Global-in-time behavior of a Gierer-Meinhardt system

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a mathematics for cell biology
~ top down modeling

1) <u>reinforce-consumption</u>

$u_t = \alpha,\ v_t = -\beta$

2) <u>production-extinction</u>

$u_t = \alpha u,\ v_t = -\beta v$

3) <u>transport</u>

$u_t = -\nabla \cdot j$

$j\ldots$ fllux

4) <u>gradient</u>

$j = -d_u \nabla u\ldots$ diffusion

$j = d_v \nabla v\ldots$ chemotaxis

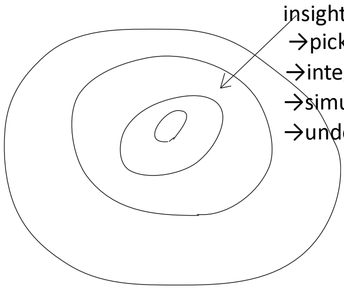
5) <u>chemical reaction</u>

$A + B \to C\ (k)$

$\Rightarrow$ (mass action)

$$\frac{d[A]}{dt} = -k[A][B]$$

$$\frac{d[B]}{dt} = -k[A][B]$$

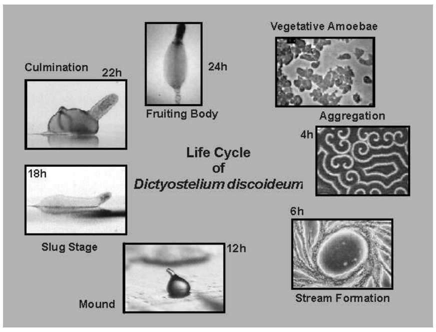


insight from experiments
→pick up key factors
→integrate formulae
→simulation check
→understand the evens as a system

Chemotaxis

Keller-Segel 70

$$u_t = \nabla \cdot (d_1(u,v)\nabla u) - \nabla \cdot (d_2(u,v)\nabla v)$$
$$v_t = d_v \Delta v - k_1 vw + k_{-1}p + f(v)u$$
$$w_t = d_w \Delta w - k_1 vw + (k_{-1}+k_2)p + g(v,w)u$$
$$p_t = d_p \Delta p + k_1 vw - (k_{-1}+k_2)p$$



moving clustered cells   aggregating cells

$u = u(x,t)$ cellular slime molds
$v = v(x,t)$ chemical substances
$w = w(x,t)$ enzymes
$p = p(x,t)$ comlices

1. transport, gradient

(a) diffusion u, v, w, p

(b) chemotaxis $v \to u$

2. production $u \to (v,w)$

3. chemical reaction v, w, p

$$V + W \underset{\leftarrow (k_{-1})}{\overset{(k_1) \rightarrow}{}} P \overset{(k_2)}{\rightarrow} W + A$$

$$v_t = -k_1 vw + k_{-1}p$$
$$w_t = -k_1 vw + (k_{-1}+k_2)p$$
$$p_t = k_1 vw - (k_{-1}+k_2)p$$

a mathematical phenomenon

blowup of the solution

$$\frac{du}{dt} = u^2,\ u(0) = T^{-1} > 0$$
$$\Rightarrow$$
$$u(t) = (T-t)^{-1}$$
$$\lim_{t \uparrow T} u(t) = +\infty$$

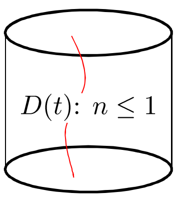
quantity distributed in space - time

Ω bounded set, $T > 0$

$u = u(x,t)$:

$\Omega \times [0,T] \to (-\infty, +\infty]$ continuous

$$D(t) = \overline{\{x \in \Omega \mid u(x,t) = +\infty\}}$$
$$D = \bigcup_{0 \le t \le T} D(t) \times \{t\} \subset \Omega \times [0,T]$$



Ω: $n = 3$

Temperature infinite region enclosed in a bounded domain in a positive time interval takes a dimension lower than 2

$u_t - \Delta u \ge 0$ in $\Omega \times (0,T) \setminus D$

$u = u(x,t)$ Lip. conti. near in $\partial\Omega$ unif. in $t \in [0,T]$

Theorem [F. Takahashi-S. 08]

$$\int_0^T \mathrm{Cap}_2(D(t))dt \le \frac{L^n(\Omega)}{2}$$

scale invariant estimate

Reaction-Diffusion System in Biology
- Population Dynamics and Morphogenesis

$\Omega \subset \mathbf{R}^N$ bounded domain
$\partial\Omega$ smooth, ν outer unit normal

$0 < \varepsilon \ll 1$, $D \gg 1$ diffusion coefficients
$0 < \tau \ll 1$ relaxization time

$u_t = \varepsilon^2 \Delta u + f(u,v)$

$\tau v_t = D\Delta v + g(u,v)$ in $\Omega \times (0,T)$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

$u|_{t=0} = u_0(x) \geq 0,\ v|_{t=0} = v_0(x) \geq 0$

$u = u(x,t) \geq 0$ activator (prey)
$v = v(x,t) \geq 0$ inihivitor (predator)

$f = f(u,v)$, $g = g(u,v)$
nonlinearity
self-growth (birth/death) + interaction

PDE system

$u_t = \varepsilon^2 \Delta u + f(u,v)$

$\tau v_t = D\Delta v + g(u,v)$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

ODE part

$u_t = f(u,v)$

$\tau v_t = g(u,v)$

constant stationary solution (u_*, v_*)

$\Rightarrow$ an equilibrium of ODE

$f(u_*, v_*) = g(u_*, v_*) = 0$

stationary problem

$\varepsilon^2 \Delta u + f(u,v) = 0$

$D\Delta v + g(u,v) = 0$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

stability controlled by the real parts
of eigenvalues of the linearized matrix

$$\begin{pmatrix} f_u(u_*, v_*) & f_v(u_*, v_*) \\ \tau^{-1} g_u(u_*, v_*) & \tau^{-1} g_v(u_*, v_*) \end{pmatrix}$$

reaction-diffusion sysetm

$$u_t = \varepsilon^2 \Delta u + f(u,v)$$

$$\tau v_t = D\Delta v + g(u,v)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

$\Rightarrow$

$$\tau \frac{d}{dt}\int_\Omega v = \int_\Omega g(u,v)$$

$$D \to +\infty \Rightarrow \Delta v \to 0$$

$$\Delta v = 0,\ \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0 \Rightarrow v(\cdot,t) = \xi(t)$$

Turing 52

diffusion

$\Rightarrow$ instabilization of stable constant stationary solutions

$\Rightarrow$ pattern formation

shadow system

$$u_t = \varepsilon^2 \Delta u + f(u,v)$$

$$\tau \frac{d\xi}{dt} = \frac{1}{|\Omega|}\int_\Omega g(u,\xi)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = 0$$

reaction-diffusion sysetm

$$u_t = \varepsilon^2 \Delta u + f(u,v)$$

$$\tau v_t = D\Delta v + g(u,v)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

ODE part

$$u_t = f(u,v)$$

$$\tau v_t = g(u,v)$$

transient and asymptotic dynamics

stationary problem

$$\varepsilon^2 \Delta u + f(u,v) = 0$$

$$D\Delta v + g(u,v) = 0$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

shadow system

$$u_t = \varepsilon^2 \Delta u + f(u,v)$$

$$\tau \frac{d\xi}{dt} = \frac{1}{|\Omega|}\int_\Omega g(u,\xi)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = 0$$

Lotka-Volterra system

$a, b, c, d > 0$ constants

$$\frac{\partial u}{\partial t} = \varepsilon^2 \Delta u + u(a - bv)$$

$$\tau \frac{\partial v}{\partial t} = D\Delta v + v(-c + du)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

$$u|_{t=0} = u_0(x) \geq 0$$

$$v|_{t=0} = v_0(x) \geq 0$$

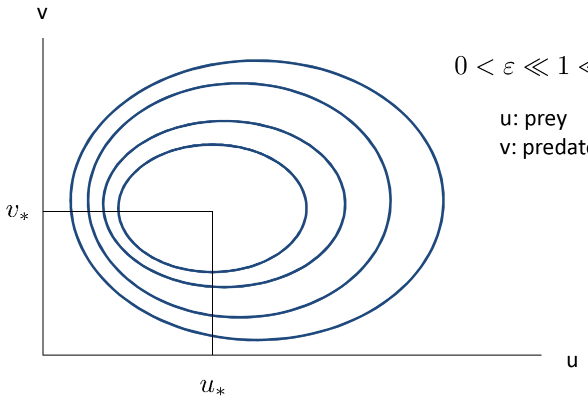
ODE part

$$\frac{du}{dt} = u(a - bv)$$

$$\tau \frac{dv}{dt} = v(-c + du)$$

$0 < \varepsilon \ll 1 \ll D$

u: prey
v: predator



stationary states
… spatially homogeneous

$(u_*, v_*) = (c/d, a/b)$

no Turing pattern →

Theorem 1 [Alikakos 79]

1. $\forall\ u_0, v_0 \in C^2(\overline{\Omega})$

$\exists 1$ classical solution
$(u, v) = (u(x,t), v(x,t))$ global-in-time

$$u_t = \varepsilon^2 \Delta u + u(a - bv)$$

$$\tau v_t = D\Delta v + v(-c + du)$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

$$u|_{t=0} = u_0(x) \geq 0, \ v|_{t=0} = v_0(x) \geq 0$$

2. $u_0 \not\equiv 0,\ v_0 \not\equiv 0$

$\Rightarrow$

$\exists 1$ ODE solution $(\tilde{u}, \tilde{v}) = (\tilde{u}(t), \tilde{v}(t))$

$$\lim_{t \uparrow +\infty} \mathrm{dist}_{C^2}((u(\cdot,t), v(\cdot,t)), \mathcal{O}) = 0$$

$$\mathcal{O} = \{(\tilde{u}(t), \tilde{v}(t))\}_{t \geq 0} \text{ (period } \tilde{T})$$

ODE part

$$\frac{du}{dt} = u(a - bv)$$

$$\tau \frac{dv}{dt} = v(-c + du)$$

$$u_t = \varepsilon^2 \Delta u + u(a - bv)$$
$$\tau v_t = D\Delta v + v(-c + du)$$
$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$
$$u|_{t=0} = u_0(x) \geq 0,\ v|_{t=0} = v_0(x) \geq 0$$

$$u = u_D(x,t),\ v = v_D(x,t)$$

Theorem 2

[transient control of shadow system]

$\forall T > 0$

$$\lim_{D\uparrow+\infty} \sup_{t\in[0,T]} \{\|u_D(\cdot,t) - U(\cdot,t)\|_{C^2}$$
$$+\|v_D(\cdot,t) - V(t)\|_{C^2}\} = 0$$

shadow system

$$U_t = \varepsilon^2 \Delta U + U(a - bV)$$
$$\tau \frac{dV}{dt} = \frac{1}{|\Omega|}\int_\Omega V(-c + dU)$$
$$\left.\frac{\partial U}{\partial \nu}\right|_{\partial\Omega} = 0,\ U|_{t=0} = u_0(x) \geq 0$$
$$V|_{t=0} = \overline{v}_0 = \frac{1}{|\Omega|}\int_\Omega v_0$$

Theorem 3

[shadow system $(U,V) \to$ ODE]

$(\hat{u},\hat{v}) = (\hat{u}(t),\hat{v}(t))$ ODE solution

$$\hat{u}(0) = \overline{u}_0 \equiv \frac{1}{|\Omega|}\int_\Omega u_0$$
$$\hat{v}(0) = \overline{v}_0 \equiv \frac{1}{|\Omega|}\int_\Omega v_0$$

(period $\hat{T}$)

$\Rightarrow$

$$\frac{1}{|\Omega|}\int_\Omega U(\cdot,t) = \hat{u}(t),\ V(t) = \hat{v}(t)$$
$$\lim_{t\uparrow+\infty} \|U(\cdot,t) - \hat{u}(t)\|_\infty = 0$$

$$U(\cdot,t) - \hat{u}(t) \approx e^{-\varepsilon^2 \mu_2 t}\varphi_2$$

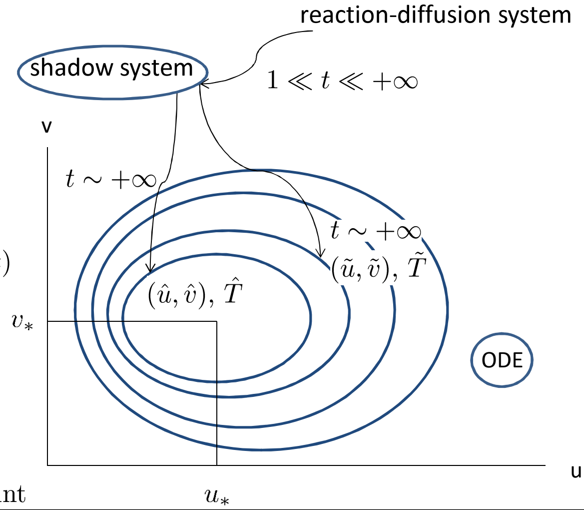
$\tilde{T} > 0 \Rightarrow \mathcal{O}$ non-shrink to a point

Theorem 4 [Discrepancy]

$\forall \delta > 0,\ \exists D_0 > 0$ s.t.

$D \geq D_0 \Rightarrow \tilde{T} > \hat{T} - \delta$

$\hat{T}$, ultimate period of $(u(\cdot,t), v(\cdot,t))$



Gierer-Meinhardt 72

morphogenesis
spatial tissue structure of hydra

cut → duplicate

local self-enhancement (direct, indirect)
+
long-range inhibition
(prevent the spreading into surrounding tissue)

↓

local concentration maxima
stripelike distributions of substances

u=u(x,t) activator
v=v(x,t) inhibitor

$$f(u,v) = -u + \frac{u^p}{v^q}$$
$$g(u,v) = -v + \frac{u^r}{v^s}$$
$$p > 1,\ q, r > 0,\ s > -1$$

spiky patterns in stationary states

.. Wei-Wintner 08
J. Wei, HB DE, Stationary PDE, vol. 5

spiky patterns discovered by
Ni-Takagi 86

stationary state

$$\varepsilon^2 \Delta u - u + \frac{u^p}{v^q} = 0$$
$$D\Delta v - v + \frac{u^r}{v^s} = 0$$
$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

shadow stationary state

$$\varepsilon^2 \Delta u - u + \frac{u^p}{\xi^q} = 0,\ \left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = 0$$
$$\xi = \left(\frac{1}{|\Omega|}\int_\Omega u^r\right)^{1/(s+1)}$$

A chemotaxis system shares the shadow stationary state

Gierer-Meinhardt PDE

$$u_t = \varepsilon^2 \Delta u - u + \frac{u^p}{v^q}$$
$$\tau v_t = D\Delta v - v + \frac{u^r}{v^s}$$
$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

global-in-time existence case

Masuda-Takahashi 87
Jiang 06

Question 1 compactness of the orbit

shadow system $D \to +\infty$

$$u_t = \varepsilon^2 \Delta u - u + \frac{u^p}{\xi^q}$$
$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = 0$$
$$\tau \frac{d\xi}{dt} = -\xi + \frac{1}{|\Omega|}\int_\Omega \frac{u^r}{\xi^s} dx$$

global-in-time existence case
blowup case

Li-Ni 09

Question 2 dynamical control to PDE

Gierer-Meihardt ODE

$$\frac{du}{dt} = -u + \frac{u^p}{v^q}$$
$$\tau \frac{dv}{dt} = -v + \frac{u^r}{v^s}$$

spatially homogeneous (constant) stationary state

$$f(u_*, v_*) = -u_* + \frac{u_*^p}{v_*^q} = 0$$
$$g(u_*, v_*) = -v_* + \frac{u_*^r}{v_*^s} = 0$$

$\Rightarrow$

$$u_*^{p-1} = v_*^q,\ u_*^r = v_*^{s+1}$$

$\Rightarrow$

$$(p-1)\log u_* = q \log v_*$$
$$r \log u_* = (s+1)\log v_*$$

Gierer-Meinhardt condition

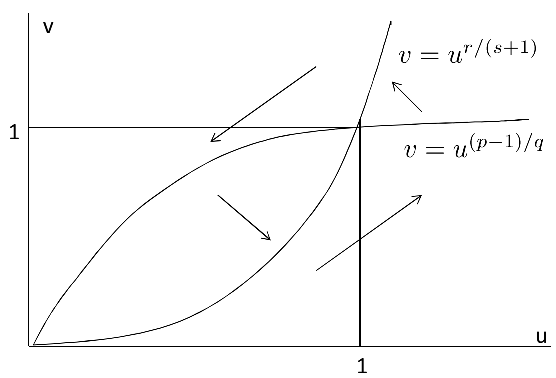
$$0 < \frac{p-1}{r} < \frac{q}{s+1}$$

$\Rightarrow$

equilibrium $(u_*, v_*) = (1,1)$

activator $\leftrightarrow$ inhibitor (**oscillating**)
(**near equilibrium**)

ODE phase plane



Gierer-Meihardt ODE

$$\frac{du}{dt} = -u + \frac{u^p}{v^q}$$
$$\tau\frac{dv}{dt} = -v + \frac{u^r}{v^s}$$

Ni-K. Suzuki-Takagi 06

$\tau = \dfrac{s+1}{p-1} \Rightarrow$

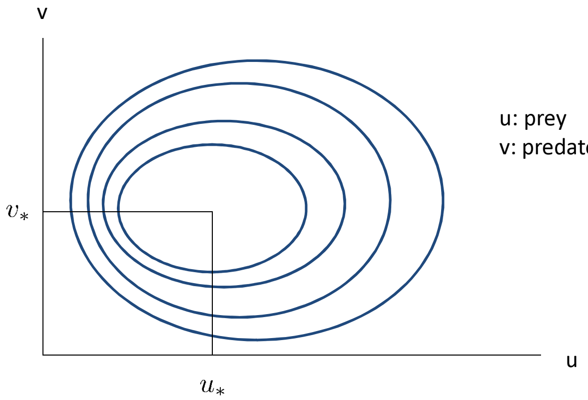
$\forall$ ODE orbit is closed

u: activator
v: inhibitor

$(u_*, v_*) = (1,1)$

Lotka-Volterra ODE

$$\frac{du}{dt} = u(a - bv)$$
$$\tau\frac{dv}{dt} = v(-c + du)$$



u: prey
v: predator

$(u_*, v_*) = (c/d, a/b)$

Abstract

Gierer-Meihardt system models morphogenesis of hydra in the context of Turing patterns. There is a parameter region, however, where the ODE part takes periodic orbits. If two diffusion coefficients are comparable in this parameter region, then any solution exists global-in-time and is absorbed into an ODE orbit. A variational structure is hidden there, common and applicable to the study of other reaction-diffusion systems; joint work with G. Karali and Y. Yamada

Plan

1. Lotka-Volterra system (7)
2. Variational structure (4)
3. Compactness of the orbit (2)
4. Main theorem (1)

1. Lotka-Volterra system

$$\frac{du}{dt} = u(a - bv)$$
$$\tau\frac{dv}{dt} = v(-c + du)$$

$$\xi = \log u,\ \eta = \log v$$
$$\Rightarrow$$
$$\frac{d\xi}{dt} = a - be^{\eta}$$
$$\frac{d\eta}{dt} = -\frac{c}{\tau} + \frac{d}{\tau}e^{\xi}$$

Observation

u_t/u, v_t/v are growth rates

$$H(\xi,\eta) = -a\eta + be^{\eta} - \tau^{-1}c\xi + \tau^{-1}de^{\xi}$$
$$\Rightarrow$$
$$a - be^{\eta} = -H_{\eta}$$
$$-\frac{c}{\tau} + \frac{d}{\tau}e^{\xi} = H_{\xi}$$

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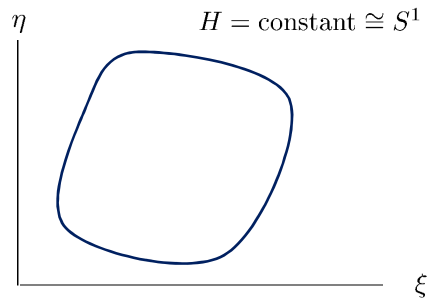
Lotka-Volterra ODE is a Hamilton system

$$\frac{d\xi}{dt} = -H_{\eta}$$
$$\frac{d\eta}{dt} = H_{\xi}$$
$$\Rightarrow$$
$$\frac{d}{dt}H(\xi,\eta) = 0$$

$$H(\xi,\eta) \equiv -a\eta + be^{\eta} - \tau^{-1}c\xi + \tau^{-1}de^{\xi}$$



2/14

Lotka-Volterra PDE

$$u_t = \varepsilon^2 \Delta u + u(a - bv)$$
$$\tau v_t = D\Delta v + v(-c + du)$$
$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

growth rate formulation

$\xi = \log u,\ \eta = \log v$

$$H(\xi, \eta) = -a\eta + be^{\eta} - \tau^{-1}c\xi + \tau^{-1}de^{\xi}$$

$$\xi_t = \varepsilon^2 e^{-\xi}\Delta e^{\xi} - H_\eta$$
$$\eta_t = \tau^{-1}De^{-\eta}\Delta e^{\eta} + H_\xi$$
$$\left.\frac{\partial \xi}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial \eta}{\partial \nu}\right|_{\partial\Omega} = 0$$

$$\mathcal{H}(\xi, \eta) = \int_\Omega H(\xi(\cdot), \eta(\cdot))$$

$\Rightarrow$

$$\frac{d}{dt}\mathcal{H}(\xi(\cdot,t), \eta(\cdot,t)) = \int_\Omega H_\xi \xi_t + H_\eta \eta_t \ dx$$

$$= \int_\Omega (-\tau^{-1}c + \tau^{-1}de^{\xi})\varepsilon^2 e^{-\xi}\Delta e^{\xi} \ dx$$
$$+ \int_\Omega (-a + be^{\eta})\tau^{-1}De^{-\eta}\Delta e^{\eta} \ dx$$
$$= -\tau^{-1}\int_\Omega c\varepsilon^2|\nabla\xi|^2 + aD|\nabla\eta|^2 \ dx$$

a Lyapunov function

stationary states

$\Rightarrow$

spatially homogeneous

no Turing pattern

3/14

A priori estimates via Lyapunov function

$$H(\xi, \eta)$$
$$= -a\eta + be^{\eta} - \tau^{-1}c\xi + \tau^{-1}de^{\xi}$$

$$H(\xi, \eta) \geq \delta_1(e^{\xi} + e^{\eta}) - C_2$$

$\Rightarrow$

$$\int_\Omega e^{\xi} + e^{\eta}$$
$$= \|u(\cdot,t)\|_1 + \|v(\cdot,t)\|_1 \leq C_3$$

$$\mathcal{H}(\xi, \eta) = \int_\Omega H(\xi(\cdot), \eta(\cdot))dx$$

$\Rightarrow$

$$\mathcal{H}(\log u(\cdot,t), \log v(\cdot,t)) \leq C_1$$

$$H(\xi, \eta) \geq \delta_2(\xi_- + \eta_-) - C_4$$

$\Rightarrow$

$$\|\log u(\cdot,t)\|_1 + \|\log v(\cdot,t)\|_1 \leq C_5$$

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comparison theorem

$u_t = \varepsilon^2 \Delta u + u(a - bv)$

$\leq \varepsilon^2 \Delta u + au$

$= (\varepsilon^2 \Delta + a - \lambda)u + \lambda u$

$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = 0,\ u|_{t=0} = u_0(x) \geq 0$

$\overline{u} = \overline{u}(x,t),\ \lambda \gg 1$

$\overline{u}_t = (\varepsilon^2 \Delta + a - \lambda)\overline{u} + \lambda u$

$\left.\frac{\partial \overline{u}}{\partial \nu}\right|_{\partial\Omega} = 0,\ \overline{u}|_{t=0} = u_0(x)$

$\Rightarrow$

$0 \leq u \leq \overline{u}$

semigroup estimate

$\|u(\cdot,t)\|_1 \leq C_3$

$\Rightarrow$

$\|\overline{u}(\cdot,t)\|_r \leq C_6(r)$

$\Rightarrow$

$\|u(\cdot,t)\|_r \leq C_6(r),\ 1 \leq r < \infty$

$\Rightarrow$

$\|\overline{u}(\cdot,t)\|_\infty \leq C_7$

$\Rightarrow$

$\|u(\cdot,t)\|_\infty \leq C_7$

$\tau v_t = D\Delta v + v(-c + du)$

$\leq D\Delta v + dC_7 v$

$\Rightarrow$

$\|v(\cdot,t)\|_\infty \leq C_8$

5/14

Theory of dynamical systems

ω-limit set

$\omega(u_0, v_0) = \{(u_*, v_*) \mid \exists t_k \uparrow +\infty$ s.t.
$\|(u(\cdot,t_k), v(\cdot,t_k)) - (u_*, v_*)\|_{C^2} = 0\}$

$\Rightarrow$

compact, connected in $C^2(\overline{\Omega}) \times C^2(\overline{\Omega})$

invariant under the flow

$u_t = \varepsilon^2 \Delta u + u(a - bv)$

$\tau v_t = D\Delta v + v(-c + du)$

$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$

$\forall\ (u_*, v_*) \in \omega(u_0, v_0)$

$u_* \geq 0,\ v_* \geq 0$

$\|\log u(\cdot,t)\|_1 + \|\log v(\cdot,t)\|_1 \leq C_5$

$\Rightarrow$ (Fatou's lemma)

$\log u_* \in L^1(\Omega),\ \log v_* \in L^1(\Omega)$

$\mathcal{H}_* = \int_\Omega H(\log u_*, \log v_*)$

well-defined, invariant on $\omega(u_0, v_0)$

i.e.,

$\mathcal{H}_* = \mathcal{H}_\infty$

$\mathcal{H}_\infty = \lim_{t\uparrow+\infty} \mathcal{H}(\log u(\cdot,t), \log v(\cdot,t))$

6/14

$(\tilde{u}, \tilde{v}) = (\tilde{u}(\cdot, t), \tilde{v}(\cdot, t))$

solution to LV PDE with

$\tilde{u}|_{t=0} = u_* \geq 0, \ \tilde{v}|_{t=0} = v_* \geq 0$

strong maximum principle

$u_* \not\equiv 0, \ v_* \not\equiv 0$

$\Rightarrow$

$\tilde{u}(\cdot, t), \tilde{v}(\cdot, t) > 0, \ t > 0$

$(\tilde{u}(\cdot, t), \tilde{v}(\cdot, t)) \in \omega(u_0, v_0), \ \forall t \geq 0$

$\mathcal{H}$ invariant on $\omega(u_0, v_0)$

$\Rightarrow \forall t > 0$

$$0 = \frac{d}{dt}\mathcal{H}(\log \tilde{u}(\cdot, t), \log \tilde{v}(\cdot, t))$$

$$= -\tau^{-1} \int_\Omega c\varepsilon^2 |\nabla \log \tilde{u}|^2 + aD|\nabla \log \tilde{v}|^2$$

(u_*, v_*) spatially homogeneous

$\Rightarrow$

$\forall t_k \uparrow +\infty, \ \exists \{t'_k\} \subset \{t_k\}$ s.t.

$(\tilde{u}(\cdot, t + t'_k), \tilde{v}(\cdot, t + t'_k) \to (\hat{u}(t), \hat{v}(t))$

in C^2, a solution to the ODE

$$|\Omega| \cdot H(\hat{u}(t), \hat{v}(t)) = \mathcal{H}_\infty$$

$$= \lim_{t \uparrow +\infty} \mathcal{H}(\log u(\cdot, t), \log v(\cdot, t))$$

ODE orbit $\{(\hat{u}(t), \hat{v}(t))\}_{-\infty < t < +\infty}$

determined by the Hamiltonian

$\Rightarrow$

Theorem 1

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2. Variational structure

Gierer-Meinhardt ODE

$$\frac{du}{dt} = -u + \frac{u^p}{v^q}$$

$$\tau \frac{dv}{dt} = -v + \frac{u^r}{v^s}$$

$$u^{-p} u_t = u^{-p+1} + v^{-q}$$

$$v^s v_t = -\tau^{-1} v^{s+1} + \tau^{-1} u^r$$

growth rate formulation

$\xi = u^{-p+1}/(p-1)$

$\eta = v^{s+1}/(s+1)$

$\Rightarrow$

$\xi_t = -u_t u^{-p}$

$\eta_t = v^s v_t$

$$\xi_t = (p-1)\xi - \{(s+1)\eta\}^{-\frac{q}{s+1}}$$

$$\eta_t = -\tau^{-1}(s+1)\eta + \tau^{-1}\{(p-1)\xi\}^{-\frac{r}{p-1}}$$

$$p - 1 = \tau^{-1}(s+1) \Leftrightarrow \tau = \frac{s+1}{p-1}$$

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<u>assume</u> $p-1=\tau^{-1}(s+1)$

$$H=(p-1)\xi\eta+\left(\frac{r}{p-1}-1\right)^{-1}A(\xi)+\left(\frac{q}{s+1}-1\right)^{-1}B(\eta)$$

$A(\xi)=\tau^{-1}(p-1)^{-\frac{r}{p-1}}\xi^{1-\frac{r}{p-1}}$

$B(\eta)=(s+1)^{-\frac{q}{s+1}}\eta^{1-\frac{q}{s+1}}$

$\xi_t=(p-1)\xi-\{(s+1)\eta\}^{-\frac{q}{s+1}}$

$\eta_t=-\tau^{-1}(s+1)\eta+\tau^{-1}\{(p-1)\xi\}^{-\frac{r}{p-1}}$

$\Rightarrow$

$$\frac{d\xi}{dt}=H_\eta$$

$$\frac{d\eta}{dt}=-H_\xi$$

Hamilton formalism

Gierer-Meinhardt PDE

$$u_t=d_1\Delta u-u+\frac{u^p}{v^q}$$

$$v_t=d_2\Delta v-\tau^{-1}\left(v+\frac{u^r}{v^s}\right)$$

$$\left.\frac{\partial u}{\partial\nu}\right|_{\partial\Omega}=\left.\frac{\partial v}{\partial\nu}\right|_{\partial\Omega}=0$$

$d_1=\varepsilon^2,\ d_2=\tau^{-1}D$

$\xi=u^{-p+1}/(p-1)$

$\eta=v^{s+1}/(s+1)$

$\Rightarrow$

$$\xi_t=-d_1(p-1)\xi^{\frac{p}{p-1}}\Delta\xi^{-\frac{1}{p-1}}+H_\eta$$

$$\eta_t=d_2(s+1)\eta^{\frac{s}{s+1}}\Delta\eta^{\frac{1}{s+1}}-H_\xi$$

$$\left.\frac{\partial\xi}{\partial\nu}\right|_{\partial\Omega}=\left.\frac{\partial\eta}{\partial\nu}\right|_{\partial\Omega}=0$$

$$\frac{d}{dt}\int_\Omega H(\xi,\eta)\ dx =$$
$$-\int_\Omega Q(\xi^{-1/2}\eta^{1/2}|\nabla\xi|, \xi^{1/2}\eta^{-1/2}|\nabla\eta|)$$
$$+c_1|\nabla\xi^{-\alpha/2}|^2\ +c_2|\nabla\eta^{-\beta/2}|^2\ dx$$

$$\alpha = \frac{r}{p-1} > \frac{1}{p-1}$$
$$\beta = \frac{q}{s+1} > 1$$
$$\Rightarrow$$
$$c_i > 0,\ i=1,2$$

$$Q(X,Y) = d_1\cdot\frac{p}{p-1}X^2\ +d_2\cdot\frac{s}{s+1}Y^2$$
$$+(d_1+d_2)XY$$

$$\frac{2\sqrt{d_1d_2}}{d_1+d_2} \geq \sqrt{\frac{(s+1)(p-1)}{sp}}$$
$$\Rightarrow$$
$$Q(X,Y)\geq 0$$

Lemma 1

$$\frac{2\sqrt{d_1d_2}}{d_1+d_2} \geq \sqrt{\frac{(s+1)(p-1)}{sp}}$$
$$\frac{p}{r} < 1 < \frac{q}{s+1},\ \tau = \frac{s+1}{p-1}$$
$$\Rightarrow$$
$$\mathcal{H}(\xi,\eta) = \int_\Omega H(\xi(\cdot,t),\eta(\cdot,t))$$

a Lyapunov function

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3. Compactness of the orbit

$$\mathcal{H}(\xi,\eta)\approx$$
$$\int_\Omega u^{-p+1}v^{s+1} + u^{r-p+1} + v^{-q+s+1}$$

$$\frac{q}{s+1} > 1 \Rightarrow q-s-1>0$$
$$\ell > \max\{n/2, 1\}$$
$$a = \frac{\ell}{q-s-1} > 0$$
$$v = w^{-a} > 0$$
$$\Rightarrow$$
$$\|w(\cdot,t)\|_\ell \leq C_1$$

$$w_t = d_2\Delta w - d_2(a+1)w^{-1}|\nabla w|^2$$
$$+a^{-1}\tau^{-1}(w - u^r w^{a(s+1)+1})$$
$$\leq d_2\Delta w + a^{-1}\tau^{-1}w$$
$$\left.\frac{\partial w}{\partial \nu}\right|_{\partial\Omega} = 0$$

comparison + semigroup estimate

$$\Rightarrow$$
$$\|w(\cdot,t)\|_\infty \leq C_2$$
$$\Rightarrow$$
$$\boxed{\|v(\cdot,t)^{-1}\|_\infty \leq C_3}$$

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Lemma 2 (Masuda-K.Takahashi-Jiang)

$$0 < \frac{p-1}{r} < \min\{\frac{q}{s+1},\ 1\},\ a > 1,\ b > 0$$

$$\frac{2\sqrt{d_1 d_2}}{d_1 + d_2} \geq \sqrt{\frac{ab}{(a-1)(b+1)}}$$

$\Rightarrow$

$$\frac{d}{dt}\int_\Omega u^a v^{-b} \leq (-a + \tau^{-1} b)\int_\Omega u^a v^{-b} + C_4(a,b)\left(\int_\Omega v^{-\theta/\varepsilon}\right)^{\varepsilon}\left(\int_\Omega u^a v^{-b}\right)^{1-\varepsilon}$$

$$\theta = \frac{r}{r-p+1-\delta}\left[q - \frac{(p-1)(s+1)}{r} - \left(\frac{s+1}{r} - \frac{b}{a}\right)\delta\right]$$

$$\varepsilon = \frac{\delta}{a}\left(\frac{r}{r-p+1-\delta}\right)$$

$$0 < \delta \ll 1 \Rightarrow 0 < \varepsilon < 1,\ \theta > 0$$

$$\boxed{\forall a > 1,\ 0 < \exists b \ll 1 \text{ s.t. } \int_\Omega u^a v^{-b} dx \leq C_5(a,b)}$$

4. Main Theorem

Theorem [Gierer-Meinhardt system]

$$\frac{2\sqrt{d_1 d_2}}{d_1 + d_2} \geq \sqrt{\frac{(s+1)(p-1)}{sp}}$$

$$\tau = \frac{s+1}{p-1}$$

$$\frac{p}{r} < 1 < \frac{q}{s+1}$$

$\Rightarrow$

$\exists 1$ ODE solution $(\tilde{u}, \tilde{v}) = (\tilde{u}(t), \tilde{v}(t))$

$$\lim_{t\uparrow+\infty} \mathrm{dist}_{C^2}((u(\cdot,t), v(\cdot,t)), \mathcal{O}) = 0$$

$$\mathcal{O} = \{(\tilde{u}(t), \tilde{v}(t))\}_{t\geq 0}$$

Remark 1 [Jiang 06]

$$\frac{p-1}{r} < 1 \Rightarrow T = +\infty$$

Gierer-Meinhardt PDE

$$u_t = \varepsilon^2 \Delta u - u + \frac{u^p}{v^q}$$

$$\tau v_t = D\Delta v - v + \frac{u^r}{v^s}$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

$$d_1 = \varepsilon^2,\ d_2 = \tau^{-1} D$$

Gierer-Meinhardt ODE

$$\frac{du}{dt} = -u + \frac{u^p}{v^q}$$

$$\tau\frac{dv}{dt} = -v + \frac{u^r}{v^s}$$

the only case where the compactness of the orbit is known so far

Remark 2 [Yanagida 01, 02]

skew-gradient formalism
(Kuhn-Tucker duality)

$p+1=r,\ q+1=s$

non-degenerate saddle of a Lagrangean is dynamically stable

Gierer-Meinhardt PDE

$$u_t = \varepsilon^2 \Delta u - u + \frac{u^p}{v^q}$$

$$\tau v_t = D\Delta v - v + \frac{u^r}{v^s}$$

$$\left.\frac{\partial u}{\partial \nu}\right|_{\partial\Omega} = \left.\frac{\partial v}{\partial \nu}\right|_{\partial\Omega} = 0$$

a spatially homogeneous
- temporally oscillation criterion

$$\frac{2\sqrt{d_1 d_2}}{d_1+d_2} \geq \sqrt{\frac{(s+1)(p-1)}{sp}}$$

$$\boxed{d_1 = \varepsilon^2 \approx d_2 = \tau^{-1} D}$$

$$\boxed{\tau = \frac{s+1}{p-1}},\ \frac{p}{r} < 1 < \frac{q}{s+1}$$

Remark 3 [expected Turing pattern]

local self-enhancement

$\Leftrightarrow$

$0 < \varepsilon \ll 1 \ll D$

long-range inhibition

$\Leftrightarrow$

$0 < \tau \ll 1$

Pattern formation is certainly based on the interaction of many components. Since the interaction are expected to be nonlinear, our intuition is insufficient to check whether a particular assumption really accounts for the experimental observation. By modeling, the weak points of an hypothesis become evident and the initial hypothesis can be modified or improved. Models often contain simplifying assumptions, and different models may account equally well for a particular observation. This diversity should, however, be considered as an advantage: multiplicity of models stimulates the design of experimental tests in order to discriminate between the rival theories.

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