Turing patterns: analysis and computation

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MMSC modelling case studies

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Turing patterns

- pattern formation is an important topic in biology

Images: Left: Florham Park, "Alan Turing: Calico Cats, Zebras, and Daylilies". Right: When Math Meets Nature: Turing Patterns and Form Constants - Scientific American Blog Network

- Chemicals can react and diffuse in such a way as to produce steady state heterogeneous spatial patterns of chemical or morphogen concentration.
- Turing mechanism: chemical distribution is determined by a reaction-diffusion equation. In the absence of diffusion, steady state solutions are uniform (spatially constant). This steady state solution becomes linearly unstable in the presence of certain diffusion terms, a phenomenon known as *diffusion driven instability*.

- governing equations:

$$\frac{\partial A}{\partial t} = F(A,B) + D_A \Delta A, \tag{1a}$$
$$\frac{\partial B}{\partial t} = G(A,B) + D_B \Delta B, \tag{1b}$$

where $A(\boldsymbol{x},t)$ and $B(\boldsymbol{x},t)$ are two chemical species, F and G are reaction terms which are in general nonlinear, and ΔA and ΔB are diffusion terms.

- dimensionless form:

$$\frac{\partial u}{\partial t} = \gamma f(u,v) + \Delta u, \tag{2a}$$
$$\frac{\partial v}{\partial t} = \gamma g(u,v) + d\Delta v. \tag{2b}$$

Here γ has the dimension of L^2, where L is the characteristic length.

Assume that (u_0, v_0) is a steady state solution for the system without diffusion (i.e., $f(u_0,v_0)=0,\ g(u_0,v_0)=0$). The *linear stability analysis of Turing mechanism* consists of the following steps:

1. Find conditions such that the linearised solution is stable in the absence of diffusion.
2. In the presence of diffusion, we are interested in the parameters d, γ, geometry of domain etc. such that the linearised solution is linearly unstable.

Consider the linearised equation

$$\boldsymbol{w}_t = \gamma A \boldsymbol{w} + D \Delta \boldsymbol{w}, \tag{3}$$

where

$$\boldsymbol{w} = \begin{pmatrix} u - u_0 \\ v - v_0 \end{pmatrix}, \quad A = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}, \quad D = \begin{pmatrix} 1 & 0 \\ 0 & d \end{pmatrix}.$$

The above requirements lead to the following necessary (not sufficient) conditions:

$$f_u + g_v < 0, \quad f_u g_v - f_v g_u > 0, \tag{4}$$

$$d f_u + g_v > 0, \quad (d f_u + g_v)^2 - 4d(f_u g_v - f_v g_u) > 0. \tag{5}$$

To further analyse the linear instability, we first want to transform the PDEs to algebraic equations. To this end, consider the Fourier decomposition of $\boldsymbol{w}$ by eigenfunctions of the Laplacian:

$$\boldsymbol{w}(\boldsymbol{x}, t) = \sum_k c_k e^{\lambda t} \boldsymbol{W}_k(\boldsymbol{x}), \tag{6}$$

where $(k^2, \boldsymbol{W}_k)$ are eigenpairs, i.e.,

$$-\Delta \boldsymbol{W}_k = k^2 \boldsymbol{W}_k, \tag{7}$$

with the boundary condition

$$(\boldsymbol{n} \cdot \nabla) \boldsymbol{W}_k = 0, \quad \text{on } \partial\Omega.$$

Eigenpairs $(k^2, \boldsymbol{W}_k)$ only depend on the domain.

Substituting the Fourier mode (6) into (3), we get

$$\lambda \boldsymbol{W}_k = \gamma A \boldsymbol{W}_k - Dk^2 \boldsymbol{W}_k,$$

and therefore

$$|\lambda I - \gamma A + Dk^2| = 0. \tag{8}$$

Given any $k^2 > 0$, we can solve two values of λ from (8). The function $\lambda = \lambda(k^2)$ is called the dispersion relation.

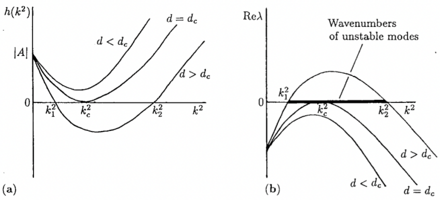

Figure 2.5. (**a**) Plot of $h(k^2)$ defined by (2.23) for typical kinetics illustrated in Figure 2.2. When the diffusion coefficient ratio d increases beyond the critical value d_c, $h(k^2)$ becomes negative for a finite range of $k^2 > 0$. (**b**) Plot of the largest of the eigenvalues $\lambda(k^2)$ from (2.23) as a function of k^2. When $d > d_c$ there is a range of wavenumbers $k_1^2 < k^2 < k_2^2$ which are linearly unstable.

Murray, J.D., 2001. Mathematical biology II: spatial models and biomedical applications. Chapter 2

Bifurcation parameter $d = d_c$: for $d > d_c$, the following condition implies that *there exists* $k^2 > 0$ such that at least one λ (solved from (8)) has positive real part, and thus the steady state is linearly unstable:

$$\alpha := \frac{\gamma}{2d}[(df_u + g_v) - [(df_u + g_v)^2 - 4d|A|]^{1/2}] < k^2 < \frac{\gamma}{2d}[(df_u + g_v) + [(df_u + g_v)^2 - 4d|A|]^{1/2}] := \beta.$$

The corresponding $\boldsymbol{W}_k$ is the Turing pattern predicted by this linear theory.

The project has the following concrete goals:

1. Learn about the Turing mechanism. For specific examples (e.g., $f = a - u + u^2 v$, $g = b - u^2 v$), analyse the effect of parameters (e.g., (a, b, d)), scaling (γ) and geometry in 1D and 2D rectangular domains. Explain the emergence of strips/spots etc. (different patterns correspond to different $\boldsymbol{W}_k$).
2. Investigate how the linear analysis fails when the solutions leave steady state, i.e., how solutions to the nonlinear problem (2) deviate from $\boldsymbol{W}_k$ (in 1D and possibly in 2D). The nonlinear equations can be solved by numerical computation.
3. Investigate the effect of other factors, e.g., growing domains where the domain is a function of t, and effects of curvature (in this case, the Laplacian $-\Delta$ should be replaced by the Laplace-Beltrami operator).

References

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   Chapter 2: background, equations, linear stability analysis etc.
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3. Plaza, R.G., Sanchez-Garduno, F., Padilla, P., Barrio, R.A. and Maini, P.K., 2004. The effect of growth and curvature on pattern formation. Journal of Dynamics and Differential Equations, 16(4), pp.1093-1121.