Spatiotemporal dynamics induced by nonlocal competition in a diffusive predator-prey system with habitat complexity

Ruizhi Yang · Chenxuan Nie · Dan Jin

Received: 4 December 2021 / Accepted: 9 June 2022 / Published online: 27 June 2022
© The Author(s), under exclusive licence to Springer Nature B.V. 2022

Abstract In this paper, we study a delayed diffusive predator–prey model with nonlocal competition in prey and habitat complexity. The local stability of coexisting equilibrium is studied by analyzing the eigenvalue spectrum. Time delay inducing Hopf bifurcation is investigated by using time delay as bifurcation parameter. We give some conditions for determining the bifurcation direction and the stability of the bifurcating periodic solution by utilizing the normal form method and center manifold theorem. Our results suggest that only nonlocal competition and diffusion together can induce stably spatial inhomogeneous bifurcating periodic solutions.

Keywords Predator–prey · Nonlocal competition · Delay · Hopf bifurcation

1 Introduction

Predator–prey model is an important model in biomathematics, which is used to study the growth law of two populations with predator–prey relationship [1–5]. A classical predator–prey model is Lotka–Volterra model [6], which is investigated widely from different aspects [7–9]. In order to improve the realistic application of the Lotka–Volterra model, many scholars modified the functional response which is used to describe the effect of predators on prey. The classical functional response functions are Holling type I–III [10], Beddington–DeAngelis type [11], Crowley–Martin type [12], Hassell–Varley type [13], etc.

In the ecological environment, habitat complexity plays an important role, which can be used to control the size and growth trend of the population. Many works have shown that habitat complexity has a stabilizing effect on the predator–prey model [17–19]. Ma and Wang [21] proposed a predator–prey model with habitat complexity and time delay based on the Lotka–Volterra model, that is

\[
\begin{aligned}
\frac{du}{dt} &= ru \left(1 - \frac{u}{K}\right) - \frac{c(1-\beta)u^\alpha v}{1+ch(1-\beta)^{\alpha^2}}, \\
\frac{dv}{dt} &= ec(1-\beta)u^\alpha v(t-\tau) - dv.
\end{aligned}
\]  

(1.1)

All parameters are positive. The biological description of parameters is in Table 1. The authors assume there is a gestation delay in predator. In particular, parameter \( \beta \) is used to measure the strength of habitat complexity, such as oyster and coral reefs, mangroves, sea grass beds, and salt marshes [20]. The habitat complexity can be used to control the population growth. If \( \alpha = 1 \) (\( \alpha = 2 \)), the functional response is Holling type I (II). Ma and Wang [21] studied the positivity, boundedness, stability, and Hopf bifurcation of the model (1.1). They observed the stabilizing and destabilizing effects of habitat complexity and periodic oscil-
lation caused by time delay under some parameters. After that, assuming the habitat is heterogeneous, Li et al. [14] analyzed the effect of reaction–diffusion on the model (1.1), and suggested that spatially inhomogeneous periodic solutions may exist. But they did not show the existence of stably inhomogeneous periodic solutions. Motivated by the model (1.1), Wang [15] proposed a predator–prey model with modified Holling type III functional response to incorporate the effect of habitat complexity, the production delay, the gestation delay, and the linear harvesting effort. Ma [16] proposed a delay-induced nonautonomous predator–prey system with variable habitat complexity based on the model (1.1), and studied the permanence, positivity and boundedness, local and global stabilities, and Hopf bifurcation.

\[
\begin{align*}
\frac{\partial u(x, t)}{\partial t} &= d_1 \Delta u + ru \left(1 - \frac{1}{K} \int_{\Omega} G(x, y)u(y, t)dy \right) - \frac{c(1 - \beta)u^a v}{1 + ch(1 - \beta)u^a}, \\
\frac{\partial v(x, t)}{\partial t} &= d_2 \Delta v + \frac{ec(1 - \beta)u^a(t - \tau)v(t - \tau)}{1 + ch(1 - \beta)u^a(t - \tau)} - dv, \quad x \in \Omega, \ t > 0 \\
\frac{\partial u(x, t)}{\partial v} &= \frac{\partial v(x, t)}{\partial v} = 0, \quad x \in \partial \Omega, \ t > 0 \\
u(x, \theta) &= u_0(x, \theta) \geq 0, \quad v(x, \theta) = v_0(x, \theta) \geq 0, \quad x \in \bar{\Omega}, \theta \in [-\tau, 0].
\end{align*}
\]

In the ecological environment, the space is often inhomogeneous, and the spatial diffusion often occurs in population. Therefore, the reaction–diffusion equation may be more realistic when we study the predator–prey model. In addition, many scholars have studied the predator–prey model with reaction–diffusion, and suggested that diffusion can induce spatial pattern, inhomogeneous periodic solution [22, 23]. However, spatially homogeneous periodic solutions often appear in numerical simulation, which means the inhomogeneous periodic solutions are usually unstable. Therefore, we want to study the effect of diffusion term on the model (1.1), and whether inhomogeneous periodic solutions will appear?

In fact, the resources are limited in nature, and competition within the population always exists. This competition is usually nonlocal. In [24, 25], the authors suggested that the consumption of resources in spatial location is related not only to the local population density, but also to the number of nearby population density. They measured this effect by weighting and integrating, and modified the \( \frac{\partial u}{\partial t} \) as \( \frac{1}{\kappa} \int_{\Omega} G(x, y)u(y, t)dy \). \( G(x, y) \) is some kernel function. In [26], the authors studied a diffusive predator–prey model with nonlocal competition effect, including stability of positive constant steady state and Hopf bifurcation. Geng et al. [27] studied Hopf, Turing, double-Hopf, and Turing–Hopf bifurcations of a diffusive predator–prey model with nonlocal competition. Liu et al. [28] studied a diffusive predator–prey model with nonlocal competition and time delay. These works show that spatially inhomogeneous bifurcating periodic solutions are stable, which is different from the model without nonlocal competition. Therefore, we want to study the effect of nonlocal competition on the model (1.1), and whether some new dynamic phenomena will appear?

Motivated by these, we incorporate nonlocal competition and spatial diffusion on the model (1.1), as follow

\[
G(x, y) = \frac{1}{|\Omega|} = \frac{1}{l\pi}, \quad x, y \in \Omega.
\]

This is based on the assumption that the competition strength among prey individuals in the habitat is the same, that is the competition between any two prey is the same [27]. The boundary condition is Newman boundary, which is be explained by the fact that the habitat of the population is closed and no prey or predator can entering or leaving the habitat.

With the scope of our knowledge, there is no work to study the dynamics of the predator–prey model (1.2) with the nonlocal competition in prey, habitat complexity, reaction–diffusion, and gestation delay in predator, although it seems more realistic. In addition, almost no literature shows the existence of stably inhomogeneous periodic solutions induced by time delay in predator–
prey models with habitat complexity through numerical simulation. The aim of this paper is to study the dynamics of the predator–prey model (1.2), mainly focuses on the stability and Hopf bifurcation by using time delay as bifurcating parameter.

The rest of this paper is organized as follows. In Sect. 2, we study the stability of coexisting equilibrium and existence of Hopf bifurcation. In Sect. 3, we study the Property of Hopf bifurcation. In Sect. 3, we give some numerical simulations to illustrate the theoretical results. In Sect. 4, we give a conclusion.

### 2 Stability analysis

In this section, we will study the stability and existence of Hopf bifurcation at coexisting equilibrium. Denote \( \mathbb{N} \) as positive integer set, and \( \mathbb{N}_0 \) as nonnegative integer set. \((0, 0) \) and \((K, 0) \) are boundary equilibria of system (1.2). Make the following hypothesis

\[
\textbf{(H}_0\textbf{)} \quad \beta < \beta_* := 1 - \frac{d}{cK^n(e - dh)}, \quad e > dh.
\]

Ma and Wang [21] have studied the existence of the coexisting equilibrium, they obtained that system (1.2) has a unique coexisting equilibrium \( E_*(u_*, v_*) \) when hypothesis \((\textbf{H}_0) \) holds, where

\[
u_* = \left[ \frac{c}{d} \left( 1 - \beta \right)(e - dh) \right]^{-\frac{1}{n}}, \quad u_* = \frac{eru_*(K - u_*)}{dK}.
\]

In addition, Ma and Wang [21] showed that increasing the habitat complexity \( \beta \) has a positive impact on prey’s equilibrium density and a negative impact on predator’s equilibrium density. But the lower degree of habitat complexity has a positive effect predator’s density.

Linearize system (1.2) at \( E_*(u_*, v_*) \)

\[
\frac{\partial u}{\partial t} \begin{pmatrix} u(x, t) \\ v(x, t) \end{pmatrix} = D \left( \frac{\Delta u(t)}{\Delta v(t)} \right) + L_1 \begin{pmatrix} u(x, t) \\ v(x, t) \end{pmatrix} \\
+ L_2 \begin{pmatrix} u(x, t - \tau) \\ v(x, t - \tau) \end{pmatrix} + L_3 \begin{pmatrix} \dot{u}(x, t) \\ \dot{v}(x, t) \end{pmatrix}, \tag{2.1}
\]

where

\[
D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}, \quad L_1 = \begin{pmatrix} a_1 & a_2 \\ 0 & -d \end{pmatrix}, \quad L_2 = \begin{pmatrix} 0 & 0 \\ b_1 & d \end{pmatrix}, \quad L_3 = \begin{pmatrix} \hat{a} & 0 \\ 0 & 0 \end{pmatrix},
\]

\[
a_1 = r \left( 1 - \frac{u_*}{K} \right) + \frac{\alpha(1 - \beta)cv_*u_*^{a-1}}{(1 - \beta)chu_*^{a} + 1}^2, \]

\[
a_2 = -\frac{(1 - \beta)cu_*^a}{(1 - \beta)chu_*^{a} + 1} < 0,
\]

\[
b_1 = \frac{\alpha(1 - \beta)cev_*u_*^{a-1}}{(1 + (1 - \beta)chu_*^{a})^2} > 0, \quad \hat{a} = -\frac{ru_*}{K} < 0,
\]

and \( \hat{u} = \frac{1}{1 + \pi} \int_0^{\pi} u(y, t)dy \). The characteristic equation are

\[
\lambda^2 + A_n\lambda + B_n + (C_n - d\lambda)e^{-\lambda \tau} = 0, \quad n \in \mathbb{N}_0,
\]

where

\[
A_0 = -(a_1 + \hat{a} - d), \quad B_0 = -(a_1 + \hat{a})d, \quad C_0 = \hat{a}d + a_1d - a_2b_1,
\]

\[
A_n = (d_1 + d_2)\frac{n^2}{l^2} - a_1 + d, \quad B_n = d_1
\]

\[
d_2\frac{n^4}{l^4} + (dd_1 - a_1d_2)\frac{n^2}{l^2} - a_1d,
\]

\[
C_n = -dd_1\frac{n^2}{l^2} + a_1d - a_2b_1, \quad n \in \mathbb{N}.
\]

#### 2.1 The case of \( \tau = 0 \)

We will first discuss the stability of the coexisting equilibrium when the delay \( \tau = 0 \). Make the following hypothesis

\[
\text{...}
\]
(H₁) \( a_1 + \hat{a} < 0, \ A_n - d > 0, \ B_n + C_n > 0, \)
for \( n \in \mathbb{N} \).

Lemma 2.1 Assume \((H_0)\) and \((H_1)\) hold. Equation (2.3) has a pair of purely imaginary roots \( \pm io_n \) at \( \tau^{*}_n, \ j \in \mathbb{N}_0, \ n \in \mathbb{S}, \) where

\[
\omega_n = \sqrt{\frac{1}{2} - \left( A_n^2 - 2B_n - d^2 \right) + \sqrt{(A_n^2 - 2B_n - d^2)^2 - 4(B_n^2 - C_n^2)}}. 
\]

(H₂) \( a_1 + \hat{a} < 0, \ A_k - d < 0 \) (or \( B_k + C_k < 0 \)),
for some \( k \in \mathbb{N} \).

Theorem 2.1 For system (1.2), assume \( \tau = 0 \) and \((H_0)\) holds. If \((H_1)\) hold, \( E_s(u_s, v_s) \) is locally asymptotically stable. If \((H_2)\) holds, \( E_s(u_s, v_s) \) is Turing unstable.

Proof When \( \tau = 0 \), the characteristic Eq. (2.3) are
\[
\lambda^2 - (a_1 + \hat{a})\lambda - a_2 b_1 = 0, \quad n = 0. \tag{2.5}
\]
and
\[
\lambda^2 - (A_n - d)\lambda + B_n + C_n = 0, \quad n \in \mathbb{N}. \tag{2.6}
\]
If \((H_1)\) holds, we can obtain that the characteristic root of (2.5) and (2.6) all have negative real parts. Then, \( E_s(u_s, v_s) \) is locally asymptotically stable. If \((H_2)\) holds, we can obtain that the characteristic roots of (2.5) all have negative real parts. And the characteristic equation (2.6) at least have one root with positive real part. Then, \( E_s(u_s, v_s) \) is Turing unstable.

Remark 2.1 Since the hypothesis \((H_1)\) is too complicated, we just give a sufficient condition to ensure that \((H_1)\) holds, that is
\[
r > r_s := \left[ \left( 1 - \frac{a_2}{K} \right) \left( \alpha (1 - \frac{d}{\tau}) - 1 \right) \right]^{-1} > 0. \text{This is equivalent to } a_1 < 0, \text{thus ensuring that the hypothesis } (H_1) \text{ holds. When } \tau = 0, \text{by Theorem 2.1, } E_s(u_s, v_s) \text{ is locally asymptotically stable when } (H_0) \text{ holds and } r \text{ is larger than the critical value } r_s. \text{This means that the prey and predator will coexist when } (H_0) \text{ holds and } r \text{ is large enough, and their densities will tend to the coexisting equilibrium and distribute homogeneously in space.}
\]

2.2 The case of \( \tau > 0 \)

Now, We will discuss the stability of the coexisting equilibrium when the delay \( \tau > 0 \).

Next, we verify the transversal condition for the existence of Hopf bifurcation.

Lemma 2.2 Assume \((H_0)\) and \((H_1)\) hold. Then,
\[
\text{Re} \left[ \frac{d}{d\tau} \right]_{\tau=\tau} > 0 \quad \text{for } n \in \mathbb{S}, \quad j \in \mathbb{N}_0.
\]
Proof By (2.3), we have
\[
\left( \frac{d\lambda}{d\tau} \right)^{-1} = \frac{2\lambda + A_n - de^{-\lambda \tau} - \frac{\tau}{\lambda}}{(C_n - d\lambda)\lambda e^{-\lambda \tau} - \frac{\tau}{\lambda}}.
\]
Then,
\[
\text{Re}\left( \frac{d\lambda}{d\tau} \right)^{-1}\bigg|_{\tau = \tau'_n} = \text{Re}\left[ \frac{2\lambda + A_n - de^{-\lambda \tau} - \frac{\tau}{\lambda}}{(C_n - d\lambda)\lambda e^{-\lambda \tau} - \frac{\tau}{\lambda}} \right]\bigg|_{\tau = \tau'_n}
\]
\[
= \left[ \frac{1}{C_n^2 + d^2\omega^2(2\omega^2 + A_n^2 - 2B_n - d^2)} \right]_{\tau = \tau'_n} > 0.
\]
Denote \( \tau_s = \min\{\tau'_n | n \in \mathbb{S} \} \). According to the above analysis, we have the following theorem.

\[Δ\]

Remark 2.2 Comparing Theorem 2.2 with Theorem 2.1, we can see that the gestation delay \( \tau \) can induce the instability of the coexisting equilibrium, although other parameters have ensured that the coexisting equilibrium is stable when \( \tau = 0 \). The prey and predator will coexist when \( \tau \in [0, \tau_s) \), and their densities will tend to the coexisting equilibrium and distribute homogeneously in space. But when the delay \( \tau > \tau_s \), the prey and predator will coexist with the form of periodic oscillation. However, whether the spatial oscillation is homogeneous or inhomogeneous requires us to analyze next.

3 Property of Hopf bifurcation

To better understand the properties of bifurcating periodic solutions, such as bifurcating direction, stability of bifurcating periodic solutions, we give detailed computation of some parameters determining these properties of Hopf bifurcation by the method in [29,30]. For fixed \( j \in \mathbb{N}_0 \) and \( n \in \mathbb{S} \), we denote \( \bar{\tau} = \tau'_n \). Let \( \bar{u}(x, t) = u(x, \tau t) - u_s \) and \( \bar{v}(x, t) = v(x, \tau t) - v_s \).

We rewrite system (1.2) as following system

\[
\frac{\partial u}{\partial t} = \tau[d_1\Delta u + r(u + u_s)\left(1 - \frac{1}{K}\int_0^{\bar{\tau}} (u(y, t) + u_s)dy\right) - \frac{c(1 - \beta)(u + u_s)^\alpha(v + v_s)}{1 + c\bar{h}(1 - \beta)(u + u_s)^\alpha}] + h.o.t.,
\]
\[
\frac{\partial v}{\partial t} = \tau[d_2\Delta v + \frac{ec(1 - \beta)(u(t - 1) + u_s)^\alpha(v(t - 1) + v_s)}{1 + c\bar{h}(1 - \beta)(u(t - 1) + u_s)^\alpha} - d(v + v_s)] + h.o.t.,
\]

\[
\frac{\partial u}{\partial t} = \tau[d_1\Delta u + a_1u + a_2v + \hat{\alpha}u + \alpha_1u^2 + \alpha_2uv + \alpha_3u^3 + \alpha_4u^2v] + h.o.t.,
\]
\[
\frac{\partial v}{\partial t} = \tau[d_2\Delta v + b_1u(t - 1) + dv(t - 1) - dv + \beta_1u^2(t - 1) + \beta_2u(t - 1)v(t - 1) + \beta_3u^3(t - 1) + \beta_4u^2(t - 1)v(t - 1)] + h.o.t.,
\]

**Theorem 2.2** Assume (H0) and (H1) hold, then the following statements are true for system (1.2).

- \( E_s(u_s, v_s) \) is locally asymptotically stable for \( \tau \in [0, \tau_s) \).
- \( E_s(u_s, v_s) \) is unstable for \( \tau > \tau_s \).
- \( \tau = \tau_j \) or \( \tau'_n \) \( (n \in \mathbb{S}, j \in \mathbb{N}_0) \) are Hopf bifurcation values of system (1.2).
where

\[
\begin{align*}
\alpha_1 &= -\frac{\alpha(\beta - 1)cv_\ast u_\ast^{-2}(\alpha + (\alpha + 1)(\beta - 1)chu_\ast^{\alpha} - 1)}{2 ((\beta - 1)chu_\ast^{\alpha} - 1)^3}, \\
\alpha_2 &= \frac{\alpha(\beta - 1)cv_\ast u_\ast^{-1}}{((\beta - 1)chu_\ast^{\alpha} - 1)^2}, \\
\alpha_3 &= \frac{\alpha(\beta - 1)cv_\ast u_\ast^{-3}(\alpha^2 - 3\alpha + (\alpha^2 + 3\alpha + 2)(\beta - 1)^2c^2h^2u_\ast^{2\alpha} + 4(\alpha^2 - 1)(\beta - 1)chu_\ast^{\alpha} + 2)}{6 ((\beta - 1)chu_\ast^{\alpha} - 1)^4}, \\
\alpha_4 &= \frac{\alpha(\beta - 1)cev_\ast u_\ast^{-2}(\alpha + (\alpha + 1)(\beta - 1)chu_\ast^{\alpha} - 1)}{2 ((\beta - 1)chu_\ast^{\alpha} - 1)^3}, \\
\beta_1 &= \frac{\alpha(\beta - 1)cev_\ast u_\ast^{-1}(\alpha + (\alpha + 1)(\beta - 1)chu_\ast^{\alpha} - 1)}{2 ((\beta - 1)chu_\ast^{\alpha} - 1)^2}, \\
\beta_2 &= \frac{\alpha(\beta - 1)cev_\ast u_\ast^{-3}(\alpha^2 - 3\alpha + (\alpha^2 + 3\alpha + 2)(\beta - 1)^2c^2h^2u_\ast^{2\alpha} + 4(\alpha^2 - 1)(\beta - 1)chu_\ast^{\alpha} + 2)}{6 ((\beta - 1)chu_\ast^{\alpha} - 1)^4}, \\
\beta_3 &= \frac{\alpha(\beta - 1)cev_\ast u_\ast^{-2}(\alpha + (\alpha + 1)(\beta - 1)chu_\ast^{\alpha} - 1)}{2 ((\beta - 1)chu_\ast^{\alpha} - 1)^3}.
\end{align*}
\]

Define the real-valued Sobolev space \( X := \{(u, v)^T : u, v \in H^2(0, l\pi), (u_x, v_x)|_{x=0,l\pi}=0 \} \), the complexification of \( X \) \( X_\mathbb{C} := X \oplus iX = \{x_1 + ix_2 | x_1, x_2 \in X \} \). and the inner product \( \langle \tilde{u}, \tilde{v} \rangle := \int_0^{l\pi} \bar{u}_1v_1dx + \int_0^{l\pi} \bar{u}_2v_2dx \) for \( \tilde{u} = (u_1, u_2)^T, \tilde{v} = (v_1, v_2)^T, \tilde{u}, \tilde{v} \in X_\mathbb{C} \). The phase space \( \mathcal{C} \) \( \mathcal{C} := C([-1,0], X) \) is with the sup norm, then we can write \( \phi_t \in \mathcal{C}, \phi_t(\theta) = \phi(t+\theta) \) or \( -1 \leq \theta \leq 0 \). Denote \( \beta_n^{(j)}(x) = (\gamma_n(x), x)^T, \beta_n^{(j)}(x) = (0, \gamma_n(x))^T, \) and \( \beta_n = \{ \beta_n^{(1)}(x), \beta_n^{(2)}(x) \} \), where \( \{ \beta_n^{(j)}(x) \} \) is an orthonormal basis of \( X \). We define the subspace of \( \mathcal{C} \) as \( \mathcal{B}_n := \text{span}\{< \phi(\cdot), \beta_n^{(j)}(\cdot) > \beta_n^{(j)}(\phi \in \mathcal{C}), j = 1, 2 \}, n \in \mathbb{N} \). There exists a \( 2 \times 2 \) matrix function \( \eta^\ast(\sigma, \xi) -1 \leq \sigma \leq 0, \) such that \( -\dot{\tau}D^2_{\tau\xi} \phi(0) + \dot{\tau}L(\phi) = \int_{-1}^{0} d\eta^\ast(\sigma, \tau) \phi(\sigma) \) for \( \phi \in \mathcal{C} \). The bilinear form on \( \mathcal{C}^\ast \times \mathcal{C} \) is defined by

\[
(\psi, \phi) = \psi(0)\phi(0) - \int_{-1}^{0} \int_{\xi=0}^{\sigma} \psi(\xi - \sigma) d\eta^\ast(\sigma, \tau) \phi(\xi) d\xi,
\]

for \( \phi \in \mathcal{C}, \psi \in \mathcal{C}^\ast \). Define \( \tau = \tilde{\tau} + \mu \), then the system undergoes a Hopf bifurcation at \((0, 0)\) when \( \mu = 0 \), with a pair of purely imaginary roots \( \pm io\omega_0 \). Let \( A_0 \) denote the infinitesimal generators of semigroup, and \( A_0^* \) be the formal adjoint of \( A \) under the bilinear form (3.3). Define the following function

\[
\delta(n_0) = \begin{cases} 
1 & n_0 = 0, \\
0 & n_0 \in \mathbb{N}.
\end{cases}
\]

Choose \( \eta_0(\sigma, \tilde{\tau}) = (-n_0^2/\pi^2)D + L_1 + L_3\delta(n_0) \),

\( \eta_0(-1, \tilde{\tau}) = -\dot{\tau}L_2, \eta_0(\sigma, \tilde{\tau}) = 0 \) for \( -1 < \sigma < 0 \).

Let \( p(\theta) = p(0)e^{io_0\tilde{\tau}} \) \( (\theta \in [-1, 0]), q(\theta) = q(0)e^{-io_0\tilde{\tau}} \) \( (\theta \in [0, 1]) \), be the eigenfunctions of \( A(\tilde{\tau}) \) and \( A^* \) corresponds to \( i o_0 \tilde{\tau} \), respectively. We can choose \( p(0) = (1, p_1)^T, q(0) = M(1, q_2) \), where \( p_1 = \frac{1}{a_2}(io_0 + dl_2^2/\pi^2 - a_1 - i\delta(n_0)), q_2 = a_2/(io_0 + dl_2^2/\pi^2 + d + d_2a^2/\pi^2) \), and \( M = (1 + p_1q_2 + \tilde{\tau}(q_2b_1 + dp_1q_2)e^{-io_0\tilde{\tau}})^{-1} \). Then, (3.1) can be rewritten in an abstract form

\[
\frac{dU(t)}{dt} = (\tilde{\tau} + \mu)D\Delta U(t) + (\tilde{\tau} + \mu)[L_1(U_i) + L_2U(t - 1) + L_3\dot{U}(t)] + F(U_i, \dot{U}_i, \mu).
\]
\[ F(\phi, \mu) = (\tilde{\tau} + \mu) \left( \alpha_1 \phi_1^2(0) + \hat{\alpha}_1 \phi_1(0) \hat{\phi}_1(0) + \alpha_2 \phi_1(0) \phi_2(0) + \alpha \phi_1^3(0) + \alpha^4 \phi_1^2(0) \phi_2(0) \right), \]

\[ \gamma_n(x) = A \omega + H(z, \bar{z}, \theta), \]
Theorem 3.1 For any critical value $\tau^j_n$ ($n \in \mathbb{S}$, $j \in \mathbb{N}_0$), we have the following results.

- When $\mu_2 > 0$ (resp. <0), the Hopf bifurcation is forward (resp. backward).
- When $\beta_2 < 0$ (resp. >0), the bifurcating periodic solutions on the center manifold are orbitally asymptotically stable (resp. unstable).
- When $T_2 > 0$ (resp. $T_2 < 0$), the period increases (resp. decreases).

Remark 3.1 In Theorem 3.1, when Hopf bifurcation is forward (backward), then the bifurcating periodic solutions exist for $\tau > \tilde{\tau}$ ($\tau < \tilde{\tau}$), where $\tilde{\tau}$ is some critical value $\tau = \tau^j_n$. Then, the prey and predator’s densities will oscillate periodically when $\tau > \tilde{\tau}$ ($\tau < \tilde{\tau}$). If the periodic solution is stable, the densities of prey and predator will produce periodic oscillation and converge to a stable periodic solution. In addition, the periodic solutions corresponding with the critical $\tau^j_n$ are spatially homogeneous, and the periodic solutions corresponding with the critical $\tau^j_{n+1}$ ($n > 0$) are spatially inhomogeneous.

4 Numerical simulations

To analyze the effect of diffusion term and nonlocal competition, we compare our results with the work [21] and the following model without nonlocal competition.

\[
\begin{align*}
\frac{\partial u(x, t)}{\partial t} &= d_1 \Delta u + ru \left(1 - \frac{u}{K}\right) - \frac{c(1 - \beta)u^\sigma v}{1 + ch(1 - \beta)u^\alpha}, \\
\frac{\partial v(x, t)}{\partial t} &= d_2 \Delta v + \frac{ev(1 - \beta)u^\alpha(t - \tau)v(t - \tau)}{1 + ch(1 - \beta)u^\alpha(t - \tau)} - dv, \quad x \in \Omega, \ t > 0 \\
\frac{\partial u(x, t)}{\partial \nu} &= \frac{\partial v(x, t)}{\partial \nu} = 0, \quad x \in \partial \Omega, \ t > 0 \\
u(x, \theta) &= u_0(x, \theta) \geq 0, \quad v(x, \theta) = v_0(x, \theta) \geq 0, \quad x \in \bar{\Omega}, \ \theta \in [-\tau, 0].
\end{align*}
\]

By Theorem 3.1, when Hopf bifurcation occurs when $\tau = \tau_*$.

Choose the same parameters with [21].

\[
d = 1.16, \ K = 300, \ c = 0.23, \ h = 0.054, \ e = 0.115, \ \alpha = 1, \ \tau = 2.65.
\]

Fix $d_1 = 0.1$, $d_2 = 0.1$, $l = 0.5$, the bifurcation diagram of system (1.2) for $\beta$ and $\tau$ is in Fig. 1. It shows that the habitat complexity has stabilizing effect which is consistent with [21]. However, with the increase in the habitat complexity, spatially inhomogeneous periodic solutions will appear.

If we choose $\beta = 0.18$, then $(u_*, v_*) = (117.4610, 18.7768)$ is a unique coexisting equilibrium. By direct computation, we have $\tau_* = \tau_0^1 \approx 0.883 < \tau_0^0 \approx 0.2860$. By Theorem 2.2, we know that $E_t(u_*, v_*)$ is locally asymptotically stable when $\tau \in (0, \tau_0^1)$ (Fig. 2a, b), in which the densities of prey and predator will tend to the coexisting equilibrium and distribute homogeneously in space. This is consistent with the results in [21] and for model (4.1) (Fig. 2c, d).

For model (1.2), Hopf bifurcation occurs when $\tau = \tau_*$. By Theorem 3.1, we have $\mu_2 \approx 1.6767 * 10^{-6} > 0$, $\beta_2 \approx -2.0497 * 10^{-6} < 0$, $T_2 \approx 4.3181 * 10^{-7} > 0$.

Hence, the stably spatially inhomogeneous bifurcating periodic solutions exist for $\tau > \tau_*$ (Fig. 3a, b, c, d), in which the densities of prey and predator will oscillate periodically and distribute inhomogeneously in space. This is inconsistent with the results in [21] and for model (4.1) (Fig. 3e, f), where $(u_*, v_*)$ is local.
Fig. 1 Bifurcation diagram of system (1.2) for $\beta$ and $\tau$

Spatiotemporal dynamics induced by nonlocal competition

stable when $\tau = 0.15$. In the model (4.1), the densities of prey and predator will still tend to the coexisting equilibrium and distribute homogeneously in space.

When $\tau^0_0 < \tau < \tau^0_1$, we can still observe stably spatially inhomogeneous bifurcating periodic solutions for model (1.2) (Fig. 4a, b, c, d), but spatially homogeneous bifurcating periodic solutions for model (4.1) (Fig. 4e, f, g, h). This means that although the density of prey and predator will oscillate periodically with the increase in time delay, the final spatial distribution form is different. This show that only nonlocal competition and diffusion together can induce stably spatially inhomogeneous periodic solutions. In addition, from Figs. 2, 3, and 4, we know that time delay can destroy the stability of coexistence equilibrium and cause spatially inhomogeneous periodic oscillation.

4.2 $\alpha = 2$

Choose the same parameters with [21].

Fix $d_1 = 0.3$, $d_2 = 0.1$, $l = 1.2$, the bifurcation diagram of system (1.2) for $\beta$ and $\tau$ is in Fig. 5. It shows that the habitat complexity has stabilizing effect which is consistent with [21]. However, with the increase in the habitat complexity, spatially inhomogeneous periodic solutions will appear.

We choose $\beta = 0.68$, then $(u_\star, v_\star) = (39.2236, 8.9574)$ is a unique coexisting equilibrium. Hypothesis (H0) and (H1) is satisfied. By direct computation, we have $\tau_\star = \tau_1^0 \approx 0.0301 < \tau_0^1 \approx 0.0644$. By Theorem 2.2, we know that $E_\star(u_\star, v_\star)$ is locally asymptotically stable when $\tau \in [0, \tau_\star)$ (Fig. 6a, b), in which the densities of prey and predator will tend to the coexisting equilibrium and distribute homogeneously in space. This is consistent with the results in [21] and for model (4.1) (Fig. 6c, d).

For model (1.2), Hopf bifurcation occurs when $\tau = \tau_\star$. By Theorem 3.1, we have

$$
\mu_2 \approx 2.1269 \times 10^{-6} > 0, \quad \beta_2 \\
\approx -4.81928 \times 10^{-6} < 0, \quad T_2 \approx 5.6381 \times 10^{-5} > 0.
$$

Hence, the stably spatially inhomogeneous bifurcating periodic solutions exist for $\tau > \tau_\star$ (Fig. 7a, b, c, d), in which the densities of prey and predator will oscillate periodically and distribute inhomogeneously.
in space. This is inconsistent with the results in [21] and for model (4.1), in which \((u_*, v_*)\) is local stable with the same parameters (Fig. 7e, f). In the model (4.1), the densities of prey and predator will still tend to the coexisting equilibrium and distribute homogeneously in space.

When \(\tau_1^0 < \tau < \tau_0^0\), we can still observe stably spatially inhomogeneous bifurcating periodic solutions for model (1.2) (Fig. 8a, b, c, d), but spatially homogeneous bifurcating periodic solutions for model (4.1) (Fig. 8e, f, g, h). This also means that although the density of prey and predator will oscillate periodically with the increase in time delay, the final spatial distribution form is different. In addition, from Figs. 6, 2, and 8, we know that time delay can destroy the stability of coexistence equilibrium and cause spatially inhomogeneous periodic oscillation.

4.3 \(\alpha = 3\)

Choose the same parameters with [21].

\[
d = 1.16, \quad K = 30, \quad c = 0.24, \quad h = 0.054, \quad e = 0.07, \quad \alpha = 3, \quad r = 2.65.
\]

Fix \(d_1 = 0.5, \ d_2 = 0.1, \ l = 0.75\), the bifurcation diagram of system (1.2) for \(\beta\) and \(\tau\) is in Fig. 9. It shows that the habitat complexity has stabilizing effect which is consistent with [21].

Fix \(\beta = 0.68\), then \((u_*, v_*) = (12.7079, 1.1714)\) is a unique coexisting equilibrium. By direct computa-
Spatiotemporal dynamics induced by nonlocal competition

Fig. 3 The numerical simulations for the models (1.2) (a, d) and (4.1) (e, f) with $\beta = 0.18, \tau = 0.15$ and initial values $u_0(x) = u^* + 0.1\cos x, v_0(x) = v^* - 0.1\cos x$. The coexisting equilibrium $(u^*, v^*)$ is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u^*, v^*)$ is stable for the model (4.1).

By Theorem 2.2, we know that $E_*(u^* \approx 12.7079, v^* \approx 1.1714)$ is locally asymptotically stable when $\tau \in [0, \tau_*)$ for models (1.2) and (4.1) (Fig. 10), in which the densities of prey and predator will oscillate periodically and distribute inhomogeneously in space.

The Hopf bifurcation occurs when $\tau = \tau_*$. By Theorem 3.1, we have

$$\mu_2 \approx 2.8642 \times 10^{-4} > 0, \quad \beta_2 \approx -2.0057 \times 10^{-4} < 0, \quad T_2 \approx 7.7547 \times 10^{-4} > 0.$$ 

Hence, the stably spatially inhomogeneous bifurcating periodic solutions exist for $\tau > \tau_*$ (Fig. 11a, b,
Fig. 4 The numerical simulations for the models (1.2) (a, b, c, d) and (4.1) (e, f, g, h) with $\beta = 0.18 \tau = 0.3$ and initial values

$u_0(x) = u_* + 0.1\cos x, \quad v_0(x) = v_* - 0.1\cos x$. The coexisting equilibrium $(u_*, v_*)$ is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u_*, v_*)$ is unstable and there exists a spatially homogeneous periodic solution for the model (4.1)
Inhomogeneous oscillation
Homogeneous oscillation
Stable region

5 Conclusion and discussion

In this paper, we study a delayed diffusive predator–prey model with nonlocal competition in prey and habitat complexity, which seems more realistic. We mainly study the local stability of coexisting equilibrium and existence of Hopf bifurcation. We also studied the property of bifurcating periodic solutions by the normal form method and center manifold theorem.

Our work shows that the habitat complexity has stabilizing effect when \( \alpha = 1, 2, 3 \), which is consistent with [21]. Under the same parameters with [21], when \( \beta \) cross some values, the spatial inhomogeneous Hopf bifurcation curve is below the homogeneous Hopf bifurcation curve. Then, the stably spatial inhomogeneous periodic solutions will appear first when \( \alpha = 1, 2 \). Under some parameters, the inhomogeneous oscillation curve is always below the homogeneous oscillation curve when \( \alpha = 3 \). Then, the stably spatial inhomogeneous periodic solutions will always appear first.

We compared the model (1.2) with the model (4.1) through numerical simulations under the same parameters, and obtained different results. In the model (4.1), the stable periodic solutions are always spatially homogeneous, but the inhomogeneous periodic solutions emerge in the model (1.2). In the real world, the spatial distribution of prey and predator is always inhomogeneous, so the inhomogeneous periodic solution seems...
Fig. 6 The numerical simulations for the models (1.2) (a, b) and (4.1) (c, d) with $\beta = 0.68 \tau = 0.02$ and initial values $u_0(x) = u_0 + 0.1\cos x$, $v_0(x) = v_0 - 0.1\cos x$. The coexisting equilibrium $(u_*, v_*)$ is stable for these two models.

more realistic. In addition, we show that only nonlocal competition and diffusion together can induce stably spatial inhomogeneous periodic solutions under some parameters.

In the model (1.2), time delay can affect the stability of the coexistence equilibrium. When the time delay is smaller than the critical value, the densities of prey and predator will tend to the coexisting equilibrium and distribute homogeneously in space. But when the time delay crosses the critical value, the densities of prey and predator will oscillate periodically and distribute inhomogeneously in space. In addition, we observe that increasing the gestation delay will increase the amplitude of the periodic solution. This may be due to the long gestation period, which leads to a long feedback time for predator growth, resulting in large fluctuations in population density.

By the numerical simulations, we show that the amplitude of spatially inhomogeneous periodic solution is large near the boundary of the region. Because the prey wants to avoid the hunting of predator, it will escape the survival region and immigrate to the boundary. However, due to the Newman boundary conditions, the prey cannot escape the survival region, so it will reverse in the middle of the space after reaching the boundary. The predator will follow the movement of the prey to get more food. This results in a large amplitude near the boundary.
Fig. 7 The numerical simulations for the models (1.2) (a–d) and (4.1) (e–f) with $\beta = 0.68$, $\tau = 0.04$ and initial values $u_0(x) = u^* + 0.1 \cos x$, $v_0(x) = v^* - 0.1 \cos x$. The coexisting equilibrium $(u^*, v^*)$ is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u^*, v^*)$ is stable for the model (4.1).
The numerical simulations for the models (1.2) (a–d) and (4.1) (e–h) with $\beta = 0.68$ $\tau = 0.07$ and initial values $u_0(x) = u^* + 0.1\cos x$, $v_0(x) = v^* - 0.1\cos x$. The coexisting equilibrium $(u^*, v^*)$ is unstable and there exists a spatially homogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u^*, v^*)$ is unstable and there exists a spatially homogeneous periodic solution for the model (4.1).
Fig. 9  Bifurcation diagram of system (1.2) for $\beta$ and $\tau$

![Bifurcation diagram](image-url)

- Homogeneous oscillation
- Inhomogeneous oscillation
- Stable region

Axes:
- $\beta$ (x-axis)
- $\tau$ (y-axis)
Fig. 10 The numerical simulations for the models (1.2) (a, b) and (4.1) (c, d) with $\beta = 0.68 \tau = 0.01$ and initial values $u_0(x) = u_* + 0.001\cos x$, $v_0(x) = v_* - 0.001\cos x$. The coexisting equilibrium $(u_*, v_*)$ is stable for these two models.
Fig. 11 The numerical simulations for the models (1.2) (a–d) and (4.1) (e–f) with $\beta = 0.68$, $\tau = 0.15$ and initial values $u_0(x) = u_\ast + 0.001 \cos x$, $v_0(x) = v_\ast - 0.001 \cos x$. The coexisting equilibrium $(u_\ast, v_\ast)$ is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u_\ast, v_\ast)$ is stable for the model (4.1)
Fig. 12 The numerical simulations for the models (1.2) (a–d) and (4.1) (e–h) with $\beta = 0.68$, $\tau = 0.35$ and initial values $u_0(x) = u_\ast + 0.001\cos x$, $v_0(x) = v_\ast - 0.001\cos x$. The coexisting equilibrium $(u_\ast, v_\ast)$ is unstable and there exists a spatially inhomogeneous periodic solution with mode-1 spatial pattern for the model (1.2). The coexisting equilibrium $(u_\ast, v_\ast)$ is unstable and there exists a spatially homogeneous periodic solution for the model (4.1).
Author contributions All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Ruizhi Yang. Numerical simulations were performed by Ruizhi Yang and Chenxuan Nie. All authors read and approved the final manuscript.

Funding This research is supported by the Fundamental Research Funds for the Central Universities (Grant No. 2572022DJ05), Postdoctoral program of Heilongjiang Province (No. LBH-Q21060), and College Students Innovations Special Project funded by Northeast Forestry University (No. 202210225157), National Nature Science Foundation of China (No. 11601070) and Heilongjiang Provincial Natural Science Foundation (No. A2018001).

Statements and Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Data availability Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

References

1. Zhou, Y., Yan, X., Zhang, C.: Turing patterns induced by self-diffusion in a predator-prey model with schooling behavior in predator and prey. Nonlinear Dyn. 105, 3731–3747 (2021)
2. Du, Y., Hsu, S.B.: A diffusive predator-prey model in heterogeneous environment. J. Differ. Equ. 203(2), 331–364 (2004)
3. Freedman, H.I., Rao, V.: The trade-off between mutual interference and time lags in predator-prey systems. Bull. Math. Biol. 45(6), 991–1004 (1983)
4. Zhang, X., An, Q., Wang, L.: Spatiotemporal dynamics of a delayed diffusive ratio-dependent predator-prey model with fear effect. Nonlinear Dyn. 105, 3775–3790 (2021)
5. Wang, L., Zhang, M., Jia, M.: A delayed predator-prey model with prey population guided anti-predator behaviour and stage structure. J. Appl. Anal. Comput. 11(4), 1811–1824 (2020)
6. Volterra, V.: Fluctuations in the abundance of species considered mathematically. Nature 118(2972), 558–560 (1926)
7. Yang, R., Song, Q., An, Y.: Spatiotemporal dynamics in a predator-prey model with functional response increasing in both predator and prey densities. Mathematics 10(1), 17 (2021)
8. Maji, C.: Impact of fear effect in a fractional-order predator-prey system incorporating constant prey refuge. Nonlinear Dyn. 107, 1329–1342 (2022)
9. Yang, R., Zhao, X., An, Y.: Dynamical analysis of a delayed diffusive predator-prey model with additional food provided and anti-predator behavior. Mathematics 10(3), 469 (2022)
10. Holling, C.S.: The functional response of predators to prey density and its role in mimicry and population dynamics. Mem. Entomol. Soc. Can 97(45), 1–60 (1965)
11. Beddington, J.R.: Mutual interference between parasites or predators and its effect on searching efficiency. J. Anim. Ecol. 44(1), 331–340 (1975)
12. Crowley, P.H., Martin, E.K.: Functional responses and interference within and between year classes of a dragonfly population. J. N. Am. Benthol. Soc. 8(3), 211–221 (1989)
13. Hassell, M.P., Varley, G.C.: New inductive population model for insect parasites and its bearing on biological control. Nature 223(5211), 1133–1137 (1969)
14. Li, Y., Liu, H., Yang, R.: Time-delay effect on a diffusive predator-prey model with habitat complexity. Adv. Differ. Equ. 2021(1), 1–24 (2021)
15. Wang, S., Tang, H., Ma, Z.: Hopf bifurcation of a multiple-delayed predator-prey system with habitat complexity. Math. Comput. Simul. 180, 1–23 (2021)
16. Ma, Z.: Hopf bifurcation of a generalized delay-induced predator-prey system with habitat complexity. Int. J. Bifurc. Chaos 30(06), 1495–1507 (2020)
17. Ekhl, P.: Effects of habitat complexity and prey abundance on the spatial and temporal distributions of perch (Perca fluviatilis) and pike (Esox lucius). Canad. J. Fisher. Aquat. Sci. 54(54), 1520–1531 (1997)
18. August, P.V.: The role of habitat complexity and heterogeneity. Ecology 64(6), 1495–1507 (2003)
19. Canion, C.R., Heck, K.L.: Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. Mar. Ecol. Prog. 393(393), 37–46 (2009)
20. Jana, D., Bairagi, N.: Habitat complexity, dispersal and metapopulations: macroscopic study of a predator-prey system. Ecol. Complex. 17, 131–139 (2014)
21. Ma, Z., Wang, S.: A delay-induced predator-prey model with Holling type functional response and habitat complexity. Nonlinear Dyn. 93, 1519–1544 (2018)
22. Song, Y., Peng, Y., Zhang, T.: The spatially inhomogeneous Hopf bifurcation induced by memory delay in a memory-based diffusion system. J. Differ. Equ. 300, 597–624 (2021)
23. Yi, F.: Turing instability of the periodic solutions for reaction-diffusion systems with cross-diffusion and the patch model with cross-diffusion-like coupling. J. Differ. Equ. 281, 379–410 (2021)
24. Britton, N.F.: Aggregation and the competitive exclusion principle. J. Theor. Biol. 136(1), 57–66 (1989)
25. Furter, J., Grinfeld, M.: Local vs. non-local interactions in population dynamics. J. Math. Biol. 27(1), 65–80 (1989)
26. Chen, S., Yu, J.: Stability and bifurcation on predator-prey systems with nonlocal prey competition. Discrete Contin. Dyn. Syst. 38(1), 43–62 (2018)
27. Geng, D., Jiang, W., Lou, Y., et al.: Spatiotemporal patterns in a diffusive predator-prey system with nonlocal intraspecific prey competition. Stud. Appl. Math. 1–27 (2021)
28. Liu, Y., Duan, D., Niu, B.: Spatiotemporal dynamics in a diffusive predator-prey model with group defense and nonlocal competition. Appl. Math. Lett. 103, 106175 (2020)
29. Wu, J.: Theory and Applications of Partial Functional Differential Equations. Springer, Berlin (1996)
30. Hassard, B.D., Kazarinoff, N.D., Wan, Y.H.: Theory and Applications of Hopf Bifurcation. Cambridge University Press, Cambridge, New York (1981)
31. Jost, C., Ellner, S.P.: Testing for predator dependence in predator-prey dynamics: a non-parametric approach. Proc. R. Soc. B 267, 1611–1620 (2000)
32. Harrison, G.W.: Comparing predator-prey models to Luckinbill’s experiment with Didinium and Paramecium. Ecology 76(2), 357–374 (1995)
33. Luckinbill, L.S.: Coexistence in laboratory populations of Paramecium aurelia and its predator Didinium nasutum. Ecology 54, 1220–1327 (1973)
34. Salt, G.W.: Predator and prey densities as controls of the rate of capture by the predator Didinium nasutum. Ecology 55, 434–439 (1974)
35. Reukauf E. Zur biologie von Didinium nasutum. Zeitschrift für vergleichende Physiologie 11, 689–701 (1930)

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.