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Research article

Stability dynamics of a nonlocal interaction model with memory and Allee effect

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Abstract: Interaction dynamics among species yield to Allee effects, spatial memory, and nonlocal competition. When predators are not subject to the Allee effect, the coexistence equilibrium point remains locally asymptotically stable despite nonlocal competition. However, in the presence of the Allee effect, nonlocal competition leads to the destabilization of the coexistence point. Moreover, the model will undergo stability switches, Hopf bifurcation, and Turing bifurcation, and induced complex dynamics will appear. It is also found that when the memory diffusion is small, it has no effect on the stability switches; as it increases, only the nonlocal model exhibits the spatially inhomogeneous Hopf bifurcation. When it exceeds the maximum threshold, this phenomenon occurs in both models. Furthermore, when the memory diffusion coefficient exceeds the threshold, the stability range of the coexistence equilibrium will decrease in both the local and nonlocal models. Finally, numerical simulations verify the theoretical results.

Keywords: nonlocal competition; spatial memory; Allee effect; Hopf bifurcation; Turing bifurcation

1. Introduction

Predator-prey interactions constitute one of the most fundamental and extensively studied topics in theoretical ecology, as they underpin the structure, stability, and dynamics of ecological communities. For decades, mathematical modeling of population dynamics has been rooted in the local interaction hypothesis, which posits that the competitive pressure experienced by a population at a spatial location x is determined solely by its own density at that exact position. A standard instance of this framework, proposed independently by Fisher [1] and Kolmogoroff [2], is given by

$$u_t = u_{xx} + u(1 - u).$$

In this model, the quadratic term $u(x, t) \cdot u(x, t)$ encapsulates intraspecific competition: Individuals at position x compete only with conspecifics at the same location x at time t, a mechanism termed local competition. However, growing empirical evidence has revealed that the local interaction assumption is often an oversimplification of real ecological systems. In nature, individuals interact with conspecifics across finite spatial ranges via sensory cues such as vision, hearing, and olfaction, leading to competitive effects that extend beyond the immediate locality [3]. The level of competition at x depends on the local population density as well as the distribution of individuals in surrounding habitats [4–6]. Mathematically, this nonlocal interaction is formalized by replacing the local competition term $-u^2(x,t)$ with a convolution-based nonlocal term

$$-u(x,t)\int_{\Omega} G(x,y)u(x,t)\mathrm{d}x,$$

where $G(x,y)$ is a spatial kernel that quantifies the strength of interaction between individuals at locations x and y [7], and Ω represents the species' habitat domain. This modeling approach encapsulates the fundamental ecological principle that individuals at position x compete for scarce resources with conspecifics across the entire habitat, with the competitive strength weighted by their spatial distance.

Nonlocal prey competition has emerged as a prominent research focus in theoretical ecology, with a wealth of studies exploring its implications for pattern formation and stability. Wu and Song [8] demonstrated that incorporating a nonlocal term can generate Turing patterns, a phenomenon absent in the original local model. Shi et al. [9] further revealed that such nonlocal spatial averaging can induce instability in the constant steady state, a mechanism distinct from classical Turing instability. Duan et al. [10] identified the coexistence of stable homogeneous and inhomogeneous periodic solutions in the vicinity of double Hopf bifurcation points. Recently, Dong et al. [11] investigated a diffusive Rosenzweig-MacArthur system with nonlocal prey competition and prey-taxis, and showed that their interaction can induce rich spatiotemporal patterns. In addition, Li and Ding [12] revealed that nonlocal competition and host-taxis can provide a new mechanism for the formation of spatial heterogeneity patterns in a two-dimensional pine wilt disease model. For more research on nonlocal prey competition, see [13, 14].

Beyond nonlocal competition, animal movement is another critical factor shaping predator-prey dynamics. While traditional models assume random diffusion, empirical observations show that both predators and prey exhibit directed movement (chemotaxis) in response to environmental signals. Kareiva and Odell [15] first observed this in ladybugs and aphids, showing predators migrate to resource-rich areas to improve foraging efficiency. Examples include fruit flies tracking food odors [16] and nematodes responding to environmental cues [17]. Fagan et al. [18] noted that spatial mobility is linked to memory, meaning prey's danger perception depends on both the environment and prior experience. The role of spatial memory in animal movement has been a key research focus. Wang et al. [19] found that slow memory-based diffusion in prey facilitates Turing patterns, while fast diffusion leads to richer dynamics in a diffusive predator-prey model. Peng et al. [20] derived stability conditions and proved Hopf bifurcation in a model with predator memory-based diffusion. Wu et al. [21] showed that spatial memory delay induces inhomogeneous Hopf bifurcation in an Allee effect model, while prey-taxis stabilizes the steady state. Liu and Jiang [22] demonstrated that memory-based diffusion and memory period lead to more complex dynamics in a spatially heterogeneous model. For more on memory-based diffusion, see [23, 24].

In addition to movement and competition, the Allee effect, a fundamental ecological phenomenon first described by Warder Clyde Allee, plays a critical role in population persistence. The Allee effect refers to the positive correlation between individual fitness and population density at low densities, meaning a species requires a minimum population threshold to sustain itself in natural environments. While the majority of predator-prey studies have focused on the Allee effect occurring in prey species [25], ample evidence suggests that this effect is also prevalent in predator populations. The underlying mechanisms include mate limitation at low population densities [26] and cooperative foraging among predators [27]. Recently, Kumar et al. [28] investigated an ecological model with fear and group defense in prey and the Allee effect in predators, and showed that the Allee strength plays an important role in the survival and extinction of the predators. Therefore, incorporating the Allee effect into predator populations is biologically meaningful for describing realistic ecological dynamics. In this case, the predator population requires a certain density threshold to maintain effective reproduction and cooperative predation. When the predator density is too low, the Allee effect weakens predator growth and makes predator persistence more difficult. Based on the above analysis, we propose a spatial memory and nonlocal prey competition on a diffusive predator-prey model with Allee effect as follows:

$$\begin{cases}\dfrac{\partial u(x,t)}{\partial t} =& d_{11}\Delta u(x,t)+u(1-\overline{u}-v), x\in\Omega, t>0,\\ \dfrac{\partial v(x,t)}{\partial t} =& d_{22}\Delta v(x,t)-d_{21}div(v(x,t)\nabla u(x,t-\tau))\\ & +ev\left(\dfrac{uv}{\theta+v}-d\right), x\in\Omega, t>0,\\ \dfrac{\partial u(x,t)}{\partial n} =& 0, \dfrac{\partial v(x,t)}{\partial n}=0, x\in\partial\Omega, t>0,\\ u(x,t) =& u_0(x,t)\geq 0, v(x,t)=v_0(x)\geq 0, x\in\Omega, t\in[-\tau,0],\end{cases} \tag{1.1}$$

where $u(x,t)$ and $v(x,t)$ denote density of prey and predator at location x and time t, respectively. d_{11} and d_{22} denote the Fickian diffusion coefficient of prey and predator, respectively. d_{21} is the spatial memory diffusion coefficient. e is the conversion efficiency. d is the mortality rate of the predator and θ is the Allee effect constant.

$$\overline{u}(x,t)=\frac{1}{|\Omega|}\int_{\Omega}u(x,t)\mathrm{d}x,$$

where Ω is the bounded domain with smooth boundary in $\mathbb{R}^1$. From an ecological perspective, spatial contexts such as river systems, pressure gradients, temperature variations, and latitudinal/longitudinal gradients can all be abstracted as one-dimensional spatial domains. For the convenience of mathematical analysis, the one-dimensional spatial domain is consistently defined as $\Omega=(0,l\pi)$. Let $\mathbb{N}_0=\mathbb{N}\cup\{0\}$, where $\mathbb{N}$ is the positive integer set.

The rest of the paper is organized as follows. Section 2 is divided into two subsections: In Subsection 2.1, the local prey competition model (2.2) is mainly investigated, the effects of memory diffusion and delay on the stability of the coexistence equilibrium of this model are discussed, and it is found that delay cannot induce spatially homogeneous Hopf bifurcation. In Subsection 2.2, the nonlocal prey competition model (1.1) is studied, the stability of the coexistence equilibrium under memory diffusion is analyzed, and the conditions for the occurrence of Hopf bifurcation and Turing bifurcation between the local model (2.2) and the nonlocal model (1.1) are compared. Section 3 verifies the theoretical results through numerical simulations.

2. Stability and bifurcation analysis of model

In this section, we conduct a comparative analysis of the effects of local and nonlocal terms on a class of predator-prey models with spatial memory and the Allee effect. We investigate the influence of memory diffusion and time delay on the stability of the coexistence equilibrium and present the conditions for the occurrence of Hopf bifurcation and Turing instability. Some of the conclusions have been discussed in [29]. The positive equilibrium satisfies the following algebraic equations:

$$\begin{cases} u\,(1-u-v)=0, \\ ev\left(\dfrac{uv}{\theta+v}-d\right)=0. \end{cases} \tag{2.1}$$

Therefore, $v^2+(d-1)v+d\theta=0$. Denote

$$S_1=\{0<\theta<\theta^*\}\cap\{0<d<1\},\quad \theta^*=\frac{(d-1)^2}{4d}.$$

Theorem 2.1. *Suppose* $0<d<1$.

(1) *If* $0<\theta<\theta^*$*, then Eq* (2.1) *admits two positive solutions, denoted as*

$$v_1=\frac{1-d+\sqrt{(1-d)^2-4d\theta}}{2},v_2=\frac{1-d-\sqrt{(1-d)^2-4d\theta}}{2},$$

and $u_i=1-v_i$.

(2) *If* $\theta=\theta^*$*, then Eq* (2.1) *admits a unique positive solution* $u=\frac{1+d}{2}$ *and* $v=\frac{1-d}{2}$.

(3) *If* $\theta>\theta^*$*, then Eq* (2.1) *admits no positive solution.*

According to Theorem 2.1, as the Allee effect increases, the number of coexisting equilibrium points decreases from 2 to 1 and eventually becomes 0. When $0<\theta<\theta^*$, the model has two coexisting equilibrium points, one of which is unstable. When $\theta=\theta^*$, there exists only one coexisting equilibrium point, which is also unstable. When $\theta>\theta^*$, no coexisting equilibrium point exists in the model, as shown in Figure 1. Ecologically, the Allee effect reflects that predators can successfully accomplish vital life activities such as cooperative predation and synchronized reproduction only when their population size reaches a sufficient level. If predator density is too low, effective cooperation among individuals cannot be formed, which directly leads to reduced predation efficiency and restricted population growth. As a result, the predator becomes difficult to sustain survival and thus cannot coexist with the prey in the long run. Ultimately, only the prey population survives.

The stability properties of these equilibria for the ODE model corresponding to model (2.2) have been discussed in [29]. For completeness, we briefly recall the main results: the equilibrium $E(0,0)$ is unstable, while a predator-free equilibrium $E(1,0)$ is locally asymptotically stable. For the positive equilibrium $E_i(u_i,v_i),(i=1,2)$, the characteristic equation of the ODE model corresponding to model (2.2) is

$$\lambda^2-\mathrm{Tr}_0(u_i,v_i)\lambda+D_0(u_i,v_i)=0,$$

where

$$\mathrm{Tr}_0(u_i,v_i)=\frac{\theta e u_i v_i}{(\theta+v_i)^2}-u_i,$$

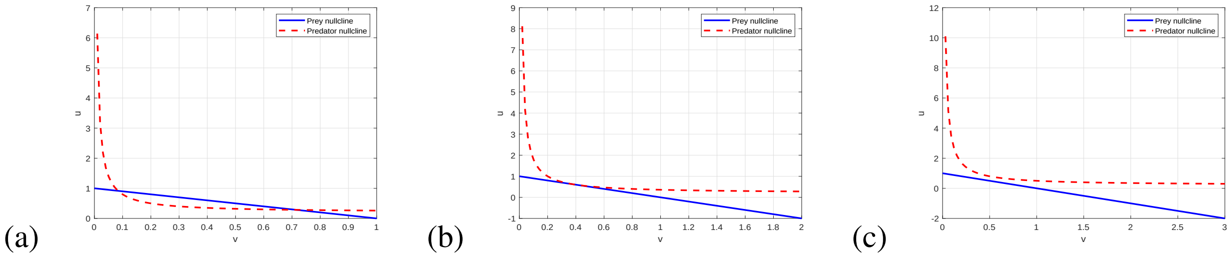


Figure 1. Plots of nullclines with possible coexistence equilibrium points for (a) $\theta = 0.3$, (b) $\theta = 0.8$, and (c) $\theta = 1.3$. The other parameter values are $d = 0.2$ and $\theta^* = 0.8$.

and

$$D_0(u_i, v_i) = \frac{eu_iv_i}{\theta + v_i}(2v_i + d - 1).$$

Combining the expressions for v_1 and v_2, we obtain

$$D_0(u_1, v_1) > 0, \qquad D_0(u_2, v_2) < 0.$$

Therefore, $E_2(u_2, v_2)$ is a saddle point of the ODE model corresponding to model (2.2), and it is unstable. For the other positive equilibrium $E_1(u_1, v_1)$, since $D_0(u_1, v_1) > 0$, its stability in the corresponding ODE model is determined by the sign of $\mathrm{Tr}_0(u_1, v_1)$. In particular, $E_1(u_1, v_1)$ is locally asymptotically stable if $e < \frac{(\theta+v_1)^2}{\theta v_1}$ and loses its stability if $e > \frac{(\theta+v_1)^2}{\theta v_1}$. The critical case $e = \frac{(\theta+v_1)^2}{\theta v_1}$ corresponds to the spatially homogeneous Hopf bifurcation.

2.1. *Spatial memory model with local prey competition*

A predator-prey model with spatial memory and local prey competition is considered:

$$\begin{cases} \dfrac{\partial u(x,t)}{\partial t} =d_{11}\Delta u(x,t) + u(1-u-v), x \in \Omega, t > 0, \\ \dfrac{\partial v(x,t)}{\partial t} =d_{22}\Delta v(x,t) - d_{21}div(v(x,t)\nabla u(x,t-\tau)) \\ \qquad\qquad + ev\left(\dfrac{uv}{\theta + v} - d\right), x \in \Omega, t > 0, \\ \dfrac{\partial u(x,t)}{\partial n} =0, \dfrac{\partial v(x,t)}{\partial n} = 0, x \in \partial\Omega, t > 0, \\ \quad u(x,t) =u_0(x,t) \geq 0, v(x,t) = v_0(x) \geq 0, x \in \Omega, t \in [-\tau, 0]. \end{cases} \tag{2.2}$$

At the coexistence equilibrium point $E_1(u_1, v_1)$, the linearized system of model (2.2) is given by

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = D_1\begin{pmatrix} \Delta u(x,t) \\ \Delta v(x,t) \end{pmatrix} + D_2\begin{pmatrix} \Delta u(x,t-\tau) \\ \Delta v(x,t-\tau) \end{pmatrix} + J\begin{pmatrix} u(x,t) \\ v(x,t) \end{pmatrix}, \tag{2.3}$$

where

$$D_1 = \begin{pmatrix} d_{11} & 0 \\ 0 & d_{22} \end{pmatrix}, D_2 = \begin{pmatrix} 0 & 0 \\ -d_{21}v_1 & 0 \end{pmatrix}, J = \begin{pmatrix} -u_1 & -u_1 \\ \frac{ev_1{}^2}{\theta+v_1} & \frac{\theta eu_1v_1}{(\theta+v_1)^2} \end{pmatrix}.$$

Therefore, we derive the characteristic equation

$$\lambda^2 - Tr_i\lambda + D_i = 0, i \in \mathbb{N}_0. \tag{2.4}$$

For $i \in \mathbb{N}_0$,

$$Tr_i = \frac{\theta e u_1 v_1}{(\theta + v_1)^2} - u_1 - (d_{11} + d_{22})\frac{i^2}{l^2}$$

and

$$D_i = d_{11}d_{22}\frac{i^4}{l^4} + u_1\left(d_{21}v_1 e^{-\lambda\tau} + d_{22} - \frac{d_{11}\theta e v_1}{(\theta + v_1)^2}\right)\frac{i^2}{l^2} - \frac{\theta e {u_1}^2 v_1}{(\theta + v_1)^2} + \frac{e u_1 {v_1}^2}{\theta + v_1}. \tag{2.5}$$

Defining

$$\tilde{l} = (\theta + v_1)\sqrt{\frac{d_{22}}{\theta e u_1 v_1}}, \quad \Pi(i, l) = \theta e u_1 v_1 l^2 - (\theta + v_1)^2 d_{22} i^2,$$

for $l > \tilde{l}$,

$$N^* = \begin{cases} \frac{l}{\tilde{l}} - 1, & \frac{l}{\tilde{l}} \in \mathbb{N}, \\ \left\lfloor \frac{l}{\tilde{l}} \right\rfloor, & \frac{l}{\tilde{l}} \notin \mathbb{N}. \end{cases} \tag{2.6}$$

Remark 2.1. *Taking e as the bifurcation parameter, the critical value for the spatially homogeneous Hopf bifurcation of the local model* (3) *is*

$$e_H = \frac{(\theta + v_1)^2}{\theta v_1}.$$

If $e < e_H$, then $Tr_i < 0$ for $i \in \mathbb{N}_0$. Therefore, the local model does not exhibit diffusion-driven spatially inhomogeneous Hopf bifurcation.

When $\tau = 0$, the stability of the predator-free equilibrium point $E(1, 0)$ and the coexistence equilibrium point $E_1(u_1, v_1)$ are discussed for the model (2.2).

Theorem 2.2. *Suppose that $d \geq 1$, i.e., the coexistence equilibrium does not exist. Then, the predator-free equilibrium point $E(1, 0)$ is globally asymptotically stable.*

Proof. Define the time-evolution Lyapunov function

$$L(t) = e\int_\Omega (u - 1 - lnu)\,\mathrm{d}x + \int_\Omega v\mathrm{d}x \geq 0.$$

Taking the derivative of both sides with respect to t yields

$$\begin{aligned} \dot{L}(t) &= e\int_\Omega \left(1 - \frac{1}{u}\right)u_t\mathrm{d}x + \int_\Omega v_t\mathrm{d}x \\ &= e\left(\int_\Omega \left(1 - \frac{1}{u}\right)d_{11}\Delta u\mathrm{d}x + \int_\Omega \left(1 - \frac{1}{u}\right)u\,(1 - u - v)\,\mathrm{d}x\right) + \int_\Omega ev\left(\frac{uv}{\theta + v} - d\right)\mathrm{d}x \\ &\leq e\left(-d_{11}\int_\Omega \left(\frac{\nabla u}{u}\right)^2\mathrm{d}x + \int_\Omega (u - 1)(1 - u - v)\mathrm{d}x\right) + e\int_\Omega uv\mathrm{d}x - ed\int_\Omega v\mathrm{d}x \\ &= -d_{11}e\int_\Omega \left(\frac{\nabla u}{u}\right)^2\mathrm{d}x - e\int_\Omega (u - 1)^2\mathrm{d}x + e(1 - d)\int_\Omega v\mathrm{d}x. \end{aligned} \tag{2.7}$$

When $d \geq 1$, $\dot{L}(t) \leq 0$. Meanwhile, $\dot{L}(t) = 0$, if and only if $(u, v) = (1, 0)$. By Lasalle's invariance principle [30, Theorem 3], $E(1, 0)$ is globally asymptotically stable.

Denote

$$D^H_{11,i} = \frac{\Pi(i,l)}{(\theta + v_1)^2 i^2} - \frac{u_1 l^2}{i^2},$$

and

$$D^T_{21,i} = \frac{(d_{11} i^2 + u_1 l^2)\Pi(i,l)}{u_1 v_1 (\theta + v_1)^2 i^2 l^2} - \frac{e v_1 l^2}{(\theta + v_1) i^2}.$$

Lemma 1. *Suppose S_1 holds.*

(1) *When $l \leq \tilde{l}$, it can be verified that D_i is strictly positive for all $i \in \mathbb{N}$.*

(2) *When $l > \tilde{l}$, $D_i > 0$ is guaranteed for all $i > N^*$, and for $1 \leq i \leq N^*$ the sign of D_i is as follows:*

$$D_i \begin{cases} < 0 & d_{21} < D^T_{21,i}, \\ = 0 & d_{21} = D^T_{21,i}, \\ > 0 & d_{21} > D^T_{21,i}. \end{cases} \tag{2.8}$$

Theorem 2.3. *Suppose S_1 holds.*

(1) *For $l \leq \tilde{l}$, $E_1(u_1, v_1)$ is locally asymptotically stable for the local model* (2.2) *if* $\frac{\theta e v_1}{(\theta+v_1)^2} < 1$.

(2) *For $l > \tilde{l}$, $E_1(u_1, v_1)$ is locally asymptotically stable for the local model* (2.2) *provided* $\frac{\theta e v_1}{(\theta+v_1)^2} < 1$ *and $d_{21} > D^T_{21,i}$ for $1 \leq i \leq N^*$.*

Together with Remark 2.1, Theorem 2.3 gives the stability conditions of the coexistence equilibrium $E_1(u_1, v_1)$ for the local model (2.2) when $\tau = 0$. When $l > \tilde{l}$ and $1 \leq i \leq N^*$, the condition $d_{21} = D^T_{21,i}$ gives a possible Turing bifurcation point. Moreover, $D_i < 0$, namely $d_{21} < D^T_{21,i}$, implies that the coexistence equilibrium $E_1(u_1, v_1)$ loses stability through a Turing-type mechanism.

Next, we discuss the case of $\tau > 0$. Assume that $\lambda = \pm \mathrm{i}\omega$ are roots of the Eq (2.4). Thus, ω satisfies

$$\begin{aligned} &-\omega_i^2 - \mathrm{i}\omega_i Tr_i + d_{11} d_{22} \mu_i^2 + u_1 \left(d_{21} v_1 e^{-\lambda\tau} + d_{22} - \frac{d_{11}\theta e v_1}{(\theta + v_1)^2} \right) \frac{i^2}{l^2} \\ &- \frac{\theta e {u_1}^2 v_1}{(\theta + v_1)^2} + \frac{e u_1 {v_1}^2}{\theta + v_1} = 0. \end{aligned}$$

Separate the real and imaginary parts as follows:

$$\begin{cases} A_i - \omega_i^2 = -\mu_i d_{21} u_1 v_1 \cos(\omega_i \tau), \\ Tr_i \omega_i = -\mu_i d_{21} u_1 v_1 \sin(\omega_i \tau), \end{cases} \tag{2.9}$$

where

$$A_i = d_{11} d_{22} \mu_i^2 + \left(d_{22} u_1 - \frac{d_{11}\theta e u_1 v_1}{(\theta + v_1)^2} \right) \mu_i - \frac{\theta e {u_1}^2 v_1}{(\theta + v_1)^2} + \frac{e u_1 {v_1}^2}{\theta + v_1}.$$

From Eq (2.9), for $i = 0$,

$$\omega^4 + B_0 \omega^2 + C_0 = 0, \tag{2.10}$$

where

$$B_0 = \left(\frac{\theta e u_1 v_1}{(\theta + v_1)^2} \right)^2 - \frac{2 e u_1 {v_1}^2}{\theta + v_1} + {u_1}^2, \quad C_0 = A_0^2 > 0.$$

Let

$$\triangle_{10} = B_0^2 - 4C_0 = Tr_0^2(Tr_0^2 - 4A_0),$$

where

$$Tr_0^2 - 4A_0 = \left(\frac{\theta e u_1 v_1}{(\theta + v_1)^2}\right)^2 + {u_1}^2 + \frac{2\theta e {u_1}^2 v_1}{(\theta + v_1)^2} - \frac{4 e u_1 {v_1}^2}{\theta + v_1}.$$

Remark 2.2. *Assume that* $Tr_0 < 0$ *and* $D_0 > 0$*. If Eq* (2.10) *has positive roots, then* $B_0 < 0$ *and* $\triangle_{10} \geq 0$*. When* $D_0 > 0$ *and* $B_0 < 0$*, then* $\triangle_{10} < 0$*. This is in contradiction with* $\triangle_{10} \geq 0$*. Therefore, Eq* (2.10) *has no positive roots. This means that the spatially homogeneous Hopf bifurcation cannot be induced by delay in model* (2.2).

For $i \in \mathbb{N}$,

$$\omega^4 + B_i \omega^2 + C_i = 0, \tag{2.11}$$

where

$$\begin{aligned} B_i &= {Tr_i}^2 - 2A_i \\ &= \left(d_{11}^2 + d_{22}^2\right){\mu_i}^2 - 2\left(\frac{\theta e u_1 v_1 d_{22}}{(\theta + v_1)^2} - u_1 d_{11}\right)\mu_i + \left(\frac{\theta e u_1 v_1}{(\theta + v_1)^2}\right)^2 \\ &\quad - \frac{2 e u_1 {v_1}^2}{\theta + v_1} + {u_1}^2, \\ C_i &= {A_i}^2 - (d_{21} u_1 v_1 \mu_i)^2 . \end{aligned} \tag{2.12}$$

Let

$$\triangle_{1i} = B_i^2 - 4C_i = Tr_i^4 - 4Tr_i^2 A_i + 4(d_{21} u_1 v_1 \mu_i)^2.$$

For fixed $i \in \mathbb{N}$, define

$$d_{21}^{(1i)} = \frac{A_i}{u_1 v_1 \mu_i} > 0, \quad d_{21}^{*(1i)} = \frac{|Tr_i| \sqrt{4A_i - {Tr_i}^2}}{2 u_1 v_1 \mu_i} > 0. \tag{2.13}$$

It can be verified that

$$\left(d_{21}^{(1i)}\right)^2 - \left(d_{21}^{*(1i)}\right)^2 = \frac{(2A_i - Tr_i)^2}{4(u_1 v_1 \mu_i)^2} \geq 0,$$

which implies $d_{21}^{(1i)} \geq d_{21}^{*(1i)} > 0$. Based on the above analysis, the signs of C_{1i} and $\triangle_{1i}$ can be described as

$$C_{1i} \begin{cases} > 0, & 0 < d_{21} < d_{21}^{(1i)}, \\ = 0, & d_{21} = d_{21}^{(1i)}, \\ < 0, & d_{21} > d_{21}^{(1i)}. \end{cases} \tag{2.14}$$

and

$$\triangle_{1i} \begin{cases} > 0, & d_{21} > d_{21}^{*(1i)}, \\ = 0, & d_{21} = d_{21}^{*(1i)}, \\ < 0, & 0 < d_{21} < d_{21}^{*(1i)}. \end{cases} \tag{2.15}$$

The conclusion about the number of positive roots of Eq (2.11) is as follows.

Lemma 2. *Suppose* S_1 *holds.*
(i) *For* $0 < d_{21} < d_{21}^{*(1i)}$, *Eq* (2.11) *has no positive roots.*
(ii) *For* $d_{21}^{*(1i)} \leq d_{21} < d_{21}^{(1i)}$, *Eq* (2.11) *has no positive roots when* $B_i \geq 0$ *and two positive roots when* $B_i < 0$.
(iii) *For* $d_{21} = d_{21}^{(1i)}$, *Eq* (2.11) *has no positive roots if* $B_i \geq 0$, *and has one positive root if* $B_i < 0$.
(iv) *For* $d_{21} > d_{21}^{(1i)}$, *Eq* (2.11) *has a positive root.*

Lemma 3. *If Eq* (2.11) *has positive roots, then the corresponding critical values of delay* τ *are*

$$\tau_{i,j}^{\pm} = \frac{1}{\omega_i^{\pm}}\left[\arccos\left(\frac{\omega_i^{\pm 2} - A_i}{\mu_i d_{21} u_1 v_1}\right) + 2j\pi\right], i \in \mathbb{N}, j \in \mathbb{N}_0.$$

Next, we verify the transversality condition.

Lemma 4. *Suppose* S_1 *holds. Then,* $\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}|_{\tau=\tau_{i,j}^{+}} > 0$ *and* $\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}|_{\tau=\tau_{i,j}^{-}} < 0$ *for* $i \in \mathbb{N}$ *and* $j \in \mathbb{N}_0$,.

Proof. From Eq (2.4),

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{2\lambda - Tr_i}{u_1 v_1 \mu_i d_{21} \lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}.$$

Furthermore,

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1} = \frac{Tr_i^2 + 2\omega^2 - 2A_i}{(u_1 v_1 \mu_i d_{21})^2}.$$

By calculation, we can get

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1}\Big|_{\tau=\tau_{i,j}^{+}} = \frac{\sqrt{Tr_i^4 - 4Tr_i^2 A_i + 4(d_{21}u_1 v_1 \mu_i)^2}}{(u_1 v_1 \mu_i d_{21})^2} > 0,$$

and

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1}\Big|_{\tau=\tau_{i,j}^{-}} = -\frac{\sqrt{Tr_i^4 - 4Tr_i^2 A_i + 4(d_{21}u_1 v_1 \mu_i)^2}}{(u_1 v_1 \mu_i d_{21})^2} < 0.$$

For a fixed $d_{21} > 0$, denote

$$\underline{d_{21}^1} = \begin{cases} \min\left\{\min\limits_{i \notin H_B}\left\{d_{21}^{(1i)}\right\}, \min\limits_{i \in H_B}\left\{d_{21}^{*(1i)}\right\}\right\}, & H_B \neq \emptyset, \\ \min\limits_{i \in \mathbb{N}}\left\{d_{21}^{(1i)}\right\}, & H_B = \emptyset, \end{cases} \tag{2.16}$$

where $H_B = \{i \in \mathbb{N} : B_i < 0\}$, and

$$(G_0) : \left\{l \mid l \leq \tilde{l}, \text{ and } \frac{\theta e v_1}{(\theta + v_1)^2} < 1\right\}$$
$$\cup \left\{l \mid l > \tilde{l}, \frac{\theta e v_1}{(\theta + v_1)^2} < 1, \text{ and } d_{21} > D_{21,i}^{T}, \text{ for } 1 \leq i \leq N^*\right\}.$$

From Lemma 2 and Eq (2.16), we obtain the following theorem. For a detailed proof of the theorem, refer to [20].

Theorem 2.4. *Suppose S_1 and (G_0) hold.*
(i) *For $0 < d_{21} < \underline{d}^1_{21}$, that is, Eq* (2.11) *has no positive solutions for any $i \in \mathbb{N}$, then $E_1(u_1, v_1)$ of model* (2.2) *is locally asymptotically stable for any $\tau \geq 0$.*
(ii) *When $d_{21} = \underline{d}^1_{21}$, if $H_B \neq \emptyset$ and $i \in H_B$, Eq* (2.11) *admits positive solutions $\omega^{\pm}_i$, which induces a set of Hopf bifurcation values $\tau^{\pm}_{i,j}$ in model* (2.2)*. Thus, $E_1(u_1, v_1)$ may be unstable for some $\tau > 0$. If $H_B \neq \emptyset$ and $i \notin H_B$ or $H_B = \emptyset$ and $i \in N$, Eq* (2.11) *has no positive solutions, and $E_1(u_1, v_1)$ remains locally asymptotically stable for any $\tau \geq 0$.*
(iii) *If $d_{21} > \underline{d}^1_{21}$, Eq* (2.11) *has positive roots $\omega^{\pm}_i$ for any $i \in \mathbb{N}$, which generates a sequence of Hopf bifurcation points $\tau^{\pm}_{i,j}$ in model* (2.2)*. Therefore, $E_1(u_1, v_1)$ may be unstable for certain $\tau > 0$.*

In the case that $d_{21} > \underline{d}^1_{21}$, selecting τ as the bifurcation parameter, we obtain the following conclusions.

Theorem 2.5. *Suppose S_1 and (G_0) hold. For fixed $d_{21} > \underline{d}^1_{21}$, let $\tau^{\pm}_{i,0} = \min_{i \in \mathbb{N}_0}\{\tau^{\pm}_{i,j}\}$.*

(1) *When $H_B = \emptyset$, define*

$$W_1(d_{21}) = \left\{ i \in \mathbb{N} : d^{(1i)}_{21} < d_{21} \right\} \text{and} \tau^*_1(d_{21}) = \min_{i \in W_1(d_{21})} \{\tau^+_{i,0}\},$$

For $d_{21} > \underline{d_{21}}$, the coexistence equilibrium point $E_1(u_1, v_1)$ of model (2.2) *is locally asymptotically stable for $\tau < \tau^*_1(d_{21})$, unstable for $\tau > \tau^*_1(d_{21})$, and Hopf bifurcations occur at $\tau = \tau^+_{i,j}$ $(i \in W_1(d_{21}))$.*

(2) *When $H_B \neq \emptyset$, let*

$$\overline{d^1_{21}} = \max_{i \in H_B} d^{(1i)}_{21}.$$

(i) *For $\underline{d}^1_{21} < d_{21} < \overline{d^1_{21}}$, let*

$$W_2(d_{21}) = \left\{ i \in N : d^{(1i)}_{21} < d_{21} \right\}, \quad \text{and} \quad W_3(d_{21}) = \left\{ i \in H_B : d^{*(1i)}_{21} < d_{21} < d^{(1i)}_{21} \right\}.$$

The critical delay is

$$\tau^*_2(d_{21}) = \min \left\{ \min_{i \in W_2(d_{21})} \{\tau^+_{i,0}\}, \min_{i \in W_3(d_{21})} \{\tau^+_{i,0}\}, \{\tau^-_{i,0}\} \right\}.$$

$E_1(u_1, v_1)$ of model (2.2) *is locally asymptotically stable for $\tau < \tau^*_2(d_{21})$, unstable for $\tau > \tau^*_2(d_{21})$, and Hopf bifurcations occur at $\tau = \tau^+_{i,j}$ $(i \in W_2(d_{21}))$ and $\tau = \tau^{\pm}_{i,j}$ $(i \in W_3(d_{21}))$. Furthermore, when $\tau = \tau^{\pm}_{i,j}$ for $i \in W_3(d_{21})$, stability switches occur for $k \geq 0$, such that $E_1(u_1, v_1)$ is locally asymptotically stable when*

$$\tau \in (0, \tau^+_{1,0}) \bigcup (\tau^-_{1,0}, \tau^+_{1,1}) \bigcup \cdots \bigcup (\tau^-_{1,k-1}, \tau^+_{1,k})$$

and unstable when

$$\tau \in (\tau^+_{1,0}, \tau^-_{1,0}) \bigcup (\tau^+_{1,1}, \tau^-_{1,1}) \bigcup \cdots \bigcup (\tau^+_{1,k}, +\infty).$$

(ii) *For $d_{21} > \overline{d^1_{21}}$, define*

$$W_4(d_{21}) = H_B \cup \{ i \notin H_B : d^{(1i)}_{21} < d_{21} \}, \quad \tau^*_3(d_{21}) = \min_{i \in W_4(d_{21})} \{\tau^+_{i,0}\}.$$

$E_1(u_1, v_1)$ of model (2.2) *is locally asymptotically stable for $\tau < \tau^*_3(d_{21})$, unstable for $\tau > \tau^*_3(d_{21})$, and Hopf bifurcations occur at $\tau = \tau^+_{i,j}$ $(i \in W_4(d_{21}))$.*

Proof. (1) According to the definition of $W_1(d_{21})$, it follows that $W_1(d_{21})$ is finite. If $H_B = \emptyset$, then $B_i \geq 0$. For $i \in W_1(d_{21})$, $C_{1i} < 0$, which implies that Eq (2.11) admits a positive root, leading to Hopf bifurcation at $\tau = \tau_{i,j}^+$ for $i \in W_1(d_{21})$.

(2)(*i*) For $\underline{d_{21}^1} < d_{21} < \overline{d_{21}^1}$, if $i \notin H_B$ $(B_i \geq 0)$, then $C_{1i} < 0$ and $\triangle_{1i} > 0$ for $i \in W_2(d_{21})$. Eq (2.11) has a positive root. If $i \in H_B$, then $B_i < 0$. For $i \in W_3(d_{21})$, the conditions $C_{1i} > 0$ and $\triangle_{1i} > 0$ are satisfied, and thus two positive roots exist for Eq (2.11). For $i \in W_2(d_{21})$, the conditions $C_{1i} < 0$ and $\triangle_{1i} > 0$ are satisfied, and thus a positive root exists for Eq (2.11). Thus, Hopf bifurcations occur at $\tau = \tau_{i,j}^+$ $(i \in W_2(d_{21}))$ and $\tau = \tau_{i,j}^{\pm}$ $(i \in W_3(d_{21}))$. For each fixed $i \in W_3(d_{21})$, both $\{\tau_{i,j}^+\}_{j=0}^{\infty}$ and $\{\tau_{i,j}^-\}_{j=0}^{\infty}$ are increasing in j. The distance between consecutive elements of $\{\tau_{i,j}^+\}_{j=0}^{\infty}$ is $\frac{2\pi}{\omega_i^+}$, and for $\{\tau_{i,j}^-\}_{j=0}^{\infty}$, it is $\frac{2\pi}{\omega_i^-}$. Consequently, because $\omega_i^+ > \omega_i^-$, the real part of the eigenvalues undergoes more frequent positive jumps than negative ones as τ increases. Let $\{\tau_{1,s}^+\}_{s=1}^{\infty}$ and $\{\tau_{1,s}^-\}_{s=1}^{\infty}$ be the resulting sequence. Then, there exists $k \geq 0$, such that all the roots of Eq(2.11) have negative real parts for

$$\tau \in (0, \tau_{1,0}^+) \bigcup (\tau_{1,0}^-, \tau_{1,1}^+) \bigcup \cdots \bigcup (\tau_{1,k-1}^-, \tau_{1,k}^+)$$

and at least one pair of conjugate complex roots with positive real parts exists for

$$\tau \in (\tau_{1,0}^+, \tau_{1,0}^-) \bigcup (\tau_{1,1}^+, \tau_{1,1}^-) \bigcup \cdots \bigcup (\tau_{1,k}^+, +\infty).$$

(*ii*) When $d_{21} > \overline{d_{21}^1}$, the conditions $C_{1i} < 0$ and $\triangle_{1i} > 0$ are satisfied, and thus a positive root exists for Eq (2.11). Therefore, Hopf bifurcation occurs at $\tau = \tau_{i,j}^+$ for $i \in W_4(d_{21})$.

2.2. *Spatial memory model with nonlocal prey competition*

Linearizing model (1.1) at $E_1(u_1, v_1)$, we obtain

$$\begin{pmatrix} u_t \\ v_t \end{pmatrix} = D_1 \begin{pmatrix} \Delta u(x,t) \\ \Delta v(x,t) \end{pmatrix} + D_2 \begin{pmatrix} \Delta u(x,t-\tau) \\ \Delta v(x,t-\tau) \end{pmatrix} + J_U \begin{pmatrix} u(x,t) \\ v(x,t) \end{pmatrix} + J_{\bar{U}} \begin{pmatrix} \bar{u}(x,t) \\ \bar{v}(x,t) \end{pmatrix}, \tag{2.17}$$

where

$$J_U = \begin{pmatrix} 0 & -u_1 \\ \frac{ev_1{}^2}{\theta+v_1} & \frac{\theta e u_1 v_1}{(\theta+v_1)^2} \end{pmatrix}, J_{\bar{U}} = \begin{pmatrix} -u_1 & 0 \\ 0 & 0 \end{pmatrix}.$$

Thus, the characteristic equation corresponding to the linearized model (2.17) can be expressed as

$$\lambda^2 - \widetilde{Tr}_i \lambda + \widetilde{D}_i = 0, i \in \mathbb{N}_0. \tag{2.18}$$

For $i = 0$, $\widetilde{Tr}_0 = Tr_0(u_1, v_1)$ and $\widetilde{D}_0 = D_0(u_1, v_1)$. For $i \in \mathbb{N}$,

$$\widetilde{Tr}_i = \frac{\theta e u_1 v_1}{(\theta + v_1)^2} - (d_{11} + d_{22}) \frac{i^2}{l^2}$$

and

$$\widetilde{D}_i = d_{11} d_{22} \frac{i^4}{l^4} + u_1 v_1 \left(d_{21} e^{-\lambda\tau} - \frac{d_{11} \theta e}{(\theta + v_1)^2} \right) \frac{i^2}{l^2} + \frac{e u_1 v_1{}^2}{\theta + v_1}. \tag{2.19}$$

When $\tau = 0$, for the signs of $\widetilde{D}_i$ and $\widetilde{Tr}_i$, we have Lemmas 5 and 6, respectively. Denote

$$d_{11,i}^H = \frac{\Pi(i,l)}{(\theta + v_1)^2 i^2}, \quad d_{21,i}^T = \frac{d_{11} i^2 \Pi(i,l)}{u_1 v_1 (\theta + v_1)^2 i^2 l^2} - \frac{e v l^2}{(\theta + v_1) i^2}.$$

Lemma 5. *Suppose* S_1 *holds.*

(1) *For* $l \leq \tilde{l}$, $\widetilde{Tr}_i$ *remains negative for* $i \in \mathbb{N}$.

(2) *For* $l > \tilde{l}$, $\widetilde{Tr}_i < 0$ *holds for* $i > N^*$, *while for* $1 \leq i \leq N^*$, *the sign of* $\widetilde{Tr}_i$ *is as follows:*

$$\widetilde{Tr}_i \begin{cases} < 0, & d_{11} > d_{11,i}^H, \\ = 0, & d_{11} = d_{11,i}^H, \\ > 0, & d_{11} < d_{11,i}^H. \end{cases} \tag{2.20}$$

Lemma 6. *Suppose* S_1 *holds.*

(1) *For* $l \leq \tilde{l}$, $\widetilde{D}_i$ *remains positive for* $i \in \mathbb{N}$.

(2) *For* $l > \tilde{l}$, $\widetilde{D}_i > 0$ *holds for* $i > N^*$, *while for* $1 \leq i \leq N^*$, *the sign of* $\widetilde{D}_i$ *is as follows:*

$$\widetilde{D}_i \begin{cases} < 0 & d_{21} < d_{21,i}^T, \\ = 0 & d_{21} = d_{21,i}^T, \\ > 0 & d_{21} > d_{21,i}^T. \end{cases} \tag{2.21}$$

Theorem 2.6. *Suppose* S_1 *holds.*

(1) *For* $l \leq \tilde{l}$, $E_1(u_1, v_1)$ *is locally asymptotically stable for the nonlocal model* (1.1) *if* $\frac{\theta e v_1}{(\theta+v_1)^2} < 1$.

(2) *For* $l > \tilde{l}$, $E_1(u_1, v_1)$ *is locally asymptotically stable for the nonlocal model* (1.1) *if* $\frac{\theta e v_1}{(\theta+v_1)^2} < 1$, $d_{11} > d_{11,i}^H$, *and* $d_{21} > d_{21,i}^T$ *for* $1 \leq i \leq N^*$.

Remark 2.3. *Suppose* $d_{11,i}^H$, $D_{11,i}^H$ *and* $d_{21,i}^T$, $D_{21,i}^T$ *are the possible Hopf bifurcation points and the possible Turing bifurcation points, respectively. Then:*

(*a*) $d_{11,i}^H - D_{11,i}^H = \frac{u_1 l^2}{i^2} > 0$. (*b*) $d_{21,i}^T - D_{21,i}^T = -\frac{u_1 l^2 \Pi(i,l)}{u_1 v_1 (\theta+v_1)^2 i^2 l^2} < 0$.

(1) Based on conditions (*a*) *and* (*b*), *the nonlocal term extends the range of parameter region for the spatially inhomogeneous Hopf bifurcation and narrows the range of parameter region for the Turing bifurcation.*

(2) If Hopf bifurcation points of the local model (2.2) *and the nonlocal model* (1.1) *exist, then they have the same homogeneous Hopf bifurcation points. Moreover, spatial memory diffusion* d_{21} *has no effect on whether Hopf bifurcation occurs in model* (1.1).

Next, we discuss the case of $\tau > 0$. Assume that $\lambda = \pm i\omega$ are roots of Eq (2.18). Thus, ω satisfies

$$-\omega^2 - i\omega\widetilde{Tr}_i + d_{11}d_{22}\mu_i^2 + u_1 v_1 \left(d_{21}e^{-i\omega\tau} - \frac{d_{11}\theta e}{(\theta + v_1)^2} \right) \mu_i + \frac{e u_1 {v_1}^2}{\theta + v_1} = 0.$$

Separate the real and imaginary parts as follows:

$$\begin{cases} \overline{D}_i - \omega^2 = -\mu_i d_{21} u_1 v_1 \cos(\omega\tau), \\ \widetilde{Tr}_i \omega = -\mu_i d_{21} u_1 v_1 \sin(\omega\tau), \end{cases} \tag{2.22}$$

where

$$\overline{D}_i = d_{11}d_{22}\mu_i^2 - \frac{u_1 v_1 d_{11}\theta e}{(\theta + v_1)^2}\mu_i + \frac{e u_1 {v_1}^2}{\theta + v_1}.$$

From Eq (2.22), we have

$$\omega^4 + R_i\omega^2 + F_i = 0, \tag{2.23}$$

where

$$R_i = \widetilde{Tr}_i^2 - 2\overline{D}_i = \left(d_{11}^2 + d_{22}^2\right)\mu_i{}^2 - \frac{2\theta e u_1 v_1 d_{22}}{(\theta + v_1)^2}\mu_i + \frac{(\theta e u_1 v_1)^2}{(\theta + v_1)^4} - \frac{2 e u_1 v_1{}^2}{\theta + v_1}, \tag{2.24}$$

$$F_i = \overline{D}_i^2 - (d_{21} u_1 v_1 \mu_i)^2 .$$

Let

$$\triangle_{2i} = R_i^2 - 4F_i = \widetilde{Tr}_i^4 - 4\widetilde{Tr}_i^2\overline{D}_i + 4(d_{21}u_1v_1\mu_i)^2.$$

For fixed i, define

$$d_{21}^{(2i)} = \frac{\overline{D}_i}{u_1 v_1 \mu_i} > 0, \quad d_{21}^{*(2i)} = \frac{|\widetilde{Tr}_i| \sqrt{4\overline{D}_i - \widetilde{Tr}_i^2}}{2u_1 v_1 \mu_i} > 0. \tag{2.25}$$

It can be verified that

$$\left(d_{21}^{(2i)}\right)^2 - \left(d_{21}^{*(2i)}\right)^2 = \frac{(2\overline{D}_i - \widetilde{Tr}_i)^2}{4(u_1 v_1 \mu_i)^2} \geq 0,$$

which implies $d_{21}^{(2i)} \geq d_{21}^{*(2i)} > 0$. Based on the above analysis, the signs of F_i and $\triangle_{2i}$ can be described as

$$F_i \begin{cases} > 0, & 0 < d_{21} < d_{21}^{(2i)}, \\ = 0, & \quad d_{21} = d_{21}^{(2i)}, \\ < 0, & \quad d_{21} > d_{21}^{(2i)}. \end{cases} \tag{2.26}$$

and

$$\triangle_{2i} \begin{cases} > 0, & \quad d_{21} > d_{21}^{*(2i)}, \\ = 0, & \quad d_{21} = d_{21}^{*(2i)}, \\ < 0, & 0 < d_{21} < d_{21}^{*(2i)}. \end{cases} \tag{2.27}$$

Next, the conclusion about the number of positive roots of Eq (2.23) is as follows:

Lemma 7. *Suppose* S_1 *holds.*
(i) *For* $0 < d_{21} < d_{21}^{*(2i)}$, *Eq* (2.23) *has no positive roots.*
(ii) *For* $d_{21}^{*(2i)} \leq d_{21} < d_{21}^{(2i)}$, *Eq* (2.23) *has no positive roots when* $R_i \geq 0$ *and two positive roots when* $R_i < 0$.
(iii) *For* $d_{21} = d_{21}^{(2i)}$, *Eq* (2.23) *has no positive roots if* $R_i \geq 0$, *and has one positive root if* $R_i < 0$.
(iv) *For* $d_{21} > d_{21}^{(2i)}$, *Eq* (2.23) *has a positive root.*

Lemma 8. *If Eq* (2.23) *has positive roots, then the corresponding critical values of delay* τ *are*

$$\tau_{i,j}^{\pm} = \frac{1}{\omega_i^{\pm}}\left[\arccos\left(\frac{\omega_i^{\pm 2} - \overline{D}_i}{\mu_i d_{21} u_1 v_1}\right) + 2j\pi\right], i \in \mathbb{N}, j \in \mathbb{N}_0.$$

Next, we verify the transversality condition.

Lemma 9. *Suppose* S_1 *holds. Then,* $\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}|_{\tau=\tau_{i,j}^{+}} > 0$, *and* $\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}|_{\tau=\tau_{i,j}^{-}} < 0$ *for* $i \in \mathbb{N}$ *and* $j \in \mathbb{N}_0$.

Proof. This is given by Eq (2.18),

$$\left(\frac{\mathrm{d}\lambda}{\mathrm{d}\tau}\right)^{-1} = \frac{2\lambda - \widetilde{Tr}_i}{u_1 v_1 \mu_i d_{21} \lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}.$$

Furthermore,

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1} = \frac{\widetilde{Tr}_i^{2} + 2\omega^2 - 2\overline{D}_i}{(u_1 v_1 \mu_i d_{21})^2}.$$

By calculation, we get

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1}\Big|_{\tau=\tau_{i,j}^{+}} = \frac{\sqrt{\widetilde{Tr}_i^{4} - 4\widetilde{Tr}_i^{2}\overline{D}_i + 4(d_{21}u_1v_1\mu_i)^2}}{(u_1 v_1 \mu_i d_{21})^2} > 0,$$

and

$$\left(\frac{\mathrm{d}\Re(\lambda)}{\mathrm{d}\tau}\right)^{-1}\Big|_{\tau=\tau_{i,j}^{-}} = -\frac{\sqrt{\widetilde{Tr}_i^{4} - 4\widetilde{Tr}_i^{2}\overline{D}_i + 4(d_{21}u_1v_1\mu_i)^2}}{(u_1 v_1 \mu_i d_{21})^2} < 0.$$

For a fixed $d_{21} > 0$, denote

$$\underline{d_{21}^{2}} = \begin{cases} \min\left\{\min\limits_{i\notin H_R}\left\{d_{21}^{(2i)}\right\}, \min\limits_{i\in H_R}\left\{d_{21}^{*(2i)}\right\}\right\}, & H_R \neq \emptyset, \\ \min\limits_{i\in\mathbb{N}}\left\{d_{21}^{(2i)}\right\}, & H_R = \emptyset, \end{cases} \tag{2.28}$$

where $H_R = \{i \in \mathbb{N} : R_i < 0\}$, and

$$\begin{aligned}(G_1) : &\left\{ l \mid l \leq \tilde{l} \text{ and } \frac{\theta e v_1}{(\theta + v_1)^2} < 1 \right\} \\ &\cup \left\{ l \mid l > \tilde{l}, \frac{\theta e v_1}{(\theta + v_1)^2} < 1, d_{11} > d_{11,i}^{H} \text{ and } d_{21} > d_{21,i}^{T} \text{ for } 1 \leq i \leq N^* \right\}.\end{aligned}$$

From Lemma 7 and Eq (2.28), we obtain Theorem 2.7.

Theorem 2.7. *Suppose* S_1 *and* (G_1) *hold.*
(*i*) *For* $0 < d_{21} < \underline{d_{21}^{2}}$, *meaning Eq* (2.23) *has no positive solutions for any* $i \in \mathbb{N}$, *we find that* $E_1(u_1, v_1)$ *of model* (1.1) *is locally asymptotically stable for any* $\tau \geq 0$.
(*ii*) *When* $d_{21} = \underline{d_{21}^{2}}$, *if* $H_R \neq \emptyset$ *and* $i \in H_R$, *Eq* (2.23) *admits positive solutions* $\omega_i^{\pm}$, *which induces a set of Hopf bifurcation values* $\tau_{i,j}^{\pm}$ *in model* (1.1). *Thus,* $E_1(u_1, v_1)$ *may be unstable for some* $\tau > 0$. *If* $H_R \neq \emptyset$ *and* $i \notin H_R$ *or* $H_R = \emptyset$ *and* $i \in N$, *Eq* (2.23) *has no positive root, and* $E_1(u_1, v_1)$ *remains locally asymptotically stable for any* $\tau \geq 0$.
(*iii*) *If* $d_{21} > \underline{d_{21}^{2}}$, *Eq* (2.23) *has positive roots* $\omega_i^{\pm}$ *for any* $i \in \mathbb{N}$, *which generates a sequence of Hopf bifurcation points* $\tau_{i,j}^{\pm}$ *in model* (2.17). *Therefore,* $E_1(u_1, v_1)$ *may be unstable for certain* $\tau > 0$.

In the case that $d_{21} > \underline{d_{21}^{2}}$, selecting τ as the bifurcation parameter, we obtain the following conclusions.

Theorem 2.8. *Suppose* S_1 *and* (G_1) *hold. For fixed* $d_{21} > \underline{d_{21}^2}$*, let* $\tau_{i,0}^{\pm} = \min\limits_{i\in\mathbb{N}_0}\{\tau_{i,j}^{\pm}\}$.

(1) *When* $H_R = \emptyset$*, define*

$$M_1(d_{21}) = \left\{i \in \mathbb{N} : d_{21}^{(2i)} < d_{21}\right\}, and \tau_4^*(d_{21}) = \min_{i\in M_1(d_{21})}\{\tau_{i,0}^{+}\}.$$

For $d_{21} > \underline{d_{21}^2}$*, the coexistence equilibrium point* $E_1(u_1, v_1)$ *of model* (1.1) *is locally asymptotically stable for* $\tau < \tau_4^*(d_{21})$*, unstable for* $\tau > \tau_4^*(d_{21})$*, and Hopf bifurcations occur at* $\tau = \tau_{i,j}^{+}$ $(i \in M_1(d_{21}))$.

(2) *When* $H_R \neq \emptyset$*, let*

$$\overline{d_{21}^2} = \max_{i\in H_R} d_{21}^{(2i)}.$$

(i) *For* $\underline{d_{21}^2} < d_{21} < \overline{d_{21}^2}$*, let*

$$M_2(d_{21}) = \left\{i \in N : d_{21}^{(2i)} < d_{21}\right\}, \quad and \quad M_3(d_{21}) = \left\{i \in H_R : d_{21}^{*(2i)} < d_{21} < d_{21}^{(2i)}\right\}.$$

The critical delay is

$$\tau_5^*(d_{21}) = \min\left\{\min_{i\in M_2(d_{21})}\{\tau_{i,0}^{+}\}, \min_{i\in M_3(d_{21})}\{\tau_{i,0}^{+}\}, \{\tau_{i,0}^{-}\}\right\}.$$

$E_1(u_1, v_1)$ *of model* (1.1) *is locally asymptotically stable for* $\tau < \tau_5^*(d_{21})$*, and unstable for* $\tau > \tau_5^*(d_{21})$ *with Hopf bifurcations occurring at* $\tau = \tau_{i,j}^{+}$ $(i \in M_2(d_{21}))$ *and* $\tau = \tau_{i,j}^{\pm}$ $(i \in M_3(d_{21}))$*. Furthermore, when* $\tau = \tau_{i,j}^{\pm}$ *for* $i \in M_3(d_{21})$*, stability switches occur for* $k \geq 0$*, such that* $E_1(u_1, v_1)$ *is locally asymptotically stable when*

$$\tau \in (0, \tau_{1,0}^{+})\bigcup(\tau_{1,0}^{-}, \tau_{1,1}^{+})\bigcup\cdots\bigcup(\tau_{1,k-1}^{-}, \tau_{1,k}^{+})$$

and unstable when

$$\tau \in (\tau_{1,0}^{+}, \tau_{1,0}^{-})\bigcup(\tau_{1,1}^{+}, \tau_{1,1}^{-})\bigcup\cdots\bigcup(\tau_{1,k}^{+}, +\infty).$$

(ii) *For* $d_{21} > \overline{d_{21}^2}$*, define*

$$M_4(d_{21}) = H_R \cup \{i \notin H_R : d_{21}^{(2i)} < d_{21}\},$$

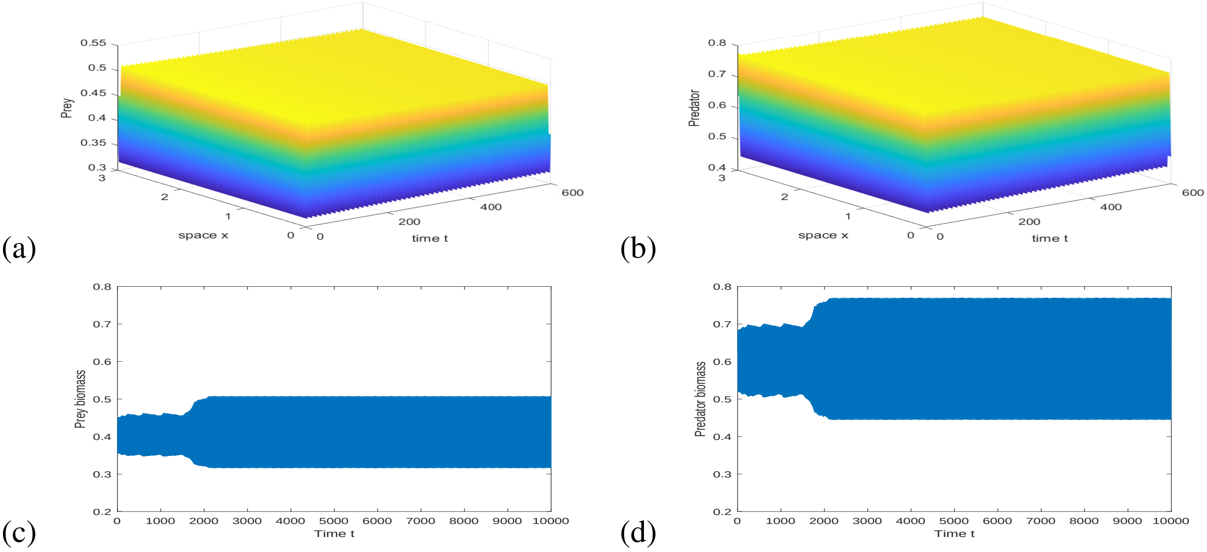
and

$$\tau_6^*(d_{21}) = \min_{i\in M_4(d_{21})}\{\tau_{i,0}^{+}\}.$$

$E_1(u_1, v_1)$ *of model* (1.1) *is locally asymptotically stable for* $\tau < \tau_6^*(d_{21})$*, and unstable for* $\tau > \tau_6^*(d_{21})$ *with Hopf bifurcations occurring at* $\tau = \tau_{i,j}^{+}$ $(i \in M_4(d_{21}))$.

3. Numerical simulations

In the present section, we verify and complement the theoretical findings through a series of numerical simulations. From an ecological point of view, these numerical simulations also illustrate the underlying mechanisms of population interaction in the model. The predator Allee effect describes the density threshold required for predator persistence: when predator density is too low, effective reproduction and cooperative predation become difficult, which weakens predator growth. The nonlocal prey competition reflects that prey individuals compete not only with nearby individuals but also with individuals distributed over a spatial range. Spatial memory represents directed movement based on previous spatial information. Therefore, the observed stability switches, spatially heterogeneous patterns, and spatially inhomogeneous Hopf bifurcations are caused by the combined effects of predator Allee effect, nonlocal prey competition, and spatial memory. Choosing $e = 4$, $d = 0.2$ and $\theta = 0.6$. By calculation, we obtain $u_1 = 0.4$, $v_1 = 0.6$, and $Tr_0(0.4, 0.6) = 0$. The local model (2.2) and the nonlocal model (1.1) have the same spatially homogeneous Hopf bifurcation. Meanwhile, we observe that the prey population exhibits relatively small fluctuations, whereas the predator population shows larger fluctuations, indicating that predator population fluctuations are more sensitive to prey resources. This reflects the ecological mechanism that predator growth is constrained by prey availability and the predator Allee effect, as shown in Figure 2.



(a) (b) (c) (d)

Figure 2. Choosing $e = 4$, $d = 0.2$, and $\theta = 0.6$, local and nonlocal models have the same spatially homogeneous Hopf bifurcations.

Choosing $e = 2$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 1$, and $d_{22} = 0.01$. By calculation, we obtain $u_1 = 0.4$, $v_1 = 0.6$, $\widetilde{l} = 0.22$, and $\frac{\theta e v_1}{(\theta+v_1)^2} = 0.5 < 1$. Choosing $l = 3 > 0.22$. By calculation, we obtain $N^* = 13$, $\max\{D^T_{21,i}\} = 0.48$ for $1 \leq i \leq 13$. According to Theorem 2.3, choosing $d_{21} = 0.4$, and the coexistence equilibrium point $E_1(u_1, v_1)$ loses stability and spatially heterogeneous patterns appear for the local prey competition model (2.2), as shown in Figure 3.

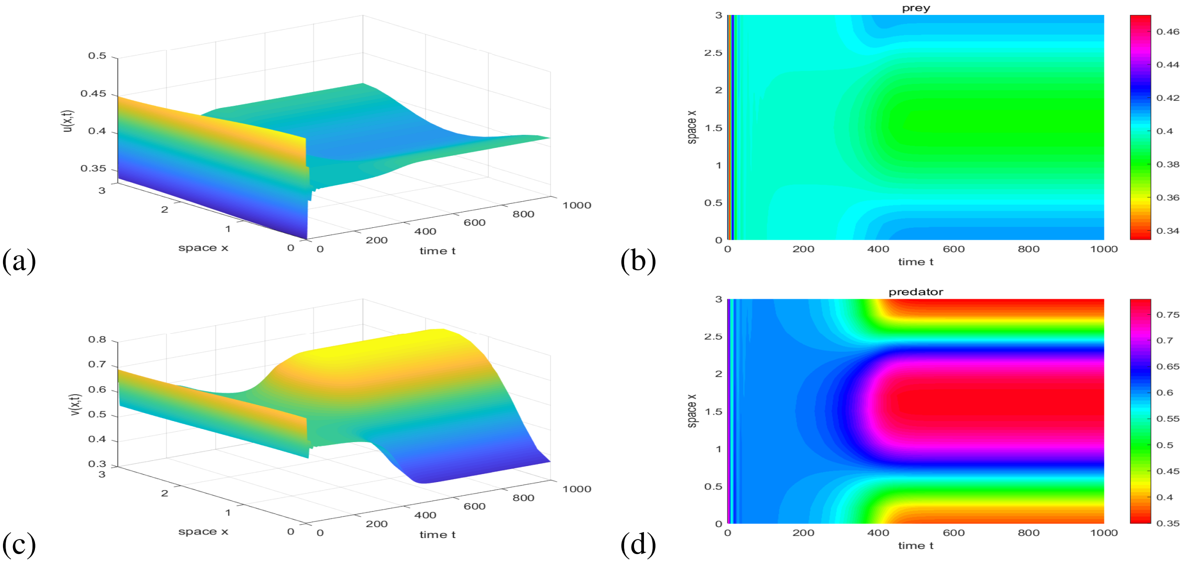


Figure 3. Choosing $e = 2$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 1$, $d_{22} = 0.01$, $l = 3$, and $d_{21} = 0.4$. Results for the local model.

Choosing $d_{21} = 0.5 > 0.48$, the stability condition in Theorem 2.3 is satisfied, and the coexistence equilibrium point $E_1(u_1, v_1)$ is locally asymptotically stable for the local model (2.2), as shown in Figure 4. This comparison shows that memory diffusion can change the spatial distribution of both prey and predator populations by affecting the stability of the coexistence equilibrium.

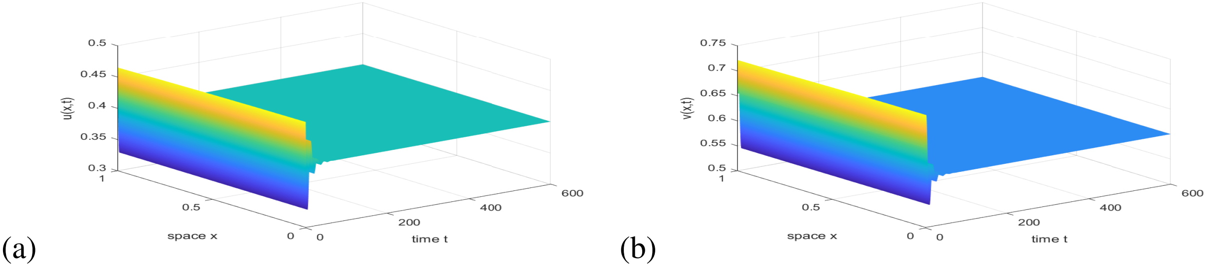


Figure 4. Choosing $e = 2$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 1$, $d_{22} = 0.01$, $l = 3$, and $d_{21} = 0.5$. Results for the local model.

Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, and $d_{22} = 1.2$. Computation yields $\widetilde{l} = 3.46$, and $\frac{\theta e v_1}{(\theta+v_1)^2} = 0.25 < 1$. For $l = 3 < 3.46$, according to Theorem 2.3, the coexistence equilibrium point $E_1(u_1, v_1)$ is locally asymptotically stable for the local model (2.2). By calculation, we obtain $H_B = \{1\}$, $d_{21}^{*(11)} = 4.89$, $d_{21}^{(11)} = 5.02$, $d_{21}^{(12)} = 3.11$, $d_{21}^{(13)} = 3.25$, $d_{21}^{(14)} = 3.88$, $d_{21}^{(15)} = 4.81$, and $d_{21}^{(16)} = 6$. Therefore, $\underline{d_{21}^1} = 3.11$, and $\overline{d_{21}^1} = 5.02$. Similarly, we obtain $H_R = \{1, 2\}$, $d_{21}^{*(21)} = 0.72$, $d_{21}^{*(22)} = 1.47$, $d_{21}^{(21)} = 4.53$, $d_{21}^{(22)} = 1.48$, $d_{21}^{(23)} = 1.41$, $d_{21}^{(24)} = 1.97$, and $d_{21}^{(25)} = 2.87$. Therefore, $\underline{d_{21}^2} = 0.72$, and $\overline{d_{21}^2} = 4.53$.

Choosing $d_{21} = 0.6 < 0.72$. According to Theorem 2.4 and Theorem 2.7, the coexistence equilibrium point $E_1(u_1, v_1)$ is locally asymptotically stable for local prey competition model (2.2) and nonlocal prey competition model (1.1) for any $\tau \geq 0$, as shown in Figure 5.

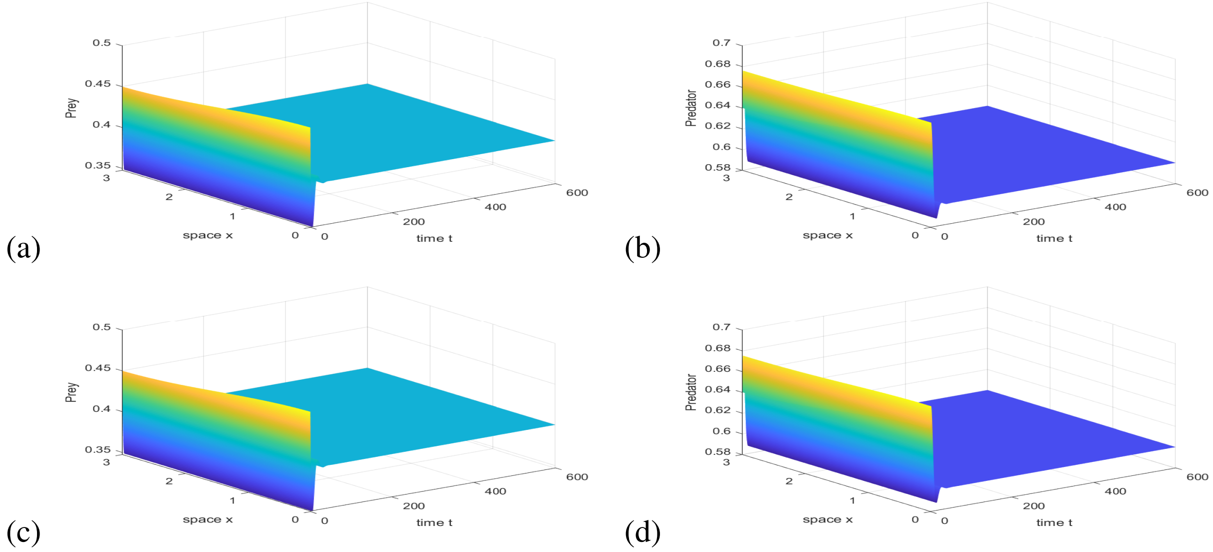


Figure 5. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, and $d_{21} = 0.6$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

Choosing $3.11 < d_{21} = 4.3 < 5.02$. By calculation, we get $W_2(d_{21}) = \{2, 3, 4\}$. Then, $\tau^+_{2,0} = 3.65$, $\tau^+_{3,0} = 3.89$, and $\tau^+_{4,0} = 6.92$. Therefore, $\tau^*_2 = 3.65$. Similarly, we can get $M_2(d_{21}) = \{2, 3, 4, 5\}$ and $M_3(d_{21}) = \{1\}$. Then, $\tau^+_{1,0} = 0.49$, $\tau^-_{1,0} = 39.55$, $\tau^+_{2,0} = 1.29$, $\tau^+_{3,0} = 1.71$, $\tau^+_{4,0} = 2.26$, and $\tau^+_{5,0} = 3.29$. Therefore, $\tau^*_5 = 0.49$. According to Theorem 2.5 and Theorem 2.8, choosing $\tau = 0.3$, $E_1(u_1, v_1)$ is locally asymptotically stable for local and nonlocal models (Figure 6). Choosing $\tau = 2$, only the nonlocal model exhibits a spatially inhomogeneous Hopf bifurcation (Figure 7). Choosing $\tau = 5$, both models undergo a spatially inhomogeneous Hopf bifurcation (Figure 8). These results are summarized in Table 1.

Table 1. $d_{21} = 4.3$, $\tau^*_2 = 3.65$ and $\tau^*_5 = 0.49$.

Model	$\tau = 0.3$	$\tau = 2$	$\tau = 5$
Local	stable (Figure 6)	stable (Figure 7)	inhomogeneous (Figure 8)
Nonlocal	stable (Figure 6)	inhomogeneous (Figure 7)	inhomogeneous (Figure 8)

Choosing $d_{21} = 6 > 5.02$. By calculation, we obtain $W_4(d_{21}) = \{1, 2, 3, 4, 5\}$. Then, $\tau^+_{1,0} = 4.68$, $\tau^+_{2,0} = 2.01$, $\tau^+_{3,0} = 1.91$, $\tau^+_{4,0} = 2.26$, and $\tau^+_{5,0} = 3.31$. Therefore, $\tau^*_3 = 1.91$. Similarly, we obtain $M_4(d_{21}) = \{1, 2, 3, 4, 5\}$, and then $\tau^+_{1,0} = 0.34$, $\tau^+_{2,0} = 0.88$, $\tau^+_{3,0} = 1.11$, $\tau^+_{4,0} = 1.36$, and $\tau^+_{5,0} = 1.73$. Therefore, $\tau^*_6 = 0.34$. Choosing $\tau = 0.3$, the coexistence equilibrium point $E_1(u_1, v_1)$ of both the local and nonlocal models is locally asymptotically stable (Figure 9). Choosing $\tau = 1.5$, only the nonlocal model exhibits a spatially inhomogeneous Hopf bifurcation at this equilibrium point (Figure 10). Choosing $\tau = 3$, both models undergo a spatially inhomogeneous Hopf bifurcation at the coexistence equilibrium point (Figure 11). These results are summarized in Table 2.

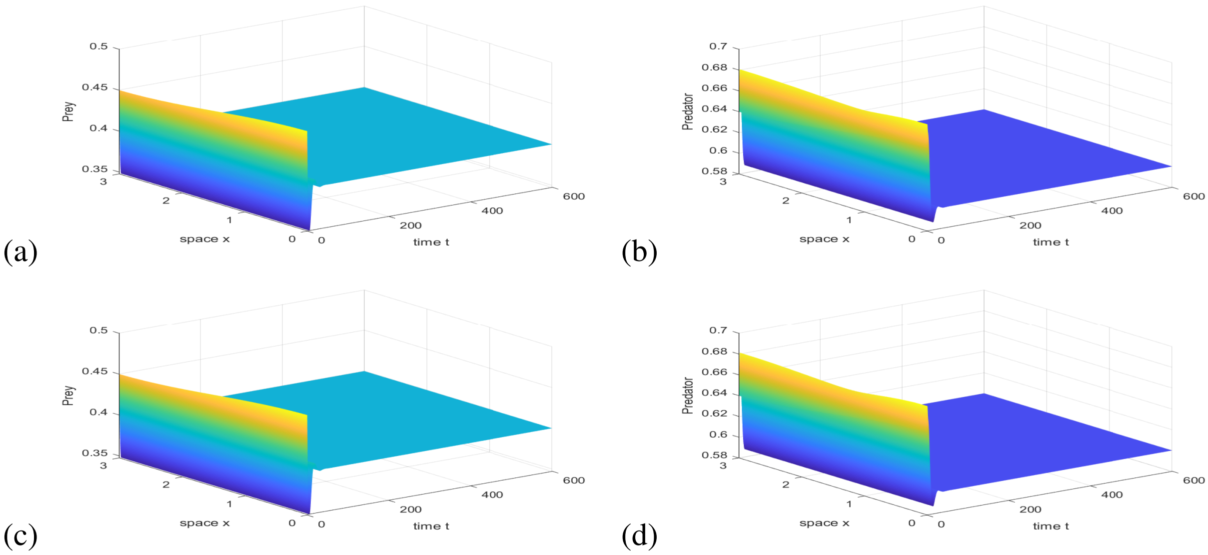


Figure 6. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 4.3$, and $\tau = 0.3$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

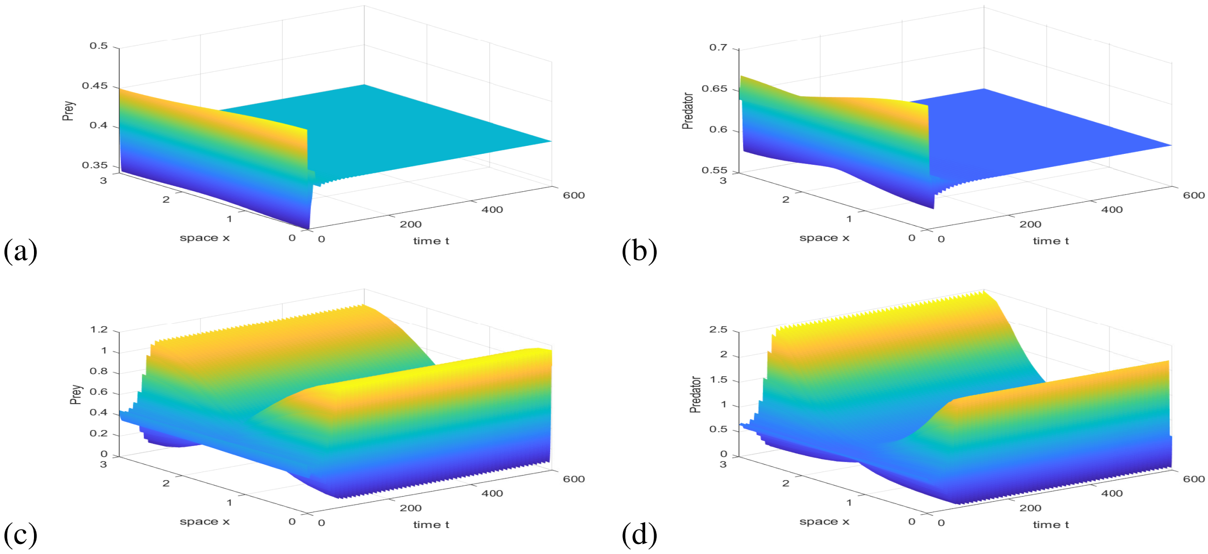


Figure 7. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 4.3$, and $\tau = 2$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

Table 2. $d_{21} = 6$, $\tau_3^* = 1.91$ and $\tau_6^* = 0.34$.

Model	$\tau = 0.3$	$\tau = 1.5$	$\tau = 3$
Local	stable (Figure 9)	stable (Figure 10)	inhomogeneous (Figure 11)
Nonlocal	stable (Figure 9)	inhomogeneous (Figure 10)	inhomogeneous (Figure 11)

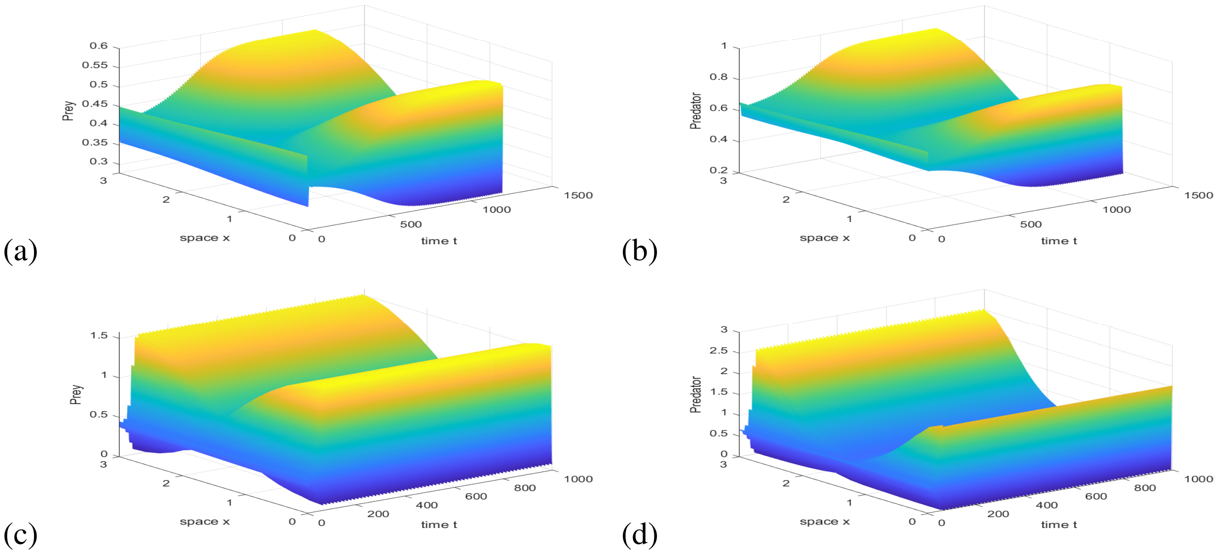


Figure 8. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 4.3$, and $\tau = 5$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

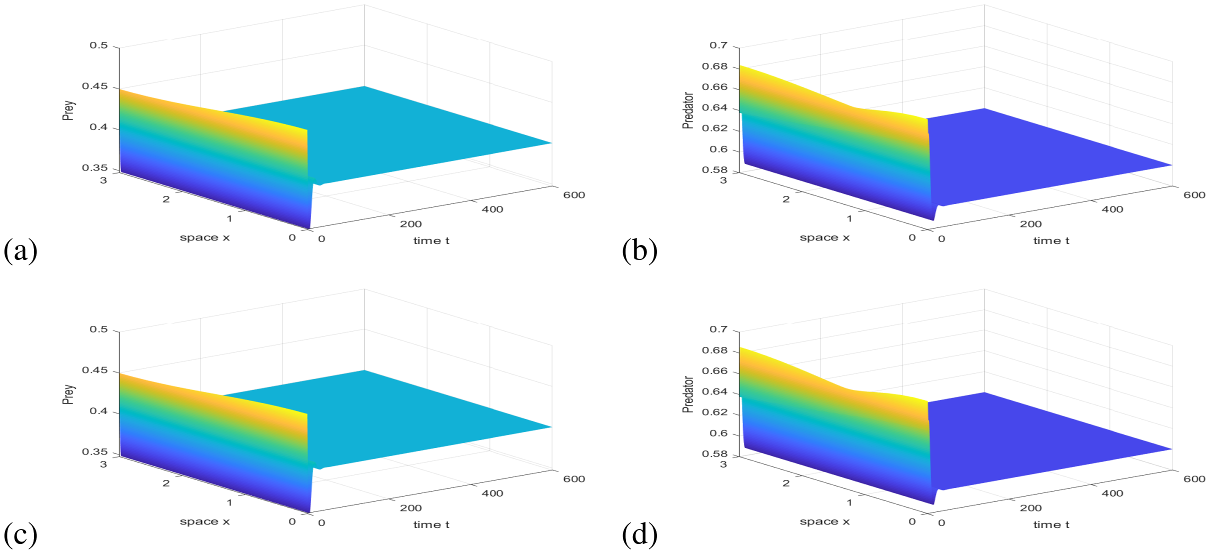


Figure 9. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 6$, and $\tau = 0.3$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

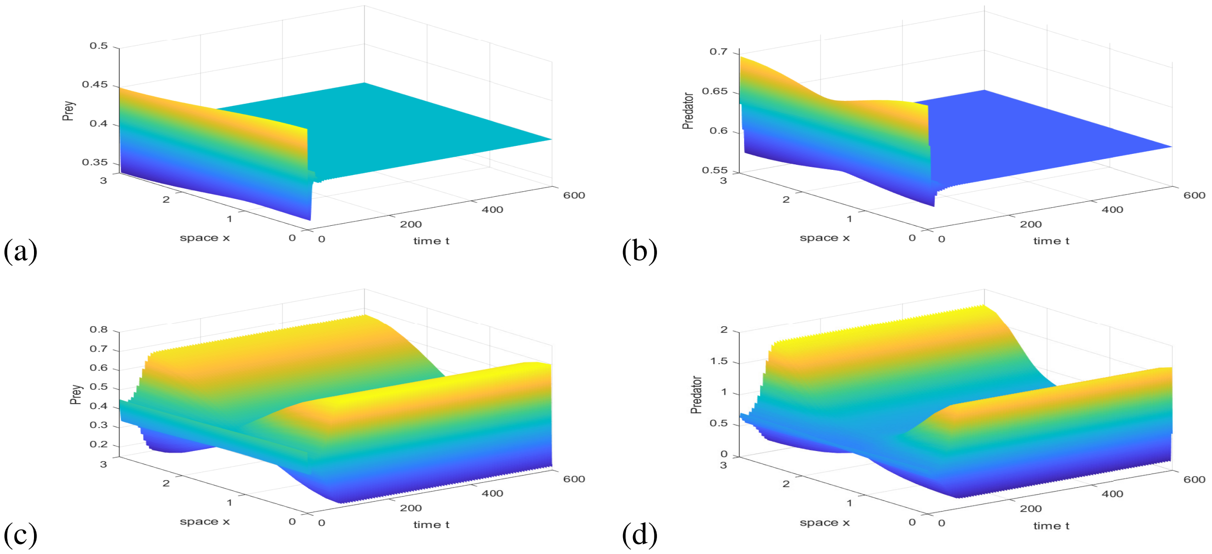


Figure 10. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 6$, and $\tau = 1.5$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

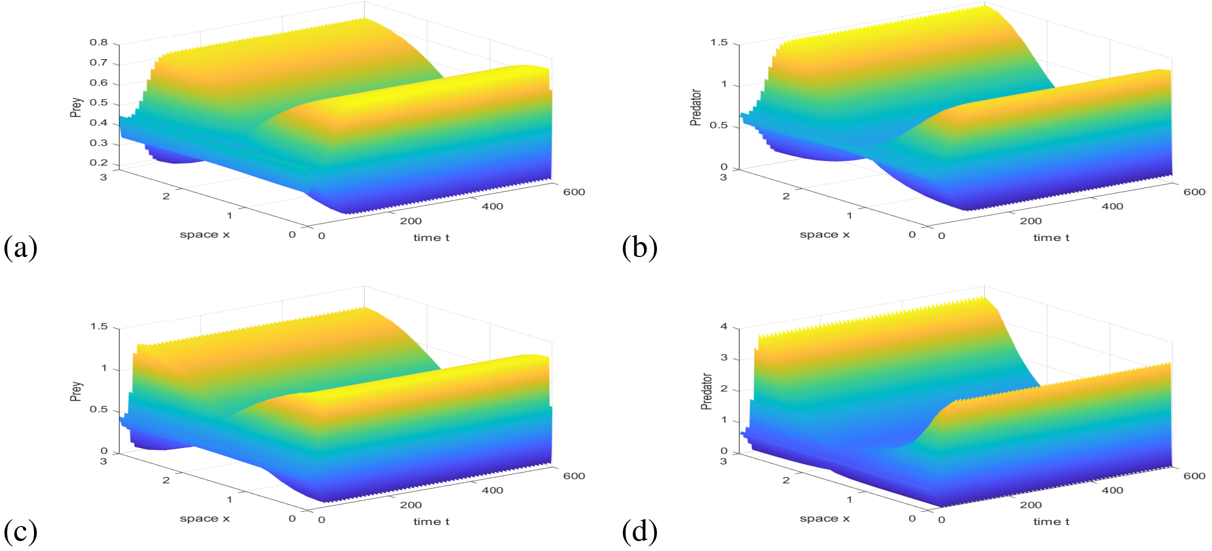


Figure 11. Choosing $e = 1$, $d = 0.2$, $\theta = 0.6$, $d_{11} = 0.2$, $d_{22} = 1.2$, $l = 3$, $d_{21} = 6$, and $\tau = 3$, (a), (b) and (c), (d) correspond to the local and nonlocal models, respectively.

4. Conclusions

In this paper, we consider the impacts of spatial memory and nonlocal prey competition on diffusive predator-prey models with an Allee effect. The Allee effect affects the number of coexisting equilibrium points. As the intensity of the Allee effect increases, the number of coexisting equilibrium points decreases from 2 to 1 and eventually to 0. Specifically, without time delay, the coexistence equilibrium point remains locally asymptotically stable despite nonlocal competition when the predator lacks the Allee effect. However, in the presence of an Allee effect for the predator, nonlocal prey competition leads to the destabilization of the coexistence equilibrium point.

In addition, if spatially inhomogeneous Hopf bifurcation points and Turing bifurcation points exist, then the nonlocal term extends the range of parameter region for the spatially inhomogeneous Hopf bifurcation and narrows the range of parameter region for Turing bifurcation. In addition, the local model and the nonlocal model share the same homogeneous Hopf bifurcation point, and the spatial memory diffusion coefficient has no influence on the occurrence of Hopf bifurcation.

Furthermore, when the spatial memory diffusion coefficient is small, the memory delay has no effect on the stability of the coexistence equilibrium point, which remains locally asymptotically stable in both the local and nonlocal models. As the spatial memory diffusion coefficient gradually increases, although both models undergo a delay-induced spatially inhomogeneous Hopf bifurcation at the coexistence equilibrium point, the nonlocal model triggers this bifurcation first. Additionally, as the memory diffusion coefficient continues to increase, the delay-induced stability regions of the coexistence equilibrium point in both the local and nonlocal models shrink.

In summary, interesting spatial patterns can be observed in the presence of nonlocal terms and spatial memory. Further, we will consider various kernel functions and higher spatial dimensions in future work to investigate the corresponding dynamical behavior.

Use of AI tools declaration

No artificial intelligence tools were used in the preparation of this manuscript.

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Conflict of interest

The authors declare no conflicts of interest regarding this article.

Author contributions

Youwei Yang: Formal analysis, Writing-original draft, Project administration. **Ranchao Wu**: Methodology, Writing-review & editing, Project administration. **Qigang Deng**: Analysis, Methodology.

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