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Delay diffusive prey predator model with hunting cooperation in predators

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Abstract

In this paper, we conduct a detailed stability analysis and investigate the occurrence of Hopf bifurcation in a temporal predator-prey model that incorporates hunting cooperation among predators. Building on this, we extend the model to a spatiotemporal domain to explore how spatial diffusion influences the dynamics. Our simulations reveal the emergence of distinct spatial patterns, such as cold spots indicating regions of low prey density and hot spots corresponding to high predator concentration. Notably, we observe that increasing the diffusion rates leads to the formation of more sharply concentrated and spatially structured patterns. To further enrich the model, we introduce a time delay representing the gestation or response time in predator-prey interactions. The inclusion of delay significantly alters the dynamics: while the non-delayed model supports stationary spatial patterns, the delayed model gives rise to complex oscillatory structures that evolve over time, highlighting the critical role of delay in generating temporal fluctuations in pattern formation.

Keywords. Spatio-temporal predator-prey model, Delayed spatio-temporal model, Stability and bifurcation analysis.
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1. INTRODUCTION

The prey-predator model, also known as the Lotka–Volterra model, is a foundational concept in the field of mathematical ecology that describes the dynamic interaction between two interdependent populations: the prey, which serves as a food source, and the predator, which depends on the prey for survival. This classical model provides critical insights into population fluctuations, species coexistence, and ecological balance. Over time, it has been extended and refined to incorporate more realistic features observed in natural systems. One such extension involves the concept of hunting cooperation, a behavior where individuals within a group work together to capture prey more effectively. This collaborative strategy increases hunting success and can significantly alter population dynamics by enhancing the predatory efficiency. The idea of cooperative hunting was first mathematically discussed in the ecological context by Alves et al. [1]. It has been observed in various social animal species, including wolves, dolphins, and killer whales, where individuals coordinate movements, roles, or timing to improve the outcome of predatory attempts [13]. Incorporating such behavioral ecology into mathematical models enriches their biological realism and helps explain patterns of survival and dominance in nature.

To study the spatial distribution and movement of species, this work extends the classical predator-prey framework by incorporating diffusion terms, allowing populations to disperse in a two-dimensional habitat. The motivation for including spatial effects stems from the seminal work of Alan Turing on the chemical basis of morphogenesis [8, 17]. Turing showed that a uniform steady state, stable in the absence of diffusion, can become unstable when spatial diffusion is introduced a process now widely known as Turing instability. This phenomenon is the mathematical underpinning of pattern formation in nature, responsible for structures such as animal skin markings, vegetation patches, and reaction-diffusion systems. In systems exhibiting Turing instability, the resulting spatial patterns are

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typically stationary and include spot and stripe formations. These are known as Turing patterns, and they occur when diffusion destabilizes an otherwise stable steady state. In contrast, non-Turing patterns emerge in regions where the system is inherently unstable, with or without diffusion. These include time-evolving patterns such as spirals, target waves, and chaotic structures. Such patterns generally arise in what is known as the Turing-Hopf or non-Turing domain, and are characterized by their dynamic, non-stationary nature [18, 24].

To further capture ecological realism, we introduce discrete time delays into the predator-prey interaction terms [7, 19, 21]. These delays account for biological lags such as gestation periods, maturation times, or delays in the effect of consumption on population growth. In natural systems, the consequences of events like successful predation do not manifest instantaneously but are reflected in population changes after a certain time lag. Time delays have been shown to introduce a range of dynamical behaviors into ecological models, including oscillatory solutions, loss or gain of stability, and the onset of complex behaviors such as chaos, depending on the magnitude of the delay and system parameters [11–14].

Despite the increasing attention to delayed and diffusive models in ecology, the literature addressing the combined effects of spatial diffusion, cooperative hunting, and discrete time delays remains scarce. Most existing studies treat these aspects in isolation. Therefore, our goal is to construct and analyze a comprehensive mathematical model that unifies all three phenomena within a two-dimensional spatial framework. This approach enables us to study how cooperation among predators, species movement, and temporal lags jointly influence the dynamics and spatial organization of ecological populations. While previous works, such as those by Yang et al. [22], Song et al. [15], and Li et al. [6], have explored the stability and bifurcation structures in diffusive predator-prey models with one-dimensional spatial variation, our study extends this to the more complex two-dimensional spatial setting. This extension allows us to examine richer pattern formations and explore how these patterns evolve under varying delay conditions. Furthermore, we plan to investigate, in future work, the stability of the system in one-dimensional spatial domains using normal form theory, particularly analyzing how the variation in the delay parameter, denoted by ω, affects system dynamics.

In this work, we first consider a temporal predator-prey model with logistic growth in the prey and cooperative hunting among predators. The delayed interaction is incorporated in the predator growth term to account for realistic time lags. In the initial analysis, presented in section 2, we establish the existence of equilibrium points, derive conditions for local stability, and identify criteria under which a Hopf bifurcation occurs at the interior equilibrium. We then extend this temporal model by incorporating spatial diffusion, resulting in a delayed spatio-temporal model described by partial differential equations. This is presented in section 3, where we analyze the Turing instability condition for both the delayed and non-delayed systems. Through linearization and perturbation analysis, we determine the parameter regimes under which spatially heterogeneous patterns can emerge. To support the theoretical findings, section 4 presents a series of numerical simulations conducted on the delayed spatio-temporal model. These simulations illustrate various types of pattern formation including spots, stripes, and oscillatory structures and demonstrate how the inclusion of delay affects the emergence and stability of these patterns. The numerical results are shown to be consistent with the analytical predictions and highlight the intricate interplay between diffusion, delay, and cooperative behavior. The paper concludes in section 5, where we summarize the main findings, discuss their ecological implications, and propose directions for future research.

2. TEMPORAL MODEL

In this section we introduce the temporal model and present a brief review of the results obtained. The temporal model considered in [1] is a prey-predator model with hunting cooperation and logistic growth in prey along with a specialist predator and is of the form

$$\frac{dn}{dt_1} = rn\left(1 - \frac{n}{k}\right) - (\lambda + ap)np, \tag{2.1a}$$

$$\frac{dp}{dt_1} = e(\lambda + ap)np - \mu P, \tag{2.1b}$$

where $n(t_1)$ and $p(t_1)$ are prey and predator densities, respectively. Parameters r are the intrinsic growth rate, k the carrying capacity of prey, μ the death rate of the predator, and e the conversion efficiency. The term $(\lambda + ap)$

incorporates the hunting cooperation of predators into the model where λ and a are the hunting cooperation parameters. All of the mentioned parameters are positive. Here we follow the non-dimensionalization process for the model (2.1) to reduce the number of parameters. Suppose N, P and t are new nondimensional variables; we use the transformation $N = \frac{n}{k}$, $P = \frac{\lambda}{r}p$ and $t = rt_1$. The non-dimensional prey-predator model is given by

$$\frac{dN}{dt} = N(1-N) - (1+\alpha P)NP, \tag{2.2a}$$

$$\frac{dP}{dt} = c(1+\alpha P)NP - mP, \tag{2.2b}$$

where, $\alpha = \frac{ar}{\lambda^2}$, $c = \frac{e\lambda k}{r}$ and $m = \frac{\mu}{r}$. Initial conditions are $N(0) = N_0 > 0$, $P(0) = P_0 > 0$. The ecologically feasible steady states are points of intersection of $N(1-N) - (1+\alpha P)NP = 0$ and $c(1+\alpha P)NP - mP = 0$ in $\mathbb{R}^2_+$. Irrespective of the parameter values, the system of Eq. (2.2) possesses three equilibrium points on the boundary of $\mathbb{R}^2_+$, (a) $E_0 = (0,0)$, the trivial equilibrium, and (b) $E_1 = (1,0)$, the axial equilibrium point. Coexisting equilibrium point(s) $E = (N,P)$ is given by $P = \frac{m-cN}{\alpha cN}$, where N is positive roots of the cubic equation

$$\alpha c^2 N^3 - \alpha c^2 N^2 - mcN + m^2 = 0. \tag{2.3}$$

In the Eq. (2.3) we can say that the sign changes two times, so by Descartes rule of signs, either two positive roots are possible or zero positive roots. It is very difficult to find the explicit expression for equilibrium points. So, we discuss the dynamics for the considered model by choosing the set of parameters as below.

2.1. **Hopf bifurcation for temporal model.** The Jacobian evaluated at the coexisting equilibrium point (N^*, P^*) is given by

$$J = \begin{bmatrix} a_{10} & a_{01} \\ b_{10} & b_{01} \end{bmatrix},$$

where, $a_{10} = -N^*$, $a_{01} = -(1+2\alpha P^*)N^*$, $b_{10} = c(1+\alpha P^*)P^*$ and $b_{01} = c\alpha N^* P^*$. The Hopf-bifurcation condition can obtained by equating $\text{trace}(J_{E^*})|_{\alpha=\alpha_H} = 0$, $\det(J_{E^*})\,|_{\alpha=\alpha_H} > 0$ and $\frac{d}{dc}(trace(J_{E^*}))\,|_{\alpha=\alpha_H} \neq 0$. The Hopf-bifurcation threshold value α_H is obtained by the equation $(c+1)N^* = m$. Here we cannot find the bifurcation threshold in terms of parameters. So, we take a set of parameters $c = 0.85$, $m = 0.8$ for which one interior equilibrium point is calculated whose stability changes at the Hopf bifurcation point $\alpha_H = 4.5195$ where the stability of (N^*, P^*) changes from stable to unstable, as shown in Figure 1.

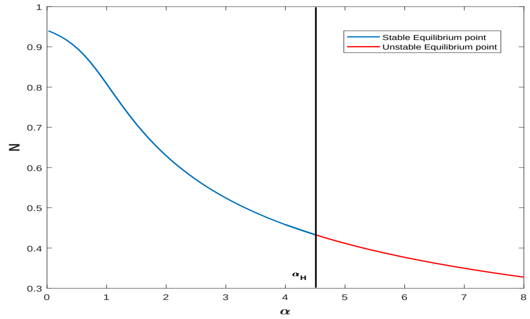


FIGURE 1. One-dimensional bifurcation diagram with respect to α for fix parameters $m = 0.8$, $c = 0.85$. The blue curve represents the stable equilibrium, and the red curve represents the unstable equilibrium.

3. Delayed Spatio-temporal model

Generally, most of the prey-predator models typically consider temporal changes in species densities without accounting for spatial heterogeneity or biological delays. However, in realistic ecosystems, both spatial movement and time delays due to processes such as gestation or maturation significantly influence population behavior.
In this work, we extend a standard predator-prey model by incorporating spatial diffusion and a discrete time delay, resulting in a spatio-temporal reaction-diffusion system with delay. The prey and predator populations, denoted by $n(x,t)$ and , $p(x,t)$ respectively, diffuse through space with diffusion coefficients d_1 and d_2. The predator's reproduction depends on the past densities of both species, introducing a biologically motivated delay τ_1. The resulting model captures more realistic dynamics, including pattern formation and potential destabilization due to delay effects. The newly obtained spatio-temporal model with delay is given by

$$\frac{dn}{dt} = rn\left(1-\frac{n}{k}\right) - (\lambda + ap)np + d_1\nabla^2 n, \tag{3.1a}$$

$$\frac{dp}{dt} = e(\lambda + ap_{\tau_1})n_{\tau_1}p_{\tau_1} - \mu p + d_2\nabla^2 p, \tag{3.1b}$$

where $p_{\tau_1} = p(t_1 - \tau_1)$ and $n_{\tau_1} = n(t_1 - \tau_1)$. Now, under the same transformation used above for the dimensional variable n, p and t_1 and the transformation for the dimensional space variable $\bar{x}$, $\bar{y}$ are given by $x = \frac{\bar{x}}{\sqrt{rd_1}}$ and $y = \frac{\bar{y}}{\sqrt{rd_1}}$, the non-dimensional equation is given by

$$\frac{\partial N}{\partial t} = N(1-N) - (1+\alpha P)NP + \nabla^2 N, \tag{3.2a}$$

$$\frac{\partial P}{\partial t} = c(1+\alpha P_\tau)N_\tau P_\tau - mP + d\nabla^2 P \tag{3.2b}$$

where $d = \frac{d_2}{d_1}$, $\tau = r\tau_1$ and $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$. Here, we discuss the stability criteria for the system of Eq. (3.2) for two scenarios. The first is for without delay, and the second is for with delay. The stability criteria is discussed by perturbing the system of Eq. (3.2) around the homogeneous steady-state (N^*, P^*) assuming the perturbation to be small and the linearized model of Eq. (3.2) at (N^*, P^*) is given by

$$\frac{\partial N}{\partial t} = a_{10}N + a_{01}P + \nabla^2 N, \tag{3.3a}$$

$$\frac{\partial P}{\partial t} = b'_{01}P + c_{10}N(t-\tau) + c_{01}P(t-\tau) + d\nabla^2 P, \tag{3.3b}$$

where $b'_{01} = -m$, $c_{10} = b_{10}$, $c_{01} = c(1+2\alpha P)N$ and such that $b_{01} = b'_{01} + c_{01}$. Assume the perturbed solution of model (3.2) is of the following form [20, 25]:

$$\begin{pmatrix} N \\ P \end{pmatrix} = \begin{pmatrix} N^* \\ P^* \end{pmatrix} + \epsilon \begin{pmatrix} N_k \\ P_k \end{pmatrix} e^{\lambda_k t} e^{ikx}, \tag{3.4}$$

where λ_k is the growth rate and k is the wave number. Substituting Eq. (3.4) in the system of Eq. (3.3), we get the characteristic equation for the delayed spatio-temporal model, which is given by

$$\lambda^2 + (-a_{10} - b'_{01} + (1+d)k^2)\lambda + (k^2 - a_{10})(dk^2 - b'_{01}) + (-c_{01}\lambda + (a_{10} - k^2)c_{01} - a_{01}c_{10})e^{-\lambda\tau} = 0. \tag{3.5}$$

3.1. **Turing instability condition for $\tau = 0$.** Put $\tau = 0$ in Eq. (3.5), we get the characteristic equation for the non delayed diffusive model of system of Eq. (3.2) is given by

$$\lambda^2 + (a_{10} + b_{01} - k^2 - dk^2)\lambda + dk^4 - k^2(a_{10}d + b_{01}) + a_{10}b_{01} - a_{01}b_{10} = 0. \tag{3.6}$$

As discussed in [5, 16, 23], the Turing instability condition is the condition where the steady state is stable for the temporal model and becomes unstable for the diffusive model. The mathematical condition for the Turing instability for without delay model is given by

$$a_{10} + b_{01} < 0, \quad a_{10}b_{01} - a_{01}b_{10} > 0 \quad \text{and} \quad a_{10}d + b_{01} > 2\sqrt{d(a_{10}b_{01} - a_{01}b_{10})}.$$

The wave threshold value is $k_c = \sqrt{\frac{a_{10}d + b_{01}}{2d}}$.

3.2. **Hopf-bifurcation for $\tau \neq 0$.** In order to derive the Hopf bifurcation condition, assume that $\lambda = i\omega$ $(\omega > 0)$ is a root of Eq. (3.5). Then we have

$$-\omega^2+(-a_{10}-b'_{01}+(1+d)k^2)i\omega+(k^2-a_{10})(dk^2-b'_{01})+(-c_{01}i\omega+(a_{10}-k^2)c_{01}-a_{01}c_{10})e^{-i\omega\tau}=0. \tag{3.7}$$

Comparing the real and imaginary parts of the Eq. (3.7) we get,

$$pcos(\omega\tau)-c_{01}\omega sin(\omega\tau)=\omega^2-q, \tag{3.8a}$$

$$psin(\omega\tau)+c_{01}\omega cos(\omega\tau)=\omega r, \tag{3.8b}$$

where $p=a_{10}c_{01}-a_{01}c_{10}-c_{01}k^2$, $q=(k^2-a_{10})(dk^2-b'_{01})$ and $r=(1+d)k^2-a_{10}-b'_{01}$. Now, squaring and adding Eq. (3.8)a and (3.8)b we get,

$$\omega^4+P_k\omega^2+Q_k=0, \tag{3.9}$$

where $P_k=-c_{01}^2-2q+r^2$ and $Q_k=q^2-p^2$. On the basis of the roots of the Eq. (3.9), we can discuss the behavior of the considered diffusive model. If $P_k>0$ and $Q_k>0$ are positive, then no positive ω, i.e., no effect of delay. If either $P_k>0$ and $Q_k<0$ or $P_k<0$ and, $Q_k<0$ then only one positive ω and only one Hopf bifurcation occur in this case. If $P_k<0$, $Q_k>0$ and $P_k^2-4Q_k>0$ then two positive ω exists and in this multiple Hopf bifurcation, the Hopf threshold value is given by

$$\tau_T=\frac{2\pi j}{\omega}+\frac{1}{\omega}cos^{-1}\left(\frac{(\omega^2-q)p-c_{01}r\omega^2}{p^2+c_{01}^2\omega^2}\right), \tag{3.10}$$

where $j=0,1,2,3...$, see [2, 3].

4. NUMERICAL SIMULATION

The system of Eq. (3.2) can be solved numerically based on the finite difference method for spatial derivatives and an explicit Euler method for temporal derivatives at the time interval [0, T] with time step $\Delta t=0.01$ and space step $\Delta x=\Delta y=0.25$. The initial condition taken for numerical simulations is a small perturbation around the homogeneous steady state (N^*,P^*) given by $N(x,y,0)=N^*+\epsilon\xi_{xy}$ and $P(x,y,0)=P^*+\epsilon\eta_{xy}$ where $\epsilon=0.001$ and ξ_{xy}, η_{xy} are spatially uncorrelated Gaussian terms.

4.1. **Pattern formation without delay.** The Turing instability curve is drawn by the equation $a_{10}d+b_{01}=2\sqrt{d(a_{10}b_{01}-a_{01}b_{10})}$. This curve divides the $\alpha-d$ plane into two regions, as shown in Figure 2 and the blue temporal Hopf curve divides these two regions into four regions. The region is denoted by HSS (homogeneous steady state), where the steady state is stable and no patterns appear in this region. The region denoted by OSC where oscillatory patterns appear. In the region denoted below the red curve, only Turing patterns appear, as shown in Figures 3 and 4. Figure 3 shows the pattern obtained for the spatio-temporal model without delay for the prey population. In this

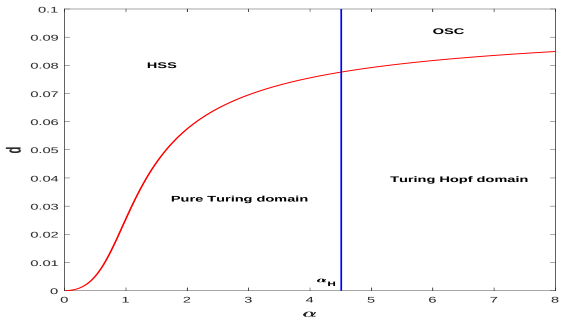
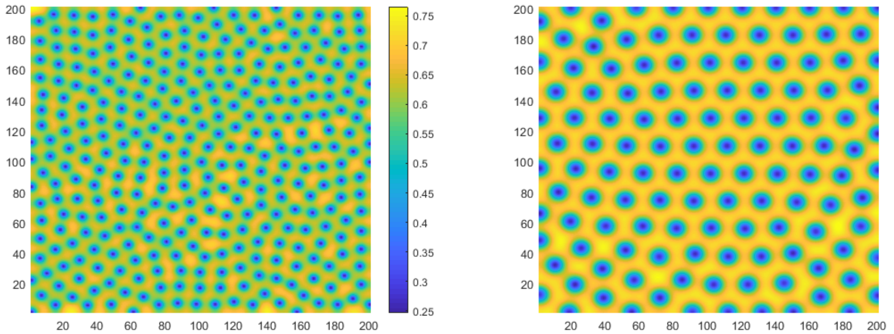


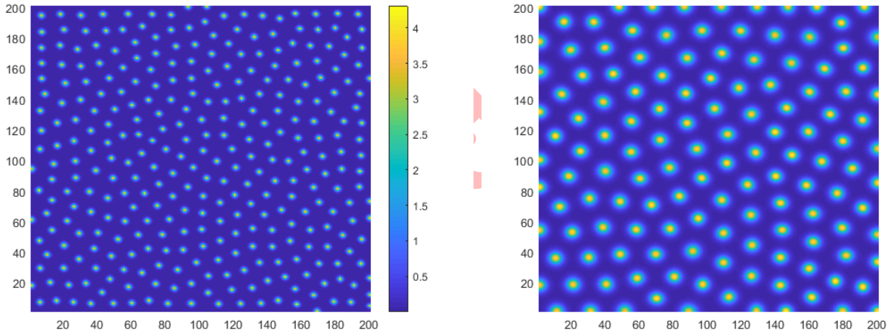
FIGURE 2. Turing and non-Turing regions in $\alpha-d$ the plane for the parameters $m=0.8$ and $c=0.85$. The green curve represents the Turing curve, and the blue vertical line represents the Hopf-bifurcation threshold line for the temporal model.



(a) (b)

Figure 3. Snapshots of pattern for prey at the time $t = 2000$ for $\alpha = 1$ different values of d: (a) $d = 0.01$ (b) $d = 0.024$.

pattern, we observe that for a low diffusion coefficient, prey density is spreading, and for a higher diffusion coefficient, prey density appears in small patches of spots having low density at the center. Figure 4 shows the pattern obtained for the spatio-temporal model without delay for the predator population. In this pattern, we observe that for a low diffusion coefficient, predator density appears in small patches of spots having high density at the center, and for a higher diffusion coefficient, predator density appears in large patches of spots having a high density at the center.



(a) (b)

Figure 4. Snapshots of the pattern for the predator at the time $t = 2000$ for $\alpha = 1$ different values of d: (a) $d = 0.01$, (b) $d = 0.021$.

4.2. **Pattern formation with delay.** In this section, we see the effect of delay on the diffusive model by numerical simulation. We have used the Eq. (3.10) to draw the Hopf threshold value as shown in Figure 5. If we take $\alpha < 4.263$ then no any ω obtained, i.e., the steady state is always stable. If we take $\alpha \in (4.263, \alpha_H)$ them, two ω exist. So, two Hopf-threshold values were obtained as given in the paper [10, 15, 22]. This is clearly drawn in Figure 5 which shows that delay destabilizes the steady state. In the case without delay, the steady state is stable in the region where $\alpha < \alpha_H$ and unstable in the region where $\alpha < \alpha_H$. In case of delay, we got a red curve in the stable as well as unstable region in which the steady state is stable on the left side of the blue curve and unstable on the right side of the blue curve. If we introduce diffusion in the delayed model, then the red curve shifts towards the right, i.e., the stability region increases as we increase the diffusion coefficient from $d = 0$ to $d = 0.01$. So, we can say that the diffusion stabilizes the steady state and delay destabilizes the steady state, as shown in Figure 5. This concept has been discussed in the paper [3] in detail.

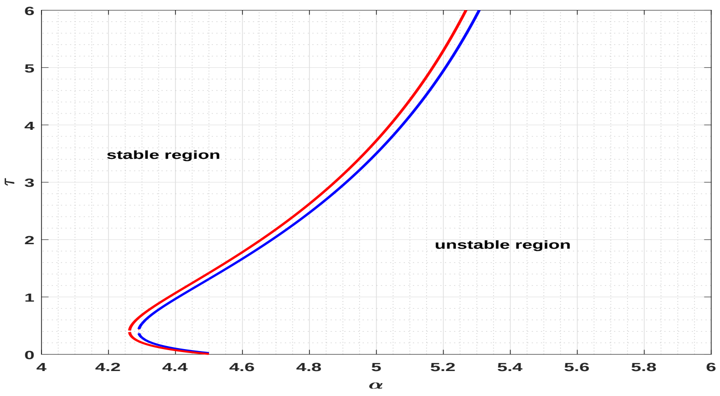


FIGURE 5. Effect of diffusion on a delayed temporal model for the fixed parameters $c = 0.85$, and $m = 0.8$. The red curve represents the delayed temporal model, and the blue curve represents the Hopf bifurcation curve for wave number $k = 0.05$ and diffusion coefficient $d = 0.01$.

Next, we draw the pattern for the different regions of the bifurcation diagram for both delayed and without delayed spatio-temporal models and compare the results. If we fix the parameter $\alpha = 5$ and $d = 0.02$ then the cold spot pattern appears as shown in Figure 6(a) for the $\tau = 0$ and it is stationary with respect to time as shown in Figure 6(b). If we further increase the delay parameter $\tau = 5.8$ for the fix value, α and d the the cold spot pattern changes to an oscillatory pattern as shown in Figure 6(c) and it is non stationary with respect to time as shown in Figure 6(d).

5. CONCLUSION

The proposed spatio-temporal predator-prey model with delay offers a more comprehensive framework for analyzing ecological systems by incorporating both diffusion and time delay. The diffusion terms account for species dispersal across space, which is crucial for understanding spatial pattern formation. Meanwhile, the inclusion of a time delay reflects the natural lag in the predator's response to prey availability, commonly seen in ecosystems due to gestation periods or behavioral interactions.

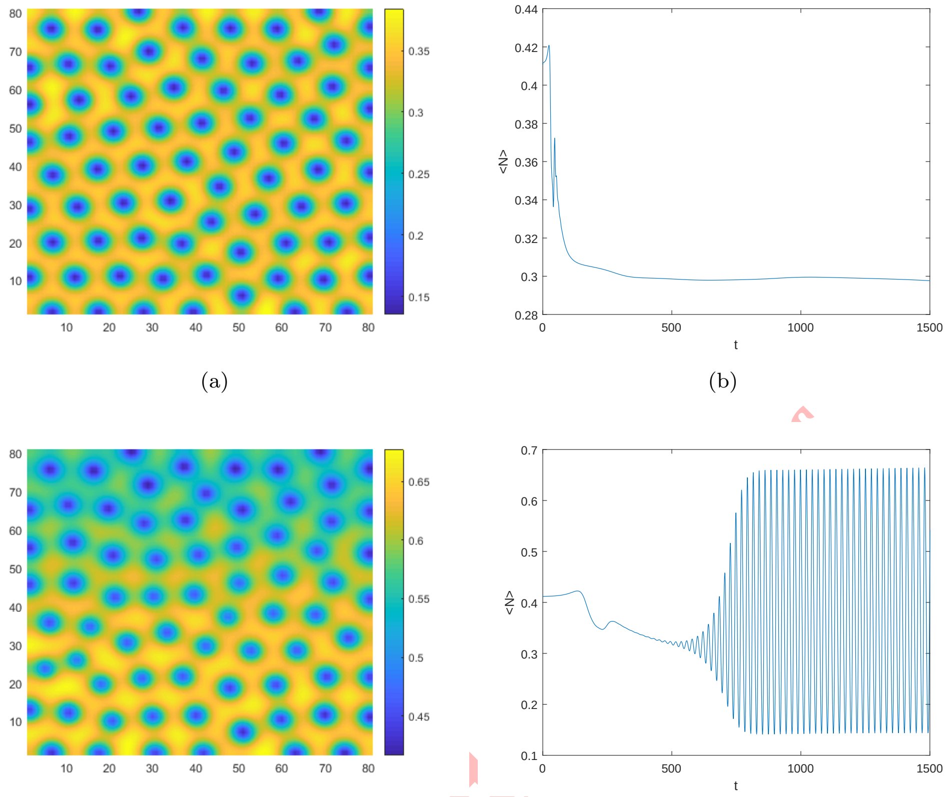
In this work, we explored two scenarios:

- Pattern formation in the spatio-temporal model without delay, and
- Pattern formation in the delayed spatio-temporal model.

For the spatio-temporal model without delay, we observed the emergence of cold spot patterns for prey density and hot spot patterns for predator density under Turing instability conditions, as shown in Figures 3 and 4. It is evident from the figures that increasing the diffusion coefficient d leads to a corresponding increase in the size of the spatial patches. Ecologically, this implies that both prey and predator populations tend to spread in localized groups as diffusion increases. This behavior aligns with cooperative hunting strategies in predators and grouped movement in prey species for survival.

In the case of the delayed spatio-temporal model, the dynamics become more complex due to the appearance of exponential delay terms such as $e^{-\lambda\tau}$ in the characteristic equation [2]. This makes direct analytical study challenging. Therefore, we employed Hopf bifurcation analysis by assuming purely imaginary roots $\lambda = i\omega$. Two key behaviors emerged:

Stabilizing effect of diffusion and destabilizing effect of delay: As illustrated in Figure 5, increasing the diffusion coefficient expands the stability region of the system, while introducing or increasing the delay reduces stability.



(a) (b)

(c) (d)

FIGURE 6. Snapshots of the pattern for the parameters $\alpha = 5$ and $d = 0.02$ at the time $t = 1500$ for different values of τ: (a) $\tau = 0$ (b) Spatial average (c) $\tau = 5.8$ (d) spatial average.

Transition in pattern formation due to delay: Figure 6 demonstrates that the stationary patterns observed in the non delayed case transform into oscillatory patterns when delay is introduced. From an ecological perspective, this indicates that, while populations may form static spatial patterns in the absence of delay, time delays can induce temporal fluctuations, leading to dynamic oscillations in population densities.

In conclusion, the delayed spatio-temporal model captures a richer set of ecological behaviors compared to its non delayed counterpart. Future studies may consider extending this framework to include the Allee effect and interactions involving generalist predators, which could offer further insight into population stability and ecosystem resilience also introduce diffusion in the epidemic model with delay studied in the paper [4].

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