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Oscillations Induced by Quiescent Adult Female in a Reaction–Diffusion Model of Wild Aedes Aegypti Mosquitoes

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This paper takes the reaction–diffusion approach to deal with the quiescent females phase, so as to describe the dynamics of invasion of aedes aegypti mosquitoes, which are divided into three subpopulations: eggs, pupae and female. We mainly investigate whether the time of quiescence (delay) in the females phase can induce Hopf bifurcation. By means of analyzing the eigenvalue spectrum, we show that the persistent positive equilibrium is asymptotically stable in the absence of time delay, but loses its stability via Hopf bifurcation when time delay crosses some critical value. Using normal form and center manifold theory, we investigate the stability of the bifurcating branches of periodic solutions and the direction of the Hopf bifurcation. Numerical simulations are carried out to support our theoretical results.

Keywords: Aedes aegypti dynamics; reaction–diffusion system; DDE; Hopf bifurcation.

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1. Introduction and Mathematical Model

Aedes aegypti mosquitoes are the first and principle vector which transmit dengue fever, chikungunya, Zika, and yellow fever viruses, etc., by biting human and animal populations. This kind of mosquitoes can be found in tropical and subtropical regions of the world [Cauchemez *et al.*, 2014; Fauci & Morens, 2016; Gao *et al.*, 2016]. In order to better understand vector-borne diseases, a significant mathematical model is developed, some authors used ordinary/delay differential equations (see [Carmona Toro *et al.*, 2017; Aghriche *et al.*, accepted]) and others used partial differential equations (see [Zhang & Lin, 2019; Takahashi *et al.*, 2005]). To study the dynamics of Aedes aegypti mosquitoes, a delayed mathematical model was proposed in [Aghriche *et al.*, accepted] to describe the interactions between three biological stages of mosquito life cycle: adult females F, eggs E and pupae P and the model is given by (see [Aghriche *et al.*, accepted])

$$\begin{cases} \dfrac{dF(t)}{dt} = \alpha P(t) - \mu_F F(t-\tau), \\ \dfrac{dE(t)}{dt} = \beta\sigma F(t-\tau)\left(1 - \dfrac{E(t)+P(t)}{k}\right) - (\gamma+\mu_E)E(t), \\ \dfrac{dP(t)}{dt} = \gamma E(t) - (\alpha+\mu_P)P(t), \\ F(\theta) \geq 0, \quad \theta \in [-\tau, 0], \quad E(0) = E_0 \geq 0, \quad P(0) = P_0 \geq 0, \end{cases} \tag{1}$$

where σ (day^{-1}) is the oviposition rate, γ (day^{-1}) is the developing rate from egg to larva, α (day^{-1}) is the developing rate from pupa to adult stage, μ_E (day^{-1}) is the eggs unviability rate, μ_F (day^{-1}) the death rate of the female mosquitoes, μ_P (day^{-1}) the death rate of the pupae, β (day^{-1}) the eggs fraction that turn into female mosquitoes, k is the charge capacity of the breeding places. The meaning of time delay τ and the biological modeling can be found in [Aghriche *et al.*, accepted].

For the virus transmission model, since the disease is transmitted by the adult female mosquitoes, we consider only the spatial mobility of females and the corresponding model is given as follows

$$\begin{cases} \dfrac{\partial F(t,x,y)}{\partial t} = d\triangle F(t,x,y) + \alpha P(t,x,y) - \mu_F F(t-\tau,x,y), \\ \dfrac{\partial E(t,x,y)}{\partial t} = \beta\sigma F(t-\tau,x,y)\left(1 - \dfrac{E(t,x,y)+P(t,x,y)}{k}\right) - (\gamma+\mu_E)E(t,x,y), \\ \dfrac{\partial P(t,x,y)}{\partial t} = \gamma E(t,x,y) - (\alpha+\mu_P)P(t,x,y), \\ \dfrac{\partial F}{\partial \eta} = \dfrac{\partial E}{\partial \eta} = \dfrac{\partial P}{\partial \eta} = 0 \quad \text{on } \partial\Omega, \\ F(\theta,x,y) = \phi(\theta,x,y) \geq 0, \\ E(0,x,y) = E_0(x,y) \geq 0, \quad (x,y) \in \Omega, \quad \theta \in [-\tau, 0], \\ P(0,x,y) = P_0(x,y) \geq 0, \end{cases} \tag{2}$$

where $\phi(\theta,\cdot,\cdot) \in C([-\tau,0],\mathbb{R}^2)$, and Ω is a bounded domain in $\mathbb{R}^2$ with smooth boundary $\partial\Omega$, with Neumann boundary condition. η is the unit outer normal to $\partial\Omega$. The diffusion symbol $\triangle = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$ denotes the Laplacian operator, and the positive constant d is the diffusion coefficient of female mosquitoes.

The main purpose of this paper is to investigate the spatiotemporal dynamics of system (2). More concretely, we shall focus on the asymptotic stability of the mosquito-free equilibrium and persistent positive equilibrium, the existence of the Hopf bifurcation around the persistent positive equilibrium point induced by time delay, the direction of the bifurcation and the properties of the periodic solutions. The rest of the paper is organized as follows. In Secs. 2 and 3, we study the effect of diffusion and time delay. In Sec. 4, we establish the existence of the Hopf bifurcation by analyzing the corresponding characteristic equation. In Sec. 5, we present the formulae of determining the bifurcation properties by computing the normal forms. In Sec. 6, we give some numerical simulations supporting our theoretical results and conclusions.

2. The Effect of Diffusion

In this section, we study the stability of the possible equilibrium points of system (2) without delay

$$\begin{cases} \dfrac{\partial F(t,x,y)}{\partial t} = d\triangle F(t,x,y) + \alpha P(t,x,y) - \mu_F F(t,x,y), \\ \dfrac{\partial E(t,x,y)}{\partial t} = \beta\sigma F(t,x,y)\left(1 - \dfrac{E(t,x,y)+P(t,x,y)}{k}\right) - (\gamma+\mu_E)E(t,x,y), \\ \dfrac{\partial P(t,x,y)}{\partial t} = \gamma E(t,x,y) - (\alpha+\mu_P)P(t,x,y), \\ \dfrac{\partial F}{\partial \eta} = \dfrac{\partial E}{\partial \eta} = \dfrac{\partial P}{\partial \eta} = 0 \quad \text{on } \partial\Omega, \\ F(0,x,y) = F_0(x,y) > 0, \quad E(0,x,y) = E_0(x,y) > 0, \quad P(0,x,y) = P_0(x,y) > 0 \quad \text{on } \Omega. \end{cases} \tag{3}$$

System (3) has two equilibria: mosquito-free equilibrium $E_0 = (0,0,0)$ and a persistent positive equilibrium $E_1 = (F^*, E^*, P^*)$, where

$$F^* = \frac{\alpha\gamma k(R-1)}{\mu_F R(\alpha+\mu_P+\gamma)},$$

$$E^* = \frac{k(\alpha+\mu_P)(R-1)}{R(\alpha+\mu_P+\gamma)},$$

$$P^* = \frac{\gamma k(R-1)}{R(\alpha+\mu_P+\gamma)},$$

which are positive if $R = \frac{\gamma\alpha\sigma\beta}{\mu_F(\gamma+\mu_E)(\alpha+\mu_P)} > 1$.

Remark 2.1. R denotes the mosquito population reproduction number (the computation of R is given in detail in [Aghriche *et al.*, accepted]).

2.1. *Stability of mosquito-free equilibrium*

Note that the operator $-\triangle$ with the homogeneous Neumann boundary condition on Ω has the eigenvalues $0 = \mu_0 < \mu_1 < \mu_2 < \cdots < \mu_n < \cdots$ and $\lim_{n\to+\infty} \mu_n = \infty$. Let $S(\mu_n)$ be the eigenspace corresponding to μ_n with multiplicity $m_n \geq 1$. Let Φ_{nj} $(1 \leq j \leq m_n)$ be the normalized eigenfunctions corresponding to μ_n. Then, the set $\{\Phi_{ji} : i \geq 0, 1 \leq j \leq m_n\}$ forms a complete orthonormal basis [Faria, 2001; Ouyang, 2000]. The linearized system of (3) at the mosquito-free equilibrium E_0 can be expressed as

$$\begin{pmatrix} F_t \\ E_t \\ P_t \end{pmatrix} = L\begin{pmatrix} F \\ E \\ P \end{pmatrix} = D\begin{pmatrix} \triangle F \\ \triangle E \\ \triangle P \end{pmatrix} + J_0\begin{pmatrix} F \\ E \\ P \end{pmatrix},$$

$$D = \begin{pmatrix} d & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

$$J_0 = \begin{pmatrix} -\mu_F & 0 & \alpha \\ \beta\sigma & -(\gamma+\mu_E) & 0 \\ 0 & \gamma & -(\alpha+\mu_P) \end{pmatrix}. \tag{4}$$

Let $X_{nj} = \{c \cdot \Phi_{nj} : c \in \mathbb{R}^3\}$ where $\{\Phi_{nj} : 1 \leq j \leq \mathrm{Dim}[S(\mu_n)]\}$ is an orthonormal basis of $S(\mu_n)$. For $n \geq 0$, it can be observed that $X = \bigoplus_{n=1}^{\infty} X_n$,

$X_n = \bigoplus_{j=1}^{\mathrm{Dim}[S(\mu_n)]} X_{nj}$ is invariant under the operator L and λ is an eigenvalue of L if and only if λ is an eigenvalue of the matrix $J_n = -\mu_n D + J_0$ for some $n \geq 0$. Therefore, the stability is translated into the distribution of roots of the following characteristic equation:

$$\lambda^3 + a_{2n}\lambda^2 + a_{1n}\lambda + a_{0n} = 0, \tag{5}$$

where

$$\begin{aligned} a_{2n} &= \gamma + \mu_E + \alpha + \mu_P + \mu_n d + \mu_F, \\ a_{1n} &= (\mu_n d + \mu_F)(\alpha + \mu_P + \gamma + \mu_E) \\ &\quad + (\gamma + \mu_E)(\alpha + \mu_P), \\ a_{0n} &= \mu_n d(\gamma + \mu_E)(\alpha + \mu_P) \\ &\quad + \mu_F(\gamma + \mu_E)(\alpha + \mu_P)(1 - R). \end{aligned}$$

It is clear that all coefficients a_{2n}, a_{1n}, a_{0n} are positives when $R \leq 1$. Thus, $\lambda = 0$ is not a root of (5). Moreover, the characteristic Eq. (5) does not change sign and from the Descartes' method we deduce that all roots of Eq. (5) have negative real parts for any $n \in \mathbb{N}$ with $R \leq 1$. Then, we obtain the following lemma.

Proposition 1. *If $R \leq 1$ and $\tau = 0$, then the mosquito-free equilibrium E_0 is locally asymptotically stable.*

2.2. *Stability of persistent positive equilibrium*

In this section, we study the locally asymptotical stability of the persistent positive equilibrium E_1 of system (3). Linearizing system (3) at E_1, we obtain the following linearized system

$$\begin{pmatrix} F_t \\ E_t \\ P_t \end{pmatrix} = L\begin{pmatrix} F \\ E \\ P \end{pmatrix} = D\begin{pmatrix} \triangle F \\ \triangle E \\ \triangle P \end{pmatrix} + J_1\begin{pmatrix} F \\ E \\ P \end{pmatrix}, \tag{6}$$

where

$$D = \begin{pmatrix} d & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad J_1 = \begin{pmatrix} -\mu_F & 0 & \alpha \\ \beta\sigma\left(1 - \dfrac{E^* + P^*}{k}\right) & -\left(\dfrac{\beta\sigma F^*}{k} + \gamma + \mu_E\right) & -\dfrac{\beta\sigma F^*}{k} \\ 0 & \gamma & -(\alpha + \mu_P) \end{pmatrix}.$$

The corresponding characteristic equation is given by

$$\lambda^3 + b_{2n}\lambda^2 + b_{1n}\lambda + b_{0n} = 0, \tag{7}$$

where

$$\begin{aligned} b_{2n} &= \frac{\beta\sigma F^*}{k} + \gamma + \mu_E + \alpha + \mu_P + \mu_n d + \mu_F, \\ b_{1n} &= (\alpha + \mu_P)\left(\frac{\beta\sigma F^*}{k} + \gamma + \mu_E\right) \\ &\quad + (\mu_n d + \mu_F)\left(\frac{\beta\sigma F^*}{k} + \gamma + \mu_E + \alpha + \mu_P\right) \\ &\quad + \frac{\beta\sigma\gamma F^*}{k}, \\ b_{0n} &= (\mu_n d + \mu_F)(\alpha + \mu_P + 1)\frac{\beta\sigma F^*}{k} \\ &\quad + \mu_n d(\alpha + \mu_P)(\gamma + \mu_E). \end{aligned}$$

By the same way as in the previous paragraph, all coefficients b_{2n}, b_{1n}, b_{0n} are positives and we deduce the following result.

Proposition 2. *Let $R > 1$ and $\tau = 0$, then*

- *the persistent positive equilibrium E_1 is locally asymptotically stable,*
- *the mosquito-free equilibrium E_0 is unstable.*

3. The Effect of Time Delay and Diffusion

The linearization of system (2) at the trivial steady state E_0 can be expressed by:

$$\begin{pmatrix} F_t \\ E_t \\ P_t \end{pmatrix} = L\begin{pmatrix} F \\ E \\ P \end{pmatrix}$$

$$= D\begin{pmatrix}\triangle F\\ \triangle E\\ \triangle P\end{pmatrix} + J_{11}\begin{pmatrix}F\\ E\\ P\end{pmatrix} + J_{22}\begin{pmatrix}F(t-\tau,x,y)\\ E(t-\tau,x,y)\\ P(t-\tau,x,y)\end{pmatrix}, \tag{8}$$

with

$$D = \begin{pmatrix} d & 0 & 0\\ 0 & 0 & 0\\ 0 & 0 & 0\end{pmatrix},$$

$$J_{11} = \begin{pmatrix} 0 & 0 & \alpha\\ 0 & -(\gamma+\mu_E) & 0\\ 0 & \gamma & -(\alpha+\mu_P)\end{pmatrix},$$

$$J_{22} = \begin{pmatrix} -\mu_F e^{-\lambda\tau} & 0 & 0\\ \beta\sigma e^{-\lambda\tau} & 0 & 0\\ 0 & 0 & 0\end{pmatrix}.$$

Note that λ is an eigenvalue of L if and only if λ is an eigenvalue of the matrix $J_n = -\mu_n D + J_{11} + J_{22}$ for some $n \geq 0$. Therefore, the stability is translated into the distribution of roots of the following characteristic equation:

$$\lambda^3 + \alpha_{2n}\lambda^2 + \alpha_{1n}\lambda + \alpha_{0n} + [\beta_2\lambda^2 + \beta_1\lambda + \beta_0]e^{-\lambda\tau} = 0, \tag{9}$$

where

$$\begin{aligned}
\alpha_{2n} &= \gamma + \mu_E + \alpha + \mu_P + \mu_n d,\\
\alpha_{1n} &= (\gamma+\mu_E)(\alpha+\mu_P) + \mu_n d(\gamma+\mu_E+\alpha+\mu_P),\\
\alpha_{0n} &= \mu_n d(\gamma+\mu_E)(\alpha+\mu_P),\\
\beta_2 &= \mu_F,\\
\beta_1 &= \mu_F(\gamma+\mu_E+\alpha+\mu_P),\\
\beta_0 &= \mu_F(\gamma+\mu_E)(\alpha+\mu_P)(1-R).
\end{aligned}$$

It is known that the mosquito-free equilibrium is locally asymptotically stable if and only if all roots of Eq. (9) have negative real parts for every $n \in \mathbb{N}$ (see [Cooke & Van Den Driessche, 1986, 1998]). Conversely, the mosquito-free equilibrium is unstable if there exists $n \in \mathbb{N}$, such that Eq. (9) has at least one root with positive real part.

Assume that $\lambda = i\omega$ ($\omega > 0$) is a root of (9), then we have

$$-i\omega^3 - \alpha_{2n}\omega^2 + i\alpha_{1n}\omega + \alpha_{0n} + (-\beta_2\omega^2 + i\beta_1\omega + \beta_0) \times (\cos\omega\tau - i\sin\omega\tau) = 0. \tag{10}$$

Separating the real and imaginary parts, we have

$$\begin{cases} -\alpha_{2n}\omega^2 + \alpha_{0n} = (\beta_2\omega^2 - \beta_0)\cos\omega\tau - \beta_1\omega\sin\omega\tau,\\ -\omega^3 + \alpha_{1n}\omega = (\beta_0 - \beta_2\omega^2)\sin\omega\tau - \beta_1\omega\cos\omega\tau. \end{cases} \tag{11}$$

Adding up the squares of both the equations, we obtain

$$\omega^6 + A_{2n}\omega^4 + A_{1n}\omega^2 + A_{0n} = 0. \tag{12}$$

Let $z = \omega^2$, Eq. (12) becomes

$$h(z) = z^3 + A_{2n}z^2 + A_{1n}z + A_{0n} = 0, \tag{13}$$

where

$$\begin{aligned}
A_{2n} &= \alpha_{2n}^2 - 2\alpha_{1n} - \beta_2^2,\\
A_{1n} &= \alpha_{1n}^2 - 2\alpha_{2n}\alpha_{0n} + 2\beta_2\beta_0 - \beta_1^2,\\
A_{0n} &= \alpha_{0n}^2 - \beta_0^2.
\end{aligned}$$

For $n = 0$, we have $A_{00} = -\beta_0^2 < 0$. Hence h is continuous and $\lim_{z\to+\infty} h(z) = +\infty$, then h crosses the x-axis at some positive value. As E_0 is asymptotically stable for $\tau = 0$, then it becomes unstable for time delay greater than some critical value (see [Cooke & Van Den Driessche, 1986, 1998]).

4. Occurrence of the Hopf Bifurcation

In this section, we study the local asymptotic stability of the persistent positive equilibrium E_1 of system (2) and the occurrence of Hopf bifurcation by considering time delay τ as a bifurcation parameter.

By linearizing system (2) at E_1, we get the following corresponding characteristic equation

$$\lambda^3 + A_n\lambda^2 + B_n\lambda + C_n + (D\lambda^2 + \overline{E}_1\lambda + F_1)e^{-\lambda\tau} = 0, \tag{14}$$

where

$$A_n = \frac{\beta\sigma F^*}{k} + \gamma + \mu_E + \alpha + \mu_P + \mu_n d,$$

$$B_n = \left(\frac{\beta\sigma F^*}{k} + \gamma + \mu_E\right)(\alpha + \mu_P) + \mu_n d\left(\frac{\beta\sigma F^*}{k} + \gamma + \mu_E + \alpha + \mu_P\right) + \frac{\beta\sigma\gamma F^*}{k},$$

$$C_n = \mu_n d\frac{\beta\sigma F^*}{k}(\alpha + \mu_P + \gamma) + \mu_n d(\gamma + \mu_E)(\alpha + \mu_P),$$

$$D = \mu_F,$$

$$\overline{E}_1 = \mu_F\left(\frac{\beta\sigma F^*}{k} + \gamma + \mu_E + \alpha + \mu_P\right),$$

$$F_1 = \mu_F\frac{\beta\sigma F^*}{k}(\alpha + \mu_P + \gamma).$$

If $\lambda = i\omega$ ($\omega > 0$) is a root of (14), we have

$$-i\omega^3 - A_n\omega^2 + iB_n\omega + C_n + (-D\omega^2 + i\overline{E}_1\omega + F_1) \times (\cos\omega\tau - i\sin\omega\tau) = 0. \quad (15)$$

Separating the real and imaginary parts, we have

$$\begin{cases} -A_n\omega^2 + C_n = (D\omega^2 - F_1)\cos\omega\tau - \overline{E}_1\omega\sin\omega\tau, \\ -\omega^3 + B_n\omega = (F_1 - D\omega^2)\sin\omega\tau - \overline{E}_1\omega\cos\omega\tau. \end{cases} \quad (16)$$

Adding up the squares of both the equations, we obtain

$$\omega^6 + \eta_{2n}\omega^4 + \eta_{1n}\omega^2 + \eta_{0n} = 0. \quad (17)$$

Let $z = \omega^2$, Eq. (17) becomes

$$g(z) = z^3 + \eta_{2n}z^2 + \eta_{1n}z + \eta_{0n} = 0, \quad (18)$$

where

$$\eta_{2n} = A_n^2 - 2B_n - D^2,$$
$$\eta_{1n} = B_n^2 - 2A_nC_n + 2DF_1 - \overline{E}_1^2,$$
$$\eta_{0n} = C_n^2 - F_1^2.$$

To attest the instability of E_1, we assume $n = 0$, we have $\eta_{00} = -F_1^2 < 0$ and $g(z) \to +\infty$ when $z \to +\infty$.

We conclude that, there exists $N_1 \in \mathbb{N}_0$ such that all roots of Eq. (18) are positive and real (noted z_n) for all $n \le N_1$ and there are no positive real roots for $n \ge N_1 + 1$. According to the above analysis, we deduce the following result.

Proposition 3. *Assume that $R > 1$ holds, then (14) has a pair of purely imaginary roots $\pm i\omega_n$ with $\omega_n = \sqrt{z_n}$ for each $n \le N_1$ and from (16), we obtain*

$$\tau_{nj} = \tau_{n0} + \frac{2j\pi}{\omega_n}; \quad j = 0, 1, 2, \ldots \quad (19)$$

and

$$\tau_{n0} = \frac{1}{\omega_n}\left(\arccos\frac{(\overline{E}_1 - DA_n)\omega_n^4 + (A_nF_1 - B_n\overline{E}_1 + DC_n)\omega_n^2 - F_1C_n}{D^2\omega_n^4 + (\overline{E}_1^2 - 2DF_1)\omega_n^2 + F_1^2}\right). \quad (20)$$

Let $\lambda(\tau) = \eta(\tau) + i\omega(\tau)$ be the root of Eq. (14) near τ_{nj} such that $\eta(\tau_{nj}) = 0$ and $\omega(\tau_{nj}) = \omega_n$. Then, one needs to verify the transversality condition

$$\frac{d}{d\tau}\operatorname{Re}\lambda(\tau)\bigg|_{\tau=\tau_{nj}} = \frac{d}{d\tau}\eta(\tau)\bigg|_{\tau=\tau_{nj}} \neq 0.$$

Lemma 1 [Zhou *et al.*, 2009]. *Let $z_n = \omega_n^2$ and $F \neq D\omega_n^2$ and $g'(z_n) \neq 0$ where g is given by (18). Then*

$$\left(\frac{d\operatorname{Re}\lambda}{d\tau}\right)_{|\tau=\tau_{nj}} \neq 0 \quad \textit{and}$$

$$\operatorname{sign}\left(\frac{d\operatorname{Re}\lambda}{d\tau}\right)_{|\tau=\tau_{nj}} = \operatorname{sign}(g'(z_n)).$$

Let $\tau^* = \min_{0\le n\le N_1}\{\tau_{nj}\}$. Then from Lemma 1 and the above analysis, we deduce the following theorem.

Theorem 1. *Suppose $R > 1$ and $g'(z_n) \neq 0$, then*

— *the persistent positive equilibrium E_1 is asymptotically stable when $\tau < \tau^*$ and unstable when $\tau > \tau^*$,*
— *a Hopf bifurcation occurs near E_1 at $\tau = \tau_{nj}$ for $0 \le n \le N_1$ and $j \in \{0, 1, 2, \ldots\}$.*

5. Stability of Bifurcating Branch

In this section, we establish an algorithm detecting the direction of the Hopf bifurcation obtained in Theorem 1 and the stability of the bifurcating periodic solutions. The methods used here follow the normal form theory and center manifold theorem (see [Wu, 1996; Hassard *et al.*, 1981]). Without loss of generality, we denote any one of the critical values τ_{nj}, $0 \le n \le N_1$ and $j \in \{0,1,2,\ldots\}$ by τ_0 and ω_n by ω_0.

Let $w_1(t) = F(t) - F^*(t)$, $w_2(t) = E(t) - E^*(t)$, $w_3(t) = P(t) - P^*(t)$, $\mu = \tau - \tau_0$; then $\mu = 0$ is the Hopf bifurcation value of (2). Rescale the time by $t \to t/\tau$ to normalize the delay. Define $\mathbf{C} = \mathrm{C}([-1,0],\mathbb{R}^3)$; then system (2) can be transformed into a functional differential equation as:

$$\dot{w}_t = \mathrm{L}_\mu w_t + f(\mu, w_t), \tag{21}$$

where $w(t) = (w_1(t), w_2(t), w_3(t))^T \in \mathbb{R}^3$ and $\mathrm{L}_\mu : \mathbf{C} \to \mathbb{R}^3$ and $f : \mathbb{R} \times \mathbf{C} \to \mathbb{R}^3$ are respectively represented by:

$$\mathrm{L}_\mu\phi = \tau\begin{pmatrix} -d\mu_n & 0 & \alpha \\ 0 & -\left(\dfrac{\beta\sigma F^*}{k} + \gamma + \mu_E\right) & -\dfrac{\beta\sigma F^*}{k} \\ 0 & \gamma & -(\alpha + \mu_P) \end{pmatrix}\begin{pmatrix}\phi_1(0)\\ \phi_2(0)\\ \phi_3(0)\end{pmatrix} + \tau\begin{pmatrix} -\mu_F & 0 & 0 \\ \beta\sigma\left(1 - \dfrac{E^* + P^*}{k}\right) & 0 & 0 \\ 0 & 0 & 0\end{pmatrix}\begin{pmatrix}\phi_1(-1)\\ \phi_2(-1)\\ \phi_3(-1)\end{pmatrix}$$

and

$$f(\mu, \Phi) = \tau\begin{pmatrix} 0 \\ \beta\sigma\phi_1(-1)\left(\dfrac{\phi_2(0) + \phi_3(0)}{k}\right) \\ 0 \end{pmatrix},$$

where $\phi = (\phi_1, \phi_2, \phi_3)^T \in \mathbf{C}$.

By the Riesz representation theorem, there exists a 3×3 matrix $\eta(\theta, \mu)$, whose elements are of bounded variation functions, such that

$$\mathrm{L}_\mu\phi = \int_{-1}^{0} [d\eta(\theta, \mu)]\phi(\theta), \quad \text{for } \phi \in \mathbf{C}.$$

Choose

$$\eta(\theta, \mu) = \tau\begin{pmatrix} -d\mu_n & 0 & \alpha \\ 0 & -\left(\dfrac{\beta\sigma F^*}{k} + \gamma + \mu_E\right) & -\dfrac{\beta\sigma F^*}{k} \\ 0 & \gamma & -(\alpha + \mu_P) \end{pmatrix}\delta(\theta) + \tau\begin{pmatrix} -\mu_F & 0 & 0 \\ \beta\sigma\left(1 - \dfrac{E^* + P^*}{k}\right) & 0 & 0 \\ 0 & 0 & 0\end{pmatrix}\delta(\theta + 1),$$

where δ is a Dirac delta function. For $\phi \in \mathrm{C}([-1,0], \mathbb{R}^3)$, define

$$A(\mu)\phi = \begin{cases} \dfrac{d\phi(\theta)}{d\theta}, & \text{for } \theta \in [-1, 0), \\ \displaystyle\int_{-1}^{0} d\eta(s,\mu)\phi(s) = \mathrm{L}_\mu\phi, & \text{for } \theta = 0 \end{cases}$$

and

$$R(\mu)\phi = \begin{cases} 0, & \text{for } \theta \in [-1, 0), \\ f(\mu, \phi), & \text{for } \theta = 0. \end{cases}$$

System (21) is equivalent to

$$\dot{w}_t = A(\mu)w_t + R(\mu)w_t, \tag{22}$$

where $w_t(\theta) = w(t + \theta)$ for $\theta \in [-1, 0]$.

For $\psi \in \mathrm{C}([-1,0], (\mathbb{R}^3)^*)$, the adjoint operator A^* of $A = A(0)$ is defined as

$$A^*\psi(s) = \begin{cases} -\dfrac{d\psi(s)}{ds} & s \in (0, 1], \\ \displaystyle\int_{-1}^{0} d\eta^T(t, 0)\psi(-t) & s = 0, \end{cases}$$

and a bilinear product is defined as

$$\langle\psi(s),\phi(\theta)\rangle = \overline{\psi}(0)\cdot\phi(0) - \int_{\theta=-1}^{0}\int_{\xi=0}^{\theta}\overline{\psi}(\xi-\theta)d\eta(\theta)\phi(\xi)d\xi,$$

where $\eta(\theta)=\eta(\theta,0)$. From the discussion in Sec. 4, we know that $\pm i\omega_0\tau_0$ are eigenvalues of A, and so they are also eigenvalues of A^*.

We assume that

$$q(\theta)=(q_1,q_2,q_3)^T e^{i\omega_0\tau_0\theta}$$

is the eigenvector of A corresponding to eigenvalue $i\omega_0\tau_0$. Then, we have

$$Aq(\theta)=i\omega_0\tau_0 q(\theta).$$

Based on the definition of A, we can get the following linear algebraic equations:

$$\begin{pmatrix} i\omega_0+d\mu_n+\mu_F e^{i\omega_0\tau_0} & 0 & -\alpha \\ -\beta\sigma\left(1-\dfrac{E^*+P^*}{k}\right)e^{i\omega_0\tau_0} & i\omega_0+\left(\dfrac{\beta\sigma F^*}{k}+\gamma+\mu_E\right) & \dfrac{\beta\sigma F^*}{k} \\ 0 & -\gamma & i\omega_0+(\alpha+\mu_P)\end{pmatrix}\begin{pmatrix}q_1\\q_2\\q_3\end{pmatrix}=0. \tag{23}$$

Solving system (23) and choosing $q_1=1$, we get

$$q_2=\frac{i\omega_0+(\alpha+\mu_P)}{\gamma}q_3;\quad q_3=\frac{i\omega_0+d\mu_n+\mu_F e^{i\omega_0\tau_0}}{\alpha}.$$

Analogously, if $q^*(s)=M(q_1^*,q_2^*,q_3^*)^T e^{i\omega_0\tau_0 s}$ is the eigenvector of A^* corresponding to eigenvalue $-i\omega_0\tau_0$, we have

$$\begin{pmatrix} -i\omega_0+d\mu_n+\mu_F e^{i\omega_0\tau_0} & -\beta\sigma\left(1-\dfrac{E^*+P^*}{k}\right)e^{i\omega_0\tau_0} & 0 \\ 0 & -i\omega_0+\left(\dfrac{\beta\sigma F^*}{k}+\gamma+\mu_E\right) & -\gamma \\ -\alpha & \dfrac{\beta\sigma F^*}{k} & -i\omega_0+(\alpha+\mu_P)\end{pmatrix}\begin{pmatrix}q_1^*\\q_2^*\\q_3^*\end{pmatrix}=0,$$

where

$$q_1^*=1,\quad q_2^*=\frac{-i\omega_0+d\mu_n+\mu_F e^{i\omega_0\tau_0}}{\beta\sigma\left(1-\dfrac{E^*+P^*}{k}\right)e^{i\omega_0\tau_0}},\quad q_3^*=\frac{-i\omega_0+\left(\dfrac{\beta\sigma F^*}{k}+\gamma+\mu_E\right)}{\gamma}q_2^*.$$

From

$$\begin{aligned}\langle q^*(s),q(\theta)\rangle &= \bar{q}^*(0)q(0)-\int_{\theta=-1}^{0}\int_{\xi=0}^{\theta}\bar{q}^*(\xi-\theta)d\eta(\theta)q(\xi)d\xi \\ &= \overline{M}(\bar{q}_1^*,\bar{q}_2^*,\bar{q}_3^*)(q_1,q_2,q_3)^T-\int_{\theta=-1}^{0}\int_{\xi=0}^{\theta}\bar{q}^*(\xi-\theta)d\eta(\theta)q(\xi)d\xi \\ &= \overline{M}\left(q_1\bar{q}_1^*+q_2\bar{q}_2^*+q_3\bar{q}_3^*-q_1\bar{q}_2^*\tau_0\beta\sigma\left(1-\frac{E^*+P^*}{k}\right)e^{-i\omega_0\tau_0}+q_3\bar{q}_2^*\tau_0\frac{\beta\sigma F^*}{k}\right).\end{aligned}$$

We can determine M by $\langle q^*(s),q(\theta)\rangle=1$. Thus, we obtain

$$M=\left[\bar{q}_1q_1^*+\bar{q}_2q_2^*+\bar{q}_3q_3^*-\bar{q}_1q_2^*\tau_0\beta\sigma\left(1-\frac{E^*+P^*}{k}\right)e^{i\omega_0\tau_0}+\bar{q}_3q_2^*\tau_0\frac{\beta\sigma F^*}{k}\right]^{-1}.$$

Now, we compute the coordinates to describe the center manifold $\mathcal{C}_0$ at $\mu = 0$ (see [Hassard *et al.*, 1981]). Let w_t be the solution of Eq. (22) when $\mu = 0$. Define

$$z(t) = \langle q^*, w_t \rangle \tag{24}$$

and

$$W(t,\theta) = w_t(\theta) - 2\,\mathrm{Re}\{z(t)q(\theta)\}. \tag{25}$$

On the center manifold $\mathcal{C}_0$, we have

$$\begin{aligned} W(t,\theta) &= W(z(t), \bar{z}(t), \theta) \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta) z\bar{z} \\ &\quad + W_{02}(\theta)\frac{\bar{z}^2}{2} + \cdots, \end{aligned} \tag{26}$$

z and $\bar{z}$ are local coordinates on center manifold $\mathcal{C}_0$ in the directions of q^* and $\bar{q}^*$. Noting that W is also real if w_t is real, we are only concerned with the real solutions. For solution $w_t \in \mathcal{C}_0$ of Eq. (22), we get:

$$\begin{aligned} \dot{z}(t) &= \langle q^*, \dot{w}_t \rangle \\ &= i\omega_0\tau_0 z + \bar{q}^*(0) \cdot f(0, W(z, \bar{z}, 0) \\ &\quad + 2\,\mathrm{Re}\{zq(0)\}) \\ &= i\omega_0\tau_0 z + \bar{q}^*(0) f_0(z, \bar{z}). \end{aligned}$$

The above equation can be rewritten as

$$\dot{z}(t) = i\omega_0\tau_0 z + g(z, \bar{z}),$$

where

$$\begin{aligned} g(z,\bar{z}) &= \bar{q}^*(0) \cdot f_0(z, \bar{z}) \\ &= g_{20}\frac{z^2}{2} + g_{11} z\bar{z} + g_{02}\frac{\bar{z}^2}{2} + g_{21}\frac{z^2\bar{z}}{2}. \end{aligned} \tag{27}$$

Then, we obtain

$$\begin{aligned} w_t(\theta) &= W(z, \bar{z}, \theta) + 2\,\mathrm{Re}\{zq(\theta)\} \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} \\ &\quad + zq + z\bar{q} \\ &= W_{20}(\theta)\frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta)\frac{\bar{z}^2}{2} \\ &\quad + z(1, q_2, q_3)^T e^{i\omega_0\tau_0\theta} \\ &\quad + \bar{z}(1, \bar{q}_2, \bar{q}_3)^T e^{-i\omega_0\tau_0\theta} + \cdots. \end{aligned}$$

Substituting the values of f and $w_t(\theta)$ into (27), we have:

$$\begin{aligned} g(z,\bar{z}) &= \bar{q}^*(0) f_0(z, \bar{z}) \\ &= \bar{q}^*(0) f_0(z, w_t) \\ &= \tau_0 \overline{M}(1, \bar{q}_2^*, \bar{q}_2^*) \\ &\quad \cdot \begin{pmatrix} 0 \\ \beta\sigma\phi_1(-1)\left(\dfrac{\phi_2(0) + \phi_3(0)}{k}\right) \\ 0 \end{pmatrix}. \end{aligned}$$

Simplifying the above equation and comparing with Eq. (27), we get

$$\begin{cases} g_{20} = 4\tau_0\overline{M}\dfrac{q_2^* q_2 \beta\sigma}{k} e^{-i\omega_0\tau_0}, \\ g_{11} = 4\tau_0\overline{M}\dfrac{q_2^*\beta\sigma}{k}(\bar{q}_2 e^{-i\omega_0\tau_0} + q_2 e^{i\omega_0\tau_0}), \\ g_{02} = 4\tau_0\overline{M}\dfrac{q_2^*\beta\sigma}{k}\bar{q} e^{i\omega_0\tau_0}, \\ g_{21} = \tau_0\overline{M}\dfrac{q_2^*\beta\sigma}{k}(2\bar{q}_2 W_{20}^{(1)}(-1) + (W_{20}^{(2)}(0) \\ \qquad + W_{20}^{(3)}(0))e^{i\omega_0\tau_0} + 8q_2 W_{11}^{(1)}(-1) \\ \qquad + 2(W_{11}^{(2)}(0) + W_{11}^{(3)}(0))e^{i\omega_0\tau_0}). \end{cases} \tag{28}$$

Since g_{21} depends on $W_{20}(\theta)$ and $W_{11}(\theta)$, we should also compute the values of $W_{20}(\theta)$ and $W_{11}(\theta)$. Following the procedures in [Tian & Zhang, 2013; Wang *et al.*, 2006], we have

$$\begin{aligned} W_{20}(\theta) &= \frac{ig_{20}}{\omega_0\tau_0} q(0) e^{i\omega_0\tau_0\theta} + \frac{i\bar{g}_{02}}{3\omega_0\tau_0}\bar{q}(0) e^{-i\omega_0\tau_0\theta} \\ &\quad + H_1 e^{2i\omega_0\tau_0\theta} \end{aligned}$$

and

$$\begin{aligned} W_{11}(\theta) &= \frac{ig_{11}}{\omega_0\tau_0} q(0) e^{i\omega_0\tau_0\theta} \\ &\quad + \frac{i\bar{g}_{11}}{\omega_0\tau_0}\bar{q}(0) e^{-i\omega_0\tau_0\theta} + H_2, \end{aligned}$$

where H_1 and H_2 are the solutions of the following linear algebraic equations, respectively:

$$\begin{pmatrix} 2i\omega_0 + d\mu_n & \mu_F e^{-i\omega_0\tau_0} & -\alpha \\ -\beta\sigma\left(1 - \dfrac{E^* + P^*}{k}\right)e^{-i\omega_0\tau_0} & 2i\omega_0 + \left(\dfrac{\beta\sigma F^*}{k} + \gamma + \mu_E\right) & \dfrac{\beta\sigma F^*}{k} \\ 0 & -\gamma & 2i\omega_0 + (\alpha + \mu_P) \end{pmatrix} H_1 = \begin{pmatrix} 0 \\ \beta\sigma\left(\dfrac{q_2 + q_3}{k}\right) \\ 0 \end{pmatrix}$$

and

$$\begin{pmatrix} 0 & \mu_F & -\alpha \\ -\beta\sigma\left(1 - \dfrac{E^* + P^*}{k}\right)e^{-i\omega_0\tau_0} & \dfrac{\beta\sigma F^*}{k} + \gamma + \mu_E & \dfrac{\beta\sigma F^*}{k} \\ 0 & -\gamma & (\alpha + \mu_P) \end{pmatrix} H_2 = \begin{pmatrix} 0 \\ \beta\sigma\left(\dfrac{\mathrm{Re}\{q_2\} + \mathrm{Re}\{q_3\}}{k}\right) \\ 0 \end{pmatrix}.$$

Referring to [Hassard *et al.*, 1981], we have the following formulae

$$c_1(0) = \frac{i}{2\omega_0\tau_0}\left(g_{11}g_{20} - 2\|g_{11}\|^2 - \frac{\|g_{02}\|^2}{3}\right) + \frac{g_{21}}{2},$$

$$\mu_2 = -\frac{\mathrm{Re}\{c_1(0)\}}{\mathrm{Re}\{\lambda'(\tau_0)\}},$$

$$\beta_2 = 2\,\mathrm{Re}\{c_1(0)\},$$

$$T_2 = -\frac{\mathrm{Im}\{c_1(0)\} + \mu_2\,\mathrm{Im}\{\lambda'(\tau_0)\}}{\omega_0\tau_0}.$$

Thus, we have the results on the direction of the Hopf bifurcation and the stability of the bifurcating branch of periodic solutions.

Theorem 2

— *If* $\mu_2 > 0$ ($\mu_2 < 0$), *then the Hopf bifurcation is supercritical* (*subcritical*) *and the bifurcating periodic solutions exist for* $\tau > \tau_0$ ($\tau < \tau_0$).
— *If* $\beta_2 < 0$ ($\beta_2 > 0$), *then the bifurcating periodic solutions are stable* (*unstable*). *The period of the bifurcating periodic solutions is determined by* T_2: *if* $T_2 > 0$ ($T_2 < 0$), *then the period increases* (*decreases*).

6. Numerical Simulations

In this section, we aim to provide a 1D numerical simulation of the considered model to substantiate the theoretical results established in the previous sections by using Matlab software with the parameters given in Table 1.

Table 1. Parameters estimation.

Parameter	Value	Reference
γ	0.90	Assumed
α	0.6	Assumed
σ	4	[Carmona Toro *et al.*, 2017]
β	0.4	[Carmona Toro *et al.*, 2017]
μ_E	0.15	Assumed
μ_P	0.01	Assumed
k	500	Assumed

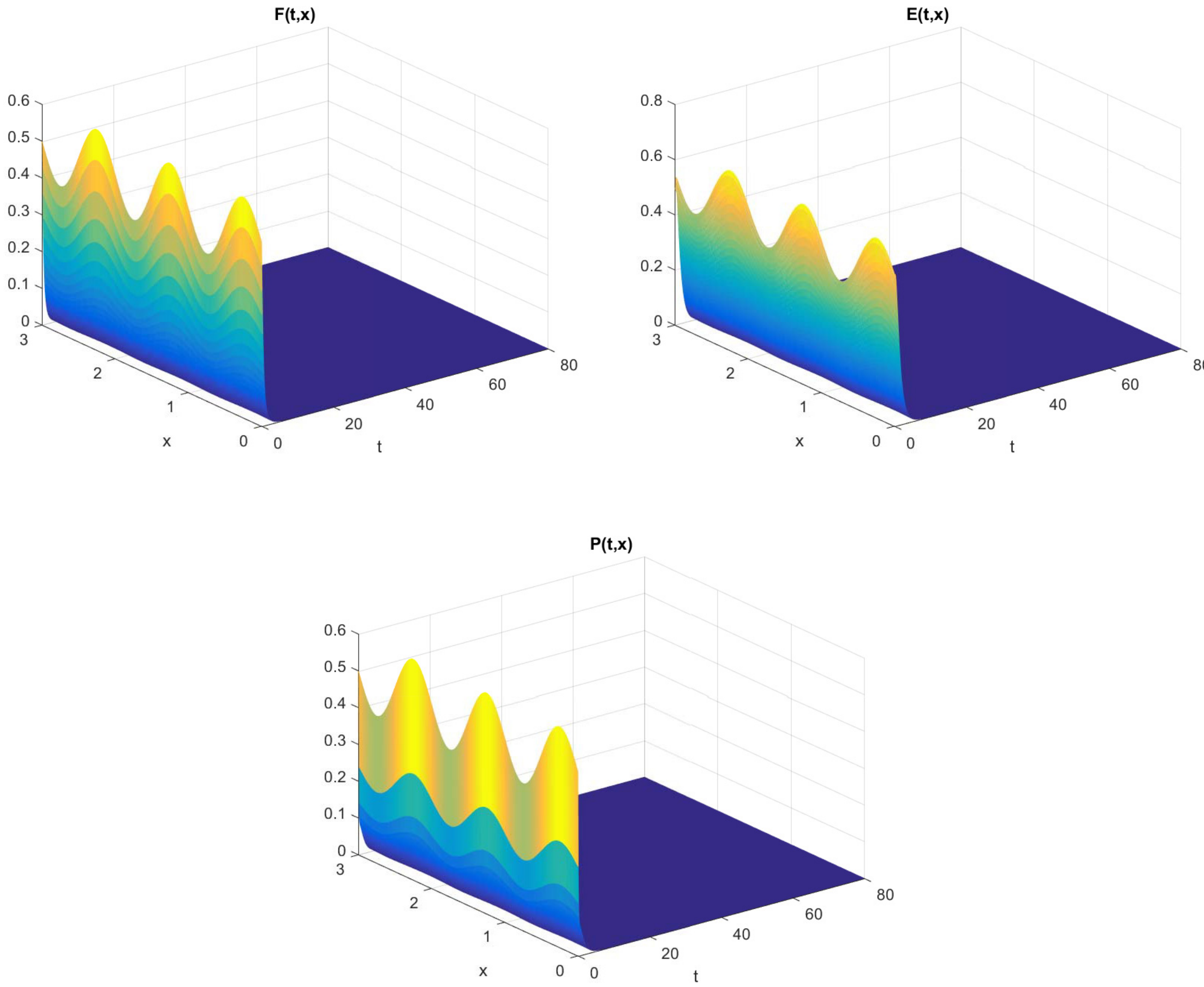

Fig. 1. Stability of E_0 for $\tau = 0$, $d = 0.0004$ and nonexistence of E_1 for $\mu_F = 2$, in this case $R = 0.6745$.

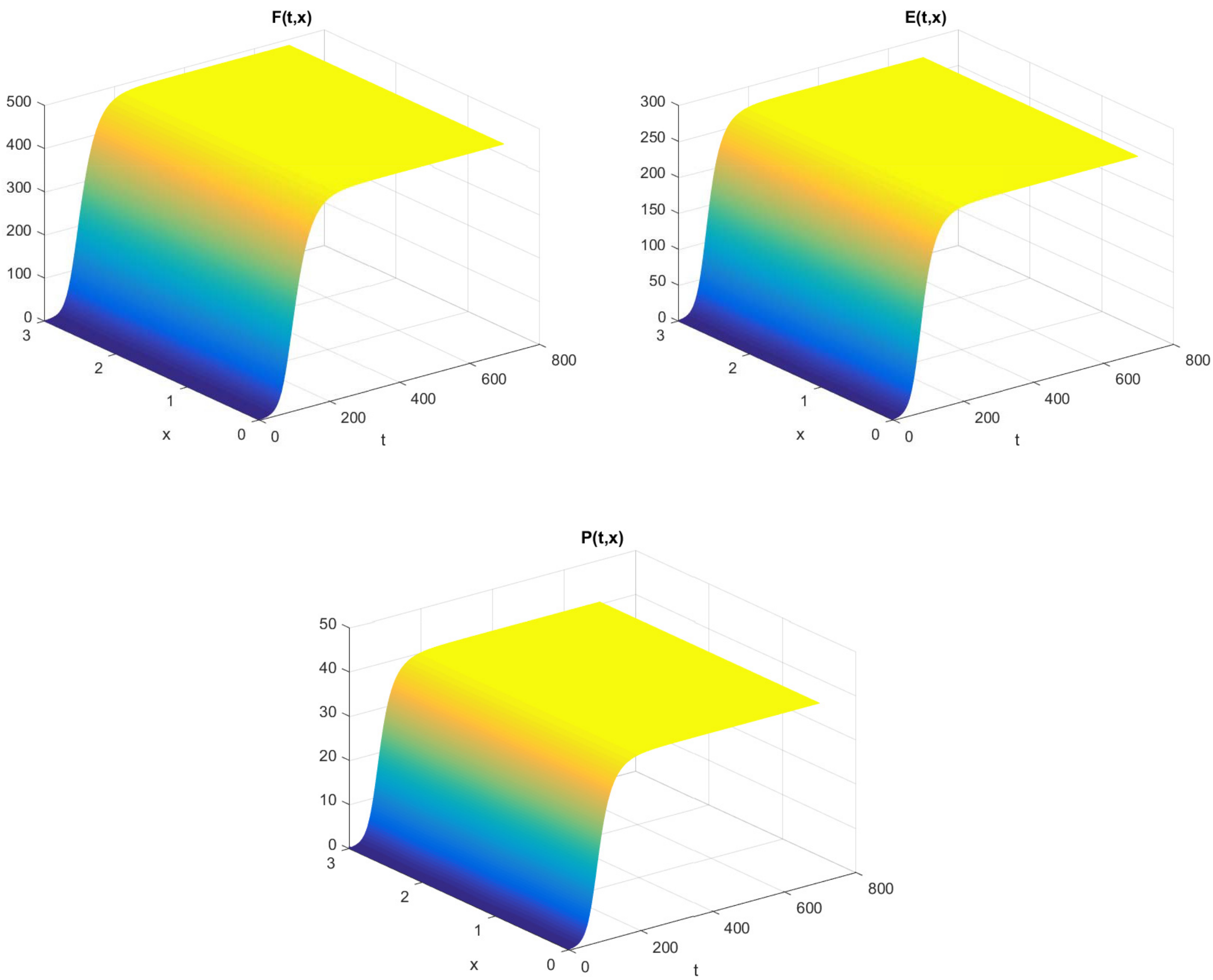

Fig. 2. Instability of E_0 and stability of E_1 for $\tau = 0$, $\mu_F = 0.05$, $d = 0.05$ and $R = 26.97$.

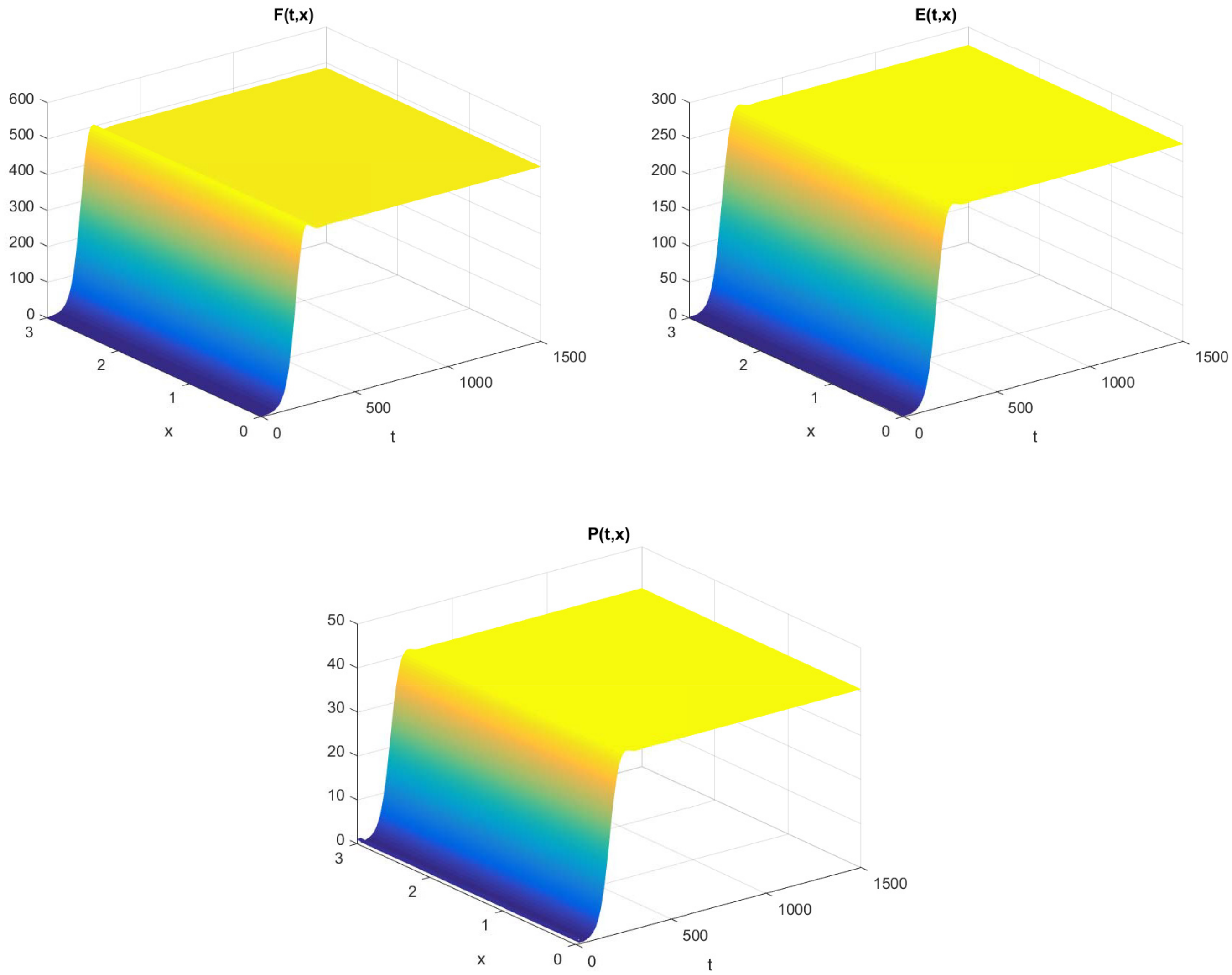

Fig. 3. Stability of E_1 for $\tau = 20.5$, $\mu_F = 0.05$, $d = 0.05$ and $R = 26.97$.

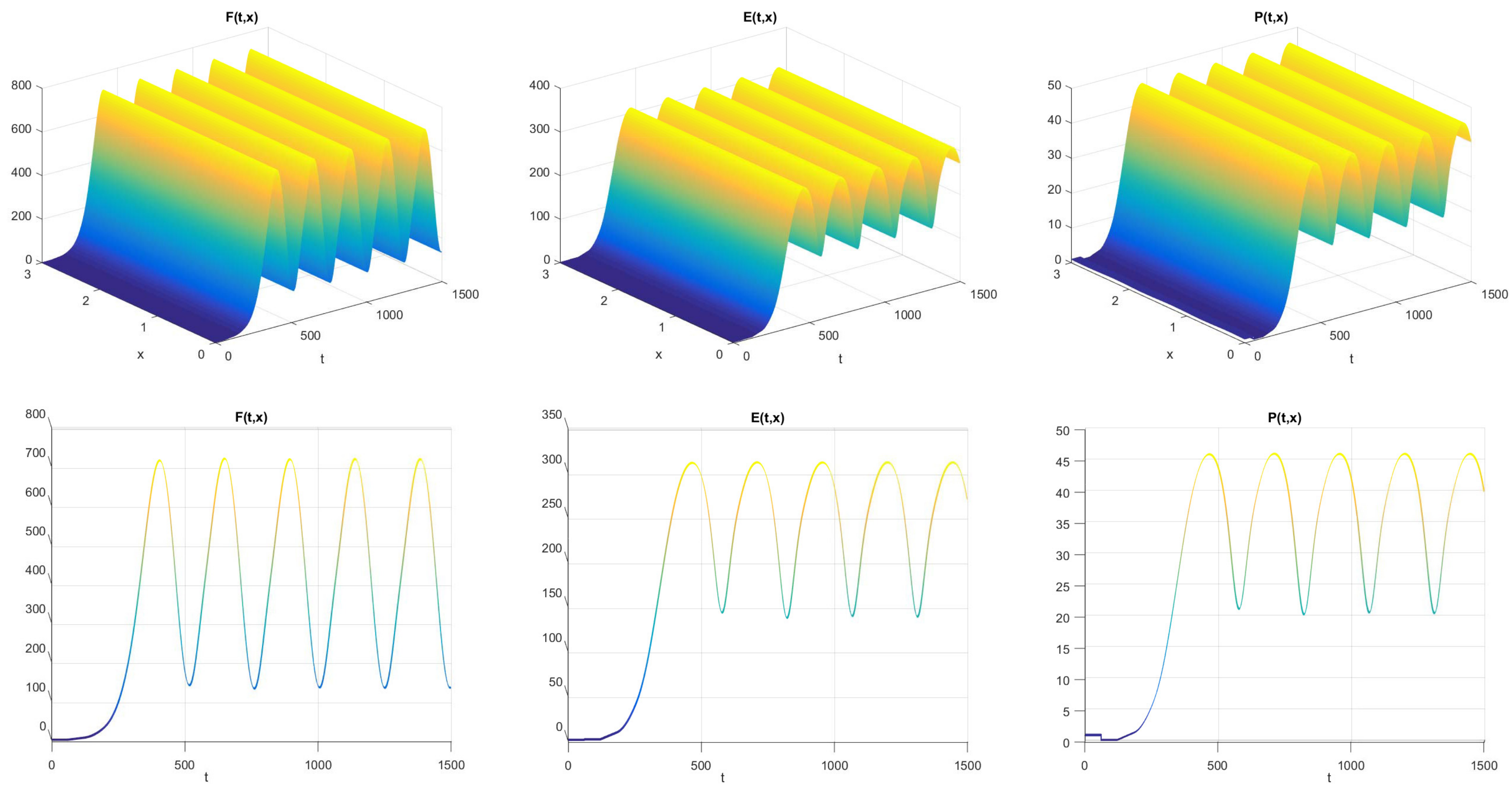

Fig. 4. Periodic solutions for $\tau = \tau_0 = 60$, $\mu_F = 0.05$, $d = 0.05$ and $R = 26.97$ with respect to varying time space variables (above) and varying time and fixed space variables (below).

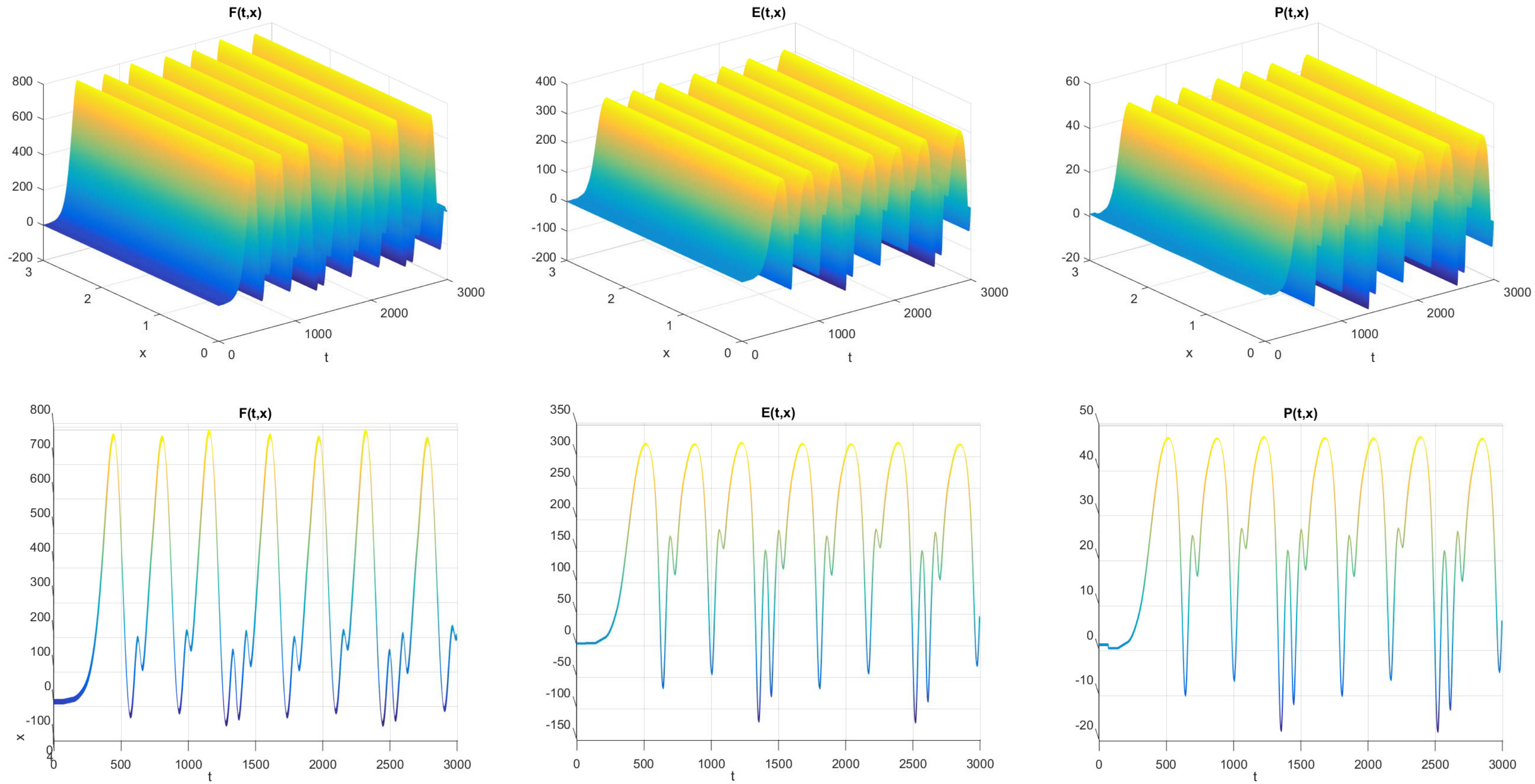

Fig. 5. Chaotic solutions for $\tau = 70.5 > \tau_0$, $\mu_F = 0.05$, $d = 0.05$ and $R = 26.97$ with respect to varying time space variables (above) and varying time and fixed space variables (below).

(i) For $\mu_F = 2$, we have $R = 0.6745$ and E_0 is the only steady state which is asymptotically stable (see Fig. 1).

(ii) For $\mu_F = 0.05$, we have $R = 26.97$ and E_0 and $E_1 = (3443.6, 194.49, 286.96)$ are the steady states of the model. The trivial one is unstable and the nontrivial one is asymptotically stable (see Fig. 2).

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