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Dynamics of a spatially coupled model with delayed prey dispersal

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ABSTRACT

Dispersal of species from one region to another one is a common occurrence in ecology. Several studies have been conducted on predator–prey interactions subjected to population dispersal between patches. In this paper, we consider a two-patch Rosenzweig–MacArthur predator–prey model with prey dispersal. In absence of predator, the movement of prey is density-independent. Predator-influenced prey dispersal is also taken into account because predators have a potential to control prey movement. Travelling time (time delay) linked with the movement mechanism among the prey community is incorporated. The positivity and boundedness of the solutions in the spatially coupled system are established. Stability behaviours of the coexisting equilibrium are explored by considering delay as the bifurcating parameter. It is found that, delayed prey dispersal can potentially alter the stability (resp. instability), and even causes stability switching (resp. instability switching) around the interior equilibrium. However, after some consecutive changes in stability, the equilibrium undergoes instability for larger delay. Analysis of the stability is performed by estimating the distance between critical values of the time delay. In addition, numerical examples are provided to illustrate the findings.

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1 Introduction

Establishing mechanisms to understand the interactions between species in ecological systems are very complex. Starting from the third decade of nineteenth century, several pioneer scientists developed mathematical models to explore dynamics between prey and predator [1–6]. These classical models have been investigated further by making use of fractional-order systems [7–8], square root functional response [9], nonlinear harvesting strategies [10–11], etc. in the recent years. Successive developments, including time delay parameters in the models appeared in population dynamics to capture more complex and realistic scenarios [12–15]. The time delay factors evolved due to gestation, maturity, predation response, and other factors in many real ecological systems. Several articles in the current decades studied the effects of time delay on the stability of steady state in predator–prey models. Li and Takeuchi [16], proved that delay does not have any destabilizing effect in a model having Beddington–DeAngelis functional response. Jana and Roy [17], have incorporated two delays in a Holling–Tanner predator–prey model with Beddington–DeAngelis functional response and detected stability switching with respect to the gestation delay. In a class of predator–prey models, it was demonstrated that delay always had a destabilizing effect [18].

An improved modelling approach in a stage-structured community, Banerjee and Takeuchi [19], established that maturation delay could enhance stability of the equilibrium. Anacleto and Vidal [20], have studied a delayed predator–prey model combined with type II response function and Allee effect. They established that the stability switching scenario happens due to the increasing values of time delay parameter. It is worthwhile to note that, the delay induced stability is studied when the equilibrium of the above non-delayed models are locally stable. On the other hand, when the equilibrium of the non-delayed models are unstable, increasing time delay does not have any influence to stabilize the solutions [21]. Shu et al. [22], have studied a delayed intraguild community and found that if the system is unstable prior to incorporation of delay, either the delay has no effect in changing the instability or instability switching can occur. Souna et al. [23], have studied a delayed predator–prey model with a single predator group feeding upon two different prey groups: grouped prey and solitary prey. The growth term of the grouped prey involved time lag. They discussed the effect of time delay in the stability of the periodic solution of the system. Chen et al. [24], have studied the combined effects of time delay and impreciseness on the stability of a two-species competition model. They concluded

that under certain conditions, time delay does not have a significant role in the stability of the system as compared to the fuzziness of biological parameters.

Interactions between predator and prey are not only limited to a single patch. The movement of species from one place to another is an indispensable part of ecology. Various factors like food availability, competition, safe breeding, environmental changes, predation, etc., lead to movement of the predators or prey from one patch to another. Thus, spatial models (patchy models) find their popularity in stability analysis [25–28], fishery management [29–30], biological pest control [29–31].

Travel time of species between patches cannot be ignored while dealing with spatial systems. Hence, incorporating time delay in dispersal is more appropriate in modelling. Takeuchi [32], proposed a single-species patchy model using autonomous equations. They have established that delay has no impact in destabilizing the coexisting equilibrium (which is globally stable in the absence of delay). Sun and Mai [33], have considered a two-species competition model over multiple patches. They have shown that the delayed dispersal does not effect the stability and instability of the coexistence equilibrium. On the other hand, Xu et al. [34], have designed a two-patch prey-predator model with prey dispersal. The delay is incorporated in gestation as well as in functional response. They have proved that the increasing delay causes instability. Likewise, non-spatial models, the stability results in patchy models were derived by Takeuchi et al. [32] and Xu et al. [34], when the coexisting equilibrium is asymptotically stable without time delay.

Recently, a very limited number of articles have paid attention to analyse delay-induced stability in spatial models when the coexisting steady state is unstable without delay. Zhang et al. [35], have considered the predator-induced prey dispersal where the dispersal was based on the predation risk of the prey. They have incorporated the delay in its dispersal term. It was found that, incorporation of time delay can destabilize (resp. stabilize) a stable (resp. unstable) coexisting equilibrium. Several stability switching phenomena were illustrated by computational simulations in a two-patch predator-prey model with delayed dispersal on both predator and prey [36]. Later, Mai et al. [37], have considered the predator dispersal and explained switching of stability analytically when the coexisting equilibrium of the non-delayed model was unstable. It was also proved that delay had no influence in altering the stability when the equilibrium was stable.

Obviously, a limited literature has investigated the impacts of dispersal delay in spatial models. Henceforth, a need arises, to study in greater depth, the effect of

dispersal delay in predator-prey models. Further, the spatial models mentioned in the above discussion were formulated based on the concept of patchy model, in which populations can disperse between distinct locations or regions. Another popular framework to develop spatial population model is to make use of partial differential equations (i.e. reaction-diffusion models). It is important to note that the population dynamics using reaction-diffusion systems are defined in a domain. Therefore, populations do not disperse between two distinct locations. Consequently, incorporating the time-lag in dispersal is not found in the existing reaction-diffusion models. For instance, we cannot include time delay in the diffusion terms of the models studied by Polyanin and Zhurov [38] and Dos Anjos [39]. On the other hand, time delay can easily be plugged into the dispersal terms for patchy models. Hence, investigating the influence of delayed dispersal in population dynamics through patchy models could be an alternative option to consider in comparison to the reaction-diffusion systems. Our main objective is to develop a two-patch predator-prey model with new kind of prey-dispersal process. Further, we would like to study the positivity and boundedness of the solutions to our model. We examine whether time delay in dispersal has any effect on the stability of the coexisting equilibrium. We also compare our results with the existing contributions and reveal the future scope in this direction.

The rest of the article is divided into three sections. [Section 2](#) deals with the formulation of our model. In [Section 3](#), the positivity and boundedness of the solutions of our model is discussed. In [Section 4.1](#), we evaluated the stability of the model in the absence of delay. In [Section 4.2](#), we have analyzed the delayed model taking delay as the bifurcation parameter. The effect of dispersal in the stability of the system was also analyzed in this section. Finally, in [Section 5](#) we have concluded by stating all our results.

2 Model formulation

We deal with a two-patch predator-prey model with prey dispersal. In each patch, the prey species, in the absence of predators, grow logistically. We assume that the predators in each patch are specialist and decay exponentially in the absence of prey. The predator-prey interaction in each patch is described with Holling type II functional response. In the absence of predator, the prey species follow density-independent dispersal between patches. However, in the presence of predators, the prey should avoid predation pressure. Hence, movement of prey should be influenced by predator. Hence, we have incorporated predator-influenced

prey dispersal in our model. The prey populations tend to move more in number from their own patch when the number of predator is higher in the same patch. It is fairly acceptable that spatial range of prey is smaller than predator. If the patches are not too close to each other, a travel time should be involved in the movement process of prey from one patch to another. Hence, a time delay is now included to more realistically capture the dispersal mechanism. Based on the above assumptions, we formulate the following strategic model:

$$\begin{aligned} \dot{x}_1 &= rx_1 \left(1 - \frac{x_1}{K}\right) - \frac{ax_1y_1}{h + x_1} + D \left(\alpha \frac{\rho y_2(t - \tau)}{L + y_2(t - \tau)} + (1 - \alpha) \right) x_2(t - \tau) \\ &\quad - D \left(\alpha \frac{\rho y_1}{L + y_1} + (1 - \alpha) \right) x_1, \\ \dot{y}_1 &= \frac{bx_1y_1}{h + x_1} - my_1, \\ \dot{x}_2 &= rx_2 \left(1 - \frac{x_2}{K}\right) - \frac{ax_2y_2}{h + x_2} + D \left(\alpha \frac{\rho y_1(t - \tau)}{L + y_1(t - \tau)} + (1 - \alpha) \right) x_1(t - \tau) \\ &\quad - D \left(\alpha \frac{\rho y_2}{L + y_2} + (1 - \alpha) \right) x_2, \\ \dot{y}_2 &= \frac{bx_2y_2}{h + x_2} - my_2, \end{aligned} \quad (1)$$

where $x_1(\theta), x_2(\theta), y_1(\theta), y_2(\theta) \geq 0$ and continuous on $\theta \in [-\tau, 0)$, $x_1(0), x_2(0), y_1(0), y_2(0) > 0$. Here $x_i(t)$ and $y_i(t)$ are the number of prey and predator populations, respectively, at time t in the i -th patch ($i = 1, 2$). The intrinsic growth rate and carrying capacities of the prey, in the two patches, are denoted by r and K , respectively. Here a is the attack rate during predation and $b = ac$ where c is the conversion coefficient of prey biomass into predator. We define m as the specific mortality rate of predator and h as the half-saturation constant.

Density-independent dispersal of prey species in the dynamics of $x_1(t)$ can be defined as $D(x_2 - x_1)$, where D is the inherent dispersal rate of the prey. Clearly, Dx_2 amount prey population from patch 2 contributes to the dynamics of x_1 in the patch 1. On the other hand, Dx_1 is the measure of prey leaving the patch 1 and contributes to the dynamics of x_2 in the second patch. Similarly, $D(x_1 - x_2)$ is the density-independent dispersal term in the dynamics of x_2 in the patch 2. Such density-independent dispersal is very common in theoretical models. Some significant attentions were also paid to develop and analyze models involving the impact of density-dependent dispersal [25–26–40]. However, only Zhang et al. [35], have proposed density-dependent dispersal among prey with time delay and a density-dependent dispersal model was formulated due to the predator-avoidance factor of prey species. We have proposed similar type of density-dependent dispersal in model (1) to examine how time delay can change the dynamics.

We now describe the density-dependent dispersal proposed in the model (1). We assume that the prey species x_1 moves from the patch 1 to avoid predation and the movement depends upon the density of y_1 in the respective patch. The predator-influenced dispersal of prey in patch 1 is proportional to $\frac{y_1}{L+y_1}x_1$. Similarly, $\frac{y_2}{L+y_2}x_2$ is linked with the dispersal of prey in the second patch. Here, we assume L is a parameter with the same dimension of biomass and control the dispersal rate at a maximum limit. When the predator is large in number, $\frac{y_1}{L+y_1} \rightarrow 1$. Now we can write the density-dependent dispersal term, without time delay, in the dynamics of x_1 as

$$D \left(\frac{\rho y_2}{L + y_2} x_2 - \frac{\rho y_1}{L + y_1} x_1 \right),$$

where ρ is a proportionality constant. When the dispersal is not instantaneous, incorporation of travel time τ converts the dispersal term as

$$D \left(\frac{\rho y_2(t - \tau)}{L + y_2(t - \tau)} x_2(t - \tau) - \frac{\rho y_1}{L + y_1} x_1 \right).$$

In the same way, we construct the dispersal term in the dynamics of x_2 and incorporate the time delay in the density-dependent dispersal term. A constant α ($0 \leq \alpha \leq 1$) has been plugged into our system, where α and $(1 - \alpha)$ represent the weights of predator-dependent dispersal and density-independent dispersal, respectively. When $\alpha = 0$ (resp. $\alpha = 1$), the prey populations follow only state-independent (resp. predator-influenced) dispersal between regions.

We have chosen the same value of the parameters in both the patches. Hence, both regions are homogeneous and populations would be in balanced dynamics in the absence of time delay. When travel time is taken into account in dispersal, the balanced dynamics could be lost. We now investigate how the delay can change the stability due to the new dispersal framework.

3 Positivity and boundedness

In this section, we would like to show two qualitative features of the spatially coupled system. It is relatively easy to show positivity and boundedness of the solutions in Gauss-type predator-prey models. Because of the presence of dispersal, the spatial model cannot be written in Gauss-type form. Therefore, it is interesting to establish the following propositions.

Proposition 3.1. The solution of system (1) starting from $x_i(0) > 0$, $y_i(0) > 0$, ($i = 1, 2$) is positive.

Proof. Note that the dynamics of predator equations follow Gauss-type form. Hence, the solution $y_i(t)$ can be written as

$$y_i(t) = y_i(0)e^{\int_0^t \left(-m + \frac{bx_i(s)}{h+x_i(s)}\right) ds} > 0 \text{ for all } t > 0.$$

Now let us suppose that, the solution $x_i(t)$'s are not positive for all $t > 0$. Since $x_i(0) > 0$, so there exist a least $t = t^* > 0$ such that either (i) $x_1(t^*) = 0$, (ii) $x_2(t^*) = 0$ or (iii) both $x_1(t^*) = x_2(t^*) = 0$. We first assume the third case $x_1(t^*) = x_2(t^*) = 0$. Then, for $t \in [0, t^*)$ we have $x_1(t), x_2(t) > 0$. Now

$$\dot{x}_i \geq -x_i(t) \left\{ r \frac{x_i(t)}{K} + \frac{ay_i(t)}{h+x_i(t)} + D \left(\alpha \frac{\rho y_i(t)}{L+y_i(t)} + (1-\alpha) \right) \right\},$$

where $y_i(t) > 0, i = 1, 2$.

Hence, by comparison theorem, we can write

$$x_i(t) \geq x_i(0)e^{-\int_0^t \left\{ r \frac{x_i(s)}{K} + \frac{ay_i(s)}{h+x_i(s)} + D \left(\alpha \frac{\rho y_i(s)}{L+y_i(s)} + (1-\alpha) \right) \right\} ds} > 0.$$

Since $x_i(t)$ is continuous, so $x_i(t^*) = x_i(t^* - 0) > 0$, which is a contradiction to our assumption that $x_i(t^*) = 0$. Thus, the solution $x_i(t) > 0$ for all $t > 0$. A similar justification can be applied to prove the case (i) and (ii). Therefore, the solution is positive. \square

Proposition 3.2. The solutions of system (1) starting from $x_i(0), y_i(0) > 0, (i = 1, 2)$ are bounded.

Proof. We prove the boundedness of the solutions $x_i(t), y_i(t), (i = 1, 2)$ by contradiction.

Let us assume that $y_1(t)$ is unbounded. Then, there exists a $t > t_1$ such that $y_1(t) > N$, where $N > 0$ is sufficiently large. Consequently, the first equation of system (1) reduces to

$$\dot{x}_1(t) \approx -\frac{ax_1(t)y_1(t)}{h+x_1(t)} < 0.$$

Thus, $x_1(t)$ is a decreasing function in time. We now fix a $t > t_2, (t_2 > t_1)$ such that $x_1(t) \rightarrow 0$. Then, for $t > t_2$, the second equation of system (1) takes the form

$$\dot{y}_1(t) = \left(\frac{bx_1(t)}{h+x_1(t)} - m \right) y_1(t) \approx -my_1(t) < 0.$$

This implies that $y_1(t) \rightarrow 0$ for increasing time, a contradiction. A similar argument can be provided for $y_2(t)$. Thus, $y_1(t)$ and $y_2(t)$ can never be unbounded.

Now, suppose x_1 is unbounded. Then, there exists a t_3 such that for all $t > t_3$, the first equation of system (1) can be approximated as

$$\dot{x}_1(t) \approx -r \frac{x_1^2(t)}{K},$$

since for large values of $x_1(t)$, the quadratic term is dominant over other terms. This implies that x_1 is decreasing, which is contradicting the fact that $x_1(t)$ is unbounded. Similar arguments can be presented for $x_2(t)$. Thus, all solutions of system (1) are bounded. \square

4 Model analysis

The two patches in system (1) are identical in nature in the absence of dispersal. The dynamics of the system (1) in absence of dispersal ($D = 0$) is discussed by Sun and Mai [36], Mai et al. [37]. The system (1) have three equilibrium: the trivial equilibrium $(0, 0, 0, 0)$, the boundary equilibrium $(K, 0, K, 0)$ and the co-existence equilibrium $(x_1^*, y_1^*, x_2^*, y_2^*)$, where $x_1^* = x_2^* = \frac{mh}{b-m} := x^*$ and $y_1^* = y_2^* = \frac{r}{a} \left(1 - \frac{x^*}{K}\right) (h + x^*) := y^*$. The coexisting equilibrium exists when $0 < m < \frac{Kb}{h+K}$. The stability analysis of these steady states is followed from single-isolated Rosenzweig-MacArthur model. Besides these three equilibrium, when the dispersal is in action, the model has two more boundary equilibria: $(\bar{x}, 0, x^*, \bar{y})$ and $(x^*, \bar{y}, \bar{x}, 0)$, where \bar{x}, \bar{y} are positive. One can easily establish that these equilibria are unstable in our model. We are interested in studying the dynamics of the system (1) around the coexisting equilibrium. Linearizing the system (1) around the coexisting equilibrium, we get

$$\begin{aligned} \dot{x}_1 &= (A - M)x_1 - \left(a \frac{x^*}{h+x^*} + C \right) y_1 + Mx_2(t - \tau) \\ &\quad + Cy_2(t - \tau), \\ \dot{y}_1 &= \frac{hby^*}{(h+x^*)^2} x_1, \\ \dot{x}_2 &= (A - M)x_2 - \left(a \frac{x^*}{h+x^*} + C \right) \\ &\quad + Mx_1(t - \tau) + Cy_1(t - \tau), \\ \dot{y}_2 &= \frac{hby^*}{(h+x^*)^2} x_2, \end{aligned} \tag{2}$$

where

$$A = r - \frac{2rx^*}{K} - \frac{ahy^*}{(h+x^*)^2},$$

$$M = D \left(\alpha \frac{\rho y^*}{L+y^*} + (1-\alpha) \right) > 0, C = D\alpha \rho \frac{Lx^*}{(L+y^*)^2} > 0.$$

To obtain the characteristic equation, we look for a non-trivial solution in the form of

$$X = \hat{C}e^{\lambda t}, \tag{3}$$

where $X = (x_1 \ y_1 \ x_2 \ y_2)^T$ and $\hat{C} = (\hat{C}_1 \ \hat{C}_2 \ \hat{C}_3 \ \hat{C}_4)^T$ is a non-trivial vector of arbitrary constants. Here λ is

a parameter, called eigenvalue, which needs to be determined later. Substituting equation (3) into the system (2), we obtain $J\hat{C} = 0$, where the matrix J is given by

$$J = \begin{pmatrix} J_1 & J_2 \\ J_2 & J_1 \end{pmatrix} \quad (4)$$

with

$$J_1 = \begin{pmatrix} A - M - \lambda & -a\frac{x^*}{h+x^*} - C \\ \frac{bhy^*}{(h+x^*)^2} & -\lambda \end{pmatrix}$$

$$\text{and } J_2 = \begin{pmatrix} Me^{-\lambda\tau} & Ce^{-\lambda\tau} \\ 0 & 0 \end{pmatrix}.$$

In order to obtain a non-trivial solution (i.e., λ) of the equation $J\hat{C} = 0$, we impose the condition $\det(J) = 0$. Since $\det(J) = \det(J_1 + J_2)\det(J_1 - J_2)$, thus, we have either $\det(J_1 + J_2) = 0$ or $\det(J_1 - J_2) = 0$, or both of them are zero. These facts produce the following two characteristic equations:

$$\lambda^2 - (A - M)\lambda + B + N - (M\lambda + N)e^{-\lambda\tau} = 0, \quad (5)$$

$$\lambda^2 - (A - M)\lambda + B + N + (M\lambda + N)e^{-\lambda\tau} = 0, \quad (6)$$

where $B = \frac{bhy^*}{(h+x^*)^2} \frac{ax^*}{h+x^*} > 0$ and $N = \frac{bhy^*}{(h+x^*)^2} C > 0$.

Based on the nature of the solution of the characteristic equation, we can determine the state of the system.

4.1 Analysis of the non-delayed model

We first consider the case when the dispersal from one patch to another is instantaneous (i.e., $\tau = 0$). The characteristic equations reduce to

$$\begin{aligned} \lambda^2 - A\lambda + B &= 0, \\ \lambda^2 - (A - 2M)\lambda + B + 2N &= 0. \end{aligned} \quad (7)$$

If $A < 0$, then the roots of the characteristic equation (7) have no positive real parts and thus is asymptotically stable. However, when $A > 0$, two cases arises: (a) If $A > 2M$, then the roots of the characteristic equation (7) have four positive real parts, (b) If $A < 2M$, there exist two roots with positive real parts and two roots with negative real parts. However, the presence of positive real parts in the roots of the equation (7) indicates that the system will be unstable whenever $A > 0$.

4.2 Analysis of the delayed model

We now want to study the dynamics of the system (1) with respect to the time delay. Since the characteristic equations (5) and (6) are transcendental, we want to check if change of sign in the real part of the roots occur when τ varies. When $\tau = 0$, the four eigenvalues can be determined from quadratic equations. Hence, we know

the position of the roots in the complex \mathbb{C} -plane. Since change in the dynamics (viz. stability) will only take place when the roots cross the imaginary axis \mathbb{C}^0 of the complex plane, we look for the existence of purely imaginary roots of equations (5) and (6) for some critical values of τ . Suppose there exists delay for which $\lambda = i\omega$, $\omega > 0$. Substituting $\lambda = i\omega$ into characteristic equation (5) and separating the real and imaginary parts, we obtain

$$-\omega^2 + B + N - M\omega \sin \omega\tau - N \cos \omega\tau = 0, \quad (8)$$

$$-(A - M)\omega - M\omega \cos \omega\tau + N \sin \omega\tau = 0. \quad (9)$$

Equations (8) and (9) can further be written as

$$\begin{aligned} \cos \omega\tau &= \frac{-N\omega^2 - (A - M)M\omega^2 + NB + N^2}{(M\omega)^2 + N^2} =: C_1(\omega), \\ \sin \omega\tau &= \frac{AN\omega - M\omega^3 + MB\omega}{(M\omega)^2 + N^2} =: S_1(\omega). \end{aligned} \quad (10)$$

Adding squares of both equations into equation (10), we obtain

$$\omega^4 + \omega^2(A^2 - 2B - 2N - 2MA) + B(B + 2N) = 0. \quad (11)$$

Solving for ω^2 , we obtain

$$\omega^2 = \frac{1}{2} \left\{ (2B + 2N + 2MA - A^2) \pm \sqrt{\Delta} \right\},$$

where $\Delta = (A^2 - 2B - 2N - 2MA)^2 - 4B(2N + B)$.

Hence, ω (if exist) has at most two positive value of the form

$$\omega_{\pm} = \sqrt{\frac{1}{2} \left\{ (2B + 2N + 2MA - A^2) \pm \sqrt{\Delta} \right\}}. \quad (12)$$

Similarly, substituting $\lambda = i\omega$, $\omega > 0$ into characteristic equation (6), we obtain

$$\begin{aligned} \cos \omega\tau &= -\frac{-N\omega^2 - (A - M)M\omega^2 + NB + N^2}{(M\omega)^2 + N^2} = -C_1(\omega), \\ \sin \omega\tau &= -\frac{AN\omega - M\omega^3 + MB\omega}{(M\omega)^2 + N^2} = -S_1(\omega). \end{aligned} \quad (13)$$

Obviously, the system (13) leads to the same value ω_{\pm} .

Now, we determine the value of τ from equation (10) at which Hopf-bifurcation occurs. We define

$$\theta_+ = \cos^{-1}(C_1(\omega_+)) \in (0, \pi),$$

$$\theta_- = \cos^{-1}(C_1(\omega_-)) \in (0, \pi).$$

When $\omega = \omega_+$,

$$S_1(\omega_+) = \frac{\omega_+(NA + MB - M\omega_+^2)}{N^2 + M^2\omega_+^2} \\ = \frac{\omega_+(N(A - M) - MA(M - A/2) - M\sqrt{\Delta}/2)}{N^2 + M^2\omega_+^2}.$$

It is difficult to determine the sign of $S_1(\omega_+)$ in full parameter space. Later, we compute the value of $S_1(\omega_+)$ for case basis along with simulation. The general form of critical delay at which the characteristic equation (5) will have purely imaginary roots are

$$\tau_{n,1}^+ = \begin{cases} \frac{(2\pi - \theta_+)}{\omega_+} + \frac{2n\pi}{\omega_+}, & \text{if } S_1(\omega_+) < 0 \\ \frac{\theta_+}{\omega_+} + \frac{2n\pi}{\omega_+}, & \text{if } S_1(\omega_+) > 0 \end{cases} \quad (14)$$

where $n = 0, 1, 2, \dots$

On the other hand, when $\omega = \omega_-$,

$$S_1(\omega_-) = \frac{\omega_-(NA + MB - M\omega_-^2)}{N^2 + M^2\omega_-^2} \\ = \frac{\omega_-(N(A - M) - MA(M - A/2) + M\sqrt{\Delta}/2)}{N^2 + M^2\omega_-^2}.$$

Therefore, we compute

$$\tau_{n,1}^- = \begin{cases} \frac{(2\pi - \theta_-)}{\omega_-} + \frac{2n\pi}{\omega_-}, & \text{if } S_1(\omega_-) < 0 \\ \frac{\theta_-}{\omega_-} + \frac{2n\pi}{\omega_-}, & \text{if } S_1(\omega_-) > 0 \end{cases} \quad (15)$$

where $n = 0, 1, 2, \dots$

Consequently, we determine two sequences $\{\tau_{n,1}^+\}$ and $\{\tau_{n,1}^-\}$ from the relations (14) and (15), respectively for a fixed value of $S_1(\omega_{\pm})$. Hence, Hopf-bifurcation occurs at these values of delay due to the occurrence of purely complex eigenvalues in the characteristic equation (5).

In the similar way, we can find the two sequences of threshold values of τ at which characteristic equation (6) have purely imaginary roots $\pm i\omega_{\pm}$ as follows:

$$\tau_{n,2}^+ = \begin{cases} \frac{(\pi - \theta_+)}{\omega_+} + \frac{2n\pi}{\omega_+}, & \text{if } S_1(\omega_+) < 0 \\ \frac{(\pi + \theta_+)}{\omega_+} + \frac{2n\pi}{\omega_+}, & \text{if } S_1(\omega_+) > 0 \end{cases} \quad (16)$$

where $n = 0, 1, 2, \dots$ and

$$\tau_{n,2}^- = \begin{cases} \frac{(\pi - \theta_-)}{\omega_-} + \frac{2n\pi}{\omega_-}, & \text{if } S_1(\omega_-) < 0 \\ \frac{(\pi + \theta_-)}{\omega_-} + \frac{2n\pi}{\omega_-}, & \text{if } S_1(\omega_-) > 0 \end{cases} \quad (17)$$

where $n = 0, 1, 2, \dots$

Hence, we obtain another two sets of critical values at which the characteristic equation (6) has purely imaginary roots. Finally, we present the following results.

Result: When ω_{\pm} exist, the model experience Hopf-bifurcation at each value $\{\tau_{n,1}^{\pm}\}$ and $\{\tau_{n,2}^{\pm}\}$, where $n = 0, 1, 2, \dots$

Generally, Hopf-points (critical thresholds of time delay parameter) are the indicators of generating (or

describing) cyclic dynamics in our spatial system. Ecologically, once the delay parameter crosses a critical value to produce a stable coexisting equilibrium, all the populations maintain a positive stock in long run with no variation. On the other hand, the populations exhibit oscillations when the delay crosses a Hopf-point to induce instability around the coexisting equilibrium. However, populations experience non-equilibrium dynamics when the value of the Hopf-points are larger than a certain critical threshold.

Now, we examine if the eigenvalues on \mathbb{C}^0 change their signs when delay crosses the threshold values $\tau = \tau_{n,j}^{\pm}$, $j \in \{1, 2\}$.

Differentiating characteristic equation (5) w.r.t. τ , we obtain

$$(2\lambda - (A + M) + \tau e^{-\lambda\tau}(M\lambda + N) - Me^{-\lambda\tau}) \frac{d\lambda}{d\tau} + (M\lambda + N)\lambda e^{-\lambda\tau} = 0. \quad (18)$$

Thus,

$$\left(\frac{d\lambda}{d\tau}\right)^{-1} = \frac{Me^{-\lambda\tau} + (A + M) - 2\lambda}{(M\lambda + N)\lambda e^{-\lambda\tau}} - \frac{\tau}{\lambda}. \quad (19)$$

From equation (5), we found

$$e^{\lambda\tau} = \frac{M\lambda + N}{\lambda^2 - (A - M)\lambda + B + N}.$$

Using the above fact,

$$\begin{aligned} & \text{sign} \left\{ \left[\frac{d(\text{Re}\lambda)}{d\tau} \right]_{\tau=\tau_{n,1}^{\pm}} \right\} \\ &= \text{sign} \left\{ \text{Re} \left[\left(\frac{d\lambda}{d\tau} \right)^{-1} \right]_{\tau=\tau_{n,1}^{\pm}} \right\} \\ &= \text{sign} \left\{ \text{Re} \left[\frac{M}{(M\lambda^2 + N\lambda)} \right. \right. \\ & \quad \left. \left. + \frac{(A - M) - 2\lambda}{\lambda^3 - (A - M)\lambda^2 + (B + N)\lambda} \right]_{\lambda=i\omega_{\pm}} \right\} \\ &= \text{sign} \{ -M^2 + (A - M)^2 - 2(B + N - \omega_{\pm}^2) \} \\ &= \text{sign} \{ \pm\sqrt{\Delta} \}. \end{aligned}$$

Similarly, when $\tau = \tau_{n,2}^{\pm}$, from characteristic equation (6), we get

$$\text{sign} \left\{ \left[\frac{d(\text{Re}\lambda)}{d\tau} \right]_{\tau=\tau_{n,2}^{\pm}} \right\} = \text{sign} \{ \pm\sqrt{\Delta} \}. \quad (20)$$

Hence, we obtain the transversality conditions

$$\left[\frac{d(\operatorname{Re}\lambda)}{d\tau} \right]_{\tau=\tau_{n,1}^+, \tau_{n,2}^+} > 0 \quad \text{and} \quad \left[\frac{d(\operatorname{Re}\lambda)}{d\tau} \right]_{\tau=\tau_{n,1}^-, \tau_{n,2}^-} < 0.$$

Also, it is easy to verify from equation (18) that the purely imaginary roots ω_{\pm} are simple. As a consequence, a pair of eigenvalues will enter into \mathbb{C}^+ (resp. \mathbb{C}^-) when τ increases through $\tau_{n,1}^+$, $\tau_{n,2}^+$ (resp. $\tau_{n,1}^-$, $\tau_{n,2}^-$). However, there is no specific rule to count the number of eigenvalues for the characteristic equations in \mathbb{C}^- when delay is varied. We shall show that increasing delay can generate many eigenvalues with negative real part. On the other hand, the number of eigenvalues in \mathbb{C}^+ will increase or decrease by 2 when delay passes through critical threshold. This fact is true from the following Lemma due to Cooke and Grossman [41].

Lemma 4.1 [41] Let $f(\lambda, \tau) = \lambda^2 + d_1\lambda + d_2\lambda e^{-\lambda\tau} + d_3 + d_4e^{-\lambda\tau}$, where d_i 's ($i = 1, 2, 3, 4$) and τ are real numbers and $\tau > 0$. Then, as τ varies, the sum of the multiplicities of zeros of f in the open right half-plane can change only if a zero appears on or crosses the imaginary axis.

Overall the above methodology would be implemented to understand stability change phenomenon due to the change of time delay parameter. In our analysis, members of the sequences of critical delays would be arranged in ascending order irrespective of their indices.

Remark 4.1. Since $\omega_+ > \omega_-$, $\tau_{n+1,j}^+ - \tau_{n,j}^+ = \frac{2\pi}{\omega_+} < \frac{2\pi}{\omega_-} = \tau_{n+1,j}^- - \tau_{n,j}^-$ i.e. the distance between two consecutive $\tau_{n,j}^+$ is less than the distance between two consecutive $\tau_{n,j}^-$. So, it is trivially clear that, two consecutive members from the sequence $\{\tau_{n,j}^+\}_{n=0}^{\infty}$ must lie between two consecutive members of $\{\tau_{n,j}^-\}_{n=0}^{\infty}$, for some $n > n^* \in \mathbb{Z}^+$ and $j = \{1, 2\}$. However, the opposite phenomenon never happen.

Remark 4.2. It can be noted that $|\tau_{n,j}^+ - \tau_{n,k}^+| = \frac{\pi}{\omega_+} < \frac{\pi}{\omega_-} = |\tau_{n,j}^- - \tau_{n,k}^-|$, i.e. the distance between $\tau_{n,j}^-$ and $\tau_{n,k}^-$ is always greater than the distance between $\tau_{n,j}^+$ and $\tau_{n,k}^+$ for all $n \in \mathbb{Z}^+$ ($j = \{1, 2\}$, $k = \{1, 2\}$, $j \neq k$).

Remark 4.3. From Remark 4.1 and 4.2, it is clear that between any two consecutive thresholds from the sequence $\{\tau_{n,j}^+\}_{n=0}^{\infty}$, there exist a threshold $\tau_{s,k}^+$ which is equidistant from both the consecutive members of $\{\tau_{n,j}^+\}_{n=0}^{\infty}$ where $j \neq k$ and $|n - s| = 1$ or $n = s$.

Similarly, between any two consecutive members from $\{\tau_{n,j}^-\}_{n=0}^{\infty}$, there exist a critical delay $\tau_{s,k}^-$ which is equidistant from both the two consecutive thresholds of $\{\tau_{n,j}^-\}_{n=0}^{\infty}$ where $j \neq k$ and $|n - s| = 1$ or $n = s$. Mathematically, we can write $|\tau_{n,j}^+ - \tau_{s,k}^+| = \frac{\pi}{\omega_+} < \frac{\pi}{\omega_-} = |\tau_{n,j}^- - \tau_{s,k}^-|$, where $j \neq k$ with suitable indices n and s such that $|n - s| = 1$ or $n = s$.

So we can conclude from Remark 4.1–4.3 that two consecutive thresholds from $\{\tau_{n,1}^+\}_{n=0}^{\infty} \cup \{\tau_{n,2}^+\}_{n=0}^{\infty}$ must lie between two consecutive thresholds from $\{\tau_{n,1}^-\}_{n=0}^{\infty} \cup \{\tau_{n,2}^-\}_{n=0}^{\infty}$ after some $n > n^* \in \mathbb{Z}^+$. This key information is the backbone to analyze the stability in our delayed model. We now present two different situations based on the stability of the identical patches.

4.2.1 The isolated patches are stable

In this case, we assume that $A < 0$, which indicates that the isolated patches are stable. It can be seen that when the isolated patches are stable, the combined effect of instantaneous predator-influenced dispersal and density-independent dispersal have no effect in destabilizing the patches. Furthermore, it is mentioned by 35, that density-independent delayed dispersal (i.e., when $\alpha = 0$) cannot destabilize the equilibrium alone. However, in the presence of combined dispersal, the system gets destabilized for increasing values of delay. We would like to explore the impacts of predator-influenced delay dispersal for several parameter ranges. To proceed further, we first establish the following Lemma.

Lemma 4.2. Let $A < 0$ along with $A^2 < 2(B + N + MA)$ and $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$. Then, $\tau_{0,j}^+ < \tau_{0,j}^-$ ($j = 1, 2$) holds true.

Proof. Since $A < 0$, the characteristic equation of the non-delayed system (7) will have two pairs of eigenvalues in \mathbb{C}^- plane. Also, $A^2 < 2(B + N + MA)$ and $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$ indicates that ω_{\pm} will exist and corresponding critical delays too will come into existence. We assume that the condition $\tau_{0,j}^+ < \tau_{0,j}^-$ ($j = 1, 2$) is not true. Let us assume that $\tau_{0,j}^+ > \tau_{0,j}^-$ ($j = 1, 2$). Without loss of generality, suppose that $\tau_{0,1}^-$ be the least threshold among the four sequences where Hopf-bifurcation occurs. Note that no eigenvalue crosses \mathbb{C}^0 from \mathbb{C}^- to \mathbb{C}^+ when $\tau \in [0, \tau_{0,1}^-]$. In addition, Lemma 4.2 alternatively suggests that no eigenvalue would be created in \mathbb{C}^+ for varying delay within $[0, \tau_{0,1}^-]$. However, by virtue of transversality condition,

one pair of eigenvalues having positive real parts cross \mathbb{C}^0 and enter into \mathbb{C}^- when delay exceeds $\tau_{0,1}^-$. Since there is no eigenvalue in \mathbb{C}^+ when $\tau = 0$, it is impossible to happen first Hopf-bifurcation when $\tau = \tau_{0,j}^-$. Hence, $\tau_{0,j}^+ < \tau_{0,j}^-$ must be a true relation. \square

We now present necessary conditions for destabilization of the dynamics at equilibrium.

Theorem 4.1. When $A < 0$, the coexistence equilibrium E^* is locally asymptotically stable in absence of dispersal delay τ . Due to increase in τ , three situations can occur:

(i) If $A^2 > 2(B + N + MA)$ or $4B(2N + B) > (A^2 - 2B - 2N - 2MA)^2$, then the coexistence equilibrium E^* of system (1) remains stable for all time delay;

(ii) If $A^2 < 2(B + N + MA)$, $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$ and $\tau_{0,j}^+ < \tau_{0,j}^- < \tau_{0,k}^+$ ($j = \{1, 2\}$, $k = \{1, 2\}$, $j \neq k$), then the system undergoes stability switching for a finite number of times;

(iii) If $A^2 < 2(B + N + MA)$, $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$ and the first two critical delays are $\tau_{0,1}^+$ and $\tau_{0,2}^+$, then the system undergo only stability change such that the system remains stable for $\tau < \min\{\tau_{0,1}^+, \tau_{0,2}^+\}$ but is unstable for all $\tau > \min\{\tau_{0,1}^+, \tau_{0,2}^+\}$.

Proof. (i) The coexisting equilibrium is stable when $\tau = 0$ i.e. the eigenvalues of the characteristic equations (5) and (6) are located in the \mathbb{C}^- plane. Since $A^2 > 2(B + N + MA)$ or $4B(2N + B) > (A^2 - 2B - 2N - 2MA)^2$, clearly ω_{\pm} does not exist. It suggests that there does not appear any critical delay where Hopf-bifurcation can shift the eigenvalue from left half complex plane to right half one. As a result, the eigenvalues of the characteristic equation (5) and (6) remains in the \mathbb{C}^- plane for all $\tau > 0$. Thus, the co-existing equilibrium remains stable for all time delay.

(ii) Conditions $A^2 < 2(B + N + MA)$, $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$ ensure the existence of ω_{\pm} and hence the four sequences of threshold values of τ . Again, Lemma 4.2.1 guarantees the relation $\tau_{0,j}^+ < \tau_{0,j}^-$ ($j = 1, 2$). Also, from the values of $\tau_{0,j}^{\pm}$ computed in (14), (15), (16) and (17), it is clear that either $\tau_{0,2}^+ < \tau_{0,1}^+$ (resp. $\tau_{0,2}^- < \tau_{0,1}^-$) or $\tau_{0,2}^+ < \tau_{0,1}^+$ (resp. $\tau_{0,2}^- < \tau_{0,1}^-$). So, the first Hopf-bifurcation needs to take place when $\tau = \tau_{0,j}^+$ ($j = 1$ or 2). After the first Hopf-bifurcation, the multiplicity of eigenvalue in \mathbb{C}^+ is two. Thus, the system becomes unstable after the first Hopf-bifurcation (a supercritical Hopf-bifurcation). As per

our assumption $\tau_{0,j}^+ < \tau_{0,j}^- < \tau_{0,k}^+$ ($j, k = \{1, 2\}$, $j \neq k$), the second Hopf-bifurcation (a subcritical Hopf-bifurcation) occurs when $\tau = \tau_{0,j}^-$. Hence, the multiplicity of eigenvalue in \mathbb{C}^+ will decrease to zero when τ increases through $\tau_{0,j}^-$. Consequently, the system becomes stable once again after the second Hopf-bifurcation and the first stability switching have occurred. The third Hopf-bifurcation needs to occur when $\tau = \tau_{0,k}^+$. The eigenvalue in \mathbb{C}^+ will again become 2 and instability occur in the system. Depending upon the distribution of threshold values, multiplicity of eigenvalue in \mathbb{C}^+ will keep on changing to either 0 or 2. Now we prove that number of stability switching is finite. From Remark 4.1–4.3, there must exist two consecutive thresholds from $\{\tau_{n,1}^+\} \cup \{\tau_{n,2}^+\}$ between two consecutive thresholds in $\{\tau_{n,1}^-\} \cup \{\tau_{n,2}^-\}$ for some $n \in \mathbb{Z}^+$. Thus, the multiplicity of the eigenvalue in \mathbb{C}^+ will change to 4 when delay increases. From the same Remark 4.1–4.3, it is clear that no two thresholds from $\{\tau_{n,1}^-\} \cup \{\tau_{n,2}^-\}$ can occur consecutively in between two consecutive thresholds in $\{\tau_{n,1}^+\} \cup \{\tau_{n,2}^+\}$. Thus, the number of eigenvalues in \mathbb{C}^+ cannot be reduced from 2 for further increase in delay. Hence, instability will persist after some critical threshold and the number of switches become finite.

(iii) As stated above, the first two Hopf-bifurcation occurs at $\tau = \tau_{0,j}^+$ and $\tau_{0,k}^+$. Thus, the multiplicity of eigenvalue in \mathbb{C}^+ increase to 4 once delay exceeds the threshold at which second Hopf-bifurcation takes place. The system cannot gain its stability back as $\tau_{n,j}^-$ and $\tau_{n,k}^-$ can never occur consecutively as seen from the above analysis in case (ii) above. Thus, the instability will persist in the system for $\tau > \min\{\tau_{0,1}^+, \tau_{0,2}^+\}$. \square

We illustrate the possible of dynamics for varying delay through some examples for better understanding.

Example 4.1 Invariant stability: In this example, we show that time delay cannot change the local asymptotic stability for special combinations of both types of dispersal. We take the parameters as $r = 0.05$, $K = 2.1$, $a = 0.08$, $b = 0.07$, $h = 1$, $m = 0.03$ in the system (1). Because of balanced dynamics between patches, the equilibrium of the system is found to be $(x_1^*, y_1^*, x_2^*, y_2^*) = (0.75, 0.703, 0.75, 0.703)$. Regardless the value of the dispersal parameters, this equilibrium is stable without time delay. We choose the dispersal parameters as $L = 1$, $\alpha = 0.7$, $\rho = 1$, $D = 10$. It is found that there does not exist any positive ω for the given parameter set. As a result, no stability change happens

Table 1. The critical time delays are presented for up to $n = 4$.

$\tau_{n,1}^+$	$\tau_{n,1}^-$	$\tau_{n,2}^+$	$\tau_{n,2}^-$
$\tau_{0,1}^+ \approx 76.1244$	$\tau_{0,1}^- \approx 90.6352$	$\tau_{0,2}^+ \approx 37.984$	$\tau_{0,2}^- \approx 45.2423$
$\tau_{1,1}^+ \approx 152.405$	$\tau_{1,1}^- \approx 181.421$	$\tau_{1,2}^+ \approx 114.265$	$\tau_{1,2}^- \approx 136.028$
$\tau_{2,1}^+ \approx 228.686$	$\tau_{2,1}^- \approx 272.207$	$\tau_{2,2}^+ \approx 190.546$	$\tau_{2,2}^- \approx 226.814$
$\tau_{3,1}^+ \approx 304.967$	$\tau_{3,1}^- \approx 362.993$	$\tau_{3,2}^+ \approx 266.826$	$\tau_{3,2}^- \approx 317.6$
$\tau_{4,1}^+ \approx 381.248$	$\tau_{4,1}^- \approx 453.779$	$\tau_{4,2}^+ \approx 343.107$	$\tau_{4,2}^- \approx 408.386$

due to delay in dispersal. In addition, it can be seen that for any $\alpha \in [0, 0.701)$, there exists no positive ω and as such the system remains stable for the given range of α . \square

Example 4.2 Stability switching: We take the same parameter set with increase in the value of α from 0.7 to 0.703. Now positive ω comes into existence since $\alpha \geq 0.701$. Due to the existence of two positive ω , sequences of τ can be obtained at which Hopf-bifurcation takes place. The first five members of each sequence of the critical delays is given in Table 1:

The list of critical τ in increasing order is:

$$\tau_{0,2}^+ < \tau_{0,2}^- < \tau_{0,1}^+ < \tau_{0,1}^- < \tau_{1,2}^+ < \tau_{1,2}^- < \tau_{1,1}^+ < \tau_{1,1}^- < \tau_{2,2}^+ < \tau_{2,2}^- < \tau_{2,1}^+ < \tau_{2,1}^- < \tau_{3,2}^+ < \tau_{3,2}^- < \tau_{3,1}^+ < \tau_{3,1}^- < \tau_{4,2}^+ < \dots$$

The first Hopf-bifurcation occurs when $\tau_{0,2}^+ = 37.984$ and hence a pair of eigenvalues from the \mathbb{C}^- plane will enter the \mathbb{C}^+ plane. Henceforth, the equilibrium of the system becomes unstable. Now, the second Hopf-bifurcation occurs when $\tau_{0,2}^- = 45.2423$. Thus, the pair of eigenvalue from the \mathbb{C}^+ plane will enter the \mathbb{C}^- plane, leaving behind no eigenvalue in the \mathbb{C}^+ plane. Consequently, the system restores back its stability. Again when τ is increased and reaches its critical value $\tau_{0,1}^+ = 76.1244$, instability rebounds. With further increase in τ to $\tau_{0,1}^- = 90.6352$, the system restores its stability. Such change from stable to unstable and back to stable continues till $\tau = \tau_{2,1}^+$, after which, appearance of two consecutive $\tau_{2,1}^+$ and $\tau_{3,2}^+$ will increase the multiplicity of eigenvalue with positive real parts in \mathbb{C}^+ and the system can never regain its stability. The persistence of instability can be explained from the following fact (see equations (14)-(17)):

$$\tau_{n+1,1}^- - \tau_{n,1}^- = \tau_{n+1,2}^- - \tau_{n,2}^- = \frac{2\pi}{\omega_-} \approx 90.79,$$

$$\tau_{n+1,1}^+ - \tau_{n,1}^+ = \tau_{n+1,2}^+ - \tau_{n,2}^+ = \frac{2\pi}{\omega_+} \approx 76.27,$$

$$|\tau_{n,1}^- - \tau_{n,2}^-| = \frac{\pi}{\omega_-} \approx 45.3929,$$

and

$$|\tau_{n,1}^+ - \tau_{n,2}^+| = |\tau_{2,1}^+ - \tau_{3,2}^+| = \frac{\pi}{\omega_+} \approx 38.1404.$$

It can be observed that the distance between two consecutive threshold from the $\{\tau_{n,1}^+\}$ and $\{\tau_{n,2}^+\}$ are the least among all. When the stability switches occur, the multiplicities of eigenvalues in \mathbb{C}^+ vary between 0 and 2. A situation must exist for which two consecutive critical delays from the class $\{\tau_{n,1}^+\} \cup \{\tau_{n,2}^+\}$ will occur consecutively. Here in this example, $\tau_{2,1}^+$ and $\tau_{3,2}^+$ are occurring consecutively. Thus, the multiplicity of eigenvalues in \mathbb{C}^+ increases to 4. In order to restore the stability, two consecutive threshold from $\{\tau_{n,1}^-\}$ and $\{\tau_{n,2}^-\}$ have to appear just right after the two consecutive $\tau_{2,1}^+$ and $\tau_{3,2}^+$. But from Remark 4.1–4.3, it is clear that no two threshold from $\{\tau_{n,1}^-\}$ and $\{\tau_{n,2}^-\}$ can appear consecutively. As a consequence, once delay exceeds $\tau_{3,2}^+$, there would be an increase of eigenvalue to 4 which can never decrease to 0. Thus instability phenomenon continues after delay crosses $\tau_{2,1}^+$.

Finally, we can observe that stability persists when

$$\tau \in (0, \tau_{0,2}^+) \cup (\tau_{0,2}^-, \tau_{0,1}^+) \cup (\tau_{0,1}^-, \tau_{1,2}^+) \cup (\tau_{1,2}^-, \tau_{1,1}^+) \cup (\tau_{1,1}^-, \tau_{2,2}^+)$$

and instability persists when

$$\tau \in (\tau_{0,2}^+, \tau_{0,2}^-) \cup (\tau_{0,1}^+, \tau_{0,1}^-) \cup (\tau_{1,2}^+, \tau_{1,2}^-) \cup (\tau_{1,1}^+, \tau_{1,1}^-) \cup (\tau_{2,2}^+, \tau_{2,2}^-) \cup (\tau_{2,1}^+, \infty).$$

In this illustration, stability switching occurs 5 times in the system. \square

Example 4.3 Stability change: In particular, when weight on the density dependent-dispersal is 20% (i.e., $\alpha = 0.8$), there exist two positive ω . Consequently, we can construct four sequences of τ at which Hopf-bifurcation occurs. We provide the first three members of each sequences in Table 2.

The list of critical τ in increasing order are:

$$\tau_{0,2}^+ < \tau_{0,1}^+ < \tau_{1,2}^+ < \tau_{0,2}^- < \tau_{1,1}^+ < \dots$$

The least entry of the above list is $\tau_{0,2}^+ = 20.6883$ and hence two eigenvalues enter into \mathbb{C}^+ as increasing delay crosses $\tau_{0,2}^+$. Hence, the equilibrium of the system becomes unstable due to varying delay. There exist only two eigenvalues with positive real part of the characteristics equations when $\tau \in (\tau_{0,2}^+, \tau_{0,1}^+)$. However,

Table 2. The critical time delays are presented for up to $n = 2$.

$\tau_{n,1}^+$	$\tau_{n,1}^-$	$\tau_{n,2}^+$	$\tau_{n,2}^-$
$\tau_{0,1}^+ \approx 41.5605$	$\tau_{0,1}^- \approx 155.477$	$\tau_{0,2}^+ \approx 20.6883$	$\tau_{0,2}^- \approx 77.676$
$\tau_{1,1}^+ \approx 83.3049$	$\tau_{1,1}^- \approx 311.079$	$\tau_{1,2}^+ \approx 62.4327$	$\tau_{1,2}^- \approx 233.278$
$\tau_{2,1}^+ \approx 125.049$	$\tau_{2,1}^- \approx 466.68$	$\tau_{2,2}^+ \approx 104.177$	$\tau_{2,2}^- \approx 388.879$

four (resp. six) eigenvalues persist in \mathbb{C}^+ for $\tau \in (\tau_{0,1}^+, \tau_{1,2}^+)$ (resp. $(\tau_{1,2}^+, \tau_{0,2}^-)$) as two additional eigenvalues enter into \mathbb{C}^+ at $\tau_{0,1}^+$ (resp. $\tau_{1,2}^+$). On the other hand, when $\tau \in (\tau_{0,2}^-, \tau_{1,1}^+)$, only four eigenvalues remain in \mathbb{C}^+ as two eigenvalues jump from \mathbb{C}^+ into \mathbb{C}^- at $\tau_{0,2}^-$. Thus, we conclude that the equilibrium is unstable for all $\tau \in (\tau_{0,2}^-, \tau_{1,1}^+)$.

We further explain that the system remains unstable for $\tau > \tau_{0,2}^+$. Theoretically, we observe from equations (14)-(17), that

$$\tau_{n+1,1}^- - \tau_{n,1}^- = \tau_{n+1,2}^- - \tau_{n,2}^- = \frac{2\pi}{\omega_-} \approx 155.609,$$

$$\tau_{n+1,1}^+ - \tau_{n,1}^+ = \tau_{n+1,2}^+ - \tau_{n,2}^+ = \frac{2\pi}{\omega_+} \approx 41.7444,$$

$$|\tau_{n,1}^- - \tau_{n,2}^-| = \frac{\pi}{\omega_-} \approx 77.8045,$$

and

$$|\tau_{n,1}^+ - \tau_{n,2}^+| = \frac{\pi}{\omega_+} \approx 20.8722.$$

Since $\tau_{0,2}^+$ and $\tau_{0,1}^+$ are the first critical delay and second critical delay, respectively, so instability can be changed only when two $\tau_{0,2}^-$ and $\tau_{0,1}^-$ appear consecutively. But looking at the distances between them, it is impossible that two $\tau_{0,2}^-$ and $\tau_{0,1}^-$ appear consecutively. Henceforth, the system cannot get back its stability and remains unstable when $\tau > \tau_{0,2}^+$. \square

It can be noted that when $\alpha = 1$ for the parameter set used in the above examples, the first and second bifurcation takes place at $\tau_{0,2}^+ = 13.872$ and $\tau_{0,1}^+ = 27.9833$ respectively. Also, the difference between two consecutive threshold from $\{\tau_{n,j}^+\}$ and $\{\tau_{n,k}^+\}$ is found to be 14.1113 and the difference between two consecutive $\{\tau_{n,j}^-\}$ and $\{\tau_{n,j}^+\}$ is found to be 103.012. So, the system remain stable when $\tau \in (0, 13.875)$ and unstable when $\tau \in (13.875, \infty)$. It can be seen that the stability range gets narrower when α is increased. Although the above examples depicts that α have impact on the stability of the delayed dispersal, but it is not always true. The example below supports our argument.

Example 4.4 We take the parameter set $r = 0.05$, $K = 1.1$, $a = 0.08$, $b = 0.07$, $h = 1$, $m = 0.03$, $D = 1$, $\rho = 1$ and $L = 1$. Coexisting equilibrium is stable for non-delayed model. It was observed that irrespective of any value of α , there exist no positive ω . Thus, the system remains stable for all $\tau > 0$. \square

4.2.2 The isolated patches are unstable

When $A > 0$, the equilibrium in both the isolated patches is unstable. It can be seen that the instantaneous dispersal have no influence (follows from equation (5)-(6)) in stabilizing the patches when the isolated patches are unstable. We want to investigate if delayed dispersal have any role in stabilizing the system. The necessary conditions for the system to change its instability are stated in the next theorem.

Theorem 4.2. When $A > 0$ and $A > 2M$, the interior equilibrium is unstable for all $\tau > 0$.

Proof. When $A > 0$ and $A > 2M$, the two pair of eigenvalues from characteristic equation (7a) and (7b) for the non-delayed model are in the \mathbb{C}^+ plane. Instability can be changed to stability only when the two pair of eigenvalues in \mathbb{C}^+ plane shifts to \mathbb{C}^- plane. This is possible only when two consecutive thresholds from $\{\tau_{n,1}^-\} \cup \{\tau_{n,2}^-\}$ ($n \in \mathbb{Z}^+$) occurs. From Remark 4.1-4.3, it is clear that no two consecutive threshold from $\{\tau_{n,1}^-\} \cup \{\tau_{n,2}^-\}$ can occur in between two consecutive threshold from $\{\tau_{n,1}^+\} \cup \{\tau_{n,2}^+\}$. The only possibility is when $\tau_{0,1}^-$ and $\tau_{0,2}^-$ occur consecutively which result the first and second Hopf-bifurcation.

Without loss of generality, we suppose that the first and second Hopf-bifurcations occur corresponding at $\tau_{0,1}^-$ and $\tau_{0,2}^-$, respectively. Now, from the computations provided in Eqns. (14)-(17), we obtain $\tau_{0,1}^- = \frac{\theta_-}{\omega_-}$ (since $\tau_{0,2}^- > \tau_{0,1}^-$). The value of $\tau_{0,2}^-$ needs to be $\frac{\pi + \theta_-}{\omega_-}$. Now if $\tau_{0,1}^+ = \frac{\theta_+}{\omega_+}$, then it is contradicting the fact that $\tau_{0,2}^-$ is the second threshold delay since $\frac{\pi}{\omega_-} > \frac{\pi}{\omega_+} > \frac{\theta_+}{\omega_+}$. Also, if $\tau_{0,1}^+ = \frac{2\pi - \theta_+}{\omega_+}$, then $\tau_{0,2}^+ = \frac{\pi - \theta_+}{\omega_+}$, which is again contradicting the fact that $\tau_{0,2}^-$ is the second threshold delay, since $\frac{\pi}{\omega_-} > \frac{\pi}{\omega_+} > \frac{\pi - \theta_+}{\omega_+}$. Thus, $\tau_{0,2}^-$ cannot be the second threshold delay.

Similar argument follows if we consider the first critical value as $\tau_{0,2}^-$ and the second critical value as $\tau_{0,1}^-$. Here $\tau_{0,2}^- = \frac{\pi - \theta_-}{\omega_-}$. Also $|\tau_{0,1}^- - \tau_{0,2}^-| = \frac{\pi}{\omega_-}$. If $\tau_{0,2}^+ = \frac{\pi - \theta_+}{\omega_+}$, then $\tau_{0,2}^+$ must lies between $\tau_{0,2}^-$ and $\tau_{0,1}^-$ as $|\tau_{0,1}^- - \tau_{0,2}^-| = \frac{\pi}{\omega_-} > \frac{\pi - \theta_+}{\omega_+}$. Also, if $\tau_{0,2}^+$ takes the value $\frac{\pi + \theta_+}{\omega_+}$, then corresponding $\tau_{0,1}^+$ is $\frac{\theta_+}{\omega_+}$, which must lie between $\tau_{0,2}^-$ and $\tau_{0,1}^-$. \square

Theorem 4.3. When $A > 0$ and $A < 2M$, then the coexistence equilibrium E^* experiences instability switching only when the following conditions are satisfied:

- (i) $A^2 < 2(B + N + MA)$ and $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$;
- (ii) $\tau_{0,1}^- < \tau_{0,1}^+$, $\tau_{0,2}^+ < \tau_{0,2}^-$ and $\tau_{0,1}^- < \tau_{0,2}^+$.

Otherwise, the equilibrium remains unstable for all $\tau > 0$.

Proof. Obviously, the characteristic equation (7a) yields a pair of eigenvalues with positive real parts and the characteristic equation (7b) yields a pair of eigenvalues with negative real parts when $A > 0$ and $A < 2M$. Clearly $A^2 < 2(B + N + MA)$ and $4B(2N + B) < (A^2 - 2B - 2N - 2MA)^2$ will lead to existence of purely imaginary roots $\pm \omega_{\pm}$.

When $\tau_{0,1}^- < \tau_{0,1}^+$, $\tau_{0,2}^+ < \tau_{0,2}^-$ and $\tau_{0,1}^- < \tau_{0,2}^+$, the possible combinations of the arrangement of the critical delays are: (a1) $\tau_{0,1}^- < \tau_{0,2}^+ < \tau_{0,2}^- < \tau_{0,1}^+$ and (a2) $\tau_{0,1}^- < \tau_{0,2}^+ < \tau_{0,1}^+ < \tau_{0,2}^-$. In both the combinations, it can be seen that the first Hopf-bifurcation occurs when $\tau = \tau_{0,1}^-$. After the first bifurcation, the equilibrium gets stable. The second bifurcation occurs when $\tau = \tau_{0,2}^+$, after which, the system regains back its instability. Hence, at least one switching occurs. From Remark 4.1–4.3, we can claim that number of switches is finite.

Now, we show that the equilibrium is unstable when the thresholds do not follow condition (ii). Consider the case when $\tau_{0,1}^- > \tau_{0,2}^+$. Then, the possible combinations of the arrangement of the critical delays are: (b1) $\tau_{0,2}^+ < \tau_{0,1}^- < \tau_{0,1}^+ < \tau_{0,2}^-$ and (b2) $\tau_{0,2}^+ < \tau_{0,1}^- < \tau_{0,2}^- < \tau_{0,1}^+$. Since the distance between two $\tau_{n,j}^+$ is always less than distance between two $\tau_{n,j}^-$, so the case (b2) is invalid. Now in the case of (b1), the first Hopf-bifurcation occurs when $\tau = \tau_{0,2}^+$. So the eigenvalues of (7b) enters the \mathbb{C}^+ plane. Thus, the multiplicity of the eigenvalues in \mathbb{C}^+ is 4. Now when $\tau = \tau_{0,1}^-$, multiplicity of the roots having positive real parts in \mathbb{C}^+ reduces to 2 and so the instability persists. Thus, we see that the multiplicity of the positive real part never reduces to 0 as two consecutive members of $\{\tau_{n,1}^-\} \cup \{\tau_{n,2}^-\}$ can never occur. Henceforth, the system remains unstable throughout. \square

Now, we present few examples to understand the dynamics of the equilibrium based on the conditions mentioned in the above theorems.

Example 4.5 Persistence of instability: To achieve our goal, we choose the parameter set as $r = 0.5$, $K = 150$, $a = 0.8$, $b = 0.6$, $h = 1$, $m = 0.2$. Since the equilibrium points of the system are independent of the dispersal parameters, the coexisting equilibrium is calculated as $(0.5, 0.934, 0.5, 0.934)$. If we chose the dispersal rate $D = 1$, $L = 1$, $\rho = 1$ and $\alpha = 0.4$, we obtain $A < 2M$ as $A = 0.164444$, $M = 0.793215$. Consequently, in the absence of delay in the dispersal, both the roots of the characteristic equation (5) has positive real parts, but both the roots of the equation (6) has negative real parts. First few critical values of τ where Hopf-bifurcation takes place for increasing delay are given in Table 3:

The list of critical τ in increasing order are:

$$\tau_{0,2}^+ < \tau_{0,1}^- < \tau_{0,1}^+ < \tau_{1,2}^+ < \tau_{1,1}^+ < \tau_{2,2}^+ < \tau_{0,2}^- < \tau_{2,1}^+ < \dots$$

It can be seen that first Hopf-bifurcation occurs when $\tau_{0,2}^+ = 4.00375$. As a result, both the roots of characteristic equation (6) having negative real part cross the \mathbb{C}^0 at $\tau_{0,2}^+ = 4.00375$ and then enter the \mathbb{C}^+ plane. No change in instability occurs when τ lies between $\tau_{0,2}^+$ and $\tau_{0,1}^-$. When τ crosses $\tau_{0,1}^- = 4.1862$, the \mathbb{C}^+ plane contains exactly two roots with positive real parts. Thus, stability cannot be installed into the system even when $\tau \in (\tau_{0,1}^-, \tau_{0,1}^+)$. In a similar way, we can conclude that for $\tau \in (\tau_{0,1}^+, \tau_{1,2}^+)$ no change in instability can be seen. Furthermore, it is observed that:

$$\begin{aligned} |\tau_{n,1}^- - \tau_{n,2}^-| &= |\tau_{0,1}^- - \tau_{0,2}^-| = \frac{\pi}{\omega_-} \approx 24.52655, \\ |\tau_{n,1}^+ - \tau_{n,2}^+| &= |\tau_{0,1}^+ - \tau_{1,2}^+| = \frac{\pi}{\omega_+} \approx 5.1169. \end{aligned}$$

It is clear that between the two consecutive threshold $\tau_{0,1}^-$ and $\{\tau_{0,2}^-\}$ there exist more than one thresholds from $\{\tau_{n,1}^+\} \cup \{\tau_{n,2}^+\}$. Further from Remark 4.1–4.3, it is clear that no two threshold from $\{\tau_{n,1}^-\}$ and $\{\tau_{n,2}^-\}$ can appear consecutively. Hence, at least one pair of eigenvalues will persist in \mathbb{C}^+ when $\tau > \tau_{1,2}^+$. Thus, we can conclude that the instability cannot be altered due to succeeding delays. For the same parameter set, it is computed that no instability change can take place for $\alpha \in [0, 0.47)$. \square

Table 3. The critical time delays are presented for up to $n = 2$.

$\tau_{n,1}^+$	$\tau_{n,1}^-$	$\tau_{n,2}^+$	$\tau_{n,2}^-$
$\tau_{0,1}^+ \approx 9.12063$	$\tau_{0,1}^- \approx 4.1862$	$\tau_{0,2}^+ \approx 4.00375$	$\tau_{0,2}^- \approx 28.7127$
$\tau_{1,1}^+ \approx 19.3544$	$\tau_{1,1}^- \approx 53.2393$	$\tau_{1,2}^+ \approx 14.2375$	$\tau_{1,2}^- \approx 77.7658$
$\tau_{2,1}^+ \approx 29.5881$	$\tau_{2,1}^- \approx 102.292$	$\tau_{2,2}^+ \approx 24.4713$	$\tau_{2,2}^- \approx 126.819$

Table 4. The critical time delays are presented for up to $n = 2$.

$\tau_{n,1}^+$	$\tau_{n,1}^-$	$\tau_{n,2}^+$	$\tau_{n,2}^-$
$\tau_{0,1}^+ \approx 9.21512$	$\tau_{0,1}^- \approx 3.93668$	$\tau_{0,2}^+ \approx 4.01408$	$\tau_{0,2}^- \approx 27.247$
$\tau_{1,1}^+ \approx 19.6172$	$\tau_{1,1}^- \approx 50.5572$	$\tau_{1,2}^+ \approx 14.4161$	$\tau_{1,2}^- \approx 73.8675$
$\tau_{2,1}^+ \approx 30.0192$	$\tau_{2,1}^- \approx 97.1778$	$\tau_{2,2}^+ \approx 24.8182$	$\tau_{2,2}^- \approx 120.488$

Example 4.6 *Instability switching*: Taking the same parameter sets as in the example above along with $\alpha = 0.5$, we compute the first three critical values of τ for each sequence in the given Table 4.

The list of critical τ in increasing order are: $\tau_{0,1}^- < \tau_{0,2}^+ < \tau_{0,1}^+ < \tau_{1,2}^+ < \tau_{1,1}^+ < \dots$. Unlike the earlier cases, $\tau_{0,1}^-$ is the least member in the table. When τ crosses $\tau_{0,1}^- = 3.93668$, two eigenvalues corresponding to the equation (5) enter the \mathbb{C}^- plane. Thus, coexisting equilibrium of the system becomes stable. But when τ crosses $\tau_{0,2}^+$, the system restores instability. Again when $\tau = \tau_{0,1}^+$ and $\tau_{1,2}^+$, a pair of eigenvalue from the \mathbb{C}^- enters the \mathbb{C}^+ and the instability does not change. Thus, a switching of instability occurs in the dynamics. Using similar arguments mention in the earlier

discussion, the equilibrium is unstable for $\tau > \tau_{0,2}^+$. Thus, the system becomes stable when $\tau \in (\tau_{0,1}^-, \tau_{0,2}^+)$ and becomes unstable when $\tau \in [0, \tau_{0,1}^-) \cup (\tau_{0,2}^+, \infty)$. The instability switching pattern is presented in Figure 1 by choosing three τ viz. $\tau = 3.6, 4, 4.4$. The unstable solution for $\tau = 3.6 \in [0, \tau_{0,1}^-)$ is depicted in Figure 1a whereas the stable solution for $\tau = 4 \in (\tau_{0,1}^-, \tau_{0,2}^+)$ is provided in Figure 1b. We choose $\tau = 4.4 > \tau_{0,2}^+$ to achieve oscillatory solution in Figure 1c. \square

It can be seen from Example 4.6 that the system is stable when $\tau \in (\tau_{0,1}^-, \tau_{0,2}^+)$. The range of the critical delays within which the co-existing equilibrium is stable is $|\tau_{0,2}^+ - \tau_{0,1}^-| \approx 0.0774$, which is a narrow range. But when α is increased, the range of the critical delays within which stability occurs gets increased. Further,

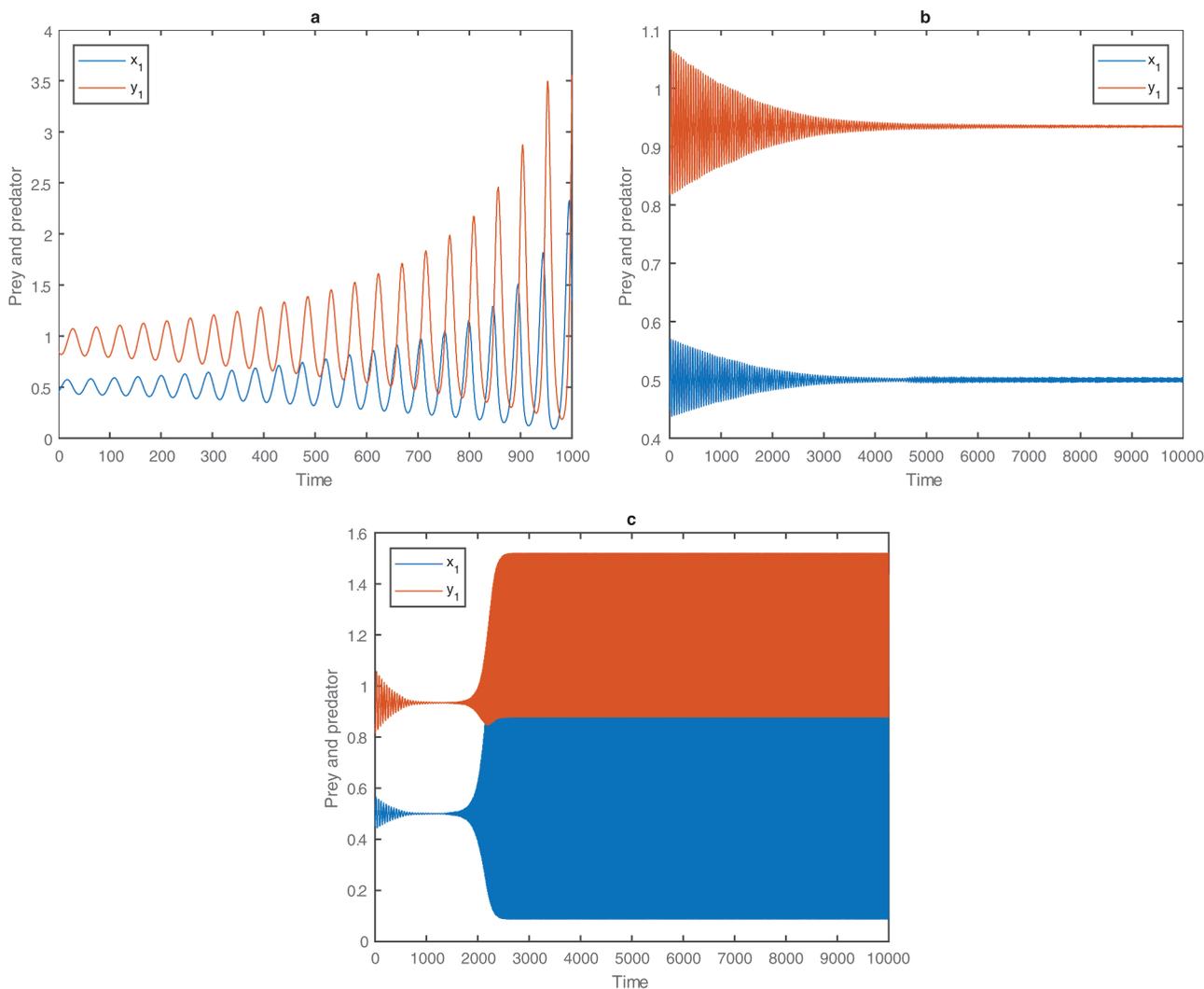


Figure 1. Taking the set of parameters from Example 4.6 with the initial conditions $(0.45, 0.85, 0.45, 0.85)$, solutions of the spatially coupled system (1) are plotted for (a) $\tau = 3.6$, (b) $\tau = 4$, (c) $\tau = 4.4$. We have shown the time response of $x_1(t)$ and $y_1(t)$ only as $x_2(t)$ and $y_2(t)$ also exhibit the same stability and oscillatory behavior for a fixed delay.

when α is increased to its maximum value 1, the range of the critical delays within which the system is stable is the longest, measuring $|\tau_{0,2}^- - \tau_{0,1}^+| \approx 0.83425$.

5 Conclusion

Our model comprised of two isolated identical Rosenzweig-MacArthur model in which dispersal of prey species between patches follow both density-independent and density-dependent patterns. Since the movement from one patch to another takes time, a time-lag was incorporated in the dispersal. Analytically, we have proved that all the solutions of the delayed system are positive and bounded. We have shown that when the dispersal was instantaneous, equilibrium in our two-patch strategic model was stable (resp. unstable) if the equilibria in the isolated patches were stable (resp. unstable). Hence, the instantaneous prey dispersal did not have any effect in changing the stability of the equilibrium. This result is in well agreement with Hauzy et al. [26].

Taking the delay as the bifurcating parameter, we have analyzed the two cases viz. (i) when the isolated systems (equilibria) were stable, (ii) when the isolated systems were unstable. Mai et al. [37], analyzed their model for predator dispersal analytically to show the jumps of eigenvalues from \mathbb{C}^+ to \mathbb{C}^- and vice-versa by constructing a very special sequence. In our study, we have used the distances between critical delays to establish the stability. When the isolated patches were stable, following three cases could occur:

- (i) the connected system could remain stable for all time delay,
- (ii) the connected system could have stability switching,
- (iii) the connected system could change its stability once.

It is to be noted that results (i) and (iii) are also observed by Zhang et al. [35]. We have explained the stability switching result (ii) for our model in a great detail.

Numerical simulations were provided to explain the dynamics of all the three cases. It was observed that the weight parameter α plays a very crucial role in the stability of the system. When the value of α is larger, predator-influenced prey dispersal and larger time delay together can cause non-equilibrium dynamics (See Examples 4.1–4.3). Consequently, predators may face uncertainty in searching their resources to maintain their steady density. If the patchy model is considered as a marine ecosystem, uncertain yield (due to the non-nonequilibrium dynamics) may lead economic slowdown in a fishery industry.

A similar analysis of the system was done when the equilibria of the isolated systems were unstable. It was found, that under some parametric conditions ($A > 2M$), the delay had no effect in changing its instability. However, when $A < 2M$, the delay could induce instability switching. Numerical experiments were performed for the case when $A < 2M$. A suitable weight parameter α could not alter the instability for any time delay. For some values of α , stability switching could take place for the varying delay.

Clearly, spatial models due to dispersal delay reveal more complex dynamics in comparison to non-spatial predator-prey models. Describing the delay-induced dynamics can also emerge new and more complex mathematical theories and techniques. Zhang et al. [35], have proved that a stable system could be destabilized due to delayed prey dispersal. We considered several spatial systems (not detailed here) with different migration terms to produce the same outcome obtained by Zhang et al. [35]. However, we are successful in obtaining the same outcome in our discussed model (1). Hence, identifying many more systems to validate such a result could be interesting. On the other hand, delayed predator dispersal always maintains local stability of the steady state [37]. Therefore, attention could be paid to develop models with new kind of predator dispersal, in which delayed predator dispersal could destabilize the local stability of the equilibrium. Till date, the analysis of such kind of models have been investigated when all the patches were identical. Analysis of the heterogeneous patchy models might be very complex. For instance, harvesting in patchy model could induce heterogeneity. As proposed by Sun and Mai [36], exploring dynamics in harvested models under delayed dispersal certainly be challenging from mathematical viewpoint.

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