

Reaction-Diffusion Models and Bifurcation Theory

Lecture 6: Stability of constant steady state

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Stability

$$\begin{cases} u_t = d\Delta u - V \cdot \nabla u + f(x, u), & x \in \Omega, \quad t > 0, \\ u(x, t) = 0, \text{ or } \nabla u \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Suppose that $v(x)$ is a steady state solution. Let X be an open set of Banach space such that $u_0, v \in X$, and the solution $u(x, t; u_0)$ exists.

- 1 A steady state solution v is stable (Lyapunov stable) in X if for any $\varepsilon > 0$, there exists a $\delta > 0$ such that when $\|u_0 - v\|_X < \delta$, then $\|u(\cdot, t; u_0) - v(\cdot)\|_X < \varepsilon$ for all $t > 0$; v is unstable if it is not stable.
- 2 A steady state solution v is (locally) asymptotically stable (attractive) in X if v is stable, and there exists $\eta > 0$, such that when $\|u_0 - v\|_X < \eta$, then $\lim_{t \rightarrow \infty} \|u(\cdot, t; u_0) - v(\cdot)\|_X = 0$.
- 3 If $v(x)$ is locally asymptotically stable, then the set $X_v = \left\{ u_0 \in X : \lim_{t \rightarrow \infty} \|u(\cdot, t; u_0) - v(\cdot)\|_X = 0 \right\}$ is the basin of attraction of v . A steady state solution v is globally asymptotically stable if $X_v = X$.

Examples of X : $C(\overline{\Omega})$, $W^{1,p}(\Omega)$, $C^{2,\alpha}(\overline{\Omega})$, $C_+(\overline{\Omega}) = \{u_0 \in C(\overline{\Omega}) : u_0(x) \geq 0, x \in \overline{\Omega}\}$.
[\[Brown-Dunne-Gardner, 1981, JDE\]](#) these stabilities are same (under some conditions).

Principle of Linearized Stability

$$\begin{cases} u_t = d\Delta u - V \cdot \nabla u + f(x, u), & x \in \Omega, \quad t > 0, \\ u(x, t) = 0, \text{ or } \nabla u \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Principle of Linearized Stability: Suppose that $v(x)$ is a steady state solution. Consider the eigenvalue problem:

$$\begin{cases} L\phi \equiv d\Delta\phi - V \cdot \nabla\phi + f_u(x, v(x))\phi = \mu\phi, & x \in \Omega, \\ \phi(x) = 0, \text{ or } \nabla\phi \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

If all the eigenvalues of L have negative real part, then v is locally asymptotically stable; and if at least one of eigenvalues of L has positive real part, then v is unstable.

Corollary.

1. Let ρ_1 be the principal eigenvalue of L , then v is locally asymptotically stable if $\rho_1 < 0$, and v is unstable if $\rho_1 > 0$.

2. Define $I(\phi) = \int_{\Omega} [|\nabla\phi(x)|^2 - f_u(x, v(x))\phi^2(x)]dx$. If $V = 0$, then v is locally

asymptotically stable if $I(\phi) > 0$ for any $\phi \in W^{1,2}(\Omega)$, and v is unstable if there exists a $\phi \in W^{1,2}(\Omega)$ for Neumann or $\in W_0^{1,2}(\Omega)$ for Dirichlet) such that $I(\phi) < 0$.

[Smoller, 1982, book, Chapter 11], [Webb, 1985, book]

Autonomous Neumann Problem

$$\begin{cases} u_t = d\Delta u + f(u), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Linearized equation at a steady state solution v :

$$\begin{cases} d\Delta\phi + f'(v)\phi = \mu\phi, & x \in \Omega, \\ \nabla\phi \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

Theorem. Suppose that $v(x) = c$ is a constant steady state solution (so $f(c) = 0$). Then $v(x) = c$ is locally asymptotically stable if $f'(c) < 0$, and $v(x) = c$ is unstable if $f'(c) > 0$.

Note: for $u_t = f(u)$, if $f(c) = 0$, then c is a steady state. Moreover $u = c$ is locally asymptotically stable if $f'(c) < 0$, and $u = c$ is unstable if $f'(c) > 0$. Hence the stability for the ODE and the PDE are the **same** for this case.

Systems

Suppose that Ω is a bounded smooth domain in $\mathbb{R}^n$ with $n \geq 1$.

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Suppose that $(u_*(x), v_*(x))$ is a steady state solution. Then from the Principle of Linearized Stability, we shall consider the eigenvalues of

$$\begin{cases} d_1 \Delta \phi + f_u(u_*, v_*)\phi + f_v(u_*, v_*)\psi = \mu\phi, & x \in \Omega, \\ d_2 \Delta \psi + g_u(u_*, v_*)\phi + g_v(u_*, v_*)\psi = \mu\psi, & x \in \Omega, \\ \nabla \phi \cdot n = \nabla \psi \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

$(u_*(x), v_*(x))$ is locally asymptotically stable if all eigenvalues have negative real part.

Cooperative: $f_v(u, v) \geq 0$, $g_u(u, v) \geq 0$ for $(u, v) \in \mathbb{R}^+ \times \mathbb{R}^+$

Competitive: $f_v(u, v) \leq 0$, $g_u(u, v) \leq 0$ for $(u, v) \in \mathbb{R}^+ \times \mathbb{R}^+$

Consumer-resource, Predator-prey: $f_v(u, v) \leq 0$, $g_u(u, v) \geq 0$ for $(u, v) \in \mathbb{R}^+ \times \mathbb{R}^+$

If the system is cooperative, then the eigenvalue with largest real part is real-valued, and it is a principal eigenvalue μ_1 with a positive eigenfunction. [Sweers, Math Z, 1992] Dirichlet BC

Constant solutions

If the steady state solution $(u_*(x), v_*(x)) \equiv (u_*, v_*)$, then the eigenvalue problem

$$\begin{cases} d_1 \Delta \phi + f_u(u_*, v_*)\phi + f_v(u_*, v_*)\psi = \mu\phi, & x \in \Omega, \\ d_2 \Delta \psi + g_u(u_*, v_*)\phi + g_v(u_*, v_*)\psi = \mu\psi, & x \in \Omega, \\ \nabla \phi \cdot n = \nabla \psi \cdot n = 0, & x \in \partial\Omega. \end{cases}$$

is **solvable**.

$$L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d_1 \Delta \phi \\ d_2 \Delta \psi \end{pmatrix} + \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}$$

Fourier series solution

$$\begin{pmatrix} \phi(x) \\ \psi(x) \end{pmatrix} = \sum_{j=0}^{\infty} \begin{pmatrix} a_j \\ b_j \end{pmatrix} \varphi_j(x).$$

where $0 = \mu_0 < \mu_1 \leq \mu_2 \leq \dots \mu_j \rightarrow \infty$, and

$$\Delta \varphi_j(x) = -\mu_j \varphi_j(x), \quad x \in \Omega, \quad \nabla \varphi \cdot n = 0, \quad x \in \partial\Omega.$$

Reduction to matrix eigenvalues

$$L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d_1 \Delta \phi \\ d_2 \Delta \psi \end{pmatrix} + \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}$$

From the uniqueness of Fourier expansion, we obtain

$$\sum_{j=0}^{\infty} (-\mu_j d_1 a_j + f_u a_j + f_v b_j - \mu a_j) \varphi_j = 0,$$

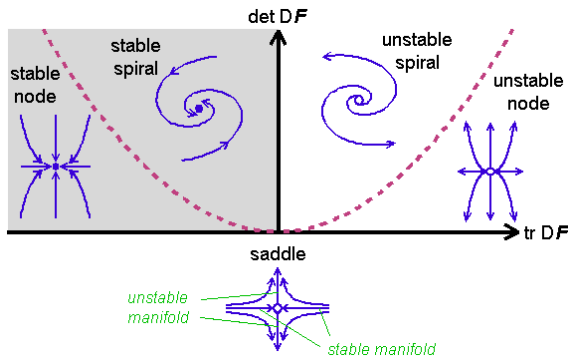
$$\sum_{j=0}^{\infty} (-\mu_j d_2 b_j + g_u a_j + g_v b_j - \mu b_j) \varphi_j = 0,$$

and (a_j, b_j) satisfies

$$L_j \begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} -d_1 \mu_j + f_u & f_v \\ g_u & -d_2 \mu_j + g_v \end{pmatrix} = \lambda \begin{pmatrix} a_j \\ b_j \end{pmatrix}.$$

Theorem 6.1. If $L(\phi, \psi) = \mu(\phi, \psi)$, then there exists $j_i \in \mathbb{N} \cup \{0\}$ ($i = 1, \dots, k$) such that $(\phi, \psi) = \sum_{i=1}^k (a_{j_i}, b_{j_i}) \varphi_{j_i}$ and $L_{j_i}(a_{j_i}, b_{j_i}) = \mu(a_{j_i}, b_{j_i})$. In particular if $i = 1$, then $(\phi, \psi) = (a_j, b_j) \varphi_j$ and $L_j(a_j, b_j) = \mu(a_j, b_j)$.

Trace-determinant plane



Jacobian matrix $J = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$

characteristic equation

$$\lambda^2 + a_1\lambda + a_2 = \lambda^2 - (a + d)\lambda + (ad - bc) = (\lambda - \lambda_1)(\lambda - \lambda_2) = 0$$

$$a_1 = -(a + d) = -\text{Trace}(J) \text{ and } a_2 = ad - bc = \text{Det}(J)$$

Stability: $a_1 > 0$ and $a_2 > 0$, or $\text{Trace}(J) < 0$ and $\text{Det}(J) > 0$.

Stability of (u_*, v_*) w.r.t. R-D system

$$L_j \begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} -d_1\mu_j + f_u & f_v \\ g_u & -d_2\mu_j + g_v \end{pmatrix} = \lambda \begin{pmatrix} a_j \\ b_j \end{pmatrix}.$$

$$T_j = \text{Trace}(L_j) := -(d_1 + d_2)\mu_j + f_u + g_v = -(d_1 + d_2)\mu_j + T_0,$$

$$D_j = \text{Det}(L_j) := d_1d_2\mu_j^2 - (d_1g_v + d_2f_u)\mu_j + f_ug_v - f_vg_u = d_1d_2\mu_j^2 - (d_1g_v + d_2f_u)\mu_j + D_0.$$

Stable with ODE: if $T_0 < 0$ and $D_0 > 0$

Stable with R.D. system: if $T_j < 0$ and $D_j > 0$ for all $j \in \mathbb{N} \cup \{0\}$, and unstable otherwise

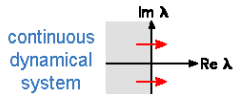
$T_n = 0$: possible Hopf bifurcation occurs

$D_n = 0$: possible steady state bifurcation (pitchfork) occurs

stationary bifurcation



Hopf bifurcation



When the stability is preserved

Let (u_*, v_*) be a constant steady state solution of the R.-D. system

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

The corresponding ODE system is

$$u_t = f(u, v), \quad v_t = g(u, v).$$

Theorem 6.2. If $d_1 = d_2 = d$, then the stability of (u_*, v_*) w.r.t. R.-D. system is same as the one w.r.t. ODE system.

Proof: If λ is an eigenvalue of L_0 , then $\lambda - d\mu_j$ is an eigenvalue of L_j .

Theorem 6.3. If (u_*, v_*) is stable w.r.t. ODE system, then there exists $M > 0$ such that when $d_1, d_2 > M$, then (u_*, v_*) is stable w.r.t. R.-D. system.

Proof: $T_j = \text{Trace}(L_j) = -(d_1 + d_2)\mu_j + f_u + g_v = -(d_1 + d_2)\mu_j + T_0 < 0$ if $T_0 < 0$.
 $D_j = \text{Det}(L_j) = d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + D_0 \geq M^2 \mu_j^2 - C_1 M \mu_j + D_0 =$
 $M \mu_j (M \mu_j - C_1) + D_0 > 0$ if $M > C_1 / \mu_1$ where $C_1 = |f_u| + |g_v|$.

Theorem 6.4. If (u_*, v_*) is stable w.r.t. ODE system, and the function $D(p) = d_1 d_2 p^2 - (d_1 g_v + d_2 f_u)p + D_0 > 0$ for all $p \geq 0$, then (u_*, v_*) is stable w.r.t. R.-D. system.

Alan Turing (1912-1954)



THE CHEMICAL BASIS OF MORPHOGENESIS

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It is suggested that a system of chemical substances, called morphogens, reacting together and diffusing through a tissue, is adequate to account for the main phenomena of morphogenesis. Such a system, although it may originally be quite homogeneous, may later develop a pattern or structure due to an instability of the homogeneous equilibrium, which is triggered off by random disturbances. Such reaction-diffusion systems are considered in some detail in the case of an isolated ring of cells, a mathematically convenient, though biologically unusual system. The investigation is chiefly concerned with the onset of instability. It is found that there are six essentially different forms which this may take. In the most interesting form stationary waves appear on the ring. It is suggested that this might account, for instance, for the tetradic pattern on *Drosophila* and for whorled leaves. A system of reactions and diffusion on a sphere is also considered. Such a system appears to account for gastrulation. Another reaction system in two dimensions gives rise to patterns reminiscent of dappling. It is also suggested that stationary waves in two dimensions could account for the phenomena of phyllotaxis.

The purpose of this paper is to discuss a possible mechanism by which the genes of a cytotype may determine the anatomical structure of the resulting organism. The theory does not make any new hypotheses; it merely suggests that certain well-known physical laws are sufficient to account for many of the facts. The full understanding of the paper requires a good knowledge of mathematics, some biology, and some elementary chemistry. Since readers cannot be expected to be experts in all of these subjects, a number of elementary facts are explained, which can be found in text-books, but whose omission would make the paper difficult reading.

1. A MODEL OF THE EMBRYO. MORPHOGENS

In this section a mathematical model of the growing embryo will be described. This model will be a simplification and an idealization, and consequently a falsification. It is to be hoped that the features retained for discussion are those of greatest importance in the present state of knowledge.

The model takes two slightly different forms. In one of them the cell theory is recognized but the cells are idealized into geometrical points. In the other the matter of the organism is imagined as continuously distributed. The cells are not, however, completely ignored, for various physical and physico-chemical characteristics of the matter as a whole are assumed to have values appropriate to the cellular matter.

With either of the models one proceeds as with a physical theory and defines an entity called 'the state of the system'. One then describes how that state is to be determined from the state at a moment very shortly before. With either model the description of the state consists of two parts, the mechanical and the chemical. The mechanical part of the state describes the positions, masses, velocities and elastic properties of the cells, and the forces between them. In the continuous form of the theory essentially the same information is given in the form of the stress, velocity, density and elasticity of the matter. The chemical

[Turing, 1952] The Chemical Basis of Morphogenesis.

Phil. Trans. Royal Society London B

Turing instability

$$L_j \begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} -d_1\mu_j + f_u & f_v \\ g_u & -d_2\mu_j + g_v \end{pmatrix} = \lambda \begin{pmatrix} a_j \\ b_j \end{pmatrix}.$$

$$T_j = \text{Trace}(L_j) := -(d_1 + d_2)\mu_j + f_u + g_v = -(d_1 + d_2)\mu_j + T_0,$$

$$D_j = \text{Det}(L_j) := d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + f_u g_v - f_v g_u = d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + D_0.$$

If (u_*, v_*) is stable w.r.t. ODE system, then $T_0 < 0$ and $D_0 > 0$.

For $j \geq 1$, $T_j = -(d_1 + d_2)\mu_j + f_u + g_v = -(d_1 + d_2)\mu_j + T_0 < 0$.

So for (u_*, v_*) to be unstable, we must have $D_j < 0$ for some $j \in \mathbb{N}$.

Then $d_1 g_v + d_2 f_u > 0$, f_u and g_v must be of different signs.

We assume that $\underline{f_u > 0}$ and $\underline{g_v < 0}$.

Solving $D_j = d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + D_0 < 0$,

we obtain $0 < d_1 < \frac{d_2 f_u \mu_j - D_0}{\mu_j(d_2 \mu_j - g_v)}$ or $d_2 > \frac{D_0 - d_1 g_v \mu_j}{\mu_j(f_u - d_1 \mu_j)}$.

More stability

Let (u_*, v_*) be a constant steady state solution of the R.-D. system

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

The corresponding ODE system is

$$u_t = f(u, v), \quad v_t = g(u, v).$$

Theorem 6.5. Suppose that (A) $f_u > 0$ (activator), $g_v < 0$ (inhibitor);

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

1. For fixed $d_2 > 0$, if $d_1 > \max_{j \in \mathbb{N}} \frac{d_2 f_u \mu_j - D_0}{\mu_j (d_2 \mu_j - g_v)}$, then (u_*, v_*) is stable w.r.t. R.-D. system.
2. For fixed $d_1 > 0$, if $0 < d_2 < \min_{j \in \mathbb{N}} \frac{D_0 - d_1 g_v \mu_j}{\mu_j (f_u - d_1 \mu_j)}$, then (u_*, v_*) is stable w.r.t. R.-D. system.

Note: 1. there are only finitely many $j \in \mathbb{N}$ such that $\frac{D_0 - d_1 g_v \mu_j}{\mu_j (f_u - d_1 \mu_j)} > 0$.

2. there are infinitely many $j \in \mathbb{N}$ such that $\frac{d_2 f_u \mu_j - D_0}{\mu_j (d_2 \mu_j - g_v)} > 0$, but as $j \rightarrow \infty$,

$$\frac{d_2 f_u \mu_j - D_0}{\mu_j (d_2 \mu_j - g_v)} \rightarrow 0.$$

Turing Instability

Let (u_*, v_*) be a constant steady state solution of the R.-D. system

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

The corresponding ODE system is

$$u_t = f(u, v), \quad v_t = g(u, v).$$

Theorem 6.6. [Turing, 1952] Suppose that (A) $f_u > 0$ (activator), $g_v < 0$ (inhibitor); (B) $D_1 = f_u g_v - f_v g_u > 0$ and $f_u + g_v < 0$.

1. For fixed $d_2 > 0$, if $0 < d_1 < \max_{j \in \mathbb{N}} \frac{d_2 f_u \mu_j - D_0}{\mu_j (d_2 \mu_j - g_v)}$, then (u_*, v_*) is unstable w.r.t. R.-D. system.

2. For fixed $d_1 > 0$, if $d_2 > \min_{j \in \mathbb{N}} \frac{D_0 - d_1 g_v \mu_j}{\mu_j (f_u - d_1 \mu_j)}$, then (u_*, v_*) is unstable w.r.t. R.-D. system.

Turing instability can be caused by small d_1 and large d_2 .

[Gierer-Meinhardt, 1972] short-range activator and long-range inhibitor causes Turing instability.

An artificial example

$$J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} = \begin{pmatrix} 2 & -4 \\ 2 & -3 \end{pmatrix}$$

For ODE, it is stable, since $T_0 = f_u + g_v = -1 < 0$ and $D_0 = f_u g_v - f_v g_u = 2 > 0$.

We also have $f_u = 2 > 0$ and $g_v = -3 < 0$.

Then when $d_2 > \min_{j \in \mathbb{N}} \frac{2 + 3d_1\mu_j}{\mu_j(2 - d_1\mu_j)}$, the Turing instability holds.

Example: $n = 1$, $\Omega = (0, \pi)$, $\mu_j = j^2$, $d_1 = 0.1$

Then for $j = 1, 2, 3, 4$, $\mu_j = 1, 4, 9, 16$, $d_2 > \min \left\{ \frac{23}{19}, \frac{1}{2}, \frac{47}{99}, \frac{17}{16} \right\} = \frac{47}{99}$.

So the steady state loses the stability when $d_2 > 47/99$, and the corresponding eigen-mode is $j = 3$, or $\cos(3x)$.

When $d_2 = 0.5$, the matrix $L_3 = \begin{pmatrix} 2 - d_1\mu_3 & -4 \\ 2 & -3 - d_2\mu_3 \end{pmatrix} = \begin{pmatrix} 1.1 & -4 \\ 2 & -7.5 \end{pmatrix}$,

eigenvalue $\lambda_1 = -6.44$ (eigenvector $(0.47, 0.88)$), $\lambda_2 = 0.039$ (eigenvector $(0.97, 0.26)$)

So the solution is unstable like $(u(x, t), v(x, t)) = (u_*, v_*) + e^{0.039t} (0.97, 0.26) \cos(3x)$

Pattern formation matrix sign patterns

Condition for Turing instability:

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

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

Activator-inhibitor type: $\begin{pmatrix} + & - \\ + & - \end{pmatrix}$

positive feedback type: $\begin{pmatrix} + & + \\ - & - \end{pmatrix}$

Lotka-Volterra equations

[Volterra, 1928] (non-diffusion)

Two species model: $u(t)$, $v(t)$

self growth: logistic; interaction: uv

Cooperative:

$$\begin{cases} u_t = u(a - u + bv) & t > 0, \\ v_t = v(d + cu - v), & t > 0. \end{cases}$$

Competitive:

$$\begin{cases} u_t = u(a - u - bv) & t > 0, \\ v_t = v(d - cu - v), & t > 0. \end{cases}$$

Consumer-resource, Predator-prey:

$$\begin{cases} u_t = u(a - u - bv) & t > 0, \\ v_t = v(d + cu - v), & t > 0. \end{cases}$$

Cooperative system

$$\begin{cases} u_t = u(a - u + bv) & t > 0, \\ v_t = v(d + cu - v), & t > 0. \end{cases}$$

$$\text{Jacobian } J = \begin{pmatrix} a - 2u + bv & bu \\ cv & d - 2v + cu \end{pmatrix},$$

Trivial equilibrium: $(0, 0)$ (unstable)

Semi-trivial equilibrium: $(a, 0)$ (saddle), $(0, d)$ (saddle)

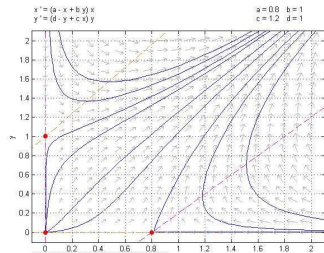
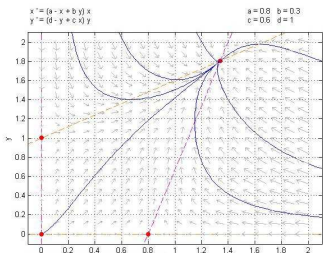
Coexistence equilibrium: $(u_*, v_*) = \left(\frac{ac + d}{1 - bc}, \frac{a + bd}{1 - bc} \right)$ (exists and stable when $bc < 1$)

$$J(u_*, v_*) = \begin{pmatrix} -u_* & bu_* \\ cv_* & -v_* \end{pmatrix}, \quad T_0 = -(u_* + v_*) < 0 \text{ and } D_0 = (1 - bc)u_*v_* > 0$$

Case 1: weak cooperation $0 < bc < 1$: (u_*, v_*) is globally asymptotically stable

Case 2: strong cooperation $bc \geq 1$: no coexistence equilibrium, all solutions are divergent

Cooperative system



Left: weak cooperation; Right: strong cooperation.

Consumer-resource system

$$\begin{cases} u_t = u(a - u - bv) & t > 0, \\ v_t = v(d + cu - v), & t > 0. \end{cases}$$

$$\text{Jacobian } J = \begin{pmatrix} a - 2u - bv & -bu \\ cv & d - 2v + cu \end{pmatrix},$$

Trivial equilibrium: $(0, 0)$ (unstable)

Semi-trivial equilibrium: $(a, 0)$ (saddle), $(0, d)$ (stable if $a < bd$, saddle if $a > bd$)

Coexistence equilibrium: $(u_*, v_*) = \left(\frac{ac + d}{1 + bc}, \frac{a - bd}{1 + bc} \right)$ (exists and stable when $a > bd$)

$$J(u_*, v_*) = \begin{pmatrix} -u_* & -bu_* \\ cv_* & -v_* \end{pmatrix}, \quad T_0 = -(u_* + v_*) < 0 \text{ and } D_0 = (1 + bc)u_*v_* > 0$$

Case 1: strong predation $0 < a \leq bd$ (or $b \geq a/d$): $(0, d)$ is globally asymptotically stable

Case 2: weak predation $a > bd$ (or $0 < b < a/d$): (u_*, v_*) is globally asymptotically stable

Global stability

$$\begin{cases} u_t = u(a - u - bv) & t > 0, \\ v_t = v(d + cu - v), & t > 0. \end{cases}$$

Case 1: strong predation $0 < a \leq bd$ (or $b \geq a/d$): equilibrium $(0, d)$

$$V(u, v) = ku + v - d - d \ln(v/d)$$

$$\dot{V} = ku_t + v_t - dv_t/v = ku(a - u - bv) + v(d + cu - v) - d(d + cu - v) = (ka - cd)u + (c - kb)uv - (v - d)^2 - ku^2$$

So choosing $\frac{c}{b} \leq k \leq \frac{cd}{a}$, then $\dot{V} < 0$ for $u, v \geq 0$.

$\dot{V} = 0$ if and only if $(u, v) = (0, d)$.

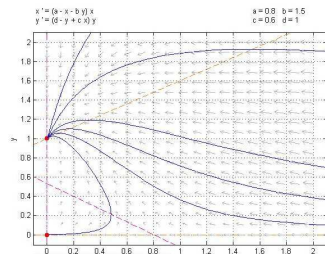
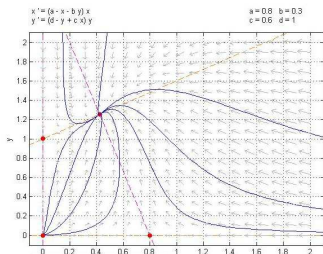
Case 2: weak predation $a > bd$ (or $0 < b < a/d$): $(u_*, v_*) = \left(\frac{ac + d}{1 + bc}, \frac{a - bd}{1 + bc} \right)$

$$V(u, v) = k[u - u_* - u_* \ln(u/u_*)] + v - v_* - v_* \ln(v/v_*)$$

$$\begin{aligned} \dot{V} &= k(1 - u_*/u)u_t + (1 - v_*/v)v_t = k(u - u_*)(a - u - bv) + (v - v_*)(d + cu - v) \\ &= k(u - u_*)(a - u - u_* + u_* - bv - bv_* + bv_*) + (v - v_*)(d + cu + cu_* - cu_* - v - v_* + v_*) \\ &= k(u - u_*)[-(u - u_*) - b(v - v_*)] + (v - v_*)[c(u - u_*) - (v - v_*)] \\ &= (c - kb)(u - u_*)(v - v_*) - k(u - u_*)^2 - (v - v_*)^2 < 0 \text{ (if we choose } k = c/b) \end{aligned}$$

$\dot{V} = 0$ if and only if $(u, v) = (u_*, v_*)$.

Consumer-resource system



Left: weak predation; right: strong predation

Competition system

$$\begin{cases} u_t = u(a - u - bv) & t > 0, \\ v_t = v(d - cu - v), & t > 0. \end{cases}$$

$$\text{Jacobian } J = \begin{pmatrix} a - 2u - bv & -bu \\ -cv & d - 2v - cu \end{pmatrix},$$

Trivial equilibrium: $(0, 0)$ (unstable)

Semi-trivial equilibrium: $(a, 0)$ (saddle if $d > ac$, stable if $d < ac$)

Semi-trivial equilibrium: $(0, d)$ (stable if $a < bd$, saddle if $a > bd$)

Coexistence equilibrium: $(u_*, v_*) = \left(\frac{d - ac}{1 - bc}, \frac{a - bd}{1 - bc} \right)$

(exists and stable when $1 - bc > 0$, $d > ac$ and $a > bd$)

(exists and saddle when $1 - bc < 0$, $d < ac$ and $a < bd$)

$$J(u_*, v_*) = \begin{pmatrix} -u_* & -bu_* \\ -cv_* & -v_* \end{pmatrix}, \quad T_0 = -(u_* + v_*) < 0 \text{ and } D_0 = (1 - bc)u_*v_* > 0$$

(if $0 < bc < 1$); $D_0 = (1 - bc)u_*v_* < 0$ (if $bc > 1$)

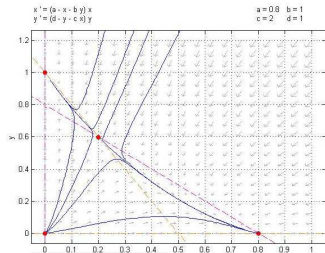
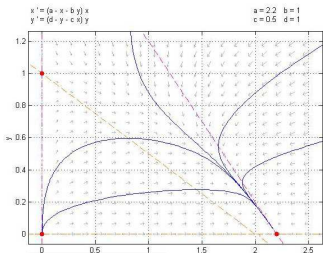
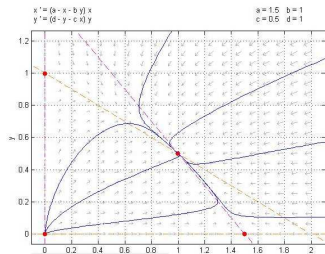
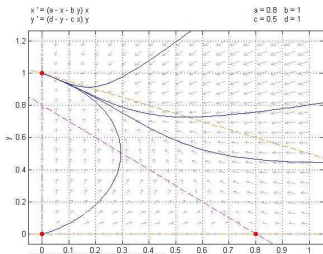
Case 1: **u strong v weak** $a > \max\{d/c, bd\}$: $(a, 0)$ is globally asymptotically stable

Case 2: **u weak v strong** $a < \min\{d/c, bd\}$: $(0, d)$ is globally asymptotically stable

Case 3: **weak competition** $bd < a < d/c$: (u_*, v_*) is globally asymptotically stable

Case 4: **strong competition** $d/c < a < bd$: $(a, 0)$ and $(0, d)$ are bistable

Competition system



Diffusive Lotka-Volterra systems

[Hsu, 2005, TJM]

Theorem 6.7. If $V(u, v) = V_1(u) + V_2(v)$ is a Lyapunov function for the system $x' = f(u, v)$, $v' = g(u, v)$, $V_1''(u) \geq 0$ for $u \geq 0$ and $V_2''(v) \geq 0$ for $v \geq 0$. Then

$W(u, v) = \int_{\Omega} V(u(x, \cdot), v(x, \cdot)) dx$ is a Lyapunov function for the reaction-diffusion system

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Proof. $\dot{W} = \int_{\Omega} (V_1'(u)u_t + V_2'(v)v_t) dx$

$$= \int_{\Omega} (V_1'(u)f(u, v) + V_2'(v)g(u, v)) dx + \int_{\Omega} (d_1 V_1'(u)\Delta u + d_2 V_2'(v)\Delta v) dx$$

$$\leq -d_1 \int_{\Omega} V_1''(u)|\nabla u|^2 dx - d_2 \int_{\Omega} V_2''(v)|\nabla v|^2 dx \leq 0$$

Corollary. For diffusive Lotka-Volterra systems (cooperative, competitive, and consumer-resource), if a constant equilibrium is globally asymptotically stable for the ODE system, then it is globally asymptotically stable for the R.-D. system.

Strong competition case

Only one case: bistable (strong competition) case for the Lotka-Volterra competitive system, there is no globally asymptotically stable equilibrium.

$$\begin{cases} u_t = d_1 \Delta u + u(a - u - bv), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + v(d - v - cu), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

$d/c < a < bd$ and $bc > 1$: $(a, 0)$ and $(0, d)$ are bistable, and (u_*, v_*) is a saddle.

$$\begin{aligned} T_j &= -(d_1 + d_2)\mu_j - (u_* + v_*) < 0 \\ D_j &= d_1 d_2 \mu_j^2 + (d_1 u_* + d_2 v_*)\mu_j - (bc - 1)u_* v_* \end{aligned}$$

From $D_j = 0$, we obtain

$d_1 = \frac{v_*((bc - 1)u_* - d_2\mu_j)}{\mu_j(d_2\mu_j + u_*)}$ is a possible bifurcation point for non-constant steady state solutions bifurcating from (u_*, v_*) . But all bifurcating solutions are unstable.

Open question: is there a periodic orbit in this case?

From monotone dynamical system theory, there are no stable periodic orbits, or stable steady states solutions other than $(a, 0)$ and $(0, d)$.

Rosenzweig-MacArthur model

$$\frac{du}{dt} = u \left(1 - \frac{u}{K} \right) - \frac{muv}{1+u}, \quad \frac{dv}{dt} = -dv + \frac{muv}{1+u}$$

$$\text{Nullcline: } u = 0, v = \frac{(K-u)(1+u)}{m}; \quad v = 0, d = \frac{mu}{1+u}.$$

$$\text{Solving } d = \frac{mu}{1+u}, \text{ one have } u = \lambda \equiv \frac{d}{m-d}.$$

$$\text{Equilibria: } (0, 0), (K, 0), (\lambda, v_\lambda) \text{ where } v_\lambda = \frac{(K-\lambda)(1+\lambda)}{m}$$

We take λ as a bifurcation parameter

Case 1: $\lambda \geq K$: $(K, 0)$ is globally asymptotically stable

Case 2: $(K-1)/2 < \lambda < K$: $(K, 0)$ is a saddle, and (λ, v_λ) is a locally stable equilibrium

Case 3: $0 < \lambda < (K-1)/2$: $(K, 0)$ is a saddle, and (λ, v_λ) is a locally unstable equilibrium ($\lambda = (K-1)/2$ is a Hopf bifurcation point)

Global stability

[Hsu, Hubble, Waltman, SIAM-AM, 1978] [Hsu, Math. Biosci., 1978]

(λ, v_λ) is globally asymptotically stable if $K \leq 1$, or $K > 1$ and $(K - 1)/2 < \lambda < K$.

Lyapunov function for $u' = g(u)(-v + h(u))$, $v' = v(-d + g(u))$ where

$$g(u) = \frac{mu}{1+u} \text{ and } h(u) = \frac{(K-u)(1+u)}{m}$$

$$V(u, v) = \int_\lambda^u \frac{g(s) - g(\lambda)}{g(s)} ds + \int_{v_\lambda}^v \frac{t - v_\lambda}{t} dt$$

$$\dot{V} = \frac{g(u) - g(\lambda)}{g(u)} u_t + \frac{v - v_\lambda}{v} v_t = (g(u) - g(\lambda))(-v + h(u)) + (v - v_\lambda)(-d + g(u))$$

$$= (g(u) - g(\lambda))(h(u) - h(\lambda)) \leq 0$$

if $h(u) - h(\lambda) \geq 0$ for $0 \leq u \leq \lambda$ and $h(u) - h(\lambda) \leq 0$ for $u \geq \lambda$.

[Ardito-Ricciardi, 1995, JMB]

$$V(u, v) = v^\theta \int_\lambda^u \frac{g(s) - g(\lambda)}{g(s)} ds + \int_{v_\lambda}^v t^{\theta-1} \frac{t - v_\lambda}{t} dt$$

[Cheng, SIAM-MA, 1981] If $0 < \lambda < (K - 1)/2$, then (λ, v_λ) is unstable, and there is a unique periodic orbit which is globally asymptotically stable.

More on uniqueness of limit cycle:

[Zhang, 1986, Appl. Anal.], [Kuang-Freedman, 1988, Math. Biosci.]

[Hsu-Hwang, 1995, 1998], [Xiao-Zhang, 2003, 2008]

Summary of ODE

$$\frac{du}{dt} = u \left(1 - \frac{u}{K} \right) - \frac{mu v}{1+u}, \quad \frac{dv}{dt} = -d v + \frac{mu v}{1+u}$$

$$\text{Nullcline: } u = 0, v = \frac{(K-u)(1+u)}{m}; v = 0, d = \frac{mu}{1+u}.$$

$$\text{Solving } d = \frac{mu}{1+u}, \text{ one have } u = \lambda \equiv \frac{d}{m-d}.$$

$$\text{Equilibria: } (0, 0), (K, 0), (\lambda, v_\lambda) \text{ where } v_\lambda = \frac{(K-\lambda)(1+\lambda)}{m}$$

We take λ as a bifurcation parameter

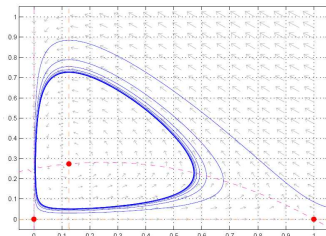
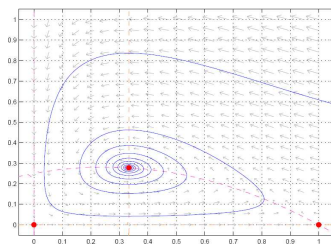
Case 1: $\lambda \geq K$: $(K, 0)$ is globally asymptotically stable

Case 2: $(K-1)/2 < \lambda < K$: (λ, v_λ) is globally asymptotically stable

Case 3: $0 < \lambda < (K-1)/2$: the unique limit cycle is globally asymptotically stable

$(\lambda = (K-1)/2$: Hopf bifurcation point)

Phase Portraits



Left: $(K - 1)/2 < \lambda < K$: $(K, 0)$ is a saddle, and (λ, v_λ) is a locally stable equilibrium

Right: $0 < \lambda < (K - 1)/2$: $(K, 0)$ is a saddle, and (λ, v_λ) is a locally unstable equilibrium; there exists a limit cycle

A supercritical Hopf bifurcation occurs.

Reaction-diffusion model

$$\begin{cases} u_t - d_1 u_{xx} = u \left(1 - \frac{u}{K} \right) - \frac{muv}{u+1}, & x \in (0, \ell\pi), \ t > 0, \\ v_t - d_2 v_{xx} = -dv + \frac{muv}{u+1}, & x \in (0, \ell\pi), \ t > 0, \\ u_x = v_x = 0, \ x = 0, \ell\pi, & t > 0, \\ u(x, 0) = u_0(x), \ v(x, 0) = v_0(x), & x \in (0, \ell\pi). \end{cases}$$

All bifurcations for ODE still occur for PDE as spatial homogeneous solutions.

Case 1: $\lambda \geq K$: $(K, 0)$ is globally stable

Case 2: $K - 1 < \lambda < K$: (λ, v_λ) is globally stable

(when $(K - 1)/2 < \lambda < K - 1$, (λ, v_λ) is locally stable)

Case 3: $0 < \lambda < (K - 1)/2$: a spatial homogeneous periodic orbit

Does the stability change with the addition of diffusion?

Determine the bifurcation points

Linearization at (λ, v_λ) :

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

$$\text{and } L_n(\lambda) := \begin{pmatrix} -\frac{d_1 n^2}{\ell^2} + \frac{\lambda(K-1-2\lambda)}{K(1+\lambda)} & -d \\ \frac{K-\lambda}{K(1+\lambda)} & -\frac{d_2 n^2}{\ell^2} \end{pmatrix}.$$

$$\begin{cases} T_n(\lambda) = \frac{\lambda(K-1-2\lambda)}{K(1+\lambda)} - \frac{(d_1 + d_2)n^2}{\ell^2}, \\ D_n(\lambda) = \frac{d(K-\lambda)}{K(1+\lambda)} - \left[\frac{d_2 \lambda(K-1-2\lambda)}{K(1+\lambda)} \right] \frac{n^2}{\ell^2} + \frac{d_1 d_2 n^4}{\ell^4}. \end{cases}$$

$$L \begin{pmatrix} \phi \\ \psi \end{pmatrix} = \begin{pmatrix} d_1 \Delta \phi \\ d_2 \Delta \psi \end{pmatrix} + \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix} \begin{pmatrix} \phi \\ \psi \end{pmatrix}$$

$$L_j \begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} -d_1 \mu_j + f_u & f_v \\ g_u & -d_2 \mu_j + g_v \end{pmatrix} = \lambda \begin{pmatrix} a_j \\ b_j \end{pmatrix}.$$

$$T_j = \text{Trace}(L_j) := -(d_1 + d_2)\mu_j + f_u + g_v = -(d_1 + d_2)\mu_j + T_0,$$

$$D_j = \text{Det}(L_j) := d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + f_u g_v - f_v g_u = d_1 d_2 \mu_j^2 - (d_1 g_v + d_2 f_u)\mu_j + D_0.$$

Stable with ODE: if $T_0 < 0$ and $D_0 > 0$

Stable with R.D. system: if $T_j < 0$ and $D_j > 0$ for all $j \in \mathbb{N} \cup \{0\}$

$T_n = 0$: possible Hopf bifurcation occurs

$D_n = 0$: possible steady state bifurcation (pitchfork) occurs

$$T(\lambda, p) = -p(d_1 + d_2) + T_0(\lambda),$$

$$D(\lambda, p) = d_1 d_2 p^2 - (d_1 g_v(\lambda) + d_2 f_u(\lambda))p + D_0(\lambda).$$

$\{(\lambda, p) \in \mathbb{R}_+^2 : T(\lambda, p) = 0\}$: Hopf bifurcation curve

$\{(\lambda, p) \in \mathbb{R}_+^2 : D(\lambda, p) = 0\}$: steady state bifurcation curve.

$T(\lambda, \mu_j) = 0$: possible Hopf bifurcation occurs at mode j

$D(\lambda, \mu_j) = 0$: possible steady state bifurcation (pitchfork) occurs at mode j

Spatial non-homogeneous periodic orbits

Condition for Hopf bifurcation:

$$T_n(\lambda_0) = 0, \quad D_n(\lambda_0) > 0, \quad T_j(\lambda_0) \neq 0, \quad D_j(\lambda_0) \neq 0 \quad \text{for } j \neq n.$$

Theorem [Yi-Wei-Shi, JDE, 2009] Suppose $d_1, d_2, d > 0$ and $K > 1$

$$\frac{d_1}{d_2} > \frac{\max h(\lambda)}{4d}, \quad \text{where} \quad h(\lambda) := \frac{\lambda^2(K-1-2\lambda)^2}{K(1+\lambda)(K-\lambda)}.$$

Then there exists $\ell_n > 0$, such that any ℓ in $(\ell_n, \ell_{n+1}]$, there exists $2n$ points $\lambda_{j,\pm}^H(\ell)$, $1 \leq j \leq n$, satisfying

$$0 < \lambda_{1,-}^H(\ell) < \lambda_{2,-}^H(\ell) < \cdots < \lambda_{2,+}^H(\ell) < \lambda_{1,+}^H(\ell) < \frac{K-1}{2},$$

such that a Hopf bifurcation occurs at $\lambda = \lambda_{j,\pm}^H$, and the bifurcating periodic solution at $\lambda = \lambda_{j,\pm}^H$ is in form of

$$(u, v) = (\lambda_{j,\pm}^H, v(\lambda_{j,\pm}^H)) + s(a_0, b_0) \cos\left(\frac{ix}{\ell}\right) \cos(\omega_{j,\pm} t) + h.o.t.$$

(There is no spatial non-homogeneous steady state solutions bifurcating for these parameters.)

More bifurcation: periodic orbits, steady states

Theorem [Yi-Wei-Shi, JDE, 2009] [Peng-Shi, JDE, 2009]

Suppose $d_1, d_2, d > 0$ and $K > 1$ satisfy

$$\frac{d_1}{d_2} < \frac{\max h(\lambda)}{4d}, \quad \text{where} \quad h(\lambda) := \frac{\lambda^2(K-1-2\lambda)^2}{K(1+\lambda)(K-\lambda)}.$$

Then there exist $\tilde{\ell}_{n,\pm}$ such that if for each $\ell \in (\tilde{\ell}_{n,+}, \tilde{\ell}_{n,-})$ except a finite many exceptional ℓ , there exists exactly two points $\lambda_{n,\pm}^S$ such that a smooth curve $\Gamma_{n,\pm}$ of positive solutions of the system bifurcating from $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, and $\Gamma_{n,\pm}$ is contained in a global branch $\mathcal{C}_{n,\pm}$ of the positive solutions. Near $(\lambda, u, v) = (\lambda_{n,\pm}^S, \lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S})$, $\Gamma_{n,\pm} = \{(\lambda(s), u(s), v(s)) : s \in (-\epsilon, \epsilon)\}$, where $(u(s), v(s)) = (\lambda_{n,\pm}^S, v_{\lambda_{n,\pm}^S}) + s(a_n, b_n) \cos(n\pi/\ell) + h.o.t..$ Moreover each $\mathcal{C}_{n,\pm}$ contains another $(\lambda_{j,\pm}^S, \lambda_{j,\pm}^S, v_{\lambda_{j,\pm}^S})$.

A priori estimate of steady states

Theorem[Peng-Shi, JDE, 2009]

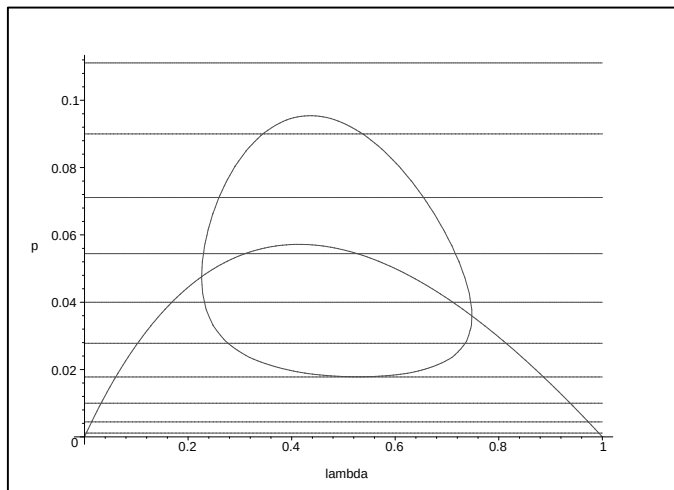
Consider

$$\begin{cases} -d_1 \Delta u = u \left(1 - \frac{u}{K} \right) - \frac{muv}{u+1} & \text{in } \Omega, \\ -d_2 \Delta v = -dv + \frac{muv}{u+1} & \text{in } \Omega, \\ \partial_\nu u = \partial_\nu v = 0 & \text{on } \partial\Omega. \end{cases}$$

Here Ω is a general bounded domain in $\mathbb{R}^n$ with $n \leq 3$. For any given constants $d_1, d_2, d > 0, K > 1$ and a fixed domain Ω , there exists a positive constant M_1 , which depends only on d_1, d_2, K, d and Ω , such that the equation has no non-constant positive solution provided that $m \geq M_1$.

Recall that $\lambda = \frac{d}{m-d}$.

Bifurcation points: periodic orbits and steady states

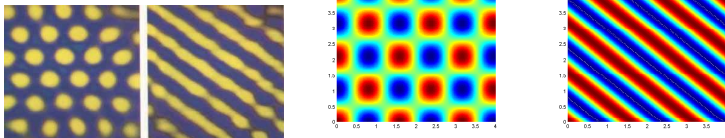


Bifurcation diagram: $d_1 = d_2 = 1$, $k = 3$, $\theta = 0.003$ and $\ell = 30$.

Turing patterns in real experiment

The first experimental evidence of Turing pattern was observed in 1990, nearly 40 years after Turing's prediction, by the Bordeaux group in France, on the chlorite-iodide-malonic acid-starch (CIMA) reaction in an open unstirred gel reactor. This observation represents a significant breakthrough for one of the most fundamental ideas in morphogenesis and biological pattern formation.

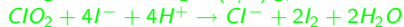
[\[Castets, et.al., 1990, PRL\]](#)



Left: CIMA experiment photos; Right: graph of $\cos(4x)\cos(3y)$ and $\cos(4x + 4y)$

Modeling for CIMA reaction

[Lengyel-Epstein, 1991, Science]



$[ClO_2]$, $[I_2]$ and $[MA]$ varying slowly, assumed to be constant

Let $I^- = X$, $ClO_2 = Y$ and $I_2 = A$. Then the reaction becomes



Reaction rates k_1 , k_2 are constants, and k_3 is proportional to $\frac{[X] \cdot [Y]}{u + [X]^2}$

Reaction-diffusion system for CIMA reaction

Nondimensionalized reaction-diffusion system:

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

Here $[I^-] = u(x, t)$, $[ClO_2] = v(x, t)$, $x \in \Omega$ (reactor)

no flux boundary condition: closed chemical reaction

$a, b, \sigma, c > 0$. Key parameter: $a > 0$ (the feeding rate)

[\[Lengyel-Epstein, 1991, Science\]](#)

Change of parameters:

$$d = \frac{c}{b}, \quad m = \sigma b, \quad \alpha = \frac{a}{5},$$

New equation:

$$\begin{cases} u_t = \Delta u + 5\alpha - u - \frac{4uv}{1+u^2}, & x \in \Omega, t > 0, \\ v_t = m \left(d\Delta v + u - \frac{uv}{1+u^2} \right), & x \in \Omega, t > 0. \end{cases}$$

Turing bifurcation in CIMA model

$$\begin{cases} u_t = u_{xx} + 5\alpha - u - \frac{4uv}{1+u^2}, & x \in (0, \ell\pi), \quad t > 0, \\ v_t = m \left(dv_{xx} + u - \frac{uv}{1+u^2} \right), & x \in (0, \ell\pi), \quad t > 0, \\ u_x(x, t) = v_x(x, t) = 0, & x = 0, \ell\pi, \quad t > 0, \\ u(x, 0) = u_0(x), \quad v(x, 0) = v_0(x), & x \in (0, \ell\pi), \end{cases} \quad (1)$$

Constant equilibrium: $(u_*, v_*) = (\alpha, 1 + \alpha^2)$

Jacobian at (u_*, v_*) : $J = \frac{1}{1 + \alpha^2} \begin{pmatrix} 3\alpha^2 - 5 & -4\alpha \\ 2\alpha^2 & -\alpha \end{pmatrix}$.

Assume $0 < 3\alpha^2 - 5 < \alpha$ (or $1.291 < \alpha < 1.468$)

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

Bifurcation points: $d_j = \frac{\alpha}{1 + \alpha^2} \cdot \frac{5 + \lambda_j}{\lambda_j(f_0 - \lambda_j)}$,

where $f_0 = \frac{3\alpha^2 - 5}{1 + \alpha^2}$, and $\lambda_j = j^2/\ell^2$.

[Ni-Tang, 2005] also true for higher dimensions

Global Turing Bifurcation for CIMA reaction

[Ni-Tang, 2005, Tran. AMS] :

(A) For $d > 0$ small, (u_*, v_*) is the only steady state solution;

(B) All non-negative steady state solution satisfies $0 < u(x) < 5\alpha$,
 $0 < v(x) < 1 + 25\alpha^2$.

[Jang-Ni-Tang, 2004, JDDE] :

(C) Each connected component bifurcated from (d_j, u_*, v_*) is unbounded in the space of (d, u, v) , and its projection over d -axis covers (d_j, ∞) .

(D) For each $d > \min\{d_j\}$ and $d \neq d_k$, there exists a non-constant steady state solution.

Their results are only for steady state solutions.

[Yi-Wei-Shi, 2009, NARW, AML], [Jin-Shi-Wei-Yi, RMJM, 2013 to appear]

ODE Dynamics

Kinetic equation:

$$\begin{cases} u_t = 5\alpha - u - \frac{4uv}{1+u^2}, & t > 0, \\ v_t = m \left(u - \frac{uv}{1+u^2} \right), & t > 0, \end{cases}$$

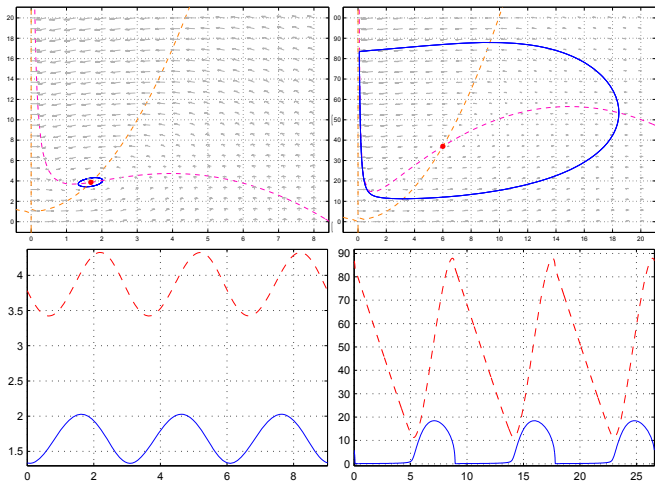
Equilibrium: $(u_*, v_*) = (\alpha, 1 + \alpha^2)$

- (i) For $\alpha < \alpha_0 = \frac{m + \sqrt{m^2 + 60}}{6}$, (u_*, v_*) is locally stable;
- (ii) For $\alpha > \alpha_0$, (u_*, v_*) is locally unstable, and the system has a periodic orbit (α_0 is a Hopf bifurcation point);
- (iii) For $\alpha < \sqrt{27}/5 \approx 1.0392$, (u_*, v_*) is globally asymptotically stable (even for R-D system in higher dimensional domains)

Comparison of bifurcation points:

$$\frac{\sqrt{27}}{5} \approx 1.0392 < \sqrt{\frac{5}{3}} \approx 1.291 < \frac{m + \sqrt{m^2 + 60}}{6} \quad (\text{if } m > 0)$$

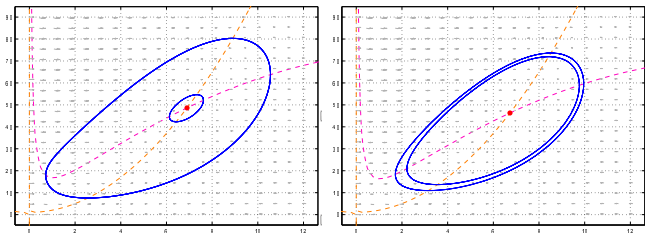
Limit cycle generated from Hopf bifurcation



Here $m = 2$, $\alpha_0 = 5/3 \approx 1.667$. Left: $\alpha = 1.69$; Right: $\alpha = 6$.

Top: phase portraits; Bottom: solution curves (solid curve $u(t)$, dotted curve: $v(t)$)

Multiple periodic orbits for ODE



$$u' = 5\alpha - u - \frac{4uv}{1+u^2}, \quad v' = m \left(u - \frac{uv}{1+u^2} \right).$$

Hopf bifurcation point: $\alpha_0 = (\sqrt{m^2 + 60} + m)/6$
 supercritical if $0 < m < M_0$, and subcritical if $m > M_0$

$$M_0 = \frac{\sqrt{19\sqrt{769} - 147}}{2} \approx 9.7453.$$

Example: $m = 20$, Hopf bifurcation point $\alpha_0 = 6.908$ (subcritical)

Left: $\alpha = 6.90$, Right: $\alpha = 6.73$

(Open Q: how to prove unique or exactly 2 periodic orbits?)

Stability of (u_*, v_*) w.r.t. R-D system

Linearized operator

$$L(\alpha) := \begin{pmatrix} \frac{\partial^2}{\partial x^2} + \frac{3\alpha^2 - 5}{1 + \alpha^2} & -\frac{4\alpha}{1 + \alpha^2} \\ \frac{2m\alpha^2}{1 + \alpha^2} & md\frac{\partial^2}{\partial x^2} - \frac{m\alpha}{1 + \alpha^2} \end{pmatrix}.$$

From Fourier expansion, the eigenvalues of $L(\alpha)$ are the ones of

$$L_n(\alpha) := \begin{pmatrix} -\frac{n^2}{\ell^2} + \frac{3\alpha^2 - 5}{1 + \alpha^2} & -\frac{4\alpha}{1 + \alpha^2} \\ \frac{2m\alpha^2}{1 + \alpha^2} & -md\frac{n^2}{\ell^2} - \frac{m\alpha}{1 + \alpha^2} \end{pmatrix}, \quad n = 0, 1, 2, \dots.$$

The characteristic equation of $L_n(\alpha)$ is

$$\mu^2 - \mu T_n + D_n = 0, \quad n = 0, 1, 2, \dots,$$

Stability of (u_*, v_*) w.r.t. R-D system

$$T_n(\alpha) := \frac{3\alpha^2 - 5 - m\alpha}{1 + \alpha^2} - \frac{n^2}{\ell^2}(1 + md),$$
$$D_n(\alpha) := m \left[\frac{5\alpha}{1 + \alpha^2} - \frac{n^2}{\ell^2} \left(\frac{d(3\alpha^2 - 5) - \alpha}{1 + \alpha^2} \right) + \frac{n^4}{\ell^4} d \right],$$

Stable: if all $T_n < 0$ and $D_n > 0$, and unstable otherwise

$T_n = 0$: possible Hopf bifurcation occurs

$D_n = 0$: possible steady state bifurcation (pitchfork) occurs

$T_0 = 0$ ($3\alpha^2 - 5 - m\alpha = 0$): bifurcation of spatially constant periodic orbit

$D_n = 0$ ($\alpha = 0$): bifurcation of spatially constant steady state

Other bifurcations: We use $\alpha > 0$ as bifurcation parameter.

Spatial Hopf Bifurcation

[Jin-Shi-Wei-Yi]: For any $n \in \mathbb{N}$, $m > 0$, if $\ell > \sqrt{2/3}n$, then there exists $d_* = d_*(m, \ell, n) > 0$ such that when $0 < d < d_*$, there exists $n + 1$ points $\alpha_j^H = \alpha_j^H(d, m, \ell)$, $0 \leq j \leq n$, satisfying

$$0 < \alpha_0^H < \alpha_1^H < \alpha_2^H < \cdots < \alpha_n^H < \infty;$$

At each $\alpha = \alpha_j^H$, the system has a Hopf bifurcation, and the bifurcating periodic solutions near $(\alpha, u, v) = (\alpha_j^H, \alpha_j^H, 1 + (\alpha_j^H)^2)$ can be parameterized as $(\alpha(s), u(s), v(s))$ so that $\alpha(s) = \alpha_j^H + o(s)$,

$$\begin{cases} u(s)(x, t) = \alpha_j^H + s \left(a_n e^{2\pi i t / T(s)} + \overline{a_n} e^{-2\pi i t / T(s)} \right) \cos \frac{n}{\ell} x + o(s), \\ v(s)(x, t) = 1 + (\alpha_j^H)^2 + s \left(b_n e^{2\pi i t / T(s)} + \overline{b_n} e^{-2\pi i t / T(s)} \right) \cos \frac{n}{\ell} x + o(s). \end{cases}$$

[Ni-Tang, 2005]: when d small, there is only the constant steady state.
 $\Rightarrow$ when d small and α large, oscillatory patterns dominate.

Steady state bifurcation

[Jin-Shi-Wei-Yi]: For any $d > 0$, if $\tilde{\ell}_n < \ell < \tilde{\ell}_{n+1}$ for some $n \in \mathbb{N}$ and ℓ is not in a countable subset of $\mathbb{R}^+$, then there exists n points $\alpha_j^S = \alpha_j^S(d, \ell)$, $1 \leq j \leq n$, satisfying

$$\alpha_* < \alpha_1^S < \alpha_2^S < \cdots < \alpha_n^S < \infty,$$

and $\alpha = \alpha_n^S$ is a bifurcation point for steady state solutions.

- (i) There exists a C^∞ smooth curve Γ_j of steady states bifurcating from $(\alpha, u, v) = (\alpha_j^S, u_{\alpha_j^S}, v_{\alpha_j^S})$, with Γ_j contained in a global branch $\mathcal{C}_j$ of the solution set, and near bifurcation point, the solutions on the curve Γ_j has the form $u_j(s) = \alpha_j^S + sa_j \cos(k_j x / \ell) + o(s)$, $v_j(s) = 1 + (\alpha_j^S)^2 + sb_j \cos(k_j x / \ell) + o(s)$ for some $k_j \in \mathbb{N}$;
- (ii) Each $\mathcal{C}_j$ is unbounded, that is, the projection of $\mathcal{C}_j$ on the α -axis contains (α_j^S, ∞) .

$\Rightarrow$ when $\alpha > \alpha_1^S$, and $\alpha \neq \alpha_i^S$, then the system has a non-constant steady state solution.

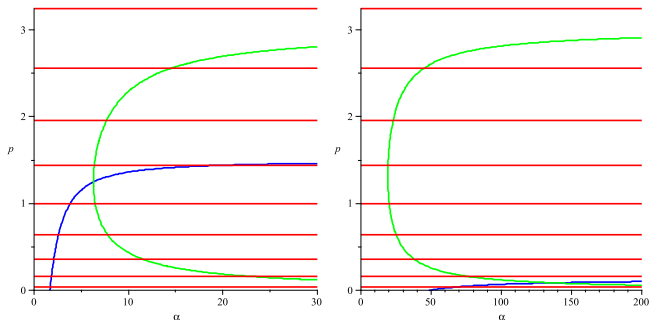
Global Bifurcation picture

- (i) If $\alpha < 1.0392$, (u_*, v_*) is globally asymptotically stable;
- (ii) If $1.0392 < \alpha < 1.2910$, (u_*, v_*) is locally asymptotically stable;
- (iii) If $1.2910 < \alpha < (\sqrt{m^2 + 60} + m)/6$, it is Turing instability zone, bifurcation of non-constant steady states, also possible backward Hopf bifurcation;
- (iv) If $\alpha > (\sqrt{m^2 + 60} + m)/6$, then many intervening Hopf and steady bifurcations occur as $\alpha \rightarrow \infty$.

Hopf bifurcation occurs not only when d is small, but also any $d > 0$, but m is small.

Steady state bifurcation also occurs for all $d > 0$ (so not necessarily Turing type).

Global Bifurcation diagram



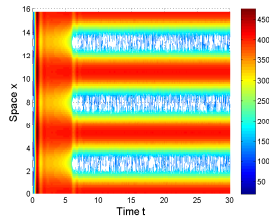
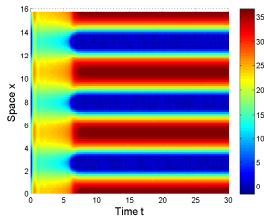
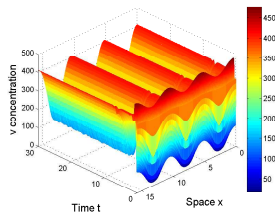
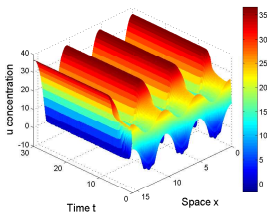
Intersection of **green** and **red** curves: Steady state bifurcation points

Intersection of **blue** and **red** curves: Hopf bifurcation points

Left: Hopf bifurcation first; Right: Steady state bifurcation first

Numerical simulations

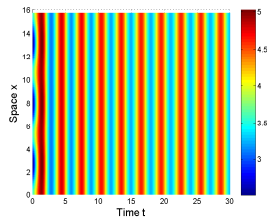
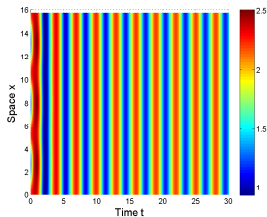
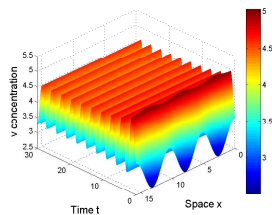
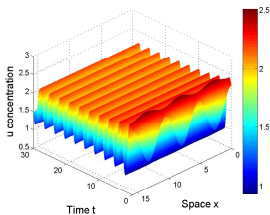
Turing pattern: non-constant steady state solution



Left: $u(x, t)$, Right: $v(x, t)$

Numerical simulations

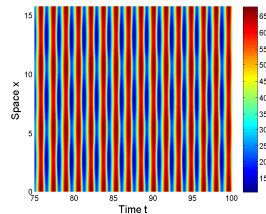
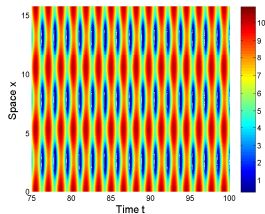
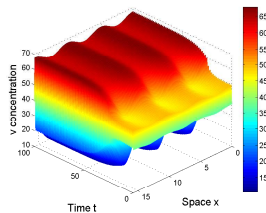
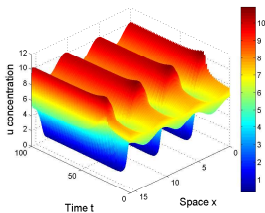
Hopf pattern: constant periodic orbit



Left: $u(x, t)$, Right: $v(x, t)$

Numerical simulations

Turing-Hopf pattern: non-constant periodic orbit



Left: $u(x, t)$, Right: $v(x, t)$

Methods to prove global stability in reaction-diffusion systems

(a) Upper-lower solution method.

[Pao, 1982, JMAA] [Pao, 1996, JMAA]

(b) Fluctuation Method.

[Thieme-Zhao, 2001, NA-RW], [Zhao, 2010, Cana.Appl.Math.Q]

(c) Lyapunov method.

[Hsu, 2005, TMJ]

$$\text{Lotka-Volterra: } V(u, v) = k[u - u_* - u_* \ln(u/u_*)] + v - v_* - v_* \ln(v/v_*) = k \int_{u_*}^u \frac{s - u_*}{s} ds + \int_{v_*}^v \frac{t - v_*}{t} dt \text{ for } u' = u(a - u \pm bv), v' = v(d - v \pm cu).$$

$$\text{Rosenzweig-MacArthur: } V(u, v) = \int_{\lambda}^u \frac{g(s) - g(\lambda)}{g(s)} ds + \int_{v_{\lambda}}^v \frac{t - v_{\lambda}}{t} dt$$

for $u' = g(u)(-v + h(u))$, $v' = v(-d + g(u))$

Delayed Diffusive Leslie-Gower Predator-Prey Model

[Chen-Shi-Wei, 2012, IJBC]

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} - d_1 \Delta u(t, x) = u(t, x)(p - \alpha u(t, x) - \beta v(t - \tau_1, x)), & x \in \Omega, t > 0, \\ \frac{\partial v(t, x)}{\partial t} - d_2 \Delta v(t, x) = \mu v(t, x) \left(1 - \frac{v(t, x)}{u(t - \tau_2, x)} \right), & x \in \Omega, t > 0, \\ \frac{\partial u(t, x)}{\partial \nu} = \frac{\partial v(t, x)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, t) = u_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_2, 0], \\ v(x, t) = v_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_1, 0]. \end{cases}$$

Constant steady state: $(u_*, v_*) = \left(\frac{p}{\alpha + \beta}, \frac{p}{\alpha + \beta} \right)$.

Delayed Diffusive Leslie-Gower Predator-Prey Model

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$$\begin{cases} \frac{\partial u(t, x)}{\partial t} - d_1 \Delta u(t, x) = u(t, x)(p - \alpha u(t, x) - \beta v(t - \tau_1, x)), & x \in \Omega, t > 0, \\ \frac{\partial v(t, x)}{\partial t} - d_2 \Delta v(t, x) = \mu v(t, x) \left(1 - \frac{v(t, x)}{u(t - \tau_2, x)} \right), & x \in \Omega, t > 0, \\ \frac{\partial u(t, x)}{\partial \nu} = \frac{\partial v(t, x)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, t) = u_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_2, 0], \\ v(x, t) = v_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_1, 0]. \end{cases}$$

Constant steady state: $(u_*, v_*) = \left(\frac{p}{\alpha + \beta}, \frac{p}{\alpha + \beta} \right)$.

Main result: (a) If $\alpha > \beta$, then (u_*, v_*) is globally asymptotically stable for any $\tau_1 \geq 0, \tau_2 \geq 0$. (proved with upper-lower solution method)

(b) If $\alpha < \beta$, then there exists $\tau_* > 0$ such that (u_*, v_*) is stable for $\tau_1 + \tau_2 < \tau_*$, and it is unstable for $\tau_1 + \tau_2 > \tau_*$.

Delayed Diffusive Leslie-Gower Predator-Prey Model

[Chen-Shi-Wei, 2012, IJBC]

$$\begin{cases} \frac{\partial u(t, x)}{\partial t} - d_1 \Delta u(t, x) = u(t, x)(p - \alpha u(t, x) - \beta v(t - \tau_1, x)), & x \in \Omega, t > 0, \\ \frac{\partial v(t, x)}{\partial t} - d_2 \Delta v(t, x) = \mu v(t, x) \left(1 - \frac{v(t, x)}{u(t - \tau_2, x)} \right), & x \in \Omega, t > 0, \\ \frac{\partial u(t, x)}{\partial \nu} = \frac{\partial v(t, x)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, t) = u_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_2, 0], \\ v(x, t) = v_0(x, t) \geq 0, & x \in \Omega, t \in [-\tau_1, 0]. \end{cases}$$

Constant steady state: $(u_*, v_*) = \left(\frac{p}{\alpha + \beta}, \frac{p}{\alpha + \beta} \right)$.

Main result: (a) If $\alpha > \beta$, then (u_*, v_*) is globally asymptotically stable for any $\tau_1 \geq 0, \tau_2 \geq 0$. (proved with upper-lower solution method)

(b) If $\alpha < \beta$, then there exists $\tau_* > 0$ such that (u_*, v_*) is stable for $\tau_1 + \tau_2 < \tau_*$, and it is unstable for $\tau_1 + \tau_2 > \tau_*$.

[Du-Hsu, 2004, JDE] When $\tau_1 = \tau_2 = 0$, if $\alpha > s_0 \beta$, for some $s_0 \in (1/5, 1/4)$, then (u_*, v_*) is globally asymptotically stable. (proved with Lyapunov function, and it is conjectured that the global stability holds for all $\alpha, \beta > 0$.)

Global stability (Lyapunov)

[Du-Hsu, 2004, JDE]

$$\begin{cases} u_t - d_1 \Delta u = u(p - \alpha u - \beta v), & x \in \Omega, \ t > 0, \\ v_t - d_2 \Delta v = \mu v \left(1 - \frac{v}{u}\right), & x \in \Omega, \ t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \geq 0, \ v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

$$W(u, v) = \int_{\Omega} V(u, v) dx, \quad V(u, v) = k \int_{u_*}^u \frac{s - u_*}{s^2} ds + \int_{v_*}^v \frac{t - v_*}{t} dt$$

$$\begin{aligned} \dot{V} &= k \frac{u - u_*}{u^2} u_t + \frac{v - v_*}{v} v_t = k \frac{u - u_*}{u} (p - \alpha u - \beta v) + \mu (v - v_*) (1 - v/u) \\ &= (\mu - k\beta) \frac{(u - u_*)(v - v_*)}{u} - k\alpha \frac{(u - u_*)^2}{u} - \mu \frac{(v - v_*)^2}{u} < 0 \quad (\text{choose } k = \frac{\mu}{\beta}) \end{aligned}$$

$$\dot{W} = -d_1 \int_{\Omega} \frac{2u_* - u}{u^3} |\nabla u|^2 dx - d_2 \int_{\Omega} \frac{v_*}{v^2} |\nabla v|^2 dx.$$

$$u(x, t) \leq \frac{p}{\alpha}, \quad u_* = \frac{p}{\alpha + \beta} \quad \text{so } 2u_* - u \geq 0 \text{ if } \alpha \geq \beta.$$

$$V(u, v) = k \int_{u_*}^u \frac{s^2 - u_*^2}{s^2} ds + \int_{v_*}^v \frac{t - v_*}{t} dt: \text{ prove the global stability for } \alpha > q\beta \text{ for } q \in (0.2, 0.25).$$

Global stability (comparison)

[Chen-Shi-Wei, 2012, IJBC]

$$\begin{cases} u_t - d_1 \Delta u = u(p - \alpha u - \beta v), & x \in \Omega, \ t > 0, \\ v_t - d_2 \Delta v = \mu v \left(1 - \frac{v}{u}\right), & x \in \Omega, \ t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \geq 0, \ v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Step 1: $u_t - d_1 \Delta u = u(p - \alpha u - \beta v(t - \tau_1)) \leq u(p - \alpha u)$, so there exists $t_1 > 0$ such that $u(t, x) < \frac{p}{\alpha} + \epsilon$ for $t \geq t_1$.

Step 2: $v_t - d_2 \Delta v = \mu v \left(1 - \frac{v}{u}\right) < \mu v \left(1 - \frac{v}{(p/\alpha) + \epsilon}\right)$, so there exists $t_2 > t_1$

such that $v(t, x) < \frac{p}{\alpha} + \epsilon$ for any $t \geq t_2$.

Step 3: There exists $\delta > 0$ such that

$$(u(t, x), v(t, x)) > \left(\frac{\delta}{\alpha} \left(p - \beta \left(\frac{p}{\alpha} + \epsilon \right) \right), \frac{\delta}{\alpha} \left(p - \beta \left(\frac{p}{\alpha} + \epsilon \right) \right) \right) > (0, 0).$$

Step 4: $\left(\frac{p}{\alpha} + \epsilon, \frac{p}{\alpha} + \epsilon \right)$ is an upper solution, and

$\left(\frac{\delta}{\alpha} \left(p - \beta \left(\frac{p}{\alpha} + \epsilon \right) \right), \frac{\delta}{\alpha} \left(p - \beta \left(\frac{p}{\alpha} + \epsilon \right) \right) \right)$ is a lower solution. Then two constant iterative sequences can be defined, and the sequences converge to a unique limit.

Types of systems

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Quasi-monotone nondecreasing (cooperative): $f(u, v)$ nondecreasing in v and $g(u, v)$ nondecreasing in u

Quasi-monotone nonincreasing (competitive): $f(u, v)$ nonincreasing in v and $g(u, v)$ nonincreasing in u

Mixed Quasi-monotone (consumer-resource): $f(u, v)$ nonincreasing in v and $g(u, v)$ nondecreasing in u

Upper solution $(\bar{u}, \bar{v})$ and lower solution $(\underline{u}, \underline{v})$

$$\bar{u}(x, t) \geq \underline{u}(x, t), \quad \bar{v}(x, t) \geq \underline{v}(x, t), \quad x \in \Omega, \quad t > 0,$$

$$\nabla \bar{u} \cdot n \geq \nabla \underline{u} \cdot n \geq \nabla \underline{u} \cdot n, \quad x \in \partial\Omega, \quad t > 0,$$

$$\nabla \bar{v} \cdot n \geq \nabla \underline{v} \cdot n \geq \nabla \underline{v} \cdot n, \quad x \in \partial\Omega, \quad t > 0,$$

$$\bar{u}(x, 0) \geq u_0(x) \geq \underline{u}(x, 0), \quad \bar{v}(x, 0) \geq v_0(x) \geq \underline{v}(x, 0), \quad x \in \Omega.$$

Solution from upper-lower solutions

Quasi-monotone nondecreasing (cooperative): $f(u, v)$ nondecreasing in v and $g(u, v)$ nondecreasing in u

$$\begin{cases} \bar{u}_t - d_1 \Delta \bar{u} - f(\bar{u}, \bar{v}) \geq 0 \geq \underline{u}_t - d_1 \Delta \underline{u} - f(\underline{u}, \underline{v}), \\ \bar{v}_t - d_2 \Delta \bar{v} - g(\bar{u}, \bar{v}) \geq 0 \geq \underline{v}_t - d_2 \Delta \underline{v} - g(\underline{u}, \underline{v}), \end{cases}$$

Quasi-monotone nonincreasing (competitive): $f(u, v)$ nonincreasing in v and $g(u, v)$ nonincreasing in u

$$\begin{cases} \bar{u}_t - d_1 \Delta \bar{u} - f(\bar{u}, \underline{v}) \geq 0 \geq \underline{u}_t - d_1 \Delta \underline{u} - f(\underline{u}, \bar{v}), \\ \bar{v}_t - d_2 \Delta \bar{v} - g(\underline{u}, \bar{v}) \geq 0 \geq \underline{v}_t - d_2 \Delta \underline{v} - g(\bar{u}, \underline{v}), \end{cases}$$

Mixed Quasi-monotone (consumer-resource):

$$\begin{cases} \bar{u}_t - d_1 \Delta \bar{u} - f(\bar{u}, \underline{v}) \geq 0 \geq \underline{u}_t - d_1 \Delta \underline{u} - f(\underline{u}, \bar{v}), \\ \bar{v}_t - d_2 \Delta \bar{v} - g(\bar{u}, \bar{v}) \geq 0 \geq \underline{v}_t - d_2 \Delta \underline{v} - g(\underline{u}, \underline{v}), \end{cases}$$

Theorem. [Pao, 1982, JMAA], [Pao, 2002, NA] If there exists a pair of upper and lower solutions $(\bar{u}, \bar{v})$ and $(\underline{u}, \underline{v})$, then the system has a unique solution $(u(x, t), v(x, t))$ satisfying $\underline{u} \leq u \leq \bar{u}$ and $\underline{v} \leq v \leq \bar{v}$. Moreover if $(\bar{u}, \bar{v})$ and $(\underline{u}, \underline{v})$ are constants, then the limits of iterative sequences starting from $(\bar{u}, \bar{v})$ and $(\underline{u}, \underline{v})$ exist; if the limits are same, then the solutions all converge to the limit.

Iterative sequences

Quasi-monotone nondecreasing (cooperative): $f(u, v)$ nondecreasing in v and $g(u, v)$ nondecreasing in u

$$\begin{cases} \overline{u^k}_t - d_1 \Delta \overline{u^k} + M \overline{u^k} = M \overline{u^{k-1}} + f(\overline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \overline{v^k}_t - d_2 \Delta \overline{v^k} + M \overline{v^k} = M \overline{v^{k-1}} + g(\overline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{u^k}_t - d_1 \Delta \underline{u^k} + M \underline{u^k} = M \underline{u^{k-1}} + f(\underline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{v^k}_t - d_2 \Delta \underline{v^k} + M \underline{v^k} = M \underline{v^{k-1}} + g(\underline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0. \end{cases}$$

Quasi-monotone nonincreasing (competitive): $f(u, v)$ nonincreasing in v and $g(u, v)$ nonincreasing in u

$$\begin{cases} \overline{u^k}_t - d_1 \Delta \overline{u^k} + M \overline{u^k} = M \overline{u^{k-1}} + f(\overline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \overline{v^k}_t - d_2 \Delta \overline{v^k} + M \overline{v^k} = M \overline{v^{k-1}} + g(\underline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{u^k}_t - d_1 \Delta \underline{u^k} + M \underline{u^k} = M \underline{u^{k-1}} + f(\underline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{v^k}_t - d_2 \Delta \underline{v^k} + M \underline{v^k} = M \underline{v^{k-1}} + g(\overline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0. \end{cases}$$

Mixed Quasi-monotone (consumer-resource):

$$\begin{cases} \overline{u^k}_t - d_1 \Delta \overline{u^k} + M \overline{u^k} = M \overline{u^{k-1}} + f(\overline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \overline{v^k}_t - d_2 \Delta \overline{v^k} + M \overline{v^k} = M \overline{v^{k-1}} + g(\underline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{u^k}_t - d_1 \Delta \underline{u^k} + M \underline{u^k} = M \underline{u^{k-1}} + f(\underline{u^{k-1}}, \overline{v^{k-1}}), & x \in \Omega, \quad t > 0, \\ \underline{v^k}_t - d_2 \Delta \underline{v^k} + M \underline{v^k} = M \underline{v^{k-1}} + g(\overline{u^{k-1}}, \underline{v^{k-1}}), & x \in \Omega, \quad t > 0. \end{cases}$$

Fluctuation Method

[Zhao, 2010, CAMQ] (for scalar equation with diffusion, delay and nonlocal terms)

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Theorem. Assume that

- (consumer-resource type) Suppose that $f(u, v)$ is nonincreasing in v and $g(u, v)$ is nondecreasing in u .
- (solution bound) There exist $\bar{u} \geq \underline{u}$ and $\bar{v} \geq \underline{v}$ such that, for any (u_0, v_0) , there exists $T > 0$ such that when $t \geq T$, $\bar{u} \geq u(x, t) \geq \underline{u}$ and $\bar{v} \geq v(x, t) \geq \underline{v}$.
- (upper-lower solution) $(\bar{u}, \bar{v})$ and $(\underline{u}, \underline{v})$ satisfy

$$f(\bar{u}, \underline{v}) \leq 0 \leq f(\underline{u}, \bar{v}), \quad g(\bar{u}, \bar{v}) \leq 0 \leq g(\underline{u}, \underline{v}).$$

- (uniqueness) For any $(\bar{w}, \bar{z})$ and $(\underline{w}, \underline{z})$ satisfying $\bar{u} \geq \bar{w} \geq \underline{w} \geq \underline{u}$, $\bar{v} \geq \bar{z} \geq \underline{z} \geq \underline{v}$, if

$$f(\bar{w}, \underline{z}) \geq 0 \geq f(\underline{w}, \bar{z}), \quad g(\bar{w}, \bar{z}) \geq 0 \geq g(\underline{w}, \underline{z}),$$

then $\bar{w} = \underline{w}$, $\bar{z} = \underline{z}$.

Then there exists a unique constant steady state (u_*, v_*) satisfying $\bar{u} \geq u_* \geq \underline{u}$ and $\bar{v} \geq v_* \geq \underline{v}$ and (u_*, v_*) is globally asymptotically stable.

Fluctuation Method

Define $u^\infty(x) = \limsup_{t \rightarrow \infty} u(x, t)$, $u_\infty(x) = \liminf_{t \rightarrow \infty} u(x, t)$

$v^\infty(x) = \limsup_{t \rightarrow \infty} v(x, t)$, $v_\infty(x) = \liminf_{t \rightarrow \infty} v(x, t)$

$u^\infty = \sup_{x \in \overline{\Omega}} u^\infty(x)$, $u_\infty = \inf_{x \in \overline{\Omega}} u_\infty(x)$, $v^\infty = \sup_{x \in \overline{\Omega}} v^\infty(x)$, $v_\infty = \inf_{x \in \overline{\Omega}} v_\infty(x)$.

Let $M > 0$ be a constant such that $f_M(u, v) = Mu + f(u, v)$ is increasing in u , and $g_M(u, v) = Mv + g(u, v)$ is increasing in v . Then

$$u(x, t) = e^{-Mt} \int_{\Omega} \Gamma_1(x, y, t) u_0(y) dy + \int_0^t e^{-Ms} \int_{\Omega} \Gamma_1(x, y, s) f_M(u(y, s), v(y, s)) dy ds$$

$$v(x, t) = e^{-Mt} \int_{\Omega} \Gamma_2(x, y, t) v_0(y) dy + \int_0^t e^{-Ms} \int_{\Omega} \Gamma_2(x, y, s) g_M(u(y, s), v(y, s)) dy ds$$

where $\Gamma_i(x, y, t)$ ($i = 1, 2$) is the Green's function of $w_t = d_i \Delta w$ on Ω with Neumann boundary condition.

From Fatou's lemma, $u^\infty(x) \leq \int_0^\infty e^{-Ms} \int_{\Omega} \Gamma_1(x, y, s) f_M(u^\infty(y), v_\infty(y)) dy ds$

Then from $\int_{\Omega} \Gamma(x, y, s) dy = 1$ and $\int_0^\infty e^{-Ms} ds = 1/M$, we have

$$u^\infty \leq \frac{f_M(u^\infty, v_\infty)}{M} = \frac{Mu^\infty + f(u^\infty, v_\infty)}{M} = u^\infty + \frac{f(u^\infty, v_\infty)}{M}.$$

Hence $f(u^\infty, v_\infty) \geq 0$.

Fluctuation Method

Similarly we obtain

$$f(u^\infty, v_\infty) \geq 0, f(u_\infty, v^\infty) \leq 0, g(u^\infty, v^\infty) \geq 0, g(u_\infty, v_\infty) \leq 0.$$

From condition 3 (Uniqueness), $u^\infty = u_\infty$ and $v^\infty = v_\infty$.

Since

$$0 \geq f(\bar{u}, \underline{v}) \geq f(u^\infty, v_\infty) \geq 0, \text{ then}$$

$$f(u^\infty, v_\infty) = 0, f(u_\infty, v^\infty) = 0, g(u^\infty, v^\infty) = 0, g(u_\infty, v_\infty) = 0. \text{ Hence}$$
$$u^\infty = u_\infty = u_* \text{ and } v^\infty = v_\infty = v_* \text{ from the condition 3 (Uniqueness).}$$

Conclusions.

1. For autonomous reaction-diffusion equation with no-flux boundary condition, the global stability of the constant equilibrium can be established by this new theorem.
2. For this type of equations, the upper-lower solution method and the fluctuation method are essentially same.

Invariant rectangle

$$\begin{cases} u_t = d_1 \Delta u + f(u, v), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v), & x \in \Omega, \quad t > 0, \\ \nabla u \cdot n = \nabla v \cdot n = 0, & x \in \partial\Omega, \quad t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Suppose that there exist $(\bar{u}, \bar{v})$ and $(\underline{u}, \underline{v})$ satisfy

$$\begin{aligned} f(\bar{u}, v) &\leq 0, \quad \underline{v} \leq v \leq \bar{v}, \quad f(\underline{u}, v) \geq 0, \quad \underline{v} \leq v \leq \bar{v}, \\ g(u, \bar{v}) &\leq 0, \quad \underline{u} \leq u \leq \bar{u}, \quad g(\underline{u}, \underline{v}) \geq 0, \quad \underline{u} \leq u \leq \bar{u}. \end{aligned}$$

Then $R = (\underline{u}, \bar{u}) \times (\underline{v}, \bar{v})$ is an invariant rectangle for the system, in the sense that, if $(u_0(x), v_0(x)) \in R$ for all $x \in \bar{\Omega}$, then $(u(x, t), v(x, t)) \in R$ for all $x \in \bar{\Omega}$ and $t > 0$.