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SURVEY ARTICLE

Bifurcation in infinite dimensional spaces and applications in spatiotemporal biological and chemical models*

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Abstract Recent advances in abstract local and global bifurcation theory is briefly reviewed. Several applications are included to illustrate the applications of abstract theory, and it includes Turing instability of chemical reactions, pattern formation in water limited ecosystems, and diffusive predator-prey models.

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1 Introduction

Bifurcation theory is the mathematical study of changes in the qualitative or topological structure in the asymptotical dynamical behavior of natural or engineering systems. Such systems are usually described by continuous and discrete mathematical models like differential equations and mappings. Bifurcation occurs when certain physical parameters cross through critical thresholds.

The earliest example of bifurcation is the buckling of an elastic beam. In engineering, buckling is a failure mode characterized by a sudden failure of a structure subjected to high compressive stresses, where the actual compressive stresses at failure are greater than the ultimate compressive stresses that the material is capable of withstanding. This mode of failure is also described as failure due to elastic instability. Bifurcation of buckling can be found in classical Euler-Bernoulli beam theory due to Leonhard Euler and

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Daniel Bernoulli with earlier contribution of Jacob Bernoulli. Other famous people such as Galileo Galilei and Leonardo da Vinci also have made unsuccessful attempts before Isaac Newton invented the powerful tool of differential and integral calculus [14,41].

For example, a pinned inextensible rod subject to prescribed axial thrust can be described by a boundary value problem (see Refs. [35,36]):

$$\begin{cases} \phi'' + \lambda \sin\phi = 0, & 0 < x < 1, \quad \phi'(0) = \phi'(1) = 0, \\ u' = \cos\phi - 1, & 0 < x < 1, \quad u(0) = 0, \\ w' = \sin\phi, & 0 < x < 1, \quad w(0) = w(1) = 0. \end{cases} \tag{1.1}$$

Here, the length of the elastic column is normalized so that $0 \leqslant x \leqslant 1$, the horizontal and vertical displacements of the buckled axis are denoted by $u(x)$ and $w(x)$, respectively, $\phi(x)$ is the angle between the tangent to the column's axis and the x-axis, and λ is a parameter proportional to the thrust. Clearly, the solutions of (1.1) is determined by the equation of ϕ. The linearization of the equation of ϕ around $\phi = 0$ is

$$\psi'' + \lambda\psi = 0, \quad 0 < x < 1, \quad \psi'(0) = \psi'(1) = 0, \tag{1.2}$$

and it is well known that the eigenvalues of (1.2) are $\lambda_n = (n\pi)^2$ for $n = 0, 1, 2, \ldots$. When $0 < \lambda \leqslant \lambda_1$, $\phi = 0$ is the only solution, but for each $n \geqslant 1$, a new branch of solutions $(\lambda, \phi_n^{\pm}(\lambda, x))$ bifurcates from the eigenvalue λ_n and $\phi_n^{\pm}(\lambda, \cdot)$ exists for $\lambda > \lambda_n$. Each $\phi_n^{\pm}(\lambda, \cdot)$ represents a new bend-state when the thrust λ is larger.

Many more examples of bifurcation can be found in the mathematical studies of physics, chemistry, biology and engineering. All these problems can be written as an abstract form:

$$F(\lambda, u) = 0, \tag{1.3}$$

where $F\colon\ \mathbb{R} \times X \to Y$ is a nonlinear differentiable mapping, and X, Y are Banach spaces. Very often the solutions of (1.3) are also the steady state solutions of evolution equation

$$\frac{\mathrm{d}u}{\mathrm{d}t} = F(\lambda, u). \tag{1.4}$$

In this article, we survey some basic bifurcation results for equation (1.3) in a setting of infinite dimensional Banach spaces, and we use some important examples from reaction-diffusion models in biochemical reactions and population ecology to illustrate the abstract theory. For a more general introduction to bifurcation theory and other related methods in nonlinear analysis, see for example, Refs. [1,3,5,10,15,20,24,30,39]. On the other hand, Refs. [2,12,13,27,28,32] provide a more detailed introduction to mathematical models in chemical reactions and population ecology. For surveys of related problems but focusing on (a) bifurcation in diffusive predator-prey systems, see Ref. [11]; and (b) bistability in ecological systems, see Ref. [19].

In Section 2, we recall abstract bifurcation theorems including some recent new results; and in Section 3, we illustrate our abstract results by showing the application of bifurcation theory to three spatiotemporal models from ecology and biochemistry: Turing instability and bifurcation in chemical reaction models; cross-diffusion induced instability and bifurcation in water-limited ecosystems; and bifurcations in classical diffusive predator-prey models which shows the patchiness (spatial heterogeneity) of plankton distributions in phytoplankton-zooplankton interaction. We denote by $\mathbb{N}$ the set of all the positive integers, and $\mathbb{N}_0 = \mathbb{N} \cup \{0\}$.

2 Abstract bifurcation theory

We consider a nonlinear equation:

$$F(\lambda, u) = 0, \tag{2.1}$$

where $F\colon\ \mathbb{R} \times X \to Y$ is a differentiable mapping, and X, Y are Banach spaces. We use $F_\lambda(\lambda, u)$ and $F_u(\lambda, u)$ to denote the partial derivatives of F, and $F_{\lambda u}(\lambda, u)$, etc. for the higher order derivatives. For a linear operator L, we use $N(L)$ as the null space of L and $R(L)$ as the range of L. Our main interest is on the solution set of (2.1). We review the classical bifurcation results and also some new variants without proofs. Detailed proofs can be found in Ref. [38,39] or original papers cited below.

If (λ_0, u_0) is a solution of (2.1), and $F_u(\lambda_0, u_0)$ is an invertible linear mapping, then the solution set is locally a curve with same smoothness as F. That is the classical implicit function theorem.

Theorem 2.1 (Implicit Function Theorem) *Let $(\lambda_0, u_0) \in \mathbb{R} \times X$ and let F be a continuously differentiable mapping of an open neighborhood V of (λ_0, u_0) into Y. Let $F(\lambda_0, u_0) = 0$ and $F_u(\lambda_0, u_0)$ is an isomorphism, i.e., $F_u(\lambda_0, u_0)$ is one-to-one and onto, and $F_u^{-1}(\lambda_0, u_0)\colon\ Y \to X$ is a linear bounded operator. Then the solutions of $F(\lambda, u) = 0$ near (λ_0, u_0) form a curve $(\lambda, u(\lambda))$, $u(\lambda) = u_0 + (\lambda - \lambda_0)w_0 + z(\lambda)$, where $w_0 = -[F_u(\lambda_0, u_0)]^{-1}(F_\lambda(\lambda_0, u_0))$ and $\lambda \mapsto z(\lambda) \in X$ is a continuously differentiable function near $\lambda = \lambda_0$ with $z(\lambda_0) = z'(\lambda_0) = 0$.*

When $F_u(\lambda_0, u_0)$ is not invertible, we call (λ_0, u_0) a *degenerate solution* of $F(\lambda, u) = 0$. Here, we discuss the case when the kernel of $F_u(\lambda_0, u_0)$ is nonempty, and in particular, we discuss the case that $\mu = 0$ is a simple eigenvalue of $F_u(\lambda_0, u_0)$, i.e.,

($\mathbf{F_1}$) $\dim N(F_u(\lambda_0, u_0)) = \operatorname{codim} R(F_u(\lambda_0, u_0)) = 1$, and $N(F_u(\lambda_0, u_0)) = \operatorname{span}\{w_0\}$.

This is equivalent to that the algebraic and geometric multiplicity of the eigenvalue 0 of the linear operator $F_u(\lambda_0, u_0)$ are both 1. First we have the following result of Crandall and Rabinowitz [8].

Theorem 2.2 (Saddle-node Bifurcation Theorem) *Let $F\colon \mathbb{R}\times X \to Y$ be continuously differentiable. $F(\lambda_0,u_0)=0$, F satisfies* (F_1) *and*

$(\mathbf{F_2})$ $F_\lambda(\lambda_0,u_0)\notin R(F_u(\lambda_0,u_0))$.

Then the solutions of $F(\lambda,u)=0$ near (λ_0,u_0) form a continuously differentiable curve $(\lambda(s),u(s))$ for $s\in(-\delta,\delta)$, $(\lambda(0),u(0)=(\lambda_0,u_0)$, $\lambda'(0)=0$ and $u'(0)=w_0$. Moreover, if F is C^2 in u, then

$$\lambda''(0)=-\frac{\langle l,F_{uu}(\lambda_0,u_0)[w_0,w_0]\rangle}{\langle l,F_\lambda(\lambda_0,u_0)\rangle}, \tag{2.2}$$

where $l\in Y^*$ (the conjugate space of Y) satisfying $N(l)=R(F_u(\lambda_0,u_0))$.

If $\lambda''(0)\neq 0$, and the solution set $\{(\lambda(s),u(s))\colon\ |s|<\delta\}$ is a parabola-like curve which reaches an extreme point at (λ_0,u_0). The degenerate solution (λ_0,u_0) in this case is a *turning point* on the solution curve. We notice that although the local solution set in this case cannot be parameterized by λ, it is still a parameterized curve. We call it saddle-node bifurcation theorem to follow the terminology in dynamical systems.

Next, it is natural to consider the case when (F_2) fails. We still assume F satisfies (F_1) at (λ_0,u_0). Then we have decompositions of X and Y:

$$X=N(F_u(\lambda_0,u_0))\oplus Z,\quad Y=R(F_u(\lambda_0,u_0))\oplus Y_1,$$

where Z is a complement of $N(F_u(\lambda_0,u_0))$ in X, and Y_1 is a complement of $R(F_u(\lambda_0,u_0))$. In particular, $F_u(\lambda_0,u_0)|_Z\colon\ Z\to R(F_u(\lambda_0,u_0))$ is an isomorphism. Since $R(F_u(\lambda_0,u_0))$ is codimension one, there exists $l\in Y^*$ such that $R(F_u(\lambda_0,u_0))=\{v\in Y\colon\ \langle l,v\rangle=0\}$. We assume the opposite of (F_2):

$(\mathbf{F_2'})$ $F_\lambda(\lambda_0,u_0)\in R(F_u(\lambda_0,u_0))$.

Then the equation

$$F_\lambda(\lambda_0,u_0)+F_u(\lambda_0,u_0)[v]=0 \tag{2.3}$$

has a unique solution $v_1\in Z$. The following 'crossing curve bifurcation' theorem was proved by Liu, Shi and Wang [23].

Theorem 2.3 *Let U be a neighborhood of (λ_0,u_0) in $\mathbb{R}\times X$, and let $F\colon\ U\to Y$ be a twice continuously differentiable mapping. Assume that $F(\lambda_0,u_0)=0$, F satisfies* (F_1) *and* (F_2') *at (λ_0,u_0). Let $X=N(F_u(\lambda_0,u_0))\oplus Z$ be a fixed splitting of X, let $v_1\in Z$ be the unique solution of* (2.3)*, and let $l\in Y^*$ such that $R(F_u(\lambda_0,u_0))=\{v\in Y\colon\ \langle l,v\rangle=0\}$. We assume that the matrix* (*all derivatives are evaluated at* (λ_0,u_0))

$$H_0\equiv\begin{pmatrix}\langle l,F_{\lambda\lambda}+2F_{\lambda u}[v_1]+F_{uu}[v_1,v_1]\rangle & \langle l,F_{\lambda u}[w_0]+F_{uu}[w_0,v_1]\rangle\\ \langle l,F_{\lambda u}[w_0]+F_{uu}[w_0,v_1]\rangle & \langle l,F_{uu}[w_0,w_0]\rangle\end{pmatrix} \tag{2.4}$$

is non-degenerate, i.e., $\det(H_0)\neq 0$.

(1) *If H_0 is definite, i.e.,* $\det(H_0)>0$, *then the solution set of $F(\lambda,u)=0$ near $(\lambda,u)=(\lambda_0,u_0)$ is the single point set $\{(\lambda_0,u_0)\}$.*

(2) *If* H_0 *is indefinite, i.e.,* $\det(H_0) < 0$, *then the solution set of* $F(\lambda, u) = 0$ *near* $(\lambda, u) = (\lambda_0, u_0)$ *is the union of two intersecting* C^1 *curves, and the two curves are in the form of*

$$(\lambda_i(s), u_i(s)) = (\lambda_0 + \mu_i s + s\theta_i(s), u_0 + \eta_i s w_0 + s v_i(s)), \quad i = 1, 2,$$

where $s \in (-\delta, \delta)$ *for some* $\delta > 0$, $\theta_i(0) = 0$, $v_i(s) \in Z$, $v_i(0) = 0$ $(i = 1, 2)$, *and* (μ_i, η_i) $(i = 1, 2)$ *are non-zero linear independent solutions of the equation*

$$\langle l, F_{\lambda\lambda} + 2F_{\lambda u}[v_1] + F_{uu}[v_1, v_1]\rangle \mu^2$$
$$+2\langle l, F_{\lambda u}[w_0] + F_{uu}[w_0, v_1]\rangle \eta\mu + \langle l, F_{uu}[w_0, w_0]\rangle \eta^2 = 0. \tag{2.5}$$

A special case of Theorem 2.3 is the well-known 'bifurcation form simple eigenvalue' theorem of Crandall and Rabinowitz [7].

Theorem 2.4 (Transcritical and Pitchfork Bifurcation Theorem) *Let* $F\colon \mathbb{R} \times X \to Y$ *be continuously differentiable. Suppose that* $F(\lambda, u_0) = 0$ *for* $\lambda \in \mathbb{R}$, *the partial derivative* $F_{\lambda u}$ *exists and is continuous. At* (λ_0, u_0), F *satisfies* (F_1) *and*

$(\mathbf{F_3})$ $F_{\lambda u}(\lambda_0, u_0)[w_0] \notin R(F_u(\lambda_0, u_0))$, *where* $w_0 \in N(F_u(\lambda_0, u_0))$.

Then the solutions of $F(\lambda, u) = 0$ *near* (λ_0, u_0) *consists precisely of the curves* $u = u_0$ *and* $(\lambda(s), u(s))$, $s \in I = (-\delta, \delta)$, *where* $(\lambda(s), u(s))$ *are continuously differentiable functions such that* $\lambda(0) = \lambda_0$, $u(0) = u_0$, $u'(0) = w_0$. *Moreover, if* F *is* C^2 *in* u, *then* $\lambda(s)$ *is differentiable, and*

$$\lambda'(0) = -\frac{\langle l, F_{uu}(\lambda_0, u_0)[w_0, w_0]\rangle}{2\langle l, F_{\lambda u}(\lambda_0, u_0)[w_0]\rangle}. \tag{2.6}$$

If $\lambda'(0) \neq 0$, then a transcritical bifurcation occurs; while $\lambda'(0) = 0$ and $\lambda''(0) \neq 0$, a pitchfork bifurcation occurs. In fact, the word 'bifurcation' is from the Latin *bifurcus*, which means 'two forks'. Again, the names transcritical and pitchfork bifurcations are from dynamical system terms.

The implicit function theorem (transversal curve), saddle-node bifurcation (bending curve), and transcritical/pitchfork bifurcation (two crossing curves) illustrate the impact of different levels of degeneracy of the nonlinear mapping on the structure of local solution sets.

Finally, we state the following global bifurcation theorem due to Pejsachowicz and Rabier [33] (see also Shi and Wang [40]).

Theorem 2.5 *Assume that all conditions in Theorem* 2.4 *hold. If in addition,* $F_u(\lambda, u)$ *is a Fredholm operator for all* $(\lambda, u) \in \mathbb{R} \times X$, *then the curve* $\{(\lambda(s), u(s))\colon\ s \in I\}$ *in Theorem* 2.4 *is contained in* $\mathscr{C}$, *which is a connect component of* $\overline{S}$, *where* $S = \{(\lambda, u) \in \mathbb{R} \times X\colon\ F(\lambda, u) = 0,\ u \neq u_0\}$; *and either* $\mathscr{C}$ *is not compact, or* $\mathscr{C}$ *contains a point* (λ_*, u_0) *with* $\lambda_* \neq \lambda_0$.

Here we recall that a bounded linear mapping L from a Banach space X to another Banach space Y is said to be *Fredholm* if the dimension of its kernel $N(L)$ and the co-dimension of its range $R(L)$ are both finite. A more general global result is proved in Refs. [33,40], which extends the celebrated global bifurcation theorem of Rabinowitz [34].

3 Bifurcations in biological and chemical models

3.1 Turing bifurcation

A pure diffusion process usually leads to a smoothing effect so that the system tends to a constant equilibrium state. However, the combined effect of diffusion and chemical reaction may result in destabilizing the constant equilibrium. In 1952, Alan Turing published a paper 'The chemical basis of morphogenesis' [42] which is now regarded as the foundation of basic chemical theory or reaction diffusion theory of morphogenesis. Turing suggested that, under certain conditions, chemicals can react and diffuse in such a way to produce non-constant equilibrium solutions, which represent spatial patterns of chemical or morphogen concentration.

Turing's idea is a simple but profound one. He considered a reaction-diffusion system

$$u_t = D_u \Delta u + f(u,v), \quad v_t = D_v \Delta v + g(u,v), \tag{3.1}$$

and its corresponding kinetic equation

$$u' = f(u,v), \quad v' = g(u,v). \tag{3.2}$$

He said that if, in the absence of the diffusion (considering (3.2)), u and v tend to a linearly stable uniform steady state, then, with the presence of diffusion and under certain conditions, the uniform steady state can become unstable, and spatial non-homogeneous patterns can evolve through bifurcations. In another word, a constant equilibrium can be asymptotically stable with respect to (3.2), but it is unstable with respect to (3.1). Therefore, this constant equilibrium solution becomes unstable because of the diffusion, which is called *diffusion driven instability*.

To illustrate the bifurcation theory introduced earlier, we consider the one-dimensional system:

$$\begin{cases} u_t = u_{xx} + f(u,v), & x \in (0,\ell\pi),\ t>0, \\ v_t = dv_{xx} + g(u,v), & x \in (0,\ell\pi),\ t>0, \\ u_x(t,0) = u_x(t,\ell\pi) = v_x(t,0) = v_x(t,\ell\pi) = 0, & t>0, \\ u(0,x) = u_0(x), \quad v(0,x) = v_0(x), & x \in (0,\ell\pi). \end{cases} \tag{3.3}$$

Here $d > 0$ is the ratio D_v/D_u of the two diffusion coefficients, $\ell > 0$ represents the length of the interval. It is well known that the eigenvalue problem

$$-\varphi'' = \mu\varphi, \quad x \in (0,\ell\pi), \quad \varphi'(0) = \varphi'(\ell\pi) = 0,$$

has eigenvalues $\mu_n = n^2/\ell^2$ $(n = 0,1,2,\dots)$, with corresponding eigenfunctions $\varphi_n(x) = \cos \frac{n}{\ell} x$. Suppose that (u_0,v_0) is a solution of $f(u,v) = g(u,v) =$

0, then (u_0, v_0) is a constant equilibrium solution of (3.3). The stability of (u_0, v_0) with respect to (3.3) is determined by the linearized operator

$$L\begin{pmatrix}\phi\\ \psi\end{pmatrix} = \begin{pmatrix}\phi_{xx}\\ d\psi_{xx}\end{pmatrix} + \begin{pmatrix}f_u & f_v\\ g_u & g_v\end{pmatrix}\begin{pmatrix}\phi\\ \psi\end{pmatrix}.$$

We assume that (u_0, v_0) is locally stable with respect to the ordinary differential equation (ODE) dynamics (3.2), hence,

$$D_1 = f_u g_v - f_v g_u > 0, \quad f_u + g_v < 0.$$

Let

$$k = \frac{n}{\ell}, \quad \begin{pmatrix}\phi\\ \psi\end{pmatrix} = \begin{pmatrix}A\\ B\end{pmatrix}\cos kx, \quad J = \begin{pmatrix}f_u & f_v\\ g_u & g_v\end{pmatrix}, \quad D = \begin{pmatrix}1 & 0\\ 0 & d\end{pmatrix}.$$

Then the eigenvalues of L are determined by the eigenvalue problem

$$(J - k^2 D)\begin{pmatrix}A\\ B\end{pmatrix} \equiv \begin{pmatrix}f_u - k^2 & f_v\\ g_u & g_v - k^2 d\end{pmatrix}\begin{pmatrix}A\\ B\end{pmatrix} = \mu\begin{pmatrix}A\\ B\end{pmatrix}.$$

The trace and determinant of $J - k^2 D$ are

$$\mathrm{tr}\,(J - k^2 D) = (f_u + g_v) - k^2(1 + d),$$
$$\det(J - k^2 D) = (f_u g_v - f_v g_u) - k^2(d f_u + g_v) + k^4 d.$$

For (u_0, v_0) to be unstable with respect to (3.3), we must have $\det(J - k^2 D) < 0$ since $\mathrm{tr}\,(J - k^2 D) < 0$ always holds. This requires $d f_u + g_v > 0$ while we have $f_u + g_v < 0$. Thus f_u and g_v must have opposite signs. Here we assume that $f_u > 0$ and $g_v < 0$, hence u is an activator and v is an inhibitor. Then we can apply the theory in Section 2 to obtain the following general bifurcation result.

Theorem 3.1 *Suppose that $f, g \in C^1(\mathbb{R}^2)$, there exists $(u_0, v_0) \in \mathbb{R}^2$ such that $f(u_0, v_0) = g(u_0, v_0) = 0$, and at (u_0, v_0),*

(A) $f_u > 0$ (*activator*), $g_v < 0$ (*inhibitor*);

(B) $D_1 = f_u g_v - f_v g_u > 0$ *and* $f_u + g_v < 0$.

Define $\ell_n = f_u^{-1/2} n$, and for fixed ℓ satisfying $\ell_{j-1} < \ell < \ell_j$, for $n = 1, 2, \ldots, j$, define

$$d_n(\ell) = \frac{D_1 - n^2\ell^{-2} g_v}{n^2\ell^{-2}(f_u - n^2\ell^{-2})} > 0.$$

If for some $n = 1, 2, \ldots, j$, $d_n(\ell) \neq d_k(\ell)$ for any $k = 1, 2, \ldots, j$, $k \neq n$, then

(1) *$d = d_n(\ell)$ is a bifurcation point where a continuum Σ of non-trivial solutions of*

$$\begin{cases} u_{xx} + f(u, v) = 0, \quad d v_{xx} + g(u, v) = 0, \quad x \in (0, \ell\pi),\\ u_x(0) = u_x(\ell\pi) = v_x(0) = v_x(\ell\pi) = 0, \end{cases}$$

bifurcates from the line of trivial solutions (d, u_0, v_0).

(2) *The continuum* Σ *is either unbounded in the space of* (d, u, v), *or it connects to another* $(d_k(\ell), u_0, v_0)$.

(3) Σ *is locally a curve near* $(d_n(\ell), u_0, v_0)$ *in the form of*

$$(d, u, v) = \Big(d(s), u_0 + sA\cos\frac{nx}{\ell} + o(s), v_0 + sB\cos\frac{nx}{\ell} + o(s)\Big), \quad |s| < \delta,$$

and $d'(0) = 0$ *thus the bifurcation is of pitchfork type* ($d''(0)$ *can be computed in terms of higher derivatives of* f *and* g).

The proof of Theorem 3.1 is a direct application of Theorems 2.4 and 2.5, and is omitted here. Similar proofs can be found in Refs. [6,18,31] for special cases.

Over the years, Turing's idea has attracted the attention of a great number of investigators and was successfully developed on the theoretical backgrounds. Not only has it been studied in biological and chemical fields, but some investigations range as far as economics, semiconductor physics, and star formation (see Ref. [12]). However, the search for Turing patterns in real chemical or biological systems turned out to be difficult. Almost 40 years after Turing's seminal paper, the first experimental observation of a Turing pattern in a chemical reactor was due to De Kepper's group, who observed a spotty pattern in a chlorite-iodide-malonic acid (CIMA) reaction [9] in 1990. The experiment on the CIMA reaction has revealed the existence of stationary spatial periodic concentration patterns, the so-called Turing structures, in open gel reactors. Later, Lengyel and Epstein have suggested [22] that these patterns could arise because the iodine activator species forms a reversible complex of low mobility with the starch molecules used as color indicator for this reaction. In particular, they have also developed a simple two-variable model [21] that includes the three overall stoichiometric processes that lie at the heart of the mechanism of the CIMA reaction: the chlorine dioxide-iodine-malonic acid model. The corresponding dimensionless reaction-diffusion equations take the following form:

$$\begin{cases} u_t = \Delta u + a - u - \dfrac{4uv}{1+u^2}, & x \in \Omega,\ t > 0, \\ v_t = \sigma\Big[c\Delta v + b\Big(u - \dfrac{uv}{1+u^2}\Big)\Big], & x \in \Omega,\ t > 0, \\ u(x,0) = u_0(x), \quad v(x,0) = v_0(x), & x \in \Omega, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega,\ t > 0, \end{cases} \tag{3.4}$$

where Ω is a bounded connected domain (the reactor) in $\mathbb{R}^n$ $(n \geqslant 1)$, with smooth boundary $\partial\Omega$; the reactor is assumed to be closed, thus reflexive Neumann boundary condition is imposed (here $\partial_\nu u$ is the outer normal derivative of u); $u(x,t)$ and $v(x,t)$ denote the dimensionless iodide (I^-) and chlorite (ClO_2^-) concentrations respectively; a and b are parameters related to the feed concentrations; and c is the ratio of the diffusion coefficients;

$\sigma > 0$ is a rescaling parameter depending on the concentration of the starch, which enlarges the effective diffusion ratio to σc.

One can apply Theorem 3.1 to the corresponding one-dimensional version of (3.4), see Ref. [18] (and also Ref. [29] for higher dimensional case). System (3.4) has a unique fixed point $(u^*, v^*) = (\alpha, 1 + \alpha^2)$, where $\alpha = a/5$. The Jacobian matrix at (u^*, v^*) is

$$J := \begin{pmatrix} \dfrac{3\alpha^2 - 5}{1 + \alpha^2} & -\dfrac{4\alpha}{1 + \alpha^2} \\ \dfrac{2\sigma\alpha^2 b}{1 + \alpha^2} & -\dfrac{\sigma\alpha b}{1 + \alpha^2} \end{pmatrix}.$$

Hence, when $0 < 3\alpha^2 - 5 < \sigma\alpha b$, conditions (A) and (B) in Theorem 3.1 are satisfied. Therefore, for the system (here we denote $d = c/b$)

$$\begin{cases} u_{xx} + a - u - \dfrac{4uv}{1 + u^2} = 0, & x \in (0, \ell\pi), \\ dv_{xx} + u - \dfrac{uv}{1 + u^2} = 0, & x \in (0, \ell\pi), \\ u'(0) = u'(\ell\pi) = v'(0) = v'(\ell\pi) = 0, \end{cases}$$

the bifurcation points are

$$d_n = \frac{\alpha}{1 + \alpha^2} \cdot \frac{5 + \mu_n}{\mu_n(f_0 - \mu_n)},$$

where $f_0 = (3\alpha^2 - 5)/(1 + \alpha^2)$, and $\mu_n = n^2/\ell^2$. In fact, in Ref. [18], it was showed that all the bifurcating branches are unbounded in positive d-direction but bounded in (u, v) norm with the *a priori* estimates.

A complete understanding of the asymptotical behavior of solutions to Lengyel-Epstein system (3.4) or any other systems with complicated spatiotemporal dynamics is still beyond reach. Yi, Wei and Shi [44,46] showed that (3.4) also possess periodic orbits through Hopf bifurcation for certain parameters, but the dynamics is relatively simpler when a is small, or when a is large but the domain Ω is small. Jin, Shi, Wei and Yi[1)] consider the global bifurcation diagrams with intervening steady state and Hopf bifurcations. In particular, they showed that (3.4) has spatially non-homogeneous periodic orbits, which is another indication of complex spatiotemporal dynamics.

3.2 Cross-diffusion induced bifurcation

Some of these self-organized patterns have been attributed to the cross-diffusion and advection in the systems. Shi, Xie and Little[2)] further explored Turing's diffusion-induced instability for the cross-diffusion systems. The idea can be summarized as follows: assume that in the absence of self-diffusion

1) Jin J Y, Shi J P, Wei J J, Yi F Q. Bifurcations of patterned solutions in diffusive Lengyel-Epstein system. Preprint, 2008

2) Shi J P, Xie Z F, Little K. Cross-diffusion induced instability and stability in reaction-diffusion systems. Preprint, 2008

and cross-diffusion, there is a spatial homogeneous stable steady state; in the presence of self-diffusion but not cross-diffusion, this steady state remains stable hence it does not belong to the classical Turing instability scheme, but it could become unstable when cross-diffusion also comes to play a role in the system; thus it is a *cross-diffusion induced instability.* On the other hand, if Turing instability does occur, i.e., a spatial uniform steady state is stable with respect to the diffusion-free system, and it is unstable when diffusion (but not cross-diffusion) presents; this steady state could become stable with the inclusion of cross-diffusion influence, which represents a *cross-diffusion induced stability.*

Similar to the analysis in Subsection 3.1, one could consider the system

$$\begin{cases} u_t = d_{11}u_{xx} + d_{12}v_{xx} + f(u,v), & t>0,\ x\in(0,\ell\pi), \\ v_t = d_{21}u_{xx} + d_{22}v_{xx} + g(u,v), & t>0,\ x\in(0,\ell\pi), \\ u_x(t,0) = u_x(t,\ell\pi) = v_x(t,0) = v_x(t,\ell\pi) = 0, & t>0, \\ u(0,x) = h(x), \quad v(0,x) = l(x), & x\in(0,\ell\pi). \end{cases} \tag{3.5}$$

Again we assume $f(u_0,v_0) = g(u_0,v_0) = 0$ for some $(u_0,v_0)\in\mathbb{R}^2$. Define

$$D = \begin{pmatrix} d_{11} & d_{12} \\ d_{21} & d_{22} \end{pmatrix}, \quad J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}, \tag{3.6}$$

where the derivatives of f and g are evaluated at (u_0,v_0). The following instability result was shown[1)].

Theorem 3.2 *Suppose that $f,g\in C^1(\mathbb{R}^2)$, there exists $(u_0,v_0)\in\mathbb{R}^2$ such that $f(u_0,v_0) = g(u_0,v_0) = 0$, and at (u_0,v_0), the Jacobian matrix J satisfies*

(A) $f_u > 0$ (*activator*), $g_v < 0$ (*inhibitor*);

(B) $\det J = f_u g_v - f_v g_u > 0$ *and* $\operatorname{tr} J = f_u + g_v < 0$;

and the diffusion matrix D satisfies

(C) $d_{11} > 0,\ d_{22} > 0,\ d_{12}, d_{21}\in\mathbb{R}$ *such that* $\det D = d_{11}d_{22} - d_{12}d_{21} > 0$.

If in addition,

$$-F(J,D) - 2\sqrt{\det D \det J} \geqslant \frac{\det D}{\ell^2}, \tag{3.7}$$

where

$$F(J,D) = -d_{22}f_u + d_{21}f_v + d_{12}g_u - d_{11}g_v,$$

then (u_0,v_0) is an unstable equilibrium solution with respect to (3.5).

To demonstrate the cross-diffusion induced instability, we consider a reaction-diffusion model proposed by von Hardenberg, Meron, et al. [26,43], which gives a theoretical explanation of desertification phenomena in water limited systems. The model predicts no vegetation at low water levels and homogeneous vegetation at high water levels, with intermediate states of spots, stripes, and labyrinths. These patterns have all been documented in

1) See footnote 2) on p. 415

desert systems. The model also predicts the coexistence of steady states for several precipitation ranges. The non-dimensional form of the equations is

$$\begin{aligned} n_t &= \frac{\gamma w}{1+\sigma w} n - n^2 - \mu n + \Delta n, \\ w_t &= p - (1-\rho n)w - w^2 n + \delta \Delta (w - \beta n) - v(w - \alpha n)_x, \end{aligned} \tag{3.8}$$

where $n(x,t)$ is the vegetation biomass density and $w(x,t)$ is the soil water density. More explanation on the model can be found in Ref. [43][1]. Here, we only consider the case of $v = 0$, and concentrate on the impact of cross-diffusion term $-\beta \Delta n$ on the stability of equilibrium solutions. Again for simplicity, we only consider the one-dimensional problem:

$$\begin{cases} n_t = n_{xx} + \dfrac{\gamma w}{1+\sigma w} n - n^2 - \mu n, & t > 0,\ x \in (0, \ell\pi), \\ w_t = \delta w_{xx} - \beta \delta n_{xx} + p - (1-\rho n) w - w^2 n, & t > 0,\ x \in (0, \ell\pi), \\ n_x(t,0) = n_x(t,\ell\pi) = w_x(t,0) = w_x(t,\ell\pi) = 0, & t > 0, \\ n(0,x) = h(x), \quad w(0,x) = l(x), & x \in (0, \ell\pi). \end{cases} \tag{3.9}$$

It was shown that[1] if

$$0 < \gamma - \mu\sigma < \frac{\sigma}{\rho}, \quad w > \rho, \tag{3.10}$$

then

$$(n_0, w_0) = \Big(\frac{\gamma w}{1+\sigma w} - \mu, w \Big)$$

is a constant equilibrium solution of (3.9) satisfying $1 - \rho n > 0$. Moreover, this equilibrium is linearly stable with respect to the corresponding ODE dynamics of (3.9). For the reaction-diffusion system (3.9), one can show that (n_0, w_0) is still stable with respect to the dynamics of (3.9) if $\beta = 0$. But from Theorem 3.2, if

$$\beta > \frac{(\delta n_0 + p w_0^{-1} + w_0 n_0 + 2\sqrt{\delta \det J} + \delta \ell^{-2})(1+\sigma w_0)^2}{\delta \gamma n_0}, \tag{3.11}$$

then (n_0, w_0) becomes unstable. Hence the instability is induced by strong cross-diffusion effect.

(3.11) is a sufficient condition for instability but not necessary. In fact, if

$$\beta > \frac{(\delta n_0 + p w_0^{-1} + w_0 n_0 + 2\sqrt{\delta \det J})(1+\sigma w_0)^2}{\delta \gamma n_0}, \tag{3.12}$$

then the instability holds for (3.9) and certain length $\ell\pi$, and the bifurcations to non-homogeneous steady states occur. To formulate the bifurcation

1) See footnote 2) on p. 415

problem, we make a change of variables $y = \ell^{-1}x$, and the steady state equation for (3.9) becomes

$$\begin{cases} n_{yy} + \lambda\Big[\dfrac{\gamma w}{1+\sigma w}n - n^2 - \mu n\Big] = 0, & y \in (0,\pi), \\ \delta w_{yy} - \beta\delta n_{yy} + \lambda[p - (1-\rho n)w - w^2 n] = 0, & y \in (0,\pi), \\ n'(0) = n'(\pi) = w'(0) = w'(\pi) = 0, \end{cases} \tag{3.13}$$

where $\lambda = \ell^2$ is a parameter representing the characteristic wave length of the spatial pattern. If (3.12) is satisfied, then one can show that if $\lambda^{\pm}$ are the two positive real roots of

$$(\det J)\lambda^2 + (\delta n_0 + p w_0^{-1} + w_0 n_0 - \beta\delta\gamma n_0(1+\sigma w_0)^{-2})\lambda + \delta = 0, \tag{3.14}$$

such that $0 < \lambda^- < \lambda^+$, then $\lambda = \lambda_k^{\pm} = k^2\lambda^{\pm}$ for integer $k \geqslant 1$ are bifurcation points for (3.13). Indeed essentially only one branch of periodic non-homogeneous steady state solutions bifurcates from the curve (λ, n_0, w_0) since the ones bifurcating from $\lambda_k^{\pm}$ correspond to the mode $\cos(ky)$ but after a rescaling they are the same as the one from $\lambda_1^{\pm}$. Pitchfork bifurcation theorem (Theorem 2.4) can be applied here, and we omit the details. Notice that the global branch from each $\lambda_k^{\pm}$ must be unbounded, but it is not clear whether the 'essential branch' (the branch of monotone solutions bifurcating from $\lambda_1^{\pm}$) is unbounded or not.

3.3 Pattern formation with arbitrary diffusion coefficients

In our final example, we consider a diffusive predator-prey system with Holling type II functional response, which has been considered in ecological literature, especially when studying the patchiness of plankton distributions in phytoplankton-zooplankton interaction (see Ref. [25]). The nondimensionalized equation in one space dimension is in the form:

$$\begin{cases} u_t - d_1 u_{xx} = u\Big(1 - \dfrac{u}{k}\Big) - \dfrac{muv}{u+1}, & x \in (0,\ell\pi),\ t > 0, \\ v_t - d_2 v_{xx} = -\theta v + \dfrac{muv}{u+1}, & x \in (0,\ell\pi),\ t > 0, \\ u_x(0,t) = v_x(0,t) = 0, \quad u_x(\ell\pi,t) = v_x(\ell\pi,t) = 0, & t > 0, \\ u(x,0) = u_0(x) \geqslant 0, \quad v(x,0) = v_0(x) \geqslant 0, & x \in (0,\ell\pi). \end{cases} \tag{3.15}$$

For the ODE system in (3.15) without the diffusion:

$$u' = u\Big(1 - \frac{u}{k}\Big) - \frac{muv}{u+1}, \quad v' = -\theta v + \frac{muv}{u+1}, \tag{3.16}$$

there is a rich dynamics which we shall describe briefly, see Refs. [16,17] for more details and related references. System (3.16) has three non-negative equilibrium solutions: $(0,0)$, $(k,0)$, (λ, v_λ), where

$$\lambda = \frac{\theta}{m-\theta}, \quad v_\lambda = \frac{(k-\lambda)(1+\lambda)}{km}.$$

The coexistence equilibrium (λ, v_λ) is in the first quadrant if and only if $m > \theta(1+k)/k$ (or $0 < \lambda < k$). In the following, we shall fix θ and k and use λ as the main bifurcation parameter (or equivalently, m as a parameter). We have the following stability information for the dynamics of (3.16): when $\lambda \geqslant k$, $(k, 0)$ is globally asymptotically stable; when $(k-1)/2 < \lambda < k$, the coexistence equilibrium (λ, v_λ) is globally asymptotically stable; and when $0 < \lambda < (k-1)/2$, there is a globally asymptotically stable periodic orbit [4]. $\lambda = (k-1)/2$ is a bifurcation point where a subcritical Hopf bifurcation occurs. The appearance of the limit cycle is related to the famous paradox of enrichment of Rosenzweig [37].

In Ref. [45], Yi, Wei and Shi considered the bifurcation of steady state solutions and also periodic solutions of (3.15) from the curve of constant steady state solution (λ, v_λ), and gave the following results. Similar to the setting in Subsection 3.1, the linearization operators at (λ, v_λ) are

$$L(\lambda) := \begin{pmatrix} d_1 \dfrac{\partial^2}{\partial x^2} + \dfrac{\lambda(k-1-2\lambda)}{k(1+\lambda)} & -\theta \\ \dfrac{k-\lambda}{k(1+\lambda)} & d_2 \dfrac{\partial^2}{\partial x^2} \end{pmatrix},$$

$$L_n(\lambda) := \begin{pmatrix} -\dfrac{d_1 n^2}{\ell^2} + \dfrac{\lambda(k-1-2\lambda)}{k(1+\lambda)} & -\theta \\ \dfrac{k-\lambda}{k(1+\lambda)} & -\dfrac{d_2 n^2}{\ell^2} \end{pmatrix}.$$

The trace and the determinant of $L_n(\lambda)$ are

$$T_n(\lambda) = \frac{\lambda(k-1-2\lambda)}{k(1+\lambda)} - \frac{(d_1+d_2)n^2}{\ell^2},$$
$$D_n(\lambda) = \frac{\theta(k-\lambda)}{k(1+\lambda)} - \frac{d_2\lambda(k-1-2\lambda)}{k(1+\lambda)}\frac{n^2}{\ell^2} + \frac{d_1 d_2 n^4}{\ell^4}.$$

If there exists an $n \in \mathbb{N}_0$ such that

$$D_n(\lambda_0) = 0, \quad T_n(\lambda_0) \neq 0; \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0, \quad j \neq n, \tag{3.17}$$

and

$$\frac{\mathrm{d}}{\mathrm{d}\lambda} D_n(\lambda_0) \neq 0, \tag{3.18}$$

then $\lambda = \lambda_0$ is a bifurcation point for the steady state solutions, and one can apply Theorems 2.4 and 2.5 to obtain a global branch of nontrivial steady state solutions of (3.15). On the other hand, if there exists an $n \in \mathbb{N}_0$ such that

$$T_n(\lambda_0) = 0, \quad D_n(\lambda_0) > 0; \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0, \quad j \neq n, \tag{3.19}$$

and for the unique pair of complex eigenvalues near the imaginary axis $\alpha(\lambda) \pm \mathrm{i}\,\omega(\lambda)$,

$$\alpha'(\lambda_0) \neq 0, \tag{3.20}$$

then a Hopf bifurcation occurs for (3.15), and a branch of nontrivial periodic orbits bifurcate from the curve of constant steady states.

We know that $\lambda_0^H := (k-1)/2$ is always a Hopf bifurcation point where a spatial homogeneous periodic solution of (3.15) bifurcates. Define

$$A(\lambda) := \frac{\lambda(k-1-2\lambda)}{k(1+\lambda)}$$

for $\lambda \in [0, \lambda_0^H]$. Then $A(0) = A(\lambda_0^H) = 0$, and $A(\lambda) > 0$ in $(0, \lambda_0^H)$, and $A(\lambda)$ has a unique critical point $\lambda = \lambda_*$ at which $A(\lambda)$ achieves a local maximum $A(\lambda_*) = 2\lambda_*^2/k := M_* > 0$. Define

$$\ell_n = n\sqrt{\frac{d_1+d_2}{M_*}}, \quad n \in \mathbb{N}, \tag{3.21}$$

where

$$M_* = \frac{(\sqrt{k+1}-\sqrt{2})^2}{k} > 0.$$

Then for $\ell_n < \ell \leqslant \ell_{n+1},\ 1 \leqslant j \leqslant n$, we define $\lambda_{j,-}^H$ and $\lambda_{j,+}^H$ to be the roots of $A(\lambda) = (d_1+d_2)j^2/\ell^2$ satisfying $0 < \lambda_{j,-}^H < \lambda_* < \lambda_{j,+}^H < \lambda_0^H$. And these $\lambda_{j,\pm}^H$ satisfy

$$\begin{aligned} 0 &< \lambda_{1,-}^H(\ell) < \lambda_{2,-}^H(\ell) < \cdots < \lambda_{n,-}^H(\ell) < \lambda_* \\ &< \lambda_{n,+}^H(\ell) < \cdots < \lambda_{2,+}^H(\ell) < \lambda_{1,+}^H(\ell) < \lambda_0^H, \end{aligned}$$

Clearly, $T_j(\lambda_{j,\pm}^H) = 0$ and $T_i(\lambda_{j,\pm}^H) \neq 0$ for $i \neq j$. Hence, $\lambda_{j,\pm}^H$ are potential Hopf bifurcation points.

Define

$$h(\lambda) := \frac{\lambda^2(k-1-2\lambda)^2}{k(1+\lambda)(k-\lambda)}. \tag{3.22}$$

One can show that for all $\lambda \in (0, \lambda_0^H),\ h(\lambda) > 0,\ h(0) = h(\lambda_0^H) = 0$, and there exists a unique $\lambda^\# \in (0, \lambda_0^H)$, such that $h'(\lambda^\#) = 0,\ h'(\lambda) > 0$ in $(0, \lambda^\#)$ and $h'(\lambda) < 0$ in $(\lambda^\#, \lambda_0^H)$. Then we have the following result on the Hopf bifurcations.

Theorem 3.3 *Suppose that the constants $d_1, d_2, m, \theta > 0$ and $k > 1,\ \ell_n$ are defined as in* (3.21), *and $\lambda_{j,\pm}^H$ are defined as above.*

(1) *If*

$$\frac{d_1}{d_2} > \frac{h(\lambda^\#)}{4\theta}, \tag{3.23}$$

then system (3.15) *undergoes a Hopf bifurcation at $\lambda = \lambda_{j,\pm}^H$, and there is no steady state bifurcation along the curve $\{(\lambda, v_\lambda):\ 0 < \lambda < \lambda_0^H\}$.*

(2) *If*

$$\frac{d_1}{d_2} < \frac{h(\lambda^\#)}{4\theta}, \tag{3.24}$$

and $\lambda^H_{j,\pm} \notin [\underline{\lambda}, \overline{\lambda}]$, *where* $0 < \underline{\lambda} < \overline{\lambda}$ *are the only two roots of* $h(\lambda) = 4\theta d_1/d_2$ *in* $(0, \lambda^H_0)$, *then system* (3.15) *undergoes a Hopf bifurcation at* $\lambda = \lambda^H_{j,\pm} \notin [\underline{\lambda}, \overline{\lambda}]$.

Moreover, the periodic solutions bifurcating from $\lambda = \lambda^H_{j,\pm}$ *are spatially non-homogeneous, and can be parameterized in the form*

$$(u(s), v(s)) = (\lambda^H_{j,\pm}, v_{\lambda^H_{j,\pm}}) + s(a_0, b_0)\cos\frac{jx}{\ell}\cos(\omega_{j,\pm}t) + o(|s|)$$

for small $s > 0$.

For the steady state bifurcations, we notice that

$$D_n(\lambda) = \theta C(\lambda) - d_2 A(\lambda)p + d_1 d_2 p^2,$$

where

$$p = \frac{n^2}{\ell^2}, \quad C(\lambda) = \frac{k-\lambda}{k(1+\lambda)}.$$

Solving p from $D_n(\lambda) = 0$, we have

$$p = p_\pm(\lambda) := \frac{d_2 A(\lambda) \pm \sqrt{C(\lambda)(d_2^2 h(\lambda) - 4d_1 d_2 \theta)}}{2d_1 d_2}.$$

Then we have the result on steady state bifurcation based on Theorems 2.4 and 2.5.

Theorem 3.4 *Suppose that the constants* $d_1, d_2, m, \theta > 0$ *and* $k > 1$ *satisfy* (3.24), *and define*

$$\widetilde{\ell}_{n,+} := \frac{n}{\sqrt{\max p_+(\lambda)}}, \quad \widetilde{\ell}_{n,-} := \frac{n}{\sqrt{\min p_-(\lambda)}}.$$

If for some $n \in \mathbb{N}$, $\ell \in (\widetilde{\ell}_{n,+}, \widetilde{\ell}_{n,-})$ *except a finite many values, there exists exactly two points* $\lambda^S_{n,\pm} \in (\underline{\lambda}, \overline{\lambda})$, *with* $\lambda^S_{n,-} < \lambda^S_{n,+}$, *such that* $p_\pm(\lambda^S_{n,\pm}) = n^2/\ell^2$, *then there is a smooth curve* $\Gamma_{n,\pm}$ *of positive solutions of*

$$\begin{cases} d_1 u_{xx} + u\Big(1 - \dfrac{u}{k}\Big) - \dfrac{muv}{1+u} = 0, & x \in (0, \ell\pi), \\ d_2 v_{xx} - \theta v + \dfrac{muv}{1+u} = 0, & x \in (0, \ell\pi), \\ u'(0) = u'(\ell\pi) = v'(0) = v'(\ell\pi) = 0, \end{cases} \tag{3.25}$$

bifurcating from $(\lambda, u, v) = (\lambda^S_{n,\pm}, \lambda^S_{n,\pm}, v_{\lambda^S_{n,\pm}})$, *with* $\Gamma_{n,\pm}$ *contained in a global branch* $\mathscr{C}_{n,\pm}$ *of the positive solutions of* (3.25). *Moreover,*

(1) *Near* $(\lambda, u, v) = (\lambda^S_{n,\pm}, \lambda^S_{n,\pm}, v_{\lambda^S_{n,\pm}})$,

$$\Gamma_{n,\pm} = \{(\lambda(s), u(s), v(s)) \colon \ s \in (-\varepsilon, \varepsilon)\},$$

where

$$(u(s,x), v(s,x)) = (\lambda^H_{n,\pm}, v_{\lambda^H_{n,\pm}}) + s(a_0, b_0)\cos\frac{nx}{\ell} + o(|s|)$$

for $|s|$ small.

(2) *Either $\mathscr{C}_{n,\pm}$ contains another $(\lambda^S_{j,\pm}, \lambda^S_{j,\pm}, v_{\lambda^S_{j,\pm}})$, or the projection of $\mathscr{C}_{n,\pm}$ onto λ-axis contains the interval $(0, \lambda^S_{n,\pm})$.*

We remark that all the bifurcating spatial non-homogeneous periodic solutions and steady state solutions are unstable, but nevertheless, it shows the richness of spatiotemporal patterns for $\lambda \in (0, (k-1)/2)$. These patterns exist no matter what the effective diffusion coefficient d_1/d_2 is, although d_1/d_2 may affect the type of spatiotemporal patterns. Thus the mechanism of pattern formation here is different from Turing's idea described earlier.

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