Pattern formation and Turing instability

D. Gurarie

Topics:

- Pattern formation through "symmetry breaking" and "loss of stability"
- Activator-inhibitor systems with diffusion

Turing proposed a mechanism for growth and development of patterns (morphogenesis) in biological systems (embryonic development, et al). According to Turing

- Active genes stimulate production/activation of chemical agents (morphogenes)
- Chemical reactions alone is too "symmetric" for pattern generation
- But diffusion-driven instabilities create initial patterns and those can lead to further development

Basic mathematical questions:

Q1: can diffusion be *stabilizing factor* for reactive system ? (Answer: yes in 1D and some other cases)

Q2: can diffusion destabilize a reactive system?

Under what conditions?

What are the resulting patterns?

Examples of "symmetry breaking", and patterns

- Physical systems: Phase transition "solid-fluid-gas", fluid & gas have large continuous symmetries (all rotations, translations), solid – a rigid (discrete) crystalline symmetry.
- Mathematics: Hopf bifurcation from "stable equilibrium" (symmetric?) -> "limit cycle" (pattern?)

Turing analysis involves

i) Symmetric (e.g. spatially uniform) equilibria
ii) Bifurcations in various parameters, e.g. diffusivity, domain size
iii) Activation/inhibition type reactions

Stabilizing diffusion

For single reactant $u(x,t)$ there is no Turing instability.

$$\begin{aligned} u_t &= Du_{xx} + f(u);\ \text{on } \mathbf{R} \text{ or } [0,l] + \text{BC} \\ u_t &= D\Delta u + f(u);\ \text{on } \mathbf{R}^n \text{ or } \Omega + \text{BC} \end{aligned}$$, or multi-D

Indeed, a "uniform" (*x* - independent) ODE $\dot{u} = f(u)$ has either stable $m = f'(u^*) < 0$, or unstable (*m>0*) equilibrium. The diffusion will maintain a stable one, and it can stabilize the unstable one.

To check it we take the linearized problem about u^*, for $v(x,t) = u(x,t) - u^*$

$$\begin{aligned} v_t &= Dv_{xx} + mv; \\ m &= f'(u^*) \end{aligned} \tag{1}$$

Solution on R / Rⁿ

$$v(x,t) = \int_{-\infty}^{\infty} \frac{e^{mt-(x-\xi)^2/4Dt}}{\sqrt{4\pi Dt}} v_0(\xi)\, d\xi \tag{2}$$

For *m>0,* $v(x,t)$ grows with t

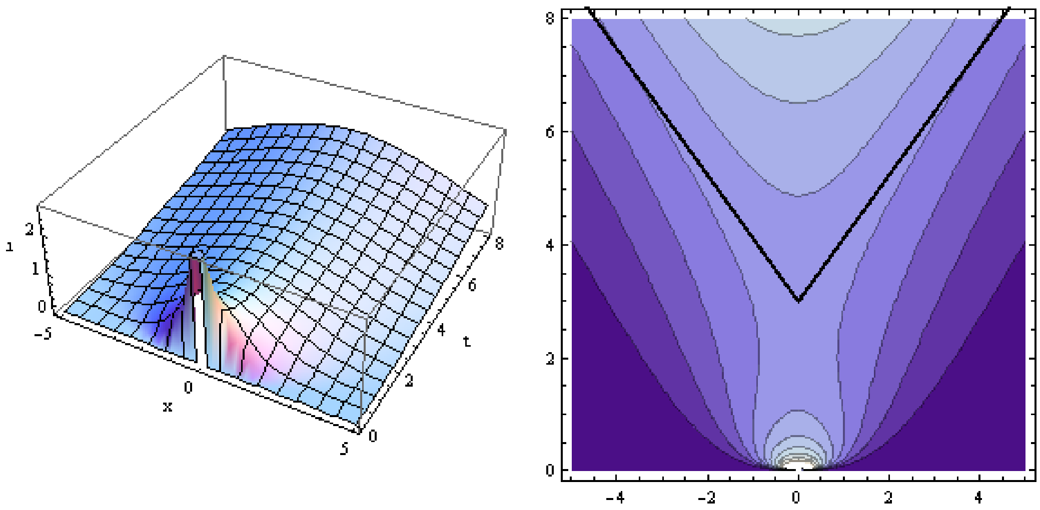

Figure 1: Point-source solution (2) on R for m>0

For *m<0*, all $v(x,t)$ decay exponentially ($v(x,t) < Ce^{-mt}$).

Finite interval [*0,l*]

Use Neumann BC (no flux) and eigenfunction expansion

$$\begin{cases} \partial_x{}^2\psi + \mu\psi = 0; \text{ on } [0,l] \\ \partial_x\psi\,|_{0,l} = 0 \end{cases} \Rightarrow \begin{cases} \mu_k = \left(\dfrac{\pi k}{l}\right)^2 \\ \psi_k(x) = \cos\left(\dfrac{\pi k x}{l}\right) \end{cases}; k = 0,1,\ldots \tag{3}$$

The eigenvalues of BV problem (1) are $\mu_k = -D(\pi k / l)^2 + m$. So stable case (m<0) remains stable, For unstable case get bifurcation values at $D(\pi / l)^2 = m; D(2\pi / l)^2 = m; \ldots$

The resulting would be "unstable mode" (pattern) is the corresponding cos-Fourier mode (3).

Turing instability for double-diffusive systems

A pair of reaction-diffusion species obeys a coupled system

$$\begin{cases} u_t = D_1 u_{xx} + f(u,v) \\ v_t = D_2 v_{xx} + g(u,v) \end{cases} \tag{4}$$

or its multi-D version in (x,y,…) space, with Neumann BC. So symmetric (x-independent) (u,v) solve a pure reaction ODS with equilibrium (u^*, v^*), and Jacobian

$$J = \begin{bmatrix} f_u{}^* & f_v{}^* \\ g_u{}^* & g_v{}^* \end{bmatrix}$$

Then we get a linearized system for $u'(x,t) = u(x,t) - u^*; v'(x,t) = v(x,t) - v^*$ by

$$\begin{cases} u'_t = D_1 u'_{xx} + au' + bv' \\ v'_t = D_2 v'_{xx} + cu' + dv' \end{cases}; \text{ with Jacobian } J = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

or in vector notation

$$U_t = \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix} \partial_x^{\,2} U + J \cdot U; U(x,t) = \begin{pmatrix} u' \\ v' \end{pmatrix} \tag{5}$$

Stability of system (5) depends on eigenvalues of a *matrix-differential operator*

$$L = \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix} \partial_x^{\,2} + J \tag{6}$$

We denote by μ eigenvalues of scalar laplacian $L_0 = \partial_x^{\,2}$ or Δ.

Examples of eigenvalue problem for Laplacian: $\Delta\psi + \mu\psi = 0$ ➔ $\{\mu, \psi(x)\}$: ?

	μ	$\psi(x)$
Free space $\mathbf{R}; \mathbf{R}^n$	$0 \le \mu_k = k^2 < \infty$ $\mathbf{k} = (k_1, k_2, \ldots) \in \mathbf{R}^n;$ $k = \lvert \mathbf{k} \rvert$	$\{\psi_{\mathbf{k}}(\mathbf{x}) = e^{i\mathbf{k}\cdot\mathbf{x}}\}$ or $\{\cos \mathbf{k}\cdot\mathbf{x}, \sin \mathbf{k}\cdot\mathbf{x}\}$
Finite interval $[0,l]$ Dirichlet: Neuman: Periodic	 $\{\mu_k = (\pi k / l)^2 : k = 1, 2 \ldots\}$ $\{\mu_k = (\pi k / l)^2 : k = 0, 1, \ldots\}$ $\{\mu_k = (2\pi k / l)^2 : -\infty < k < \infty\}$	$\psi_k = \sin\left(\frac{\pi k x}{l}\right)$ $\psi_k = \cos\left(\frac{\pi k x}{l}\right)$ $\{\psi_k(x) = e^{i2\pi kx/l}\}$ or {cos, sin}
2D (nD) Square, box $0 < x < a; 0 < y < b$	Product type: $\{\mu_{k,m} = \pi^2\left[(k/a)^2 + (m/b)^2\right] : k, m = 1, 2 \ldots\}$	$\psi_{km} = \sin\left(\frac{\pi k x}{a}\right)\sin\left(\frac{\pi k y}{b}\right)$
Polar disk (annulus) $0 < r < a;$ $0 < \theta < 2\pi$	product type (radial x angular modes): $\mu_{km} = (z_{km} / a)^2$	$\psi_{k,m}(r,\theta) = J_m(z_{mk} r / a) e^{\pm im\theta}$

1.

Having compute eigenvalues of L_0 we can pass to matrix-operator (6). We search for eigenmodes of L in the form "scalar x vector" = $\psi(\mathbf{x})X$, ψ - eigenmode of Laplace L_0 . It gives

$$\left(\lambda I + \mu \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix} - J\right) \cdot X = 0;\ J = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

The eigenvalue problem for "diagonalized" operator L is then reduced to 2D matrix-problem for a family of matrices

$$B(\mu, J) = J - \mu \begin{bmatrix} D_1 & \\ & D_2 \end{bmatrix} = \begin{bmatrix} a - \mu D_1 & b \\ c & d - \mu D_2 \end{bmatrix} \tag{7}$$

Specifically, eigenvalues of L

$$\Rightarrow \lambda(L) = \lambda(\mu, J) = \text{eigen}\left[B(\mu, J)\right] \tag{8}$$

where $\{\mu\}$ vary over the entire spectrum of Laplacian.

Turing instability analysis

Basic question: given positive Laplace eigens $\{\mu\}$ can a stable chemistry (Jacobian J) producecan unstable matrix $B(\mu)$ for specific diffusivities $D_{1,2}$, domain size l, or "norm" of J (proportional to reaction rates in *f,g*).

Table 1: stability test

Stable J	Stable B- ?
$\mathrm{tr}J = a + d < 0$	$\mathrm{tr}B = -\mu(D_1 + D_2) + \mathrm{tr}J < 0$ - always true!
$\det J = ad - bc > 0$	$\det B = D_1 D_2 \mu^2 - \underbrace{(aD_2 + dD_2)}_{a_1}\mu + \underbrace{(ad - bc)}_{a_2} = Q(\mu)$

The answer depends on quadratic function $Q(\mu)$ -? Specifically,

Case 1: Having symmetric (negative-definite) $J = \begin{bmatrix} a & b \\ b & d \end{bmatrix}$, matrix function $B(\mu)$ (7) is negative-definite for all $\mu > 0$. So $\lambda(\mu, J)$ remain negative, and diffusion leads to stabilization (no patterns).

Case 2: Scalar diffusivity $D_1 = D_2 = D$. Clearly, for stable J and $\mu > 0$, "eigens B" = "eigens(J) - μD" are more negative (stable).

In general case (Turing) it depends on coefficients of quadratic function $Q(\mu) = \det B(\mu)$ in Table 1. Namely, (i) $Q(\mu) > 0$ for all μ means "stable $B(\mu)$", hence stable L; (ii) $Q(\mu)$ changing sign for some $\mu > 0$, gives unstable $B(\mu)$, hence "unstable mode" for L. Turing conditions for "unstable" (negative) $p(\mu)$ are

$$\begin{array}{lll} (T1) & a_1 = aD_2 + dD_1 > 0 & \text{- negative slope } Q'(0) \\ (T2) & (aD_2 + dD_1)^2 \geq 4D_1D_2(ad - bc) & \text{- discriminant} \end{array} \tag{9}$$

From (T1) and tr(J) <0 => coefficients (a,d) should have opposite signs, then (b,c) are also opposite. The only choice are

Case 3: Activation-inhibition systems: (i) "u" grows, "v" decays; (ii) "u" inhibits "v" and "v" enhances "u", or vice versa

$$J = \begin{bmatrix} + & - \\ + & - \end{bmatrix}; \text{ or } \begin{bmatrix} + & + \\ - & - \end{bmatrix}$$

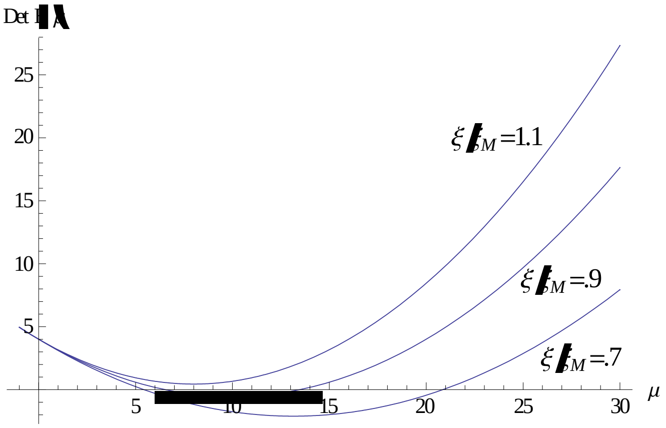

Figure 2: Cases of stable and unstable det(B) in terms of parameter $\xi = \sqrt{D_1 / D_2}$

One can rewrite Turing condition (9) for $J = \begin{bmatrix} a & \pm b \\ \mp c & -d \end{bmatrix}$ (a,b,c,d – positive), as

$$a/\xi + d\xi \geq 2\sqrt{bc};\ \text{with parameter } \xi{=}\sqrt{D_1/D_2} \tag{10}$$

Combined set conditions (tr(J)<0, det(J)>0, tr(B)<0, det(B)<0) gives

$$a/d \leq 1;$$

$$\xi = \sqrt{D_1/D_2} \leq \frac{\sqrt{bc}-\sqrt{bc-ad}}{d}$$

It sets a limit (Fig.3) of ratio D_1/D_2 to get unstable Turing mode.

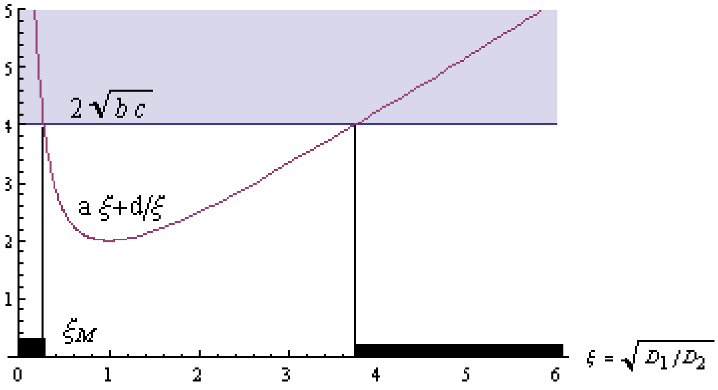

Figure 3: Parameter range for D_1/D_2 to get Turing instability

A positive (unstable) eigenvalue $\lambda(L)$ for some μ within the "unstable" interval of Fig.2 will give a spatial (eigenmode) part $\psi(\mathbf{x})$(e.g. $\cos\left(\frac{\pi k x}{l}\right)$ for $= -\partial_x{}^2$, with $\mu_k = \left(\frac{\pi k}{l}\right)^2$) to "seed" the follow up development of a ***spatial pattern*** for nonlinear reaction-diffusion (4), spawn by its "symmetric" unstable equilibrium (u^*, v^*).

Bifurcation analysis in terms of D_i, depends on how "parabola" $\sigma(\mu)$ of Fig.2 will hit the positive μ axis. It can be "saddle-node" or Hopf bifurcation(?).