

Bifurcation Theory and its applications in PDEs and Mathematical Biology

Lecture 5: Nonlocal Models

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First word

Terence McKenna (1946-2000)

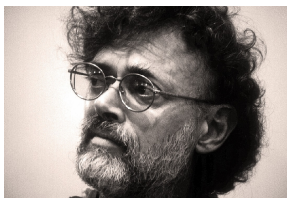
The imagination is a dimension of nonlocal information.

Deepak Chopra (1946-)

DNA is a quantum computer that localizes a non-local omnipresent consciousness or spirit into space time energy information and matter.

Bernie S. Siegel (1932-)

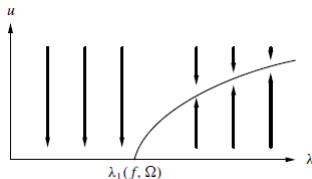
Consciousness is non-local and does not depend on words to communicate.



Logistic equation

$$\frac{dP(t)}{dt} = aP(t) \left(1 - \frac{P(t)}{K}\right)$$

Here $P(t)$ is the quantity of a substance at time t , a is the growth rate per capita, and K is the carrying capacity. It has been extensively used in mathematical modeling of physical, chemical, and biological events.



Notice sur la loi que la population suit dans son accroissement,
par P.-F. VERHULST.

On sait que le célèbre *Malthus* a établi comme principe que la population humaine *tend* à croître en progression géométrique, de manière à se doubler après une certaine période, par exemple, tous les vingt-cinq ans. Cette proposition est incontestable, si l'on fait abstraction de la difficulté toujours croissante de se

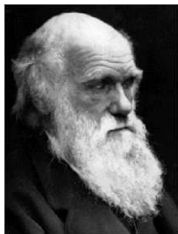
Logistic equation was first proposed Belgium mathematician Pierre Francois Verhulst (1804-1849) in 1838. But it did not get any attention in 19th century.

Fisher-Haldane-Wright law

Darwin-Mendel's gene evolution theory assumes that the advantageous gene replaces other gene in the long run through mutations or genetic drift. Suppose that for a gene with two possible alleles: P (advantageous) and Q (non-advantageous). Then the frequency of the advantageous gene in the n -th and $(n+1)$ -th generations is described by the Fisher-Haldane-Wright law:

$$p_{n+1} = \frac{(w_x p_n^2 + w_y p_n q_n) p_n}{w_x p_n^2 + 2w_y p_n q_n + w_z q_n^2}, q_{n+1} = 1 - p_{n+1}.$$

where $w_x : w_y : w_z$ are the fitness parameters of $PP : PQ : QQ$ type genes.



Left: Charles Darwin (1809-1882), right: Gregor Mendel (1822-1884)

Fisher-Haldane-Wright equation

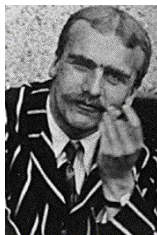
Fisher-Haldane-Wright equation can be written as

$$p_{n+1} - p_n = p_n(1 - p_n) \frac{(w_x - w_y)p_n + (w_y - w_z)(1 - p_n)}{w_x p_n^2 + 2w_y p_n(1 - p_n) + w_z(1 - p_n)^2}$$

Making the discrete process continuous, then we have

$$\frac{dp}{dt} = p(1 - p) \frac{(w_x - w_y)p + (w_y - w_z)(1 - p)}{w_x p^2 + 2w_y p(1 - p) + w_z(1 - p)^2}$$

Finally we assume that $w_z = 1$, $w_y = 1 + s$, $w_x = 1 + 2s$ and s is a small positive number, $\frac{dp}{dt} = sp(1 - p)$



Left: Ronald Fisher (1890-1962), middle: J. B. S. Haldane (1892-1964), right: Sewall Wright (1889-1988)

Fisher-KPP equation

In the Fisher-Haldane-Wright Law, if the species also moves freely in the space, then its population density also satisfies a diffusion equation. Hence we obtain a reaction-diffusion equation assuming 1-D spatial domain:

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

Here $p(x, t)$ is the density function of the advantageous gene at location x and time t . This equation was first proposed by Fisher in 1937, and in the same year Soviet Union mathematicians Kolmogorov, Petrovski, Piskunov considered this nonlinear parabolic partial differential equation. They introduced the concept of **traveling wave**. Today this equation is called Fisher equation, KPP equation, or Fisher-KPP equation.



Left: Ronald Fisher (1890-1962), middle: Andrey Nikolaevich Kolmogorov (1903-1987), right: Ivan Georgievich Petrovsky (1901-1973)

Ecological Explanation of Fisher-KPP, nonlocal competition

$$\frac{\partial u(x, t)}{\partial t} = D\Delta u(x, t) + r(x)u(x, t) - a(x)u^2(x, t).$$

- ❶ Dispersal of population: diffusion $D\Delta u(x, t)$ (can also be nonlocal dispersal, advection)
- ❷ Growth and death: $r(x)u(x, t)$ with $r(x) = b(x) - d(x)$ (birth-death)
- ❸ Crowding effect: $-a(x)u(x, t) \cdot u(x, t)$ (interaction: mass action)

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With proper boundary conditions, the Fisher-KPP equation has at most one positive steady state solution, and it is globally asymptotically stable when it exists.

[Lou, 2006, JDE] [Liang-Lou, 2012, DCDSB]

[He-Ni, 2016, CVPDE] [DeAngelis-Ni-Zhang, 2016, JMB]

The crowding effect is caused by the intraspecific competition with peers of the same species, which may be not at the same spatial location. Hence the crowding effect can be modeled as

$$- \int_{\Omega} K(x, y) u(y, t) u(x, t) dy.$$

Here $K(x, y)$ is probability of an individual at y competes with the one at x , and $u(x, t)$, $u(y, t)$ are the population density at x , y respectively.

Nonlocal dispersal

[Hutson-Martinez-Mischaikow-Vickers, JMB, 2003]

[Bates-Fife-Ren-Wang, ARMA, 1997] [Bates-Chmaj, JSP, 1999]

Divide \mathbb{R} (the habitat) into contiguous sites, each of length Δx . Discretize time into steps of size Δt . Let $u(i, t)$ be the density of individuals in site n at time t . Assume that the probability of individuals leaving site i and going to site j is $\alpha(j, i)$. Then the number of individuals leaving site i during the interval $[t, t + \Delta t]$ is

$\sum_{j=-\infty}^{\infty} \alpha(j, i)u(i, t)(\Delta x)^2 \Delta t$. During this same time interval, the number of arrivals to

site i from elsewhere is $\sum_{j=-\infty}^{\infty} \alpha(i, j)u(j, t)(\Delta x)^2 \Delta t$. Finally let $f(u(i, t), i)$ denote the

per capita net reproduction rate at site i at the given population density.

$$u(i, t + \Delta t) = u(i, t) + \left(\sum_{j=-\infty}^{\infty} \alpha(i, j)u(j, t) - \sum_{j=-\infty}^{\infty} \alpha(j, i)u(i, t) \right) \Delta x \Delta t + f(u(i, t), i)u(i, t)\Delta t$$

Limit as $\Delta x, \Delta t \rightarrow 0$:

$$u_t(x, t) = \int_{\mathbb{R}} [\alpha(x, y)u(y, t) - \alpha(y, x)u(x, t)]dy + f(u(x, t), x)u(x, t).$$

Relation to diffusion model

If $\int_{\mathbb{R}} \alpha(y, x) dy = 1$ (probability), then

$$u_t(x, t) = \int_{\mathbb{R}} \alpha(x, y) u(y, t) dy - u(x, t) + f(u(x, t), x) u(x, t).$$

If $\alpha(x, y) = k(x - y)$ (only depends on distance between x and y), then

$$u_t(x, t) = \int_{\mathbb{R}} k(x - y) u(y, t) dy - u(x, t) + f(u(x, t), x) u(x, t)$$

$$\begin{aligned} \int_{\mathbb{R}} k(x - y) u(y, t) dy &= \int_{\mathbb{R}} k(y) u(x - y, t) dy = \int_{\mathbb{R}} k(y) \sum_{j=0}^{\infty} \frac{u_x^{(j)}(x, t)}{j!} (-y)^j dy \\ &= \sum_{j=0}^{\infty} \frac{u_x^{(j)}(x, t)}{j!} \int_{\mathbb{R}} k(y) (-y)^j dy = u(x, t) + \frac{1}{2} u_{xx}(x, t) \int_{\mathbb{R}} k(y) (-y)^2 dy + \dots \end{aligned}$$

So by using Taylor expansion, we can see the diffusion equation is the first approximation of the nonlocal dispersal model.

[Lutscher-Pachevsky-Lewis, SIAM-AM, SIAM-Rev, 2005]

[Cortazar-Coville-Elgueta-Martinez, JDE, 2007], [Bates-Zhao, JMAA, 2007]

[Coville-Da'vila-Martinez, JDE, 2008], [Coville-Da'vila-Martinez, SIAM-MA, 2008]

and many others

Nonlocal competition

Fisher-KPP equation: $u_t = Du_{xx} + au(1 - u)$

Nonlocal Fisher-KPP equation: $u_t = Du_{xx} + au \left(1 - \int_{\Omega} k(x - y)u(y, t)dy \right)$

[Britton, JTB, 1989], [Britton, SIAM-AM, 1990], [Gourley, JMB, 2000]

[Fuentes-Kuperman-Kenkre, PRL, 2003; JPC, 2004]

The nonlocal term represents intra-specific competition for resources and having this particular form implies that individuals are competing not only with others at their own point in space but also with individuals at other points in the domain.

[Martinez-Garcia, et.al. 2012, PTRS]

Nonlocal growth. $u_t = Du_{xx} + a \int_{\Omega} k(x - y)u(y, t)dy u(1 - u) - \alpha u.$

Nonlocal death. $u_t = Du_{xx} + au(1 - u) - \alpha \int_{\Omega} k(x - y)u(y, t)dy.$

Nonlocal Fisher-KPP Equation

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + \lambda u(x, t) \left(1 - \int_{\Omega} K(x, y) u(y, t) dy \right), & x \in \Omega, \ t > 0, \\ Bu(x, t) = 0, & x \in \partial\Omega, \ t > 0, \end{cases}$$

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- 1 Ω is a bounded domain with smooth boundary in \mathbb{R}^n or R^n , $n \geq 1$.
- 2 Boundary condition $Bu = u$ (Dirichlet), $Bu = \frac{\partial u}{\partial n}$ (Neumann).
- 3 Integral kernel $K : \overline{\Omega} \times \overline{\Omega} \rightarrow [0, \infty)$ is an integrable function.
(Or more generally, $K[u]$ is a bounded linear operator.)

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Typical kernels:

- Constant (even distribution): $K(x, y) \equiv |\Omega|^{-1}$; ($|\Omega|$ = Lebesgue measure of Ω)
- Separable: $K(x, y) = K_1(x)K_2(y)$;
- Symmetric: $K(x, y) = K(y, x)$ (Distance-dependent: $K(x, y) = K_3(|x - y|)$);
- Diffusion: $K(x, y) = \text{Green's function of } -d\Delta + c$:
 $(-d\Delta_x + c)K(x, y) = \delta(x, y)$ where $c \geq 0$;
- Dirac delta (local): $K(x, y) = \delta(x, y)$;

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Questions:

1. Is there a positive steady state solution?
2. Is the positive steady state unique? and (globally asymptotically) stable?

Constant or symmetric kernel

[Allegretto-Barabanova, 1997, Funk. Ekva.], [Chen-Shi, 2012, JDE]

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + u(x, t) \left(\lambda - \int_{\Omega} u(y, t) dy \right), & x \in \Omega, \quad t > 0, \\ u(x, t) = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

Theorem. The equation has a unique positive equilibrium $u_{\lambda}(x) = (\lambda - d\lambda_1)\phi_1(x)$ for any $\lambda > d\lambda_1$, where (λ_1, ϕ_1) is the principal eigenvalue-eigenfunction pair of $-\Delta\phi = \lambda\phi$ in $H_0^1(\Omega)$. Moreover it is globally asymptotically stable for $\lambda > d\lambda_1$.

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$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + u(x, t) \left(\lambda - b(x)u(x, t) - \int_{\Omega} K(x, y)u^p(y, t) dy \right), & x \in \Omega, \quad t > 0, \\ u(x, t) = 0, & x \in \partial\Omega, \quad t > 0 \end{cases}$$

Here $b(x) \geq (\neq)0$, and $p > 0$.

[Yamada, 2015, NA]

Theorem. If $K(x, y) = K(y, x)$, $K > 0$ and $p = 2$, then the equation has a unique positive steady state solution when $\lambda \in (\lambda_1, \infty)$, which is globally asymptotically stable.

If $p \neq 2$, then the positive steady state still exists, but the uniqueness and stability is not known.

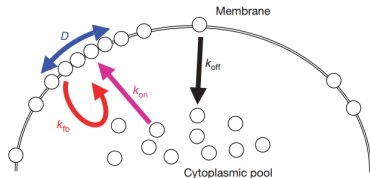
An application

[Altschuler-Angent-Wang-Wu, Nature, 2008]
On the spontaneous emergence of cell polarity

A partial differential equation model for the polarization of the GTPase Cdc42 in budding yeast

$$u_t = Du_{xx} + k_{on} \left(1 - \frac{1}{2L_0} \int_{-L_0}^{L_0} u \right) - k_{off} u + k_{fb} \left(1 - \frac{1}{2L_0} \int_{-L_0}^{L_0} u \right) u,$$

where $u(x, t)$ is the density of membrane-bound molecules (GTPase Cdc42) defined on the membrane $-L_0 < x < L_0$. Here spontaneous association of cytoplasmic molecules to random locations on the PM is modeled by k_{on} term, random disassociation of signaling molecules from the membrane is described by k_{off} term, and recruitment of cytoplasmic molecules to the locations of membrane-bound signaling molecules is indicated by k_{fb} term.



Separable kernel

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + u^q(x, t) \left(\lambda - a(x) \int_{\Omega} b(y) u^p(y, t) dy \right), & x \in \Omega, \ t > 0, \\ u(x, t) = 0, & x \in \partial\Omega, \ t > 0, \end{cases}$$

Here $b(x) \geq (\neq) 0$, $0 < q \leq 1$, and $p > 0$.

[Correa-Delgado-Suarez, 2011, ADE] [Yamada, 2015, NA]

If $q = 1$ and $a(x) \geq 0$, then the equation has a unique positive steady state solution when $\lambda \in (\lambda_1(\Omega), \lambda_1(\Omega_0))$, where $\lambda_1(O)$ is the principal eigenvalue of $-\Delta$ in $H_0^1(O)$, and $\Omega_0 = \{x \in \Omega : a(x) = 0\}$ (so $\lambda_1(\Omega_0) = \infty$ if $\Omega_0 = \emptyset$.) Moreover when $a(x) = b(x)$ and $p = 2$, then the unique steady state solution is globally asymptotically stable.

Note:

- 1 Also results for $0 < q < 1$ and $a(x) \leq 0$.
- 2 [Ouyang, 1992, TAMS] similar results for $\Delta u + au - h(x)u^p = 0$

Diffusion kernel (Dirichlet BC)

[Zuo-Shi, 2016, preprint]

$$\begin{cases} u_t = d_1 \Delta u + u \left(a - u - b \int_{\Omega} K_1(x, y) F(u(y)) dy \right), & x \in \Omega, \ t > 0, \\ u(x, t) = 0, & x \in \partial\Omega, \ t > 0, \end{cases}$$

where $F(u)$ is a continuous function with $F(0) = 0$ and $F'(u) > 0$ for $u > 0$. Here $K_1(x, y)$ is the Green's function of $-d_3 \Delta + c$ with Dirichlet boundary condition ($c \geq 0$). Hence the equation is equivalent to

$$\begin{cases} u_t = d_1 \Delta u + u(a - u - bw), & x \in \Omega, \ t > 0, \\ 0 = d_3 \Delta w - cw + F(u), & x \in \Omega, \ t > 0, \\ u(x, t) = w(x, t) = 0, & x \in \partial\Omega, \ t > 0. \end{cases}$$

This is a parabolic-elliptic system of predator-prey type.

Theorem. For $a > d\lambda_1$, there exists a positive steady state solution. If $n = 1$, then the positive steady state solution is unique and non-degenerate.

Existence: bifurcation theory and *a priori* estimates.

Uniqueness: [Casal-Eilbeck-Lopez-Gomez, 1994, DIE]

Stability: not known

Diffusion kernel (Neumann BC)

[Ni-Shi-Wang, 2018, JDE]

$$\begin{cases} u_t = d_1 \Delta u + u \left(a - u - b \int_{\Omega} K_1(x, y) F(u(y)) dy \right), & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega, \end{cases} \quad (1)$$

where $F(u)$ is a continuous function with $F(0) = 0$ and $F'(u) > 0$ for $u > 0$. Here $K_1(x, y)$ is the Green's function of $-d_3 \Delta + 1$ with Neumann boundary condition. Hence (17) is equivalent to

$$\begin{cases} u_t = d_1 \Delta u + u(a - u - bw), & x \in \Omega, t > 0, \\ 0 = d_3 \Delta w - w + F(u), & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = \frac{\partial w(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases} \quad (2)$$

This is a parabolic-elliptic system of predator-prey type.

Diffusion kernel (Neumann BC)

[Ni-Shi-Wang, 2018, JDE]

Consider the following fully parabolic system:

$$\begin{cases} u_t = d_1 \Delta u + u(a - u - bw), & x \in \Omega, t > 0, \\ \tau w_t = d_3 \Delta w - w + F(u), & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = \frac{\partial w(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Theorem. Suppose that $d_1, d_3, a, b > 0$, and $F(u)$ is a continuous function with $F(0) = 0$ and $F'(u) > 0$ for $u > 0$. Then for any $\tau \geq 0$, the unique positive constant steady state solution of the above parabolic system is globally asymptotically stable.

Corollary. For the nonlocal Fisher-KPP equation with diffusion kernel

$$\begin{cases} u_t = d_1 \Delta u + u \left(a - u - b \int_{\Omega} K_1(x, y) F(u(y)) dy \right), & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega, \end{cases}$$

there is a unique positive steady state solution, which is a constant. Moreover it is globally asymptotically stable with respect to all non-negative initial condition which is not identically zero.

Proof

$$\begin{cases} u_t = d_1 \Delta u + u(a - u - bw), & x \in \Omega, t > 0, \\ \tau w_t = d_3 \Delta w - w + F(u), & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = \frac{\partial w(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Proof 1. Use lower-upper solution method.

$$\begin{aligned} \bar{u}_1 &= a, \quad \bar{w}_1 = F(\bar{u}_1), \\ \underline{u}_1 &= a - b\bar{w}_1, \quad \underline{w}_1 = F(\underline{u}_1), \quad \bar{u}_2 = a - b\underline{w}_1 \end{aligned}$$

Proof 2. Use Lyapunov function method.

$$Q(u, w) = \int_{\Omega} \int_{\tilde{u}}^u \frac{F(s) - F(\tilde{u})}{s} ds dx + \frac{b\tau}{2} \int_{\Omega} (w - \tilde{w})^2 dx.$$

Note: if $-d_3\Delta + 1$ is replaced by $-d_3\Delta$, the original nonlocal problem is not well-defined as $-d_3\Delta$ is not invertible in H^1 .

Existence in general case

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + \lambda u(x, t) \left(1 - \int_{\Omega} K(x, y) u^p(y, t) dy \right), & x \in \Omega, \ t > 0, \\ Bu(x, t) = 0, & x \in \partial\Omega, \ t > 0, \end{cases}$$

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[Sun-Shi-Wang, 2013, ZAMP], [Yamada, 2015, NA]

[Alves-Delgado-Suarez, 2015, ZAMP]

Theorem. If $K \in L^{\infty}$ and $K(x, y) > 0$, then the equation has a positive steady state solution. Moreover when $p = 1$, the positive steady state solution is unique and locally asymptotically stable if the eigenvalue problem

$$L[\phi] = \Delta\phi(x) + \lambda\phi(x) - \lambda\phi(x) \int_{\Omega} f(x, y) u(y) dy - \lambda u(x) \int_{\Omega} f(x, y) \phi(y) dy,$$

has a principal eigenvalue (real-valued with positive eigenfunction).

Existence in general case

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + \lambda u(x, t) \left(1 - \int_{\Omega} K(x, y) u^p(y, t) dy\right), & x \in \Omega, \quad t > 0, \\ Bu(x, t) = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

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[Alves-Delgado-Suarez, 2015, ZAMP]

Theorem. If $K \in L^{\infty}$ and $K(x, y) > 0$, then the equation has a positive steady state solution. Moreover when $p = 1$, the positive steady state solution is unique and locally asymptotically stable if the eigenvalue problem

$$L[\phi] = \Delta\phi(x) + \lambda\phi(x) - \lambda\phi(x) \int_{\Omega} f(x, y) u(y) dy - \lambda u(x) \int_{\Omega} f(x, y) \phi(y) dy,$$

has a principal eigenvalue (real-valued with positive eigenfunction).

[Sun-Shi-Wang, 2015, ZAMP, Erratum] there are examples that the real eigenvalue with positive eigenfunction is not the principal one.

Open Question: Prove (or disprove) the uniqueness and/or (local or global) stability of the positive steady state solution for general kernel function $K(x, y)$. [Lam, 2019 to appear, DCDSB](non-uniqueness?)

Other non-local Fisher-KPP equations

[Lou-Nagylaki-Su, 2013, JDE]

$$\begin{cases} u_t = \sum V_{ij} u_{x_i x_j} + b \cdot \nabla u + B \left(\int_{\Omega} u(y) dy - u \right) u + \lambda g(x) u(1 - u), & x \in \Omega, t > 0, \\ \nu \cdot \nabla u = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

The positive steady state solution is unique and globally stable when it exists.
(in this case, the maximum principle holds and the principal eigenvalue of associated linearized operator exists.)

[Delgado et.al., 2016, TMNA]

$$\begin{cases} u_t = \Delta u + u(a + b \int_{\Omega} u^r(y) dy - u), & x \in \Omega, t > 0, \\ u = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega. \end{cases}$$

where $r > 0$. The positive steady state is unique when $r \leq 1$, but the solution may blow up in finite time for large $b > 0$.

[Correa-Delgado-Suarez, 2011, MCM] [Correa-Suarez, 2012, MMAS]

[Li-Coville-Wang, 2017, DCDSA] principal eigenvalue, maximum principle

Nonlocal Fisher in \mathbb{R}^n

$$\frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + \mu u(x, t) \left(1 - \int_{\mathbb{R}^n} K(x - y) u(y, t) dy \right), \quad x \in \mathbb{R}^n, \quad t > 0.$$

Here $K \in C^1$, $K \geq 0$ and $\int_{\mathbb{R}^n} K(x) dx = 1$.

[Berestycki-Nadin-Perthame-Ryzhik, 2009, Nonlinearity]

[Hamel-Ryzhik, 2014, Nonlinearity]

Theorem.

1. For $n = 1$, if $0 < \mu < \mu_0$ or the Fourier transform $\hat{K} > 0$, then the only non-negative bounded steady state solutions are $u = 0$ and $u = 1$.
2. For $n = 1$, if there exists $k_0 \in \mathbb{N}$ such that $\hat{K}(k_0/L) < 0$, and all other $\hat{K}(k/L) > 0$, then there exist non-constant positive steady state solution for large μ .

Also results on traveling wave solutions. [Fang-Zhao, 2011, Nonlinearity]

Nonlocal Lotka-Volterra two-species competition system

[Ni-Shi-Wang, 2018, JDE]

$$\left\{ \begin{array}{ll} u_t = d_1 \Delta u + u \left(\alpha - u - c_{11} \int_{\Omega} K_1(x, y) u(y, t) dy \right) \\ \quad - u \left(c_{12} \int_{\Omega} K_2(x, y) v(y, t) dy + a_1 v \right), & x \in \Omega, \ t > 0, \\ v_t = d_2 \Delta v + v \left(\beta - v - c_{22} \int_{\Omega} K_2(x, y) v(y, t) dy \right) \\ \quad - v \left(c_{21} \int_{\Omega} K_1(x, y) u(y, t) dy + a_2 u \right), & x \in \Omega, \ t > 0, \\ \partial_{\nu} u(x, t) = \partial_{\nu} v(x, t) = 0, & x \in \partial\Omega, \ t > 0. \end{array} \right.$$

Nonlocal Lotka-Volterra two-species competition system

[Ni-Shi-Wang, 2018, JDE]

$$\begin{cases} u_t = d_1 \Delta u + u \left(\alpha - u - c_{11} \int_{\Omega} K_1(x, y) u(y, t) dy \right) \\ \quad - u \left(c_{12} \int_{\Omega} K_2(x, y) v(y, t) dy + a_1 v \right), & x \in \Omega, t > 0, \\ v_t = d_2 \Delta v + v \left(\beta - v - c_{22} \int_{\Omega} K_2(x, y) v(y, t) dy \right) \\ \quad - v \left(c_{21} \int_{\Omega} K_1(x, y) u(y, t) dy + a_2 u \right), & x \in \Omega, t > 0, \\ \partial_{\nu} u(x, t) = \partial_{\nu} v(x, t) = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

When $c_{ij} = 0$, it becomes the well-known Lotka-Volterra competition system

$$\begin{cases} u_t = d_1 \Delta u + u(\alpha - u - a_1 v), & x \in \Omega, t > 0, \\ v_t = d_2 \Delta v + v(\beta - v - a_2 u), & x \in \Omega, t > 0, \\ \partial_{\nu} u(x, t) = \partial_{\nu} v(x, t) = 0, & x \in \partial\Omega, t > 0. \end{cases}$$

- ① If $\alpha > \max\{\beta/a_2, \beta a_1\}$, then $(\alpha, 0)$ is globally asymptotically stable.
- ② If $\alpha < \max\{\beta/a_2, \beta a_1\}$, then $(0, \beta)$ is globally asymptotically stable.
- ③ If $\beta a_1 < \alpha < \beta/a_2$, then $(\frac{\beta - \alpha a_2}{1 - a_1 a_2}, \frac{\alpha - \beta a_1}{1 - a_1 a_2})$ is globally asymptotically stable.
- ④ If $\beta/a_2 < \alpha < \beta a_1$, then $(\alpha, 0)$ and $(0, \beta)$ are bistable.

Nonlocal Lotka-Volterra two-species competition system

Convert it into a parabolic-elliptic system:

$$\begin{cases} u_t = d_1 \Delta u + u(\alpha - u - c_{11}w - c_{12}z - a_1 v), & x \in \Omega, t > 0, \\ v_t = d_2 \Delta v + v(\beta - v - c_{21}w - c_{22}z - a_2 u), & x \in \Omega, t > 0, \\ 0 = d_3 \Delta w - w + u, & x \in \Omega, t > 0, \\ 0 = d_4 \Delta z - z + v, & x \in \Omega, t > 0, \\ \frac{\partial u(x, t)}{\partial \nu} = \frac{\partial v(x, t)}{\partial \nu} = \frac{\partial w(x, t)}{\partial \nu} = \frac{\partial z(x, t)}{\partial \nu} = 0, & x \in \partial\Omega, t > 0, \\ u(x, 0) = u_0(x) \geq 0, v(x, 0) = v_0(x) \geq 0, & x \in \Omega. \end{cases}$$

Theorem. If the parameters α, β, a_1, a_2 and $c_{11}, c_{12}, c_{21}, c_{22}$ satisfy

$$\frac{c_{12} + a_1}{c_{22} + 1} \beta < \alpha < \frac{c_{11} + 1}{c_{21} + a_2} \beta,$$

and

$$c_{11} < \frac{c_{21}}{c_{21} + 2a_2}, \quad c_{22} < \frac{c_{12}}{c_{12} + 2a_1},$$

then the unique positive constant steady state solution $(\tilde{u}, \tilde{v}, \tilde{w}, \tilde{z})$ is globally asymptotically stable.

Proof is based on Lyapunov function method.

Segregation coexistence

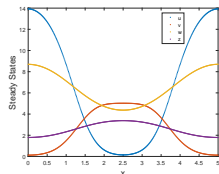
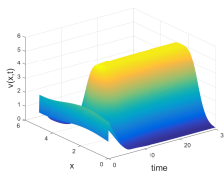
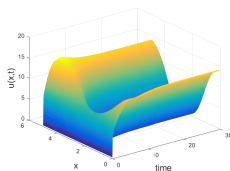
Theorem. If the parameters α, β, a_1, a_2 and $c_{11}, c_{12}, c_{21}, c_{22}$ satisfy

$$\frac{c_{12} + a_1}{c_{22} + 1} \beta < \alpha < \frac{c_{11} + 1}{c_{21} + a_2} \beta,$$

and

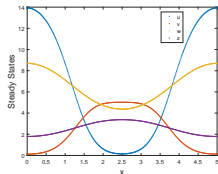
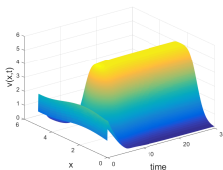
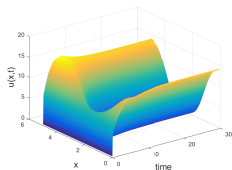
$$c_{11}, c_{22} > 1, \quad 0 < 1 - a_1, 1 - a_2 \ll 1, \quad 0 < c_{12} \ll c_{21},$$

then when $0 < d_1, d_2 < d_0$ for some d_0 , there exists a non-constant positive steady state solution.



Segregated coexistence steady states for weak competition case. Here $c_{11} = c_{22} = 4$, $c_{12} = 19.2$, $c_{21} = 0.3$, $\alpha = 83.32$, $\beta = 20$, $d_1 = d_2 = 0.3$ and $a_1 = a_2 = 0.9$. Initial density $u(x, 0) = 0.3$ and $v(x, 0) = 1.2 + 0.2 \sin(x)$.

Mechanisms of segregated coexistence in Lotka-Volterra system



- [Kishimoto-Weinberger, 1985, JDE] If Ω is convex, then a locally asymptotically stable steady state solution must be constant.
- [Mimura-Kawasaki, 1980, JMB] Segregated coexistence is possible in 1-D if there is cross-diffusion between species.
- [Matano-Mimura, 1983, PRIMS] Segregated coexistence is possible in n-D if the domain is dumbbell-shaped.
- [Mimura et.al., 1984, Hiroshima MJ] Segregated coexistence is possible in 1-D if there is nonlinear diffusion.
- [Chen-Lam-Lou, 2012, DCDSA], [Lam-Ni, 2014, JDE] Segregated coexistence is possible in 1-D if there is advection.
- [Ni-Shi-Wang, 2018, JDE] Segregated coexistence is possible in 1-D if there is nonlocal competition.

Two chemical-reaction models

Autocatalytic chemical reaction model with decay

$$\begin{cases} -\Delta u_1 = \lambda u_2 - \lambda u_1 u_2, & x \in \Omega, \\ -d\Delta u_2 = \lambda u_2 - \lambda u_1 u_2 - k u_2^q, & x \in \Omega, \\ u_1 = u_2 = 0, & x \in \partial\Omega. \end{cases}$$

$d, \lambda > 0$, $k \geq 0$, and $q \geq 1$.

$k = 0$: [\[Shi-Wang, 2006, JDE\]](#), [\[Jiang-Shi, 2008, DCDS-A\]](#)

$k > 0$: [\[Zhao-Shi-Wang, 2012, JDE\]](#) [\[Zhou-Shi, 2014, PRSE\]](#)

Two chemical-reaction models

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$k > 0$: [\[Zhao-Shi-Wang, 2012, JDE\]](#) [\[Zhou-Shi, 2014, PRSE\]](#)

Nuclear reactor model

$$\begin{cases} -\Delta u_1 = a u_1 - b u_1 u_2, & x \in \Omega, \\ -\Delta u_2 = c u_1 - d u_1 u_2 - e u_2, & x \in \Omega, \\ u_1 = u_2 = 0, & x \in \partial\Omega. \end{cases}$$

$a, b, c, d, e > 0$.

[\[Arioli, 2007, JDE\]](#) [\[Lopez-Gomez, 2009, JDE\]](#)

[\[Peng-Wei-Yang, 2010, PRSE\]](#) [\[Zhou-Shi, 2013, AML\]](#)

Converting to nonlocal Fisher

[Zhou-Shi, 2013, AML] [Zhou-Shi, 2014, PRSE]

$$\begin{cases} -\Delta u_1 = \lambda u_2 - \lambda u_1 u_2, & x \in \Omega, \\ -d\Delta u_2 = \lambda u_2 - \lambda u_1 u_2 - k u_2^q, & x \in \Omega, \\ u_1 = u_2 = 0, & x \in \partial\Omega. \end{cases}$$

Let $z = u_1 - d u_2$ and $v = u_2$. Then (z, v) satisfies $-\Delta z = k v^q$ and $-d\Delta v = (\lambda - k v^{q-1} - \lambda d v - \lambda z) v$. By using Green's function $G(x, y)$, v satisfies

$$-d\Delta v = v \left[\lambda - k v^{q-1} - \lambda d v - \lambda k \int_{\Omega} G(x, y) v^q(y) dy \right].$$

$$\begin{cases} -\Delta u_1 = a u_1 - b u_1 u_2, & x \in \Omega, \\ -\Delta u_2 = c u_1 - d u_1 u_2 - e u_2, & x \in \Omega, \\ u_1 = u_2 = 0, & x \in \partial\Omega. \end{cases}$$

Set $w = u - b v / d$, then (w, u) satisfies

$$\begin{cases} -\Delta w + e w = \left(a + e - \frac{bc}{d} \right) u, & x \in \Omega, \\ -\Delta u = u(a - d u + d w), & x \in \Omega, \\ w = u = 0, & x \in \partial\Omega. \end{cases}$$

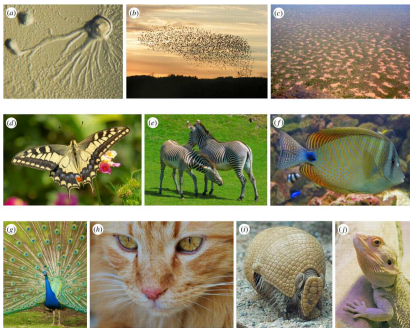
Uniqueness of positive solution of nonlocal Fisher-KPP equation will imply the uniqueness of positive solution to these two systems. ($n=1$, the uniqueness is known)

Conclusion

$$\begin{cases} \frac{\partial u(x, t)}{\partial t} = d\Delta u(x, t) + \lambda u(x, t) \left(a - bu(x, t) - \int_{\Omega} K(x, y) u^p(y, t) dy \right), & x \in \Omega, \quad t > 0, \\ Bu(x, t) = 0, & x \in \partial\Omega, \quad t > 0, \end{cases}$$

- 1 Nonlocal Fisher-KPP equation arises in various mathematical models in population ecology, cell biology and other disciplines. The existence of positive steady state solution can be established using bifurcation theory or topological degree theory.
- 2 When the kernel function is symmetric, separable, or diffusion type, the uniqueness of steady state solution has been proved, and very often the uniqueness is proved by proving the global stability of the positive steady state with respect to associated dynamics.
- 3 The uniqueness and/or stability of positive steady state solution for general kernel function is not known. It is an interesting question to prove or disprove it.
- 4 There have been extensive studies in nonlocal spatial dispersal in recent years. The studies of nonlocal dependence on the growth rate or crowding effect is another interesting questions.

Pattern formation in biology



[Turing, 1952] The Chemical Basis of Morphogenesis. *Phil. Trans. Royal Soc. London. B*

Reaction-diffusion system (R-D): $u_t = d_1 \Delta u + f(u, v)$, $v_t = d_2 \Delta v + g(u, v)$

A spatially homogenous steady state is stable w.r.t. homogenous perturbation, but is unstable w.r.t. inhomogeneous perturbation. Hence some stable non-constant non-equilibrium state (patterns) exist to show the complex spatial-temporal structure, as a result of **symmetry breaking bifurcation**.

Figure (left) from: Towards an integrated experimentaltheoretical approach for assessing the mechanistic basis of hair and feather morphogenesis, by K. J. Painter et.al. *Interface Focus*. 2012 Aug 6;2(4):433-50

Spatial patterns in ecology

Left: Tiger bush in Niger; Right: fairy circles in Namibia



Left: mussel patterning in Netherland; Right: marsh grass along York River, VA, USA



Photo from: en.wikipedia.org/wiki/Tiger_bush,
lainfo.es/en/2014/05/21/competition-between-plants-...
mainsequenceblog.com/2008/11/18/dance-of-the-mussels/,

Turing instability

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

Equilibrium point: $f(u_0, v_0) = g(u_0, v_0) = 0$.

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

stability of matrix $L_j \begin{pmatrix} a_j \\ b_j \end{pmatrix} = \begin{pmatrix} -d\mu_j + f_u & f_v \\ g_u & -\mu_j + g_v \end{pmatrix} = \lambda \begin{pmatrix} a_j \\ b_j \end{pmatrix}$,

where μ_j satisfies $\Delta \phi_j + \mu_j \phi_j = 0$, $x \in \Omega$, $\partial_\nu \phi = 0$, $x \in \partial\Omega$.

Stable for ODE: $f_u + g_v < 0$, and $f_u g_v - f_v g_u > 0$.

Unstable for PDE: $f_u < 0$ (inhibitor), $g_v > 0$ (activator), d_1 is small or d_2 is large.

[Turing, 1952] If the above conditions are satisfied, then the constant steady state (u_0, v_0) is stable w.r.t. the ODE system, but it is unstable w.r.t. the PDE system; for some $j \in \mathbb{N}$, one of the eigenvalues of L_j is positive, then the PDE system may have a non-constant steady state with spatial profile $\phi_j(x)$.

Turing's classification of patterns

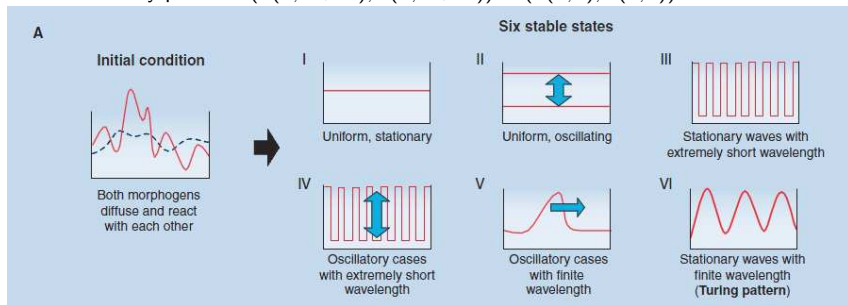
Steady state pattern: $(u(x, t), v(x, t)) = (u(x), v(x))$.

Time-oscillatory pattern: $(u(x, t + T), v(x, t + T)) = (u(x, t), v(x, t))$

Turing's classification of patterns

Steady state pattern: $(u(x, t), v(x, t)) = (u(x), v(x))$.

Time-oscillatory pattern: $(u(x, t + T), v(x, t + T)) = (u(x, t), v(x, t))$

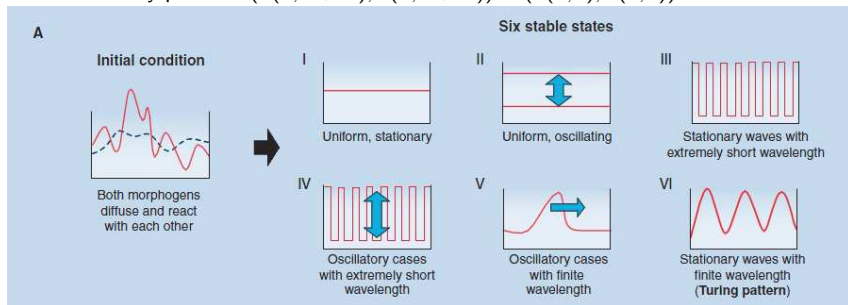


(Figure from: [\[Kondo-Miura, 2010, Science\]](#))

Turing's classification of patterns

Steady state pattern: $(u(x, t), v(x, t)) = (u(x), v(x))$.

Time-oscillatory pattern: $(u(x, t + T), v(x, t + T)) = (u(x, t), v(x, t))$



(Figure from: [\[Kondo-Miura, 2010, Science\]](#))

[\[Turing, 1952\]](#): “The two remaining possibilities (oscillatory cases) can only occur with three or more morphogens.”

Conjecture?: If (u_0, v_0) is a constant steady state for a 2-D RD system which is stable for ODE dynamics, then the diffusive system cannot have (stable) periodic orbits.

Known: If (u_0, v_0) is a constant steady state for a 2-D RD system which is unstable for ODE dynamics, then the diffusive system can have (a lot of) periodic orbits.

[\[Yi-Wei-Shi, 2009, JDE\]](#) [\[Jin-Shi-Wei-Yi, 2013, Rocky Moun. J. Math\]](#)

When there is no pattern formation?

- 1 Scalar reaction-diffusion equation: $u_t = d\Delta u + f(u)$, $x \in \Omega$, $\partial_n u = 0$, $x \in \partial\Omega$.
[Casten-Holland, 1978, JDE] [Matano, 1979, PRIMS]
any stable steady state on a convex domain is constant.
- 2 Nearly same diffusion coefficients: the constant steady remains stable.
- 3 Gradient/dissipative systems: Lyapunov functional/LaSalle invariance principle.
- 4 Cooperative or competitive reaction-diffusion systems: not activator-inhibitor (consumer-resource, predator-prey) systems; Usually no stable non-constant steady state on convex domain, and no stable time-periodic solutions.
[Kishimoto-Weinberger, 1985, JDE] [Hirsch, Smith, monotone system]

What additional structure can cause spatial patterns? (mostly competitive systems)

- [Mimura-Kawasaki, 1980, JMB] cross-diffusion
- [Matano-Mimura, 1983, PRIMS] non-convex dumbbell-shaped domain
- [Mimura et.al., 1984, Hiroshima MJ] nonlinear diffusion
- [Chen-Lam-Lou, 2012, DCDSA], [Lam-Ni, 2014, JDE] advection
- [Ni-Shi-Wang, 2018, JDE] nonlocal competition
- [Shi-Shi-Song, 2018, preprint] nonlocal spatial average

RD equation with spatial average

Define $\bar{u} = \frac{1}{|\Omega|} \int_{\Omega} u(x, t) dx$.

$$\begin{cases} u_t = d\Delta u + \lambda f(u, \bar{u}), & x \in \Omega, \ t > 0, \\ \partial_{\nu} u = 0, & x \in \partial\Omega, \ t > 0, \end{cases} \quad (3)$$

and its “localized equation”:

$$\begin{cases} u_t = d\Delta u + \lambda f(u, u), & x \in \Omega, \ t > 0, \\ \partial_{\nu} u = 0, & x \in \partial\Omega, \ t > 0, \end{cases} \quad (4)$$

Theorem 1. Suppose that $u = u_*$ satisfying $f(u_*, u_*) = 0$ is a constant steady state which is locally asymptotically stable w.r.t. (4), i.e. $f_u(u_*, u_*) + f_{\bar{u}}(u_*, u_*) < 0$.

- (i) If $f_u(u_*, u_*) < 0$, then u_* is locally asymptotically stable for all $d, \lambda > 0$.
- (ii) If $f_u(u_*, u_*) > 0$, then there exists $\lambda^1 = d\mu_1/f_u(u_*, u_*) > 0$ such that u_* is locally asymptotically stable for $0 < \lambda < \lambda^1$, and it is unstable for $\lambda > \lambda^1$. A stable spatial pattern can emerge at $\lambda = \lambda^1$.

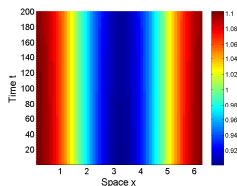
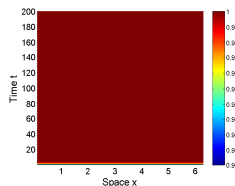
- A scalar RD equation can generate a spatial pattern if there is a proper effect by the spatial average: local activator ($f_u > 0$), and nonlocal inhibitor ($f_{\bar{u}} < 0$ and $f_u + f_{\bar{u}} < 0$).
- [Furter-Grinfeld, 1989, JMB] special case.

Example of pattern formation

[Furter-Grinfeld, 1989, JMB]

$$\begin{cases} u_t = d\Delta u + \lambda u(1 + au - b\bar{u}), & x \in \Omega, \ t > 0, \\ \partial_\nu u = 0, & x \in \partial\Omega, \ t > 0, \\ u(x, 0) = u_0(x) \geq 0, & x \in \Omega, \end{cases}$$

Here $a, b, d, \lambda > 0$. Then $\lambda^1 = d\mu_1/a$ is the bifurcation point. For $\lambda > \lambda^1$, there is a spatial pattern.



Left: converges to constant steady state with a homogeneous perturbation from steady state;

Right: generates a spatial pattern with a nonhomogeneous perturbation from steady state.

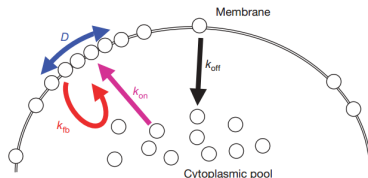
Example of no pattern formation

[Altschuler et.al., 2008, Science]

A partial differential equation model for the polarization of the GTPase Cdc42 in budding yeast

$$\begin{cases} u_t = d\Delta u + k_{on}(1 - \bar{u}) + k_{fb}(1 - \bar{u})u - k_{off}u, & x \in \Omega, \quad t > 0, \\ \partial_\nu u = 0, & x \in \partial\Omega, \quad t > 0. \end{cases}$$

where $u(x, t)$ is the density of membrane-bound molecules (GTPase Cdc42) defined on the cell membrane. Here spontaneous association of cytoplasmic molecules to random locations on the PM is modeled by k_{on} term, random disassociation of signaling molecules from the membrane is described by k_{off} term, and recruitment of cytoplasmic molecules to the locations of membrane-bound signaling molecules is indicated by k_{fb} term.



Proposition 2. The unique positive equilibrium $u = u_*$ is globally asymptotically stable. So there is no any spatial pattern.

System with spatial average

Nonlocal system:

$$\begin{cases} u_t = d_1 \Delta u + f(u, v, \bar{u}, \bar{v}, \lambda), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v, \bar{u}, \bar{v}, \lambda), & x \in \Omega, \quad t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, \quad t > 0, \end{cases} \quad (5)$$

where $\bar{u} = \frac{1}{|\Omega|} \int_{\Omega} u(x, t) dx$, $\bar{v} = \frac{1}{|\Omega|} \int_{\Omega} v(x, t) dx$, and its “localized system”:

$$\begin{cases} u_t = d_1 \Delta u + f(u, v, u, v, \lambda), & x \in \Omega, \quad t > 0, \\ v_t = d_2 \Delta v + g(u, v, u, v, \lambda), & x \in \Omega, \quad t > 0, \\ \partial_\nu u = \partial_\nu v = 0, & x \in \partial\Omega, \quad t > 0. \end{cases} \quad (6)$$

Constant steady state: $f(u_*, v_*, u_*, v_*, \lambda) = 0$, $g(u_*, v_*, u_*, v_*, \lambda) = 0$.

Stability is determined by (all evaluated at (u_*, v_*, u_*, v_*)):

$$J_U = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}, \quad J_U + J_{\bar{U}} = \begin{pmatrix} f_u + f_{\bar{u}} & f_v + f_{\bar{v}} \\ g_u + g_{\bar{u}} & g_v + g_{\bar{v}} \end{pmatrix}, \quad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix},$$

and μ_j satisfies $\Delta \phi_j + \mu_j \phi_j = 0$, $x \in \Omega$, $\partial_\nu \phi = 0$, $x \in \partial\Omega$.

Stability

Nonlocal system: $U_t = D\Delta U + F(U, \bar{U}, \lambda)$

Local system: $U_t = D\Delta U + F(U, U, \lambda)$

- ① **Mode-0 stability** for both nonlocal and local systems: matrix $J_U + J_{\bar{U}}$,
- ② **Mode- n stability** for nonlocal system: matrix $J_U - \mu_n D$, $J_{\bar{U}}$ **only affects mode-0**
- ③ **Mode- n stability** for local system: matrix $J_U + J_{\bar{U}} - \mu_n D$.

Bifurcation scenarios:

Nonlocality induced steady state bifurcation (Turing bifurcation, spatial pattern):

- ① stable in mode-0: $\text{Tr}(J_U + J_{\bar{U}}) < 0$, and $\text{Det}(J_U + J_{\bar{U}}) > 0$;
- ② stable for local mode- n : $\text{Tr}(J_U + J_{\bar{U}} - \mu_n D) < 0$, and $\text{Det}(J_U + J_{\bar{U}} - \mu_n D) > 0$;
- ③ **unstable for nonlocal mode- n** : $\text{Tr}(J_U - \mu_n D) < 0$, and $\text{Det}(J_U - \mu_n D) < 0$.

Nonlocality induced Hopf bifurcation (spatiotemporal pattern):

- ① stable in mode-0: $\text{Tr}(J_U + J_{\bar{U}}) < 0$, and $\text{Det}(J_U + J_{\bar{U}}) > 0$;
- ② stable for local mode- n : $\text{Tr}(J_U + J_{\bar{U}} - \mu_n D) < 0$, and $\text{Det}(J_U + J_{\bar{U}} - \mu_n D) > 0$;
- ③ **unstable for nonlocal mode- n** : $\text{Tr}(J_U - \mu_n D) > 0$, and $\text{Det}(J_U - \mu_n D) > 0$.

Example 1: predator-prey model

Diffusive Rosenzweig-MacArthur predator-prey system with nonlocal carrying capacity

$$\begin{cases} u_t = d_1 u_{xx} + u \left(1 - \frac{1}{kl\pi} \int_0^{l\pi} u(x, t) dx \right) - \frac{muv}{u+1}, & x \in (0, l\pi), \quad t > 0, \\ v_t = d_2 v_{xx} - \theta v + \frac{muv}{u+1}, & x \in (0, l\pi), \quad t > 0, \\ u_x(0, t) = u_x(l\pi, t), \quad v_x(0, t) = v_x(l\pi, t), & t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in (0, l\pi), \end{cases} \quad (7)$$

[Yi-Wei-Shi, 2009, JDE]: local system has stable spatially homogeneous periodic solution, but it has no stable spatially nonhomogeneous periodic solution or spatially nonhomogeneous steady state from bifurcation

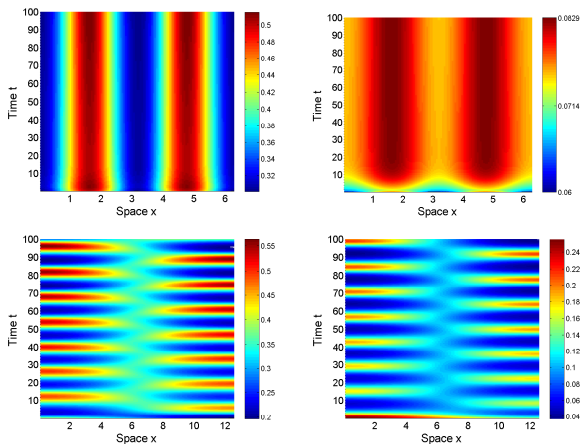
[Merchant-Nagata, 2011, JTB]: propose nonlocal system

[Chen-Yu, 2018, DCDSA]: nonlocal system has spatially nonhomogeneous periodic solution

[Shi-Shi-Song, 2018, preprint]: nonlocal system has both spatially nonhomogeneous periodic solution and spatially nonhomogeneous steady state from bifurcation

[Bayless-Volpert, 2013-1018]: pattern formation, traveling wave for similar nonlocal system on \mathbb{R}

Simulations



Top: mode-2 spatially nonhomogeneous steady state;

Bottom: mode-2 spatially nonhomogeneous periodic solution

[Yi-Wei-Shi, 2009, JDE]: localized model has globally asymptotically stable constant steady state

Example 2: Lotka-Volterra cooperative model

$$\begin{cases} u_t = \beta u_{xx} + u \left(1 - \frac{a}{l\pi} \int_0^{l\pi} u(x, t) dx + bv \right), & x \in (0, l\pi), \quad t > 0, \\ v_t = v_{xx} + v (1 + cu - dv), & x \in (0, l\pi), \quad t > 0, \\ u_x(0, t) = u_x(l\pi, t) = 0, \quad v_x(0, t) = v_x(l\pi, t) = 0, & t > 0, \\ u(x, 0) = u_0(x) \geq 0, \quad v(x, 0) = v_0(x) \geq 0, & x \in (0, l\pi). \end{cases} \quad (8)$$

If $ad - bc > 0$, then $(u_* = \frac{d+b}{ad-bc}, v_* = \frac{a+c}{ad-bc})$ is the unique positive constant steady state, and it is globally asymptotically stable w.r.t. the local system.

Theorem 3. Using $\beta > 0$ as bifurcation parameter,

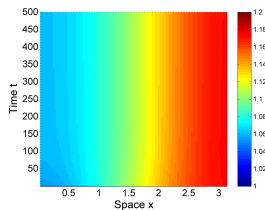
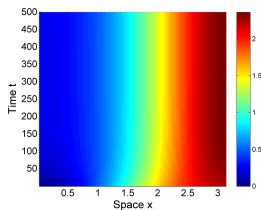
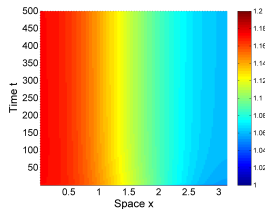
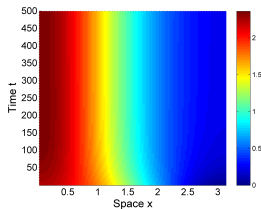
(i) there exist an infinite sequence $\beta_n = \frac{bcu_*v_*}{\lambda_n(\lambda_n + dv_*)}$ satisfying $\beta_i > \beta_{i+1} > \dots > 0$

such that system (8) undergoes a steady state bifurcation at $\beta = \beta_n$;

(ii) the nonconstant steady state solutions $(\beta, u_1^\pm(x), v_1^\pm(x))$ bifurcating at $\beta = \beta_1$ are locally asymptotically stable, and they are monotone in x .

[Kishimoto-Weinberger, 1985, JDE] stable steady state of the localized system must be constant

Simulations



Left: mode-1 spatially nonhomogeneous decreasing steady state;
Right: mode-1 spatially nonhomogeneous increasing steady state

How do the patterns emerge

Example 1: predator-prey model:

$$J_U = \begin{pmatrix} + & - \\ + & 0 \end{pmatrix}, \quad J_U + J_{\bar{U}} = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}, \quad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}.$$

$J_U + J_{\bar{U}}$ is stable, J_U is unstable.

Both Hopf and steady state bifurcations are possible.

Example 2: cooperative model:

$$J_U = \begin{pmatrix} - & + \\ + & 0 \end{pmatrix}, \quad J_U + J_{\bar{U}} = \begin{pmatrix} - & + \\ + & - \end{pmatrix}, \quad D = \begin{pmatrix} \beta & 0 \\ 0 & 1 \end{pmatrix}.$$

$J_U + J_{\bar{U}}$ is stable, J_U is unstable.

Steady state bifurcations are possible, but not Hopf ones.

Example 3: classical Turing instability

$$J_U = \begin{pmatrix} + & \pm \\ \mp & - \end{pmatrix}, \quad D = \begin{pmatrix} d_1 & 0 \\ 0 & d_2 \end{pmatrix}.$$

J_U is stable. Both Hopf and steady state bifurcations are possible, but stable bifurcating periodic orbits are spatially homogeneous.

Conclusions

- 1 In certain reaction-diffusion models, some feedback pathways are nonlocal or global. A particular case of such nonlocal effect is spatial average $\bar{u} = |\Omega|^{-1} \int_{\Omega} u$. The spatial average can cause spatiotemporal pattern formation (nonhomogeneous time-periodic solutions or steady state solutions) which do not exist in the purely local interaction models.
- 2 Nonlocality induced instability allows more flexible condition on the kinetic dynamics, and it does not require typical activator-inhibitor interaction between the two chemical species. This broadens the range of reaction-diffusion models for pattern formation.
- 3 Usually spatial heterogeneity increases the complexity of spatial patterns. Here the mechanism of pattern formation is to add some partial spatial homogeneity. Our result indicates the following scenarios of patterns verses level of locality/nonlocality of underlining reactions:

Totally nonlocal system: $U_t = D\Delta U + F(\bar{U}, \bar{U}, \lambda)$, no pattern, same as ODE

Partially nonlocal system: $U_t = D\Delta U + F(U, \bar{U}, \lambda)$, can have patterns

Totally local system: $U_t = D\Delta U + F(U, U, \lambda)$, no pattern

Future Work:

- (i) Turing-Hopf codimension-2 bifurcation in partially nonlocal system. [\[in preparation\]](#)
- (ii) Classify all 2×2 sign patterns for bifurcation in partially nonlocal system.