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INTERACTION OF DIFFUSION AND DELAY

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Abstract. For reaction-diffusion equations with delay, the joint effects of diffusion and delay are studied. In particular, for two-dimensional systems where only the interaction between species is delayed, the interdependence of stability against delay and against diffusion (Turing instability) can be clearly exhibited. Turing instabilities occur largely independent of delay. But periodic oscillations, constant in space or with low spatial frequency, can be achieved via increasing the delay or changing the diffusion rates.

1. **Introduction.** There are several mechanisms leading to bifurcations and to the emergence of spatio-temporal patterns in biological models. The most prominent among these are the Turing diffusive instability, in other context called activator/inhibitor mechanism (see, e.g. Gierer and Meinhardt [7], Hadeler [8], Levin and Segel [17], Murray [19], Okubo [20], Prigogine and Lefever [21], Ruan [22], Turing [27], etc.), and the instability caused by a delayed feedback loop (see Diekmann et al. [3], Hale and Verduyn Lunel [10] and the references therein, in particular to the early work of R. Nussbaum). Recently, reaction-diffusion equations with delay have been studied extensively. For example, Morita [18] and de Oliveira [4] have performed thorough studies of periodic solutions of diffusion equations with delay, Faria [5] and Freitas [6] investigate bifurcations in such problems. We refer to the monograph of Wu [28] for an introduction of the fundamental theory of such equations and related references on these equations.

The present note is devoted to the study, within the framework of linear or linearized systems, of the joint effects of the Turing mechanism and a delayed feedback.

In Sections 2 and 3 we recall the essentials on stable matrices and Turing instability. In Section 4 we study general delay systems, and in Section 5 we introduce a class of problems with delay restricted to the interaction of different species. In connection with these systems we introduce a notion of strong stability with respect to delay and discuss its relation to the Turing phenomenon. In Section 6 we study

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delayed diffusion equations, and in Section 7 we consider in detail delayed reaction-diffusion systems with the special type of interaction just mentioned. For this class of problems we get a complete scenario of possible instabilities. As an example, in Section 8 we apply our results to a diffusive predator-prey system with delay.

2. **Stable matrices.** Turing instability in reaction-diffusion systems can be recast in terms of matrix stability (see, for example, Cross [2], Hershkowitz [12], Satnoianu et al. [24], Satnoianu and van den Driessche [25], etc.). In this section, we review some results on stability of real matrices, which will be used throughout the paper.

Definition 1. Let A be a real $n \times n$ matrix.

- **(i):** A is said to be *stable* if all eigenvalues of A are located in the open left half-plane of the complex plane.
- **(ii):** A is said to be *strongly stable* (with respect to diffusion) if $A - D$ is stable for any nonnegative diagonal matrix D.
- **(iii):** A is said to be *excitable* (with respect to diffusion) if A is stable but not strongly stable.

Of course a strongly stable matrix is also stable. Also, for an excitable matrix A there is always a choice of D such that $A - D$ is unstable.

The problem of characterizing all strongly stable matrices, for $n \geq 4$, is yet unsolved (in spite of Satnoianu et al. [24], see also Satnoianu and van den Driessche [25]). A complete characterization, in terms of inequalities on the minors of A, has been given by Cross [2] for $n = 2$ and $n = 3$. For $n = 2$, denote

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}. \tag{1}$$

There are the following results.

Lemma 1. *The 2×2 matrix A defined in* (1) *is strongly stable if the following conditions holds:*

$$a_{11} + a_{22} < 0, \tag{2}$$

$$a_{11}a_{22} - a_{12}a_{21} > 0, \tag{3}$$

$$a_{11} \leq 0, \quad a_{22} \leq 0. \tag{4}$$

A is excitable if (2), (3) *and*

$$a_{11} > 0 \quad \text{or} \quad a_{22} > 0. \tag{5}$$

Therefore, for $n = 2$, there are two possible sign patterns of excitable matrices

$$A_1 = \begin{pmatrix} + & - \\ + & - \end{pmatrix}, \quad A_2 = \begin{pmatrix} + & + \\ - & - \end{pmatrix}. \tag{6}$$

3. **Reaction-diffusion systems – Turing instability.** In a Turing system there are several species $u = (u_1, \ldots, u_n)$ which interact according to some ordinary differential equations

$$\dot{u} = f(u). \tag{7}$$

We consider small deviations $\bar{u} + u$ from a hyperbolic equilibrium $\bar{u}$. Linearizing the equation at the equilibrium $\bar{u}$, we obtain

$$\dot{u} = Au, \tag{8}$$

where $A = f'(\bar{u})$ is the Jacobian. The exponential stability of the equilibrium $\bar{u}$ of the nonlinear system (7) is equivalent to the exponential stability of the zero solution of the linear system (8), which in turn is equivalent to the stability of the matrix A.

Now assume that the species u_i diffuses with a diffusion rate $d_i > 0$. Then we have a system of coupled reaction-diffusion equations

$$u_t = f(u) + D\Delta u, \tag{9}$$

where $D = (d_i \delta_{ij})$ is the diagonal matrix of diffusion rates and Δ is the Laplacian acting componentwise on the vector u. Thus, the linearized system reads

$$u_t = Au + D\Delta u. \tag{10}$$

Now consider the case of space dimension $n = 1$ and a bounded interval $[0, l]$ with zero Neumann boundary conditions. A Fourier ansatz

$$u(t, x) = \mathrm{Re} \sum \hat{u}_k e^{ik\pi x/l + \lambda_k t} \tag{11}$$

leads to the characteristic equation

$$\det(A - \mu D - \lambda I) = 0, \tag{12}$$

where

$$\mu = \frac{k^2 \pi^2}{l^2}. \tag{13}$$

Thus, if A is strongly stable, then $u = 0$ is a stable solution of equation (10) for any choice of D, l, and any mode k. If A is excitable, there is a choice of D and l such that at least one mode k is unstable.

In the case when $n = 2$, the sign pattern of an excitable matrix A_1 given in (6) corresponds to an activator-inhibitor dynamics. The matrix $D = (d_i \delta_{ij})$ which leads to destabilization can be characterized by an inequality for the quotient d_2/d_1 (see Hadeler [8] and Murray [19]),

$$\frac{d_2}{d_1} > \frac{1}{a_{11}^2} (\sqrt{\det A} + \sqrt{-a_{12} a_{21}})^2. \tag{14}$$

Thus, the zero solution becomes unstable (for some l and k) if a short range activator interacts with a long range inhibitor. This can be summarized as follows.

Proposition 2. *Suppose that A, with $n = 2$, is excitable. If the diffusion matrix D is chosen so that condition* (14) *is satisfied, then Turing instability occurs in system* (9) *for modes μ in some open interval depending on the a_{ij} and the d_i.*

In the sequel we consider, together with the matrix A, the matrix

$$\tilde{A} = \begin{pmatrix} -a_{11}^2 & a_{12}^2 \\ a_{21}^2 & -a_{22}^2 \end{pmatrix}. \tag{15}$$

Lemma 3. *Let A be excitable with respect to diffusion. Then*

$$\mathrm{tr}\tilde{A} < 0, \quad \det \tilde{A} < 0. \tag{16}$$

Proof. $a_{11} = a_{22} = 0$ contradicts (2), hence $\mathrm{tr}\tilde{A} < 0$. In view of (2) and (5) we have $a_{11}a_{22} < 0$. From (3) it follows that $a_{12}a_{21} < 0$, $|a_{11}a_{22}| < |a_{12}a_{21}|$, and thus $\det \tilde{A} < 0$. ☐

On the other hand, $\det \tilde{A} > 0$ does not hold for all strongly stable matrices.

4. **Delay systems – stability and bifurcation.** In this section, we study the dynamics of delay differential equations.

4.1. **The general system.** Consider the delay system

$$\dot{u}(t) = g(u(t), u(t-\tau)) \tag{17}$$

with $g : \mathbb{R}^n \times \mathbb{R}^n \to \mathbb{R}^n$ at some stationary solution $\bar{u} \in \mathbb{R}^n$; i.e., $g(\bar{u}, \bar{u}) = 0$. Assume $n = 1$. Linearizing the equation and denoting $\nu = -\partial g(u, v)/\partial u$, $\alpha = -\partial g(u, v)/\partial v$ at this solution, we get the equation

$$\dot{u}(t) = -\nu u(t) - \alpha u(t-\tau). \tag{18}$$

An exponential ansatz leads to the characteristic equation

$$\lambda + \nu + \alpha e^{-\lambda\tau} = 0. \tag{19}$$

The behavior of this characteristic equation, depending on three parameters α, ν, τ, has been described in detail (Hayes [11], Bellman and Cooke [1], Hadeler and Tomiuk [9]). The stability domain is a curvilinear wedge bounded by two curves,

$$\nu + \alpha \geq 0, \quad \tau\alpha \leq \varphi(\tau\nu), \tag{20}$$

where $\varphi : [1, \infty) \to [-1, \infty)$ is some function which increases from -1 to ∞. Stability can be lost by either leaving the stability domain through $\nu + \alpha = 0$ (one characteristic root going through the origin) or by leaving the domain by violation of $\tau\alpha \leq \varphi(\tau\nu)$ (in which case two complex conjugate roots cross the imaginary axis). This latter case can be interpreted as a Hopf bifurcation caused by a delayed feedback control.

Now assume $n \geq 2$. Linearizing the system (17) at some stationary solution yields the standard linear problem (see Hale and Verduyn Lunel [10])

$$\dot{u}(t) = Au(t) + Bu(t-\tau), \tag{21}$$

where A and B are constant quadratic matrices of order n. The characteristic equation is

$$\det(A + Be^{-\lambda\tau} - \lambda I) = 0 \tag{22}$$

where A, B are matrices of order n. The characteristic equation has not been studied in general. Special cases are mostly related to scalar second order differential delay equations. One general statement is related to positivity: Let $A = 0$ and let B generate a positive semigroup ($b_{ij} \geq 0$ for $i \neq j$). If the zero solution is stable for $\tau = 0$, then it is stable for $\tau > 0$. A similar result holds even in infinite dimensions (see Kerscher and Nagel [14, 15]).

4.2. **A system of two equations.** We specialize to a case where something more concrete can be said. We assume that the interactions within a species are instantaneous but that interactions between species are delayed. We consider (21) with $n = 2$, $A = (a_{ij})$, $B = (b_{ij})$, and

$$a_{12} = a_{21} = 0, \quad b_{11} = b_{22} = 0. \tag{23}$$

Notice that if we restrict to this case of only two species, then the case of distinct delays is formally equivalent to the case of equal delays. Indeed,

$$\begin{pmatrix} \dot{u}_1(t) \\ \dot{u}_2(t) \end{pmatrix} = \begin{pmatrix} a_{11} & 0 \\ 0 & a_{22} \end{pmatrix} \begin{pmatrix} u_1(t) \\ u_2(t) \end{pmatrix} + \begin{pmatrix} 0 & b_{12} \\ b_{21} & 0 \end{pmatrix} \begin{pmatrix} u_1(t-\tau_1) \\ u_2(t-\tau_2) \end{pmatrix}$$

leads to the characteristic equation

$$\lambda^2 - (a_{11} + a_{22})\lambda + a_{11}a_{22} - b_{12}b_{21}e^{-\lambda\tau} = 0 \tag{24}$$

with $\tau = \tau_1 + \tau_2$. We introduce the matrix

$$C = A + B = \begin{pmatrix} a_{11} & b_{12} \\ b_{21} & a_{22} \end{pmatrix}, \tag{25}$$

which plays the role of the matrix A in (8).

Definition 2. Let C be a 2×2 matrix as in (25) and let C be stable. The matrix is called *strongly stable with respect to delay* if for all $\tau \geq 0$ all roots λ of the characteristic equation (24) have strictly negative real parts. The matrix C is called *excitable with respect to delay* if it is stable but not strongly stable with respect to delay.

Proposition 4. *Assume a matrix $C = A + B$ as in (25). The following are equivalent:*

(i): *C is strongly stable with respect to delay.*
(ii): *C is stable and*

$$|a_{11}a_{22}| \geq |b_{12}b_{21}|. \tag{26}$$

Proof. For $\tau = 0$ all roots of the characteristic equation (24) have negative real parts. By continuity and Rouché's theorem, the following are equivalent,

i): For all $\tau \geq 0$, equation (24) has only roots with negative real parts.
ii): For all $\tau \geq 0$, equation (24) has no purely imaginary roots.

Equation (24) has a pair of purely imaginary roots $\pm i\omega$ if and only if ω satisfies

$$-\omega^2 - i(a_{11} + a_{22})\omega + a_{11}a_{22} - b_{12}b_{21}(\cos 2\omega\tau + i \sin 2\omega\tau) = 0.$$

Separating the real and imaginary parts gives

$$\omega^2 - a_{11}a_{22} = -b_{12}b_{21} \cos 2\omega\tau, \tag{27}$$

$$(a_{11} + a_{22})\omega = -b_{12}b_{21} \sin 2\omega\tau. \tag{28}$$

Adding up the squares of both equations gives

$$\omega^4 + (a_{11}^2 + a_{22}^2)\omega^2 + a_{11}^2 a_{22}^2 - b_{12}^2 b_{21}^2 = 0. \tag{29}$$

Solving for ω^2 in (29), we obtain two real roots $\omega_1^2 \geq \omega_2^2$, with $\omega_2^2 \leq 0$,

$$\omega_{1,2}^2 = \frac{1}{2}\big[- (a_{11}^2 + a_{22}^2) \pm \sqrt{(a_{11}^2 + a_{22}^2)^2 - 4(a_{11}^2 a_{22}^2 - b_{12}^2 b_{21}^2)}\big]. \tag{30}$$

Equation (29) has a positive real root ω if and only if $\omega_1^2 > 0$. In other words, if (26) holds then both ω_1^2 and ω_2^2 are negative, equation (29) has no positive real root. Hence all roots of equation (24) have negative real parts. The converse is now evident. □

Proposition 5. *Let C be strongly stable with respect to delay. Then C is strongly stable with respect to diffusion.*

Proof. Take squares on both sides of (26) and apply Lemma 3. □

Within the class of stable matrices introduce $X = a_{11}a_{22}$ and $Y = b_{12}b_{21}$. Then stability with respect to diffusion corresponds to $X \geq 0$ and stability with respect to delay corresponds to $|X| \geq |Y|$. These relations can be visualized as sectors in an (X, Y) plane as follows.

I=: $\{X > Y,\ X \geq 0,\ X \geq |Y|$: strongly stable with respect to diffusion and delay$\}$;

II=: $\{X > Y,\ X \geq 0,\ X < |Y|$: strongly stable with respect to diffusion, but excitable with respect to delay$\}$;
III=: $\{X > Y,\ X \leq 0$: excitable with respect to diffusion and delay$\}$;
IV=: $\{X \leq Y$: not stable$\}$.

The next result shows in which manner the delay causes instability if the matrix C is not strongly stable with respect to delay.

Proposition 6. *Suppose that the matrix C is excitable with respect to delay. There is a critical value $\tau_0 > 0$ for the delay,*

$$\tau_0 = \frac{1}{2\omega_1}\arccos\frac{a_{11}a_{22} - \omega_1^2}{b_{12}b_{21}}, \tag{31}$$

with ω_1^2 given by (30)*, such that the zero solution of system* (21) *is asymptotically stable when $\tau \in [0, \tau_0)$ and unstable when $\tau > \tau_0$.*

Proof. If C is excitable with respect to delay, according to Lemma 3, $-(a_{11}^2 + a_{22}^2) < 0$, $a_{11}^2 a_{22}^2 - b_{12}^2 b_{12}^2 < 0$. Then ω_1^2 is positive. Hence, equation (24) has a pair of purely imaginary roots $\pm i\omega_1$ whenever the delay τ takes certain values, say $\tau_j > 0$. These critical values can be determined from equation (27) (or (28)) and are given by

$$\tau_j = \frac{1}{2\omega_1}\arccos\frac{a_{11}a_{22} - \omega_1^2}{b_{12}b_{21}} + \frac{j\pi}{\omega_1}, \quad j = 0, 1, 2, ...$$

Let $\lambda(\tau) = \alpha(\tau) \pm i\omega(\tau)$ be the roots of equation (25) such that

$$\alpha(\tau_j) = 0, \quad \omega(\tau_j) = \omega_1.$$

At each value τ_j we can verify the transversality condition

$$\frac{d}{d\tau}\mathrm{Re}\lambda(\tau)\Big|_{\tau=\tau_j} = \frac{d}{d\tau}\alpha(\tau)\Big|_{\tau=\tau_j} > 0. \tag{32}$$

By continuity and Rouché's theorem, there are eigenvalues with positive real parts whenever $\tau > \tau_0$, and a Hopf bifurcation occurs at $\tau = \tau_0$. This completes the proof. □

With appropriate conditions on the nonlinearity, the system of the form (17) with linearization (21) undergoes a Hopf bifurcation at $\tau = \tau_0$; that is, a family of periodic solutions bifurcates from the zero solution when τ passes through the critical value τ_0.

5. **Delayed reaction-diffusion systems.**

Now we join reaction, diffusion and delay into one model (see Wu [28] for examples). This could be done in various complicated fashions.

5.1. **The general system.**

First we restrict ourselves to a single delay and assume that the delay and diffusion act independently.

$$u_t(t, x) = g(u(t, x), u(t - \tau, x)) + Du_{xx}(t, x). \tag{33}$$

Then the linearized equation reads

$$u_t(t, x) = Au(t, x) + Bu(t - \tau, x) + Du_{xx}(t, x). \tag{34}$$

As before, we get a family of characteristic matrix eigenvalue problems

$$(A + Be^{-\lambda\tau} - \mu D - \lambda I)u = 0$$

and the characteristic equation

$$\det(A + Be^{-\lambda\tau} - \mu D - \lambda I) = 0. \tag{35}$$

Here μ is the Fourier mode, as given in (13). If diffusion is absent, $D = 0$, then we get (22). If the delay is absent, $\tau = 0$, then we get (12) with A replaced by $C = A + B$.

Even with this generality, something interesting can be observed. We keep the matrices A and B fixed. We assume that the non-delayed well-stirred problem ($\tau = 0$, $D = 0$) is stable, i.e., the matrix $A + B$ is stable. Suppose that by variation of parameters D or τ a characteristic value passes through the origin of the complex plane at some $D = d_0$, $\tau = \tau_0$. Then, we have a root $\lambda = 0$. But for $\lambda = 0$ equation (35) reduces to

$$\det(A + B - \mu D) = 0,$$

i.e., to the characteristic equation of the non-delayed problem. Therefore, the problem without delay also has an eigenvalue zero. Hence we have found:

Proposition 7. *If, upon variation of the parameters, the delayed problem exhibits a Turing instability, then the non-delayed problem shows a Turing instability for the same set of parameters.*

Thus, the matrix $A + B$ must be excitable with respect to diffusion in order that a Turing instability should occur for any value of τ. Of course, the system can, upon variation of parameters, undergo a Hopf bifurcation before a Turing instability occurs (see the following).

5.2. **The system of two equations.** Let $n = 2$ and A and B satisfy (23); i.e., we consider a combination of the systems described above:

$$\begin{pmatrix} u_{1t}(t) \\ u_{2t}(t) \end{pmatrix} = \begin{pmatrix} a_{11} & 0 \\ 0 & a_{22} \end{pmatrix} \begin{pmatrix} u_1(t) \\ u_2(t) \end{pmatrix} + \begin{pmatrix} 0 & b_{12} \\ b_{21} & 0 \end{pmatrix} \begin{pmatrix} u_1(t-\tau_1) \\ u_2(t-\tau_2) \end{pmatrix} + \begin{pmatrix} d_1 u_{1xx} \\ d_2 u_{2xx} \end{pmatrix}. \tag{36}$$

Define, for fixed $\mu \geq 0$, the matrix

$$\hat{C} = \begin{pmatrix} \hat{a}_{11} & b_{12} \\ b_{21} & \hat{a}_{22} \end{pmatrix} \tag{37}$$

with

$$\hat{a}_{11} = a_{11} - \mu d_1, \quad \hat{a}_{22} = a_{22} - \mu d_2. \tag{38}$$

We see that $\hat{C} = C - \mu D$. The characteristic equation of (36) can be written as

$$\lambda^2 - (\hat{a}_{11} + \hat{a}_{22})\lambda + \hat{a}_{11}\hat{a}_{22} - b_{12}b_{21}e^{-\lambda\tau} = 0, \tag{39}$$

where $\tau = \tau_1 + \tau_2$. Notice that if $\mu = 0$, then $\hat{C} = C$ and equation (39) reduces to equation (24).

5.2.1. *C in sector I.* Suppose the matrix C is strongly stable with respect to delay (Sector I). Then C is strongly stable with respect to diffusion, and also the matrix $\hat{C}$ is strongly stable with respect to diffusion according to Definition 1 (if any matrix A has this property, then $A - D$ as well). But we have a stronger property, since $\hat{C}$ is also in Sector I.

Proposition 8. *Suppose the matrix C defined by* (24) *is strongly stable with respect to delay. Then the matrix $\hat{C}$ defined by* (37) *is strongly stable with respect to delay.*

Proof. Lemma 3 says that C is strongly stable with respect to diffusion, hence $a_{11} \leq 0$, $a_{22} \leq 0$. Therefore, $\hat{a}_{11}\hat{a}_{22} \geq a_{11}a_{22} \geq |b_{11}b_{22}|$. ∎

5.2.2. *C in sector II.* Now assume that C is strongly stable with respect to diffusion, but excitable with respect to delay. Then $b_{12}b_{21} \leq 0$. Then $\hat{C}$ is still strongly stable with respect to diffusion, but need not be strongly stable with respect to delay. For large μ the matrix $\hat{C}$ is strongly stable with respect to delay.

Proposition 9. *Assume C is strongly stable with respect to diffusion, but excitable with respect to delay. Let d_1 and d_2 be fixed and let μ_0 be the nonnegative root of the equation*

$$(a_{11} - \mu d_1)(a_{22} - \mu d_2) = |b_{12}b_{21}|. \tag{40}$$

Then for $\mu \geq \mu_0$ the matrix $\hat{C}$ is strongly stable with respect to delay. For $\mu < \mu_0$ the matrix $\hat{C}$ is excitable with respect to delay and there is a critical value $\hat{\tau}_0 = \hat{\tau}_0(\mu)$,

$$\hat{\tau}_0(\mu) = \frac{1}{2\hat{\omega}_1} \arccos \frac{\hat{a}_{11}\hat{a}_{22} - \hat{\omega}_1^2}{b_{12}b_{21}} \tag{41}$$

with

$$\hat{\omega}_1^2 = \frac{1}{2}\left[-(\hat{a}_{11}^2 + \hat{a}_{22}^2) + \sqrt{(\hat{a}_{11}^2 + \hat{a}_{22}^2)^2 - 4(\hat{a}_{11}^2\hat{a}_{22}^2 - b_{12}^2 b_{21}^2)} \right], \tag{42}$$

such that the zero solution of system (34) *is stable when $\tau \in [0, \hat{\tau}_0)$ and unstable when $\tau > \hat{\tau}_0$. A Hopf bifurcation occurs when $\tau = \hat{\tau}_0$.*

Proof. The proof follows from Definition 2 and Proposition 6, applied to the matrix $\hat{C}$ instead of C. □

Of course, this Hopf bifurcation can also be obtained upon variation of μ rather than of τ.

Proposition 9 says that a stable matrix of class II can lead to an oscillatory instability which is either diffusion-driven or delay-induced.

5.2.3. *C in sector III.* If the matrix C is excitable with respect to diffusion, then many different scenarios are possible.

Suppose the delay induces oscillations via Hopf bifurcation first and suppose that the bifurcating periodic solutions are stable. Now the diffusion can drive the spatially homogeneous stable periodic solutions to instability and the system could exhibit spatio-temporal patterns via Hopf and Turing mechanisms. In fact, the work of Morita [18] and de Oliveira [4] (see also Faria [5] and Freitas [6]) shows that spatially homogeneous stable oscillations can undergo Turing-like bifurcations.

Suppose the system undergoes Turing instability for some modes k with a bifurcation curve, say $\mathbb{T}$. Suppose the system also exhibits a Hopf bifurcation for some parameter values τ with a bifurcation curve, say $\mathbb{H}$. Then at the intersection points of the two bifurcation curves $\mathbb{T}$ and $\mathbb{H}$ in the $[k, \tau]-$plane, the system can undergo the so-called *Turing-Hopf bifurcation* (see Kidachi [16], Just et al. [13], Scheel [26]) and exhibit complex spatio-temporal patterns.

Of course these cannot be studied in the present framework and deserve further investigation.

5.2.4. *Remarks.* Summarizing the analysis we can say that for the case of two reactants and the delay restricted to the interaction between the two reactants, the possible bifurcation scenarios at a homogeneous equilibrium have been clarified. The essential result is a hierarchy of notions of stability where strong stability with respect to delay is the most restrictive assumption. Depending on the manner these assumptions are relaxed, various bifurcations are possible. In loose terms one can say that a Turing instability is there (or is not there) right from the onset of a delay.

A Hopf bifurcation can occur even in strongly stable systems under the influence of diffusion, but then it is restricted to lower modes.

6. **A diffusive predator-prey model with delay.** In this section, as an example we consider a diffusive predator-prey system with a single delay in the predator equation. Let Ω be an open bounded set in $R^N (N \le 3)$ with boundary $\partial\Omega$. Let $u(t,x)$ and $v(t,x)$ denote the densities of the prey and predator populations, respectively, at the time t and location x. Consider

$$\frac{\partial u}{\partial t} = d_1 \Delta u + u(t,x) g(u(t,x)) - v(t,x) p(u(t,x)), \tag{43}$$

$$\frac{\partial v}{\partial t} = d_2 \Delta v + v(t,x)[-d(v(t,x)) + cp(u(t-\tau,x))] \tag{44}$$

with the Neumann boundary value conditions

$$\frac{\partial u}{\partial n} = \frac{\partial v}{\partial n} = 0 \ \text{ on } \ \partial\Omega \tag{45}$$

and initial value conditions

$$u(\theta,x) = \phi(\theta,x) \ge 0, \ \ v(0,x) = \psi(x) \ge 0, \ \ \theta \in [-\tau,0), \ \ x \in \Omega. \tag{46}$$

We assume that the coefficient functions g, p, d are continuously differentiable and that ϕ and ψ are continuous.

The function $g(u)$ is the specific growth of the prey population in the absence of predators, it satisfies $g(0) > 0, g'(u) < 0$ and there exists a $K > 0$ such that $g(K) = 0$. A prototype is the logistic growth function $g(u) = r(1 - u/K)$.

$p(u)$ is the functional response function, it satisfies $p(0) = 0, p'(u) > 0$. An example is the Michaelis-Menten or Holling type II function $p(u) = mu/(a+u)$.

$d(v)$ is the death rate of the predator population with $d(0) > 0, d'(v) > 0$. The function $d(v) = d + ev$ satisfies the assumptions.

If $\Omega = (0,l)^N$ is a cube then we can argue as in (13). Denote the positive steady state of system (43),(44) by $E^* = (u^*, v^*)$. The Jacobian C at E^* takes the form (25) with

$$a_{11} = g(u^*) + u^* g'(u^*) - v^* p'(u^*) > 0, \tag{47}$$

$$b_{12} = -p(u^*) < 0, \tag{48}$$

$$b_{21} = cv^* p'(u^*) > 0, \tag{49}$$

$$a_{22} = -v^* d'(v^*) < 0. \tag{50}$$

In a standard situation, its elements have the signs indicated in (47)-(50), and $a_{11} + a_{22} < 0$, $a_{11}a_{22} - b_{12}b_{21} > 0$. Thus, C is excitable with respect to diffusion, and it has the sign pattern of A_1 in (6).

First we consider system (43),(44) with $\tau = 0$. By the results of section 3, if the matrix defined by (47) is excitable with respect to diffusion and if the diffusion rates d_1 and d_2 are chosen so that (14), with $a_{12} = b_{12}$ and $a_{21} = b_{21}$, holds, then Turing instability occurs in system (43),(44) with $\tau = 0$ for modes μ in some open interval depending on $a_{11}, a_{22}, b_{12}, b_{21}, d_1$ and d_2.

Now let d_1, d_2 and μ be fixed so that the matrix $\hat{C}$ is excitable with respect to delay; that is, $\hat{C}$ is stable and

$$(a_{11} - \mu d_1)^2 (a_{22} - \mu d_2)^2 < b_{12}^2 b_{21}^2.$$

Then there is a critical value $\hat{\tau}_0$ of the delay,

$$\hat{\tau}_0(\mu) = \frac{1}{\hat{\omega}_1}\arccos\frac{\hat{a}_{11}\hat{a}_{22} - \hat{\omega}_1^2}{b_{12}b_{21}}$$

with $\hat{\omega}_1^2$ given by (42), such that the steady state E^* of system (43),(44) is asymptotically stable when $\tau \in [0, \hat{\tau}_0)$ and unstable when $\tau > \hat{\tau}_0$. A Hopf bifurcation occurs at the steady state E^* when the delay τ passes through $\hat{\tau}_0$.

On the other hand, one can show that a Hopf bifurcation can occur at the steady state E^* when the delay τ passes through a critical value τ_0 while the diffusion coefficients $d_1 = d_2 = 0$. Suppose the bifurcating periodic solutions are stable. Following the techniques of Morita [18] and de Oliveira [4], one can also show that the diffusion can induce Turing type instability for the spatially homogeneous stable periodic solutions and the delayed diffusive predator-prey model (43)-(44) can exhibit spatio-temporal patterns.

It would be very interesting to study the degenerate Turing-Hopf bifurcation in the delayed diffusive predator-prey model (43)-(44), i.e., when the Turing instability and Hopf bifurcation occur simultaneously.

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REFERENCES

[1] R. Bellman and K. L. Cooke, "Differential-Difference Equations," Academic Press, New York, 1963.

[2] G. W. Cross, *Three types of matrix stability*, Lin. Alg. Appl., **20** (1978), 253-263.

[3] O. Diekmann, S. A. van Gils, S. M. Verduyn Lunel and H.-O. Walther, "'Delay Equations: Functional-, Complex-, and Nonlinear Analysis," Springer-Verlag, New York, 1995.

[4] L. A. F. de Oliveira, *Instability of homogeneous periodic solutions of parabolic-delay equations*, J. Differential Equations, **109** (1994), 42-76.

[5] T. Faria, *Bifurcation aspects for some delayed population models with diffusion*, Fields Institute Communications, **21**(1999), 143-158.

[6] P. Freitas, *Some results on the stability and bifurcation of stationary solutions of delay-diffusion equations*, J. Math. Anal. Appl., **206** (1997), 59-82.

[7] A. Gierer and H. Meinhardt, *A theory of biological pattern formation*, Kybernetik, **12** (1972), 30-39.

[8] K. P. Hadeler, *Periodic wave trains from Hopf bifurcation*, Nonlinear Times Digest, **1** (1994), 1-8.

[9] K. P. Hadeler and J. Tomiuk, *Periodic solutions of difference-differential equations*, Arch. Ration. Mech. Anal., **65** (1977), 87-95.

[10] J. K. Hale and S. M. Verduyn Lunel, "Introduction to Functional Differential Equations," Springer-Verlag, New York, 1993.

[11] N. Hayes, *Roots of the transcendental equation associated to a certain difference-differential equation*, J. London Math. Soc., **25** (1950), 226-232.

[12] D. Hershkowitz, *Recent directions in matrix stability*, Lin. Alg. Appl., **171** (1992), 161-186.

[13] W. Just, M. Bose, S. Bose, H. Engel and E. Schöll, *Spatiotemporal dynamics near a supercritical Turing-Hopf bifurcation in a two-dimensional reaction-diffusion system*, Physical Rev. E, **64** (2001), 026219-1–026219-12.

[14] W. Kerscher and R. Nagel, *Asymptotic behavior of one-parameter semigroups of positive operators*, Acta Appl. Math. **2** (1984), 297-309.

[15] W. Kerscher and R. Nagel, *Positivity and stability for Cauchy problems with delay*, in "Partial Differential Equations", Proc. Lat. Am. Sch. Math. ELAM-8, Rio de Janeiro, 1986, Lect. Notes Math. **1324** (1988), 216-235.

[16] H. Kidachi, *On mode interactions in reaction-diffusion equation with nearly degenerate bifurcations*, Prog. Theoret. Phy., **63** (1980), 1152-1169.

[17] S. A. Levin and L. A. Segel, *Pattern generation in space and aspect*, SIAM Reviews, **27** (1985), 45-67.

[18] Y. Morita, *Destabilization of periodic solutions arising in delay-diffusion systems in several space dimensions*, Japan J. Appl. Math., **1** (1984), 39-65.

[19] J. D. Murray, "Mathematical Biology," Springer-Verlag, Berlin, 1989.

[20] A. Okubo, "Diffusion and Ecological Problems: Mathematical Models," Springer-Verlag, Berlin, 1980.

[21] I. Prigogine and R. Lefever, *Symmetry breaking instability in dissipative systems, II*, J. Chem. Phys., **48** (1968), 1665-1700.

[22] S. Ruan, *Diffusion-driven instability in the Gierer-Meinhardt model of morphogenesis*, Natural Resource Modelling, **11** (1998), 131-142.

[23] S. Ruan, *Turing instability and travelling waves in diffusive plankton models with delayed nutrient recycling*, IMA J. Appl. Math., **60**(1998).

[24] R. A. Satnoianu, M. Menzinger and P. K. Maini, *Turing instabilities in general systems*, J. Math. Biol. **41** (2000), 493-512.

[25] R. A. Satnoianu and P. van den Driessche, *Some remarks on matrix stability with application to Turing instability*, Lin. Alg. Appl., **398** (2005), 69-74.

[26] A. Scheel, *Radially symmetric patterns of reaction-diffusion systems*, Mem. Amer. Math. Soc., **165** (2003), pp86.

[27] A. M. Turing, *The chemical basis of morphogenesis*, Phil. Trans. Royal Soc. B, **237**(1952), 37-72.

[28] J. Wu, "Theory and Applications of Partial Functional Differential Equations," Springer-Verlag, New York, 1996.

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