appear in (30) but a negative value of $E0$ indicates that the orbits of the systems must be computed in reverse time. In coordinates (ξ, ρ, φ) with $\zeta = \rho e^{i\varphi}$, the (truncated) normal form of (30) without $O(\|.\|^4)$-terms can be written as

$$\begin{aligned} \dot{\xi} &= \beta_1 + \xi^2 + s\rho^2, \\ \dot{\rho} &= \rho(\beta_2 + \theta\xi + \xi^2), \\ \dot{\varphi} &= \omega_1 + \vartheta\xi. \end{aligned} \tag{31}$$

To understand the bifurcations in (31), one needs to study only the planar system for (ξ, ρ) with $\rho \geq 0$:

$$\begin{aligned} \dot{\xi} &= \beta_1 + \xi^2 + s\rho^2, \\ \dot{\rho} &= \rho(\beta_2 + \theta\xi + \xi^2). \end{aligned} \tag{32}$$

System (32) is also called the truncated amplitude system.

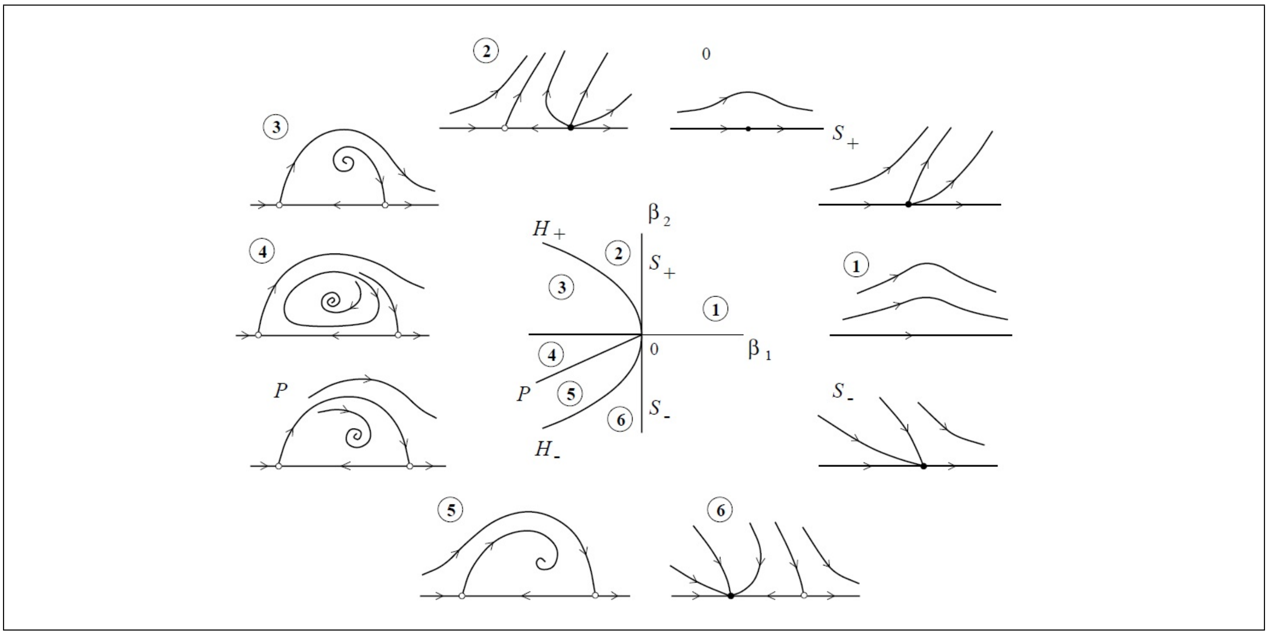


Figure 2: Unfolding of the truncated amplitude system of the fold-Hopf bifurcation in the case ($s = 1, \theta < 0$),([17],Fig. 8.16)

We will restrict to the case $s = 1, \theta < 0, E0 < 0$. The unfolding of (32) in the case ($s = 1, \theta < 0, E0 > 0$) is displayed in [17], Fig. 8.16 and shown here in Figure 2. The β_2-axis is the generic fold bifurcation curve where S^+ and S^- are two branches of the fold curve, separated by the point ZH at the origin. Crossing the branch S^+ gives rise to an unstable node and a saddle,while passing through S^- implies a stable node and a saddle. H_+, H_- are subcritical and supercritical Hopf bifurcation curves, respectively. Along the curve H_+ new equilibria of (32) are born into region 3 of Figure 2. Because of the time reversal, they are unstable if $E0 > 0$ and stable if $E0 < 0$ and correspond to limit cycles of (31). The curve $T = \{(\beta_1, \beta_2) : \beta_1 < 0, \beta_2 = 0\}$ is a Hopf bifurcation curve of (32) which corresponds to a Neimarck-Sacker bifurcation curve of (31). We can therefore expect to find invariant tori of (31) near T.
In coordinates (ξ, ρ, φ) system (30) also can be written as

$$\begin{aligned} \dot{\xi} &= \beta_1 + \xi^2 + s\rho^2 + \Theta_\beta(\xi, \rho, \varphi), \\ \dot{\rho} &= \rho(\beta_2 + \theta\xi + \xi^2) + \Psi_\beta(\xi, \rho, \varphi), \\ \dot{\varphi} &= \omega_1 + \vartheta\xi + \Phi_\beta(\xi, \rho, \varphi), \end{aligned} \tag{33}$$

where $\Theta_\beta(\xi, \rho, \varphi), \Psi_\beta(\xi, \rho, \varphi) = O((\xi^2 + \rho^2)^2)$, and $\Phi_\beta(\xi, \rho, \varphi) = O(\xi + \rho)^2$ are smooth functions that are 2π-periodic in φ. For sufficiently small β, system (33) exhibits the same local bifurcations in a small neighborhood of the origin in the phase space as (31). This system has at most two equilibria, which appear via the fold bifurcation on a curve that is close to S, and undergo a Hopf bifurcation at a curve close to H, thus giving rise to a unique limit cycle. If $s\theta < 0$, this cycle loses stability and generates a torus via the Neimark-Sacker bifurcation at some curve close to the curve T.

7. Computational results & discussion

Definition	Parameters	Values (in per day)
Reproduction rate of prey	r_1	1.5
Density factor in prey	c_1	0.1
Predation rate of prey	α	0.5
Natural death rate of prey	d_1	0.2
Reproduction rate of predator	r_2	0.5
Density factor in predator	c_2	0.1
Energy transfer rate in predator	β	0.2
Disease transformation rate	λ	0.5
Disease recovery rate	b	0.2
Density factor in recovery	δ	-
Death rate of susceptible predator	d_2	0.5
Death rate of infected predator	d_3	0.2

Table 1: Parameter values

In this section we compare our analytical results with numerical results in the case of the biologically plausible parameter set in Table 1. The parameter δ is variable. Figures are drawn with Mathematica and Matlab. For the numerical continuation of equilibria and periodic orbits we use the Matlab-based software MatCont 7.3 [9]. We start with computing orbits for $\delta = 0.02$/day from several starting points and observe that all trajectories converge to the same coexistence equilibrium $E^* = (6.12077, 0.763768, 4.52902)$, which suggests that it has a large domain of attraction, see Figure 4. Using δ as a bifurcation parameter, we perform the numerical continuation of the coexistence equilibrium. We plot D_1,D_3 and $D_1D_2 - D_3$ as defined in (17) as a function of δ. We find that for $\delta \in [0, \delta^H \approx 0.354594]$ the three species coexist, see Figure 5. For $\delta > \delta^H$ the coexistence equilibrium loses stability. During the continuation, a pair of complex eigenvalues of the Jacobian matrix crosses the imaginary axis at $\delta = \delta^H$, implying that stability is lost through a Hopf bifurcation. Ecologically, there is a threshold value for the parameter associated with the density factor in recovery, below which a stable coexistence of all the species appears. δ^H is nothing but the root of the function $D_1D_2 - D_3$. At $\delta = \delta^H$, trajectories of the system (1) start oscillating periodically, i.e., the biomass of all the species becomes unstable. From (27), $\mathrm{Re}(\kappa) = -0.0491876$ and $\mathrm{Im}(\kappa) = 0.0683601$ at $\delta = \delta^H$ which implies that the Hopf bifurcation is subcritical. The first Lyapunov coefficient computed by MatCont is found to be $1.238138e \times 10^{-02}$ which confirms the subcriticality of the Hopf point. Ecologically, the appearance of a subcritical Hopf bifurcation means that the oscillating periodic solutions are orbitally unstable. At $\delta = 0.354594/day$ we plot the center manifold of the system neglecting the order terms $O((|u|,|v|)^4)$, see (Figure 7). Continuation of the periodic orbits with free parameter δ shows a saddle-node bifurcation of limit cycles (Limit point of cycles, LPC) at $\delta = \delta^{LPC} \approx 0.3415959/day$ where the periodic orbits gain stability (Figure 6 and Figure 8(b)). Further continuation of the stable periodic orbits leads to the detection of several period doubling points, see Figure 8(a).

7.1. Codimension 2 bifurcations

Starting from the Hopf bifurcation point where $\delta = \delta^H$, we compute a Hopf bifurcation curve with δ and λ as the two free parameters (Figure 9). This leads to the detection of a generalized Hopf bifurcation (denoted as GH) at ($\delta \approx 0.304611; \lambda \approx 0.376872$) and a fold-Hopf bifurcation at ZH ($\delta \approx 0.293428; \lambda \approx 0.071447$). The equilibrium state vectors at the GH and ZH bifurcation points are $(6.989579, 0.503126, 3.453357)$ and $(4.069406, 1.379178, 5.136903)$ respectively. The normal form coefficient of the GH bifurcation is $l_2 = -1.282226 \times 10^{-03}$ and the ZH bifurcation has normal form coefficients are $s = 1, \theta = -7.217617^{-01}, E0 = -1$. At the GH point the first Lyapunov coefficient vanishes and the nature of the Hopf bifurcation changes from subcritical to supercritical. In Figure 9 we compute a LPC curve starting from the GH point with the same free parameters δ and λ. In region II, the system (1) has a unique stable limit cycle. System (1) has a stable equilibrium surrounded by two limit cycles of opposite stability in region I (region 3 in Figure 1) that collide and disappear at the LPC curve. At the ZH bifurcation point the projections of the Hopf curve and the saddle-node curve on the parameter plane are tangential. Starting from the bifurcation point ZH, we also compute a Neimark-Sacker curve with the same free parameters (Figure 9). In our case ($E0 < 0$) by the time reversal there are stable cycles in region 4 (Figure 2).

We note that the curve T in Figure 1 corresponds to the LPC curve in Figure 9. Also, the curve $\{(\beta_1, \beta_2) : \beta_1 < 0, \beta_2 = 0\}$ in Figure 2 corresponds to the Neimark-Sacker curve in Figure 9. Finally, the existence of a Neimark-Sacker curve suggests the existence of tori. In a numerical integration with starting point ($\delta \approx 0.293428, \lambda \approx 0.072447$) near the ZH point we indeed observe convergence to a stable torus, see Figure 10.

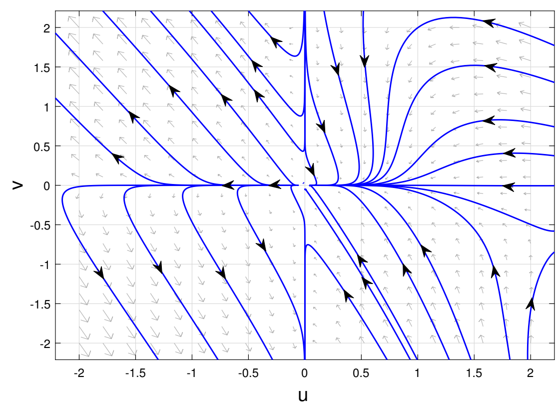


Figure 3: Phase portrait of the center manifold with parameters in Table 1 except for $r_1 = 0.2$/day and $\delta = 0.02$/day.

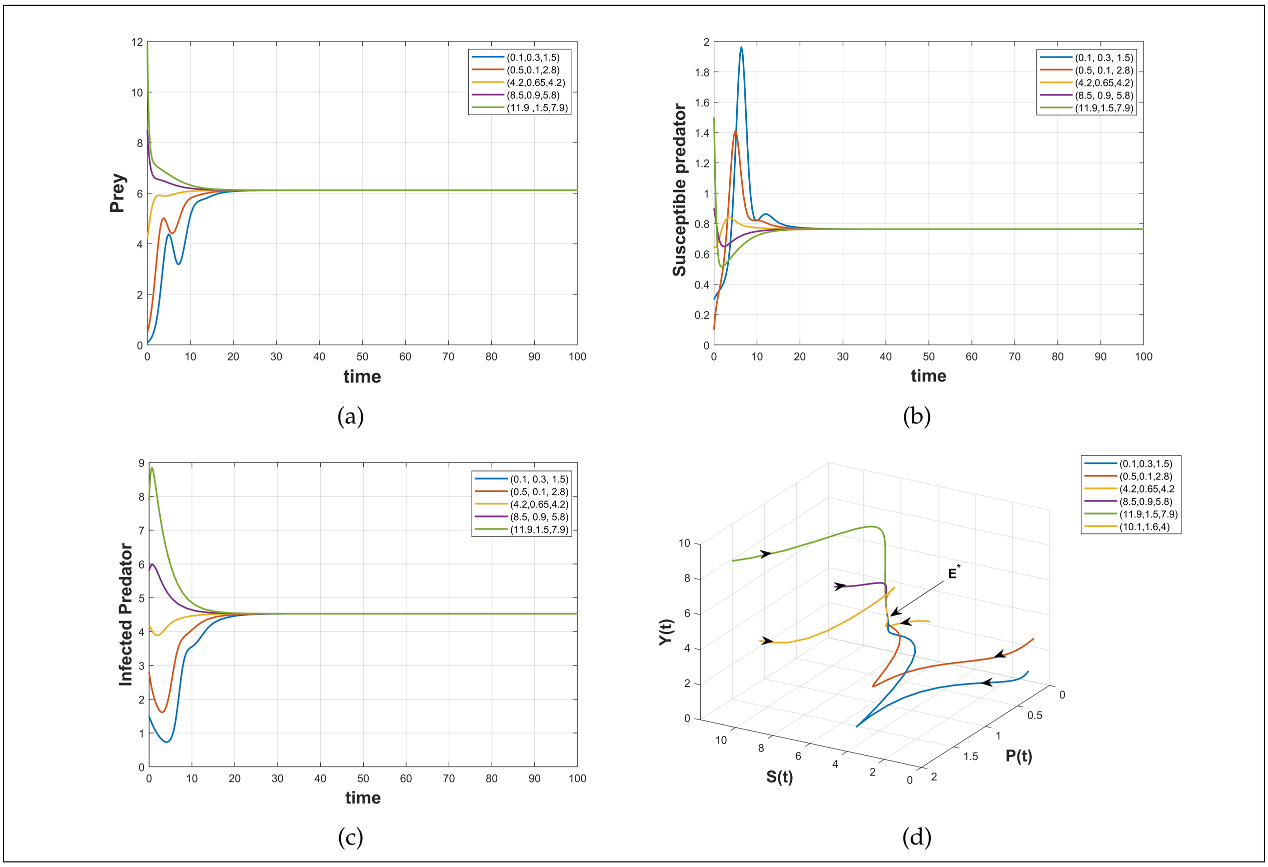


Figure 4: Time series and phase diagram for $\delta = 0.02/day$ (other parameters as in Table 1).

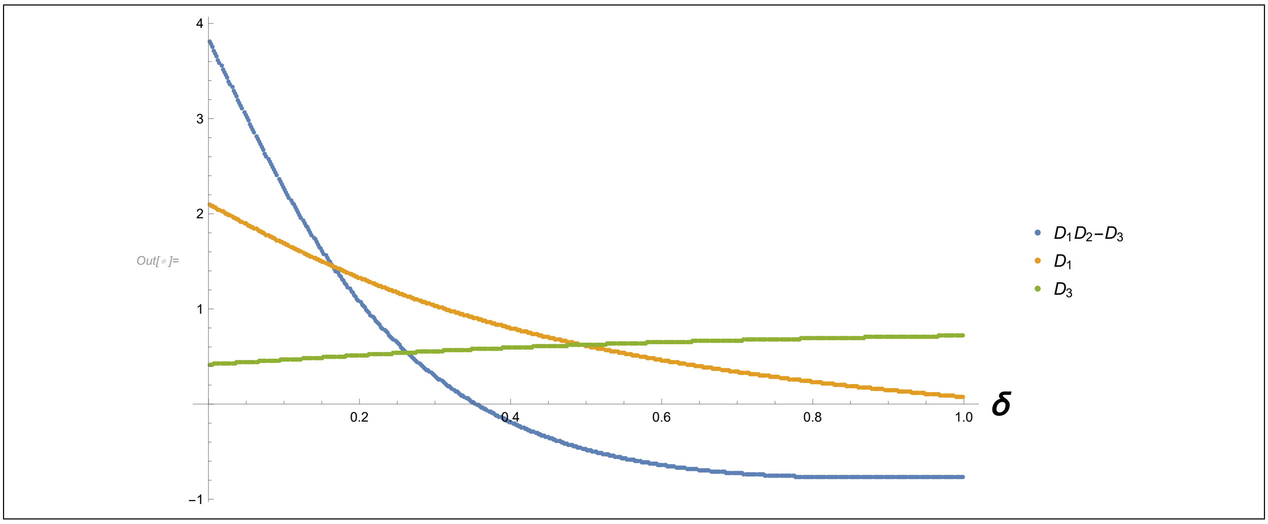


Figure 5: Plot of D_1, D_3 and $D_1 D_2 - D_3$ as functions of density factor δ.

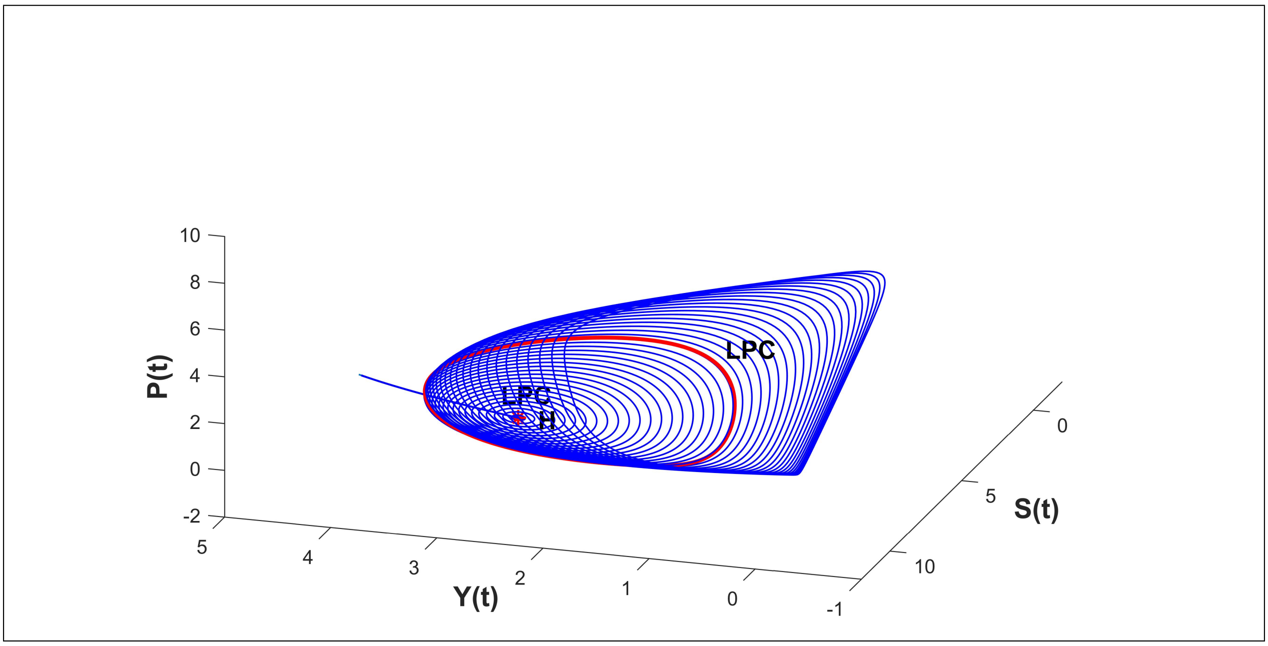


Figure 6: Bifurcation diagram of system (1) near the equilibrium E^* with respect to the bifurcation parameter δ ($\delta^H \approx 0.354594$, $\delta^{LPC} \approx 0.3415959$). H and the left LPC denote the same point, see the caption of Figure 8.

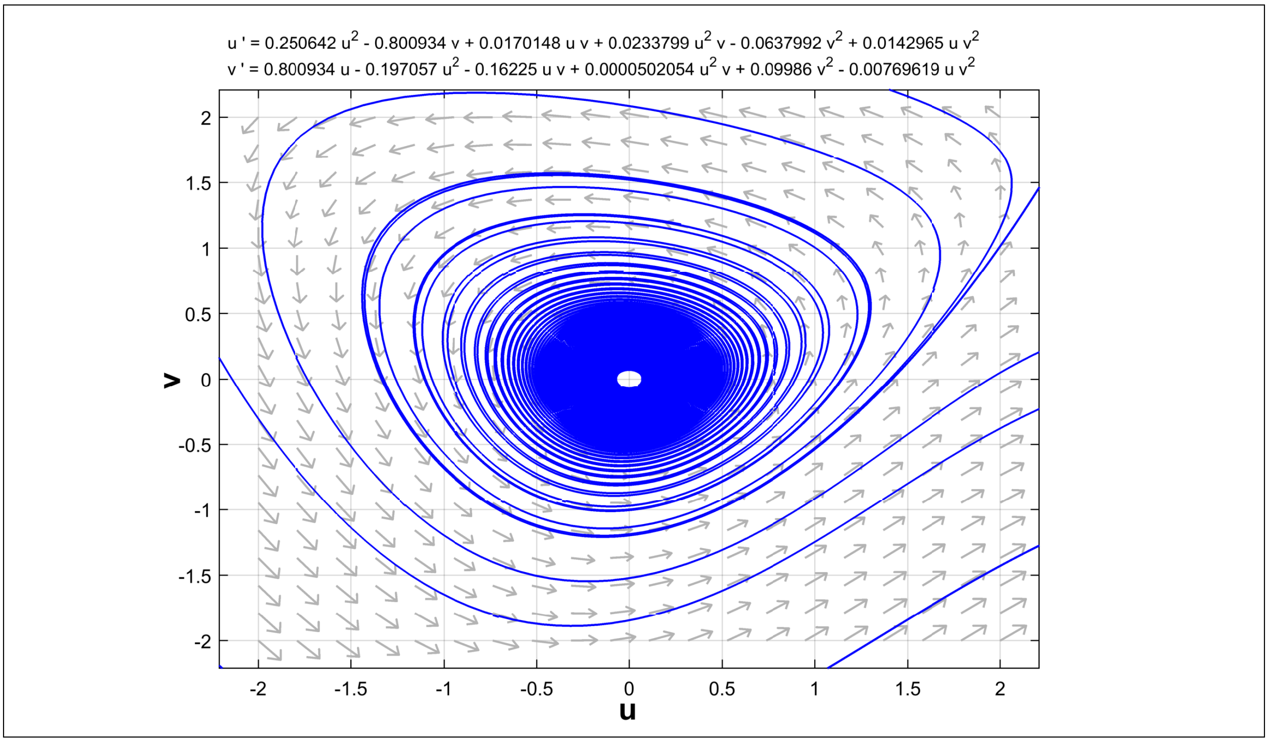
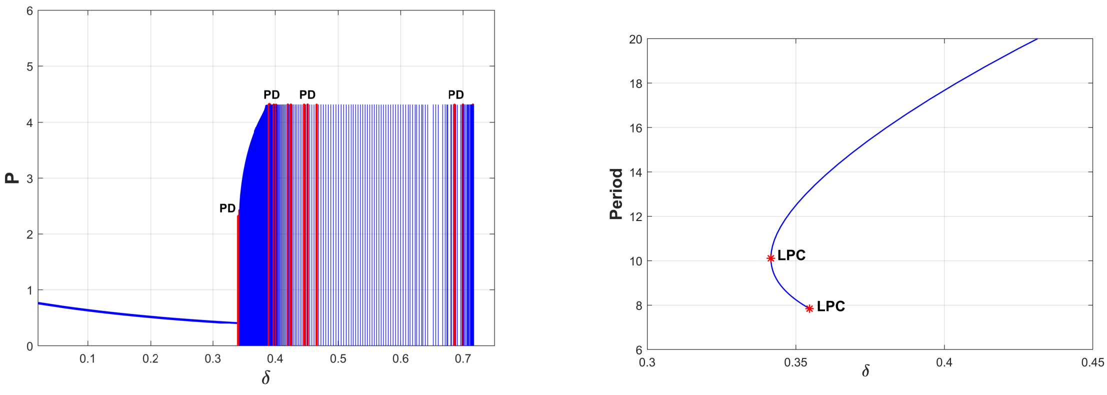


Figure 7: Phase diagram of the center manifold equations at $\delta = 0.354594/day$ neglecting the order terms $O((|u|, |v|)^4)$.



(a) (b)

Figure 8: (a) Period doubling bifurcations with respect to bifurcation parameter δ. Red coloured lines in (a) depict Period doubling points. (b) Period of the cycle versus δ. We note that in MatCont a Hopf bifurcation point is often rediscovered as an LPC curve, when a branch of periodic orbits is started from the Hopf point.

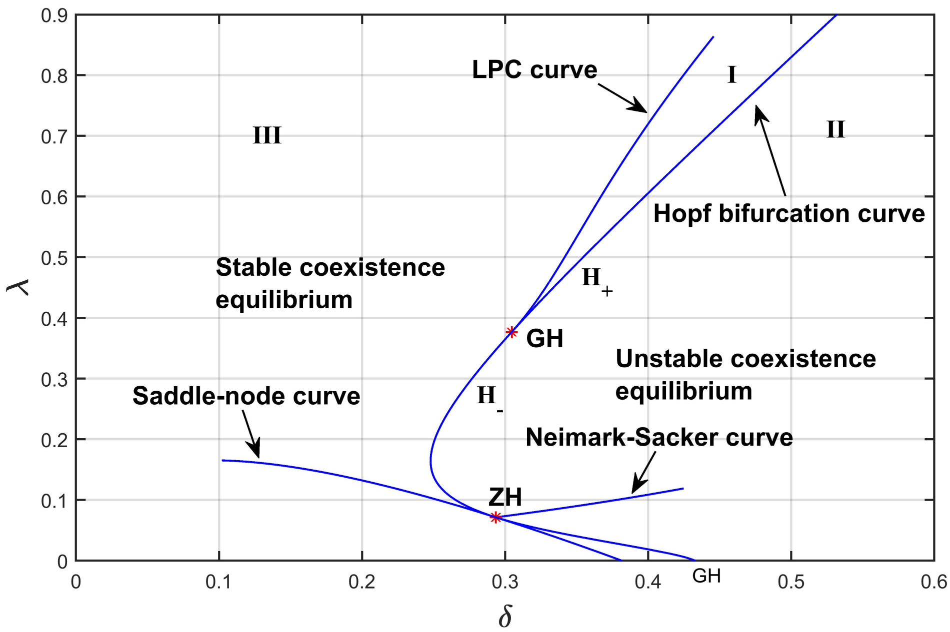


Figure 9: Two-dimensional projection of a Hopf bifurcation curve with free parameters δ and λ. H_+ and H_- denote subcritical and supercritical Hopf bifurcations, respectively.

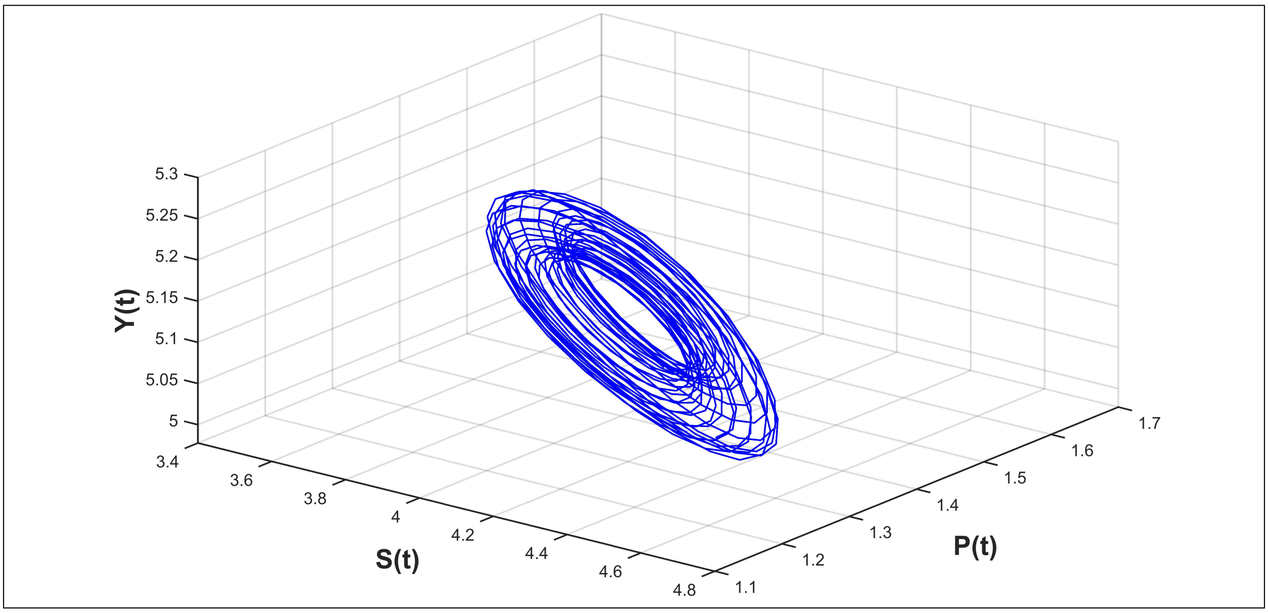


Figure 10: Formation of a torus near a ZH point.

8. Conclusion

In this article, we have proposed and investigated an epidemiological predator-prey interactive system. In this study, the disease affects only the predator species. The predator species is subdivided into susceptible and infected. The disease is assumed to be transmitted horizontally, and the recovery from the disease is assumed to be density-dependent. The asymptotic stability of different steady states of the system (1) is discussed both analytically and numerically. In each of the three cases (i) $r_1 = d_1, r_2 < d_2$, (ii) $r_2 = d_2, r_1 < d_1$, and (iii) $r_1 = d_1, r_2 = d_2$, the system (1) has a non-hyperbolic trivial equilibrium point E_0. So the linearization technique is not applicable to describe the stability nature near E_0. We compute the center manifolds of E_0 and the flow in these manifolds. In the cases (i) and (ii) E_0 turns out to be always unstable. In the case (iii) we reduce the stability of E_0 to that of the origin in a 2D problem. We also perform a numerical study using the set of parameters in Table 1. Under numerical continuation of a coexistence equilibrium of (1) with free parameter δ we observe that the equilibrium loses its stability at $\delta^H \approx 0.354594/day$ and starts oscillating due to a Hopf bifurcation (Figure 6). This bifurcation is subcritical, which implies that unstable periodic orbits are born there. We compute the dynamical equations (23) in the two-dimensional center manifold of (1) at the Hopf point ($\delta = \delta^H$) and draw the phase portrait of (23) neglecting the fourth order terms. We also symbolically compute (a version of) the normal form coefficient of the Hopf bifurcation and compare it with the numerically computed normal form coefficient in MatCont.

The numerical continuation of a Hopf bifurcation curve from the Hopf coexistence equilibrium for $\delta = \delta^H$ with δ and λ as free parameters, leads to the detection of a Generalized Hopf (GH) bifurcation point and a Zero-Hopf (ZH) bifurcation point (Figure 9). We briefly recall the mathematical results about unfoldings of GH and ZH bifurcation points in the cases of the normal form coefficients that we obtained. We apply these results to our situation and compute the predicted new bifurcation objects numerically. This includes a curve of folds of cycles (LPC) rooted in the GH point, a curve of Neimark-Sacker bifurcations rooted in the ZH point, and a stable invariant torus near the ZH point.

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Appendix

Expressions of a_{ij} and $B_i(x_1, x_2, x_3)$ in (18):

$$
\begin{aligned}
a_{11} &= r_1\left(1 - 2c_1\left(S^* + x_1\right)\right) - d_1 - \alpha\left(P^* + x_2\right),\\
a_{12} &= -\alpha\left(S^* + x_1\right),\\
a_{21} &= \beta\left(P^* + x_2\right),\\
a_{22} &= r_2\left(1 - 2c_2\left(P^* + x_2\right)\right) - d_2 + \beta S^* + \beta x_1 - \lambda x_3 - \lambda Y^*,\\
a_{23} &= -2b\delta x_3 - 2b\delta Y^* + b - \lambda P^* - \lambda x_2,\\
a_{32} &= \lambda\left(x_3 + Y^*\right)\\
a_{33} &= 2b\delta x_3 + 2b\delta Y^* - b - d_3 + \lambda P^* + \lambda x_2,\\
a_{13} &= a_{31} = 0,
\end{aligned}
$$

$$
\begin{aligned}
B_1(x_1, x_2, x_3) &= -c_1 r_1 x_1^2 - \alpha x_2 x_1,\\
B_2(x_1, x_2, x_3) &= -b\delta x_3^2 - c_2 r_2 x_2^2 + \beta x_1 x_2 - \lambda x_3 x_2,\\
B_3(x_1, x_2, x_3) &= b\delta x_3^2 + \lambda x_2 x_3.
\end{aligned}
$$

Expressions of c_{ij} in transformation matrix T:

$$c_{21} = -\frac{a_{23}a_{31}\left(a_{23}a_{32} - a_{22}a_{33} + \sigma^2\right) + a_{21}\left(a_{22}\left(a_{33}^2 + \sigma^2\right) - a_{23}a_{32}a_{33}\right)}{a_{33}^2\sigma^2 + 2a_{23}a_{32}\sigma^2 + a_{22}^2\left(a_{33}^2 + \sigma^2\right) + a_{23}^2a_{32}^2 - 2a_{22}a_{23}a_{32}a_{33} + \sigma^4},$$

$$c_{22} = \frac{\sigma\left(a_{21}\left(a_{33}^2 + a_{23}a_{32} + \sigma^2\right) - a_{23}a_{31}\left(a_{22} + a_{33}\right)\right)}{a_{33}^2\sigma^2 + 2a_{23}a_{32}\sigma^2 + a_{22}^2\left(a_{33}^2 + \sigma^2\right) + a_{23}^2a_{32}^2 - 2a_{22}a_{23}a_{32}a_{33} + \sigma^4},$$

$$c_{23} = \frac{a_{21}\left(\nu - a_{33}\right) + a_{23}a_{31}}{\nu\left(\nu - a_{33}\right) + a_{22}\left(a_{33} - \nu\right) - a_{23}a_{32}},$$

$$c_{31} = -\frac{a_{31}\left(a_{33}\sigma^2 - a_{22}a_{23}a_{32} + a_{22}^2a_{33}\right) + a_{21}a_{32}\left(a_{23}a_{32} - a_{22}a_{33} + \sigma^2\right)}{a_{33}^2\sigma^2 + 2a_{23}a_{32}\sigma^2 + a_{22}^2\left(a_{33}^2 + \sigma^2\right) + a_{23}^2a_{32}^2 - 2a_{22}a_{23}a_{32}a_{33} + \sigma^4},$$

$$c_{32} = \frac{\sigma\left(a_{31}\left(a_{22}^2 + a_{23}a_{32} + \sigma^2\right) - a_{21}a_{32}\left(a_{22} + a_{33}\right)\right)}{a_{33}^2\sigma^2 + 2a_{23}a_{32}\sigma^2 + a_{22}^2\left(a_{33}^2 + \sigma^2\right) + a_{23}^2a_{32}^2 - 2a_{22}a_{23}a_{32}a_{33} + \sigma^4},$$

$$c_{33} = \frac{a_{31}\left(\nu - a_{22}\right) + a_{21}a_{32}}{\nu\left(\nu - a_{33}\right) + a_{22}\left(a_{33} - \nu\right) - a_{23}a_{32}},$$

$$\begin{aligned}
F_1(u,v,w) = &-\frac{c_{22}\left(b\delta(c_{31}u + c_{32}v + c_{33}w)^2 + \lambda(c_{21}u + c_{22}v + c_{23}w)(c_{31}u + c_{32}v + c_{33}w)\right)}{c_{21}c_{32} - c_{22}c_{31} + c_{22}c_{33} - c_{23}c_{32}} \\
&+ \frac{(c_{22}c_{33} - c_{23}c_{32})\left(-c_1r_1(u+w)^2 - \alpha(u+w)(c_{21}u + c_{22}v + c_{23}w)\right)}{c_{21}c_{32} - c_{22}c_{31} + c_{22}c_{33} - c_{23}c_{32}} \\
&+ \frac{c_{32}\left(\beta(u+w)(c_{21}u + c_{22}v + c_{23}w) - b\delta(c_{31}u + c_{32}v + c_{33}w)^2\right)}{c_{21}c_{32} - c_{22}c_{31} + c_{22}c_{33} - c_{23}c_{32}} \\
&- \frac{c_2r_2(c_{21}u + c_{22}v + c_{23}w)^2 + \lambda(c_{21}u + c_{22}v + c_{23}w)(c_{31}u + c_{32}v + c_{33}w)}{c_{21}c_{32} - c_{22}c_{31} + c_{22}c_{33} - c_{23}c_{32}},
\end{aligned}$$

$$\begin{aligned}
F_2(u,v,w) = &\frac{(c_{21} - c_{23})\left(b\delta\left(c_{31}u + c_{32}v + c_{33}w\right)^2 + \lambda\left(c_{21}u + c_{22}v + c_{23}w\right)\left(c_{31}u + c_{32}v + c_{33}w\right)\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&+ \frac{(c_{23}c_{31} - c_{21}c_{33})\left(-c_1r_1(u+w)^2 - \alpha(u+w)\left(c_{21}u + c_{22}v + c_{23}w\right)\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&+ \frac{(c_{33} - c_{31})\left(\beta(u+w)\left(c_{21}u + c_{22}v + c_{23}w\right) - b\delta\left(c_{31}u + c_{32}v + c_{33}w\right)^2\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&- \frac{(c_{33} - c_{31})\left(\lambda\left(c_{21}u + c_{22}v + c_{23}w\right)\left(c_{31}u + c_{32}v + c_{33}w\right) - c_2r_2\left(c_{21}u + c_{22}v + c_{23}w\right)^2\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}},
\end{aligned}$$

$$\begin{aligned}
F_3(u,v,w) = &\frac{c_{22}\left(b\delta\left(c_{31}u + c_{32}v + c_{33}w\right)^2 + \lambda\left(c_{21}u + c_{22}v + c_{23}w\right)\left(c_{31}u + c_{32}v + c_{33}w\right)\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&+ \frac{(c_{21}c_{32} - c_{22}c_{31})\left(-c_1r_1(u+w)^2 - \alpha(u+w)\left(c_{21}u + c_{22}v + c_{23}w\right)\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&- \frac{c_{32}\left(\beta(u+w)\left(c_{21}u + c_{22}v + c_{23}w\right) - b\delta\left(c_{31}u + c_{32}v + c_{33}w\right)^2\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}} \\
&- \frac{c_{32}\left(\lambda\left(c_{21}u + c_{22}v + c_{23}w\right)\left(c_{31}u + c_{32}v + c_{33}w\right) - c_2r_2\left(c_{21}u + c_{22}v + c_{23}w\right)^2\right)}{-c_{22}c_{31} + c_{21}c_{32} - c_{23}c_{32} + c_{22}c_{33}}.
\end{aligned}$$

Expressions of ξ_{ij} in (24):

$$\xi_{11}=\frac{c_{21}\left(\alpha c_{23}c_{32}-\alpha c_{22}c_{33}+\beta c_{32}-c_{31}\left(c_{22}+c_{32}\right)\lambda\right)-bc_{31}^{2}\left(c_{22}+c_{32}\right)\delta}{\left(c_{21}-c_{23}\right)c_{32}+c_{22}\left(c_{33}-c_{31}\right)}+\frac{\left(c_{23}c_{32}-c_{22}c_{33}\right)c_{1}r_{1}-c_{21}^{2}c_{32}c_{2}r_{2}}{\left(c_{21}-c_{23}\right)c_{32}+c_{22}\left(c_{33}-c_{31}\right)},$$

$$\xi_{12}=\frac{c_{32}^{2}(2bc_{31}\delta+c_{21}\lambda)+2c_{2}c_{21}c_{22}c_{32}r_{2}+c_{22}^{2}(c_{31}\lambda+\alpha c_{33})}{c_{22}(c_{33}-c_{31})-c_{32}(c_{21}-c_{23})}+\frac{c_{22}c_{32}(2bc_{31}\delta-\beta+c_{21}\lambda+\alpha(-c_{23})+c_{31}\lambda)}{c_{22}(c_{33}-c_{31})-c_{32}(c_{21}-c_{23})},$$

$$\xi_{13}=\frac{bc_{22}c_{32}^{2}\delta+bc_{32}^{3}\delta+c_{2}c_{22}^{2}c_{32}r_{2}+c_{22}^{2}c_{32}\lambda+c_{22}c_{32}^{2}\lambda}{-c_{21}c_{32}+c_{22}c_{31}-c_{22}c_{33}+c_{23}c_{32}},$$

$$\xi_{21}=\frac{\left(c_{21}-c_{23}\right)\left(bc_{31}^{2}\delta+c_{21}\mathrm{c}31\lambda\right)}{c_{21}c_{32}-c_{22}c_{31}+c_{22}c_{33}-c_{23}c_{32}}+\frac{\left(c_{1}r_{1}+\alpha c_{21}\right)\left(c_{23}c_{31}-c_{21}c_{33}\right)}{-c_{21}c_{32}+c_{22}c_{31}-c_{22}c_{33}+c_{23}c_{32}}-\frac{\left(c_{31}-c_{33}\right)\left(bc_{31}^{2}\delta+c_{2}c_{21}^{2}r_{2}-\beta c_{21}+c_{21}c_{31}\lambda\right)}{-c_{21}c_{32}+c_{22}c_{31}-c_{22}c_{33}+c_{23}c_{32}},$$

$$\xi_{22}=\frac{(c_{21}-c_{23})(2bc_{31}c_{32}\delta+c_{21}c_{32}\lambda+c_{22}c_{31}\lambda)}{c_{21}c_{32}-c_{22}c_{31}+c_{22}c_{33}-c_{23}c_{32}}+\frac{\alpha c_{22}(c_{23}c_{31}-c_{21}c_{33})}{-c_{21}c_{32}+c_{22}c_{31}-c_{22}c_{33}+c_{23}c_{32}}+\frac{\left(c_{33}-c_{31}\right)\left(-2bc_{31}c_{32}\delta-2c_{2}c_{21}c_{22}r_{2}-\lambda(c_{21}c_{32}+c_{22}c_{31})+\beta c_{22}\right)}{c_{21}c_{32}-c_{22}c_{31}+c_{22}c_{33}-c_{23}c_{32}},$$

$$\xi_{23}=\frac{\left(c_{21}-c_{23}\right)\left(bc_{32}^{2}\delta+c_{22}c_{32}\lambda\right)}{c_{21}c_{32}-c_{22}c_{31}+c_{22}c_{33}-c_{23}c_{32}}-\frac{\left(c_{31}-c_{33}\right)\left(bc_{32}^{2}\delta+c_{2}c_{22}^{2}r_{2}+c_{22}c_{32}\lambda\right)}{-c_{21}c_{32}+c_{22}c_{31}-c_{22}c_{33}+c_{23}c_{32}}.$$

Expression of κ in (27):

$$\begin{aligned}\kappa=&\frac{i}{2\sigma(\sigma+2)}(4\xi_{13}^{2}\sigma^{2}-4\xi_{23}^{2}\sigma^{2}+\xi_{14}\sigma^{2}+i\xi_{15}\sigma^{2}+4i\xi_{13}\xi_{21}\sigma^{2}-2\xi_{13}\xi_{22}\sigma^{2}-2i\xi_{21}\xi_{22}\sigma^{2}+8i\xi_{13}\xi_{23}\sigma^{2}\\&-4\xi_{21}\xi_{23}\sigma^{2}-2i\xi_{22}\xi_{23}\sigma^{2}+i\xi_{24}\sigma^{2}+\xi_{12}(i\xi_{13}\left(2\sigma^{2}+\sigma-2\right)-\xi_{23}\left(2\sigma^{2}+\sigma-2\right)+\xi_{21}(2-\sigma(2\sigma+5))\\&-2i\xi_{22}\sigma)-\xi_{12}^{2}\sigma+8\xi_{13}^{2}\sigma-2\xi_{21}^{2}\sigma+\xi_{22}^{2}\sigma-8\xi_{23}^{2}\sigma+2\xi_{14}\sigma+2i\xi_{15}\sigma+6i\xi_{13}\xi_{21}\sigma-\xi_{13}\xi_{22}\sigma-5i\xi_{21}\xi_{22}\sigma\\&+16i\xi_{13}\xi_{23}\sigma-6\xi_{21}\xi_{23}\sigma-i\xi_{22}\xi_{23}\sigma+2i\xi_{24}\sigma-\xi_{25}(\sigma+2)\sigma+2\xi_{11}^{2}(\sigma+1)+\xi_{11}(i\xi_{12}(\sigma(2\sigma+5)-2)\\&+\sigma\left(\xi_{13}(4\sigma+6)-\xi_{22}(2\sigma+5)+2i\xi_{23}(2\sigma+3)+4i\xi_{21}\right)+2\left(\xi_{22}+2i\xi_{21}\right))-2\xi_{13}^{2}-2\xi_{21}^{2}+2\xi_{23}^{2}\\&+2\xi_{13}\xi_{22}+2i\xi_{21}\xi_{22}-4i\xi_{13}\xi_{23}+2i\xi_{22}\xi_{23}),\end{aligned}$$

$$\begin{aligned}\mathrm{Re}(\kappa)=&-\frac{1}{2\sigma(\sigma+2)}(\xi_{15}\sigma^{2}+4\xi_{13}\xi_{21}\sigma^{2}-2\xi_{21}\xi_{22}\sigma^{2}+8\xi_{13}\xi_{23}\sigma^{2}-2\xi_{22}\xi_{23}\sigma^{2}+\xi_{24}\sigma^{2}-\xi_{12}(2\xi_{22}\sigma\\&-\xi_{13}\left(2\sigma^{2}+\sigma-2\right))+\xi_{11}\left(\xi_{12}\left(2\sigma^{2}+5\sigma-2\right)+4\xi_{21}(\sigma+1)+2\xi_{23}\sigma(2\sigma+3)\right)+2\xi_{15}\sigma\\&+6\xi_{13}\xi_{21}\sigma-5\xi_{21}\xi_{22}\sigma+16\xi_{13}\xi_{23}\sigma-\xi_{22}\xi_{23}\sigma+2\xi_{24}\sigma+2\xi_{21}\xi_{22}-4\xi_{13}\xi_{23}+2\xi_{22}\xi_{23}),\\\mathrm{Im}(\kappa)=&\frac{1}{2\sigma(\sigma+2)}(4\xi_{13}^{2}\sigma^{2}-4\xi_{23}^{2}\sigma^{2}+\xi_{14}\sigma^{2}-2\xi_{13}\xi_{22}\sigma^{2}-4\xi_{21}\xi_{23}\sigma^{2}-\xi_{25}\sigma^{2}+\xi_{11}(\xi_{22}\left(-2\sigma^{2}-5\sigma+2\right)\\&+2\xi_{13}\sigma(2\sigma+3))-\xi_{12}\left(\xi_{21}\left(2\sigma^{2}+5\sigma-2\right)+\xi_{23}\left(2\sigma^{2}+\sigma-2\right)\right)-\xi_{12}^{2}\sigma+8\xi_{13}^{2}\sigma-2\xi_{21}^{2}\sigma\\&+\xi_{22}^{2}\sigma-8\xi_{23}^{2}\sigma+2\xi_{14}\sigma-\xi_{13}\xi_{22}\sigma-6\xi_{21}\xi_{23}\sigma-2\xi_{25}\sigma+2\xi_{11}^{2}(\sigma+1)-2\xi_{13}^{2}-2\xi_{21}^{2}\\&+2\xi_{23}^{2}+2\xi_{13}\xi_{22}).\end{aligned}$$