Turing instability and pattern generation

Turing (1952): diffusion can lead to chemical morphogenesis and pattern formation

A stable steady state of a dynamical system, usually highly symmetric (e.g. some constant concentration), can change into an unstable steady state if diffusion is added to the model. Small perturbations can then give rise to big changes in the solutions, that become less symmetric and patterns form. The first patterns to appear are not the lowest n (in $\cos nx$) as for aggregation of slime molds, but for some higher n, giving more interesting patterns.

We need two (or more) interacting chemical species with different diffusion rates. Usually diffusion increases stability, but here we shall see the opposite effect.

(Turing started with a discrete model and Fourier analysis and took some limits to come to a time and space continuous model)

First 1 spacedim. Let

$C_1(t,x), C_2(t,x)$ = concentrations of chemicals 1 and 2

D_1, D_2 = diffusion rates

$R_1(C_1,C_2), R_2(C_1,C_2)$ = rates of production of chem. 1 and 2, "kinetic" terms

Model

$$\begin{cases} \dfrac{\partial C_1}{\partial t} = R_1(C_1,C_2) + D_1 \dfrac{\partial^2 C_1}{\partial x^2} \\ \dfrac{\partial C_2}{\partial t} = R_2(C_1,C_2) + D_2 \dfrac{\partial^2 C_2}{\partial x^2} \end{cases}$$

R_1 and R_2 can also be thought of as sources for the diffusion eq.

Let $\bar{C}_1, \bar{C}_2$ be a positive spatially uniform steady state, means that

$$\frac{\partial \bar{C}_1}{\partial t} = \frac{\partial \bar{C}_2}{\partial t} = \frac{\partial^2 \bar{C}_1}{\partial x^2} = \frac{\partial^2 \bar{C}_2}{\partial x^2} = 0 \Rightarrow$$

$$\begin{cases} R_1(\bar{C}_1,\bar{C}_2) = 0 \\ R_2(\bar{C}_1,\bar{C}_2) = 0 \end{cases}$$

$\Rightarrow$ $\bar{C}_1, \bar{C}_2$ is also a steady state to the system without diffusion: $(D_1 = D_2 = 0)$

study perturbations

$$\begin{cases} C_1(t,x) = \bar{C}_1 + \hat{C}_1(t,x) \\ C_2(t,x) = \bar{C}_2 + \underbrace{\hat{C}_2(t,x)}_{\text{small}} \end{cases}$$

Taylor expansion of $R_1(C_1,C_2)$ at $(\bar{C}_1,\bar{C}_2)$:

$$R_1(C_1,C_2) = \underbrace{R_1(\bar{C}_1,\bar{C}_2)}_{=0} + \underbrace{\frac{\partial R_1}{\partial C_1}(\bar{C}_1,\bar{C}_2)}_{=a_{11}}\hat{C}_1 + \underbrace{\frac{\partial R_1}{\partial C_2}(\bar{C}_1,\bar{C}_2)}_{=a_{12}}\hat{C}_2 + \underbrace{\mathcal{O}(\hat{C}_1^2 + \hat{C}_2^2)}_{\text{order 2}}$$

Same for R_2 : $a_{21} = \frac{\partial R_2}{\partial c_1}(\bar{c}_1, \bar{c}_2)$, $a_{22} = \frac{\partial R_2}{\partial c_2}(\bar{c}_1, \bar{c}_2)$.

study the linearized system

$$\begin{cases} \dfrac{\partial \tilde{c}_1}{\partial t} = a_{11}\tilde{c}_1 + a_{12}\tilde{c}_2 + D_1 \dfrac{\partial^2 \tilde{c}_1}{\partial x^2} \\ \dfrac{\partial \tilde{c}_2}{\partial t} = a_{21}\tilde{c}_1 + a_{22}\tilde{c}_2 + D_2 \dfrac{\partial^2 \tilde{c}_2}{\partial x^2} \end{cases}$$

With $\tilde{C} = \begin{pmatrix} \tilde{c}_1 \\ \tilde{c}_2 \end{pmatrix}$, $A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$ and $D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$ we have $\underline{\tilde{C}_t = A\tilde{C} + D\tilde{C}_{xx}}$ (*)

We want (*) to be stable if $D_1 = D_2 = 0$ $\Leftrightarrow$

$$\boxed{\begin{array}{ll} \mathrm{Tr}\,A = a_{11} + a_{22} < 0 & (1) \\ \det A = a_{11}a_{22} - a_{12}a_{21} > 0 & (2) \end{array}}$$

We can solve (*) by separation of variables for $\tilde{C}$. Inspired by previous studies of $u_t = Du_{xx}$ and $u_t = Du_{xx} + ku$ with no-flux BC's, we directly look for solutions on the form (as for aggregation of slime molds)

$$\tilde{C} = \underbrace{\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}}_{\text{constants}} e^{\sigma t} \cos qx$$

$\Rightarrow \tilde{C}_t = \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} \sigma e^{\sigma t} \cos qx = \sigma \tilde{C}$, and $\tilde{C}_{xx} = \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} e^{\sigma t}(-q^2)\cos qx = -q^2 \tilde{C}$ $\overset{(*)}{\Rightarrow}$

$\sigma \tilde{C} = A\tilde{C} - q^2 D\tilde{C} \Rightarrow (A - q^2 D)\tilde{C} = \sigma \tilde{C}$. Divide by $e^{\sigma t}\cos qx$ $\Rightarrow$

$\underline{(A - q^2 D)\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix} = \sigma \begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}}$ $\Rightarrow$ $\begin{pmatrix} \alpha_1 \\ \alpha_2 \end{pmatrix}$ eigenvector and σ eigenvalue of the matrix $A - q^2 D$ $\Rightarrow$

$$0 = \det(A - q^2 D - \sigma I) = \begin{vmatrix} a_{11} - q^2 D_1 - \sigma & a_{12} \\ a_{21} & a_{22} - q^2 D_2 - \sigma \end{vmatrix} =$$

$$= \sigma^2 - \underbrace{(a_{11} + a_{22} - q^2(D_1 + D_2))}_{r}\sigma + \underbrace{(a_{11} - q^2 D_1)(a_{22} - q^2 D_2) - a_{12}a_{21}}_{s}$$

$$\Rightarrow \sigma = \sigma_{1,2} = \tfrac{1}{2}\left(r \pm \sqrt{r^2 - 4s}\right)$$

We are interested in unstable perturbations, i.e. $\mathrm{Re}(\sigma_{1,2}) > 0$.

$\mathrm{Tr}(A - q^2 D) = r = \underbrace{a_{11} + a_{22}}_{<0 \text{ by } (1)} \underbrace{- q^2(D_1 + D_2)}_{<0} < 0$ always, so any instability must come from $\underline{\det(A - q^2 D) < 0}$

$$\det(A-q^2D) = s = D_1D_2q^4 - (a_{11}D_2 + a_{22}D_1)q^2 + \underbrace{(a_{11}a_{22}-a_{12}a_{21})}_{=\det A} =$$

$$= D_1D_2\Big[q^4 - \underbrace{\frac{a_{11}D_2+a_{22}D_1}{D_1D_2}}_{u} q^2 + \underbrace{\frac{\det A}{D_1D_2}}_{w}\Big] = D_1D_2\Big[\left(q^2-\frac{u}{2}\right)^2 + w - \frac{u^2}{4}\Big]$$

Can this be negative? Yes, if $w < \frac{u^2}{4}$ and $\left(q^2-\frac{u}{2}\right)^2 < \frac{u^2}{4} - w$.

Note, $\det(A) > 0$ by (2) $\Rightarrow u > 0$ necessary if $\det(A-q^2D) < 0$. Then

$$w < \frac{u^2}{4} \Leftrightarrow 2\sqrt{w} < u \Leftrightarrow \frac{2\sqrt{\det A}}{\sqrt{D_1D_2}} < \frac{a_{11}D_2+a_{22}D_1}{D_1D_2} \Leftrightarrow$$

$$\boxed{a_{11}D_2 + a_{22}D_1 > 2\sqrt{D_1D_2\det A} \quad (3)}$$

(1), (2) and (3) are the conditions for (Turing) diffusive instability (as formulated by Segel and Jackson 1972)

Observations

1. If $D_1 = D_2$, then $a_{11}D_2 + a_{22}D_1 = \underbrace{(a_{11}+a_{22})}_{<0 \text{ by}(1)}\underbrace{D_1}_{>0} < 0 \Rightarrow u < 0 \Rightarrow$
   $\det(A-q^2D) > 0 \Rightarrow$ we need $D_1 \neq D_2$ to get diffusive instability

2. $\det(A-q^2D)$ has its minimal value for $q^2 = q_m^2 = \frac{u}{2} = \frac{1}{2}\left(\frac{a_{11}}{D_1} + \frac{a_{22}}{D_2}\right)$

   For $w > \frac{u^2}{4}$ there is no diffusive instability
   For $w = \frac{u^2}{4}$ we have the limit case $q^2 = \frac{u}{2}$
   For $w < \frac{u^2}{4}$, let $\Delta = \sqrt{\frac{u^2}{4} - w} > 0$. All q with $|q^2 - \underbrace{\tfrac{u}{2}}_{q_m^2}| < \Delta \Leftrightarrow$
   $q_m^2 - \Delta < q^2 < q_m^2 + \Delta$ correspond to unstable perturbations

3. (1) and (3) $\Rightarrow$ exactly one of a_{11} and a_{22} is positive. We may assume $a_{11} = \frac{\partial R_1}{\partial c_1}(\bar{c}_1, \bar{c}_2) > 0$ and $a_{22} = \frac{\partial R_2}{\partial c_2}(\bar{c}_1, \bar{c}_2) < 0$.
   Chemical 1 is an activator, promotes its own formation
   Chemical 2 is an inhibitor

Then $a_{11}a_{22}<0$ so (2) $\Rightarrow a_{12}a_{21}<0$ and $|a_{12}a_{21}|>|a_{11}a_{22}|$
Two cases:

I. $a_{12}<0,\ a_{21}>0 \Rightarrow A$ has signs $A=\begin{pmatrix}+&-\\+&-\end{pmatrix}$, called the activator-inhibitor case. Chemical 1 has positive effect on the synthesis of both itself and chemical 2. Chemical 2 has the opposite effect.

II $a_{12}>0,\ a_{21}<0 \Rightarrow A=\begin{pmatrix}+&+\\-&-\end{pmatrix}$, called the positive feedback case (or substrate depletion). There is positive "feedback" from both chemicals on chemical 1 (and negative on chem. 2)

4. $$\left.\begin{array}{l} a_{11}>0 \\ a_{11}+a_{22}<0 \\ a_{11}D_2+\underbrace{a_{22}}_{<0}D_1>0 \end{array}\right\} \Rightarrow |a_{22}|>a_{11} \text{ and } \underline{D_2>D_1}.$$

For $\begin{pmatrix}+&-\\+&-\end{pmatrix}$, $D_2>D_1$ means that the inhibitor diffuses away faster than the activator, and instabilities form.
For $\begin{pmatrix}+&+\\-&-\end{pmatrix}$, $D_2>D_1$ means that chemical 1, which receives positive feedback, diffuses slower

5. The numbers $L_1=\frac{D_1}{a_{11}}$ and $L_2=\frac{D_2}{|a_{22}|}$ are called ranges of activation/inhibitation. We have $L_1<L_2$ since $L_1-L_2=\frac{D_1}{a_{11}}-\left(-\frac{D_2}{a_{22}}\right)=$

$$=\frac{1}{\underbrace{a_{11}a_{22}}_{<0}}\underbrace{(a_{22}D_1+a_{11}D_2)}_{>0}<0.$$

Examples and 2D next seminars