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BIFURCATIONS AND TURING INSTABILITIES IN REACTION-DIFFUSION SYSTEMS WITH TIME-DEPENDENT DIFFUSIVITIES

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Abstract

A class of two-component,one-dimensional, reaction-diffusion systems of the type usually found in Ecology are analysed in order to establish the qualitative behaviour of solutions. It is shown that for diffusivities in the form $D_j = d_j + b_j cos(\omega t + \phi)$, relationships can be derived from which amplitude destabilisation can be assessed depending on the wavenumber k and the variable diffusion coefficients, specially the frequency ω. Therefore time-dependent diffusivities can control the Turing instability mechanism. The analysis is performed using Floquet's Theory. Numerical simulations for various kinetics are presented, and bifurcation diagrams in the plane (k, ω) are obtained.

AMS CLASSIFICATIONS: 35K57

1 Introduction

In many ecological and environmental problems it is common to find mathematical models involving reaction-diffusion systems:

$$\frac{\partial X_j}{\partial t} = F_j(\mathbf{X}) + D_j \Delta X_j$$

where $\mathbf{X} = (X_1, X_2, ..., X_n)^t$ is a n-dimensional vector of real-valued functions depending on time and k spatial variables. D_j stands for the j-th diffusivity or diffusion coefficient. The state variables X_j are most currently interpreted as concentrations or (bio)masses. Δ stands for the k-dimensional spatial laplacian operator, and the nonlinear reaction terms $F_j(\mathbf{X})$ model the interaction between the n species. On the other hand, diffusive terms can be considered as describing the ability of the various species X_j to occupy different zones in k-dimensional space either by some native transport device or through the action of small-scale mechanisms not involving advection . There is no relationship between k and n. See [Okubo 1980] for extensive examples.

The simplest case corresponds to $n = k = 1$. If a logistic reaction term is employed, the well known Fisher equation arises, see e.g. [Murray 1989] and references therein:

$$\frac{\partial X}{\partial t} = \alpha X(1 - X) + D\frac{\partial^2 X}{\partial x^2}$$

For $k = 1$ and $n = 2$ there exists a broad class of problems ranging from predator-prey models to morphogenetic ones. Reduction to $k = 1$ is a way of simplifying complicated problems by taking avantage of say, symmetries. In the rest of the study only systems of this type will be considered:

$$\frac{\partial X_j}{\partial t} = F_j(\mathbf{X}) + D_j\frac{\partial^2 X_j}{\partial x^2}\ ,\ j = 1, 2$$

In this paper it will be shown that for certain nonlinear reaction-diffusion systems with time dependent diffusivities amplitude instabilities can appear in a way somehow different to the usual Turing instability. Let $X_1(x,t)$ and $X_2(x,t)$ represent the concentrations of the two species, defined in the product set $\Omega \times \mathbb{R}^+$ of an open real interval Ω and the positive time axis, excluding 0. Moreover, adequate side conditions must be imposed at the boundaries of the spatio-temporal domain.

As a starting point for the theoretical analysis, spatially homogeneous distributions of both species are supposed on the interval Ω, thus leaving only the reaction terms:

$$\frac{\partial X_j}{\partial t} = F_j(\mathbf{X}) \qquad (j = 1, 2)$$

The presence of the diffusive terms describes both species varying their concentrations along Ω, and the diffusion coefficients $D_j > 0$ are allowed to depend on time Gourley *et al.* 1996]:

$$\frac{\partial X_j}{\partial t} = F_j(\mathbf{X}) + D_j\frac{\partial^2 X_j}{\partial x^2} \qquad (j = 1, 2)$$

$$D_j(t) = d_j + b_j \cos(\omega_j t + \phi_j) \qquad (j = 1, 2)$$

where $\phi_1 = 0$, and $d_j \geq b_j$. The d_j represent the native diffusion properties of the species, whereas the b_j reflect the impact of environmental conditions modifying the basic pattern described by the d_j. As a rule, interesting behaviours appear when $d_j \simeq b_j$. It is rather natural to take $\omega_1 = \omega_2 = \omega$, where this common frequency reflects the presence of environmental cycles in the joint evolution of the species. The delay or phase ϕ is introduced in order to simulate the mutual adaptive ability of the species, a more realistic assumption than postulating an instantaneous response. Nevertheless, it plays little or no role in the mathematical analyses to follow.

2 Stability analyses.

According to the classical Turing theory [Turing 1952] (see also [Satnoianu *et al.* 2000]) the reaction terms must describe a spatially homogeneous system with a stable singular point $\mathbf{X}_0 = (X_{01}, X_{02})$ in the first orthant, such that the system can be linearised about this point. This is equivalent to:

a) Positivity of the components of $\mathbf{X}_0$. This depends on the particular choice of the reaction terms –also called the kinetics– F_j.

b) Stability conditions for $\mathbf{X}_0$. These conditions, under the assumption of the system being linearisable at $\mathbf{X}_0$, amount to $tr\mathbf{J}_0 < 0$ and $\det \mathbf{J}_0 > 0$, where

$$\mathbf{J}_0 = [a_{jk}] = \begin{bmatrix} \dfrac{\partial F_1}{\partial X_1} & \dfrac{\partial F_1}{\partial X_2} \\ \dfrac{\partial F_2}{\partial X_1} & \dfrac{\partial F_2}{\partial X_2} \end{bmatrix} (\mathbf{X}_0)$$

is the jacobian matrix of the F_j at $\mathbf{X}_0$. For instance, the standard Lotka-Volterra reaction terms:

$$\frac{\partial X_1}{\partial t} = aX_1 - b_1 X_1 X_2 = F_1(\mathbf{X})$$
$$\frac{\partial X_2}{\partial t} = -cX_2 + b_2 X_1 X_2 = F_2(\mathbf{X})$$

will not give rise to a reaction-diffusion system of this type because $tr\mathbf{J}_0 = 0$ and the singular point $\left(\dfrac{c}{b_2}, \dfrac{a}{b_1}\right)$ is a center. Therefore these cases will be excluded and only appropriate kinetics will be dealt with. Linearisation about the singular point applies to the spatially inhomogeneous system as well, yielding:

$$\begin{bmatrix} \dfrac{\partial X_1^*}{\partial t} \\ \dfrac{\partial X_2^*}{\partial t} \end{bmatrix} = \begin{bmatrix} \dfrac{\partial F_1}{\partial X_1} & \dfrac{\partial F_1}{\partial X_2} \\ \dfrac{\partial F_2}{\partial X_1} & \dfrac{\partial F_2}{\partial X_2} \end{bmatrix}_{\mathbf{X}_0} \begin{bmatrix} X_1^* \\ X_2^* \end{bmatrix} + \begin{bmatrix} D_1 & 0 \\ 0 & D_2 \end{bmatrix} \begin{bmatrix} \dfrac{\partial^2 X_1^*}{\partial x^2} \\ \dfrac{\partial^2 X_2^*}{\partial x^2} \end{bmatrix}$$

where

$$X_j^*(t,x) = X_j(t,x) - X_{0j}, \quad (j = 1,2)$$

The classical *ansatz* $X_j^*(t,x) = a_j(t)e^{ikx}$ is now introduced, meaning that the selected spatial shape of the solutions is e^{ikx}, where the wavenumbers k are parameters to be identified later on. Plugging these expressions in the linearised spatially inhomogeneous system, a differential system for the time evolution of the amplitudes $a_j(t)$ in the neighbourhood of $\mathbf{X}_0$ is obtained:

$$\frac{d\mathbf{a}}{dt} = \frac{d}{dt}\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} = \begin{bmatrix} a_{11} - k^2 D_1 & a_{12} \\ a_{21} & a_{22} - k^2 D_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} = \mathbf{A}(k)\mathbf{a}$$

If the diffusion coefficients are time-dependent, just substitute $D_j(t) = d_j + b_j \cos(\omega t + \phi_j)$ for D_j in the matrix $\mathbf{A}(k)$. If both $b_j = 0$, then $D_j(t) = d_j$, implying that there are no cyclic enviromental influences modifying the native diffusive properties of the species. This case can be called a *basic* or *reference* state. Now the following steps are taken:

a) A classical Turing analysis of the basic state.

b) Time-dependent diffusion coefficients are allowed and the resulting system is studied.Turing Analysis

Step a) $\mathbf{A} = \mathbf{A}(k)$ is a numerical matrix depending on the wavenumber k. Therefore the origin is a stable singular point if $tr\mathbf{A}(k) < 0$ and $\det \mathbf{A}(k) > 0$. Now, remark that the stability hypotheses for the singular point $\mathbf{X}_0$ guarantee $tr\mathbf{J}_0 < 0$, so

$$tr\mathbf{A}(k) = tr\mathbf{J}_0 - k^2(D_1 + D_2) < 0$$

always holds. Thus, the only way for the origin to become an unstable point of the basic state after the introduction of the diffusive terms is that $\det \mathbf{A}(k) < 0$. This determinant is a quadratic polynomial in k^2 :

$$\det \mathbf{A}(k) = p(k^2) = d_1 d_2 k^4 - (d_2 a_{11} + d_1 a_{22})k^2 + \det \mathbf{J}_0$$

whose two roots –if they exist– determine an interval of wavenumbers for which $\det \mathbf{A}(k) < 0$, corresponding to those "modes" $a_j(t)e^{ikx}$ that would become unstable. Nevertheless, not all these modes will be physically relevant, because in the usual case of bounded Ω the boundary conditions select only a denumerable set of feasible wavenumbers, and only those whose squares belong to the interval around will develop unstable behaviour. The condition for the interval to exist is obviously

$$(d_2 a_{11} + d_1 a_{22})^2 - 4 d_1 d_2 \det \mathbf{J}_0 > 0$$

and because $\det \mathbf{J}_0 > 0$ by hypothesis, for the inequality to hold $d_1 d_2$ must be small. As a rule, if one of the diffusivities is taken as fixed, the other one being much smaller than it will provide a sufficient condition.

2.1 Floquet's theory and time-dependent diffusivities:

Enter step b). For time-dependent diffusivities of the chosen type,

$$\mathbf{A}(k,t) = \begin{bmatrix} a_{11} - k^2(d_1 + b_1 \cos \omega t) & a_{12} \\ a_{21} & a_{22} - k^2(d_2 + b_2 \cos(\omega t + \phi)) \end{bmatrix}$$

and this is a periodic matrix because $\mathbf{A}(k,t) = \mathbf{A}(k,T)$, where $T = t + \frac{2\pi}{\omega}$. The amplitudes will be given by:

$$\frac{d\mathbf{a}}{dt} = \mathbf{A}(k,t)\mathbf{a}$$

According to the Floquet theory, see *e.g.* [Jordan and Smith 1988], this system has solutions $\mathbf{a}(t)$ obeying the formula

$$\mathbf{a}(t) = \mu\mathbf{a}(t + \frac{2\pi}{\omega})$$

where μ is any eigenvalue of the constant matrix $\mathbf{E}$ transforming a fundamental matrix $\Phi(t)$ of the system into its translate $\Phi(t + \frac{2\pi}{\omega})$ –also a fundamental matrix: $\Phi(t)\mathbf{E} = \Phi(t + \frac{2\pi}{\omega})$. If $\mu = 1$ happens to be an eigenvalue of $\mathbf{E}$, a periodic solution is at hand, while for real $\mu > 1$ there is instability and for real $\mu < 1$ a stable behaviour appears. Moreover, it is known that the product of the eigenvalues is

$$\mu_1\mu_2 = \exp(\int_0^T tr\mathbf{A}(k,t)dt)$$

and this suggests considering this product as a new parameter, say b:

$$b = \mu_1\mu_2 = \exp\{\int_0^T [tr\mathbf{J}_0 - k^2(d_1 + d_2 + b_1\cos\omega t + b_2\cos(\omega t + \phi))]dt\}$$
$$= \exp\{T[tr\mathbf{J}_0 - k^2(d_1 + d_2)]\} = \exp[T\ tr\mathbf{A}(k)] < 1$$

Thus, from Cardano's relationships, the eigenvalues of $\mathbf{E}$ are the solutions of the quadratic equation

$$\mu^2 - h\mu + b = 0$$

where $h = h(k,\omega)$ is some unknown function of the wavenumber k and the frequency ω, with $b \in (0,1)$. The actual form of $h(k,\omega)$ is not relevant, only its range of values is needed. Solving for $\mu = \frac{1}{2}(h \pm \sqrt{h^2 - 4b})$, yields an analysis which can be split into three parts:

1.- If $h^2 - 4b > 0$, with $|h| > |2\sqrt{b}|$ then two positive different real roots exist.

Case 1a)

If $h > 2\sqrt{b}$ then $\mu_1 = \frac{h-\sqrt{h^2-4b}}{2} < 1$. Indeed, if it were the case that $h = a2\sqrt{b}$ for some $a > 1$, then $\mu_1 = \sqrt{b}(a - \sqrt{a^2 - 1}) = \sqrt{b}g_1(a)$, and $g_1(a) < 1$ for any $a > 1$. Therefore $\mu_1 < \sqrt{b} < 1$. On the other hand, the second root μ_2 satisfies $\mu_2 > 1$ if $h > b + 1$. This yields an unstable solution.

If $h < b + 1$, then $\mu_2 < 1$ as well, and there can exist stable solutions. If $h = b + 1$, then $\mu_2 = 1$ and there is a periodic solution. To see this, simply recall that according to the Floquet theory the solutions of $\frac{d\mathbf{a}}{dt} = \mathbf{A}(k,t)$ can be written in the form

$$\mathbf{a}(t) = \mathbf{p}_1(t)\exp(\sigma_1 t) + \mathbf{p}_2(t)\exp(\sigma_2 t)$$

where σ_j is the characteristic exponent defined through $\sigma_j = \frac{\omega}{2\pi}\log\mu_j$, and $\mathbf{p}_j(t)$ are $\frac{2\pi}{\omega}$-periodic functions (remember that $T = \frac{2\pi}{\omega}$). It is clear that for $\mu_j > 1$, $\sigma_j > 0$ and the result, as regards stability, follows immediately.

Case 1b)

If $h < -2\sqrt{b}$ then $h^2 - 4b > 0$ as well, and both roots are negative. Moreover, one of them, $\mu_1 = \frac{h+\sqrt{h^2-4b}}{2} > -1$, because $\mu_1\mu_2 < 1$. Indeed, if it were the case that $h = -a2\sqrt{b}$ with $a > 0$, the root could be written as $\mu_1 = \sqrt{b}(-a + \sqrt{a^2-1}) = \sqrt{b}g_2(a) > -1$ and $g_2(a) < 1$. The second root is $\mu_2 = \frac{h-\sqrt{h^2-4b}}{2} < -1$ whenever $h < -b-1$, and there are unstable solutions. Symmetrically, for $h > -b-1$ the second root $\mu_2 > -1$ as well, yielding stable solutions. To end up, if $h = -b-1$, then $\mu_2 = 1$ and this yields a periodic solution.

2.- At the bifurcation $h^2 - 4b = 0$ we obtain $h = \pm 2\sqrt{b}$. Two cases must be distinguished:

Case 2a)

If $h = +2\sqrt{b}$, then there exists a unique double eigenvalue $\mu = \mu_1 = \mu_2 = \sqrt{b}$, the characteristic exponent is

$$\sigma = \frac{\omega}{2\pi}\log\sqrt{b} = \frac{\omega}{4\pi}\log b < 0$$

and a stable solution follows.

Case 2b)

For $h = -2\sqrt{b}$ the eigenvalue is $-\sqrt{b}$ and $\sigma = \frac{\omega}{4\pi}\log b + \frac{\omega}{2}i$ with negative real part, and a stable solution arises as well. Note that the oscillation frequency of this solution doubles that of the original problem, a fact also occurring in the case $h < -2\sqrt{b}$ studied above.

3.- Finally, consider the case $h \in (-2\sqrt{b}, 2\sqrt{b})$, where both eigenvalues are complex conjugates and the real part of the exponents $\sigma_j = \frac{\omega}{2\pi}(\log\sqrt{b} + \sigma i)$ is negative , so there exist stable solutions with a complicated structure: In addition to the "natural oscillations" with frequency ω, there appear new oscillations associated with $\tan^{-1}(\frac{\sqrt{4b-h^2}}{h})$. Therefore there exists locally unstable behaviour for $|h(k,\omega)| > b+1$, and the instability domain is $[-2\sqrt{b}, 2\sqrt{b}]$. Once b is fixed, there exist in the (k,ω)-plane curves described by the implicit equation $h(k,\omega) = const$ that separate zones where the amplitudes have different qualitative behaviours. Note that there exist two different types of solutions according to their oscillation frequencies.

3 Numerical experiments

3.1 Activator-Inhibitor kinetics

First we consider an activator-inhibitor system [Murray 1989, p. 377]) given by the model equations where all parameters have positive values:

$$\frac{\partial u}{\partial t} = a - cu + \frac{u^2}{v(1+\eta u^2)} + \text{Diffusion}$$
$$\frac{\partial v}{\partial t} = u^2 - v + \text{Diffusion}$$

The Jacobian of the spatially homogeneous system is:

$$\mathbf{J} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} -c + \dfrac{2u}{v(1+\eta u^2)^2} & -\dfrac{u^2}{v^2(1+\eta u^2)} \\ 2u & -1 \end{bmatrix}$$

And the matrix $\mathbf{A}(k,t)$ is:

$$\mathbf{A}(k,t) = \begin{bmatrix} -c + \dfrac{2u}{v(1+\eta u^2)^2} - k^2(d_1 + b_1\cos(\omega t)) & -\dfrac{u^2}{v^2(1+\eta u^2)} \\ 2u & -1 - k^2(d_2 + b_2\cos(\omega t + \phi)) \end{bmatrix}_{\mathbf{X}_0}$$

For any parameter choice there exists a singular point in the first orthant, because the growing null cline $v = u^2$ always intersects the decreasing one $v = \frac{u^2}{(1+\eta u^2)(cu-a)}$.

For instance, for the choice $a = 1$, $c = 1$, and $\eta = .01$, the singular point is $\mathbf{X}_0 = (1.353, 1.832)$, and its Jacobian is $\begin{bmatrix} -.899 & -0.068 \\ 2.706 & -1 \end{bmatrix}$, showing that $\mathbf{X}_0$ is a stable spiral point. Adding the diffusion coefficients –without time dependence– $d_1 = 0.5$, $d_2 = 5$, the relationship

$$(d_2 a_{11} + d_1 a_{22})^2 - 4 d_1 d_2 \det \mathbf{J}_0 = 14.12 > 0$$

holds and the interval of excitable wavenumbers is $[0.49746, 1.3231]$. Now let us modulate the diffusivities using the parameter values $b_1 = 0.4$, $b_2 = 4.5$, as well as $\omega = 10$ and $\phi = 1$, and take some k in the interval of feasible wavenumbers, say $k = 1$. Figures 1 and 2 show the results: The introduction of time dependent diffusivities inhibits the Turing instabilisation mechanism.

3.2 Schnackenberg kinetics

As a second example we consider the Schnackenberg kinetics:

$$\frac{\partial u}{\partial t} = a - u + u^2 v + \text{Diffusion}$$
$$\frac{\partial v}{\partial t} = b - u^2 v + \text{Diffusion}$$

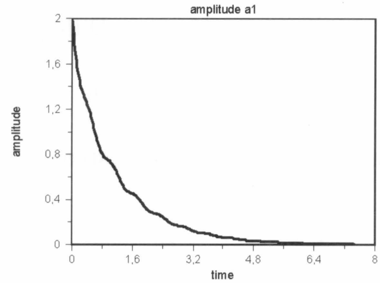


Figure 1: Inhibition of Turing instability for $k = 1$

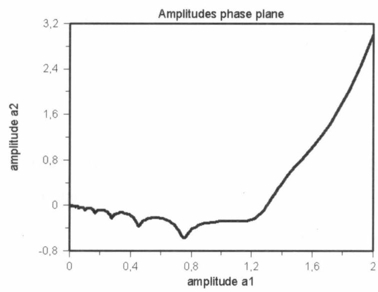


Figure 2: Both amplitudes tending to 0 for $k = 1$.

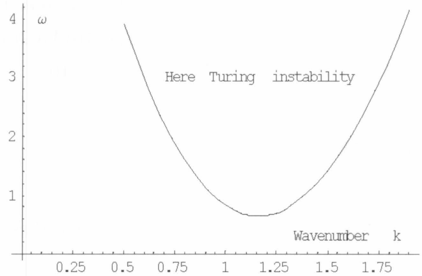


Figure 3: Bifurcation set for the Schnackenberg case.

Here the computations yield a singular point $\mathbf{X}_0 = (a+b, \frac{b}{(a+b)^2})$ in the first orthant where the Jacobian is

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} -1+2\frac{b}{a+b} & (a+b)^2 \\ -2\frac{b}{a+b} & -(a+b)^2 \end{bmatrix}$$

whose determinant is $(a+b)^2$ and the trace is negative –therefore the stationary point is a stable one– if the inequality

$$2\frac{b}{a+b} < 1 + (a+b)^2$$

holds. With the parameter values $a = 0.1$, $b = 0.9$, the spatially homogeneous singular point is $\mathbf{X}_0 = (1, 0.9)$, where the Jacobian $\mathbf{J}_0$ equals

$$\begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} = \begin{bmatrix} 0.8 & 1 \\ -1.8 & -1 \end{bmatrix}$$

and the matrix $\mathbf{A}(k,t) = \mathbf{A}(k,\omega,t)$ is:

$$\begin{bmatrix} 0.8 - k^2(0.1 + 0.2\cos(\omega t) & 1 \\ -1.8 & -1 - k^2(1.7 + 0.1\cos(\omega t + 1) \end{bmatrix}$$

There exists Turing instability for specific combinations of the solution wavenumber k and the frequency ω of the forcing on the diffusion coefficient, giving rise to the bifurcation diagram on the (k,ω) plane shown in Figure 3 where pairs (k,ω) above the parabola-like curve yield Turing instabilities for this particular kinetics:

For instance, setting $\omega = 3$, $k = .5$ –under the parabola– and the diffusion parameters $d_1 = 0.2$, $b_1 = 0.2$, $d_2 = 5$ and $b_2 = 4.9$, Figure 4 is obtained, showing no Turing instability. where modulation by the diffusion periodicity is easily seen:

On the other hand, if we take $\omega = 3$, $k = 1$ –above the parabola– and the same diffusion parameters, Turing instability is observed in Figure 5, together with the modulation through the periodicity of the diffusive coefficients:

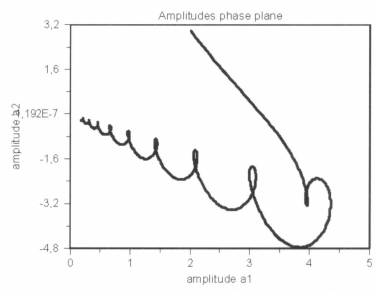
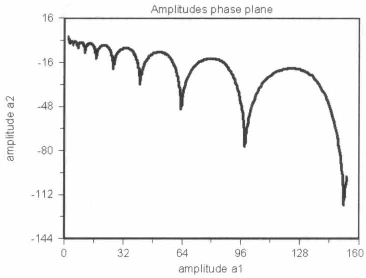


Figure 4: Both amplitudes tending to 0: No Turing instability.



Turing instability: Growing amplitudes

4 Conclusions and Views

In this work we have shown that the basic Turing istability mechanism for reaction-diffusion systems can inhibited –or enhanced– if the diffusion coefficients are allowed to have periodic time dependences, a fact that is studied through application of Floquet theory. In order to deepen this insight a bifurcation study has been started whose systematic development will be the aim of a series of papers to come.

5 References

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