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Research Article

Stability Analysis of a Two-Patch Competition Model with Dispersal Delays

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In this paper, we study a Lotka-Volterra competition model with two competing species moving randomly between two identical patches. A constant dispersal delay is incorporated into the dispersal process for each species. We show that the dispersal delays do not affect the stability and instability of all four symmetric equilibria. Numerical simulations are presented to demonstrate the effect of dispersal delays on the stability and instability of the symmetric coexistence equilibrium.

1. Introduction

As one of the basic relationships in ecological relationships, competition has been extensively studied. For competition models governed by differential equations of Lotka-Volterra type, we refer to [1, 2] and the references therein. Dispersal of species between patches is very common in nature. For example, many zooplankton species move downward into the darkness to reduce the predation risk by fish, while at night time, they move upward to consume the phytoplankton [3]. It is of great importance to examine how the dispersal affects local and global dynamics of the resulting metapopulations. To this purpose, many mathematical models incorporating the dispersal of species over patches have been proposed and studied. For instance, the movement of a single species has been considered in [4–9], and models allowing the dispersal of two species have appeared in [10–13]. See also [14–16] for studies on models with competition and predator-prey interactions in patchy environments.

We note that, in the above-mentioned work, dispersal is often assumed to be instantaneous. However, in reality, it always takes time for species dispersing from one patch to another. As a result, dispersal delays do exist and should be incorporated into modeling the dispersal process. With this in mind, recently, Zhang et al. considered a two-patch predator-prey model with delayed dispersal of prey only and showed that such dispersal delay exhibits a stabilizing role on the stability of the coexistence equilibrium [17]. Later, Mai et al. generalized the model considered in [17] into the case with an arbitrary number of patches and showed that the dispersal delay can indeed induce stability switches [18]. Sun et al. considered a two-patch predator-prey model with two dispersal delays and showed that the dispersal delays can destabilize and stabilize the coexistence equilibrium [19].

Motivated by above work, in this paper, we consider a two-species competition model and assume both species move randomly between two patches with two dispersal delays. Our objective is to explore the effects of delays on the stability and instability of symmetric equilibria of the resulting metapopulation system.

The rest of the paper is organized as follows. We present our two-patch competition model with two dispersal delays in Section 2. We carry out detailed stability analysis for the resulting symmetric equilibria in Section 3. Numerical simulations are reported in Section 4 to demonstrate the effect of dispersal delays on the stability and instability of the symmetric coexistence equilibrium. A brief summary of our work is given in last section.

2. The Two-Patch Competition Model

In this paper, we assume that the two patches are identical and the two competing species move randomly between two identical patches. Moreover, the dispersal period is relatively short compared to the lifespan of each species, and no mortality will be included in the dispersal. Therefore, our two-patch competition model with delayed dispersal of two competing species are described by the following system:

$$\begin{aligned}\frac{dX_i(t)}{dt} &= r_1 X_i(t)\left[1-\frac{X_i(t)}{K_1}-b_{12}\frac{Y_i(t)}{K_1}\right] \\ &\quad + D_1\left(X_j(t-\eta_1)-X_i(t)\right), \\ \frac{dY_i(t)}{dt} &= r_2 Y_i(t)\left[1-\frac{Y_i(t)}{K_2}-b_{21}\frac{X_i(t)}{K_2}\right] \\ &\quad + D_2\left(Y_j(t-\eta_2)-Y_i(t)\right),\end{aligned} \tag{1}$$

where $i, j \in \{1,2\}$ and $i \neq j$. X_i and Y_i denote the densities of two competing species X and Y in patch i ($i = 1,2$), respectively. r_1 and r_2 are the intrinsic growth rates of species X and Y, respectively. K_1 and K_2 are the carrying capacities of species X and Y, respectively. b_{12} and b_{21} measure the competition strengths of Y on X and X on Y, respectively. D_1 and D_2 are the dispersal rates of species X and Y, respectively. η_1 and η_2 denote the dispersal periods of species X and Y from one patch to the other, respectively. All parameters are assumed to be positive.

By rescaling $x_i = X_i/K_1$, $y_i = Y_i/K_2$, $s = r_1 t$, $\tau_i = r_1\eta_i$, $\rho = r_2/r_1$, $a = b_{12}(K_2/K_1)$, $b = b_{21}(K_1/K_2)$, and $D_i = r_1 d_i$, we obtain the dimensionless form of system (1)

$$\begin{aligned}\frac{dx_i(s)}{ds} &= x_i(s)\left[1-x_i(s)-ay_i(s)\right] \\ &\quad + d_1\left(x_j(s-\tau_1)-x_i(s)\right), \\ \frac{dy_i(s)}{ds} &= \rho y_i(s)\left[1-y_i(s)-bx_i(s)\right] \\ &\quad + d_2\left(y_j(s-\tau_2)-y_i(s)\right),\end{aligned} \tag{2}$$

where $i, j \in \{1,2\}$ and $i \neq j$.

For the case with no dispersal (i.e.,$d_i = 0$), the dynamics of the competition model in a single patch is given below (See [2]).

Theorem 1. *Consider a single patch competition model governed by*

$$\begin{aligned}\frac{dx(s)}{ds} &= x(s)\left[1-x(s)-ay(s)\right], \\ \frac{dy(s)}{ds} &= \rho y(s)\left[1-y(s)-bx(s)\right].\end{aligned} \tag{3}$$

The following conclusions hold:

(1) *There are three trivial equilibria:* $(0,0)$, $(1,0)$, *and* $(0,1)$.

(2) *The coexistence equilibrium* (x^*, y^*) *exists if and only if* $a > 1, b > 1$ *or* $a < 1, b < 1$, *where* $x^* = (1-a)/(1-ab)$ *and* $y^* = (1-b)/(1-ab)$.

(3) *If* $a > 1$ *and* $b > 1$, *then the two boundary equilibria* $(1,0)$ *and* $(0,1)$ *are both stable.*

(4) *The coexistence equilibrium* (x^*, y^*) *is stable if* $a < 1$ *and* $b < 1$ *and is a saddle point if* $a > 1$ *and* $b > 1$.

(5) *The boundary equilibrium* $(1,0)$ *is stable if* $b > 1$ *and unstable if* $b < 1$.

(6) *The boundary equilibrium* $(0,1)$ *is stable if* $a > 1$ *and unstable if* $a < 1$.

3. Stability Analysis of the Symmetric Equilibria

Since the two patches under consideration are assumed to be identical, system (2) admits four symmetric equilibria as follows:

$E_0 = (0,0,0,0)$: extinction of both species in each patch;

$E_1 = (1,0,1,0)$: extinction of species Y and persistence of species X in each patch;

$E_2 = (0,1,0,1)$: extinction of species X and persistence of species Y in each patch;

$E^* = (x^*, y^*, x^*, y^*)$: coexistence of both species in each patch, which exists as long as $a > 1$, $b > 1$ or $a < 1$, $b < 1$.

Linearizing system (2) at a symmetric equilibrium (x, y, x, y), we obtain the associated characteristic equation given by $\det\Delta_\lambda = 0$ with

$$\Delta_\lambda = \begin{bmatrix} J_1 & J_2 \\ J_2 & J_1 \end{bmatrix}, \tag{4}$$

where $J_1 = \begin{bmatrix} 1-2x-ay-d_1-\lambda & -ax \\ -\rho by & \rho(1-bx-2y)-d_2-\lambda \end{bmatrix}$ and $J_2 = \begin{bmatrix} d_1 e^{-\lambda\tau_1} & 0 \\ 0 & d_2 e^{-\lambda\tau_2} \end{bmatrix}$.

The symmetric equilibrium (x, y, x, y) is locally asymptotically stable if all characteristic roots have negative real parts [20]. Next we will study the stability of all 4 symmetric equilibria by analyzing the associated characteristic equation $\det\Delta_\lambda = 0$.

3.1. The Trivial Equilibrium E_0. Note that $\det\Delta_\lambda = \det(J_1 + J_2)\cdot\det(J_1 - J_2)$. Thus, at the trivial equilibrium E_0, the characteristic equations consist of the following 4 transcendental equations:

$$\lambda - 1 + d_1 + d_1 e^{-\lambda\tau_1} = 0 \tag{5}$$

$$\lambda - 1 + d_1 - d_1 e^{-\lambda\tau_1} = 0 \tag{6}$$

$$\lambda - \rho + d_2 + d_2 e^{-\lambda\tau_2} = 0 \tag{7}$$

$$\lambda - \rho + d_2 - d_2 e^{-\lambda\tau_2} = 0 \tag{8}$$

If $\tau_1 = \tau_2 = 0$, then the characteristic roots are $1, 1-2d_1, \rho, \rho-2d_2$. Clearly, there exist at least two positive characteristic roots 1 and ρ. Thus E_0 is unstable.

According to the results of [21–23], the change of stability at the equilibrium can happen only if characteristic roots appear on or cross the imaginary axis as τ increases. We assume that $d_1 \neq 1/2$ and $d_2 \neq \rho/2$ to ensure that zero is not a root of (5) and (7), respectively.

The following lemma will be used later in verifying the transversality condition.

Lemma 2. *Suppose, at certain τ, the characteristic equation*

$$\lambda + p + qe^{-\lambda\tau} = 0 \tag{9}$$

admits a pair of purely imaginary roots $\pm i\omega$ ($\omega > 0$). Then $(d\,\mathrm{Re}(\lambda)/d\tau)|_{\lambda=i\omega} > 0$.

Proof. For (9), it is easy to get $d\lambda/d\tau = q\lambda/(e^{\lambda\tau} - q\tau)$. Thus

$$\begin{aligned}\operatorname{sign}\left(\frac{d(\mathrm{Re}\,\lambda)}{d\tau}\right)\Bigg|_{\lambda=i\omega} \\ = \operatorname{sign}\left(\frac{\omega^2}{(\cos\omega\tau - q\tau)^2 + \sin^2\omega\tau}\right) = \operatorname{sign}\left(\omega^2\right).\end{aligned} \tag{10}$$

Consequently, $(d\,\mathrm{Re}(\lambda)/d\tau)|_{\lambda=i\omega} > 0$. The proof is complete. □

Next we look for a pair of purely imaginary roots of characteristic equations (5)-(8) by setting $\lambda = i\omega$ with $\omega > 0$. Substituting $\lambda = i\omega$ into (5)-(6), we obtain

$$\omega_{01} = \sqrt{d_1^2 - (1 - d_1)^2}. \tag{11}$$

Thus if $0 < d_1 < 1/2$, then (5)-(6) admit no purely imaginary roots; while if $d_1 > 1/2$, then there is a pair of purely imaginary roots $\pm i\omega_{01}$ for (5) and also for (6). Further we have $(d\,\mathrm{Re}(\lambda)/d\tau_1)|_{\lambda=i\omega_{01}} > 0$ by Lemma 2. This implies that if $d_1 > 1/2$, the characteristic roots of (5) and (6) cross the imaginary axis through $\pm i\omega_{01}$ at $\tau = \tau_1$ from left to right and the number of characteristic roots with positive real parts is increased by 2, as τ_1 crosses the critical value.

Similarly, for (7) and (8), we can show that there are no imaginary roots if $0 < d_2 < \rho/2$; while if $d_2 > \rho/2$, then there exists a pair of purely imaginary roots $\pm i\omega_{02}$ with $(d\,\mathrm{Re}(\lambda)/d\tau_2)|_{\lambda=i\omega_{02}} > 0$. Note that E_0 is unstable for $\tau_1 = \tau_2 = 0$. Thus the above analysis shows that the trivial equilibrium E_0 remains unstable for $\tau_1 > 0$ and $\tau_2 > 0$ and hence we have the following result on the stability of the trivial equilibrium E_0.

Theorem 3. *Consider system (2). The trivial equilibrium E_0 is unstable for $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

3.2. The Boundary Equilibrium E_1. At the boundary equilibrium E_1, the characteristic equations read as

$$\lambda + 1 + d_1 + d_1 e^{-\lambda\tau_1} = 0 \tag{12}$$

$$\lambda + 1 + d_1 - d_1 e^{-\lambda\tau_1} = 0 \tag{13}$$

$$\lambda - \rho(1 - b) + d_2 + d_2 e^{-\lambda\tau_2} = 0 \tag{14}$$

$$\lambda - \rho(1 - b) + d_2 - d_2 e^{-\lambda\tau_2} = 0 \tag{15}$$

When $\tau_i = 0$, $(i = 1, 2)$, the characteristic roots of equations (12)-(15) are $-1, -1-2d_1, \rho(1-b), \rho(1-b)-2d_2$. Here we have two cases to consider: Case (1): $b > 1$, all roots are negative, and the equilibrium E_1 is locally asymptotically stable; and Case (2): $0 < b < 1$, there are at least one positive root, and the equilibrium E_1 is unstable.

We also assume that $d_2 \neq \rho(1 - b)/2$ to ensure that 0 is not a characteristic root of (14). Substituting $\lambda = i\omega$ with $\omega > 0$ into (12)-(15), we find that if (12) or (13) admits purely imaginary roots $\pm i\omega_{11}$, then $\omega_{11} = \sqrt{d_1^2 - (1 + d_1)^2}$; and if (14) or (15) admits purely imaginary roots $\pm i\omega_{12}$, then $\omega_{12} = \sqrt{d_2^2 - (d_2 - \rho(1 - b))^2}$. However, ω_{11} does not exist since $d_1 > 0$. If $b > 1$, then ω_{12} can never exist; while if $0 < b < 1$ and $0 < d_2 < \rho(1 - b)/2$, then ω_{12} can never exist either; only if $0 < b < 1$ and $d_2 > \rho(1 - b)/2$, there are purely imaginary roots for (14) and (15). However, it follows from Lemma 2 that $(d\,\mathrm{Re}(\lambda)/d\tau_1)|_{\lambda=i\omega_{12}} > 0$. Consequently, the boundary equilibrium E_1 remains unstable for all $\tau_1 > 0$ and $\tau_2 > 0$.

Summarizing the above analysis, we have the following result.

Theorem 4. *For the boundary equilibrium E_1 of system (2), we have the following conclusions:*

(i) *If $b > 1$, then E_1 is locally asymptotically stable for $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

(ii) *If $0 < b < 1$, then E_1 is unstable for $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

3.3. The Boundary Equilibrium E_2. The stability of the boundary equilibrium E_2 can be dealt with similarly as that of E_1 and we have the following result.

Theorem 5. *For the boundary equilibrium E_2 of system (2), we have the following conclusions:*

(I) *If $a > 1$, then E_2 is locally asymptotically stable for $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

(II) *If $0 < a < 1$, then E_2 is unstable for $\tau_1 \geq 0$ and $\tau_2 \geq 0$.*

3.4. The Symmetric Coexistence Equilibrium E^*. In this subsection, we assume that $a > 1, b > 1$ or $a < 1, b < 1$ to ensure the existence of the symmetric coexistence equilibrium E^*. At the coexistence equilibrium E^*, the associated characteristic equations reduce to

$$\begin{aligned}
&\lambda^2 - \lambda(A + B - d_1 - d_2) - \lambda\left(d_1 e^{-\lambda\tau_1} + d_2 e^{-\lambda\tau_2}\right) \\
&\quad + (Bd_1 - d_1 d_2) e^{-\lambda\tau_1} + (Ad_2 - d_1 d_2) e^{-\lambda\tau_2} \\
&\quad + (1 - a) AB + d_1 d_2 - Bd_1 - Ad_2 \\
&\quad + d_1 d_2 e^{-\lambda(\tau_1+\tau_2)} = 0, \\
&\lambda^2 - \lambda(A + B - d_1 - d_2) + \lambda\left(d_1 e^{-\lambda\tau_1} + d_2 e^{-\lambda\tau_2}\right) \\
&\quad - (Bd_1 - d_1 d_2) e^{-\lambda\tau_1} - (Ad_2 - d_1 d_2) e^{-\lambda\tau_2} \\
&\quad + (1 - a) AB + d_1 d_2 - Bd_1 - Ad_2 \\
&\quad + d_1 d_2 e^{-\lambda(\tau_1+\tau_2)} = 0,
\end{aligned} \tag{16}$$

where $A = (a - 1)/(1 - ab)$ and $B = (b - 1)/(1 - ab)$. If $a > 1$, $b > 1$, or $a < 1$, $b < 1$, then $A < 0$ and $B < 0$.

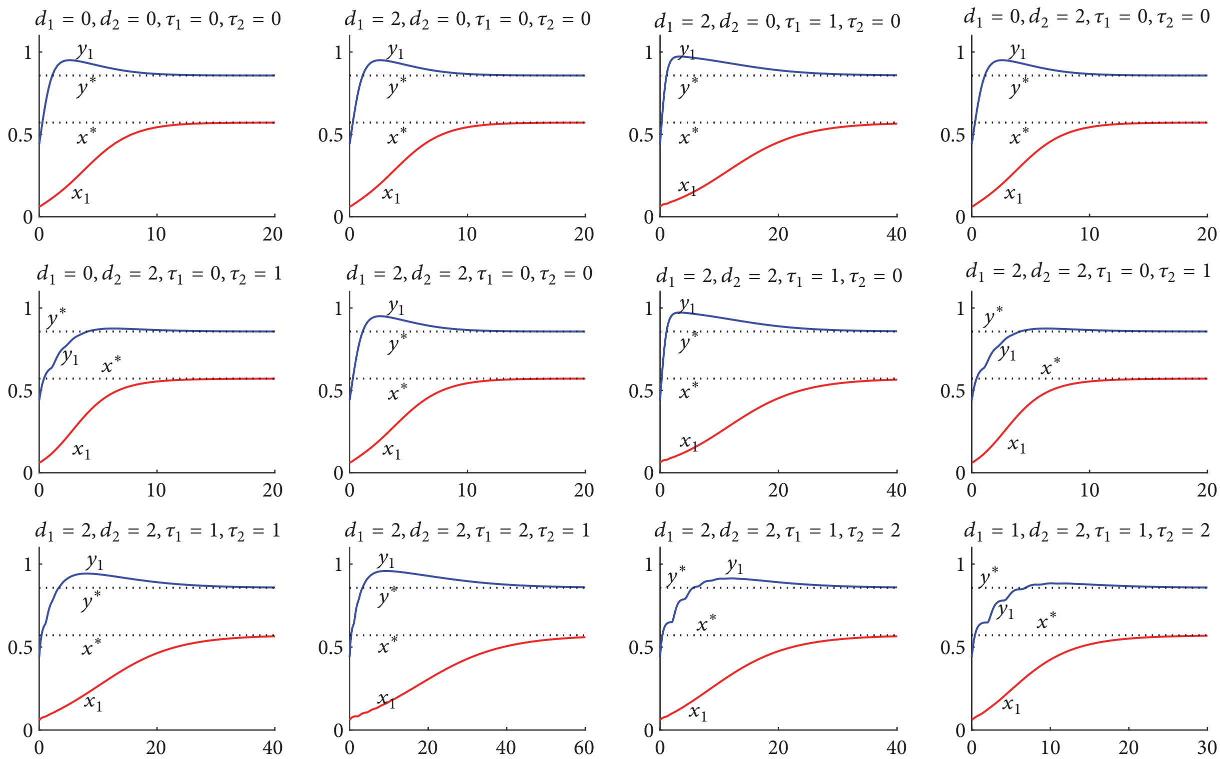

FIGURE 1: Numerical solutions of system (2) with parameter values $a = 0.5$, $b = 0.25$, $\rho = 2$. In this case, the symmetric coexistence equilibrium E^* is locally asymptotically stable.

When $\tau_1 = \tau_2 = 0$, the characteristic equations become

$$\lambda^2 - \lambda (A + B) + (1 - a) AB = 0$$
$$\lambda^2 - \lambda (A + B - 2d_1 - 2d_2) + 4d_1 d_2 - 2Ad_2 - 2Bd_1 + (1 - a) AB = 0 \quad (17)$$

Therefore, the symmetric coexistence equilibrium E^* is locally asymptotically stable if $a < 1$, $b < 1$, while it is unstable if $a > 1$, $b > 1$.

As the characteristic equations (16) have two distinct discrete delays, the analysis becomes very challenging though there has been some excellent work (see, for example, [24, 25]). We will mainly use numerical simulations to explore if the dispersal delays would affect the stability and instability of the symmetric coexistence equilibrium E^* in next section.

4. Numerical Simulations

In this section, we present some numerical simulations for model (2) to explore the effect of the dispersal delays on the stability and instability of the symmetric coexistence equilibrium E^*.

We first take parameter values $a = 0.5$, $b = 0.25$, and $\rho = 2$. This set of parameter values gives the symmetric coexistence equilibrium $E^* = (0.57, 0.86, 0.57, 0.86)$, which is locally asymptotically stable when $\tau_i = 0$ $(i = 1, 2)$ since $a < 1$ and $b < 1$. For 12 sets of different values of d_1, d_2, τ_1, and τ_2, we obtain numerical solutions in Figure 1, where we only plotted the numerical solutions in one patch. For all 12 sets of parameters values, we find that species X and Y approach x^* and y^*, respectively. This is a good indication that the dispersal delays do not affect the stability of the symmetric coexistence equilibrium E^*.

Next we take parameter values $a = 2$, $b = 4$, and $\rho = 2$. The symmetric coexistence equilibrium is $E^* = (0.14, 0.43, 0.14, 0.43)$ and is unstable for $\tau_i = 0, (i = 1, 2)$. As illustrated in Figures 2 and 3, for different initial conditions, the solutions converge to different boundary equilibria. This implies that the outcome of the competition is initial condition dependent and the dispersal delays do not change the instability of the symmetric coexistence equilibrium E^*.

5. Summary

In this paper, we have incorporated dispersal of both species between two patches into a two-species competition model. We have shown that the resulting two-patch competition model admits 4 symmetric equilibria: the trivial equilibrium E_0, two boundary equilibria E_1 and E_2, and the symmetric coexistence equilibrium E^*. For E_0, E_1, and E_2, we have analytically proven that the dispersal delays do not affect their stability and instability. For the symmetric coexistence equilibrium E^*, though we were not able to provide analytical analysis due to the complexity arisen from two delays, we have numerically demonstrated that the dispersal delays are also harmless in the sense that they do not affect the stability and instability of the symmetric coexistence equilibrium.

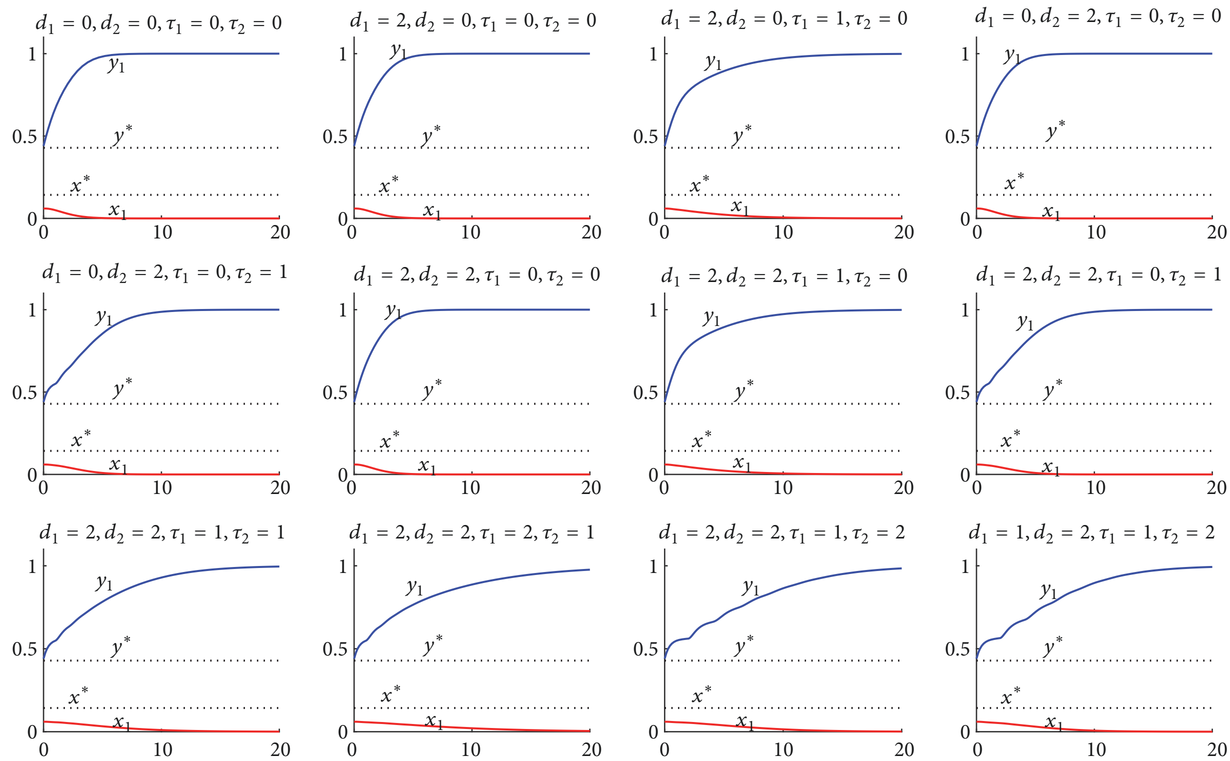

FIGURE 2: Numerical solutions of system (2). The symmetric coexistence equilibrium is unstable with parameters $a = 2$, $b = 4$, and $\rho = 2$. Initial condition is set as $(x_1(0), y_1(0), x_2(0), y_2(0)) = (0.06, 0.44, 0.06, 0.44)$.

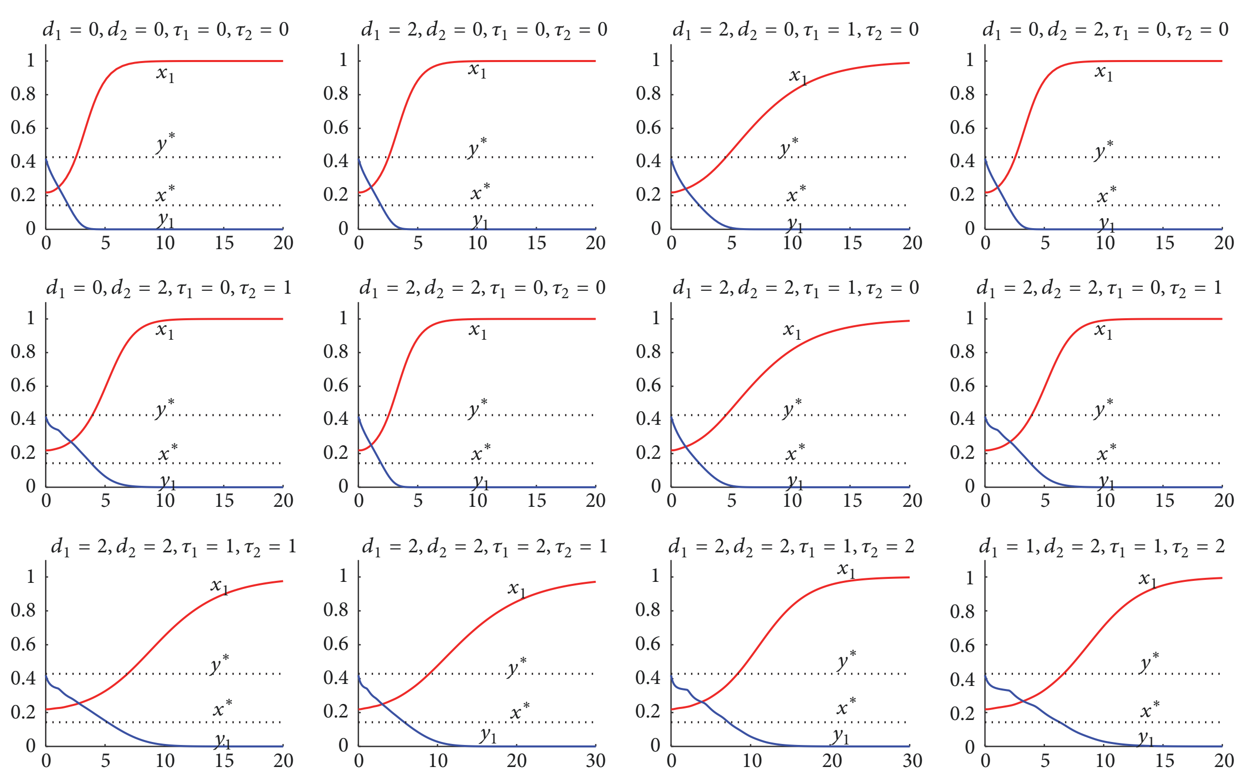

FIGURE 3: Numerical solutions of system (2). The symmetric coexistence equilibrium is unstable with parameters $a = 2$, $b = 4$, and $\rho = 2$. Initial condition is set as $(x_1(0), y_1(0), x_2(0), y_2(0)) = (0.22, 0.42, 0.22, 0.42)$.

This conclusion differs from that of predator-prey models discussed in [9, 17–19], where the dispersal delays can induce stability switches.

Data Availability

No data were used to support this study.

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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