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Stability analysis of a two-patch predator–prey model with two dispersal delays

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Abstract

This paper deals with a predator–prey model with both species in the delayed-dispersal case in a two-patch environment. The purpose of this paper is to study the effect of two dispersal delays on the stability of three equilibria. It turns out that the stability of the trivial equilibrium and the boundary equilibrium is delay-independent. However, the stability of the coexistence equilibrium is delay-dependent. Numerical simulations are performed to demonstrate the obtained results.

MSC: 92B05; 34K20; 34K18; 34K10

Keywords: Dispersal; Delay; Stability; Bifurcation; Predator–prey model

1 Introduction

The relationship of predator and prey is prevalent in nature and hence is one of the most important themes in ecological and mathematical models. Since the Lotka–Volterra predator–prey model was formulated, various predator–prey models have been studied by incorporating additional ecological concepts into the classical Lotka–Volterra model, such as functional responses, dispersal and time delay. In predator–prey models, dispersal will represent migration of either the prey population, the predator population, or both [1, 2].

Population dispersal is very common in ecology. Species migrate from one patch to another patch, due to some kinds of factor in the initial patch. For instance, a prey species will choose to move on the basis of resource availability and predation risk, while predators tend to migrate to the better patch to gain more prey. In nature, lack of food, competition, sex, age, lack of security (mainly for the prey), climatic conditions, season, overpopulation in a patch—these factors make species move from a patch to another [3]. For example, in aquatic environments, many zooplankton species exhibit vertical movements each day due to light and food. During the day time, some species migrate downwards into the darkness to reduce the predation risk by fish, while at night time, these species move upward to consume the phytoplankton [4]. There has been great interest in the study of mathematical models of populations with species dispersal among patches, such as a single population dispersal [5–8], and the dispersal of both prey and predator among patches [9–11].

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It is worth pointing out that most of the research work in population models with patchy structures assumed the dispersal to be instantaneous. In fact, species movement between patches takes some time. Recently, Zhang et al. considered a predator–prey metapopulation model with travel time delay and showed that such delay can stabilize and destabilize the system [8].

To the best of our knowledge, there is little research on joining considerations of migration and dispersal delay in biological models. It is challenging to add time delays to predator–prey models for the mathematical analysis. Delay may change the stability of dynamics and Hopf bifurcation may occur. Motivated by the above predator–prey model, we will integrate dispersal of both species and dispersal delays into a two-patch Rosenzweig–MacArthur predator–prey model. We shall investigate how the dispersal and dispersal delays interact to affect the stability of the predator–prey metapopulation model.

The rest of the paper is organized as follows. The formulation of mathematical model is presented in Sect. 2. The stability analysis of our model at three equilibria are given in Sect. 3. Then numerical simulations based on the analysis are reported in Sect. 4. Finally, we conclude the paper by a short discussion.

2 Model formulation

In this paper, our model assumes that the prey has a logistic growth rate and a predator has a Holling-type II functional response on each patch. The predator decays exponentially in the absence of prey. And we suppose that these patches are identical and the prey and predators can randomly move between two patches. During dispersal, migrating populations are assumed not to participate in the predator–prey interaction due to the two species being in different habitats. Thus, we propose a two-patch predator–prey model with dispersal of both species:

$$
\begin{cases}
\frac{dH_i}{dt} = rH_i(1 - \frac{H_i}{K}) - \frac{acH_iP_i}{b+H_i} + D(H_j(t - \eta_1) - H_i), \\
\frac{dP_i}{dt} = \frac{aH_iP_i}{b+H_i} - \delta P_i + M(P_j(t - \eta_2) - P_i),
\end{cases}
\tag{2.1}
$$

where $i, j \in \{1, 2\}$ and $i \neq j$. H_i and P_i denote the densities of prey and predators in patch i, respectively. r is the prey growth rate. K is the carrying capacity of prey. a is the maximum and constant rate of prey consumption per predator. b is the prey density where the attack rate is half-saturated. c is the inverse of yield. δ is the predator mortality. D and M are the dispersal rate of prey and predators among patches, respectively. η_1 and η_2 are the dispersal time of prey and predators, respectively.

A series of change of variables is carried out to reduce the number of parameters: $H_i = bh_i$, $P_i = \frac{br}{ac}p_i$, $t = \frac{s}{a}$, $\eta_i = \frac{\tau_i}{a}$, $\kappa = \frac{K}{b}$, $\varepsilon = \frac{r}{a}$, $d = \frac{D}{a}$, $m = \frac{M}{a}$, $\mu = \frac{\delta}{a}$, and this yields the model

$$
\begin{cases}
\frac{dh_i}{ds} = \varepsilon h_i(1 - \frac{h_i}{\kappa} - \frac{p_i}{1+h_i}) + d(h_j(s - \tau_1) - h_i), \\
\frac{dp_i}{ds} = \frac{h_ip_i}{1+h_i} - \mu p_i + m(p_j(s - \tau_2) - p_i).
\end{cases}
\tag{2.2}
$$

If $d = 0$ and $m = 0$, the single patch model has three equilibria: $(0, 0)$, $(\kappa, 0)$ and (h^*, p^*) with $h^* = \frac{\mu}{1-\mu}$ and $p^* = (1 - \frac{h^*}{\kappa})(1 + h^*)$. Its dynamics is described by the following results [12].

Theorem 2.1 *Consider* (2.2) *with* $d = 0$ *and* $m = 0$, *the following conclusions hold*:

(1) *The trivial equilibrium* $(0, 0)$ *is unstable*.

(2) *The predator-extinction equilibrium* $(\kappa, 0)$ *is stable when* $\mu > \frac{\kappa}{1+\kappa}$.

(3) *The coexistence equilibrium* (h^*, p^*) *exists if and only if* $0 < \mu < \frac{\kappa}{1+\kappa}$.

(4) *The coexistence equilibrium is globally stable when* $\frac{\kappa-1}{\kappa+1} < \mu < \frac{\kappa}{1+\kappa}$.

(5) *There is a unique globally stable limit cycle if* $0 < \mu < \frac{\kappa-1}{\kappa+1}$.

3 Stability analysis of the equilibria

Model (2.2) has three equilibria representing different outcomes of the ecological system:

$E_0 = (0, 0, 0, 0)$: extinction of both the prey and the predator in each patch;

$E_1 = (\kappa, 0, \kappa, 0)$: extinction of the predator and persistence of prey in each patch;

$E_2 = (h^*, p^*, h^*, p^*)$: coexistence of both species in each patch provided that

$$0 < \mu < \frac{\kappa}{1+\kappa}.$$

Now we linearize system (2.2) at an equilibrium (h, p, h, p) and substitute an exponential solution, and we obtain the characteristic equation $\det J = 0$ with

$$J = \begin{bmatrix} J_1 & J_2 \\ J_2 & J_1 \end{bmatrix},$$

where

$$J_1 = \begin{bmatrix} \varepsilon \cdot (1 - \frac{2h}{\kappa} - \frac{p}{(1+h)^2}) - d - \lambda & -\varepsilon \cdot \frac{h}{1+h} \\ \frac{p}{(1+h)^2} & \frac{h}{1+h} - \mu - m - \lambda \end{bmatrix}$$

and

$$J_2 = \begin{bmatrix} de^{-\lambda \tau_1} & 0 \\ 0 & me^{-\lambda \tau_2} \end{bmatrix}.$$

It is easy to calculate that $\det(J) = \det(J_1 + J_2) \cdot \det(J_1 - J_2)$. The characteristic equation determines the local stability of equilibria. The equilibrium is stable if and only if all the characteristic roots have negative real part. In the following, we will analyze the stability of our model (2.2) at three equilibria, respectively.

3.1 The stability analysis of E_0

Inserting the trivial equilibrium E_0 into the characteristic equation $\det J = 0$, we get the characteristic equations

$$\begin{cases} \lambda - \varepsilon + d + de^{-\lambda \tau_1} = 0, \\ \lambda - \varepsilon + d - de^{-\lambda \tau_1} = 0, \\ \lambda + \mu + m + me^{-\lambda \tau_2} = 0, \\ \lambda + \mu + m - me^{-\lambda \tau_2} = 0. \end{cases} \tag{3.1}$$

When the dispersal is instantaneous, i.e., $\tau_1 = \tau_2 = 0$, the roots of characteristic equations are $\varepsilon, \varepsilon - 2d, -\mu, -\mu - 2m$. Thus, there exists at least one positive root which leads to the instability of E_0.

Based on the technique of [13–15], the stability change at the equilibrium can only happen when characteristic roots appear on or cross the imaginary axis as τ increases. Here we assume that $\varepsilon \neq 2d$, then we look for a pair of purely imaginary roots of the characteristic equations (3.1).

Set $\lambda = i\omega$ with $\omega > 0$. By substituting λ into the first equation of (3.1), then separating the real and imaginary parts, we get

$$\begin{cases} d\cos\omega\tau_1 = \varepsilon - d, \\ d\sin\omega\tau_1 = \omega. \end{cases} \tag{3.2}$$

Then the first equation of (3.1) admits a pair of purely imaginary roots $\pm i\omega_0$ with $\omega_0 = \sqrt{d^2 - (\varepsilon - d)^2}$.

Similarly, for the second equation of (3.1), there is a pair of purely imaginary roots $\pm i\omega_0$ with $\omega_0 = \sqrt{d^2 - (\varepsilon - d)^2}$.

For the third equation and the last equation of (3.1), by using the same method, we have $\omega^2 = m^2 - (\mu + m)^2 < 0$. Thus, there are no purely imaginary roots for the last two equations of (3.1).

Lemma 3.1 *Suppose at certain τ_1, the first and second equation of characteristic equation* (3.1) *have purely imaginary roots $\pm i\omega$. Then*

$$\frac{d\,\mathrm{Re}(\lambda)}{d\tau_1}\bigg|_{\lambda=i\omega} > 0.$$

Proof It follows from the first equation of (3.1) that

$$\frac{d\lambda}{d\tau_1} = \frac{d\lambda}{e^{\lambda\tau_1} - d\tau_1}.$$

Thus

$$\mathrm{sign}\left(\frac{d(\mathrm{Re}\,\lambda)}{d\tau_1}\right)\bigg|_{\lambda=i\omega} = \mathrm{sign}\left(\frac{\omega^2}{(\cos\omega\tau_1 - d\tau_1)^2 + \sin^2\omega\tau_1}\right) = \mathrm{sign}(\omega^2).$$

Consequently, $\frac{d\,\mathrm{Re}(\lambda)}{d\tau_1}|_{\lambda=i\omega} > 0$.

For the second equation of (3.1), the conclusion of the lemma also holds. The proof is complete. □

By Lemma 3.1, we know that $\frac{d\,\mathrm{Re}(\lambda)}{d\tau_1}|_{\lambda=i\omega_0} > 0$. This indicates that, as τ_1 increases, for the first and second equation of (3.1), the characteristic roots cross the imaginary axis through $\pm i\omega_0$ at $\tau = \tau_1$ from left to right and the number of characteristic roots with positive real parts is increased by 2.

On the other hand, for the third and fourth equations of (3.1), there are no purely imaginary roots. Note the instability of E_0 for $\tau_1 = \tau_2 = 0$, thus E_0 remains unstable for $\tau_1 > 0$ and $\tau_2 > 0$.

3.2 The stability analysis of E_1

Using the same procedure as the stability analysis of E_0, inserting the equilibrium E_1 into the characteristic equation $\det J = 0$, we get the characteristic equations

$$
\begin{cases}
\lambda + \varepsilon + d + de^{-\lambda\tau_1} = 0, \\
\lambda + \varepsilon + d - de^{-\lambda\tau_1} = 0, \\
\lambda + m - (\frac{\kappa}{1+\kappa} - \mu) + me^{-\lambda\tau_2} = 0, \\
\lambda + m - (\frac{\kappa}{1+\kappa} - \mu) - me^{-\lambda\tau_2} = 0.
\end{cases}
\tag{3.3}
$$

When $\tau_i = 0$, the roots of the characteristic equations (3.3) are $-\varepsilon$, $-\varepsilon - 2d$, $\frac{\kappa}{1+\kappa} - \mu$, $\frac{\kappa}{1+\kappa} - \mu - 2m$. Here we have two cases to consider: (1) $\mu > \frac{\kappa}{1+\kappa}$, all roots are negative, so equilibrium E_1 is stable; (2) $0 < \mu < \frac{\kappa}{1+\kappa}$, the roots at least have a positive root, E_1 is unstable.

Substituting $\lambda = i\omega$ with $\omega > 0$ into these characteristic equations (3.3), and separating the real and imaginary parts, we can calculate that if $\mu > \frac{\kappa}{1+\kappa}$, $|\cos\omega\tau_1| = 1 + \frac{\varepsilon}{d} > 1$, $|\cos\omega\tau_2| = 1 - \frac{\frac{\kappa}{1+\kappa} - \mu}{m} > 1$, which means there is no solutions of (3.3) can appear on the imaginary axis for any τ_i. Therefore, E_1 is locally asymptotically stable when $\mu > \frac{\kappa}{1+\kappa}$.

For case (2), if $0 < \mu < \frac{\kappa}{1+\kappa}$, by the expression of $\cos\omega\tau_1$, the first and second equations of (3.3) have no imaginary roots. However, the third and fourth equations admit purely imaginary roots $\pm i\omega$ with $\omega = \sqrt{m^2 - (m - (\frac{\kappa}{1+\kappa} - \mu))^2}$ if $\frac{\kappa}{1+\kappa} - 2m < \mu < \frac{\kappa}{1+\kappa}$; the two equations have no imaginary roots while if $0 < \mu < \frac{\kappa}{1+\kappa} - 2m$. It is easy to show that $\text{sign}(\frac{d(\text{Re}\,\lambda)}{d\tau_2})|_{\lambda=i\omega} = \text{sign}(\omega^2) > 0$, Note that equilibrium E_1 is unstable with $\tau_1 = \tau_2 = 0$ in case (2). So when $0 < \mu < \frac{\kappa}{1+\kappa}$, E_1 remains unstable as τ_1 and τ_2 increase.

3.3 The stability analysis of E_2

In this subsection, we assume that $0 < \mu < \frac{\kappa}{1+\kappa}$ to ensure the coexistence equilibrium E_2 exists. Inserting E_2 into the characteristic equation $\det J = 0$, we get

$$
\begin{cases}
\lambda^2 - \lambda(A - d - m) - \lambda(de^{-\lambda\tau_1} + me^{-\lambda\tau_2}) - mde^{-\lambda\tau_1} + m(A-d)e^{-\lambda\tau_2} \\
\quad + mde^{-\lambda(\tau_1+\tau_2)} - m(A-d) + B = 0, \\
\lambda^2 - \lambda(A - d - m) + \lambda(de^{-\lambda\tau_1} + me^{-\lambda\tau_2}) + mde^{-\lambda\tau_1} - m(A-d)e^{-\lambda\tau_2} \\
\quad + mde^{-\lambda(\tau_1+\tau_2)} - m(A-d) + B = 0,
\end{cases}
\tag{3.4}
$$

where $A = \varepsilon \cdot \frac{\kappa+1}{\kappa} \cdot \frac{\mu}{1-\mu} \cdot (\frac{\kappa-1}{\kappa+1} - \mu)$ and $B = \varepsilon\mu(1 - \frac{\mu}{\frac{\kappa}{1+\kappa}}) > 0$ (since $0 < \mu < \frac{\kappa}{1+\kappa}$).

When $\tau_1 = \tau_2 = 0$, the characteristic equation becomes

$$
\begin{cases}
\lambda^2 - A\lambda + B = 0, \\
\lambda^2 - (A - 2d - 2m)\lambda - 2m(A - 2d) + B = 0.
\end{cases}
$$

Therefore, the coexistence equilibrium is stable if $A < 0$, otherwise unstable.

When $m = 0$, this implies that prey disperses only. Based on the results of [8], we summarize the related conclusions in the following theorem.

Theorem 3.2 *Consider system* (2.2) *with $m = 0$. If $A < 0$, the coexistence equilibrium E_2 is locally asymptotically stable for all $\tau_1 \geq 0$. If $A > 0$, then the coexistence equilibrium E_2 is unstable when $\tau_1 = 0$, and as τ_1 increases, we have the following results.*

Case (i) $d \in (0, A/2)$: *the coexistence equilibrium E_2 remains unstable for $\tau_1 > 0$.*
Case (ii) $d \in (A/2, A)$: *the coexistence equilibrium E_2 remains unstable for $\tau_1 > 0$.*
Case (iii) $d \in (A, \infty)$: *there may exist stability switches.*

When both species are mobile, due to the presence of two different time delays in characteristic equations, it is usually difficult to analyze the transcendental equation with two delays. Actually, finding all the characteristic roots of Eq. (3.4) have negative real parts is hopeless [16]. This indicates the difficulty in investigating the distribution of the zeros of Eq. (3.4). Thus, we mainly numerically examine how the two dispersal delays affect the stability of the coexistence equilibrium in our model in the next section.
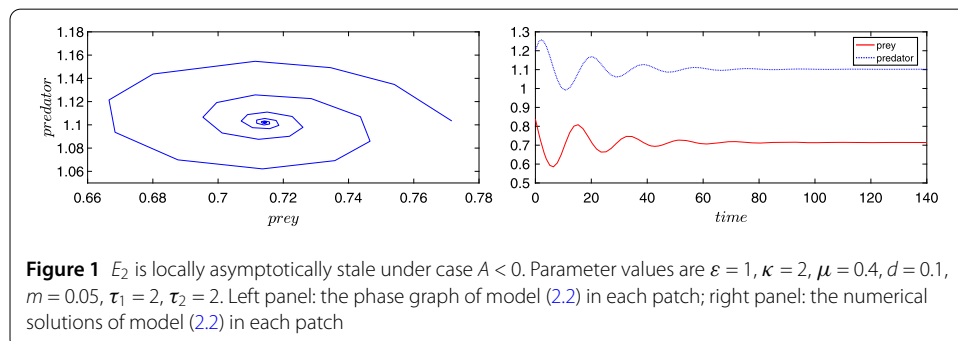
4 Numerical simulations

From the above section, we know that the stability of the trivial equilibrium E_0 and the boundary equilibrium E_1 is relatively simple. However, the stability analysis of the coexistence equilibrium E_2 is complicated. Therefore, in this section, we mainly present some numerical examples of our model (2.2) and investigate that the effect of delay on the stability and instability of the coexistence equilibrium E_2. Based on Theorem 3.2, we display the numerical simulations in each case.

Example 1 We take parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.4$, $d = 0.1$, $m = 0.05$, $\tau_1 = 2$, $\tau_2 = 2$. This set of parameter values lead to $A = -0.09 < 0$. In this case, $E_2 = (0.71, 1.10, 0.71, 1.10)$ is locally asymptotically stable. Due to the identical patch, we only plot the numerical simulations in each patch. As can be seen in Fig. 1, the prey and predators populations in each patch approach to 0.71 and 0.10, respectively.

Example 2 Chose parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.0125$, $m = 0.02$, $\tau_1 = 2$, $\tau_2 = 2$. This set of parameter values corresponds to the case $A = 0.05 > 0$ and $0 < d < A/2$. As shown in Fig. 2, the prey population in two patches will be fluctuating at same level, and so does the predators. This indicates that the coexistence equilibrium E_2 is unstable. But the prey and predator species will have long-term persistence in both patches.

Example 3 We choose $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.038$, $m = 0.05$, $\tau_1 = 2$. This leads to the case: $0 < A/2 < d < A$. If $\tau_1 = 2$ and $m = 0$, the coexistence equilibrium E_2 is unstable. As we take $m = 0.05$, we find there exists a stable interval as τ_2 increases, which is illustrated in Fig. 3.

In order to investigate our model (2.2) in the case $d > A > 0$, two dispersal delays may induce Hopf bifurcation. Thus, we first plot the numerical solutions and the τ_1-bifurcation
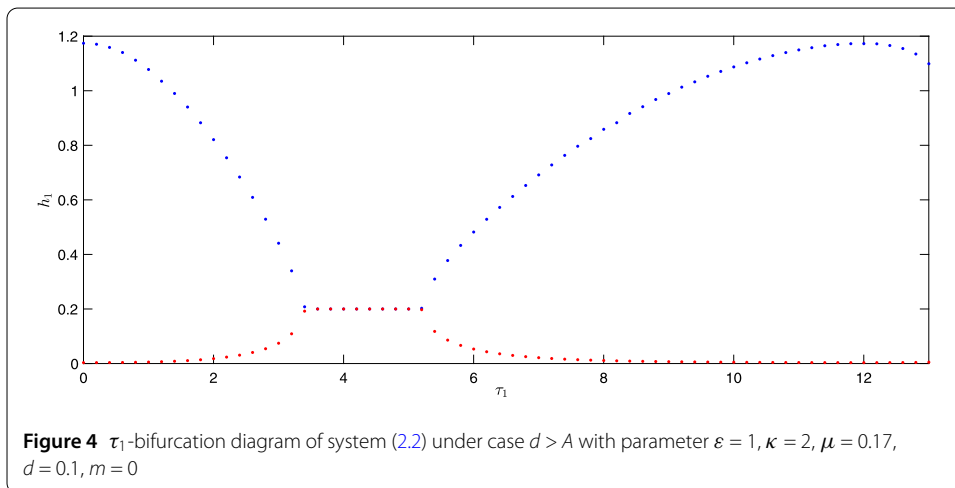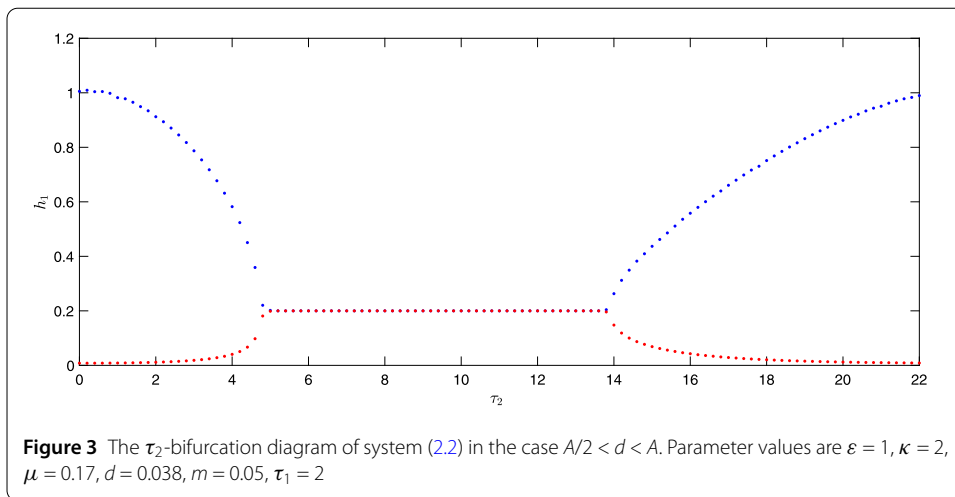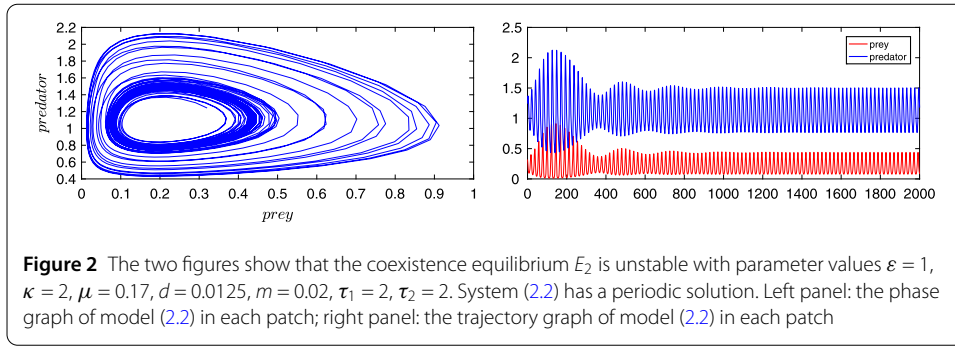

Figure 1 E_2 is locally asymptotically stale under case $A < 0$. Parameter values are $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.4$, $d = 0.1$, $m = 0.05$, $\tau_1 = 2$, $\tau_2 = 2$. Left panel: the phase graph of model (2.2) in each patch; right panel: the numerical solutions of model (2.2) in each patch

Figure 2 The two figures show that the coexistence equilibrium E_2 is unstable with parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.0125$, $m = 0.02$, $\tau_1 = 2$, $\tau_2 = 2$. System (2.2) has a periodic solution. Left panel: the phase graph of model (2.2) in each patch; right panel: the trajectory graph of model (2.2) in each patch

Figure 3 The τ_2-bifurcation diagram of system (2.2) in the case $A/2 < d < A$. Parameter values are $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.038$, $m = 0.05$, $\tau_1 = 2$

Figure 4 τ_1-bifurcation diagram of system (2.2) under case $d > A$ with parameter $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.1$, $m = 0$
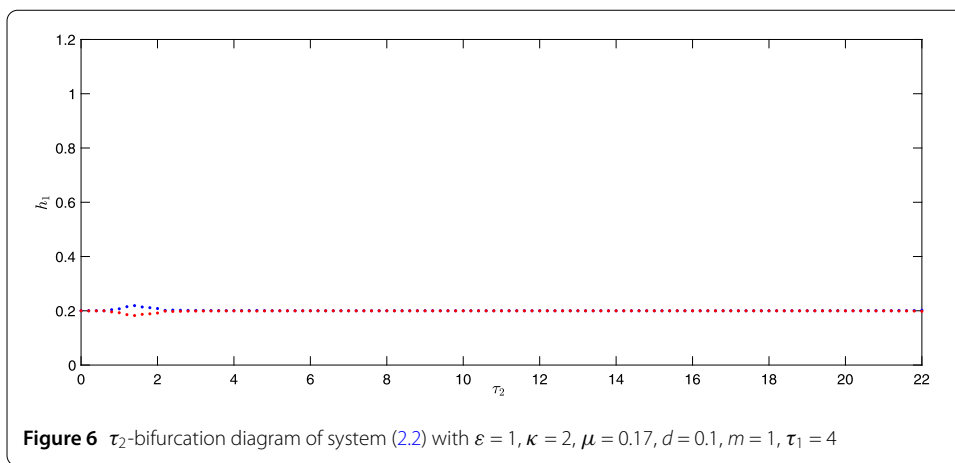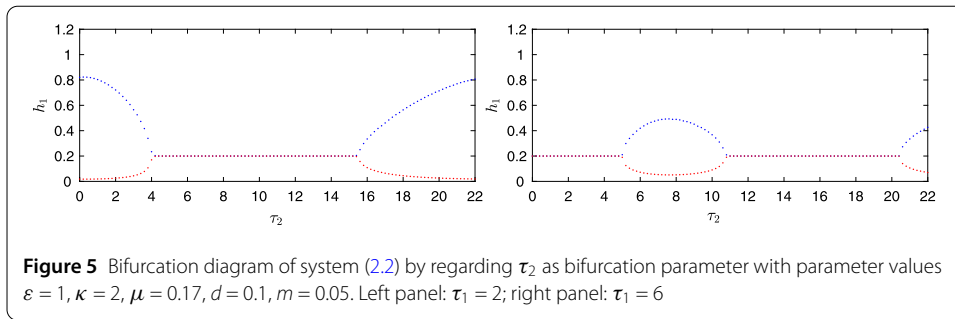
diagram of (2.2) with $m = 0$ in each cases. Then we choose values of τ_1 in its stable intervals and unstable intervals, respectively. We regard τ_2 as bifurcation parameter and display the bifurcation diagram of (2.2).

Example 4 We consider the case $d > A > 0$. Thus we first take parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.1$, $m = 0$. This means that prey individuals disperse, but predators are sedentary. In this case, there is a stable interval as shown in Fig. 4.

Figure 5 Bifurcation diagram of system (2.2) by regarding τ_2 as bifurcation parameter with parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.1$, $m = 0.05$. Left panel: $\tau_1 = 2$; right panel: $\tau_1 = 6$

Figure 6 τ_2-bifurcation diagram of system (2.2) with $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.1$, $m = 1$, $\tau_1 = 4$

Next, we take two sets of parameter values $m = 0.05$, $\tau_1 = 2$ and $m = 0.05$, $\tau_1 = 6$, respectively, and keep all other parameter values the same as above. As we see in Fig. 4, $\tau_1 = 2$ and $\tau_1 = 6$, the system (2.2) is unstable at the coexistence equilibrium E_2. We also investigate that the coexistence equilibrium is unstable if $m = 0.05$, $\tau_1 = 2$ and $\tau_2 = 0$, while it is stable if $m = 0.05$, $\tau_1 = 6$ and $\tau_2 = 0$. As τ_2 increases, there is a stable interval which is illustrated in Fig. 5.

Note that the coexistence equilibrium E_2 is stable when $\tau_1 = 4$ in Fig. 4. Thus we finally take parameter values $\varepsilon = 1$, $\kappa = 2$, $\mu = 0.17$, $d = 0.1$, $m = 1$, $\tau_1 = 4$, and present the bifurcation diagram of system (2.2) by regarding τ_2 as bifurcation parameter (see Fig. 6). We show that system (2.2) has a stable switch with $\tau_1 = 4$ as τ_2 increases.

In all, as shown in Fig. 5 and Fig. 6, dispersal delays may exhibit both stabilizing and destabilizing effects on the coexistence equilibrium.

5 Summary and discussion

This paper is concerned with a predator–prey model with two dispersal delays and the stability analysis of three equilibria. We focus attention on the effect of two dispersal delays on the dynamics of our model (2.2). Moreover, we show that, for the trivial equilibrium and the boundary equilibrium, dispersal delays have no impact on the stability and instability of two equilibria. However, the stability of the coexistence equilibrium is delay-dependent. Delays can destabilize and stabilize the coexistence equilibrium. Indeed, the dispersal delays cannot only switch the stability but also induce a Hopf bifurcation. If the species' mortality during dispersal is considered, the stability analysis becomes very dif-

ficult. Numerical simulations are carried out showing that stability switches are possible. We leave the related analysis for our future work.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors contributed equally to the writing of this paper. The authors read and approved the final manuscript.

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