STABILITY OF EQUILIBRIA IN A MUTUALISM MODEL: IMPACT OF DISCRETE DELAYS

Olfat Al Lakkies[1], Laurance Fakih[2], Paul Georgescu[3], Andrei Halanay[4]

We study a two-species mutualism delay model with two discrete lags τ_1, τ_2. For the coexistence equilibrium we derive local stability conditions from the characteristic equation. In the no-delay case, stability follows from the Routh–Hurwitz conditions. With one delay, imaginary-axis crossings reduce to a quartic equation, giving explicit critical delays when stability is lost. With two delays, we compute critical τ_2 branches for fixed τ_1 and obtain Hopf bifurcation points.

Keywords: mutualism, delay differential equations, stability analysis, Hopf bifurcation.
MSC2010: 34K20, 92D25, 34D45.

1. Introduction

Mutualisms, understood as interactions between two or more species that are beneficial for all of them, play a fundamental role in shaping ecological communities, influencing species coexistence and ecosystem stability (Bronstein [1]) and fostering biodiversity by promoting interspecies dependencies. Their ubiquitous presence is expressed, for instance, via seed dispersal (Vander Wall et al. [2]), pollination (Richman *et al.* [3]), protection from antagonists or hostile environments (Trager *et al.* [4]), or via a plethora of other fundamentally different mechanisms that often lead to an enhanced ability to survive, grow or reproduce.

From a mathematical viewpoint, mutualisms have received much less attention than their antagonistic counterparts such as parasitism and predation, fact often attributed to the idea that the former are prone to having built-in flaws, since even comparatively simpler models exhibit biologically unrealistic behaviour, in the form of unboundedness of solutions. A comprehensive framework for analyzing models of

[1]National University for Science and Technology Politehnica Bucharest, 060042 Bucharest, Romania, e-mail: `olfat.al@stud.fsa.upb.ro`

[2]Department of Mathematics and Informatics, National University for Science and Technology Politehnica Bucharest, 060042 Bucharest, Romania, e-mail: `laurance.fakih@upb.ro`, ORCID: 0009-0004-5771-5645

[3]Department of Mathematics, Technical University of Iasi, Bd. Copou 11, 700506 Iasi, Romania, e-mail: `vpgeo@tuiasi.ro`

[4]Department of Mathematics and Informatics, National University for Science and Technology Politehnica Bucharest, 060042 Bucharest, Romania; Center for Research and Training in Innovative Techniques of Applied Mathematics in Engineering, UPB, 060042 Bucharest, Romania, e-mail: `andrei.halanay@upb.ro`, ORCID: 0000-0002-2425-3008

pairwise mutualism regardless of their mode of expression (nutritional, protection, transportation) has been proposed by Hale and Valdovinos [5], with the purpose of finding robust stability patterns, being observed that mutualisms tend to exhibit stable coexistence of richer equilibria when mutualistic benefits saturate. Stability results for general models of pairwise mutualism have been obtained in Vargas-De-León [6] and Georgescu *et al.* [7] via the use of Lyapunov functionals. The global stability of positive equilibria for a general class of n-species models of mutualism has been discussed in Georgescu and Zhang [8] via conditions that are expressed in terms of per-species limits of growth-to-loss ratios computed at higher population densities, complemented by either monotonicity or sublinearity assumptions, being observed that these conditions hold for n-species versions of commonly used models of mutualism.

A fine-grained approach towards the modelling of mutualistic interactions has been taken by Moore *et al.* [9], in which birth and death processes are modeled as essentially separated phenomena, rather than being conflated in a single growth function. Further, the pairwise mutualism models of Moore *et al.* [9] relaxed the standard linearity assumptions for both per capita birth and death rates, allowing for either linear or saturating mutualistic contributions, and observed primarily via numerical arguments that decelerating (lower-powered) density dependence yields larger mutualistic benefits but tends to destabilize populations, whereas accelerating (higher-powered) density dependence always ensures stability. The numerical findings of Moore *et al.* [9] have then been confirmed in Georgescu and Zhang [10] via an approach based on the theory of monotone systems that is amenable to the treatment of higher dimensional models.

This study extends the mutualism model with saturating benefits introduced in Moore *et al.* [9] by incorporating discrete time delays in both the accrual of mutualistic benefits and per capita birth rates for each species and analyzing their effects on equilibrium stability and bifurcation phenomena. Specifically, we seek to answer the following key questions:

(1) Under what conditions do delays destabilize mutualistic coexistence?
(2) How do variations in delay magnitude influence system dynamics, potentially leading to periodic oscillations or bistability?
(3) What ecological implications arise from delayed mutualistic responses, particularly in the context of environmental changes?

Alongside the theoretical development, this paper presents *detailed numerical calculations and time-domain simulations* to explain, in detail, the stability landscape of the delayed mutualism model. We compute the coexistence equilibrium and the linearization coefficients, track the characteristic roots to identify critical delay thresholds, map stability regions in the (τ_1, τ_2)-plane, and simulate representative trajectories on both sides of the analytically predicted boundaries. These computations validate the stability criteria derived from the characteristic equation and clarify where the system remains stable and where it transitions to oscillatory behavior. By adapting techniques from Wang *et al.* [11] to our mutualistic framework, we aim to provide insights into how delayed feedback mechanisms shape ecological interactions.

2. The model

The model of interest in this study, which describes the dynamics of two interacting species with mutualistic interactions and self-regulation, modifies the model of mutualism with saturating benefits of Moore *et al.* [9] by allowing for delay in both the accrual of mutualistic benefits and the per capita birth rates for each species, being given as

$$\begin{aligned}\dot{x}_1 &= x_1\left[r_1 + \frac{\gamma_1 x_2(t-\tau_2)}{\delta_1 + x_2(t-\tau_2)} - \mu_1 x_1^{\eta_1} - \nu_1(x_1(t-\tau_1))^{\theta_1}\right]\\ \dot{x}_2 &= x_2\left[r_2 + \frac{\gamma_2 x_1(t-\tau_1)}{\delta_2 + x_1(t-\tau_1)} - \mu_2 x_2^{\eta_2} - \nu_2(x_2(t-\tau_2))^{\theta_2}\right]\end{aligned} \tag{2.1}$$

assuming that both the parameters $r_i, \gamma_i, \delta_i, \mu_i, \nu_i$, $i = 1, 2$ and the exponents η_i, θ_i, $i = 1, 2$ are strictly positive.

Here, the exponents η_i and θ_i control the nature of intraspecific density dependence: values below one correspond to decelerating density dependence, while values above one correspond to accelerating density dependence. For the corresponding model without delays, Moore *et al.* [9] showed that decelerating density dependence enhances the apparent benefits of mutualism but tends to destabilise populations, whereas accelerating density dependence is always stabilising. Allowing η_i and θ_i to depart from one lets us explore how these forms of density dependence interact with discrete delays to influence stability of equilibria.

2.1. The coexistence equilibrium

We start by investigating the feasibility of the coexistence equilibrium $E^* = (x_1^*, x_2^*)$. In this regard, its coordinates should satisfy the steady-state equations:

$$\begin{aligned}r_1 + \frac{\gamma_1 x_2^*}{\delta_1 + x_2^*} - \mu_1(x_1^*)^{\eta_1} - \nu_1(x_1^*)^{\theta_1} &= 0,\\ r_2 + \frac{\gamma_2 x_1^*}{\delta_2 + x_1^*} - \mu_2(x_2^*)^{\eta_2} - \nu_2(x_2^*)^{\theta_2} &= 0.\end{aligned}$$

To prove the existence of E^*, let us define the continuous functions $f_1, f_2 : [0,\infty) \times [0,\infty) \to \mathbb{R}$,

$$\begin{aligned}f_1(x_1, x_2) &= r_1 + \frac{\gamma_1 x_2}{\delta_1 + x_2} - \mu_1(x_1)^{\eta_1} - \nu_1(x_1)^{\theta_1},\\ f_2(x_1, x_2) &= r_2 + \frac{\gamma_2 x_1}{\delta_2 + x_1} - \mu_2(x_2)^{\eta_2} - \nu_2(x_2)^{\theta_2}.\end{aligned}$$

To apply a 2-dimensional version of Poincaré-Miranda theorem, let us consider the rectangle $R = [0, X_1] \times [0, X_2]$, where X_1 and X_2 are yet to be chosen.

For $x_1 = 0$, note that

$$f_1(0, x_2) = r_1 + \frac{\gamma_1 x_2}{\delta_1 + x_2} \geq r_1 > 0, \quad \text{for all } x_2 \in [0, X_2]$$

while for $x_1 = X_1$ one has

$$\begin{aligned}f_1(X_1, x_2) &= r_1 + \frac{\gamma_1 x_2}{\delta_1 + x_2} - \mu_1(X_1)^{\eta_1} - \nu_1(X_1)^{\theta_1}\\ &\leq r_1 + \gamma_1 - \mu_1(X_1)^{\eta_1} - \nu_1(X_1)^{\theta_1}\end{aligned}$$

Since $\lim_{x\to\infty}(\mu_1 x^{\eta_1} + \nu_1 x^{\theta_1}) = \infty$, we may choose $X_1 > 0$ in such a way that $\mu_1(X_1)^{\eta_1} + \nu_1(X_1)^{\theta_1} \geq r_1 + \gamma_1$. Consequently, for $x_1 = X_1$, $f_1(X_1, x_2) \leq 0$ for all $x_2 \in [0, X_2]$ and f_1 changes signs from one vertical side of the rectangle R to the other.

Similarly, for $x_2 = 0$, note that $f_2(x_1, 0) = r_2 + \frac{\gamma_2 x_1}{\delta_2 + x_1} \geq r_2 > 0,\quad$ for all $x_1 \in [0, X_1]$ while for $x_2 = X_2$ one has $f_2(x_1, X_2) = r_2 + \frac{\gamma_2 x_1}{\delta_2 + x_1} - \mu_2(X_2)^{\eta_2} - \nu_2(X_2)^{\theta_2} \leq r_2 + \gamma_2 - \mu_2(X_2)^{\eta_2} - \nu_2(X_2)^{\theta_2}$. Since $\lim_{x\to\infty}(\mu_2 x^{\eta_2} + \nu_2 x^{\theta_2}) = \infty$, we may choose $X_2 > 0$ in such a way that $\mu_2(X_2)^{\eta_2} + \nu_2(X_2)^{\theta_2} \geq r_2 + \gamma_2$. Consequently, for $x_2 = X_2$, $f_2(x_1, X_2) \leq 0$ for all $x_1 \in [0, X_1]$ and f_2 changes signs from one horizontal side of the rectangle R to the other.

We have obtained a rectangle $R = [0, X_1] \times [0, X_2]$ and two continuous functions $f_1, f_2 : [0, \infty) \times [0, \infty) \to \mathbb{R}$ in such a way that $f_1(0, x_2) > 0$, $f_1(X_1, x_2) \leq 0$ for all $x_2 \in [0, X_2]$ and also $f_2(x_1, 0) > 0$, $f_2(x_1, X_2) \leq 0$ for all $x_1 \in [0, X_1]$. A 2-dimensional version of Poincaré-Miranda theorem implies then the existence of $(x_1^*, x_2^*) \in R$ in such a way that $f_1(x_1^*, x_2^*) = f_2(x_1^*, x_2^*) = 0$, that is $E^* = (x_1^*, x_2^*)$ is a coexistence equilibrium. We have consequently obtained the following existence result.

Theorem 2.1. *If both the parameters $r_i, \gamma_i, \delta_i, \mu_i, \nu_i$, $i = 1, 2$ and the exponents η_i, θ_i, $i = 1, 2$ are strictly positive, then the system* (2.1) *admits at least a coexistence equilibrium E^*.*

Note that we have shown the existence of E^*, but not its uniqueness. In the most general situation, it is entirely possible to have multiple coexistence equilibria, as seen via the graphical argument presented in the supplementary online material of Moore *et al.* [9], Figures S3 and S4. However, for the "accelerating" case ($\min\{\eta_i, \theta_i\} \geq 1$, $i \in \{1, 2\}$), it has been shown in Georgescu and Zhang [10, Theorem 7] that the system (2.1) is monotone and the coexistence equilibrium E^* is unique. Still, the existence result presented in Georgescu and Zhang [10] is essentially an outcome of qualitative properties of monotone dynamical systems, while the (entirely different) existence argument presented here is perhaps more transparent.

2.2. Stability by linear approximation

To analyze the stability of E^*, we translate the equilibrium to zero through $y_i(t) = x_i(t) - x_i^*$. The linearization of the new system gives:

$$\dot{y}_1 = a_{11} y_1 + b_{11} y_1(t - \tau_1) + c_{12} y_2(t - \tau_2),$$
$$\dot{y}_2 = a_{22} y_2 + b_{21} y_1(t - \tau_1) + c_{22} y_2(t - \tau_2),$$

where the coefficients are

$$a_{11} = -\mu_1 \eta_1 (x_1^*)^{\eta_1}, \qquad a_{22} = -\mu_2 \eta_2 (x_2^*)^{\eta_2}, \qquad b_{11} = -\nu_1 \theta_1 (x_1^*)^{\theta_1},$$
$$b_{21} = \frac{\gamma_2 \delta_2 x_2^*}{(\delta_2 + x_1^*)^2}, \qquad c_{12} = \frac{\gamma_1 \delta_1 x_1^*}{(\delta_1 + x_2^*)^2}, \qquad c_{22} = -\nu_2 \theta_2 (x_2^*)^{\theta_2}.$$

The stability of E^* is determined by the roots of the characteristic equation:

$$\det\left[\lambda I - A - Be^{-\lambda\tau_1} - Ce^{-\lambda\tau_2}\right] = 0, \qquad A = \begin{bmatrix} a_{11} & 0 \\ 0 & a_{22} \end{bmatrix},\ B = \begin{bmatrix} b_{11} & 0 \\ b_{21} & 0 \end{bmatrix},\ C = \begin{bmatrix} 0 & c_{12} \\ 0 & c_{22} \end{bmatrix}$$

Expanding the above determinant, we obtain:

$$\lambda^2 + (-a_{11} - a_{22})\lambda + a_{11}a_{22} + (-b_{11}\lambda + b_{11}a_{22})e^{-\lambda\tau_1} + (-c_{22}\lambda + c_{22}a_{11})e^{-\lambda\tau_2}$$
$$+ (b_{11}c_{22} - c_{12}b_{21})e^{-\lambda(\tau_1+\tau_2)} = 0. \tag{2.2}$$

We study stability of the coexistence equilibrium under three delay configurations. We find critical delays yielding a Hopf bifurcation.

2.3. Stability in the absence of delays ($\tau_1 = 0, \tau_2 = 0$)

Theorem 2.2 (Local stability in the absence of delays). *Assume that both delays vanish, $\tau_1 = \tau_2 = 0$, and define*

$$a = -a_{11} - a_{22} - b_{11} - c_{22}$$
$$= \mu_1\eta_1(x_1^*)^{\eta_1} + \mu_2\eta_2(x_2^*)^{\eta_2} + \nu_1\theta_1(x_1^*)^{\theta_1} + \nu_2\theta_2(x_2^*)^{\theta_2} > 0,$$
$$b = a_{11}a_{22} + b_{11}a_{22} + c_{22}a_{11} + b_{11}c_{22} - c_{12}b_{21}$$
$$= \Big(\mu_1\eta_1(x_1^*)^{\eta_1} + \nu_1\theta_1(x_1^*)^{\theta_1}\Big)\Big(\mu_2\eta_2(x_2^*)^{\eta_2} + \nu_2\theta_2(x_2^*)^{\theta_2}\Big) - \frac{\gamma_1\delta_1x_1^*}{(\delta_1+x_2^*)^2}\cdot\frac{\gamma_2\delta_2x_2^*}{(\delta_2+x_1^*)^2}$$

If b is greater than 0, the equilibrium is locally asymptotically stable.

Proof. When $\tau_1 = \tau_2 = 0$, the characteristic equation simplifies to the quadratic equation

$$\lambda^2 + a\,\lambda + b = 0.$$

By the Routh–Hurwitz criterion for second-degree polynomials, both roots have negative real parts if and only if $a > 0$ and $b > 0$. □

If $b > 0$, then without delays the coexistence equilibrium is locally asymptotically stable, but since x_1^*, x_2^* are rarely explicit and depend implicitly on parameters. $b > 0$ is generally not verifiable *a priori* and is hard to interpret. In the "accelerating" case ($\min\{\eta_i, \theta_i\} \geq 1$), a more transparent outcome is possible; it is seen that:

$$\Big(\eta_1\mu_1(x_1^*)^{\eta_1} + \theta_1\nu_1(x_1^*)^{\theta_1}\Big)\Big(\eta_2\mu_2(x_2^*)^{\eta_2} + \theta_2\nu_2(x_2^*)^{\theta_2}\Big) \geq$$
$$\geq \Big(\mu_1(x_1^*)^{\eta_1} + \nu_1(x_1^*)^{\theta_1}\Big)\Big(\mu_2(x_2^*)^{\eta_2} + \nu_2(x_2^*)^{\theta_2}\Big) =$$
$$= \left(r_1 + \frac{\gamma_1x_2^*}{\delta_1+x_2^*}\right)\left(r_2 + \frac{\gamma_2x_1^*}{\delta_2+x_1^*}\right) > \frac{\gamma_1\gamma_2x_1^*x_2^*}{(\delta_1+x_2^*)(\delta_2+x_1^*)} > \frac{\gamma_1\delta_1x_1^*}{(\delta_1+x_2^*)^2}\cdot\frac{\gamma_2\delta_2x_2^*}{(\delta_2+x_1^*)^2},$$

which means that condition $b > 0$ holds, leading to the idea that higher exponents promote both the uniqueness and the stability of the coexistence equilibrium.

2.4. Stability with a single delay ($\tau_2 = 0, \tau_1 > 0$)

Theorem 2.3 (Stability with a single delay). *With the above notations, suppose that $b > 0$ (so that E^* is locally asymptotically stable for $\tau_1 = \tau_2 = 0$), $\tau_2 = 0$ and $\tau_1 > 0$. Let α_1 and α_2 denote the quantities*

$$\alpha_1 = (a_{11} + a_{22} + c_{22})^2 - 2\big(a_{11}a_{22} + c_{22}a_{11}\big) - b_{11}^2,$$
$$\alpha_2 = \big(a_{11}a_{22} + c_{22}a_{11}\big)^2 - \big(b_{11}a_{22} + b_{11}c_{22} - c_{12}b_{21}\big)^2.$$

If $\alpha_1 > 0$ and $\alpha_2 > 0$, then the equilibrium E^* remains locally asymptotically stable for all $\tau_1 > 0$. If $\alpha_1 < 0$ or $\alpha_2 > 0$, it is possible to exist a critical delay τ_{1k} at which a Hopf bifurcation occurs and stability is lost.

Proof. For $\tau_2 = 0$, the characteristic equation can be written in the form

$$\lambda^2 + (D_1 + D_5)\lambda + (D_2 + D_6) + (D_3\lambda + D_4 + D_7)e^{-\lambda\tau_1} = 0. \tag{2.3}$$

where we define

$$\begin{aligned} &D_1 := -a_{11} - a_{22}, \quad D_2 := a_{11}a_{22}, \quad D_3 := -b_{11}, \quad D_4 := b_{11}a_{22}, \\ &D_5 := -c_{22}, \quad D_6 := c_{22}a_{11}, \quad D_7 := b_{11}c_{22} - c_{12}b_{21}. \end{aligned} \tag{2.4}$$

As an outcome of the hypotheses, E^* is locally asymptotically stable for $\tau_1 = 0$. Then stability can be lost only if the roots of the characteristic equation cross the imaginary axis as τ_1 grows. To see when a purely imaginary root can appear, suppose that $\lambda = i\omega$ and substitute in (2.3). Expanding, one gets:

$$\begin{aligned} &-\omega^2 + (D_1 + D_5)(i\omega) + (D_2 + D_6) + +iD_3\omega\cos(\omega\tau_1) - i^2 D_3\omega\sin(\omega\tau_1) + \\ &+D_4\cos(\omega\tau_1) - iD_4\sin(\omega\tau_1) + D_7\cos(\omega\tau_1) - iD_7\sin(\omega\tau_1) = 0. \end{aligned}$$

The real part equals zero, so

$$-\omega^2 + (D_2 + D_6) + (D_4 + D_7)\cos(\omega\tau_1) + D_3\omega\sin(\omega\tau_1) = 0.$$

and the imaginary part equals zero too, so

$$\omega(D_1 + D_5) + D_3\omega\cos(\omega\tau_1) - (D_4 + D_7)\sin(\omega\tau_1) = 0.$$

The following system is obtained

$$\begin{cases} (D_4 + D_7)\cos(\omega\tau_1) + D_3\omega\sin(\omega\tau_1) = \omega^2 - (D_2 + D_6) \\ -(D_4 + D_7)\sin(\omega\tau_1) + D_3\omega\cos(\omega\tau_1) = -\omega(D_1 + D_5) \end{cases} \tag{2.5}$$

When both sides are squared, one obtains

$$\begin{aligned} &(D_4 + D_7)^2\cos^2(\omega\tau_1) + 2(D_4 + D_7)D_3\omega\cos(\omega\tau_1)\sin(\omega\tau_1) + D_3^2\omega^2\sin^2(\omega\tau_1) \\ &\quad = \omega^4 - 2\omega^2(D_2 + D_6) + (D_2 + D_6)^2 \\ &(D_4 + D_7)^2\sin^2(\omega\tau_1) - 2(D_4 + D_7)D_3\omega\sin(\omega\tau_1)\cos(\omega\tau_1) + D_3^2\omega^2\cos^2(\omega\tau_1) \\ &\quad = \omega^2(D_1 + D_5)^2. \end{aligned}$$

Adding those equations up gives

$$(D_4 + D_7)^2 + D_3^2\omega^2 = \omega^4 - 2\omega^2(D_2 + D_6) + (D_2 + D_6)^2 + \omega^2(D_1 + D_5)^2,$$

leading to the following equation for ω

$$\omega^4 + \omega^2\left[(D_1 + D_5)^2 - 2(D_2 + D_6) - D_3^2\right] + (D_2 + D_6)^2 - (D_4 + D_7)^2 = 0,$$

that is

$$\omega^4 + \alpha_1\omega^2 + \alpha_2 = 0 \tag{2.6}$$

with

$$\begin{aligned} \alpha_1 &= (D_1 + D_5)^2 - 2(D_2 + D_6) - D_3^2, \\ \alpha_2 &= (D_2 + D_6)^2 - (D_4 + D_7)^2 \end{aligned}$$

If $\alpha_1 > 0$ and $\alpha_2 > 0$, then equation (2.6) has no real roots, so the stability that holds for $\tau_1 = 0$ is preserved for all $\tau_1 > 0$. Substituting the values for D_i one gets

$$\alpha_1 = \big(-(a_{11}+a_{22}) - c_{22}\big)^2 - 2\big(a_{11}a_{22} + c_{22}a_{11}\big) - b_{11}^2,$$
$$\alpha_2 = \big(a_{11}a_{22} + c_{22}a_{11}\big)^2 - \big(b_{11}a_{22} + b_{11}c_{22} - c_{12}b_{21}\big)^2.$$

□

Remark

$$\alpha_1 = \Big(\mu_1\eta_1\,(x_1^*)^{\eta_1} + \mu_2\eta_2\,(x_2^*)^{\eta_2} + \nu_2\,\theta_2\,(x_2^*)^{\theta_2}\Big)^2 - 2\Big(\mu_1\eta_1\,(x_1^*)^{\eta_1}\,\mu_2\eta_2\,(x_2^*)^{\eta_2} + \nu_2\,\theta_2\,(x_2^*)^{\theta_2}\,\mu_1\eta_1\,(x_1^*)^{\eta_1}\Big) - \big[\nu_1\,\theta_1\,(x_1^*)^{\theta_1}\big]^2.$$

For $\alpha_1 > 0$ to hold, the following inequality must then be satisfied:

$$\nu_1^2\,\theta_1^2\,(x_1^*)^{2\theta_1} \;<\; \mu_1^2\eta_1^2\,(x_1^*)^{2\eta_1} + \mu_2^2\eta_2^2\,(x_2^*)^{2\eta_2} + \nu_2^2\,\theta_2^2\,(x_2^*)^{2\theta_2} + 2\,\mu_2\eta_2\,\nu_2\,\theta_2\,(x_2^*)^{\eta_2+\theta_2} \tag{2.7}$$

One also sees that $\alpha_2 = b\big(a_{11}a_{22}+c_{22}a_{11}-b_{11}a_{22}-b_{11}c_{22}+c_{12}b_{21}\big)$ and consequently for $\alpha_2 > 0$ to hold, the following inequality needs to be satisfied

$$\begin{aligned}\mu_2\eta_2\,(x_2^*)^{\eta_2} + \nu_2\,\theta_2\,(x_2^*)^{\theta_2}\big] + \frac{\gamma_1\,\delta_1\,x_1^*}{(\delta_1+x_2^*)^2}\,\frac{\gamma_2\,\delta_2\,x_2^*}{(\delta_2+x_1^*)^2} \\ >\; \nu_1\,\theta_1\,(x_1^*)^{\theta_1}\,\big[\mu_2\eta_2\,(x_2^*)^{\eta_2} + \nu_2\,\theta_2\,(x_2^*)^{\theta_2}\big].\end{aligned} \tag{2.8}$$

Note that if $\mu_1\eta_1\,(x_1^*)^{\eta_1} > \nu_1\,\theta_1\,(x_1^*)^{\theta_1}$ (that is, if for the first species the non-delayed self-regulation dominates the delayed self-regulation in absolute slopes computed at E^*), then both conditions (2.7) and (2.8) hold and E^* remains locally asymptotically stable for all $\tau_1 > 0$. That is, in a loose sense, dominated delay slopes help preserve stability. Note that conditions (2.7) and (2.8) lack symmetry since we are dealing with an *a priori* asymmetric situation, the case in which only one of the delays is 0.

If conditions (2.7) or (2.8) are not satisfied, a positive solution ω of (2.6) can exist and then, considering (2.5) as a system with unknowns $X = \cos\omega\tau_1, Y = \sin\omega\tau_1$, one can solve for X (for instance), as $X = \dfrac{\Delta X}{\Delta}$ where

$$\Delta = \begin{vmatrix} b_{11}a_{22} + b_{11}c_{22} - c_{12}b_{21} & -\omega b_{11} \\ -\omega b_{11} & -b_{11}a_{22} - b_{11}c_{22} + c_{12}b_{21} \end{vmatrix}$$

$$\Delta X = \begin{vmatrix} \omega^2 - a_{11}a_{22} - a_{11}c_{22} & -\omega b_{11} \\ \omega(a_{11}+a_{22}) + c_{22}\omega & -b_{11}a_{22} - b_{11}c_{22} + c_{12}b_{21} \end{vmatrix}.$$

The instability thresholds are then given as $\tau_{1k} = \pm\frac{1}{\omega}\left(\arccos\frac{\Delta X}{\Delta} + 2k\pi\right)$. To analyze the impact of the delay τ_1 on the stability of E^*, we differentiate the characteristic equation, which is now:

$$\begin{aligned}0 = \lambda^2 + (-a_{11} - a_{22})\,\lambda + a_{11}a_{22} + \big(-b_{11}\lambda + b_{11}a_{22}\big)e^{-\lambda\tau_1} \\ + \big(-c_{22}\lambda + c_{22}a_{11}\big) + \big(b_{11}c_{22} - c_{12}b_{21}\big)e^{-\lambda\tau_1}\end{aligned} \tag{2.9}$$

with respect to τ_1. Since $\lambda = \lambda(\tau_1)$ is implicitly a function of τ_1, this leads to:

$$\frac{d\lambda}{d\tau_1}\Big[2\lambda - (a_{11}+a_{22}) - c_{22} - \tau_1 e^{-\lambda\tau_1}(-b_{11}\lambda + b_{11}a_{22}) - \tau_1 e^{-\lambda\tau_1}(b_{11}c_{22} - c_{12}b_{21})\Big] \tag{2.10}$$

$$= (b_{11}a_{22} - b_{11}\lambda)e^{-\lambda\tau_1}\lambda + (b_{11}c_{22} - c_{12}b_{21})e^{-\lambda\tau_1}\lambda,$$

that is,

$$\frac{d\lambda}{d\tau_1} = \frac{(b_{11}a_{22} - b_{11}\lambda)e^{-\lambda\tau_1}\lambda + (b_{11}c_{22} - c_{12}b_{21})e^{-\lambda\tau_1}\lambda}{2\lambda - (a_{11} + a_{22}) - c_{22} - \tau_1 e^{-\lambda\tau_1}(-b_{11}\lambda + b_{11}a_{22}) - \tau_1 e^{-\lambda\tau_1}(b_{11}c_{22} - c_{12}b_{21})} \tag{2.11}$$

The sign of the above derivative, computed at the threshold values τ_{1k}, determines the rate of change of the eigenvalue λ with respect to τ_1, which is crucial for stability analysis. The stability of E^* depends on the sign of $\frac{d\lambda}{d\tau_1}(\tau_{1k})$.

2.5. Stability with two delays ($\tau_1 > 0$ fixed, $\tau_2 > 0$)

Theorem 2.4 (Stability with two delays)**.** *Fix $\tau_1 > 0$ such that the coexistence equilibrium E^* is locally asymptotically stable for $\tau_2 = 0$. As $\tau_2 > 0$ varies, stability can be lost only if the characteristic equation* (2.2) *admits purely imaginary roots $\lambda = \pm i\omega$ for some $\omega > 0$. If no such ω exists, then E^* remains locally asymptotically stable for all $\tau_2 > 0$. Otherwise, there exist critical delays τ_{2k} at which Hopf bifurcations occur* [14, 15].

In what follows, we look for the value of the critical delay τ_2. Let $\tau_1 > 0$ be fixed. Suppose that the stability holds for $\tau_2 = 0$ and look for a pure imaginary root that might lead to instability. Using the characteristic equation (2.2), it is seen that a root $\lambda = i\omega$ verifies:

$$- \omega^2 - i\omega(a_{11} + a_{22}) + a_{11}a_{22} - i\omega c_{22}(\cos\omega\tau_2 - i\sin\omega\tau_2) +$$
$$a_{11}c_{22}(\cos\omega\tau_2 - i\sin\omega\tau_2) - i\omega b_{11}(\cos\omega\tau_1 - i\sin\omega\tau_1) + +a_{22}b_{11}(\cos\omega\tau_1 - i\sin\omega\tau_1)$$
$$+ (b_{11}c_{22} - c_{12}b_{21})\left[\cos\omega(\tau_1 + \tau_2) - i\sin\omega(\tau_1 + \tau_2)\right] = 0$$

Separation of real and imaginary parts, respectively, leads to the following system of equations:

$$\begin{aligned} &- \omega^2 + a_{11}a_{22} - \omega c_{22}\sin\omega\tau_2 + a_{11}c_{22}(\cos\omega\tau_2) - \omega b_{11}\sin\omega\tau_1) + a_{22}b_{11}cos\omega\tau_1 \\ &\quad - (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1\cos\omega\tau_2 - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1\sin\omega\tau_2) = 0 \end{aligned} \tag{2.12}$$

$$\begin{aligned} &- \omega(a_{11} + a_{22}) - \omega c_{22}cos\omega\tau_2 - a_{11}c_{22}\sin\omega\tau_2 - \omega b_{11}\cos\omega\tau_1 - a_{22}b_{11}\sin\omega\tau_1 \\ &\quad - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1\cos\omega\tau_2 - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_2\cos\omega\tau_1 = 0 \end{aligned} \tag{2.13}$$

We denote $\tilde{X} = \cos\omega\tau_2, \quad \tilde{Y} = \sin\omega\tau_2$ Then (2.12) and (2.13) lead to the system

$$\begin{cases} (a_{11}c_{22} + (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1)\tilde{X} + (-\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1)\tilde{Y} \\ \qquad = \omega^2 - a_{11}a_{22} + b_{11}\omega\sin\omega\tau_1 - a_{22}b_{11}\cos\omega\tau_1, \\ \\ (-\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1)\tilde{X} + (-a_{11}c_{22} - (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1)\tilde{Y} \\ \qquad = \omega(a_{11} + a_{22}) + \omega b_{11}\cos\omega\tau_1 + a_{22}b_{11}\sin\omega\tau_1 \end{cases}$$

As done above, we see that

$$\cos\omega\tau_2 = \frac{\Delta_{\tilde{X}}}{\Delta}, \quad \sin\omega\tau_2 = \frac{\Delta_{\tilde{Y}}}{\Delta},$$

$$\Delta = \begin{vmatrix} a_{11}c_{22} + (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1 & -\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1 \\ -\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1 & -a_{11}c_{22} - (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1 \end{vmatrix}$$

$$\Delta_{\tilde{X}} = \begin{vmatrix} \omega^2 - a_{11}a_{22} + b_{11}\omega\sin\omega\tau_1 - a_{22}b_{11}\cos\omega\tau_1 & -\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1 \\ \omega(a_{11} + a_{22}) + \omega b_{11}\cos\omega\tau_1 + a_{22}b_{11}\sin\omega\tau_1 & -a_{11}c_{22} - (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1 \end{vmatrix}$$

$$\Delta_{\tilde{Y}} = \begin{vmatrix} a_{11}c_{22} + (b_{11}c_{22} - c_{12}b_{21})\cos\omega\tau_1 & \omega^2 - a_{11}a_{22} + b_{11}\omega\sin\omega\tau_1 - a_{22}b_{11}cos\omega\tau_1 \\ -\omega c_{22} - (b_{11}c_{22} - c_{12}b_{21})\sin\omega\tau_1 & \omega(a_{11} + a_{22}) + \omega b_{11}\cos\omega\tau_1 + a_{22}b_{11}\sin\omega\tau_1 \end{vmatrix}$$

Since

$$\cos^2\omega\tau_2 + \sin^2\omega\tau_2 = 1 \Rightarrow \Delta_{\tilde{X}}^2 + \Delta_{\tilde{Y}}^2 = \Delta^2,$$

one can eventually solve $\omega\tau_2 = \pm\arccos\frac{\Delta_{\tilde{X}}}{\Delta} + 2k\pi$ and obtain possible thresholds of stability as $\tau_{2k} = \pm\frac{1}{\omega}\left(\arccos\frac{\Delta_X}{\Delta} + 2k\pi\right)$.

To analyze the stability of the system, we differentiate the characteristic equation with respect to τ_2. Writing it as $F(\lambda, \tau_2) = 0$ (with τ_1 fixed) and using $\dfrac{d\lambda}{d\tau_2} = -\dfrac{F_{\tau_2}}{F_\lambda}$, we obtain:

$$\frac{d\lambda}{d\tau_2} = \frac{c_{22}\lambda e^{-\lambda\tau_2} + \big(b_{11}c_{22} - c_{12}b_{21}\big)\lambda e^{-\lambda(\tau_1+\tau_2)}}{\begin{array}{c} 2\lambda + (-a_{11} - a_{22}) - \tau_1 e^{-\lambda\tau_1}\big(-b_{11}\lambda + b_{11}a_{22}\big) \\ -\,\tau_2 e^{-\lambda\tau_2}\big(-c_{22}\lambda + c_{22}a_{11}\big) - (\tau_1+\tau_2)e^{-\lambda(\tau_1+\tau_2)}\big(b_{11}c_{22} - c_{12}b_{21}\big) \end{array}} \tag{2.14}$$

This derivative is to be evaluated at the threshold values τ_{2k} in order to determine the rate of change of the eigenvalue λ with respect to τ_2, which is essential for stability analysis.

3. Numerical calculations and simulations

We start with the following parameter set, used for illustrative purposes in Georgescu and Zhang [10] for the corresponding model without delays:

$$\begin{gathered} \delta_1 = \delta_2 = 4, \quad \eta_1 = \eta_2 = 1.5, \quad \theta_1 = \theta_2 = 2, \gamma_1 = \gamma_2 = 4, \\ \mu_1 = \mu_2 = 0.5, \quad \nu_1 = \nu_2 = 0.5, r_1 = r_2 = 2. \end{gathered} \tag{3.1}$$

Solving the system of equilibrium conditions

$$2 + \frac{4x_2}{4 + x_2} - 0.5x_1^{1.5} - 0.5x_1^2 = 0, \quad 2 + \frac{4x_1}{4 + x_1} - 0.5x_2^{1.5} - 0.5x_2^2 = 0$$

we obtain the coordinates of the positive equilibrium: $x_1^* = x_2^* = 1.968822$ Accordingly, the coefficients of the linearized system are

$$\begin{aligned} &a_{11} = a_{22} = -2.071910590, \quad b_{11} = -3.876260855, \quad b_{21} = 0.8841973232 \\ &c_{12} = 0.8841973232, \quad c_{22} = -3.876260855 \end{aligned}$$

and we use the auxiliary quantities $D_1, \ldots, D_7$ defined in (2.4).

The characteristic equation is: $\omega^4 + 24.64815881\,\omega^2 - 344.28642 = 0$, with the positive root $\omega = 3.154486$. Also,

$$\cos(\omega\tau_1) = -0.56097748, \quad \tau_1 = \frac{\arccos(-0.56097748)}{3.154486} \approx 0.686756.$$

With τ_1 fixed, $\tau_1 = 0.686756$, we now try to find the critical value of the delay τ_2. Define

$$A(\omega) := a_{11}c_{22} + D_7\cos(\omega\tau_1), \tag{3.2}$$

$$B(\omega) := \omega\, c_{22} + D_7\sin(\omega\tau_1). \tag{3.3}$$

Set the τ_2-auxiliaries (using the same notational pattern as in the τ_1 step, but with τ_1 substituted inside the trigonometric terms):

$$\Delta_2(\omega) := -\big(A(\omega)\big)^2 - \big(B(\omega)\big)^2, \tag{3.4}$$

$$\Delta_2^X(\omega) := -A(\omega)\Big(\omega^2 - a_{11}a_{22} + \omega b_{11}\sin(\omega\tau_1) - a_{22}b_{11}\cos(\omega\tau_1)\Big) + B(\omega)\Big(\omega(a_{11}+a_{22}) + \omega b_{11}\cos(\omega\tau_1) + a_{22}b_{11}\sin(\omega\tau_1)\Big), \tag{3.5}$$

$$\Delta_2^Y(\omega) := A(\omega)\Big(\omega(a_{11}+a_{22}) + \omega b_{11}\cos(\omega\tau_1) + a_{22}b_{11}\sin(\omega\tau_1)\Big) + \Big(\omega^2 - a_{11}a_{22} + \omega b_{11}\sin(\omega\tau_1) - a_{22}b_{11}\cos(\omega\tau_1)\Big)\, B(\omega). \tag{3.6}$$

The frequency $\omega > 0$ at which a pair of roots crosses the imaginary axis while τ_1 is fixed and τ_2 varies, is obtained by solving:

$$\big(\Delta_2(\omega)\big)^2 = \big(\Delta_2^X(\omega)\big)^2 + \big(\Delta_2^Y(\omega)\big)^2\ . \tag{3.7}$$

Numerically, (3.7) admits the positive solution $\omega_2 = 2.87426$. Evaluating (3.2)–(3.6) at $\omega = \omega_2$ gives

$$\Delta_2(\omega_2) = -9.81492, \qquad \Delta_2^X(\omega_2) = 7.34809, \qquad \Delta_2^Y(\omega_2) = -6.50679.$$

Hence $\frac{\Delta_2^X(\omega_2)}{\Delta_2(\omega_2)} = -0.748665$, $\arccos\Big(\frac{\Delta_2^X(\omega_2)}{\Delta_2(\omega_2)}\Big) = 2.41684$. Using the same cosine step as in the computation of τ_1, the critical delays form the family

$$\tau_2^{(m)} = \frac{2\pi m + \arccos\big(\Delta_2^X(\omega_2)/\Delta_2(\omega_2)\big)}{\omega_2}, \qquad m = 0, 1, 2, \dots \tag{3.8}$$

and the smallest positive (principal) branch is

$$\tau_2 \equiv \tau_2^{(0)} = \frac{2.41684}{2.87426} = 0.840857. \tag{3.9}$$

The next branch is $\tau_2^{(1)} = \frac{2\pi + 2.41684}{2.87426} = 3.02688$. For $\tau_1 = 0.686756$ and the coefficients in (3.1), the second-delay Hopf threshold is obtained for $\omega_2 = 2.87426$, so $\tau_2 = 0.840857$, with higher branches given by (3.8). We simulated in MATLAB (`dde23`) the two-delay mutualism system as follows:

Simulation setup. Parameters: $r_i = 2$, $\gamma_i = 4$, $\mu_i = \nu_i = 0.5$, $\eta_i = 1.5$, $\theta_i = 2$, $\delta_i = 4$, $(\tau_1, \tau_2) = (0.6, 0.7)$, with `lags=[`$\tau_1$`,`$\tau_2$`]`. Equilibrium E^*: solve the steady-state system with `vpasolve` to obtain $E^* = (x_1^*, x_2^*)$; here $x_1^* \approx x_2^* \approx 1.9688$. Equilibrium check: set the history buffer $Z_{eq} = [x_1^*, x_2^*;\ x_1^*, x_2^*]$ and verify $\dot{x}(E^*, Z_{eq}) \approx 0$. Simulations: two runs on $[0, 10]$: (i) history $x \equiv E^*$; (ii) history $x \equiv E^* + \varepsilon$, $\varepsilon = 10^{-4}$ (both components). Tolerances: `RelTol` $= 10^{-6}$, `AbsTol` $= 10^{-8}$. Plots: plot $x_i(t)$

and the reference line x_i^* for $i = 1, 2$. RHS implementation: in `dde_system`, use $x_1(t - \tau_1) = Z(1, 1)$, $x_2(t - \tau_2) = Z(2, 2)$.

For $(\tau_1, \tau_2) = (0.6, 0.7)$ and a very small constant perturbation of the history, the trajectories in Fig. 1 show that $x_1(t)$ and $x_2(t)$ stay close to $x_i^* \approx 1.9688$, with only small, nearly sinusoidal oscillations and no visible amplitude growth on $[0, 10]$. Further cases (different amplitudes and delays) are shown in Fig. 2.

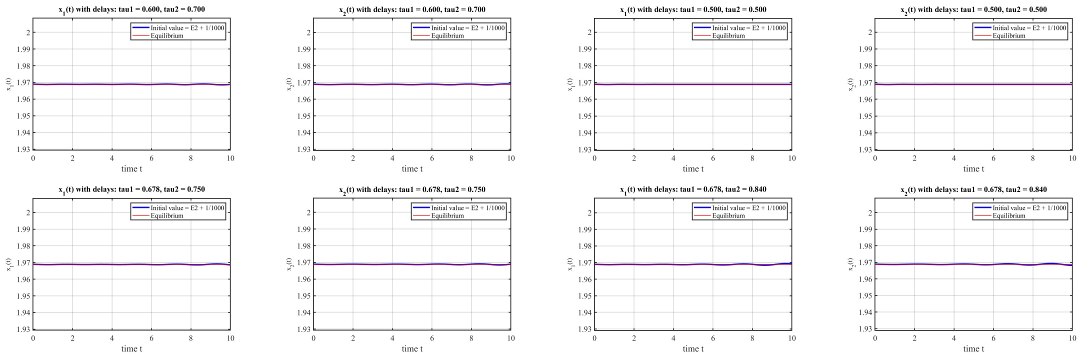

FIGURE 1. Time series and phase-plane plots for system (2.1) under representative delays and small perturbations (Section 4).

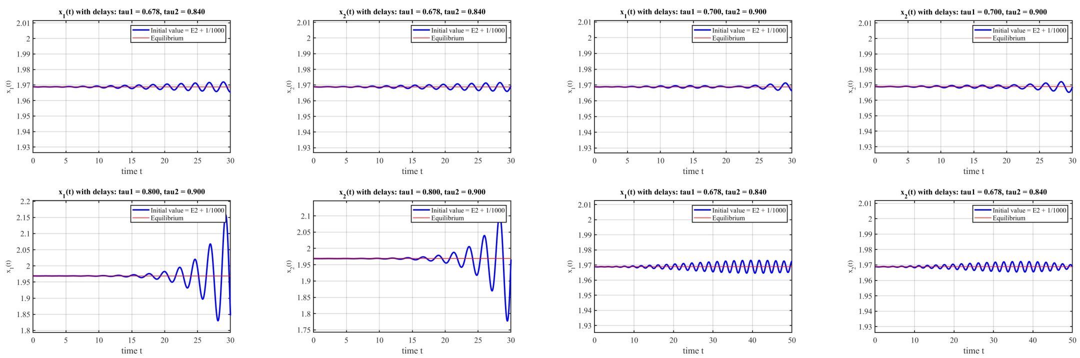

FIGURE 2. Additional simulations illustrating the effects of delays and perturbation amplitude.

Conclusion

We analyzed how discrete delays affect the local stability of the coexistence equilibrium in a two–species mutualism model with nonlinear density dependence. Extending the saturating-benefit framework of Moore *et al.* [9] (see also Georgescu and Zhang [10]) by introducing delays in mutualistic feedback and in per-capita birth terms, we derived explicit, algebraic stability and Hopf-bifurcation criteria from the characteristic equation. In the zero-delay case, stability reduces to the usual Routh–Hurwitz conditions.

When one delay is fixed and the other varies, stability can be lost through a Hopf bifurcation when a conjugate pair of characteristic roots crosses the imaginary axis; for the illustrative parameter set we obtain the smallest thresholds $\tau_1 \approx 0.6868$ and $\tau_2 \approx 0.8409$. These delay-induced oscillations are consistent with phenomena reported in other delayed ecological models (Wang *et al.* [11], Smith [13]). Ecologically, the results emphasize that response lags (e.g. maturation or resource-renewal times) can shift a system from stable coexistence to persistent oscillations (Hale and Verduyn Lunel [12], Smith [13]).

Density dependence modulates this effect: decelerating feedbacks may amplify mutualistic benefits but reduce robustness to delays (Moore *et al.* [9]), whereas accelerating feedbacks strengthen self-regulation and can mitigate delay-driven instability (Moore *et al.* [9]). Future work could address asymmetric or higher-dimensional mutualistic networks and alternative functional responses.

REFERENCES

[1] Bronstein, J. L. (1994). Our current understanding of mutualism. *Quarterly Review of Biology*, 69(1), 31–51.

[2] Vander Wall, S., Barga, S. & Seaman, A. (2017). The geographic distribution of seed-dispersal mutualisms in North America. *Evolutionary Ecology*, 31, 725-740.

[3] Richman, S., Irwin, R., Nelson, C. , & Bronstein, J. (2017). Facilitated exploitation of pollination mutualisms: fitness consequences for plants. *Journal of Ecology*, 188-196.

[4] Trager, M., Bhotika, S., Hostetler, J., Andrade, G., Rodriguez-Cabal, M., Seabird McKeon, C., Osenberg, C., Bolker, B. (2010). Benefits for plants in ant-plant protective mutualisms: a meta-analysis. *PLoS One* 5, e14308.

[5] Hale, K., & Valdovinos, F. (2021). Ecological theory of mutualism: Robust patterns of stability and thresholds in two-species population models, Ecology and Evolution 11, 17651-17671.

[6] Vargas-De-León, C. (2012). Lyapunov functions for two-species cooperative systems, *Applied Mathematics and Computation* 219, 2493-2497.

[7] Georgescu, P., Zhang, H., & Maxin, D. (2016). The global stability of coexisting equilibria for three models of mutualism, *Mathematical Biosciences and Engineering*, 13, 101-118.

[8] Georgescu, P., & Zhang, H. (2024). Global stability of coexistence equilibria for n-species models of facultative mutualism. *Journal of Theoretical Biology*, 595, Article ID 111961.

[9] Moore, C. M., Catella, S. A., & Abbott, K. C. (2018). Population dynamics of mutualism and intraspecific density dependence: How θ-logistic density dependence affects mutualistic positive feedback. *Ecological Modelling*, 368, 191–197.

[10] Georgescu, P., & Zhang, H. (2023). Facultative mutualisms and θ-logistic growth: how larger exponents promote global stability of co-existence equilibria. *Mathematics* 11, Article ID 4373.

[11] Wang, X., Kottegoda, C., Shan, C., & Huang, Q. (2024). Oscillations and coexistence generated by discrete delays in a two-species competition model. *Discrete and Continuous Dynamical Systems - Series B*, 29(4), 1798–1814.

[12] Hale, J.K., & Verduyn Lunel, S.M. (1993). *Introduction to Functional Differential Equations.* Applied Mathematical Sciences, Vol. 99. New York, NY: Springer.

[13] Smith, H.L. (2011). *An Introduction to Delay Differential Equations with Applications to the Life Sciences*. Springer.

[14] Hassard, B.D., Kazarinoff, N.D., & Wan, Y.H. (1981). *Theory and Applications of Hopf Bifurcation.* Cambridge University Press.

[15] Kuznetsov, Y.A. (2004). *Elements of Applied Bifurcation Theory* (3rd ed.). Springer.