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Spatiotemporal dynamics of a predator–prey system with prey-taxis and intraguild predation

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Abstract

This paper is concerned with a reaction-diffusion predator–prey model with prey-taxis and intraguild predation. We first discuss the basic properties of solutions with the aid of differential equation theory. Then, we investigate the local and global stability of constant equilibrium solution by linear stability analysis and Lyapunov function method, respectively. Moreover, we establish the existences of nonconstant positive steady states and time-periodic solutions through detailed bifurcation analyses. Finally, we give some numerical simulations and conclusions to illustrate the theoretical findings.

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Keywords: Predator–prey system; Prey-taxis; Diffusion; Delay; Steady state bifurcation; Hopf bifurcation

1 Introduction

Predation is a biological interaction where a predator kills and eats its prey. In ecosystem, the interaction between predator and prey is the most basic and is also ubiquitous in human society. In recent decades, the dynamic behaviors of various predator–prey models have been studied, such as the stability, Hopf bifurcation phenomenon, permanence, spatial patterns, and so on, see [1–7] for example. However, in some situations, both species rely on the same prey resources and also benefit from preying upon one another. This interaction can be called intraguild predation [8–11]. The presence and intensity of intraguild predation are important to both management and conservation of species [12]. This ecological interaction is significant, and conservation and management measures need to be taken into consideration. Therefore Holt and Polis [13] proposed the predator–prey system with a common consuming resource as follows:

$$\begin{cases} \frac{dN}{dt} = N\left(\frac{bs}{cP+sN} - dP - h\right), \\ \frac{dP}{dt} = P\left(\frac{bc}{cP+sN} + dN - g\right), \end{cases} \quad (1)$$

where $N(t)$, $P(t)$ are the densities of the prey and the predator, respectively. The parameters b , c , and s represent the consumption of the predator and the prey species for common

resources. Coefficient d measures the predation rate, g and h are the natural death rates of the predator and the prey, respectively. All the parameters in system (1) are positive constants. Based on this basic model, Fang and Wang [14] took into consideration the mobility of population individuals and investigated the modified version of (1):

$$\begin{cases} \frac{\partial N}{\partial t} = d_{11} \Delta N + d_{12} \Delta P + N \left(\frac{bs}{cP+sN} - dP - h \right), & x \in \Omega, t > 0, \\ \frac{\partial P}{\partial t} = d_{21} \Delta P + d_{22} \Delta N + P \left(\frac{bc}{cP+sN} + dN - g \right), & x \in \Omega, t > 0, \\ \frac{\partial N(x,t)}{\partial \nu} = \frac{\partial P(x,t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ N(x,0) = N_0(x) \geq 0, \quad P(x,0) = P_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (2)$$

where Δ is the Laplace operator, the self-diffusion rates d_{11} , d_{22} and cross-diffusion rates d_{12} , d_{21} are all positive, ν is the unit outer normal, and homogeneous Neumann boundary condition means that the system is a closed one. For system (2), it is shown that self-diffusion does not change the stability of the coexistence state, but cross-diffusion may induce the instability.

The directed movement of predators has attracted much attention recently and has inspired a large number of studies about the prey-taxis effect, see [15–18]. Prey-taxis can be classified as attractive or repulsive. In general, predators tend to move to habitats with higher prey density. On the other hand, some prey species are capable of fighting back against predators through communal defence, thus the predator species will move to the districts with lower prey density. It is interesting and unknown how the prey-taxis affects the spatiotemporal dynamical behaviors of reaction-diffusion systems.

Motivated by the foregoing work, we consider the following predator–prey system with prey-taxis and intraguild predation over 1D bounded domain:

$$\begin{cases} \frac{\partial N}{\partial t} = d_1 \Delta N + N \left(\frac{bs}{cP+sN} - dP - h \right), & x \in (0, L), t > 0, \\ \frac{\partial P}{\partial t} = d_2 \Delta P - \nabla \cdot (\chi \phi(P) P \nabla N) + P \left(\frac{bc}{cP+sN} + dN - g \right), & x \in (0, L), t > 0, \\ \frac{\partial N(x,t)}{\partial x} = \frac{\partial P(x,t)}{\partial x} = 0, & x = 0, L, t > 0, \\ N(x,0) = N_0(x) \geq 0, \quad P(x,0) = P_0(x) \geq 0, & x \in (0, L), \end{cases} \quad (3)$$

where $N(x, t)$ and $P(x, t)$ denote the densities of the prey and the predator at location x and time t , respectively. In system (3), all the coefficients are positive constants, d_1 and d_2 are diffusion rates. ∇ is the gradient operator, the function $\phi(P)$ denotes the prey-tactic sensitivity, L is the length of the habitat. The sensitivity coefficient χ is an arbitrary constant. The prey-taxis is attractive when $\chi > 0$ and repulsive when $\chi < 0$. In view of the volume filling effect [19, 20], we adopt the sensitivity function as follows:

$$\phi(P) = \begin{cases} 1 - \frac{P}{P_m}, & 0 \leq P \leq P_m, \\ 0, & P \geq P_m, \end{cases}$$

where P_m is the maximum number of prey that a unit volume can accommodate. If the number of predator exceeds the threshold P_m , then the tendency of directed movement vanishes. It should be mentioned that the systems with different forms of sensitivity functions were considered in [21–23].

Moreover, spatial-temporal distribution of species not only depends on the current state but also is related to the previous state. It is necessary to take account of the combined effects of prey-taxis and time delay, so we further consider the following modified predator-prey model with homogeneous Neumann boundary conditions and nonnegative initial conditions:

$$\begin{cases} \frac{\partial N}{\partial t} = d_1 \Delta N + N \left(\frac{bs}{cP+sN} - dP - h \right), \\ \frac{\partial P}{\partial t} = d_2 \Delta P - \nabla \cdot (\chi \phi(P) P \nabla N) + P \left(\frac{bc}{cP+sN} + dN(x, t - \tau) - g \right), \end{cases} \quad (4)$$

where $(x, t) \in (0, L) \times (0, +\infty)$, time delay $\tau > 0$ is the mature time of the predator. Though some significant results on prey-taxis models have been obtained (see [24–29] for example), there is no result about the predator-prey model with both time delay and prey-taxis such as (4). Therefore, the main purpose of this paper is to explore the effects of prey-taxis and time delay on stability.

The rest of the paper is organized as follows. In Sect. 2, the basic properties of solution of system (3) are discussed. In Sect. 3, the local and global stability of constant equilibrium solution of (3) is investigated. In Sect. 4, the existence of nonconstant steady states for (3) is derived by bifurcation analysis. In Sect. 5, periodic solutions of (4) induced by time delay are obtained by Hopf bifurcation theory. In Sect. 6, some numerical simulations are conducted to support the theoretical analyses. Finally, some conclusions are given in Sect. 7.

2 Basic properties of solutions

Here, we mainly discuss the basic properties of solutions of delay-free system (3) to make preparations for the posterior study.

Lemma 1 ([14]) *System (3) has the unique positive constant equilibrium solution $E^* = (N^*, P^*)$ if and only if the following assumption*

$$(H1) \quad \frac{g}{d} > \frac{bc}{gs - ch} > \frac{h}{d},$$

holds, where $N^ = \frac{g}{d} - \frac{bc}{gs - ch}$, $P^* = \frac{bs}{gs - ch} - \frac{h}{d}$.*

According to the results in [14], the equilibrium solution E^* is always globally asymptotically stable when $P > P_m$.

Lemma 2 *If $d_1 = d_2$, then the following statements hold:*

- (i) *System (3) has the unique solution $(N(x, t), P(x, t)) \in (0, L) \times [0, t_0]$, where t_0 depends on the initial conditions or $t_0 = +\infty$;*
- (ii) *$N(x, t) \geq 0$, $P(x, t) \geq 0$ for all $(x, t) \in (0, L) \times [0, t_0]$;*
- (iii) *Any solution (N, P) is bounded, that is, there exists $M > 0$ such that $0 \leq N(x, t), P(x, t) \leq M$.*

Proof Using methods similar to those in [30], we can easily obtain the local existence, uniqueness, and nonnegativity. Here we omit it.

Next, we shall establish the global existence and uniform boundedness of solution. When $P \geq P_m$, adding the first two equations of system (3), we can get

$$(N + P)_t - d_1 \Delta(N + P) = b - hN - gP \leq b - \min\{g, h\}(N + P).$$

By the comparison theorem, we have

$$\limsup_{t \rightarrow +\infty} (N + P) \leq \frac{b}{\min\{g, h\}} \triangleq M_1.$$

When $P \leq P_m$, by the first equation of (3), we obtain

$$N_t - d_1 \Delta N = N \left(\frac{bs}{cP + sN} - dP - h \right) \leq N \left(\frac{b}{N} - h \right) = b - hN,$$

hence

$$\limsup_{t \rightarrow +\infty} N \leq \frac{b}{h} \triangleq M_2.$$

Denote $M = \max\{M_1, M_2, P_m, M_3, M_4\}$, where

$$M_3 = \max_{[0, L]} \{P_0(x)\}, \quad M_4 = \max_{[0, L]} \{N_0(x)\}.$$

The proof is complete. \square

From Lemma 2, we always assume that $d_1 = d_2$ in the next context.

3 Local and global stability of positive constant equilibrium solution

In consideration of the ecological background of system (3) and biodiversity, in this section, we mainly investigate the local and global stability of constant equilibrium solution.

The linearized part of system (3) at E^* can be denoted by

$$\begin{pmatrix} \frac{\partial N}{\partial t} \\ \frac{\partial P}{\partial t} \end{pmatrix} = D \begin{pmatrix} \Delta N \\ \Delta P \end{pmatrix} + A \begin{pmatrix} N \\ P \end{pmatrix},$$

where

$$D = \begin{pmatrix} d_1 & 0 \\ -\chi \phi^* P^* & d_2 \end{pmatrix},$$

$$\phi^* = 1 - \frac{P^*}{P_m} > 0,$$

and

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} -\frac{bs^2 N^*}{(cP^* + sN^*)^2} & -\frac{bcsP^*}{(cP^* + sN^*)^2} - dN^* \\ dP^* - \frac{bcsP^*}{(cP^* + sN^*)^2} & -\frac{bc^2 P^*}{(cP^* + sN^*)^2} \end{pmatrix}.$$

Since $\Omega = (0, L)$ is one dimensional and bounded, we have the corresponding characteristic equation of the form

$$\lambda^2 - T_k \lambda + D_k = 0, \quad (5)$$

where

$$\begin{aligned} T_k &= -(d_1 + d_2) \left(\frac{k\pi}{L} \right)^2 + a_{11} + a_{22} < 0, \\ D_k &= \left[d_1 \left(\frac{k\pi}{L} \right)^2 - a_{11} \right] \left[d_2 \left(\frac{k\pi}{L} \right)^2 - a_{22} \right] - a_{12} \left(\chi \phi^* P^* \left(\frac{k\pi}{L} \right)^2 + a_{21} \right) \\ &= d_1 d_2 \left(\frac{k\pi}{L} \right)^4 - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 + d^2 P^* N^*. \end{aligned}$$

Based on the linear stability theory, for any nonnegative integer k , the constant equilibrium solution is locally asymptotically stable if and only if all roots of the characteristic equation have negative real parts. In other words, the equilibrium solution is unstable if the characteristic equation has a positive real part for some nonnegative integer.

Note that we always have $T_k < 0$ for any nonnegative integer k , therefore E^* is stable when $D_k > 0$ and is unstable when $D_k < 0$. Moreover, since $T_k \neq 0$, equation (5) has no purely imaginary root and Hopf bifurcation does not emerge at E^* for system (3).

For convenience, we denote the discriminant by

$$\Lambda = (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*)^2 - 4 d^2 d_1 d_2 P^* N^*.$$

Since $a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^* - 2d \sqrt{d_1 d_2 P^* N^*} < 0$, to guarantee $\Lambda > 0$, we only need

$$a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^* + 2d \sqrt{d_1 d_2 P^* N^*} < 0.$$

Solving the above inequation, we have

$$\chi > \chi_c = - \frac{a_{11} d_2 + a_{22} d_1 + 2d \sqrt{d_1 d_2 P^* N^*}}{a_{12} \phi^* P^*}.$$

Therefore, if $\chi > \chi_c$, then equation

$$d_1 d_2 \sigma^2 - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \sigma + d^2 P^* N^* = 0$$

has two distinct real roots:

$$\sigma_1 = \frac{-(a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) - \sqrt{\Lambda}}{2 d_1 d_2}$$

and

$$\sigma_2 = \frac{-(a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) + \sqrt{\Lambda}}{2 d_1 d_2}.$$

Assume further that

(H2) there exists $k \in \mathbb{N}^+$ such that $\sigma_1 < (\frac{k\pi}{L})^2 < \sigma_2$,

then we can get the linear stability results on the constant equilibrium solution E^* .

Theorem 1 *If assumption (H2) is satisfied, then the equilibrium solution E^* of system (3) is locally asymptotically stable when $\chi < \chi_c$, and is unstable when $\chi > \chi_c$.*

It is easy to see that the sensitivity coefficient of prey-taxis directly determines the linear stability of E^* . Theorem 1 also shows that system (3) may generate Turing pattern with prey-taxis. In contrast with the results in [14], Turing instability is not only induced by group defense of prey, but also by the attraction of prey, which mainly depends on the parameter values.

In the following, we will discuss the global stability of E^* .

Theorem 2 *If $\chi \leq \min\{\frac{2d_1}{M^2}, 2d_2\}$ and the conditions in Lemmas 1–2 are satisfied, then the equilibrium solution E^* of system (3) is globally asymptotically stable.*

Proof Let $(N(x, t), P(x, t))$ be a solution of system (3). Define the Lyapunov function

$$E(t) = \int_{\Omega} \int_{N^*}^N \frac{\xi - N^*}{\xi} d\xi dx + \int_{\Omega} \int_{P^*}^P \frac{\eta - P^*}{\eta} d\eta dx.$$

By using the equality

$$\int_{\Omega} g(u) \nabla \cdot (f(u) \nabla u) dx = \int_{\partial\Omega} g(u) f(u) \frac{\partial u}{\partial \nu} ds - \int_{\Omega} f(u) \nabla u \cdot \nabla g(u) dx,$$

we have

$$- \int_{\Omega} \nabla \cdot (\chi \phi(P) P \nabla N) dx = - \int_{\partial\Omega} \chi \phi(P) P \frac{\partial N}{\partial \nu} ds + \int_{\Omega} \chi \phi(P) P \nabla N \cdot \nabla 1 dx = 0.$$

By direct calculation, it follows that

$$\begin{aligned} \frac{dE(t)}{dt} &= \int_{\Omega} \frac{N - N^*}{N} \frac{\partial N}{\partial t} dx + \int_{\Omega} \frac{P - P^*}{P} \frac{\partial P}{\partial t} dx \\ &= \int_{\Omega} \frac{N - N^*}{N} \left[d_1 \Delta N + N \left(\frac{bs}{cP + sN} - dP - h \right) \right] dx \\ &\quad + \int_{\Omega} \frac{P - P^*}{P} \left[d_2 \Delta P - \nabla \cdot (\chi \phi(P) P \nabla N) + P \left(\frac{bc}{cP + sN} + dN - g \right) \right] dx \\ &\triangleq E_1 + E_2 + E_3, \end{aligned}$$

where

$$\begin{aligned} E_1 &= \int_{\Omega} \left[(N - N^*) \left(\frac{bs}{cP + sN} - dP - h \right) + (P - P^*) \left(\frac{bc}{cP + sN} + dN - g \right) \right] dx \\ &= - \int_{\Omega} \frac{b[cP + sN - (cP^* + sN^*)]^2}{(cP + sN)(cP^* + sN^*)} dx \\ &\leq 0, \end{aligned}$$

$$\begin{aligned}
E_2 &= \int_{\Omega} \frac{N - N^*}{N} d_1 \Delta N \, dx + \int_{\Omega} \frac{P - P^*}{P} d_2 \Delta P \, dx \\
&= -d_1 N^* \int_{\Omega} \frac{|\nabla N|^2}{N^2} \, dx - d_2 P^* \int_{\Omega} \frac{|\nabla P|^2}{P^2} \, dx, \\
E_3 &= - \int_{\Omega} \frac{P - P^*}{P} \nabla \cdot (\chi \phi(P) P \nabla N) \, dx \\
&= - \int_{\Omega} \left(1 - \frac{P^*}{P}\right) \nabla \cdot (\chi \phi(P) P \nabla N) \, dx \\
&= \int_{\Omega} \frac{P^*}{P} \nabla \cdot (\chi \phi(P) P \nabla N) \, dx \\
&= \int_{\partial\Omega} \frac{P^*}{P} \chi \phi(P) P \frac{\partial N}{\partial \nu} \, ds - \int_{\Omega} \chi \phi(P) P \nabla N \cdot \nabla \left(\frac{P^*}{P}\right) \, dx \\
&= \chi \int_{\Omega} \phi(P) \frac{P^*}{P} \nabla N \cdot \nabla P \, dx.
\end{aligned}$$

Taking into account the form of sensitivity function and Lemma 2, we have

$$\begin{aligned}
E_2 + E_3 &\leq \frac{1}{2} \chi P^* \int_{\Omega} \left(|\nabla N|^2 + \frac{|\nabla P|^2}{P^2} \right) \, dx \\
&\quad - \left(\int_{\Omega} d_1 N^* \frac{|\nabla N|^2}{M^2} \, dx + \int_{\Omega} d_2 P^* \frac{|\nabla P|^2}{P^2} \, dx \right) \\
&= - \int_{\Omega} \left(d_2 P^* - \frac{\chi P^*}{2} \right) \frac{|\nabla P|^2}{P^2} \, dx - \int_{\Omega} \left(\frac{d_1 N^*}{M^2} - \frac{\chi N^*}{2} \right) |\nabla N|^2 \, dx \\
&\leq 0.
\end{aligned}$$

It is obvious that $\frac{dE(t)}{dt} \leq 0$ and the equality holds if and only if $(N, P) = (N^*, P^*)$. It follows from LaSalle's invariance principle that the equilibrium solution E^* is globally asymptotically stable under the theorem conditions. This completes the proof. \square

According to Theorem 2, the stability of equilibrium solution can be maintained when the sensitivity coefficient χ of prey-taxis is appropriately small, and Turing pattern may occur when this coefficient is sufficiently large.

4 Existence of nonconstant steady state solution

In this section, we investigate the existence of nonconstant steady states of (3) by abstract bifurcation theory established in [31, 32]. More specifically, we shall study the nonconstant positive solutions to the following steady-state system:

$$\begin{cases} d_1 N'' + N \left(\frac{bs}{cP + sN} - dP - h \right) = 0, & x \in (0, L), \\ (d_2 P' - \chi \phi(P) P N')' + P \left(\frac{bc}{cP + sN} + dN - g \right) = 0, & x \in (0, L), \\ N'(x) = P'(x) = 0, & x = 0, L, \end{cases} \quad (6)$$

where ' denotes the differentiation with respect to x . Here we regard sensitivity coefficient χ as the bifurcation parameter and rewrite (6) into the abstract form as follows:

$$\mathcal{F}(N, P, \chi) = 0, \quad (N, P, \chi) \in \mathcal{X} \times \mathcal{X} \times \mathbb{R},$$

where

$$\mathcal{F}(N, P, \chi) = \begin{pmatrix} d_1 N'' + N(\frac{bs}{cP+sN} - dP - h) \\ (d_2 P' - \chi \phi(P)PN')' + P(\frac{bc}{cP+sN} + dN - g) \end{pmatrix},$$

$$\mathcal{X} = \{w \in H^2(0, L) | w'(0) = w'(L) = 0\}.$$

Then, any solution $(N, P) \in \mathcal{X} \times \mathcal{X}$ of $\mathcal{F} = 0$ is a classical solution of (6) by means of the standard elliptic regularity theory.

In the following, we shall verify the conditions of abstract bifurcation theory.

Firstly, the mapping $\mathcal{F} : \mathcal{X} \times \mathcal{X} \times \mathbb{R} \rightarrow \mathcal{Y} \times \mathcal{Y}$ is continuously differentiable because of the positivity of $cP + sN$, where $\mathcal{Y} = \mathcal{L}^2(0, L)$ and $\mathcal{F}(N, P, \chi) = 0$ for any $\chi \in \mathbb{R}$.

Secondly, for any fixed $(\hat{N}, \hat{P}) \in \mathcal{X} \times \mathcal{X}$, the Fréchet derivative of \mathcal{F} is given by

$$D_{(N,P)}\mathcal{F}(\hat{N}, \hat{P}, \chi)(N, P) = \begin{pmatrix} d_1 N'' + \hat{a}_{11}N + \hat{a}_{12}P \\ d_2 P'' - \chi(\hat{\phi}\hat{P}N' + \hat{\phi}\hat{N}'P + \hat{\phi}_P\hat{P}\hat{N}'P)' + \hat{a}_{21}N + \hat{a}_{22}P \end{pmatrix}, \quad (7)$$

where $\hat{\phi} = \phi(\hat{P})$, $\hat{\phi}_P = \phi_P(\hat{P})$.

Denote $\mathbf{u} = (N, P)^T$ and rewrite (7) into

$$D_{(N,P)}\mathcal{F}(\hat{N}, \hat{P}, \chi)(N, P) = A_0 \mathbf{u}'' + \mathbf{F}_0(\chi, \mathbf{u}, \mathbf{u}'), \quad (8)$$

where

$$A_0 = \begin{pmatrix} d_1 & 0 \\ -\chi\hat{\phi}\hat{P} & d_2 \end{pmatrix},$$

$$\mathbf{F}_0 = \begin{pmatrix} \hat{a}_{11}N + \hat{a}_{12}P \\ -\chi\hat{\phi}\hat{N}'P' - \chi[(\hat{\phi}\hat{N}')' + (\hat{\phi}_P\hat{P}\hat{N}')']P + \hat{a}_{21}N + \hat{a}_{22}P \end{pmatrix}.$$

It is not difficult to show that operator (8) is strictly elliptic since $d_1, d_2 > 0$. Furthermore, the Agmon condition of Remark 2.5 with one dimension in [32] is satisfied. Hence $D_{(N,P)}\mathcal{F}(\hat{N}, \hat{P}, \chi)(N, P)$ is a Fredholm operator with zero index due to Theorem 3.3 and Remark 3.4 in [32].

Thirdly, we seek the potential bifurcation values by verifying the condition

$$\mathcal{N}(D_{(N,P)}\mathcal{F}(\hat{N}, \hat{P}, \chi)) \neq \{0\}, \quad (9)$$

where \mathcal{N} represents the null space. Denote $(\hat{N}, \hat{P}) = (N^*, P^*)$, then we have

$$D_{(N,P)}\mathcal{F}(N^*, P^*, \chi)(N, P) = \begin{pmatrix} d_1 N'' + a_{11}N + a_{12}P \\ d_2 P'' - \chi\phi^*P^*N'' + a_{21}N + a_{22}P \end{pmatrix},$$

and the above null space is made up of the solutions of the following system:

$$\begin{cases} d_1 N'' + N(\frac{bs}{cP+sN} - dP - h) = 0, & x \in (0, L), \\ d_2 P'' - \chi\phi^*P^*N'' + P(\frac{bc}{cP+sN} + dN - g) = 0, & x \in (0, L), \\ N'(x) = P'(x) = 0, & x = 0, L. \end{cases} \quad (10)$$

To verify (9), we assume that $(N(x), P(x))$ is a solution of (10) and expand it into

$$N = \sum_{k=0}^{\infty} A_k \cos \frac{k\pi x}{L}, \quad P = \sum_{k=0}^{\infty} B_k \cos \frac{k\pi x}{L},$$

where A_k and B_k are constants to be determined. Thus, (9) is equivalent as that there exists at least a $k \in \mathbb{N}$ such that (A_k, B_k) is nontrivial. Plugging the expansions into (10) leads to

$$\begin{pmatrix} -d_1\left(\frac{k\pi}{L}\right)^2 + a_{11} & a_{12} \\ \chi\phi^*P^*\left(\frac{k\pi}{L}\right)^2 + a_{21} & -d_2\left(\frac{k\pi}{L}\right)^2 + a_{22} \end{pmatrix} \begin{pmatrix} A_k \\ B_k \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad k \in \mathbb{N}. \quad (11)$$

Since $a_{11}a_{22} - a_{12}a_{21} > 0$, the case $k = 0$ can be excluded. And for $k \in \mathbb{N}^+$, we can obtain that (9) holds when $\chi = \chi_k$, where

$$\chi_k = \frac{[d_1\left(\frac{k\pi}{L}\right)^2 - a_{11}][d_2\left(\frac{k\pi}{L}\right)^2 - a_{22}] - a_{12}a_{21}}{a_{12}\phi^*P^*\left(\frac{k\pi}{L}\right)^2}. \quad (12)$$

As a consequence, $\dim N(D_{(N,P)}F(N^*, P^*, \chi_k)) = 1$ and $N(D_{(N,P)}F(N^*, P^*, \chi_k)) = \text{span}\{(\overline{N}_k, \overline{P}_k)\}$, where

$$(\overline{N}_k, \overline{P}_k) = (1, S_k) \cos \frac{k\pi x}{L}, \quad (13)$$

and

$$S_k = \frac{d_1\left(\frac{k\pi}{L}\right)^2 - a_{11}}{a_{12}}, \quad k \in \mathbb{N}^+. \quad (14)$$

Basing on the analyses above, it can be sure that the local bifurcation can be found in system (3) at (N^*, P^*, χ_k) for each $k \in \mathbb{N}^+$.

Theorem 3 Assume that condition (H1) holds and

$$d_1d_2j^2k^2\left(\frac{\pi}{L}\right)^4 \neq a_{11}a_{22} - a_{12}a_{21}, \quad k \neq j, k, j \in \mathbb{N}^+.$$

Then, for each $k \in \mathbb{N}^+$, there exists $\delta > 0$ such that nonconstant positive solutions $(N_k(s, x), P_k(s, x), \chi_k(s))$ of (3) bifurcate from (N^*, P^*, χ_k) when $s \in (-\delta, \delta)$. The solutions are smooth functions of s such that

$$\begin{cases} (N_k(s, x), P_k(s, x)) = (N^*, P^*) + s(\overline{N}_k, \overline{P}_k) + s(\xi(s, x), \zeta_k(s, x)), \\ \chi_k(s) = \chi_k + s\kappa_1 + s^2\kappa_2 + O(s^3), \end{cases}$$

where κ_1 and κ_2 are constants, $(\overline{N}_k, \overline{P}_k)$ is given by (13), $(\xi(s, x), \zeta_k(s, x)) \in \mathcal{Z}$, and

$$\mathcal{Z} = \left\{ (N, P) \in \mathcal{X} \times \mathcal{X} \mid \int_0^L (N\overline{N}_k + P\overline{P}_k) dx = 0 \right\}.$$

Moreover, $(N_k(s, x), P_k(s, x), \chi_k(s))$ solves system (3) and all nonconstant solutions around (N^*, P^*, χ_k) must stay on the curve

$$\Gamma_k(s) = \{(N_k(s, x), P_k(s, x), \chi_k(s)) | s \in (-\delta, \delta)\}.$$

Proof To apply the Crandall–Rabinowitz local bifurcation theory in [31], we only need to further verify the following transversality condition:

$$\left. \frac{d}{d\chi} D_{(N,P)} \mathcal{F}(N^*, P^*, \chi)(\bar{N}_k, \bar{P}_k) \right|_{\chi=\chi_k} \notin \mathcal{R}(D_{(N,P)} \mathcal{F}(N^*, P^*, \chi_k)), \quad (15)$$

where \mathcal{R} denotes the range and

$$\left. \frac{d}{d\chi} D_{(N,P)} \mathcal{F}(N^*, P^*, \chi)(\bar{N}_k, \bar{P}_k) \right|_{\chi=\chi_k} = \begin{pmatrix} 0 \\ -\phi^* P^* \bar{N}_k'' \end{pmatrix}.$$

Then we prove (15) by contradiction. Suppose that there exists a nontrivial expression, which satisfies

$$\begin{pmatrix} d_1 \tilde{N}'' + a_{11} \tilde{N} + a_{12} \tilde{P} \\ d_2 \tilde{P}'' - \chi \phi^* P^* \tilde{N}'' + a_{21} \tilde{N} + a_{22} \tilde{P} \end{pmatrix} = \begin{pmatrix} 0 \\ -\phi^* P^* \bar{N}_k'' \end{pmatrix}.$$

Substituting the expansions

$$\tilde{N} = \sum_{k=0}^{\infty} \tilde{A}_k \cos \frac{k\pi x}{L}, \quad \tilde{P} = \sum_{k=0}^{\infty} \tilde{B}_k \cos \frac{k\pi x}{L}$$

into it, we have

$$\begin{pmatrix} -d_1 \left(\frac{k\pi}{L}\right)^2 + a_{11} & a_{12} \\ \chi \phi^* P^* \left(\frac{k\pi}{L}\right)^2 + a_{21} & -d_2 \left(\frac{k\pi}{L}\right)^2 + a_{22} \end{pmatrix} \begin{pmatrix} \tilde{A}_k \\ \tilde{B}_k \end{pmatrix} = \begin{pmatrix} 0 \\ \phi^* P^* \left(\frac{k\pi}{L}\right)^2 \end{pmatrix}. \quad (16)$$

Note that the coefficient matrix of (16) is singular, the right-hand side must be zero. It brings contradiction and (15) holds. Besides, based on the conditions of theorem, calculation may give rise to $\chi_k \neq \chi_j$ for all $k \neq j$. Thus the proof is complete. \square

5 The effect of time delay

The research in Sect. 2 indicates that prey-taxis does not cause Hopf bifurcation in delay-free system (3). For better understanding the spatiotemporal dynamics of the predator–prey system, we continue to consider the corresponding time-delay system (4) to seek the effect of digestion delay and the existence of time-periodic solutions.

If condition (H1) holds, then system (4) still has the unique equilibrium solution $E^* = (N^*, P^*)$. The characteristic equation of (4) at E^* is

$$\begin{vmatrix} \lambda + d_1 \left(\frac{k\pi}{L}\right)^2 - a_{11} & -a_{12} \\ -\chi \phi^* P^* \left(\frac{k\pi}{L}\right)^2 + \frac{bcSP^*}{(cP^* + sN^*)^2} - dP^* e^{-\lambda\tau} & \lambda + d_2 \left(\frac{k\pi}{L}\right)^2 - a_{22} \end{vmatrix} = 0,$$

which is equivalent to

$$\begin{aligned} \lambda^2 + \left[(d_1 + d_2) \left(\frac{k\pi}{L} \right)^2 - a_{11} - a_{22} \right] \lambda + d_1 d_2 \left(\frac{k\pi}{L} \right)^4 \\ - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 \\ + \frac{a_{12} bcs P^*}{(cP^* + sN^*)^2} - a_{12} d P^* e^{-\lambda \tau} + a_{11} a_{22} = 0. \end{aligned} \quad (17)$$

Obviously, equation (17) can be reduced to (5) with $\tau = 0$. When $\tau > 0$, we assume that $\lambda = i\omega$ ($\omega > 0$) is the root of characteristic equation (17). We have

$$\begin{aligned} -\omega^2 + i\omega \left[(d_1 + d_2) \left(\frac{k\pi}{L} \right)^2 - a_{11} - a_{22} \right] + d_1 d_2 \left(\frac{k\pi}{L} \right)^4 + \frac{a_{12} bcs P^*}{(cP^* + sN^*)^2} \\ + a_{11} a_{22} - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 - a_{12} d P^* (\cos \omega \tau - i \sin \omega \tau) = 0. \end{aligned}$$

Separating the real and imaginary parts leads to

$$\begin{cases} \omega^2 - d_1 d_2 \left(\frac{k\pi}{L} \right)^4 + (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 - \frac{a_{12} bcs P^*}{(cP^* + sN^*)^2} - a_{11} a_{22} \\ = -a_{12} d P^* \cos \omega \tau, \\ \omega [(d_1 + d_2) \left(\frac{k\pi}{L} \right)^2 - a_{11} - a_{22}] = a_{12} d P^* \sin \omega \tau. \end{cases}$$

Squaring the both equations and adding them, we have

$$\omega^4 + p_{1k} \omega^2 + p_{2k} = 0, \quad (18)$$

where

$$\begin{aligned} p_{1k} &= \left[(d_1 + d_2) \left(\frac{k\pi}{L} \right)^2 - a_{11} - a_{22} \right]^2 \\ &\quad - 2 \left[d_1 d_2 \left(\frac{k\pi}{L} \right)^4 - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 \right. \\ &\quad \left. + \frac{a_{12} bcs P^*}{(cP^* + sN^*)^2} + a_{11} a_{22} \right], \\ p_{2k} &= \left[d_1 d_2 \left(\frac{k\pi}{L} \right)^4 - (a_{11} d_2 + a_{22} d_1 + a_{12} \chi \phi^* P^*) \left(\frac{k\pi}{L} \right)^2 + \frac{a_{12} bcs P^*}{(cP^* + sN^*)^2} + a_{11} a_{22} \right]^2 \\ &\quad - a_{12}^2 d^2 P^{*2}. \end{aligned}$$

In order to analyze conveniently, we only discuss the spatially homogeneous case $k = 0$. In this situation equation (18) can be simplified to

$$\omega^4 + p_{10} \omega^2 + p_{20} = 0, \quad (19)$$

where

$$p_{10} = a_{11}^2 + a_{22}^2 - \frac{2a_{12}bcsP^*}{(cP^* + sN^*)^2},$$

$$p_{20} = \left[a_{11}a_{22} + \frac{a_{12}bcsP^*}{(cP^* + sN^*)^2} \right]^2 - a_{12}^2 d^2 P^{*2}.$$

Actually, if $a_{21} > 0$, then $p_{20} < 0$ and equation (19) has the unique positive root ω_0 . Thus characteristic equation (18) has a unique pair of imaginary roots $\pm i\omega_0$ with

$$\tau_j = \frac{1}{\omega_0} \left\{ 2\pi - \arccos \frac{\frac{a_{12}bcsP^*}{(cP^* + sN^*)^2} + a_{11}a_{22} - \omega_0^2}{a_{12}dP^*} + 2j\pi \right\}, \quad j = 0, 1, 2, \dots$$

Next, we prove the transversality condition. We rewrite the characteristic equation (17) when $k = 0$ and $\tau > 0$ as follows:

$$\lambda^2 - (a_{11} + a_{22})\lambda + \frac{a_{12}bcsP^*}{(cP^* + sN^*)^2} + a_{11}a_{22} + a_{12}dP^*e^{-\lambda\tau} = 0. \quad (20)$$

Differentiating both sides of (20), we have

$$2\lambda \frac{d\lambda}{d\tau} - (a_{11} + a_{22}) \frac{d\lambda}{d\tau} - a_{12}dP^*e^{-\lambda\tau} \left(\lambda + \tau \frac{d\lambda}{d\tau} \right) = 0,$$

and

$$\left[\frac{d\lambda}{d\tau} \right]^{-1} = \frac{[2\lambda - (a_{11} + a_{22})]e^{\lambda\tau}}{\lambda a_{12}dP^*} - \frac{\tau}{\lambda},$$

thus

$$\begin{aligned} \operatorname{Re} \left\{ \left[\frac{d\lambda}{d\tau} \right]^{-1} \right\}_{\lambda=i\omega_0, \tau=\tau_j} &= \operatorname{Re} \left\{ \frac{[2i\omega_0 - (a_{11} + a_{22})](\cos \omega_0 \tau_j + i \sin \omega_0 \tau_j)}{i\omega_0 a_{12}dP^*} - \frac{\tau_j}{i\omega_0} \right\} \\ &= \frac{2 \cos \omega_0 \tau_j}{a_{12}dP^*} - \frac{(a_{11} + a_{22}) \sin \omega_0 \tau_j}{\omega_0 a_{12}dP^*} \\ &= \frac{2a_{12}dP^* \cos \omega_0 \tau_j}{(a_{12}dP^*)^2} + \frac{(a_{11} + a_{22})^2}{(a_{12}dP^*)^2} \\ &= \frac{(a_{11} + a_{22})^2 - 2[\omega_0^2 - \frac{a_{12}bcsP^*}{(cP^* + sN^*)^2}]}{(a_{12}dP^*)^2} \\ &= \frac{\sqrt{p_{10}^2 - 4p_{20}}}{(a_{12}dP^*)^2} \\ &> 0. \end{aligned}$$

So far we have verified all the conditions of Hopf bifurcation theorem for partial differential equations proposed in [33, 34]. So we have the results on the existence of Hopf bifurcation solutions induced by time delay.

Theorem 4 Assume that condition (H1) holds and $a_{21} > 0$, we have:

- (i) If $\tau \in [0, \tau_0)$, then the equilibrium solution E^* of time-delay system (4) is locally asymptotically stable.
- (ii) $\tau = \tau_0$ is the Hopf bifurcation value and system (4) has spatially homogeneously time-periodic solutions around E^* .

6 Numerical simulations

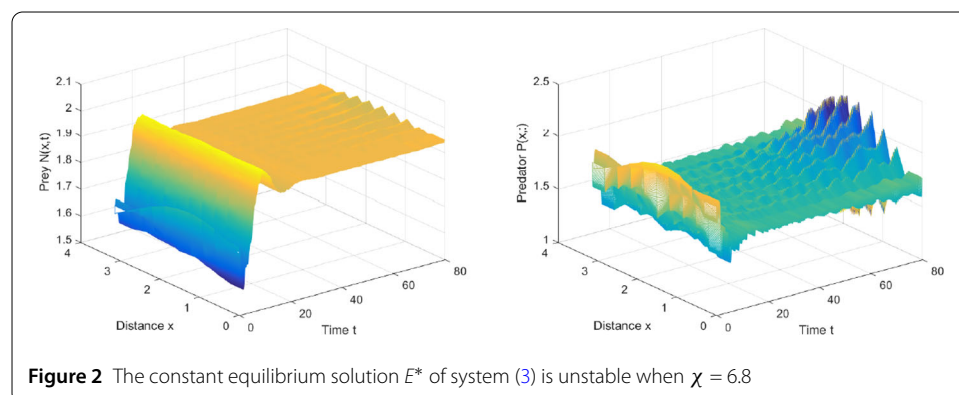
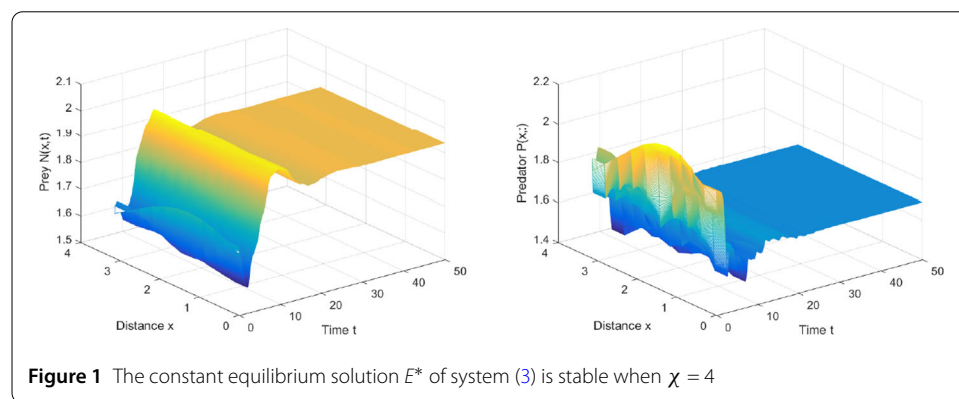
In this section, we shall conduct some numerical simulations to describe the previous theoretical analyses. For systems (3) and (4), we choose $\Omega = (0, \pi)$ and take the following system parameters:

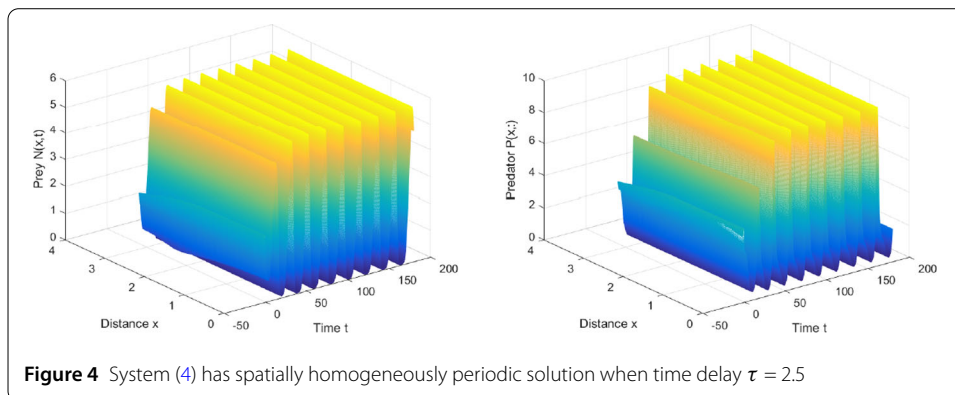
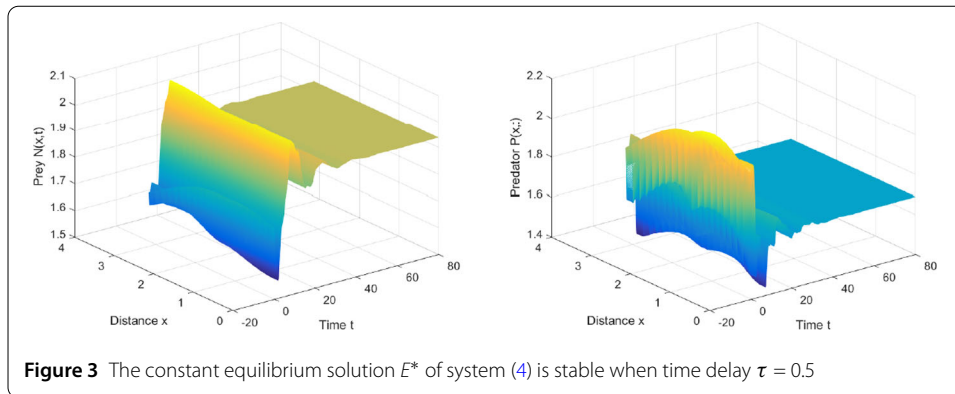
$$\begin{aligned} d_1 = d_2 = 0.01, \quad b = 1.2, \quad c = 0.1, \quad d = 0.25, \quad s = 0.2, \\ h = 0.01, \quad g = 0.7, \quad P_m = 3. \end{aligned}$$

In this situation, both systems (3) and (4) have the unique constant equilibrium solution $E^* = (1.93669, 1.68662)$.

For delay-free system (3), we can calculate the critical value $\chi_c = 5.65$. Then equilibrium solution E^* is asymptotically stable when the chemotactic coefficient χ is appropriately small (see Fig. 1). On the other hand, E^* is unstable when the coefficient χ is slightly large (see Fig. 2).

For time-delay system (4), we fix $\chi = 4$ and regard time delay τ as the bifurcation parameter. Numerical simulations in Fig. 3 show that the stability of equilibrium solution can be





maintained when time delay is small and the results in Fig. 4 illustrate that the equilibrium solution is no longer stable when time delay is large.

7 Conclusions

This paper investigates a reaction-diffusion-taxis predator–prey system without and with time delay. For the delay-free case, we first obtain the local and global stability of constant positive equilibrium solution by analyzing the distribution of characteristic roots and constructing an appropriate Lyapunov function, respectively. The stability results manifest that prey-taxis does not change the stability of equilibrium solution when the prey-taxis rate χ is small. We then regard the prey-tactic sensitivity coefficient χ as the bifurcation parameter and find the existence of nonconstant positive steady states. That is to say the prey-taxis effect can make the dynamic behaviors of the system more complicated. And for the time-delay case, we regard the digestion delay as the bifurcation parameter and obtain the existence of spatially homogeneously time-periodic solutions, which illustrates the importance of time delay effect.

Biologically, if the prey-taxis rate is weak, the distribution of both predator and prey species may tend to be stabilized over time. Otherwise, the spatial distribution of species will present inhomogeneity, which is the so-called stationary pattern. Furthermore, the periodic oscillations of species density distribution could be induced by digestion delay of predator.

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Competing interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

Authors' contributions

All authors contributed equally to the writing of this paper. All authors of the manuscript have read and agreed to its content and are accountable for all aspects of the accuracy and integrity of the manuscript.

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