

DELAY INDUCED SPATIOTEMPORAL PATTERNS IN A DIFFUSIVE INTRAGUILD PREDATION MODEL WITH BEDDINGTON-DEANGELIS FUNCTIONAL RESPONSE

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ABSTRACT. A diffusive intraguild predation model with delay and Beddington-DeAngelis functional response is considered. Dynamics including stability and Hopf bifurcation near the spatially homogeneous steady states are investigated in detail. Further, it is numerically demonstrated that delay can trigger the emergence of irregular spatial patterns including chaos. The impacts of diffusion and functional response on the model's dynamics are also numerically explored.

1. Introduction. Competition and predation are two fundamental ecological relationships among species and have been widely studied [1]. Recently, it is been recognized that intraguild predation (IGP), which is a combination of competition and predation, has significant impacts on the distribution, abundance, persistence and evolution of the species involved [2]. As a result, growing attention has been paid to IGP models [3, 4, 5, 6, 7, 8, 9].

The general framework of IGP described below was established by Holt and Polis [5]

$$\begin{cases} \dot{R}(t) = R(\varphi(R) - \rho_1(R, N, P)N - \rho_2(R, N, P)P), \\ \dot{N}(t) = N(e_1\rho_1(R, N, P)R - \rho_3(R, N, P)P - m_1), \\ \dot{P}(t) = P(e_2\rho_2(R, N, P)R + e_3\rho_3(R, N, P)N - m_2), \end{cases} \quad (1)$$

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where $R(t), N(t), P(t)$ represent the densities of basal resource, IG prey and IG predator, respectively. The quantities $\rho_2(R, N, P)R$ and $\rho_3(R, N, P)N$ are functional responses of the IG predator to the resource and IG prey, respectively; $\rho_1(R, N, P)R$ is the functional response of the IG prey to the basal resource; and m_1 and m_2 are density-independent mortality rates. The parameters e_1 and e_2 are the conversion rates of resource consumption into reproduction for the IG prey and IG predator, respectively; the parameter e_3 denotes the conversion rate of the IG predator from its consumption of IG prey; $R\varphi(R)$ is recruitment of the basal resource.

Functional response describes how the consumption rate of individual consumers varies with respect to resource density and is often used to model predator-prey interactions. For IGP models, several functional response functions have been studied. For instance, Velazquez *et al.* [10] and Hsu *et al.* [11] investigated the case with a linear functional response. Abrams and Fung [12] considered Holling type-II functional response. Verdy and Amarasekare [13] and Freeze *et al.* [14] investigated Holling type-II and ratio-dependent functional responses, respectively. Kang and Wedekin [15] considered Holling-III functional response.

Note that the reproduction of predator following the consumption of prey is not instantaneous, but rather is mediated by some reaction-time lag required for gestation. Time delay plays an important role in ecology and it can induce very complex dynamical behaviors [16, 17, 18, 19, 20, 21, 22]. For IGP models, it has been shown that a time delay greatly impacts their dynamics [23, 24]. In [24], Shu *et al.* investigated the complex dynamics of the following IGP model

$$\begin{cases} \dot{R}(t) = rR(t)\left(1 - \frac{R(t)}{K}\right) - c_1R(t)N(t) - c_2R(t)P(t), \\ \dot{N}(t) = e_1c_1R(t - \tau)N(t - \tau) - c_3N(t)P(t) - m_1N(t), \\ \dot{P}(t) = e_2c_2R(t)P(t) + e_3c_3N(t)P(t) - m_2P(t), \end{cases} \quad (2)$$

where r is the growth rate of R in the absence of N and P , K is the carrying capacity of resource. c_1 is the predation rate of IG prey for resource, c_2 is the predation rate of IG predator for resource, c_3 is the consumption rate of IG predator to IG prey and all other parameters have the same meanings as those in (1).

Note that for each species, individuals tend to migrate towards regions with lower population densities. Hence the species are distributed over space and interact with each other within their spatial domains. To take spatial effects into consideration, reaction diffusion equations become a natural choice [25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36]. In this work, we consider a reaction diffusion IGP model with delay and Beddington-DeAngelis functional response.

Suppose $\Omega \subset \mathbb{R}^n$ is a bounded domain with smooth boundary $\partial\Omega$. Let $R(t, x)$, $N(t, x)$, $P(t, x)$ represent the densities of basal resource, IG prey and IG predator at time t and location x , respectively. The basal resource is assumed to grow logistically. We assume the basal resource is consumed by the IG prey at a rate $c_1R(t, x)N(t, x)$, and the IG prey is consumed by the IG predator is $c_3N(t, x)P(t, x)$ at time t and location x . In this paper, we will assume the functional response takes the Beddington-DeAngelis (B-D) form, i.e., the consumption of the resource by the IG predator is characterized by $\frac{c_2P(t, x)R(t, x)}{1 + a_1R(t, x) + a_2P(t, x)}$. The reproduction of IG prey from consuming the basal resource is $e_1c_1R(t - \tau, x)N(t - \tau, x)$, where the time-lag parameter is introduced in a manner analogous to the treatment in [24]. We further assume the populations cannot cross the boundary of Ω . Our model then reads as

TABLE 1. Parameters definitions in model (3) and their units, where [resource] indicates basal resource density, [IG prey] indicates IG prey density, and [IG predator] indicates IG predator density

Symbol	Parameter Definition	Units
r	Basal resource intrinsic growth rate	[time] ⁻¹
K	Basal resource carrying capacity	[Basal resource density]
c_1	Predation rate of IG prey on resource	[IG prey] ⁻¹ [time] ⁻¹
c_2	Predation rate of IG predator on resource	[IG predator] ⁻¹ [time] ⁻¹
c_3	Predation rate of IG predator on IG prey	[IG prey][IG predator] ⁻¹ [time] ⁻¹
e_1	Conversion rate from resource to IG prey	[IG prey][resource] ⁻¹
e_2	Conversion rate from resource to IG predator	[IG predator][resource] ⁻¹
e_3	Conversion rate from IG prey to IG predator	[IG predator][IG prey] ⁻¹
a_1	[Half saturation constant] ⁻¹	[resource] ⁻¹
a_2	[Half saturation constant] ⁻¹	[IG predator] ⁻¹
m_1	Mortality rate of IG prey	[time] ⁻¹
m_2	Mortality rate of IG predator	[time] ⁻¹
\tilde{d}_1	Diffusion coefficient of resource	[length] ² [time] ⁻¹
\tilde{d}_2	Diffusion coefficient of IG prey	[length] ² [time] ⁻¹
\tilde{d}_3	Diffusion coefficient of IG predator	[length] ² [time] ⁻¹
L	The size of spatial domain Ω	[length]

$$\begin{cases}
 \frac{\partial R(t,x)}{\partial t} = \tilde{d}_1 \Delta R + R \left(r \left(1 - \frac{R}{K} \right) - c_1 N - \frac{c_2 P}{1+a_1 R+a_2 P} \right), t > 0, x \in \Omega \\
 \frac{\partial N(t,x)}{\partial t} = \tilde{d}_2 \Delta N + e_1 c_1 N(t-\tau, x) R(t-\tau, x) - c_3 N P - m_1 N, t > 0, x \in \Omega, \\
 \frac{\partial P(t,x)}{\partial t} = \tilde{d}_3 \Delta P + P \left(\frac{e_2 c_2 R}{1+a_1 R+a_2 P} + e_3 c_3 N - m_2 \right), t > 0, x \in \Omega, \\
 \frac{\partial R}{\partial \nu} = \frac{\partial N}{\partial \nu} = \frac{\partial P}{\partial \nu} = 0, t > 0, x \in \partial \Omega, \\
 R(t, x) = \tilde{\phi}_1(t, x) \geq 0, (t, x) \in [-\tau, 0] \times \Omega, \\
 N(t, x) = \tilde{\phi}_2(t, x) \geq 0, (t, x) \in [-\tau, 0] \times \Omega, \\
 P(t, x) = \tilde{\phi}_3(t, x) \geq 0, (t, x) \in [-\tau, 0] \times \Omega,
 \end{cases} \tag{3}$$

where $\tilde{d}_1, \tilde{d}_2, \tilde{d}_3$ denote the diffusion coefficients of the three species, respectively; Δ is the Laplacian operator in the n dimensional space, ν is the outward unit normal vector on $\partial \Omega$, and the homogeneous Neumann boundary conditions reflect the situation where the population cannot across the boundary of Ω . The meanings and units of the parameters of model (3) are summarized in Table 1.

For rescalling, we let

$$\begin{aligned}
 u_1(t, x) &= \frac{R(t, x)}{K}, u_2(t, x) = \frac{c_1 N(t, x)}{r}, u_3(t, x) = \frac{c_2 P(t, x)}{r}, \gamma_1 = \frac{m_1}{r}, \gamma_2 = \frac{m_2}{r}, \\
 \beta_1 &= \frac{e_1 c_1 K}{r}, \beta_2 = \frac{e_2 c_2 K}{r}, \alpha = \frac{c_3}{c_2}, \beta = \frac{e_3 c_3}{c_1}, b = a_1 K, c = \frac{a_2 r}{c_2}, \\
 d_1 &= \frac{\tilde{d}_1}{r L^2}, d_2 = \frac{\tilde{d}_2}{r L^2}, d_3 = \frac{\tilde{d}_3}{r L^2}, \hat{x} = \frac{x}{L}, \hat{t} = tr, \hat{\tau} = \tau r, \\
 \phi_1(t, x) &= \frac{\tilde{\phi}_1(t, x)}{K}, \phi_2(t, x) = \frac{c_1 \tilde{\phi}_2(t, x)}{r}, \phi_3(t, x) = \frac{c_2 \tilde{\phi}_3(t, x)}{r}.
 \end{aligned}$$

Then model (1.3) becomes

$$\begin{cases} \frac{\partial u_1(t,x)}{\partial t} = d_1 \Delta u_1(t,x) + f_1(\mathbf{u}, \mathbf{v}), t > 0, x \in \Omega, \\ \frac{\partial u_2(t,x)}{\partial t} = d_2 \Delta u_2(t,x) + f_2(\mathbf{u}, \mathbf{v}), t > 0, x \in \Omega, \\ \frac{\partial u_3(t,x)}{\partial t} = d_3 \Delta u_3(t,x) + f_3(\mathbf{u}, \mathbf{v}), t > 0, x \in \Omega, \\ \frac{\partial u_1(t,x)}{\partial \nu} = \frac{\partial u_2(t,x)}{\partial \nu} = \frac{\partial u_3(t,x)}{\partial \nu} = 0, t > 0, x \in \partial\Omega, \\ u_1(t,x) = \phi_1(t,x) \geq 0, (t,x) \in [-\tau, 0] \times \Omega, \\ u_2(t,x) = \phi_2(t,x) \geq 0, (t,x) \in [-\tau, 0] \times \Omega, \\ u_3(t,x) = \phi_3(t,x) \geq 0, (t,x) \in [-\tau, 0] \times \Omega, \end{cases} \tag{4}$$

where $\mathbf{u} = (u_1(t, x), u_2(t, x), u_3(t, x))$, $\mathbf{v} = (u_1(t - \tau, x), u_2(t - \tau, x))$ and

$$\begin{aligned} f_1(\mathbf{u}, \mathbf{v}) &= u_1(t, x) \left(1 - u_1(t, x) - u_2(t, x) - \frac{u_3(t, x)}{1 + bu_1(t, x) + cu_3(t, x)} \right), \\ f_2(\mathbf{u}, \mathbf{v}) &= \beta_1 u_1(t - \tau, x) u_2(t - \tau, x) - \alpha u_2(t, x) u_3(t, x) - \gamma_1 u_2(t, x), \\ f_3(\mathbf{u}, \mathbf{v}) &= u_3(t, x) \left(\frac{\beta_2 u_1(t, x)}{1 + bu_1(t, x) + cu_3(t, x)} + \beta u_2(t, x) - \gamma_2 \right). \end{aligned}$$

Throughout the paper, we denote $\bar{\Omega} = \Omega \cup \partial\Omega$, $D_T = (0, T] \times \Omega$, $\bar{D}_T = [0, T] \times \bar{\Omega}$, $Q_0 = [-\tau, 0] \times \Omega$, $\bar{Q}_0 = [-\tau, 0] \times \bar{\Omega}$, $Q_T = [-\tau, T] \times \Omega$, $\bar{Q}_T = [-\tau, T] \times \bar{\Omega}$. Denote by $C^\gamma(D_T)$ the space of Hölder continuous functions in D_T with exponent $\gamma \in (0, 1)$. The space of continuous functions in \bar{D}_T is denoted by $C(\bar{D}_T)$. For vector-value functions we use the product spaces

$$C(\bar{D}_T) \equiv C(\bar{D}_T) \times C(\bar{D}_T) \times C(\bar{D}_T), C^\gamma(\bar{D}_T) \equiv C^\gamma(\bar{D}_T) \times C^\gamma(\bar{D}_T) \times C^\gamma(\bar{D}_T).$$

Denote

$$X = \left\{ (u_1, u_2, u_3)^T \in H^2(\Omega) \times H^2(\Omega) \times H^2(\Omega) : \frac{\partial u_1}{\partial \nu} = \frac{\partial u_2}{\partial \nu} = \frac{\partial u_3}{\partial \nu} = 0 \text{ on } \partial\Omega \right\}$$

with the usual inner product $\langle \cdot, \cdot \rangle$.

The rest of the paper is organized as follows. In Section 2, we study the existence and uniqueness of solution of (4) and estimate the solution’s priori bounds. In Section 3, we discuss the existence of nonnegative spatially homogeneous steady states. In Section 4, we carry out stability analysis and Hopf bifurcation analysis about the unique positive spatially homogeneous steady state of System (4). Numerical simulations are presented in Section 5 to illustrate the impacts of delay, diffusion and the functional response on the dynamics of our IGP model. We conclude this paper with a brief summary and discussion in Section 6.

2. Existence of solution of System (4) and priori bound estimation.

Theorem 2.1. *Consider System (4), we have the following conclusions.*

(i) *Given any initial condition $(\phi_1(t, x), \phi_2(t, x), \phi_3(t, x)) \in C^\gamma(Q_0)$ with*

$$0 \leq \phi_i(t, x) \leq L_i, (t, x) \in Q_0, i = 1, 2, 3, \tag{5}$$

where $L_i, i = 1, 2, 3$ are positive constants satisfying

$$1 \leq L_1 \leq \frac{\gamma_1}{\beta_1}, L_2 < \frac{\gamma_2}{\beta}, L_3 \geq \frac{1}{c} \left[\frac{\beta_2 L_1}{\gamma_2 - \beta L_2} - bL_1 - 1 \right], \tag{6}$$

System (4) admits a unique solution $(u_1(t, x), u_2(t, x), u_3(t, x))$ satisfying

$$0 \leq u_i(t, x) \leq L_i, \text{ for } t > 0, x \in \Omega, i = 1, 2, 3.$$

(ii) For any solution $(u_1(t, x), u_2(t, x), u_3(t, x))$ of System (4), it holds true that

$$\limsup_{t \rightarrow \infty} u_1(t, x) \leq 1, \limsup_{t \rightarrow \infty} \int_{\Omega} u_2(t, x) dx \leq J_1, \limsup_{t \rightarrow \infty} \int_{\Omega} u_3(t, x) dx \leq J_2$$

where $J_1 = (\frac{\beta_1}{4\gamma_1} + \beta_1)|\Omega|$, $J_2 = (\frac{\beta_2}{4\kappa} + \frac{\beta_1\beta}{\alpha\kappa}J_1 + \beta_2)|\Omega|$ with $\kappa = \min\{\gamma_1, \gamma_2\}$.

Furthermore, if $d_1 = d_2 = d_3$ and $\tau = 0$, then for any $x \in \bar{\Omega}$,

$$\limsup_{t \rightarrow \infty} u_2(t, x) \leq \frac{\beta_2\alpha}{4\kappa\beta} + \frac{\beta_1}{\kappa}(\frac{\beta_1}{4\gamma_1} + \beta_1) + \frac{\beta_2\alpha}{\beta},$$

$$\limsup_{t \rightarrow \infty} u_3(t, x) \leq \frac{\beta_2}{4\kappa} + \frac{\beta_1\beta}{\alpha\kappa}(\frac{\beta_1}{4\gamma_1} + \beta_1) + \beta_2.$$

Proof. Note that $f_i(\mathbf{u}, \mathbf{v})$ is mixed quasi-monotone in a subset $\Lambda \times \Lambda^*$ of $\mathbb{R}^3 \times \mathbb{R}^2$ for each $i = 1, 2, 3$, we can apply [27, Theorem 2.2] to establish the existence and uniqueness of solutions to System (4). To this end, we first need to construct a pair of coupled upper and lower solutions of System (4), which we denote by $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3)$ and $(\hat{u}_1, \hat{u}_2, \hat{u}_3)$, respectively. In view of [27, Definition 2.1], the required upper and lower solutions should satisfy the boundary-initial inequalities and the following differential inequalities

$$\begin{cases} \frac{\partial \tilde{u}_1}{\partial t} \geq d_1 \Delta \tilde{u}_1 + \tilde{u}_1(1 - \tilde{u}_1 - \tilde{u}_2 - \frac{\tilde{u}_3}{1+b\tilde{u}_1+c\tilde{u}_3}) \\ \frac{\partial \tilde{u}_2}{\partial t} \geq d_2 \Delta \tilde{u}_2 + \beta_1 \tilde{u}_1 \tilde{u}_2 - \alpha \tilde{u}_3 \tilde{u}_2 - \gamma_1 \tilde{u}_2, \\ \frac{\partial \tilde{u}_3}{\partial t} \geq d_3 \Delta \tilde{u}_3 + \frac{\beta_2 \tilde{u}_1 \tilde{u}_3}{1+b\tilde{u}_1+c\tilde{u}_3} + \beta \tilde{u}_2 \tilde{u}_3 - \gamma_2 \tilde{u}_3 \end{cases} \tag{7}$$

and

$$\begin{cases} \frac{\partial \hat{u}_1}{\partial t} \leq d_1 \Delta \hat{u}_1 + \hat{u}_1(1 - \hat{u}_1 - \tilde{u}_2 - \frac{\tilde{u}_3}{1+b\hat{u}_1+c\tilde{u}_3}) \\ \frac{\partial \hat{u}_2}{\partial t} \leq d_2 \Delta \hat{u}_2 + \beta_1 \hat{u}_1 \hat{u}_2 - \alpha \tilde{u}_3 \hat{u}_2 - \gamma_1 \hat{u}_2 \\ \frac{\partial \hat{u}_3}{\partial t} \leq d_3 \Delta \hat{u}_3 + \frac{\beta_2 \hat{u}_1 \tilde{u}_3}{1+b\hat{u}_1+c\tilde{u}_3} + \beta \tilde{u}_2 \hat{u}_3 - \gamma_2 \hat{u}_3. \end{cases} \tag{8}$$

Take $(\hat{u}_1, \hat{u}_2, \hat{u}_3) = (0, 0, 0)$ and $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) = (L_1, L_2, L_3)$. Clearly, $\frac{\partial \tilde{u}_i}{\partial \nu} = 0 \geq 0 \geq 0 = \frac{\partial \hat{u}_i}{\partial \nu}$. It follows from (5) and (6) that the pair $(\hat{u}_1, \hat{u}_2, \hat{u}_3) = (0, 0, 0)$ and $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) = (L_1, L_2, L_3)$ are coupled upper and lower solutions of System (4). It is easy to check that $f_i(\mathbf{u}, \mathbf{v})$ ($i = 1, 2, 3$) satisfy the Lipschitz condition for $0 \leq u_i \leq \mathfrak{M}_i, 0 \leq v_i \leq L_i, i = 1, 2, 3$, and we denote the Lipschitz constants by $K_i, i = 1, 2, 3$. By [27, Theorem 2.2], System (4) admits a unique global solution $(u_1(t, x), u_2(t, x), u_3(t, x))$, which satisfies

$$(0, 0, 0) \leq (u_1(t, x), u_2(t, x), u_3(t, x)) \leq (L_1, L_2, L_3), \quad t \geq 0, \quad x \in \Omega.$$

This completes the proof of (i).

Next we establish the priori bound of solutions to System (4). To estimate $u_1(t, x)$, we observe that $u_1(t, x)$ satisfies

$$\begin{cases} \frac{\partial u_1(t, x)}{\partial t} \leq d_1 \Delta u_1(t, x) + u_1(t, x)(1 - u_1(t, x)), & t > 0, x \in \Omega, \\ \frac{\partial u_1(t, x)}{\partial n} = 0, & t > 0, x \in \partial\Omega. \end{cases}$$

It follows from the standard comparison principle [37, Lemma 3.4.2] of parabolic equations that $\limsup_{t \rightarrow \infty} u_1(t, x) \leq 1$. Thus for any $\varepsilon > 0$, there exists a $T_1 > 0$ such that $u_1(t, x) \leq 1 + \varepsilon$ for $t \geq T_1$.

To estimate the priori bounds of $u_2(t, x)$ and $u_3(t, x)$, we set

$$U_1(t) = \int_{\Omega} u_1(t, x) dx, U_2(t) = \int_{\Omega} u_2(t, x) dx, U_3(t) = \int_{\Omega} u_3(t, x) dx.$$

Then

$$\begin{aligned}\frac{dU_1(t)}{dt} &= \int_{\Omega} \frac{\partial u_1}{\partial t} dx = \int_{\Omega} d_1 \Delta u_1 dx + \int_{\Omega} [u_1(t, x)(1 - u_1(t, x) - u_2(t, x) - \\ &\quad \frac{u_3(t, x)}{1 + bu_1(t, x) + cu_3(t, x)})] dx, \\ \frac{dU_2(t)}{dt} &= \int_{\Omega} \frac{\partial u_2}{\partial t} dx = \int_{\Omega} d_2 \Delta u_2 dx + \int_{\Omega} [\beta_1 u_1(t - \tau, x) u_2(t - \tau, x) - \\ &\quad \alpha u_2(t, x) u_3(t, x) - \gamma_1 u_2(t, x)] dx, \\ \frac{dU_3(t)}{dt} &= \int_{\Omega} \frac{\partial u_3}{\partial t} dx = \int_{\Omega} d_3 \Delta u_3 dx + \\ &\quad \int_{\Omega} [u_3(t, x) (\frac{\beta_2 u_1(t, x)}{1 + bu_1(t, x) + cu_3(t, x)} + \beta u_2(t, x) - \gamma_2)] dx.\end{aligned}$$

From the Neumann boundary conditions, we further obtain

$$\begin{aligned}& \frac{d(\beta_1 U_1(t) + U_2(t + \tau))}{dt} \\ &= \beta_1 \int_{\Omega} \frac{\partial u_1}{\partial t} dx + \int_{\Omega} \frac{\partial u_2(t + \tau, x)}{\partial t} dx \\ &= \beta_1 \int_{\Omega} (u_1 - u_1^2) dx - \int_{\Omega} \frac{\beta_1 u_1 u_3}{1 + bu_1 + cu_3} dx \\ &\quad - \int_{\Omega} \alpha u_2(t + \tau, x) u_3(t + \tau, x) dx - \int_{\Omega} \gamma_1 u_2(t + \tau, x) dx \\ &\leq \frac{\beta_1}{4} |\Omega| + \gamma_1 \beta_1 (1 + \varepsilon) |\Omega| - \gamma_1 (\beta_1 U_1(t) + U_2(t + \tau)), \quad t > T_1.\end{aligned}$$

By the comparison principle, we have

$$\limsup_{t \rightarrow \infty} (\beta_1 U_1(t) + U_2(t + \tau)) \leq \frac{\beta_1}{4\gamma_1} |\Omega| + \beta_1 |\Omega| \equiv J_1.$$

Similarly, there exists $T_2 > T_1$ such that $\int_{\Omega} u_2(t, x) dx = U_2(t) \leq J_1 + \varepsilon$ for $t \geq T_2$. Thus, for $t \geq T_2 + \tau$, we have

$$\begin{aligned}& \frac{d(\beta_2 U_1(t) + \frac{\beta}{\alpha} U_2(t) + U_3(t))}{dt} \\ &= \beta_2 \int_{\Omega} (u_1 - u_1^2) dx + \int_{\Omega} \frac{\beta_1 \beta}{\alpha} u_1(t - \tau, x) u_2(t - \tau, x) dx - \frac{\beta \gamma_1}{\alpha} \int_{\Omega} u_2 dx - \gamma_2 \int_{\Omega} u_3 dx \\ &\leq \frac{\beta_2}{4} |\Omega| + \frac{\beta_1 \beta}{\alpha} (1 + \varepsilon) \int_{\Omega} u_2(t - \tau, x) dx - \frac{\beta \gamma_1}{\alpha} U_2 - \gamma_2 U_3 \\ &\leq \frac{\beta_2}{4} |\Omega| + \frac{\beta_1 \beta}{\alpha} (1 + \varepsilon) (J_1 + \varepsilon) |\Omega| + \beta_2 \kappa (1 + \varepsilon) |\Omega| - \kappa (\beta_2 U_1 + \frac{\beta}{\alpha} U_2 + U_3),\end{aligned}$$

where $\kappa = \min\{\gamma_1, \gamma_2\}$. This implies that

$$\limsup_{t \rightarrow \infty} (\beta_2 U_1 + \frac{\beta}{\alpha} U_2 + U_3) \leq \frac{\beta_2}{4\kappa} |\Omega| + \frac{\beta_1 \beta}{\alpha \kappa} J_1 |\Omega| + \beta_2 |\Omega| \equiv J_2.$$

and hence $\limsup_{t \rightarrow \infty} \int_{\Omega} u_3(t, x) dx = \limsup_{t \rightarrow \infty} U_3(t) \leq J_2$.

For the case with $d_1 = d_2 = d_3 = d$ and $\tau = 0$, we can similarly show that for any $\varepsilon > 0$, there exists $T_3 > T_1$ such that $0 \leq u_1(t, x) \leq 1 + \varepsilon$ and $0 \leq u_2(t, x) \leq \frac{\beta_1}{4\gamma_1} + \beta_1$ for $t > T_3$. Moreover, let $S(t, x) = \beta_2 u_1(t, x) + \frac{\beta}{\alpha} u_2(t, x) + u_3(t, x)$. Then

$$\begin{cases} \frac{\partial S}{\partial t} = d\Delta S + \beta_2(u_1 - u_1^2) - \beta_2 u_1 u_2 + \frac{\beta \beta_1}{\alpha} u_1 u_2 - \frac{\beta \gamma_1}{\alpha} u_2 - \gamma_2 u_3, & t > T_3, x \in \Omega, \\ \frac{\partial S}{\partial \nu} = 0, & t > T_3, x \in \partial\Omega, \\ S(T_3, x) = \beta_2 u_1(T_3, x) + \frac{\beta}{\alpha} u_2(T_3, x) + u_3(T_3, x), & x \in \Omega. \end{cases}$$

Thus for $t > T_3$, we have

$$\begin{aligned} & \beta_2(u_1 - u_1^2) - \beta_2 u_1 u_2 + \frac{\beta \beta_1}{\alpha} u_1 u_2 - \frac{\beta \gamma_1}{\alpha} u_2 - \gamma_2 u_3 \\ & \leq \frac{\beta_2}{4} + \frac{\beta_1 \beta}{\alpha} (1 + \varepsilon) \left(\frac{\beta_1}{4\gamma_1} + \beta_1 + \varepsilon \right) + \beta_2 \kappa (1 + \varepsilon) - \kappa S. \end{aligned}$$

Consider the system $\begin{cases} \frac{\partial W}{\partial t} = d\Delta W + \frac{\beta_2}{4} + \frac{\beta_1 \beta}{\alpha} (1 + \varepsilon) \left(\frac{\beta_1}{4\gamma_1} + \beta_1 + \varepsilon \right) + \beta_2 \kappa (1 + \varepsilon) - \kappa W, t > T_3, x \in \Omega \\ \frac{\partial W}{\partial \nu} = 0, \quad t > T_3, x \in \partial\Omega, \\ W(T_3, x) = \beta_2 u_1(T_3, x) + \frac{\beta}{\alpha} u_2(T_3, x) + u_3(T_3, x), x \in \Omega. \end{cases}$

It follows from [37, Theorem 2.4.6] that the solution $W(t, x)$ satisfies

$$\lim_{t \rightarrow \infty} W(t, x) = \frac{\beta_2}{4\kappa} + \frac{\beta_1 \beta}{\alpha \kappa} (1 + \varepsilon) \left(\frac{\beta_1}{4\gamma_1} + \beta_1 + \varepsilon \right) + \beta_2 (1 + \varepsilon).$$

The comparison argument implies that

$$\limsup_{t \rightarrow \infty} u_2(t, x) \leq \limsup_{t \rightarrow \infty} \frac{\alpha}{\beta} S(t, x) \leq \frac{\beta_2 \alpha}{4\kappa \beta} + \frac{\beta_1}{\kappa} \left(\frac{\beta_1}{4\gamma_1} + \beta_1 \right) + \frac{\beta_2 \alpha}{\beta}$$

and

$$\limsup_{t \rightarrow \infty} u_3(t, x) \leq \limsup_{t \rightarrow \infty} S(t, x) \leq \frac{\beta_2}{4\kappa} + \frac{\beta_1 \beta}{\alpha \kappa} \left(\frac{\beta_1}{4\gamma_1} + \beta_1 \right) + \beta_2.$$

This completes the proof. □

3. Spatially homogeneous steady states of System (4). Same as in [24], we denote by $\mathcal{R}_i = \frac{\beta_i}{\gamma_i} = \frac{e_i c_i K}{m_i}$ ($i = 1, 2$) the reproduction numbers for the IG prey and IG predator, respectively. Consider (4), we easily have the following existence results on trivial and semi-trivial spatially homogeneous steady states.

Proposition 1. (i) *The trivial steady state $E_0 = (0, 0, 0)$ always exists.*

(ii) *There is a weakly semi-trivial steady state in the absence of IG Prey and IG Predator $E_1 = (1, 0, 0)$.*

(iii) *The IG Prey-only strong semi-trivial steady state $E_{10} := (\frac{1}{\mathcal{R}_1}, 1 - \frac{1}{\mathcal{R}_1}, 0)$ exists if and only if $\mathcal{R}_1 > 1$.*

(iv) *The IG Predator-only strong semi-trivial steady state $E_{01} := (\hat{u}_1, 0, \mathcal{R}_2(1 - \hat{u}_1)\hat{u}_1)$ exists if and only if $\mathcal{R}_2 > 1 + b$, where*

$$\hat{u}_1 = \frac{-(\mathcal{R}_2 - c\mathcal{R}_2 - b) + \sqrt{(\mathcal{R}_2 - c\mathcal{R}_2 - b)^2 + 4c\mathcal{R}_2}}{2c\mathcal{R}_2}.$$

System (4) admits a positive steady state $E^* := (u_1^*, u_2^*, u_3^*)$ if E^* is a positive solution to the following three equations:

$$1 - u_1 - u_2 - \frac{u_3}{1 + bu_1 + cu_3} = 0, \tag{9}$$

$$\beta_1 u_1 - \alpha u_3 - \gamma_1 = 0, \tag{10}$$

$$\frac{\beta_2 u_1}{1 + bu_1 + cu_3} + \beta u_2 - \gamma_2 = 0. \tag{11}$$

It follows from (10) that

$$u_1^* = \frac{\alpha}{\beta_1} u_3^* + \frac{\gamma_1}{\beta_1}. \tag{12}$$

Combining (9), (11) and (12), we obtain

$$u_3^{*2} + pu_3^* + q = 0, \tag{13}$$

where

$$p = \frac{c\gamma_2\beta_1^2 + b\alpha\beta_1(\gamma_2 - \beta) + \alpha\beta_1(\beta - \beta_2) + c\beta\beta_1(\gamma_1 - \beta_1) + \beta\beta_1^2 + 2b\alpha\beta\gamma_1}{\alpha\beta(b\alpha + c\beta_1)},$$

$$q = \frac{\beta_1^2(\gamma_2 - \beta) + b\beta_1\gamma_1(\gamma_2 - \beta) + \beta_1\gamma_1(\beta - \beta_2) + \beta(b\gamma_1^2 - \beta_1^2)}{\alpha\beta(b\alpha + c\beta_1)}.$$

For the distribution of roots of Eq. (13), we have the following results.

- Lemma 3.1.** (i) If $p < 0, p^2 - 4q > 0$ and $q > 0$, then Eq. (13) has two positive roots $u_{3\pm}^* = \frac{-p \pm \sqrt{p^2 - 4q}}{2}$.
 (ii) If $p < 0$ and $p^2 - 4q = 0$, then Eq. (13) has a unique positive root $u_{30}^* = \frac{-p}{2}$.
 (iii) If $q < 0$, then Eq. (13) has a unique positive root $u_3^* = u_{3+}^*$.

Remark 1. Set $\mathcal{R}_3 = \frac{\beta}{\gamma_2}$, then $q < 0$ provided that $\mathcal{R}_1 > b$ and $\mathcal{R}_2 > \mathcal{R}_3 > 1$.

According to Lemma 3.1, the following proposition is valid.

- Proposition 2.** (i) When $p^2 - 4q > 0, p < 0, q > 0$ and $\mathcal{R}_2 < \min \left\{ \frac{(b\alpha + c\beta_1)(-p + \sqrt{p^2 - 4q}) + 2(b\gamma_1 + \beta_1)}{\alpha(-p + \sqrt{p^2 - 4q}) + 2\gamma_1}, \frac{(b\alpha + c\beta_1)(-p - \sqrt{p^2 - 4q}) + 2(b\gamma_1 + \beta_1)}{\alpha(-p - \sqrt{p^2 - 4q}) + 2\gamma_1} \right\}$, System (4) has two positive constant steady states $E_+^* = (u_{1+}^*, u_{2+}^*, u_{3+}^*)$ and $E_-^* = (u_{1-}^*, u_{2-}^*, u_{3-}^*)$, where $u_{1+}^* = \frac{\alpha u_{3+}^* + \gamma_1}{\beta_1}, u_{2+}^* = \frac{\gamma_2}{\beta} - \frac{\beta_2}{\beta} \times \frac{\alpha u_{3+}^* + \gamma_1}{(b\alpha + c\beta_1)u_{3+}^* + b\gamma_1 + \beta_1}, u_{3+}^* = \frac{-p + \sqrt{p^2 - 4q}}{2}$ and $u_{1-}^* = \frac{\alpha u_{3-}^* + \gamma_1}{\beta_1}, u_{2-}^* = \frac{\gamma_2}{\beta} - \frac{\beta_2}{\beta} \times \frac{\alpha u_{3-}^* + \gamma_1}{(b\alpha + c\beta_1)u_{3-}^* + b\gamma_1 + \beta_1}, u_{3-}^* = \frac{-p - \sqrt{p^2 - 4q}}{2}$.
 (ii) When $p^2 - 4q = 0, p < 0$ and $\mathcal{R}_2 < \frac{-(b\alpha + c\beta_1)p + 2(b\gamma_1 + \beta_1)}{2\gamma_1 - \alpha p}$, E_+^* and E_-^* merge, denoted by $E_0^* = (u_{10}^*, u_{20}^*, u_{30}^*)$, where $u_{10}^* = -\frac{p\alpha}{2\beta_1} + \frac{\gamma_1}{\beta_1}, u_{20}^* = \frac{\gamma_2}{\beta} - \frac{\beta_2}{\beta} \times \frac{2\gamma_1 - p\alpha}{2(b\gamma_1 + \beta_1) - (b\alpha + c\beta_1)p}, u_{30}^* = -\frac{p}{2}$.
 (iii) When $q < 0$ and $\mathcal{R}_2 < \frac{(b\alpha + c\beta_1)(-p + \sqrt{p^2 - 4q}) + 2(b\gamma_1 + \beta_1)}{\alpha(-p + \sqrt{p^2 - 4q}) + 2\gamma_1}$, System (4) has only one positive constant steady state $E^* = (u_1^*, u_2^*, u_3^*)$, where $u_1^* = u_{1+}^*, u_2^* = u_{2+}^*, u_3^* = u_{3+}^*$.

Remark 2. There exist parameter values such that Proposition 3.4 holds. For example, choosing $\alpha = 0.68, \beta = 0.9, \beta_1 = 1.9, \beta_2 = 1.8, \gamma_1 = 0.2, \gamma_2 = 0.76, b = 2.5, c = 10$. A direct calculation yields only one positive steady state $E^* = (0.1891, 0.7562, 0.2344)$.

4. Dynamics of System (4). Let $0 = \mu_1 < \mu_2 \leq \mu_3 \leq \dots$ be the eigenvalues of $-\Delta$ on Ω under no-flux boundary conditions, and $E(\mu_i)$ be the eigenspace corresponding to μ_i with multiplicity $m_i \geq 1, i \in \mathbb{N} \equiv \{1, 2, \dots\}$. Set $\mathbf{X}_{ij} := \{\mathbf{e} \cdot \phi_{ij} : \mathbf{e} \in \mathbb{R}^3\}$, where $\{\phi_{ij}\}$ is an orthonormal basis of $E(\mu_i)$ for $j = 1, 2, \dots, \dim E(\mu_i)$. For $\mathbf{X} := \{\mathbf{w} \in \mathcal{C}^1(\bar{\Omega}) : \frac{\partial w_1}{\partial \nu} = \frac{\partial w_2}{\partial \nu} = \frac{\partial w_3}{\partial \nu} = 0 \text{ on } \partial\Omega\}$, we have the following lemma from [37].

Lemma 4.1.

$$\mathbf{X} = \bigoplus_{i=1}^{\infty} \mathbf{X}_i, \text{ where } \mathbf{X}_i = \bigoplus_{j=1}^{\dim E(\mu_i)} \mathbf{X}_{ij}.$$

4.1. **Stability of E_0 and E_1 .** In the following, we consider the stability of E_0 and E_1 .

Theorem 4.2. (i) *The trivial steady state E_0 is always unstable.*

(ii) *The semi-trivial steady state E_1 is locally asymptotically stable if $\mathcal{R}_1 < 1$ and $\mathcal{R}_2 < 1 + b$ and unstable if either $\mathcal{R}_1 > 1$ or $\mathcal{R}_2 > 1 + b$.*

Proof. Linearizing System (4) at a constant steady state $\mathbf{u}^\diamond = (u_1^\diamond, u_2^\diamond, u_3^\diamond)$ gives

$$\frac{\partial \mathbf{u}}{\partial t} = (D\Delta + \hat{J}_1)\mathbf{u} + \hat{J}_2\mathbf{u}_\tau, \tag{14}$$

where $D = \text{diag}\{d_1, d_2, d_3\}$, $\mathbf{u} = (u_1(t, x), u_2(t, x), u_3(t, x))$, $\mathbf{u}_\tau = (u_1(t - \tau, x), u_2(t - \tau, x), u_3(t - \tau, x))$ and

$$\hat{J}_1 = \begin{bmatrix} 1 - 2u_1^\diamond - u_2^\diamond - \frac{u_3^\diamond + cu_3^{\diamond 2}}{(1+bu_1^\diamond + cu_3^\diamond)^2} & -u_1^\diamond & -\frac{(1+bu_1^\diamond)u_1^\diamond}{(1+bu_1^\diamond + cu_3^\diamond)^2} \\ 0 & -\alpha u_3^\diamond - \gamma_1 & -\alpha u_2^\diamond \\ \frac{\beta_2(1+cu_2^\diamond)u_2^\diamond}{(1+bu_1^\diamond + cu_3^\diamond)^2} & \beta u_3^\diamond & \frac{\beta_2 u_1^\diamond(1+bu_1^\diamond)}{(1+bu_1^\diamond + cu_3^\diamond)^2} + \beta u_2^\diamond - \gamma_2 \end{bmatrix},$$

$$\hat{J}_2 = \begin{bmatrix} 0 & 0 & 0 \\ \beta_1 u_2^\diamond & \beta_1 u_1^\diamond & 0 \\ 0 & 0 & 0 \end{bmatrix}.$$

From Lemma 4.1, we know that the eigenvalues of the System (4) is confined on the subspace \mathbf{X}_i , and λ is an eigenvalue of (14) on \mathbf{X}_i if and only if it is an eigenvalue of the matrix $-\mu_i D + J^*$, where $J^* = \hat{J}_1 + \hat{J}_2 e^{-\lambda\tau}$. Then the characteristic equation of (14) is

$$\det(\lambda I_3 + \mu_i D - J^*) = 0, \tag{15}$$

where I_3 stands for the 3×3 identity matrix.

(i) If $\mathbf{u}^\diamond = E_0$, then we obtain the following characteristic equation

$$(\lambda + d_1\mu_i - 1)(\lambda + d_2\mu_i + \gamma_1)(\lambda + d_3\mu_i + \gamma_2) = 0,$$

which gives three sets of eigenvalues, namely, $\lambda_{1i} = -d_1\mu_i + 1$, $\lambda_{2i} = -d_2\mu_i - \gamma_1$, $\lambda_{3i} = -d_3\mu_i - \gamma_2$, $i = 1, 2, \dots$. Clearly, for $i = 1$, $\lambda_{11} = 1 > 0$. From [40, Corollary 1.11], the trivial steady state E_0 is unstable.

(ii) If $\mathbf{u}^\diamond = E_1$, then we obtain the following characteristic equation

$$(\lambda + d_1\mu_i + 1)(\lambda + d_2\mu_i - \beta_1 e^{-\lambda\tau} + \gamma_1)(\lambda + d_3\mu_i - \frac{\beta_2}{1+b} + \gamma_2) = 0,$$

which gives the eigenvalues $\lambda_{1i} = -d_1\mu_i - 1$, $\lambda_{3i} = -d_3\mu_i + \frac{\beta_2}{1+b} - \gamma_2$ and λ_{2i} is determined by $\lambda_{2i} + d_2\mu_i + \gamma_1 - \beta_1 e^{-\lambda_{2i}\tau} = 0$. Clearly, $\lambda_{1i} < 0$ for all μ_i . If $\mathcal{R}_2 < 1 + b$, we get $\lambda_{3i} < 0$ for all μ_i . If $\mathcal{R}_1 < 1$, then we have $\beta_1 < \gamma_1 + d_2\mu_i$ for all μ_i . Thus it follows from [24, Lemma 6] that the eigenvalues λ_{2i} have negative real parts for all μ_i . It follows from [40, Corollary 1.11] that the equilibrium E_1 is locally asymptotically stable for $\mathcal{R}_1 < 1$ and $\mathcal{R}_2 < 1 + b$. If $\mathcal{R}_1 > 1$ then there exists $\mu_1 = 0$ such that $d_2\mu_1 + \gamma_1 < \beta_1$, so it follows from the [24, Lemma 6] that at least one of the eigenvalues λ_{2i} has a positive real part. If $\mathcal{R}_2 > 1 + b$ then there exists $\mu_1 = 0$ such that $\lambda_{31} > 0$. From [40, Corollary 1.11], the steady state E_1 is unstable in either case. \square

Theorem 4.3. *Suppose that $\mathcal{R}_1 < 1$, $\mathcal{R}_2 < 1 + b$ and $1 - \frac{\gamma_2}{\beta} > \frac{1}{c}$. Then E_1 is globally asymptotically stable.*

Proof. Let $(\hat{u}_1, \hat{u}_2, \hat{u}_3) = (\varepsilon, 0, 0)$ and $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) = (\mathfrak{M}_1, \mathfrak{M}_2, \mathfrak{M}_3)$, where $\mathfrak{M}_1 = 1 + \varepsilon < \frac{\gamma_1}{\beta}$, $\mathfrak{M}_2 = \frac{\gamma_2}{\beta} - \varepsilon > 0$, $\mathfrak{M}_3 = \frac{1}{c} \left(\frac{\beta_2 \mathfrak{M}_1}{\gamma_2 - \beta \mathfrak{M}_2} - b \mathfrak{M}_1 - 1 \right) = \frac{1}{c} \left(\frac{\beta_2(1+\varepsilon)}{\beta \varepsilon} - b(1+\varepsilon) - 1 \right) > 0$ and ε is arbitrary small positive constant.

We claim that $(\hat{u}_1, \hat{u}_2, \hat{u}_3) = (\varepsilon, 0, 0)$ and $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) = (\mathfrak{M}_1, \mathfrak{M}_2, \mathfrak{M}_3)$ are also coupled upper and lower solutions of System (4). In fact, it follows from $1 - \frac{\gamma_2}{\beta} > \frac{1}{c}$ that $1 - \frac{\gamma_2}{\beta} > \frac{\mathfrak{M}_3}{1+c\mathfrak{M}_3}$, and thus we get $\varepsilon(1 - \varepsilon - (\frac{\gamma_2}{\beta} - \varepsilon) - \frac{\mathfrak{M}_3}{1+b\varepsilon+c\mathfrak{M}_3}) \geq 0$. Hence, we obtain $\hat{u}_1(1 - \hat{u}_1 - \tilde{u}_2 - \frac{\tilde{u}_3}{1+b\hat{u}_1+c\tilde{u}_3}) \geq 0$. It is easy to check that $(\hat{u}_1, \hat{u}_2, \hat{u}_3) = (\varepsilon, 0, 0)$ and $(\tilde{u}_1, \tilde{u}_2, \tilde{u}_3) = (\mathfrak{M}_1, \mathfrak{M}_2, \mathfrak{M}_3)$ satisfy the differential inequalities in (7) and (8). Thus the claim holds. Define the iterated sequences $(\bar{u}_1^{(m)}, \bar{u}_2^{(m)}, \bar{u}_3^{(m)})$ and $(\underline{u}_1^{(m)}, \underline{u}_2^{(m)}, \underline{u}_3^{(m)})$ as follows:

$$\begin{aligned} \bar{u}_1^{(m)} &= \bar{u}_1^{(m-1)} + \frac{1}{K_1} \left[\bar{u}_1^{(m-1)} \left(1 - \bar{u}_1^{(m-1)} - \underline{u}_2^{(m-1)} - \frac{\underline{u}_3^{(m-1)}}{1 + b\bar{u}_1^{(m-1)} + c\underline{u}_3^{(m-1)}} \right) \right], \\ \underline{u}_1^{(m)} &= \underline{u}_1^{(m-1)} + \frac{1}{K_1} \left[\underline{u}_1^{(m-1)} \left(1 - \underline{u}_1^{(m-1)} - \bar{u}_2^{(m-1)} - \frac{\bar{u}_3^{(m-1)}}{1 + b\underline{u}_1^{(m-1)} + c\bar{u}_3^{(m-1)}} \right) \right], \\ \bar{u}_2^{(m)} &= \bar{u}_2^{(m-1)} + \frac{1}{K_2} \left[\bar{u}_2^{(m-1)} \left(\beta_1 \bar{u}_1^{(m-1)} - \alpha \underline{u}_3^{(m-1)} - \gamma_1 \right) \right], \\ \underline{u}_2^{(m)} &= \underline{u}_2^{(m-1)} + \frac{1}{K_2} \left[\underline{u}_2^{(m-1)} \left(\beta_1 \underline{u}_1^{(m-1)} - \alpha \bar{u}_3^{(m-1)} - \gamma_1 \right) \right], \\ \bar{u}_3^{(m)} &= \bar{u}_3^{(m-1)} + \frac{1}{K_3} \left[\bar{u}_3^{(m-1)} \left(\frac{\beta_2 \bar{u}_1^{(m-1)}}{1 + b\bar{u}_1^{(m-1)} + c\bar{u}_3^{(m-1)}} + \beta \bar{u}_2^{(m-1)} - \gamma_2 \right) \right], \\ \underline{u}_3^{(m)} &= \underline{u}_3^{(m-1)} + \frac{1}{K_3} \left[\underline{u}_3^{(m-1)} \left(\frac{\beta_2 \underline{u}_1^{(m-1)}}{1 + b\underline{u}_1^{(m-1)} + c\underline{u}_3^{(m-1)}} + \beta \underline{u}_2^{(m-1)} - \gamma_2 \right) \right], \end{aligned}$$

where $m = 1, 2, \dots$, $(\bar{u}_1^{(0)}, \bar{u}_2^{(0)}, \bar{u}_3^{(0)}) = (\mathfrak{M}_1, \mathfrak{M}_2, \mathfrak{M}_3)$, $(\underline{u}_1^{(0)}, \underline{u}_2^{(0)}, \underline{u}_3^{(0)}) = (\varepsilon, 0, 0)$ and $K_i, i = 1, 2, 3$ are the Lipschitz constants in Theorem 2.1. It is easy to see that $\mathbf{f}(\mathbf{u}, \mathbf{v}) \equiv (f_1(\mathbf{u}, \mathbf{v}), f_2(\mathbf{u}, \mathbf{v}), f_3(\mathbf{u}, \mathbf{v}))$ is a C^1 function of \mathbf{u}, \mathbf{v} and is mixed quasi-monotone in a subset $\Lambda \times \Lambda^*$ of $\mathbb{R}^3 \times \mathbb{R}^2$. We can deduce from the induction method that

$$\hat{\mathbf{u}} \leq \underline{\mathbf{u}}^{(m)} \leq \underline{\mathbf{u}}^{(m+1)} \leq \bar{\mathbf{u}}^{(m+1)} \leq \bar{\mathbf{u}}^{(m)} \leq \tilde{\mathbf{u}}. \quad (16)$$

It follows from (16) that the limits

$$\begin{aligned} \lim_{m \rightarrow \infty} \bar{u}_1^{(m)} &= \bar{u}_1, \quad \lim_{m \rightarrow \infty} \bar{u}_2^{(m)} = \bar{u}_2, \quad \lim_{m \rightarrow \infty} \bar{u}_3^{(m)} = \bar{u}_3, \\ \lim_{m \rightarrow \infty} \underline{u}_1^{(m)} &= \underline{u}_1, \quad \lim_{m \rightarrow \infty} \underline{u}_2^{(m)} = \underline{u}_2, \quad \lim_{m \rightarrow \infty} \underline{u}_3^{(m)} = \underline{u}_3 \end{aligned} \quad (17)$$

exist and satisfy the following equations

$$f_1(\bar{u}_1, \underline{u}_2, \underline{u}_3) = 0, \quad f_2(\bar{u}_1, \bar{u}_2, \underline{u}_3) = 0, \quad f_3(\bar{u}_1, \bar{u}_2, \bar{u}_3) = 0, \quad (18)$$

$$f_1(\underline{u}_1, \bar{u}_2, \bar{u}_3) = 0, \quad f_2(\underline{u}_1, \underline{u}_2, \bar{u}_3) = 0, \quad f_3(\underline{u}_1, \underline{u}_2, \underline{u}_3) = 0, \quad (19)$$

where

$$\hat{\mathbf{u}} = (\hat{u}_1, \hat{u}_2, \hat{u}_3), \quad \underline{\mathbf{u}}^{(m)} = (\underline{u}_1^{(m)}, \underline{u}_2^{(m)}, \underline{u}_3^{(m)}), \quad \underline{\mathbf{u}}^{(m+1)} = (\underline{u}_1^{(m+1)}, \underline{u}_2^{(m+1)}, \underline{u}_3^{(m+1)}),$$

$$\bar{\mathbf{u}}^{(m+1)} = (\bar{u}_1^{(m+1)}, \bar{u}_2^{(m+1)}, \bar{u}_3^{(m+1)}), \quad \bar{\mathbf{u}}^{(m)} = (\bar{u}_1^{(m)}, \bar{u}_2^{(m)}, \bar{u}_3^{(m)}), \quad \tilde{\mathbf{u}} = (\tilde{u}_1, \tilde{u}_2, \tilde{u}_3).$$

Since $\underline{u}_2^{(0)} = 0$ and $\underline{u}_3^{(0)} = 0$, we get $\underline{u}_2^{(m)} = 0$ and $\underline{u}_3^{(m)} = 0$. It follows from (17) that $\underline{u}_2 = \underline{u}_3 = 0$. Thus, it follows from the first equality of (18) that $\bar{u}_1 = 1$.

Substituting $\bar{u}_1 = 1$ into the second equality of (18) and noting that $\mathcal{R}_1 < 1$ yields $\bar{u}_2 = 0$. In view of the third equality of (18), we have $\bar{u}_3 \left(\frac{\beta_2}{1+b+c\bar{u}_3} - \gamma_2 \right) = 0$. Since $\mathcal{R}_2 < 1 + b$, we obtain $\frac{\beta_2}{1+b+c\bar{u}_3} - \gamma_2 < 0$. This implies that $\bar{u}_3 = 0$. Hence, it follows from the first equality of (19) that $\underline{u}_1 = 1$. Therefore, we have $(\bar{u}_1, \bar{u}_2, \bar{u}_3) = (1, 0, 0) = (\underline{u}_1, \underline{u}_2, \underline{u}_3)$. It follows from [27, Theorem 3.2] that for any initial function $\phi = (\phi_1(t, x), \phi_2(t, x), \phi_3(t, x))$ satisfying $\hat{\mathbf{u}} \leq \phi \leq \tilde{\mathbf{u}}$ in Q_0 , the solution $\mathbf{u} \equiv (u_1(t, x), u_2(t, x), u_3(t, x))$ of System (4) satisfies $\lim_{t \rightarrow \infty} \mathbf{u} = (1, 0, 0)$. This completes the proof. \square

4.2. Stability of E_{10} and E_{01} . Next, we consider the stability of the two strong semi-trivial steady states: E_{10} and E_{01} . For the IG prey-only strong semi-trivial steady state E_{10} , we have the following result.

Theorem 4.4. *Consider System (4) with $\mathcal{R}_1 > 1$.*

- (i) *If $-\frac{\beta_2}{\mathcal{R}_1+b} - \beta(1 - \frac{1}{\mathcal{R}_1}) + \gamma_2 < 0$, then E_{10} is unstable.*
- (ii) *If $-\frac{\beta_2}{\mathcal{R}_1+b} - \beta(1 - \frac{1}{\mathcal{R}_1}) + \gamma_2 > 0$ and $1 < \mathcal{R}_1 \leq 3$, then E_{10} is locally asymptotically stable for all $\tau \geq 0$.*
- (iii) *If $-\frac{\beta_2}{\mathcal{R}_1+b} - \beta(1 - \frac{1}{\mathcal{R}_1}) + \gamma_2 > 0$ and $\mathcal{R}_1 > 3$, then there exists $\tau_{00} > 0$ such that E_{10} is locally asymptotically stable for $\tau \in [0, \tau_{00})$ and is unstable for $\tau > \tau_{00}$. Further there exists a sequence of delays, $\{\tau_i^j\}_{j=0}^{+\infty}$ for $i = 1, 2, \dots, N_1$, at which E_{10} undergoes Hopf bifurcations. Here, τ_{00} and τ_i^j are given in the proof of this theorem.*

Proof. For E_{10} , the characteristic equation is

$$m_1(\lambda)[g_1(\lambda) + h_1(\lambda)e^{-\lambda\tau}] = 0, \tag{20}$$

with $m_1(\lambda) = \lambda + d_3\mu_i - \frac{\beta_2}{\mathcal{R}_1+b} - \beta(1 - \frac{1}{\mathcal{R}_1}) + \gamma_2$, $h_1(\lambda) = -(\lambda + d_1\mu_i + \frac{1}{\mathcal{R}_1})\frac{\beta_1}{\mathcal{R}_1} + \frac{\beta_1}{\mathcal{R}_1}(1 - \frac{1}{\mathcal{R}_1})$, and $g_1(\lambda) = (\lambda + d_1\mu_i + \frac{1}{\mathcal{R}_1})(\lambda + d_2\mu_i + \gamma_1)$. Note that $-\frac{\beta_2}{\mathcal{R}_1+b} - \beta(1 - \frac{1}{\mathcal{R}_1}) + \gamma_2 < 0$, there exists $\mu_1 = 0$ such that $-d_3\mu_1 + \frac{\beta_2}{\mathcal{R}_1+b} + \beta(1 - \frac{1}{\mathcal{R}_1}) - \gamma_2 > 0$ holds. Therefore, $m_1(\lambda)$ has at least one zero with a positive real part and the characteristic Eq. (20) has at least one positive root with a positive real part. The proof of (i) is complete.

Denote

$$\bar{E}_1 = d_1\mu_i + \frac{1}{\mathcal{R}_1} > 0, \bar{L}_1 = d_2\mu_i > 0, \quad \bar{J}_1 = \gamma_1(1 - \frac{1}{\mathcal{R}_1}) > 0.$$

Then we have

$$g_1(\lambda) + h_1(\lambda) = \lambda^2 + (\bar{E}_1 + \bar{L}_1)\lambda + \bar{E}_1\bar{L}_1 + \bar{J}_1. \tag{21}$$

Since $\bar{E}_1 + \bar{L}_1 > 0$ and $\bar{E}_1\bar{L}_1 + \bar{J}_1 > 0$, it is easy to see that Eq. (21) has no positive zeros for all μ_i .

Define

$$G(u) \equiv |g_1(i\sqrt{u})|^2 - |h_1(i\sqrt{u})|^2 \\ = u^2 + (\bar{L}_1^2 + 2\bar{L}_1\gamma_1 + \bar{E}_1^2)u + \bar{E}_1^2\bar{L}_1^2 + 2\bar{E}_1\bar{L}_1\gamma_1 - \bar{J}_1^2 + 2\bar{E}_1\gamma_1\bar{J}_1. \tag{22}$$

Since $\bar{L}_1^2 + 2\bar{L}_1\gamma_1 + \bar{E}_1^2$ is positive for all μ_i , if $\mathcal{F}(\mu_i) \equiv \bar{E}_1^2\bar{L}_1^2 + 2\bar{E}_1\bar{L}_1\gamma_1 - \bar{J}_1^2 + 2\bar{E}_1\gamma_1\bar{J}_1 > 0$ then $G(u)$ has no positive zeros.

Next, we discuss the distribution of positive zeros of $G(u)$. Clearly $\mathcal{F}(0) = \frac{\beta_1^2}{\mathcal{R}_1^2}(1 - \frac{1}{\mathcal{R}_1})(\frac{3}{\mathcal{R}_1} - 1)$. If $1 < \mathcal{R}_1 \leq 3$, then $\mathcal{F}(0) \geq 0$. Since $\mathcal{F}(\mu_i) = (d_1\mu_i + \frac{1}{\mathcal{R}_1})^2 d_2^2 \mu_i^2 + 2(d_1\mu_i + \frac{1}{\mathcal{R}_1})^2 d_2\mu_i\gamma_1 + \frac{\beta_1}{\mathcal{R}_1}(1 - \frac{1}{\mathcal{R}_1})[2(d_1\mu_i + \frac{1}{\mathcal{R}_1})\frac{\beta_1}{\mathcal{R}_1} - \frac{\beta_1}{\mathcal{R}_1}(1 - \frac{1}{\mathcal{R}_1})]$ is increasing in

μ_i , we obtain $\mathcal{F}(\mu_i) \geq 0$ for all μ_i . Thus, $G(u)$ has no positive zeros for all μ_i . It follows from [24, Lemma 11] that E_{10} is locally asymptotically stable for all $\tau \geq 0$. This completes the proof of (ii).

If $\mathcal{R}_1 > 3$, then $\mathcal{F}(0) < 0$. Since $\mathcal{F}(\mu_i)$ is increasing in μ_i and $\lim_{i \rightarrow \infty} \mathcal{F}(\mu_i) = \infty$, there exists a constant $n \in \mathbb{N}$ such that

$$\mathcal{F}(\mu_i) \geq 0 \quad \text{for } i > N_1, \quad \text{and } \mathcal{F}(\mu_i) < 0 \quad \text{for } i \leq N_1.$$

This implies that (22) has no positive root for $i > N_1$, has N_1 positive roots for $i \leq N_1$, denoted by u_1, u_2, \dots, u_{N_1} . From (22), we get $u_i = \omega_i^2 = \frac{-Tr_i + \sqrt{Tr_i^2 - 4\delta_i}}{2}$, where $Tr_i = \bar{L}_1^2 + 2\bar{L}_1\gamma_1 + \bar{E}_1^2$, $\delta_i = \bar{E}_1^2\bar{L}_1^2 + 2\bar{E}_1\bar{L}_1\gamma_1 - \bar{J}_1^2 + 2\bar{E}_1\bar{J}_1\gamma_1$. Similar to the argument of [24], we obtain

$$\tau_i^j = \frac{1}{\omega_i} \left\{ \arccos \left(\frac{\mathcal{B}_{1i}}{\sqrt{\mathcal{B}_{1i}^2 + \mathcal{C}_{1i}^2}} \right) + 2j\pi \right\}, \quad i = 1, 2, \dots, N_1, \quad j = 0, 1, 2, \dots,$$

where

$$\begin{aligned} \mathcal{B}_{1i} &= \left(\frac{\beta_1}{\mathcal{R}_1} d_1 \mu_i + \frac{\beta_1}{\mathcal{R}_1^2} - \frac{\beta_1}{\mathcal{R}_1} \left(1 - \frac{1}{\mathcal{R}_1} \right) \left(\left(d_1 \mu_i + \frac{1}{\mathcal{R}_1} \right) (d_2 \mu_i + \gamma_1) - \omega_i^2 \right) + \right. \\ &\quad \left. \frac{\beta_1}{\mathcal{R}_1} \omega_i^2 \left(d_1 \mu_i + d_2 \mu_i + \frac{1}{\mathcal{R}_1} + \gamma_1 \right), \right. \\ \mathcal{C}_{1i} &= - \left(\frac{\beta_1}{\mathcal{R}_1} d_1 \mu_i + \frac{\beta_1}{\mathcal{R}_1^2} - \frac{\beta_1}{\mathcal{R}_1} \left(1 - \frac{1}{\mathcal{R}_1} \right) \right) \left(d_1 \mu_i + d_2 \mu_i + \frac{1}{\mathcal{R}_1} + \gamma_1 \right) \omega_i + \\ &\quad \frac{\beta_1}{\mathcal{R}_1} \omega_i \left(\left(d_1 \mu_i + \frac{1}{\mathcal{R}_1} \right) (d_2 \mu_i + \gamma_1) - \omega_i^2 \right). \end{aligned}$$

Denote

$$\tau_{00} = \min_{i=1,2,\dots,N_1} \{\tau_i^0\}.$$

It follows easily from $-\frac{\beta_2}{\mathcal{R}_1+b} - \beta \left(1 - \frac{1}{\mathcal{R}_1} \right) + \gamma_2 > 0$ that $d_3 \mu_i - \frac{\beta_2}{\mathcal{R}_1+b} - \beta \left(1 - \frac{1}{\mathcal{R}_1} \right) + \gamma_2 > 0$ for all μ_i . Then all zeros of $m_1(\lambda)$ have negative real parts. Since all zeros of $g_1(\lambda) + h_1(\lambda)$ have negative real parts, we conclude that all zeros of Eq. (20) have negative real parts for $\tau = 0$. Since τ_{00} is the minimum value of τ so that Eq. (20) has purely imaginary roots, applying Lemma 1.1 of [39], we get E_{10} is locally asymptotically stable for $\tau \in [0, \tau_{00})$ and is unstable for $\tau > \tau_{00}$. From (22), we obtain $G'(u_i) > 0$ for $i = 1, 2, \dots, N_1$. Thus, E_{10} undergoes a sequence of Hopf bifurcations as τ increases through τ_i^j for $i = 1, 2, \dots, N_1, j = 0, 1, 2, \dots$. This completes the proof of (iii). \square

For the IG predator-only strong semi-trivial steady state E_{01} , we have the following result.

Theorem 4.5. *Consider System (4) with $\mathcal{R}_2 > 1 + b$.*

- (i) *If $\alpha \mathcal{R}_2 \hat{u}_1 (1 - \hat{u}_1) + \gamma_1 < \beta_1 \hat{u}_1$, then E_{01} is unstable.*
- (ii) *If $\alpha \mathcal{R}_2 \hat{u}_1 (1 - \hat{u}_1) + \gamma_1 > \beta_1 \hat{u}_1$ and $b < \hat{u}_1 (\mathcal{R}_2 + b)$, then E_{01} is locally asymptotically stable for all $\tau \geq 0$. Here \hat{u}_1 is defined in Proposition 3.1.*

Proof. For $\mathbf{u}^\diamond = (\hat{u}_1, 0, \mathcal{R}_2(1 - \hat{u}_1)\hat{u}_1)$, we get the characteristic equation

$$m_2(\lambda)g_2(\lambda) = 0, \tag{23}$$

with

$$m_2(\lambda) = (\lambda + d_2 \mu_i + \alpha \hat{u}_3 + \gamma_1 - \beta_1 \hat{u}_1 e^{-\lambda \tau}),$$

and

$$g_2(\lambda) = (\lambda + d_1\mu_i + \hat{u}_1 - \frac{b\hat{u}_1\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2})(\lambda + d_3\mu_i + \gamma_2 - \frac{\beta_2\hat{u}_1(1 + b\hat{u}_1)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}) + \frac{\beta_2\hat{u}_1\hat{u}_3(1 + b\hat{u}_1)(1 + c\hat{u}_3)}{(1 + b\hat{u}_1 + c\hat{u}_3)^4},$$

where

$$\hat{u}_1 = \frac{-(\mathcal{R}_2 - c\mathcal{R}_2 - b) + \sqrt{(\mathcal{R}_2 - c\mathcal{R}_2 - b)^2 + 4c\mathcal{R}_2}}{2c\mathcal{R}_2}, \hat{u}_3 = \mathcal{R}_2(1 - \hat{u}_1)\hat{u}_1.$$

Since $\alpha\mathcal{R}_2\hat{u}_1(1 - \hat{u}_1) + \gamma_1 < \beta_1\hat{u}_1$ and $\hat{u}_3 = \mathcal{R}_2\hat{u}_1(1 - \hat{u}_1)$ then there exists $\mu_1 = 0$ such that $d_2\mu_1 + \alpha\hat{u}_3 + \gamma_1 < \beta_1\hat{u}_1$ holds. Hence, it follows from [24, Lemma 6] that $m_2(\lambda)$ has at least one zero with a positive real part. The proof of (i) is complete.

Denote

$$\bar{E}_2 = d_1\mu_i + \hat{u}_1 - \frac{b\hat{u}_1\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}, \bar{L}_2 = d_3\mu_i + \gamma_2 - \frac{\beta_2\hat{u}_1(1 + b\hat{u}_1)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2},$$

$$\bar{J}_2 = \frac{\beta_2\hat{u}_1\hat{u}_3(1 + b\hat{u}_1)(1 + c\hat{u}_3)}{(1 + b\hat{u}_1 + c\hat{u}_3)^4}.$$

Then we have

$$g_2(\lambda) = \lambda^2 + (\bar{E}_2 + \bar{L}_2)\lambda + \bar{E}_2\bar{L}_2 + \bar{J}_2.$$

Since $\bar{E}_2 + \bar{L}_2 = d_1\mu_i + d_3\mu_i + \hat{u}_1 - \frac{b\hat{u}_1\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2} + \gamma_2 - \frac{\beta_2\hat{u}_1(1 + b\hat{u}_1)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}$ and $\bar{E}_2\bar{L}_2 + \bar{J}_2 = (d_1\mu_i + \hat{u}_1 - \frac{b\hat{u}_1\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2})(d_3\mu_i + \gamma_2 - \frac{\beta_2\hat{u}_1(1 + b\hat{u}_1)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}) + \frac{\beta_2\hat{u}_1\hat{u}_3(1 + b\hat{u}_1)(1 + c\hat{u}_3)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}$. Obviously, $\gamma_2 = \frac{\beta_2\hat{u}_1}{1 + b\hat{u}_1 + c\hat{u}_3} > \frac{\beta_2\hat{u}_1(1 + b\hat{u}_1)}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}$. Since $b < \hat{u}_1(\mathcal{R}_2 + b)$, we have $b\hat{u}_3 < \mathcal{R}_2^2\hat{u}_1^2$. Noting that $\mathcal{R}_2\hat{u}_1 = 1 + b\hat{u}_1 + c\hat{u}_3$, we obtain $\frac{b\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2} < 1$. This implies $\hat{u}_1 > \frac{b\hat{u}_1\hat{u}_3}{(1 + b\hat{u}_1 + c\hat{u}_3)^2}$. Thus $g_2(\lambda)$ has no nonnegative zeros for all $\tau \geq 0$. It follows from $\alpha\mathcal{R}_2\hat{u}_1(1 - \hat{u}_1) + \gamma_1 > \beta_1\hat{u}_1$ that all roots of $m_2(\lambda)$ have negative real parts. Thus all zeros of Eq. (23) have negative real parts for all μ_i , and hence E_{01} is locally asymptotically stable. This completes the proof of (ii). \square

4.3. Stability of the unique positive spatially homogenous steady state E^* .

4.3.1. *Stability and Hopf bifurcation.* In this subsection, by taking τ as the bifurcation parameter, we investigate the stability and the Hopf bifurcation near the unique positive spatially homogeneous steady state E^* . For this purpose, we always assume

$$(H_1) \quad q < 0 \text{ and } \mathcal{R}_2 < \frac{(b\alpha + c\beta_1)(-p + \sqrt{p^2 - 4q}) + 2(b\gamma_1 + \beta_1)}{\alpha(-p + \sqrt{p^2 - 4q}) + 2\gamma_1}.$$

The above assumption guarantees the uniqueness of the positive spatially homogeneous steady state E^* . For the spatially homogeneous positive steady state $E^* = (u_1^*, u_2^*, u_3^*)$, the characteristic equation is given below:

$$\lambda^3 + b_{2i}\lambda^2 + b_{1i}\lambda + b_{0i} + e^{-\lambda\tau}(c_2\lambda^2 + c_{1i}\lambda + c_{0i}) = 0, \tag{24}$$

where

$$b_{2i} = d_1\mu_i + d_2\mu_i + d_3\mu_i + u_1^* - bA_3 + \beta_1u_1^* + c\beta_2A_3,$$

$$b_{1i} = (d_1\mu_i + u_1^* - bA_3)(d_2\mu_i + \beta_1u_1^* + d_3\mu_i + c\beta_2A_3) + (d_2\mu_i + \beta_1u_1^*)(d_3\mu_i + c\beta_2A_3) + \alpha\beta u_2^*u_3^* + A_1A_2\beta_2u_1^*u_3^*,$$

$$\begin{aligned}
b_{0i} &= (d_1\mu_i + u_1^* - bA_3)(d_2\mu_i + \beta_1u_1^*)(d_3\mu_i + c\beta_2A_3) + (d_1\mu_i + u_1^* - bA_3)\alpha\beta u_2^*u_3^* \\
&\quad - \alpha\beta_2A_2u_1^*u_2^*u_3^* + (d_2\mu_i + \beta_1u_1^*)A_1A_2\beta_2u_1^*u_3^*, \\
c_2 &= -\beta_1u_1^*, \\
c_{1i} &= \beta_1u_1^*u_2^* - \beta_1u_1^*(d_1\mu_i + d_3\mu_i + u_1^* - bA_3 + c\beta_2A_3), \\
c_{0i} &= -d_1d_3\beta_1u_1^*\mu_i^2 + d_3\mu_i\beta_1u_1^*u_2^* - d_1\mu_i c\beta_2A_3\beta_1u_1^* - d_3\mu_i(u_1^* - bA_3)\beta_1u_1^* + \\
&\quad (c\beta_2A_3 + A_1\beta u_3^*)\beta_1u_1^*u_2^* - (u_1^* - bA_3)c\beta_2A_3\beta_1u_1^* - A_1A_2\beta_2u_1^*u_3^*\beta_1u_1^*, \\
A_1 &= \frac{1+bu_1^*}{(1+bu_1^*+cu_3^*)^2}, A_2 = \frac{1+cu_3^*}{(1+bu_1^*+cu_3^*)^2}, A_3 = \frac{u_1^*u_3^*}{(1+bu_1^*+cu_3^*)^2}.
\end{aligned}$$

Denote $M_1 = u_1^* - bA_3$, $M_2 = \beta_1u_1^*$, $M_3 = c\beta_2A_3$, $M_4 = \alpha\beta u_2^*u_3^*$, $M_5 = A_1A_2\beta_2u_1^*u_3^*$, $M_6 = \alpha\beta_2A_2u_1^*u_2^*u_3^*$, $M_7 = A_1\beta u_2^*u_3^*$. Clearly, $M_i > 0$ for $i = 2, 3, 4, 5, 6, 7$.

Furthermore, we assume that

$$\begin{aligned}
(H_2) \quad &M_1 > 0. \\
(H_3) \quad &M_6 - M_2M_7 > 0. \\
(H_4) \quad &M_1M_4 + M_2M_3u_2^* + M_2M_7 - M_6 > 0. \\
(H'_3) \quad &M_6 - M_2M_7 \leq 0. \\
(H'_4) \quad &M_1(M_1M_3 + M_5 + u_2^*M_2) + M_3(M_1M_3 + M_4 + M_5) + M_6 - M_2M_7 > 0.
\end{aligned}$$

Theorem 4.6. (i) Assume that $(H_1) - (H_4)$ hold. Then the spatially homogeneous positive steady state E^* of System (4) with $\tau = 0$ is locally asymptotically stable.

(ii) Assume that $(H_1) - (H_2)$ and $(H'_3) - (H'_4)$ hold. Then the spatially homogeneous positive steady state E^* of System (4) with $\tau = 0$ is locally asymptotically stable.

Proof. When $\tau = 0$, (24) reduces to the following equation

$$\lambda^3 + (b_{2i} + c_2)\lambda^2 + (b_{1i} + c_{1i})\lambda + b_{0i} + c_{0i} = 0. \quad (25)$$

Since $M_1 > 0$, a direct calculation yields

$$b_{2i} + c_2 = (d_1 + d_2 + d_3)\mu_i + M_1 + M_3 > 0.$$

$$\begin{aligned}
b_{1i} + c_{1i} &= (d_1d_2 + d_1d_3 + d_2d_3)\mu_i^2 + (M_3d_1 + M_3d_2 + M_1d_2 + M_1d_3)\mu_i + M_1M_3 + \\
&\quad M_4 + M_5 + u_2^*M_2 > 0.
\end{aligned}$$

$$\begin{aligned}
b_{0i} + c_{0i} &= d_1d_2d_3\mu_i^3 + (M_3d_1d_2 + M_1d_2d_3)\mu_i^2 + \\
&\quad (M_2u_2^*d_3 + M_1M_3d_2 + M_4d_1 + M_5d_2)\mu_i + M_1M_4 + M_2M_3u_2^* + \\
&\quad M_2M_7 - M_6.
\end{aligned}$$

$$\begin{aligned}
(b_{2i} + c_2)(b_{1i} + c_{1i}) - (b_{0i} + c_{0i}) &= d_1\mu_i(b_{1i} + c_{1i} - d_2d_3\mu_i^2 - M_3d_2\mu_i - M_4) + \\
&\quad d_3\mu_i(b_{1i} + c_{1i} - u_2^*M_2) + \\
&\quad d_2\mu_i(b_{1i} + c_{1i} - M_1d_3\mu_i - M_1M_3 - M_5) + \\
&\quad M_1(b_{1i} + c_{1i} - M_4) + M_3(b_{1i} + c_{1i} - u_2^*M_2) + \\
&\quad M_6 - M_2M_7.
\end{aligned}$$

Since $b_{1i} + c_{1i} - d_2d_3\mu_i^2 - M_3d_2\mu_i - M_4 > 0$, $b_{1i} + c_{1i} - u_2^*M_2 > 0$, $b_{1i} + c_{1i} - M_1d_3\mu_i - M_1M_3 - M_5 > 0$, $b_{1i} + c_{1i} - M_4 > 0$, $b_{1i} + c_{1i} - u_2^*M_2 > 0$, it follows from (H_3) that $(b_{2i} + c_2)(b_{1i} + c_{1i}) - (b_{0i} + c_{0i}) > 0$ for all μ_i .

It follows from (H_2) and (H_4) that $b_{0i} + c_{0i} > 0$ for all μ_i . Thus, by the Routh-Hurwitz stability criterion, all the roots of (25) have negative real parts. This completes the proof of part (i). Similarly, noting that $(b_{2i} + c_2)(b_{1i} + c_{1i}) - (b_{0i} + c_{0i})$ is increasing in μ_i under (H_2) , we can prove part (ii). \square

Next, we discuss the effect of the delay $\tau \neq 0$ on the stability of the positive steady state E^* . We first determine critical values of τ at which a pair of simple purely imaginary eigenvalues appears.

Let $\lambda = i\omega$ ($\omega > 0$) be a root of Eq. (24). Substituting $\lambda = i\omega$ into Eq. (24) yields

$$-i\omega^3 - b_{2i}\omega^2 + ib_{1i}\omega + b_{0i} + (-c_2\omega^2 + i\omega c_{1i} + c_{0i})e^{-i\omega\tau} = 0,$$

which implies that

$$b_{2i}\omega^2 - b_{0i} = (c_{0i} - c_2\omega^2) \cos \omega\tau + c_{1i}\omega \sin \omega\tau, \tag{26}$$

$$-\omega^3 + b_{1i}\omega = (c_{0i} - c_2\omega^2) \sin \omega\tau - c_{1i}\omega \cos \omega\tau. \tag{27}$$

It follows from (26) and (27) that

$$\omega^6 + (b_{2i}^2 - 2b_{1i} - c_2^2)\omega^4 + (b_{1i}^2 - 2b_{0i}b_{2i} + 2c_{0i}c_2 - c_{1i}^2)\omega^2 + b_{0i}^2 - c_{0i}^2 = 0. \tag{28}$$

Let $\omega^2 = s$, and denote $p_i = b_{2i}^2 - 2b_{1i} - c_2^2$, $q_i = b_{1i}^2 - 2b_{0i}b_{2i} + 2c_{0i}c_2 - c_{1i}^2$, $r_i = b_{0i}^2 - c_{0i}^2$. Then (28) is reduced to

$$h(s) \equiv s^3 + p_i s^2 + q_i s + r_i = 0. \tag{29}$$

From (24), we get

$$p_i = (d_1^2 + d_2^2 + d_3^2)\mu_i^2 + 2(M_1d_1 + M_2d_2 + M_3d_3)\mu_i + M_1^2 + M_3^2 - 2M_4 - 2M_5,$$

$$b_{0i} - c_{0i} = d_1d_2d_3\mu_i^3 + (d_1d_2M_3 + d_2d_3M_1 + 2d_1d_3M_2)\mu_i^2 + (2d_1M_2M_3 + d_2M_1M_3 + 2d_3M_1M_2 + d_1M_4 + d_2M_5 - d_3u_2^*M_2)\mu_i + 2M_1M_2M_3 + 2M_2M_5 + M_1M_4 - u_2^*M_2M_3 - M_2M_7 - M_6.$$

In the following, we need to seek conditions required for Eq. (29) to have at least one positive root. For this purpose, we further make the following hypotheses: (H_5) $2M_1M_2M_3 + 2M_2M_5 + M_1M_4 - u_2^*M_2M_3 - M_2M_7 - M_6 < 0$.

$$(H_6) \quad 2d_1M_2M_3 + d_2M_1M_3 + 2d_3M_1M_2 + d_1M_4 + d_2M_5 - d_3u_2^*M_2 \geq 0.$$

Since $b_{0i} - c_{0i}$ is increasing in μ_i under (H_2) and (H_6) , it follows from (H_5) that there exists $N_2 \in \mathbb{N}$ such that

$$b_{0i} - c_{0i} < 0 \quad \text{for } 1 \leq i \leq N_2 \quad \text{and} \quad b_{0i} - c_{0i} \geq 0 \quad \text{for } i \geq N_2 + 1, \quad i \in \mathbb{N}.$$

According to the above analysis, we have the following lemma.

Lemma 4.7. (i) Assume that $(H_2), (H_4) - (H_6)$ hold. Then Eq. (29) has at least one positive root for each $i \in \{1, 2, \dots, N_2\}$.

(ii) Assume that and $(H_2), (H_3')$ and $(H_5) - (H_6)$ hold. Then Eq. (29) has at least one positive root for each $i \in \{1, 2, \dots, N_2\}$.

Proof. It follows from (H_2) and (H_4) that $b_{0i} + c_{0i} > 0$ for all $i \in \mathbb{N}$. Thus $r_i < 0$ if and only if $b_{0i} - c_{0i} < 0$. It follows from $(H_2), (H_5)$ and (H_6) that there exists μ_i ($i = 1, 2, \dots, N_2$) such that $r_i < 0$. Since $\lim_{s \rightarrow \infty} h(s) = \infty$ for fixed μ_i , then (29) has at least one positive root for each $i \in \{1, 2, \dots, N_2\}$. This completes proof of part (i). Similarly, we can prove part (ii). \square

Remark 3. From Lemma 4.2, without loss of generality, for each $i, 1 \leq i \leq N_2$, we may assume that it has three positive roots, which are denoted by $s_{1,i}, s_{2,i}, s_{3,i}$, respectively. Then for each $i, 1 \leq i \leq N_2$, (18) has three positive roots $\omega_{k,i} = \sqrt{s_{k,i}}, k = 1, 2, 3$. By (26) and (27), we get

$$\cos \omega_{k,i} \tau_{k,i} = \frac{(c_{1i} - b_{2i}c_2)\omega_{k,i}^4 + (b_{2i}c_{0i} + b_{0i}c_2 - c_{1i}b_{1i})\omega_{k,i}^2 - b_{0i}c_{0i}}{(c_{0i} - c_2\omega_{k,i}^2)^2 + c_{1i}^2\omega_{k,i}^2}.$$

Let

$$\tau_{k,j}^i = \frac{\left(\arccos \left(\frac{(c_{1i} - b_{2i}c_2)\omega_{k,i}^4 + (b_{2i}c_{0i} + b_{0i}c_2 - c_{1i}b_{1i})\omega_{k,i}^2 - b_{0i}c_{0i}}{(c_{0i} - c_2\omega_{k,i}^2)^2 + c_{1i}^2\omega_{k,i}^2} \right) \right) + 2j\pi}{\omega_{k,i}} \quad (30)$$

for $1 \leq i \leq N_2, k = 1, 2, 3, j = 0, 1, 2, \dots$. Then $\pm i\omega_{k,i}$ is a pair of purely imaginary roots of (28) with $\tau = \tau_{k,j}^i$. Define

$$\tau^* = \tau_{k_0,0}^{i_0} = \min_{k=1,2,3, i=1,2,\dots,N_2} \tau_{k,0}^i, \quad \omega^* = \omega_{k_0,i_0}. \quad (31)$$

Lemma 4.8. *Let $\lambda(\tau) = \alpha(\tau) \pm i\beta(\tau)$ be the roots of Eq. (14) near $\tau = \tau^*$ satisfying $\alpha(\tau^*) = 0, \beta(\tau^*) = \omega^*$. Suppose that $h'((\omega^*)^2) > 0$. Then $\pm i\omega^*$ is a pair of simple purely imaginary roots of Eq. (24). Moreover, the following transversality condition holds:*

$$\text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\}_{\tau=\tau^*, \lambda=i\omega^*} > 0.$$

Proof. We denote $P(\lambda) = \lambda^3 + b_{2i}\lambda^2 + b_{1i}\lambda + b_{0i}, Q(\lambda) = c_2\lambda^2 + c_{1i}\lambda + c_{0i}$. Then (24) can be rewritten as

$$P(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0. \quad (32)$$

It is easy to know (26) and (27) are equivalent to the following equations

$$\begin{aligned} \text{Re}P(i\omega) &= -\text{Re}Q(i\omega) \cos \omega\tau - \text{Im}Q(i\omega) \sin \omega\tau, \\ \text{Im}P(i\omega) &= \text{Re}Q(i\omega) \sin \omega\tau - \text{Im}Q(i\omega) \cos \omega\tau. \end{aligned}$$

Thus

$$h(\omega^2) = (\text{Re}P(i\omega))^2 + (\text{Im}P(i\omega))^2 - ((\text{Re}Q(i\omega))^2 + (\text{Im}Q(i\omega))^2). \quad (33)$$

Differentiating both sides of (33) with respect to ω yields

$$2\omega h'(\omega^2) = i[P'(i\omega)\bar{P}(i\omega) - \bar{P}'(i\omega)P(i\omega) - Q'(i\omega)\bar{Q}(i\omega) + \bar{Q}'(i\omega)Q(i\omega)]. \quad (34)$$

Substituting $i\omega^*$ into (32) yields

$$|P(i\omega^*)| = |Q(i\omega^*)|. \quad (35)$$

If $i\omega^*$ is not simple, then $i\omega^*$ must satisfy $P'(i\omega^*) + [Q'(i\omega^*) - \tau^*Q(i\omega^*)]e^{-i\omega^*\tau^*} = 0$. Note that $e^{-i\omega^*\tau^*} = -P(i\omega^*)/Q(i\omega^*)$, we obtain $\tau^* = \frac{Q'(i\omega^*)}{Q(i\omega^*)} - \frac{P'(i\omega^*)}{P(i\omega^*)}$. Using (34) and (35), we have

$$\begin{aligned} \text{Im}\tau^* &= \text{Im} \left[\frac{Q'(i\omega^*)}{Q(i\omega^*)} - \frac{P'(i\omega^*)}{P(i\omega^*)} \right] = \text{Im} \left[\frac{Q'(i\omega^*)\bar{Q}(i\omega^*)}{Q(i\omega^*)\bar{Q}(i\omega^*)} - \frac{P'(i\omega^*)\bar{P}(i\omega^*)}{P(i\omega^*)\bar{P}(i\omega^*)} \right] \\ &= \frac{1}{Q(i\omega^*)\bar{Q}(i\omega^*)} \text{Im} [Q'(i\omega^*)\bar{Q}(i\omega^*) - P'(i\omega^*)\bar{P}(i\omega^*)] \\ &= \frac{Q'(i\omega^*)\bar{Q}(i\omega^*) - P'(i\omega^*)\bar{P}(i\omega^*) - \bar{Q}'(i\omega^*)Q(i\omega^*) + \bar{P}'(i\omega^*)P(i\omega^*)}{2i|Q(i\omega^*)|^2} \\ &= \frac{\omega^* h'((\omega^*)^2)}{|Q(i\omega^*)|^2}. \end{aligned}$$

This is a contradiction. Thus $\pm i\omega^*$ is a pair of simple purely imaginary roots of Eq. (24).

Since $\pm i\omega^*$ are simple purely imaginary roots and

$$P'(i\omega^*) + [Q'(i\omega^*) - \tau^*Q(i\omega^*)]e^{-i\omega^*\tau^*} \neq 0,$$

we may consider $\lambda = \lambda(\tau)$ to be a differentiable function. Differentiating (22) with respect to τ yields

$$\frac{d\lambda(\tau)}{d\tau} = \frac{\lambda Q(\lambda)}{P'(\lambda)e^{\lambda\tau} + Q'(\lambda) - \tau Q(\lambda)}.$$

Using (32) again, we obtain

$$\left(\frac{d\lambda(\tau)}{d\tau}\right)^{-1} = -\frac{P'(\lambda)}{\lambda P(\lambda)} + \frac{Q'(\lambda)}{\lambda Q(\lambda)} - \frac{\tau}{\lambda}. \tag{36}$$

Thus, from (36), we have

$$\begin{aligned} \text{sign} \left\{ \frac{d(\text{Re}\lambda(\tau))}{d\tau} \right\}_{\tau=\tau^*, \lambda=i\omega^*} &= \text{sign} \left\{ \text{Re} \left[-\frac{P'(\lambda)}{\lambda P(\lambda)} + \frac{Q'(\lambda)}{\lambda Q(\lambda)} - \frac{\tau}{\lambda} \right] \right\}_{\tau=\tau^*, \lambda=i\omega^*} \\ &= \text{sign} \left\{ \text{Re} \bar{\lambda} [Q'(\lambda)Q(\bar{\lambda}) - P'(\lambda)P(\bar{\lambda})] \right\}_{\lambda=i\omega^*} \\ &= \text{sign} \left\{ (\omega^*)^2 h'((\omega^*)^2) \right\} > 0. \end{aligned}$$

This completes the proof. □

When $\tau \in [0, \tau^*)$, we know that (24) has no roots on the imaginary axis. By the eigenvalue theory of [39], the sum of orders of the zeros of Eq. (24) for $\tau \in [0, \tau^*)$ is equal to Eq. (25). Then Eq. (24) only has negative real part roots for $\tau \in [0, \tau^*)$, which implies that (u_1^*, u_2^*, u_3^*) is locally asymptotically stable for $\tau \in [0, \tau^*)$. Combining Theorem 4.6, Lemma 4.7 and Lemma 4.8, we arrive the following theorem.

Theorem 4.9. *Assume that either $(H_1) - (H_6)$ or $(H_1), (H_2), (H_3), (H_4), (H_5), (H_6)$ hold. We have the following results*

- (i) *The spatially homogeneous positive steady state $E^* = (u_1^*, u_2^*, u_3^*)$ of System (4) is locally asymptotically stable for $\tau \in [0, \tau^*)$ and unstable when $\tau > \tau^*$, where τ^* is defined in (31).*
- (ii) *Furthermore, suppose that $h'((\omega^*)^2) > 0$. Then System (4) undergoes Hopf bifurcation at the positive steady state $E^* = (u_1^*, u_2^*, u_3^*)$ when $\tau = \tau_{k,j}^i$, i.e., a family of spatially periodic solutions bifurcate from $E^* = (u_1^*, u_2^*, u_3^*)$ when τ crosses through the critical values $\tau_{k,j}^i$, where $\tau_{k,j}^i$ is defined in (30).*

Remark 4. There exist parameter values such that hypotheses $(H_1) - (H_6)$ hold. For example, we choose parameter values $\alpha = 0.7, \beta = 0.9, \beta_1 = 1.95, \beta_2 = 1.8, \gamma_1 = 0.2, \gamma_2 = 0.8, b = 2.5, c = 12, d_1 = 0.25, d_2 = 0.28, d_3 = 0.2$. Using any CAS, it is easy to check that hypotheses $(H_1) - (H_6)$ are satisfied.

4.3.2. Properties of Hopf bifurcations. In this section, we investigate the direction of Hopf bifurcation and the stability of bifurcated periodic solutions by using the normal form theory and center manifold reduction. For convenience, for fixed $k \in \{1, 2, 3\}, j = 0, 1, 2, \dots$, we denote $\tau_{k,j}^i (1 \leq i \leq N_2)$ by $\hat{\tau}$, and denote $\omega_{k,i} (1 \leq i \leq N_2)$ by $\hat{\omega}$.

Let $\tau = \hat{\tau} + \mu, \mu \in \mathbb{R}$ and $\tilde{u}_1(t, \cdot) = u_1(\tau t, \cdot) - u_1^*, \tilde{u}_2(t, \cdot) = u_2(\tau t, \cdot) - u_2^*, \tilde{u}_3(t, \cdot) = u_3(\tau t, \cdot) - u_3^*$ and $\tilde{U}(t) = (\tilde{u}_1(t, \cdot), \tilde{u}_2(t, \cdot), \tilde{u}_3(t, \cdot))$ as $u_1 - u_1^*, u_2 - u_2^*, u_3 - u_3^*$, then

drop the tildes for simplicity. System (1.4) can be rewritten in the phase space $\mathcal{C} = C([-1, 0], X)$ as

$$\dot{U}(t) = \hat{\tau}D\Delta U(t) + L(\hat{\tau})(U_t) + F(U_t, \mu), \quad (37)$$

where $D = \text{diag}\{d_1, d_2, d_3\}$, $L(\delta)(\cdot) : \mathcal{C} \rightarrow X$ and $F : \mathcal{C} \times R \rightarrow X$ are given by

$$L(\delta)\phi = \delta \begin{bmatrix} \left(\frac{bu_1^*u_3^*}{(1+bu_1^*+cu_3^*)^2} - u_1^* \right) \phi_1(0) - u_1^* \phi_2(0) - \frac{(1+bu_1^*)u_1^*}{(1+bu_1^*+cu_3^*)^2} \phi_3(0) \\ \beta_1 u_2^* \phi_1(-1) + \beta_1 u_1^* \phi_2(-1) - \beta_1 u_1^* \phi_2(0) - \alpha u_2^* \phi_3(0) \\ \frac{\beta_2(1+cu_3^*)u_3^*}{(1+bu_1^*+cu_3^*)^2} \phi_1(0) + \beta u_3^* \phi_2(0) - \frac{c\beta_2 u_1^* u_3^*}{(1+bu_1^*+cu_3^*)^2} \phi_3(0) \end{bmatrix}$$

and

$$F(\phi, \mu) = \mu D\Delta\phi(0) + L(\mu)\phi + f(\phi, \mu),$$

where

$$f(\phi, \mu) = (\hat{\tau} + \mu) \times \begin{bmatrix} \left(\phi_1(0) + u_1^* \right) \left(-\phi_1(0) - \phi_2(0) - \frac{\phi_3(0) + u_3^*}{1+b(\phi_1(0)+u_1^*)+c(\phi_3(0)+u_3^*)} + \frac{u_3^*}{1+bu_1^*+cu_3^*} \right) - \left(\frac{bu_1^*u_3^*}{(1+bu_1^*+cu_3^*)^2} - u_1^* \right) \phi_1(0) - u_1^* \phi_2(0) - \frac{(1+bu_1^*)u_1^*}{(1+bu_1^*+cu_3^*)^2} \phi_3(0) \\ \beta_1 \phi_1(-1) \phi_2(-1) - \alpha \phi_2(0) \phi_3(0) \\ \left(\phi_3(0) + u_3^* \right) \left(\frac{\beta_2(\phi_1(0)+u_1^*)}{1+b(\phi_1(0)+u_1^*)+c(\phi_3(0)+u_3^*)} + \beta \phi_2(0) - \frac{\beta_2 u_1^*}{1+bu_1^*+cu_3^*} \right) - \left(\frac{\beta_2(1+cu_3^*)u_3^*}{(1+bu_1^*+cu_3^*)^2} \phi_1(0) + \beta u_3^* \phi_2(0) - \frac{c\beta_2 u_1^* u_3^*}{(1+bu_1^*+cu_3^*)^2} \phi_3(0) \right) \end{bmatrix}$$

for $\phi = (\phi_1, \phi_2, \phi_3) \in \mathcal{C}$. Let \mathcal{A} to be the infinitesimal generator of the semigroup induced by the solution of the linearized equation of (37)

$$\dot{U}(t) = \hat{\tau}D\Delta U(t) + L(\hat{\tau})(U_t).$$

Thus Eq. (37) can be written in the following abstract form

$$\frac{dU_t}{dt} = \mathcal{A}U_t + X_0 F(U_t, \mu),$$

where $X_0(\theta) = \begin{cases} 0, \theta \in [-1, 0), \\ I, \theta = 0. \end{cases}$ Recall that the Banach space decomposition $\mathbf{X} =$

$\bigoplus_{i=0}^{\infty} \mathbf{X}_i$. In view of the Resiz representation theorem, there exists a 3×3 matrix function $\eta(\theta, \hat{\tau})$ ($-1 \leq \theta \leq 0$), whose entries are bounded variation such that

$$-\hat{\tau}D\mu_i\phi(0) + L(\hat{\tau})(\phi) = \int_{-1}^0 d[\eta(\theta, \hat{\tau})]\phi(\theta),$$

for $\phi \in C([-1, 0], R^3)$. We can choose

$$\eta(\theta, \hat{\tau}) = \hat{\tau} \begin{bmatrix} -d_1\mu_i + \frac{bu_1^*u_3^*}{(1+bu_1^*+cu_3^*)^2} - u_1^* & -u_1^* & -\frac{(1+bu_1^*)u_1^*}{(1+bu_1^*+cu_3^*)^2} \\ 0 & -d_2\mu_i - \beta_1 u_1^* & -\alpha u_2^* \\ \frac{\beta_2(1+cu_3^*)u_3^*}{(1+bu_1^*+cu_3^*)^2} & \beta u_3^* & -d_3\mu_i - \frac{c\beta_2 u_1^* u_3^*}{(1+bu_1^*+cu_3^*)^2} \end{bmatrix} \\ \times \delta(\theta) + \hat{\tau} \begin{bmatrix} 0 & 0 & 0 \\ -\beta_1 u_2^* & -\beta_1 u_1^* & 0 \\ 0 & 0 & 0 \end{bmatrix} \delta(\theta + 1),$$

where δ is a Dirac delta function.

Let us define $C^* = C([0, 1], \mathbb{R}^{3*})$, where \mathbb{R}^{3*} is the 3-dimensional vector space of row vectors, \mathcal{A}^* with domain dense in C^* and range in C^* . Let \mathcal{P} and \mathcal{P}^* be the center subspace, that is, the generalized eigenspace of \mathcal{A} and \mathcal{A}^* associated with $\Lambda^* = \{i\hat{\omega}\hat{\tau}, -i\hat{\omega}\hat{\tau}\}$.

For $\Phi \in C([-1, 0], R^3), \Psi \in C([0, 1], R^{3*})$, we define

$$\mathcal{A}(\Phi(\theta)) = \begin{cases} \frac{d\Phi(\theta)}{d\theta}, & \theta \in [-1, 0), \\ \int_{-1}^0 [d\eta(\theta, \hat{\tau})]\Phi(\theta), & \theta = 0, \end{cases}$$

and

$$\mathcal{A}^*(\Psi(s)) = \begin{cases} -\frac{d\Psi(s)}{ds}, & s \in (0, 1], \\ \int_{-1}^0 \Psi(-\theta)[d\eta(\theta, \hat{\tau})], & s = 1. \end{cases}$$

Then \mathcal{A}^* is the formal adjoint of \mathcal{A} under the bilinear pairing

$$\begin{aligned} \langle \psi, \phi \rangle &= \psi(0)\phi(0) - \int_{-1}^0 \int_0^\theta \psi(\xi - \theta)d[\eta(\theta, \hat{\tau})]\phi(\xi)d\xi \\ &= \bar{\psi}(0)\phi(0) + \hat{\tau} \int_{-1}^0 \bar{\psi}(\xi + 1) \begin{bmatrix} 0 & 0 & 0 \\ \beta_1 u_2^* & \beta_1 u_1^* & 0 \\ 0 & 0 & 0 \end{bmatrix} \phi(\xi)d\xi, \end{aligned}$$

for $\phi \in C([-1, 0], R^3), \psi \in C([0, 1], R^{3*})$.

In view of the definition of the two infinitesimal generators \mathcal{A} and \mathcal{A}^* , we have the following conclusions.

Lemma 4.10. *Let*

$$\begin{aligned} \eta_1 &= \frac{(d_3\mu_i + M_3)(G_2^2 + H_2^2) - \beta u_3^*(G_1G_2 + H_1H_2)}{u_3^*\beta_2 A_2(G_2^2 + H_2^2)} + \\ &\quad i \frac{(\hat{\omega}(G_2^2 + H_2^2) - \beta u_3^*(G_2H_1 - G_1H_2))}{u_3^*\beta_2 A_2(G_2^2 + H_2^2)}, \\ \eta_1^* &= \frac{-\alpha u_2^*(G_3G_4 + H_3H_4) - (d_3\mu_i + M_3)(G_4^2 + H_4^2)}{u_1^*A_1(G_4^2 + H_4^2)} - \\ &\quad i \frac{\alpha u_2^*(G_4H_3 - G_3H_4) + \hat{\omega}(G_4^2 + H_4^2)}{u_1^*A_1(G_4^2 + H_4^2)}, \\ \eta_2 &= \frac{G_1G_2 + H_1H_2 + i(G_2H_1 - G_1H_2)}{G_2^2 + H_2^2}, \eta_2^* = \frac{G_3G_4 + H_3H_4 + i(G_4H_3 - G_3H_4)}{G_4^2 + H_4^2}, \end{aligned}$$

where $G_i, H_i (i = 1, 2, 3, 4)$ are defined as follows

$$\begin{aligned} G_1 &= M_5 - \hat{\omega} + (d_1\mu_i + M_1)(d_3\mu_i + M_3), & H_1 &= \hat{\omega}(d_1\mu_i + M_1 + d_3\mu_i + M_3), \\ G_2 &= \beta u_3^*d_1\mu_i + \beta M_1 u_3^* - \beta_2 u_1^* u_3^* A_2, & H_2 &= \beta u_3^* \hat{\omega}, \\ G_3 &= -M_5 - (d_3\mu_i + M_3)(d_1\mu_i + M_1) + (\hat{\omega})^2, & H_3 &= -\hat{\omega}(d_3\mu_i + M_3) - \hat{\omega}(d_1\mu_i + M_1), \\ G_4 &= u_2^* A_1 M_2 \cos \hat{\omega}\hat{\tau} + \alpha u_2^*(d_1\mu_i + M_1), & H_4 &= -u_2^* A_1 M_2 \sin \hat{\omega}\hat{\tau} + \alpha u_2^* \hat{\omega}. \end{aligned}$$

Then

$p(\theta) = e^{i\hat{\omega}\hat{\tau}\theta}(\eta_1, \eta_2, 1)^T$ is the eigenfunction of \mathcal{A} with respect to $i\hat{\omega}\hat{\tau}$;

$p^*(s) = e^{-i\hat{\omega}\hat{\tau}s}(\eta_1^*, \eta_2^*, 1)$ is the eigenfunction of \mathcal{A}^* with respect to $i\hat{\omega}\hat{\tau}$.

Proof. The proof is standard and we omit it here. □

Clearly, from Lemma 4.10, we know the center subspace of Eq. (37) is

$$\mathcal{P} = \text{span}\{p(\theta), \bar{p}(\bar{\theta})\}, \mathcal{P}^* = \text{span}\{p^*(s), \bar{p}^*(\bar{s})\}.$$

Then \mathcal{C} can be decomposed as $\mathcal{C} = \mathcal{P} \oplus \mathcal{Q}$, where

$$\mathcal{Q} = \{\psi \in \mathcal{C} : \langle \widehat{\psi}, \psi \rangle = 0 \text{ for all } \widehat{\psi} \in \mathcal{P}^*\}.$$

It follows from Lemma 4.12 that

$$\begin{aligned} \langle p^*(s), p(\theta) \rangle &= p^*(0)p(0) + \\ &\hat{\tau} \int_{-1}^0 e^{-i\hat{\omega}\hat{\tau}(\xi+1)} (\bar{\eta}_1^*, \bar{\eta}_2^*, 1) \begin{bmatrix} 0 & 0 & 0 \\ \beta_1 u_2^* & \beta_1 u_1^* & 0 \\ 0 & 0 & 0 \end{bmatrix} (\eta_1, \eta_2, 1)^T e^{i\hat{\omega}\hat{\tau}\xi} d\xi \\ &= \bar{\eta}_1^* \eta_1 + \bar{\eta}_2^* \eta_2 + 1 + \beta_1 u_2^* \hat{\tau} e^{-i\hat{\omega}\hat{\tau}} \eta_1 \bar{\eta}_2^* + \beta_1 u_1^* \hat{\tau} e^{-i\hat{\omega}\hat{\tau}} \eta_2 \bar{\eta}_2^*. \end{aligned}$$

Thus we choose $\mathfrak{D} = 1/(\bar{\eta}_1^* \eta_1 + \bar{\eta}_2^* \eta_2 + 1 + \beta_1 u_2^* \hat{\tau} e^{-i\hat{\omega}\hat{\tau}} \eta_1 \bar{\eta}_2^* + \beta_1 u_1^* \hat{\tau} e^{-i\hat{\omega}\hat{\tau}} \eta_2 \bar{\eta}_2^*)$. Let $\Phi = (p(\theta), \bar{p}(\theta))$, $\Psi = \mathfrak{D}(p^*(s), \bar{p}^*(s))^T \equiv (q(s), \bar{q}(s))^T$, then $\langle \Psi, \Phi \rangle = I$, where I is the identity matrix in $\mathbb{R}^{2 \times 2}$.

In what follows, in order to determine the bifurcation direction and stability, we compute the coordinates to describe the center manifold \mathcal{C}_0 . As the formulas to be developed for the bifurcation direction and stability are all relative to $\mu = 0$ only, we set $\mu = 0$ in Eq. (4.24) and obtain a center manifold

$$W(z, \bar{z})(\theta) = W_{20}(\theta) \frac{z^2}{2} + W_{11}(\theta) z\bar{z} + W_{02}(\theta) \frac{\bar{z}^2}{2} + \dots \quad (38)$$

with the range in \mathcal{Q} . The flow of Eq. (4.24) on the center manifold can be written as

$$U_t = \Phi \cdot (z(t), \bar{z}(t))^T + W(z(t), \bar{z}(t)). \quad (39)$$

Moreover, from (39), z satisfies

$$\begin{aligned} \dot{z}(t) &= \frac{d}{dt} \langle q(s), U_t \rangle = \langle q(s), \mathcal{A}U_t \rangle + \langle q(s), X_0 F(U_t, 0) \rangle \\ &= i\hat{\omega}\hat{\tau}z + q(0)f(W(z, \bar{z}) + 2\text{Re}\{zp(\theta)\}, 0) \\ &= i\hat{\omega}\hat{\tau}z + g(z, \bar{z}), \end{aligned} \quad (40)$$

where

$$g(z, \bar{z}) = g_{20} \frac{z^2}{2} + g_{11} z\bar{z} + g_{02} \frac{\bar{z}^2}{2} + g_{21} \frac{z^2 \bar{z}}{2} + \dots$$

By the Taylor expansion

$$\begin{aligned} \frac{v + v^*}{1 + b(u + u^*) + c(v + v^*)} &= \frac{v^*}{1 + bu^* + cv^*} - \frac{bv^*u}{(1 + bu^* + cv^*)^2} + \frac{(1 + bu^*)v}{(1 + bu^* + cv^*)^2} \\ &\quad + C_{11}u^2 + C_{12}uv + C_{13}v^2 + C_{14}u^2v + C_{15}uv^2 + \\ &\quad C_{16}u^3 + C_{17}v^3 + O(4), \\ \frac{u + u^*}{1 + b(u + u^*) + c(v + v^*)} &= \frac{u^*}{1 + bu^* + cv^*} + \frac{(1 + cv^*)u}{(1 + bu^* + cv^*)^2} - \frac{cu^*v}{(1 + bu^* + cv^*)^2} \\ &\quad + C_{21}u^2 + C_{22}uv + C_{23}v^2 + C_{24}u^2v + C_{25}uv^2 + \\ &\quad C_{26}u^3 + C_{27}v^3 + O(4), \end{aligned} \quad (41)$$

where

$$\begin{aligned}
 C_{11} &= \frac{b^2 v^*}{(1 + bu^* + cv^*)^3}, C_{12} = \frac{bcv^* - b(1 + bu^*)}{(1 + bu^* + cv^*)^3}, C_{13} = -\frac{c(1 + bu^*)}{(1 + bu^* + cv^*)^3}, \\
 C_{14} &= \frac{b^2(1 + bu^* - 2cv^*)}{(1 + bu^* + cv^*)^4}, C_{15} = \frac{bc(2(1 + bu^*) - cv^*)}{(1 + bu^* + cv^*)^4}, C_{16} = \frac{-b^3 v^*}{(1 + bu^* + cv^*)^4}, \\
 C_{17} &= \frac{c^3(1 + bu^*)}{(1 + bu^* + cv^*)^4}, C_{21} = -\frac{b(1 + cv^*)}{(1 + bu^* + cv^*)^3}, C_{22} = \frac{bcu^* - c(1 + cv^*)}{(1 + bu^* + cv^*)^3}, \\
 C_{23} &= \frac{c^2 u^*}{(1 + bu^* + cv^*)^3}, C_{24} = \frac{bc(2(1 + cv^*) - bu^*)}{(1 + bu^* + cv^*)^4}, C_{25} = \frac{c^2(1 + cv^* - 2bu^*)}{(1 + bu^* + cv^*)^4}, \\
 C_{26} &= \frac{b^3(1 + cv^*)}{(1 + bu^* + cv^*)^4}, C_{27} = -\frac{c^3 u^*}{(1 + bu^* + cv^*)^4}.
 \end{aligned}$$

Noting that (40), we get

$$g(z, \bar{z}) = \bar{\mathfrak{D}}(\bar{\eta}_1^*, \bar{\eta}_2^*, 1)f(W(z, \bar{z}) + zp(\theta) + \bar{z}p(\bar{\theta}), 0). \tag{42}$$

Substituting (38) into (42) and combining (41) yield

$$\begin{aligned}
 g_{20} &= 2\bar{\mathfrak{D}}\hat{\tau}[\bar{\eta}_1^* ((bA_3/u_1^* - C_{11}u_1^* - 1)\eta_1^2 - \eta_1\eta_2 - C_{13}u_1^* - (A_1 + C_{12}u_1^*)\eta_1) + \\
 &\quad \bar{\eta}_2^*(\beta_1\eta_1\eta_2 e^{-2i\hat{\omega}\tau} - \alpha\eta_2) + \bar{\eta}_3^*(u_3^*\beta_2 C_{21}\eta_1^2 + C_{23}u_3^*\beta_2 - M_3/u_3^* + \\
 &\quad (\beta_2 A_2 + \beta_2 C_{22}u_3^*)\eta_1 + \beta\eta_2)],
 \end{aligned}$$

$$\begin{aligned}
 g_{11} &= \bar{\mathfrak{D}}\hat{\tau}[\bar{\eta}_1^*(2(bA_3/u_1^* - C_{11}u_1^* - 1)\eta_1\bar{\eta}_1 - (\eta_1\bar{\eta}_2 + \eta_2\bar{\eta}_1) - 2C_{13}u_1^* - \\
 &\quad (A_1 + C_{12}u_1^*)(\eta_1 + \bar{\eta}_1)) + \bar{\eta}_2^*(\beta_1(\eta_1\bar{\eta}_2 + \bar{\eta}_1\eta_2) - \alpha(\eta_2 + \bar{\eta}_2)) + \\
 &\quad \bar{\eta}_3^*(2u_3^*\beta_2 C_{21}\eta_1\bar{\eta}_1 + 2(C_{23}u_3^*\beta_2 - M_3/u_3^*) + \\
 &\quad (\beta_2 A_2 + \beta_2 C_{22}u_3^*)(\eta_1 + \bar{\eta}_1) + \beta(\eta_2 + \bar{\eta}_2))],
 \end{aligned}$$

$$\begin{aligned}
 g_{21} &= 2\bar{\mathfrak{D}}\hat{\tau}[\bar{\eta}_1^*(2(bA_3/u_1^* - C_{11}u_1^* - 1)(\eta_1 W_{11}^{(1)}(0) + \frac{\bar{\eta}_1}{2} W_{20}^{(1)}(0)) - (\frac{W_{20}^{(1)}(0)}{2}\bar{\eta}_2 + \\
 &\quad W_{11}^{(2)}(0)\eta_1 + W_{11}^{(1)}(0)\eta_2 + \frac{W_{20}^{(2)}(0)}{2}\bar{\eta}_1) - 2C_{13}u_1^*(W_{11}^{(3)}(0) + \frac{W_{20}^{(3)}(0)}{2}) - \\
 &\quad (A_1 + C_{12}u_1^*)(\frac{W_{20}^{(1)}(0)}{2} + W_{11}^{(1)}(0) + W_{11}^{(3)}(0)\eta_1 + \frac{W_{20}^{(3)}(0)}{2}\bar{\eta}_1) - \\
 &\quad 3(C_{11} + C_{16}u_1^*)\eta_1\eta_1\bar{\eta}_1 - (C_{12} + C_{14}u_1^*)(\eta_1\eta_1 + \eta_1\bar{\eta}_1 + \bar{\eta}_1\eta_1) - 3C_{17}u_1^* - \\
 &\quad (C_{13} + C_{15}u_1^*)(2\eta_1 + \bar{\eta}_1)) + \bar{\eta}_2^*(\beta_1\eta_1 W_{11}^2(-1)e^{-i\hat{\omega}\tau} + \beta_1\bar{\eta}_1 e^{i\hat{\omega}\tau} \frac{W_{20}^2(-1)}{2} + \\
 &\quad \beta_1\bar{\eta}_2 e^{i\hat{\omega}\tau} \frac{W_{20}^1(-1)}{2} + \beta_1\eta_2 W_{11}^1(-1)e^{-i\hat{\omega}\tau} - \alpha\eta_2 W_{11}^{(3)}(0) - \alpha\bar{\eta}_2 \frac{W_{20}^{(3)}(0)}{2} - \\
 &\quad \alpha \frac{W_{20}^{(2)}(0)}{2} - \alpha W_{11}^{(2)}(0)) + \bar{\eta}_3^*(2u_3^*\beta_2 C_{21}(W_{11}^{(1)}(0)\eta_1 + \frac{\bar{\eta}_1}{2} W_{20}^{(1)}(0)) + \\
 &\quad 2(C_{23}u_3^*\beta_2 - M_3/u_3^*)(W_{11}^{(3)}(0) + \frac{W_{20}^{(3)}(0)}{2}) + (\beta_2 A_2 + \beta_2 C_{22}u_3^*)(\frac{W_{20}^{(1)}(0)}{2} + \\
 &\quad \eta_1 W_{11}^{(3)}(0) + \bar{\eta}_1 \frac{W_{20}^{(3)}(0)}{2} + W_{11}^{(1)}(0)) + \beta(\eta_2 W_{11}^{(3)}(0) + \bar{\eta}_2 \frac{W_{20}^{(3)}(0)}{2} +
 \end{aligned}$$

$$\begin{aligned} & \frac{W_{20}^{(2)}(0)}{2} + W_{11}^{(2)}(0) + 3C_{26}u_3^*\beta_2\eta_1\eta_1\bar{\eta}_1 + 3(C_{23}\beta_2 + u_3^*\beta_2C_{27}) + \\ & (C_{21}\beta_2 + u_3^*\beta_2C_{24})(\eta_1^2 + 2\eta_1\bar{\eta}_1) + (C_{22}\beta_2 + u_3^*\beta_2C_{25})(2\eta_1 + \bar{\eta}_1)], \\ & g_{02} = 2g_{20}\bar{\mathfrak{D}}/\mathfrak{D}. \end{aligned}$$

Since $W(z(t), z(\bar{t}))$ satisfies the following equation

$$\begin{aligned} \dot{W} &= \mathcal{A}W + X_0f(\Phi \cdot (z, \bar{z})^T + W(z, \bar{z}), 0) - \Phi\Psi(0)f(\Phi \cdot (z, \bar{z})^T + W(z, \bar{z}), 0) \\ &= \mathcal{A}W + H_{20}\frac{z^2}{2} + H_{11}z\bar{z} + H_{02}\frac{\bar{z}^2}{2} + \dots \end{aligned} \quad (43)$$

we obtain

$$\begin{cases} (2i\hat{\omega}\hat{\tau} - \mathcal{A})W_{20} = H_{20}, \\ -\mathcal{A}W_{11} = H_{11}, \\ (-2i\hat{\omega}\hat{\tau} - \mathcal{A})W_{02} = H_{02}. \end{cases} \quad (44)$$

Since \mathcal{A} has only two eigenvalues $\pm i\hat{\omega}\hat{\tau}$, then Eq. (44) has only a unique solution W_{ij} .

We first compute $H_{ij}(\theta)$, $\theta \in [-1, 0]$. From (43), we know that for $-1 \leq \theta < 0$,

$$H(z, \bar{z}) = -\Phi\Psi(0)f(\Phi \cdot (z, \bar{z})^T + W(z, \bar{z}), 0).$$

Therefore, by comparing the coefficients, and notice that

$$H(z, \bar{z})(0) = f(\Phi \cdot (z, \bar{z})^T + W(z, \bar{z}), 0) - \Phi\Psi(0)f(\Phi \cdot (z, \bar{z})^T + W(z, \bar{z}), 0),$$

we obtain

$$H_{20}(\theta) = \begin{cases} -(g_{20}p(\theta) + g_{02}\bar{p}(\theta)), & \theta \in [-1, 0), \\ 2\hat{\tau} \begin{bmatrix} (bA_3/u_1^* - C_{11}u_1^* - 1)\eta_1^2 - \eta_1\eta_2 - C_{13}u_1^* - (A_1 + C_{12}u_1^*)\eta_1 \\ \beta_1\eta_1\eta_2e^{-2i\hat{\omega}\hat{\tau}} - \alpha\eta_2 \\ u_3^*\beta_2C_{21}\eta_1^2 + C_{23}u_3^*\beta_2 - M_3/u_3^* + (\beta_2A_2 + \beta_2C_{22}u_3^*)\eta_1 + \beta\eta_2 \end{bmatrix} \\ -[g_{20}p(0) + g_{02}\bar{p}(0)], & \theta = 0. \end{cases}$$

$$H_{11}(\theta) =$$

$$\begin{cases} -(g_{11}p(\theta) + g_{11}\bar{p}(\theta)), & \theta \in [-1, 0), \\ 2\hat{\tau} \begin{bmatrix} (\frac{bA_3}{u_1^*} - C_{11}u_1^* - 1)\eta_1\bar{\eta}_1 - \text{Re}\{\eta_1\bar{\eta}_2\} - C_{13}u_1^* - (A_1 + C_{12}u_1^*)\text{Re}\{\eta_1\} \\ \beta_1\text{Re}\{\eta_1\bar{\eta}_2\} - \alpha\text{Re}\{\eta_2\} \\ u_3^*\beta_2C_{21}\eta_1\bar{\eta}_1 + C_{23}u_3^*\beta_2 - \frac{M_3}{u_3^*} + (\beta_2A_2 + \beta_2C_{22}u_3^*)\text{Re}\{\eta_1\} + \beta\text{Re}\{\eta_2\} \end{bmatrix} \\ -[g_{11}p(0) + g_{11}\bar{p}(0)], & \theta = 0. \end{cases}$$

It follows from (44) and the definition of \mathcal{A} that

$$\begin{aligned} \dot{W}_{20}(\theta) &= 2i\omega_n\hat{\tau}W_{20}(\theta) + [g_{20}p(\theta) + g_{02}\bar{p}(\theta)], \quad -1 \leq \theta \leq 0, \\ -\dot{W}_{11}(\theta) &= -[g_{11}p(\theta) + g_{11}\bar{p}(\theta)], \quad -1 \leq \theta \leq 0. \end{aligned}$$

Noting that $p(\theta) = p(0)e^{i\hat{\omega}\hat{\tau}\theta}$, $-1 \leq \theta \leq 0$, we have

$$\begin{aligned} W_{20}(\theta) &= [\frac{ig_{20}}{\hat{\omega}\hat{\tau}}p(\theta) + \frac{ig_{02}}{3\hat{\omega}\hat{\tau}}\bar{p}(\theta)] + E_1e^{2i\hat{\omega}\hat{\tau}\theta}, \\ W_{11}(\theta) &= [-\frac{ig_{11}}{\hat{\omega}\hat{\tau}}p(\theta) + \frac{ig_{11}}{\hat{\omega}\hat{\tau}}\bar{p}(\theta)] + E_2. \end{aligned} \quad (45)$$

Utilizing the definition of \mathcal{A} , (44) and (45) yields

$$E_1 = 2 \begin{bmatrix} (bA_3/u_1^* - C_{11}u_1^* - 1)\eta_1^2 - \eta_1\eta_2 - C_{13}u_1^* - (A_1 + C_{12}u_1^*)\eta_1 & & \\ & \beta_1\eta_1\eta_2 e^{-2i\hat{\omega}\hat{\tau}} - \alpha\eta_2 & \\ & & u_3^*\beta_2C_{21}\eta_1^2 + C_{23}u_3^*\beta_2 - M_3/u_3^* + (\beta_2A_2 + \beta_2C_{22}u_3^*)\eta_1 + \beta\eta_2 \end{bmatrix} \times$$

$$\begin{bmatrix} 2i\hat{\omega} + d_1\mu_i + M_1 & u_1^* & u_1^*A_1 \\ -\beta_1u_2^*e^{-2i\hat{\omega}\hat{\tau}} & 2i\hat{\omega} + d_2\mu_i + M_2(1 - e^{-2i\hat{\omega}\hat{\tau}}) & \alpha u_2^* \\ -\beta_2A_2u_3^* & -\beta u_3^* & 2i\hat{\omega} + d_3\mu_i + M_3 \end{bmatrix}^{-1}$$

and

$$E_2 = 2 \begin{bmatrix} d_1\mu_i + u_1^* - bA_3 & u_1^* & u_1^*A_1 \\ -\beta_1u_2^* & d_2\mu_i & \alpha u_2^* \\ -\beta_2A_2u_3^* & -\beta u_3^* & d_3\mu_i + c\beta_2A_3 \end{bmatrix}^{-1} \times$$

$$\begin{bmatrix} (\frac{bA_3}{u_1^*} - C_{11}u_1^* - 1)\eta_1\bar{\eta}_1 - \text{Re}\{\eta_1\bar{\eta}_2\} - C_{13}u_1^* - (A_1 + C_{12}u_1^*)\text{Re}\{\eta_1\} & & \\ & \beta_1\text{Re}\{\eta_1\bar{\eta}_2\} - \alpha\text{Re}\{\eta_2\} & \\ & & u_3^*\beta_2C_{21}\eta_1\bar{\eta}_1 + C_{23}u_3^*\beta_2 - \frac{M_3}{u_3^*} + (\beta_2A_2 + \beta_2C_{22}u_3^*)\text{Re}\{\eta_1\} + \beta\text{Re}\{\eta_2\} \end{bmatrix}.$$

Now, we can compute the following values

$$c_1(0) = \frac{i}{2\hat{\omega}\hat{\tau}}(g_{20}g_{11} - 2|g_{11}|^2 - \frac{|g_{02}|^2}{3}) + \frac{g_{21}}{2}, \nu_2 = -\frac{\text{Re}(c_1(0))}{\text{Re}(\lambda'(\hat{\tau}))},$$

$$\beta_2 = 2\text{Re}(c_1(0)), T_2 = -\frac{\text{Im}(c_1(0)) + \nu_2\text{Im}(\lambda'(\hat{\tau}))}{\hat{\omega}\hat{\tau}},$$

which determine the properties of bifurcating periodic solutions at critical value $\hat{\tau}$, that is, ν_2 determines the directions of the Hopf bifurcation; β_2 determines the stability of the bifurcating periodic solutions; T_2 determines the period of bifurcating periodic solutions. Moreover, by Hassard [41], we have the following result.

Theorem 4.11. *Assume that the conditions of Theorem 4.5 are satisfied, we have*

- (i) *If $\nu_2 > 0 (< 0)$, then the direction of the Hopf bifurcation is forward (backward).*
- (ii) *If $\beta_2 < 0 (> 0)$, then the bifurcating periodic solutions are orbitally stable (unstable).*
- (iii) *If $T_2 > 0 (< 0)$, then the period of the bifurcating periodic solutions increases (decreases).*

5. Numerical simulations.

5.1. The spatiotemporal dynamics in one-dimensional space. In this subsection, we numerically explore the dynamic behavior of System (4) with one-dimensional space, namely $n = 1$, $\Delta = \frac{\partial^2}{\partial x^2}$ and we take $\Omega = (0, \pi)$.

For the choice of the parameter values in System (4), we refer to [10, 11, 12, 15] and choose parameter values as follows

$$(P_1) : \alpha = 0.7, \beta = 0.9, \beta_1 = 1.95, \beta_2 = 1.8, \gamma_1 = 0.2, \gamma_2 = 0.8, b = 2.5, c = 5.5, d_1 = 0.4, d_2 = 0.3, d_3 = 0.2$$

and the initial conditions as

$$(IC_1) : \phi_1(t, x) = 0.1717 + 0.001 \cos x, \phi_2(t, x) = 0.7509 + 0.001 \cos x, \phi_3(t, x) = 0.1926 + 0.001 \cos x.$$

With these parameter values, System (4) admits a unique positive spatially homogeneous steady state $E^* = (u_1^*, u_2^*, u_3^*) \approx (0.1717, 0.7509, 0.1926)$. It is easy to

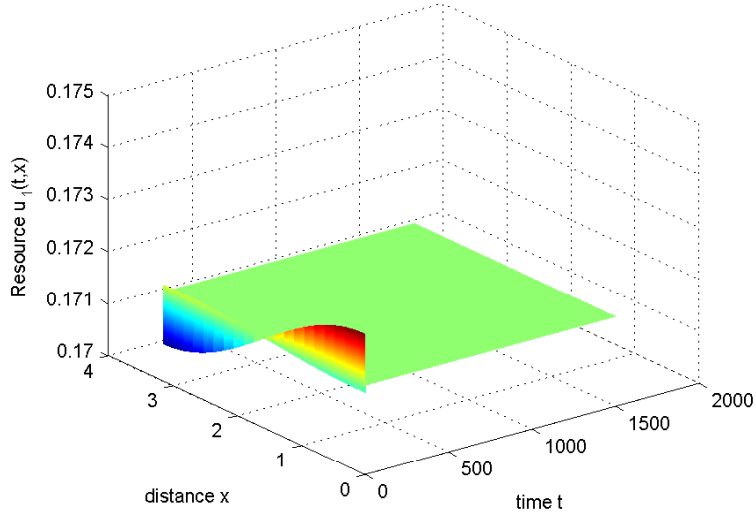


FIGURE 1. Numerical solutions of (4) with $\tau = 0.7 < \tau^* \approx 0.7895$ (only the u_1 component is plotted here): the positive spatially homogeneous steady state is locally stable.

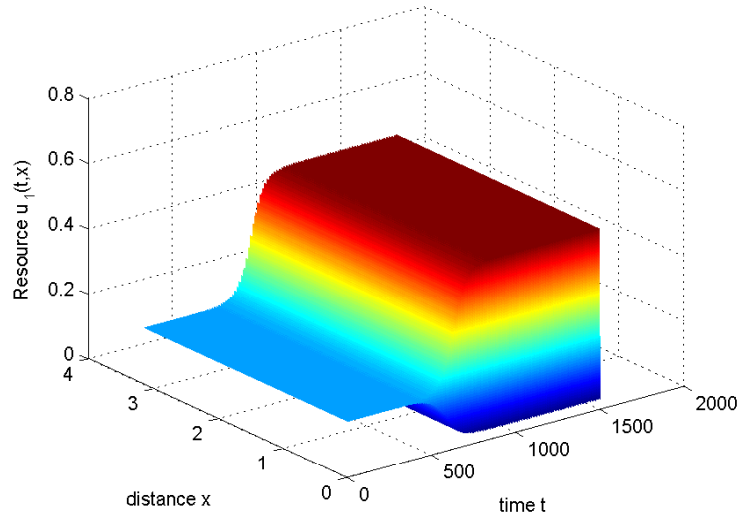


FIGURE 2. Numerical solutions of (4) with $\tau = 1.2 > \tau^* \approx 0.7895$: a periodic solution bifurcates from the positive spatially homogeneous steady state E^* .

check that the hypotheses $(H_1) - (H_6)$ hold and $h'((\omega^*)^2) = 0.0938 > 0$. By Theorem 4.9, local Hopf bifurcation occurs at $\tau^* \approx 0.7859$. We use the forward Euler method to find numerical solutions to System (4) with $\tau = 0.7 < \tau^*$ and $\tau = 1.2 > \tau^*$, respectively. As illustrated in Figures 1 and 2, when $\tau = 0.7 < \tau^*$,

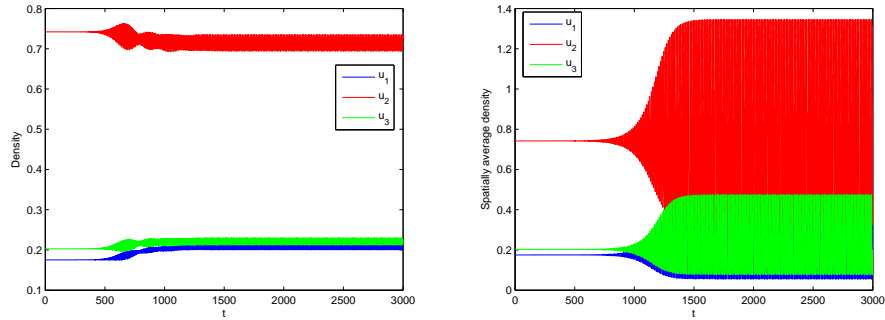


FIGURE 3. Numerical solutions of the temporal model (left) and numerical solutions of the spatiotemporal model (right) with $\tau = 1$, (P_2) and (IC_2) . Here, for the spatiotemporal model (4), average population density for each species is plotted.

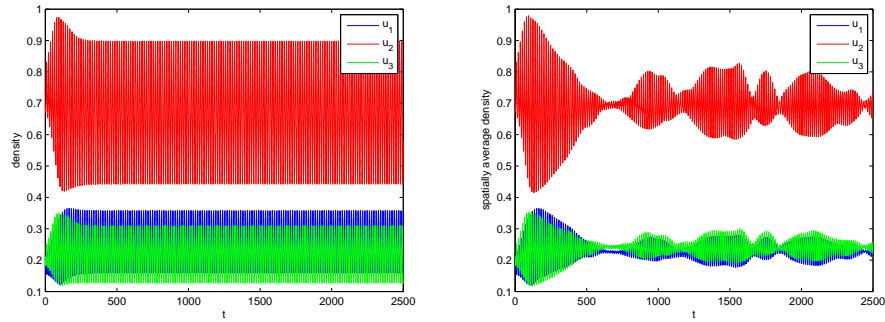


FIGURE 4. Numerical solutions of the temporal model (left) and numerical solutions of the spatiotemporal model (right) with $\tau = 1.5$, (P_2) and (IC'_2) . Here, periodic oscillations are observed for the temporal model and chaotic behavior is observed for the spatiotemporal model.

solutions of (4) approach the steady state E^* , while when $\tau > \tau^*$, sustained oscillations are observed. Calculations give $c_1(0) = -4.2942 - 30.9399i, \nu_2 = 83.06, \beta_2 = -8.5884, T_2 = 185.7969$. Thus the Hopf bifurcation is forward and the bifurcated periodic solutions from E^* are stable and the period of bifurcated periodic solution increases in τ for $\tau > \tau^*$.

5.2. The spatiotemporal dynamics in two-dimensional space. Consider System (4) with $u_1 = u_1(t, x, y), u_2 = u_2(t, x, y), u_3 = u_3(t, x, y)$ and $\Delta = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$. For this purpose, the domain of System (4) is confined to a fixed spatial domain $\Omega = [0, L] \times [0, L] \subset R^2$ with $L = 400$. we solve System (4) on a grid with 400×400 sites by a simple Euler method with a time step size of $\delta t = 0.01$ and a space step

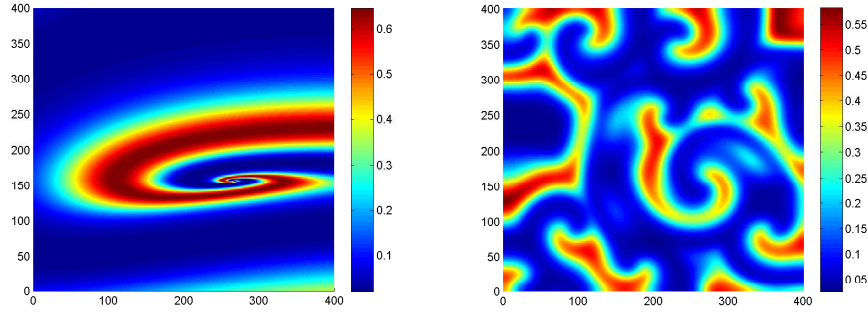


FIGURE 5. Snapshots of contour maps of the basal resource u_1 for the temporal model (left) and spatiotemporal model (right) at $t = 2000$ with $\tau = 1.5$, (P_2) and (IC'_2) .

size of $\delta x = \delta y = 1$. The discretization of the Laplacian term takes the form

$$\Delta u|_{(i,j)} = \frac{1}{s^2} [A_l(i,j)u(i-1,j) + A_r(i,j)u(i+1,j) + A_d(i,j)u(i,j-1) + A_u(i,j)u(i,j+1) - 4u(i,j)],$$

where (i, j) denote the lattice sites and $s = 1$ is the lattice constant. The matrix elements of A_l, A_r, A_d, A_u are unity except at the boundary. When (i, j) lies on the left boundary, that is $i = 0$, we define $A_l(i, j)u(i-1, j) \equiv u(i+1, j)$, which guarantees zero-flux of individuals in the left boundary. Similarly we define $A_r(i, j), A_d(i, j), A_u(i, j)$ such that the zero-flux boundary condition is satisfied.

With the given Neumann boundary conditions, the eigenvalues of $-\Delta$ on Ω are $\mu_i = \frac{\pi^2}{L^2}(n^2 + m^2), n, m \in \mathbb{Z}$, where \mathbb{Z} represents the integer set. In order to discuss the impacts of delay and diffusion on the dynamics of System (4), we will compare the temporal model (that is, System (4) without diffusion) with System (4). We take parameters as

(P_2) : $\alpha = 0.7, \beta = 0.9, \beta_1 = 1.95, \beta_2 = 1.85, \gamma_1 = 0.2, \gamma_2 = 0.8, b = 2.5, c = 5, d_1 = 1, d_2 = 2, d_3 = 4$.

We consider two types of different initial conditions:

(IC_2) : $\phi_1(t, x, y) = u_1^* + 0.001 \sin x \sin y, \phi_2(t, x, y) = u_2^* + 0.001 \sin x \sin y, \phi_3(t, x, y) = u_3^* + 0.001 \sin x \sin y,$

and

$$(IC'_2) : \begin{cases} u_1(t, x, y) = 0.1754 - \varepsilon_1(x - 0.1y - 225)(x - 0.1y - 675), \\ u_2(t, x, y) = 0.7419 - \varepsilon_2(x - 450) - \varepsilon_3(y - 150), \\ u_3(t, x, y) = 0.2029 - \varepsilon_4(x - 350) - \varepsilon_5(y - 200) \end{cases}$$

for $(t, x, y) \in [-\tau, 0] \times \Omega$. Here $\varepsilon_1 = 2 \times 10^{-7}, \varepsilon_2 = 3 \times 10^{-5}, \varepsilon_3 = 1.2 \times 10^{-3}, \varepsilon_4 = 6 \times 10^{-5}, \varepsilon_5 = 3 \times 10^{-5}$.

Under (P_2) and (IC_2) , it is easy to check that all conditions of Theorem 4.9 are satisfied and there is a unique positive steady state $E^* \approx (0.1754, 0.7419, 0.2029)$. The corresponding Hopf bifurcation value is computed as $\tau_{1,0}^1 \approx 0.8028$.

Figure 3 depicts the population dynamics of the temporal model and the spatiotemporal model at $\tau = 1$. Both the temporal model and the spatiotemporal

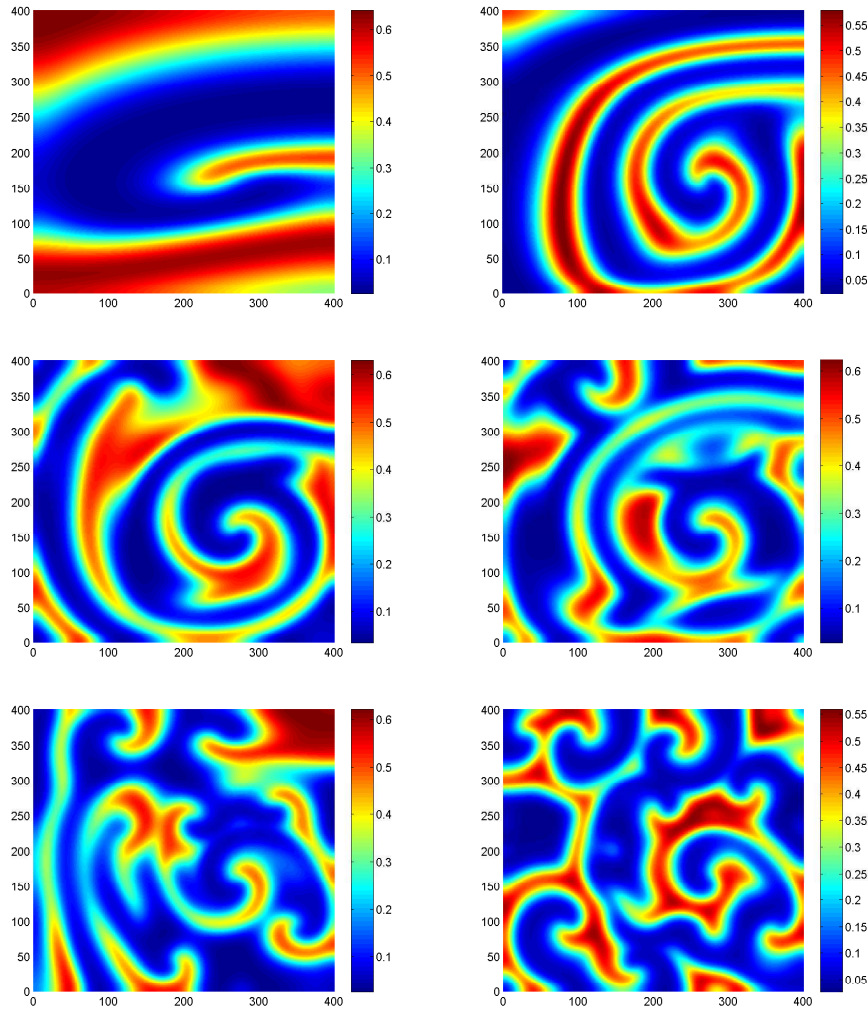


FIGURE 6. Snapshots of contour maps of the time evolution of the specie u_1 at $t = 200, 500, 1000, 1200, 1500, 2500$ with $\tau = 1.5$ under (P_2) and (IC'_2) .

model undergo periodic oscillations. However, the temporal model exhibits irregular transient oscillations initially.

If we increase τ to $\tau = 1.5$ and use initial condition (IC'_2) , as shown in Figure 4, the temporal model still exhibits regular oscillations, while the spatiotemporal model exhibits irregular oscillations and the calculated Lyapunov exponent is $0.0011 > 0$ (By the method proposed in [42]), which indicates the occurrence of chaos.

Figure 5 depicts the snapshots of the contour maps of specie u_1 for the temporal model and the spatiotemporal model at time $t = 5000$. The temporal model exhibits the spiral wave pattern. However, the spatiotemporal model presents the chaotic wave pattern. To have a better understanding on the evolution process of the

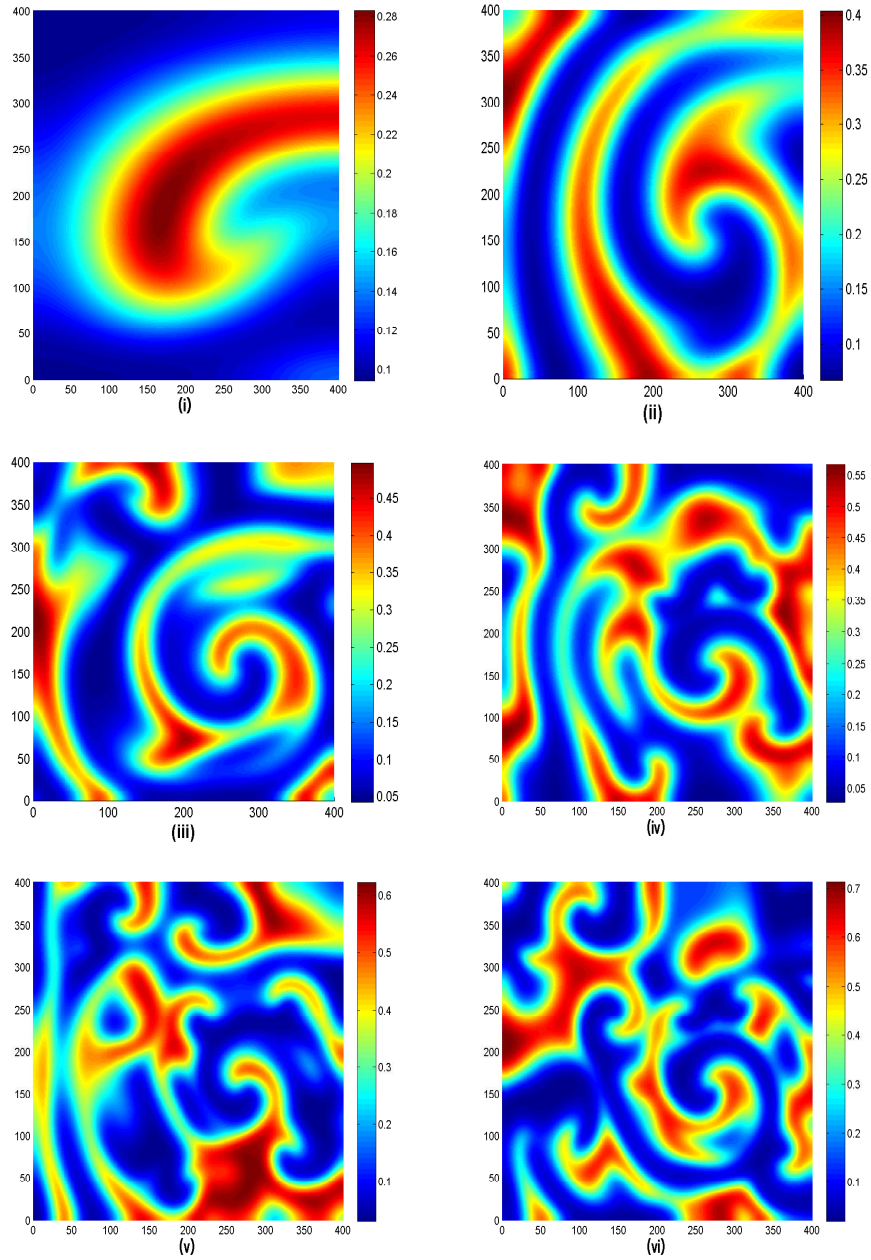


FIGURE 7. Snapshots of contour maps of the time evolution of the basal resource u_1 with different values of τ at time $t = 1500$ under (P_2) and (IC'_2) . (i) $\tau = 0.86$; (ii) $\tau = 1$; (iii) $\tau = 1.2$; (iv) $\tau = 1.4$; (v) $\tau = 1.6$; (vi) $\tau = 1.9$.

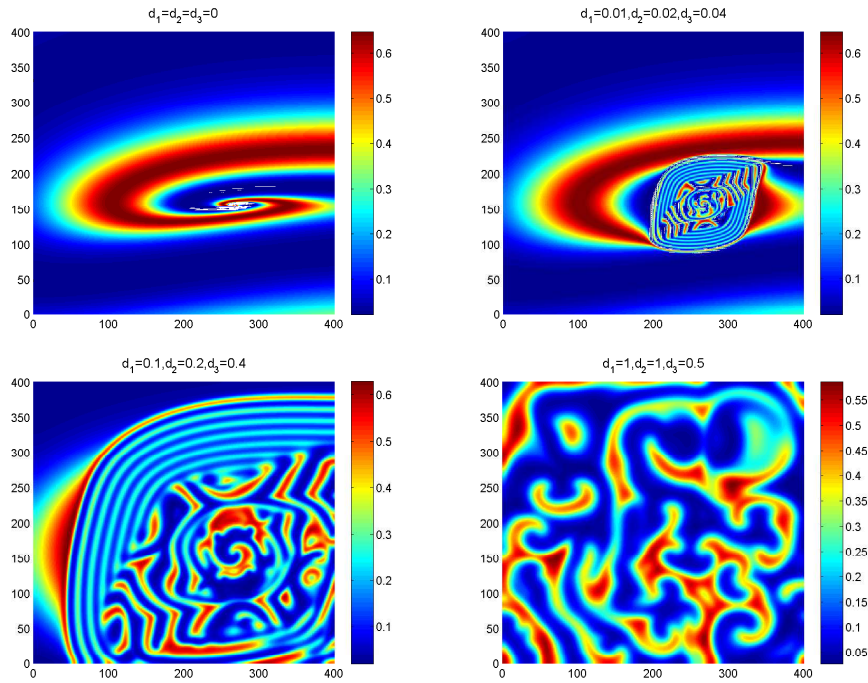


FIGURE 8. Snapshots of contour maps of the basal resource u_1 at time $t = 1500$ with different diffusion coefficients, $\tau = 1.5$, under (P_2) and (IC'_2) .

spatiotemporal pattern, in Figure 6, we present the snapshots of contour maps of the basal resource u_1 at $t=200, 500, 1000, 1200, 1500, 2500$, respectively. As pointed out in [43], the spirals are usually observed under suitable parametric conditions near Turing-Hopf bifurcation threshold. In addition, in the spatially extended system the existence of a stable limit cycle normally results in the formation of chaotic spatiotemporal patterns [44]. As can be seen from Figure 6, as time t increases, an chaotic wave spatial pattern is gradually formed starting from a regular spiral wave pattern.

5.2.1. *The effect of delay.* To explore the impact of delay, in Figure 7, we take the snapshots of the contour maps of specie u_1 at time $t = 1500$ for several different values of τ . As can be seen in Figure 7, the time delay can lead to the formation of an irregular spatial pattern from a regular spiral pattern in the whole domain as the time delay increases and surpasses some critical value.

5.2.2. *The effect of diffusion.* As seen from Figure 6, System (4) has a regular spiral wave pattern when $\tau = 1.5$, $d_1 = 1$, $d_2 = 2$ and $d_3 = 4$ at $t = 1500$. To numerically examine how the diffusion affects the pattern, we take the snapshots of contour maps of u_1 at $t = 1500$ with several different choices of the diffusion coefficients. As shown in Figure 8, spiral wave pattern emerges firstly when $d_1 = d_2 = d_3 = 0$, then as the three diffusion coefficients change to $d_1 = d_2 = 0.01, d_3 = 0.04$, the spiral wave structure disappears around the center of the spirals wave, with the increase in these diffusion coefficients, it grows steadily, and eventually the chaotic wave

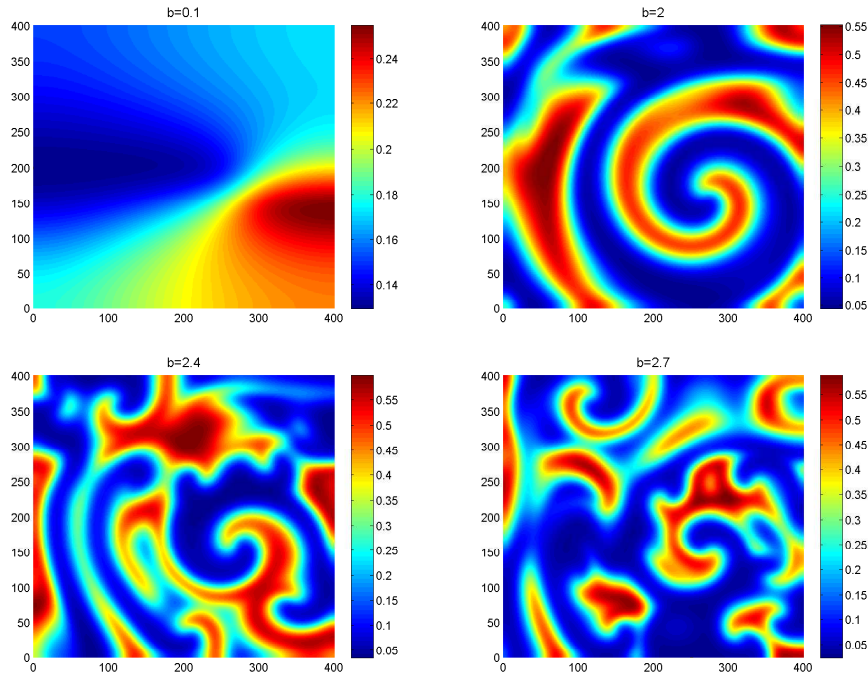


FIGURE 9. Snapshots of contour maps of the time evolution of the basal resource u_1 with different values of b and parameter values $\alpha = 0.7, \beta = 0.9, \beta_1 = 1.95, \beta_2 = 1.85, \gamma_1 = 0.2, \gamma_2 = 0.8, c = 5$ at times $t = 1500$ and $\tau = 1.5$ under (IC'_2) .

pattern dominates the whole domain. Differing from the instability mechanism in Figure 7, the spirals wave loses its stability due to the Doppler effect [45].

5.2.3. *The impact of the prey saturation constant b .* Figure 9 demonstrates how the prey saturation constant b affects the pattern formation of the basal resource u_1 at time $t = 1500$ with $\tau = 1.5$: when b is small, we observe a pattern with stripes firstly; as the constant b increases, the spiral wave pattern emerges, then it grows steadily, as b goes beyond a certain value, chaotic wave pattern appears.

5.2.4. *The impact of the predator interference constant c .* To see how the predator interference constant c influences the spatiotemporal pattern, we numerically simulation (4) with different values of c and plot the snapshots of the contour maps of the basal resource u_1 at $t = 1500$ in Figure 10. It is illustrated in Figure 10 that the predator interference constant c can also lead to the formation of chaotic wave spatial pattern, which can be preceded from the evolution of a regular spiral patterns as the predator interference constant c decreases.

6. A summary and discussion. In this work, we have investigated the spatiotemporal dynamics of a diffusive IGP model with delay and the Beddington-DeAngelis functional response. we have established locally asymptotically stability results of the trivial, semi-trivial and strong semi-trivial steady states. In the case that there is a unique positive spatially homogeneous steady state E^* , we have carried out

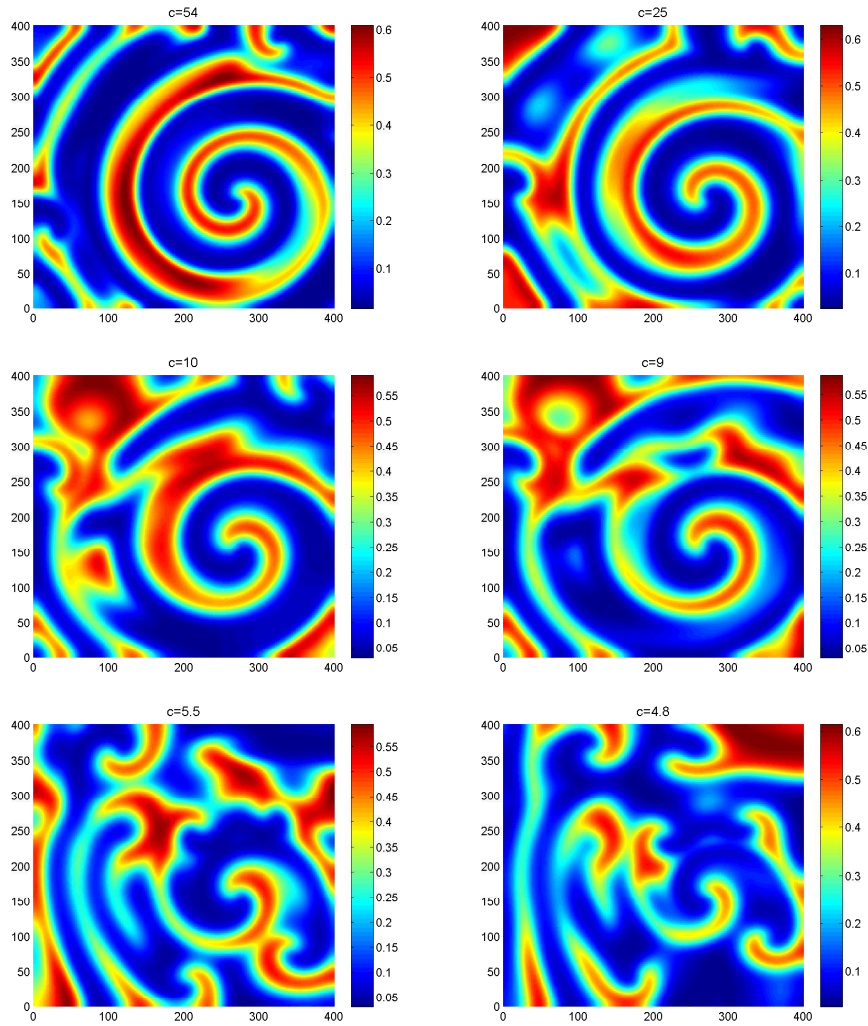


FIGURE 10. Snapshots of contour maps of the time evolution of the basal resource u_1 with different values of c and parameter values $\alpha = 0.7, \beta = 0.9, \beta_1 = 1.95, \beta_2 = 1.85, \gamma_1 = 0.2, \gamma_2 = 0.8, b = 2.5$ at times $t = 1500$ and $\tau = 1.5$ under (IC'_2) .

the Hopf bifurcation analysis. Unlike competition models with monotone response functions ([17]) where delay does not induce sustained oscillations, in our IGP models, delay promotes complex dynamics including bistability, and the emergence of spiral wave pattern and chaotic wave pattern.

Compared with the temporal model in [24], we also observe bistability is possible in System (4). In addition, the diffusion also has impacts on the formation of spatiotemporal patterns as it can change the distribution of characteristic roots of the corresponding characteristic equations, and hence has an important effect on the dynamics for the constant steady state of System (4). This has been illustrated via numerical simulations as well (See Figure 8). Moreover, we have observed that

the functional response can also influence the formation of complex patterns. As demonstrated in Figures 9 and 10, the functional responses can also trigger the emergence of spiral wave pattern and chaotic wave spatial pattern.

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