Pattern formation and Turing instability

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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.

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

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 \( v(x,t) = u(x,t) - u^* \)

\[
\begin{align*}
  v_t &= Du_{xx} + mv; \\
  m &= f'(u^*)
\end{align*}
\]

(1)

Solution on \( \mathbb{R} / \mathbb{R}^n \)

\[
v(x,t) = \int_{-\infty}^{\infty} e^{m(x-\xi)^2/4Dt} v_0(\xi) d\xi
\]

(2)

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

Figure 1: Point-source solution (2) on \( \mathbb{R} \) 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

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

(3)

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

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

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

(4)

or its multi-D version in $(x,y,\ldots)$ 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

$$
\begin{align*}
\begin{cases}
u'_t = D_1 u'_{xx} + au' + bv' \\
v'_t = D_2 v'_{xx} + cu' + dv'
\end{cases}
\end{align*}
$$

with Jacobian $J = \begin{bmatrix} a & b \\ c & d \end{bmatrix}$

or in vector notation
\[
U_t = \begin{bmatrix} D_1 \\ D_2 \end{bmatrix} \partial_x^2 U + J \cdot U; U(x,t) = \begin{pmatrix} u' \\ v' \end{pmatrix}
\]  
(5)

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

\[
L = \begin{bmatrix} D_1 \\ D_2 \end{bmatrix} \partial_x^2 + J
\]  
(6)

We denote by \( \mu \) eigenvalues of scalar laplacian \( L_0 = \partial_x^2 \) or \( \Delta \).

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

<table>
<thead>
<tr>
<th>( \mu )</th>
<th>( \psi(x) )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Free space</strong> ( \mathbb{R}; \mathbb{R}^n )</td>
<td>( 0 \leq \mu_k = k^2 &lt; \infty )</td>
</tr>
</tbody>
</table>
| \( k = (k_1, k_2, \ldots) \in \mathbb{R}^n; \)
| \( k = |k| \) | \( \{ \psi_k(x) = e^{i k \cdot x} \} \) or |
| | \( \{ \text{cos} k \cdot x, \text{sin} k \cdot x \} \) |
| **Finite interval** \( [0,l] \) | \( \{ \mu_k = (\pi k / l)^2 : k = 1, 2, \ldots \} \) |
| **Dirichlet:** | \( \{ \mu_k = (\pi k / l)^2 : k = 0, 1, \ldots \} \) |
| **Neuman:** | \( \{ \mu_k = (2\pi k / l)^2 : -\infty < k < \infty \} \) |
| **Periodic** | \( \psi_k = \sin \left( \frac{\pi k x}{l} \right) \) |
| | \( \psi_k = \cos \left( \frac{\pi k x}{l} \right) \) |
| | \( \{ \psi_k(x) = e^{i 2\pi k x/l} \} \) or \( \{ \text{cos}, \text{sin} \} \) |
| **2D (nD) Square, box** | \( 0 < x < a; 0 < y < b \) |
| \( \{ \mu_{k,m} = \pi^2 \left( \left( k/a \right)^2 + \left( m/b \right)^2 \right) : k,m = 1, 2, \ldots \} \) | \( \psi_{k,m} = \sin \left( \frac{\pi k x}{a} \right) \sin \left( \frac{\pi m y}{b} \right) \) |
| **Polar disk (annulus)** | \( 0 < r < a; \) |
| \( 0 < \theta < 2\pi \) | \( \mu_{k,m} = \left( \frac{z_{m,k}}{a} \right)^2 \) |
| **product type (radial x angular modes):** | \( \psi_{k,m}(r,\theta) = J_m \left( z_{m,k} r / a \right) e^{i m \theta} \) |

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” = \( \psi \left( x \right) X \), \( \psi \) - eigenmode of Laplace \( L_0 \). It gives

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

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

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

(7)

Specifically, eigenvalues of \( L \)

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

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

**Turing instability analysis**

Basic question: given positive Laplace eigenvalues \( \{\mu\} \) can a stable chemistry (Jacobian \( J \)) produce an 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**

<table>
<thead>
<tr>
<th>Stable J ( a + d &lt; 0 )</th>
<th>Stable B- ?</th>
</tr>
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<tbody>
<tr>
<td>( \text{tr} J = a + d &lt; 0 )</td>
<td>( \text{tr} B = -\mu \left( D_1 + D_2 \right) + \text{tr} J &lt; 0 ) - always true!</td>
</tr>
<tr>
<td>( \text{det} J = ad - bc &gt; 0 )</td>
<td>( \text{det} B = D_1 D_2 \mu^2 - \left( aD_2 + dD_2 \right) \mu + \left( ad - bc \right) = Q(\mu) )</td>
</tr>
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</table>

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($J$) - $\mu D$” 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 $\mu$ 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{align*}
(T1) & \quad a_1 = aD_2 + dD_1 > 0 \quad \text{- negative slope } Q'(0) \\
(T2) & \quad (aD_2 + dD_1)^2 \geq 4D_1D_2 (ad - bc) \quad \text{- discriminant}
\end{align*}

From (T1) and $\text{tr}(J) < 0 \Rightarrow$ 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 $\xi = \sqrt{D_1 / D_2}$](image)

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

\[\xi \bigg|_{M=1.1} = 1.1 \quad \xi \bigg|_{M=9} = 9 \quad \xi \bigg|_{M=7} = 7\]
\[ a / \xi + d / \xi \geq 2 \sqrt{bc}; \text{ with parameter } \xi = \sqrt{D_1 / D_2} \]  

(10)

Combined set conditions (\(\text{tr}(J)<0, \det(J)>0, \text{tr}(B)<0, \det(B)<0\)) 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.

\[ \text{Figure 3: Parameter range for } D_1 / D_2 \text{ to get Turing instability} \]

A positive (unstable) eigenvalue \(\lambda(L)\) for some \(\mu\) within the “unstable” interval of Fig.2 will give a spatial (eigenmode) part \(\psi(x)\) (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 \(\mu\) axis. It can be “saddle-node” or Hopf bifurcation(?).