Pattern formation II

Diffusive instability

(Turing instability)

Spatially unstructured case

$$\begin{cases} \dot{m} = f(m,n) \\ \dot{n} = g(m,n) \end{cases}$$

with equilibrium (m^*, n^*).
Linearization about the equil:

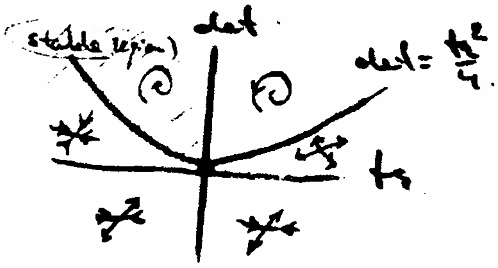
$$\begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix}^{\bullet} = A \begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix}$$

where $\Delta m = m - m^*$ and $\Delta n = n - n^*$,

$$A = \begin{pmatrix} \partial_m f(m^*,n^*) & \partial_n f(m^*,n^*) \\ \partial_m g(m^*,n^*) & \partial_n g(m^*,n^*) \end{pmatrix} =: \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

Assume hyperbolic stability, i.e.,

$$\begin{cases} a_{11} + a_{22} < 0 & (\mathrm{tr} A < 0) \\ a_{11} a_{22} > a_{12} a_{21} & (\det A > 0) \end{cases}$$



Now we add diffusion:

$$\begin{cases} \partial_t m = f(m,n) + \mu \partial_x^2 m \\ \partial_t n = g(m,n) + \nu \partial_x^2 n \end{cases}$$

with $\boxed{\text{reflecting bnds}}$ at $x = 0, L$.

Linearization about the spatially homogeneous equilibrium (m^*, n^*) gives

$$(*) \quad \boxed{\partial_t \begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix} = A \begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix} + D \partial_x^2 \begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix}}$$

where A is as before and

$$D = \begin{pmatrix} \mu & 0 \\ 0 & \nu \end{pmatrix}.$$

Given the reflecting bnd conds, it seems a good idea to write solutions of $(*)$ as a Fourier cosine series. So, we try

$$(**) \quad \boxed{\begin{pmatrix} \Delta m \\ \Delta n \end{pmatrix} = e^{\lambda t} \underbrace{\begin{pmatrix} \alpha \\ \beta \end{pmatrix} \cos \omega x}}$$

(eigen-value) (corresponding eigen function)

To satisfy the bnd conds. we must have

$$\boxed{\omega = \frac{k\pi}{L}} \qquad (k = 0, 1, 2, \dots)$$

Subst. of ⊛⊛ (prev page) into ⊛ gives:

$$\boxed{(\lambda I - A + \omega^2 D)\binom{\alpha}{\beta} = 0}$$

where I is the identity matrix. For a non-trivial solution (α, β) we need that

$$\boxed{\det(\lambda I - A + \omega^2 D) = 0} \quad \text{char. equ.}$$

which is the characteristic equation for the linear problem ⊛ on page 2.

Written out this becomes

$$\boxed{\lambda^2 + p\lambda + q = 0}$$

where

$$p = \omega^2(\mu + \nu) - (a_{11} + a_{22})$$

$$q = \omega^2\left[\omega^2 \mu\nu - \mu a_{22} - \nu a_{11}\right] + (a_{11}a_{22} - a_{12}a_{21}).$$

and so

$$\lambda = \frac{1}{2}\left(-p \pm \sqrt{p^2 - 4q}\right)$$

Hyperbolic stability of the non-spatial system (page 1) implies

$\boxed{a_{11} + a_{22} < 0}$ and $\boxed{a_{11}a_{22} - a_{12}a_{21} > 0}$

Consequently, $\boxed{p > 0 \ \forall \omega}$

$\Rightarrow$ For instability of the spatially homogeneous equil. solution it is necessary and sufficient that $q < 0$ for some $\omega > 0$.

(Because that give $\mathrm{Re}\,\lambda > 0$).

$\Rightarrow$ Necessary and sufficient condition for diffusive instability:

$$\boxed{\begin{array}{l} \exists\, \omega = \frac{k\pi}{L} \quad (k = 0, 1, 2, \dots) \text{ such that} \\ \omega^2(\omega^2\mu\nu - \mu a_{22} - \nu a_{11}) + \det A < 0 \end{array}}$$

The LHS of the above inequality is a valley parabola in ω^2.

$$\boxed{P(\omega^2) := \mu\nu (\omega^2)^2 - (\mu a_{22} + \nu a_{11})\,\omega^2 + \det A}$$

$P(\omega^2)$ has a positive real root if and only if

(i) $\boxed{(\mu a_{22}+\nu a_{11})^2 > 4\mu\nu \det A}$ (to ensure the roots are real)

and

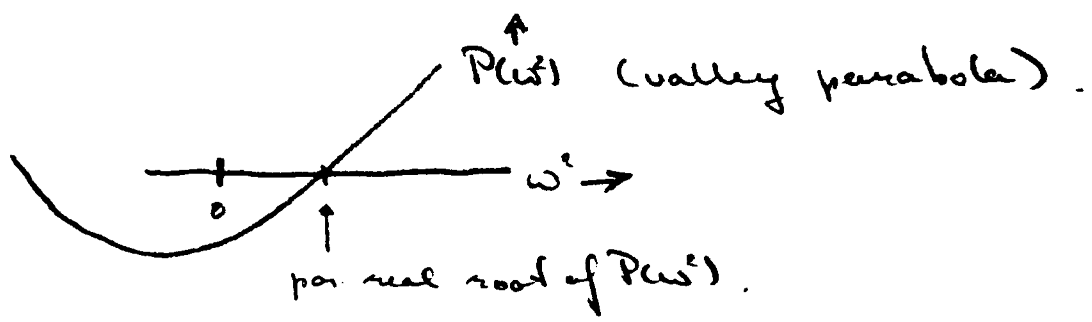
(ii) $\boxed{\mu a_{22}+\nu a_{11} > 0}$ (to ensure that the largest root is positive).

From the hyperbolic stability of the non-spatial system (page 1) we know that $\boxed{\det A > 0}$.

$\Rightarrow$ We can replace the conditions (i) and (ii) by the one condition:

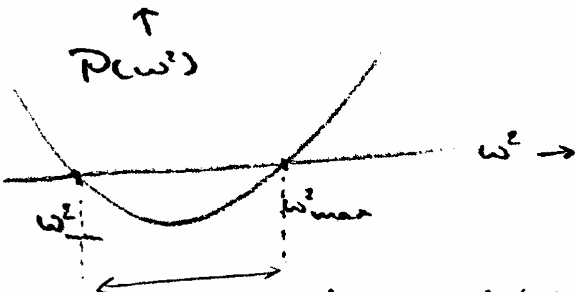
$$(*) \quad \boxed{\mu a_{22}+\nu a_{11} > 2\sqrt{\mu\nu \det A}}$$

Note that existence of a positive real root of $P(\omega^2)$ is also necessary and sufficient for the existence of an $\omega^2 > 0$ such that $P(\omega^2) < 0$.



Which $\omega > 0$ give $\mathrm{Re}\,\lambda > 0$?

(In case of diff. inst.)



(all these ω's would do)

$$\begin{cases} \omega^2_{min} = \frac{1}{2}\left(\mu a_{22} + \nu a_{11} \ominus \sqrt{(\mu a_{22} + \nu a_{11})^2 - 4\mu\nu \det A}\right) \\ \omega^2_{max} = \frac{1}{2}\left(\text{—''—} \oplus \sqrt{\text{—''—}}\right) \end{cases}$$

From ⊛ (page 5) it follows that $\boxed{\mu a_{22} + \nu a_{11} > 0}$ and hence $\boxed{0 < \omega_{min} < \omega_{max}}$ and so all $\boxed{\omega \in (\omega_{min}, \omega_{max})}$ give $\mathrm{Re}\,\lambda > 0$.

Since $\omega = \frac{k\pi}{L}$ $(k = 0, 1, 2, \dots)$ we have $\mathrm{Re}\,\lambda > 0$ for every integer $\boxed{k \in \left(\frac{L\omega_{min}}{\pi}, \frac{L\omega_{max}}{\pi}\right)}$

The emerging pattern is given by the k corresponding to the dominant eigenvalue.

(We'll give some examples later).

Summary

Necessary and sufficient conditions for diffusive instability:

① $a_{11} + a_{22} < 0$

② $a_{11}a_{22} - a_{12}a_{21} > 0$

(stability in non-spatial system)

③ $\mu a_{22} + \nu a_{11} > 2\sqrt{\mu\nu(a_{11}a_{22} - a_{12}a_{21})}$

We can write cond. ③ also as

$$a_{11}\sqrt{\frac{\nu}{\mu}} + a_{22}\sqrt{\frac{\mu}{\nu}} > 2\sqrt{a_{11}a_{22} - a_{12}a_{21}}$$

which shows that diff. instab. depends on the ratio of the diffusion coefficients and not on their absolute magnitudes.

Interpretation

(also see Edelstein-Keshet 1988).

From ① (page 6) it follows that at least one of the coefficients a_{11} or a_{22} is negative.

From ③ (page 6) it follows that not both a_{11} and a_{22} can be negative.

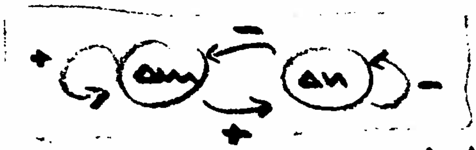
$$\boxed{a_{11} a_{22} < 0}$$

But then it follows from ② (page 6) that

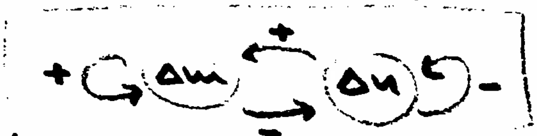
$$\boxed{a_{12} a_{21} > 0}$$

This leaves us with two sign-structures of the matrix A:

$$A = \begin{pmatrix} + & - \\ + & - \end{pmatrix} \quad \text{or} \quad A = \begin{pmatrix} + & + \\ - & - \end{pmatrix}$$



"activator-inhibitor"



"pos. feedback"

Division of ③ (page 6) by ν gives:

$$\boxed{a_{11} + a_{22}\frac{\mu}{\nu} > 0}$$

and hence $\boxed{\mu \neq \nu}$, because otherwise there would be a contradiction with ① (page 6)

|| So, the diff. coeffs. <u>must</u> <u>differ</u> for diffusion instability to occur.

$\frac{1}{|a_{11}|}$ and $\frac{1}{|a_{22}|}$ are <u>time constants</u> associated with the self-activation and self-inhibition.

Assuming that $a_{11} > 0$, $a_{22} < 0$, then from ③ (page 6):

$$\boxed{\sqrt{\frac{\mu}{|a_{11}|}} < \sqrt{\frac{\nu}{|a_{22}|}}}$$

have dimension length

i.e. u is the activator and v is the inhibitor.

|| So, the range of activation should be less than the range of inhibition for diffusion instability to occur

Diffusive instability (Examples)

The model of Gause

(also see some earlier lecture notes) (14-02-2012)

$$\begin{cases} \dot{K} = f(K) - g(K)C & \text{(resource)} \\ \dot{C} = \gamma g(K)C - \delta C & \text{(consumer)} \end{cases}$$

where

$$\begin{cases} f(0)=0 \text{ and } f(K) \gtreqless 0 \text{ for } K \lesseqgtr \underset{\text{some } K>0}{K} \\ g(0)=0 \text{ and } g'(K) > 0 \text{ for } K > 0. \end{cases}$$

Isoclines:

$$\dot{K} = 0 \iff K=0 \text{ or } C = f(K)/g(K)$$

$$\dot{C} = 0 \iff C=0 \text{ or } g(K) = \delta/\gamma.$$

(has unique root)

Positive equilibrium:

$$(K^*, C^*)$$

$$\begin{cases} K^* \text{ unique root } g(K) = \delta/\gamma \\ C^* = f(K^*)/g(K^*). \end{cases}$$

Jacobi matrix at equil.

$$A = \begin{pmatrix} \frac{\delta}{\gamma}\left(\frac{f(R^*)}{g(R^*)}\right)' & -\frac{\delta}{\gamma} \\ \gamma C^* g'(R^*) & 0 \end{pmatrix}$$

Local stability

$$\det A = \delta C^* g'(R^*) > 0$$

$$\operatorname{tr} A = \frac{\delta}{\gamma}\underbrace{\left(\frac{f(R^*)}{g(R^*)}\right)'}_{} < 0$$

slope of R-iso at the equilibrium

Diffusive stability:

Assume stability, then the sign structure of A is

$$A = \begin{pmatrix} - & - \\ + & 0 \end{pmatrix}$$

necessary condition for diffusive stability is that there is a ⊕

$\Rightarrow$ No diffusive instability possible in the Gause model.

Variation on Gause model

$$\begin{cases} \dot{R} = f(R) - g(R)\,C \\ \dot{C} = \gamma g(R) C - \underbrace{\delta C^2}_{\uparrow} \end{cases}$$

same f and g as previously.

(density-dependent mortality)

Isoclines

$$\dot{R} = 0 \iff R = 0 \text{ or } C = f(R)/g(R)$$

$$\dot{C} = 0 \iff C = 0 \text{ or } C = \frac{\gamma}{\delta} g(R).$$

Suppose a positive equilibrium (R^*, C^*) exists.

Jacobi matrix at (R^*, C^*):

$$A = \begin{pmatrix} f'(R^*) - g'(R^*)C^* & -g(R^*) \\ \gamma g'(R^*) C^* & \gamma g(R^*) - 2\delta C^* \end{pmatrix} =$$

$$= \begin{pmatrix} \frac{\delta}{\gamma} C^* \left(\frac{f(R^*)}{g(R^*)} \right)' & -\frac{\delta}{\gamma} C^* \\ \gamma C^* g'(R^*) & -\delta C^* \end{pmatrix}$$

Local stability

$$\det A = \frac{\delta^2}{\gamma}(C^*)^2\Big(\underbrace{\tfrac{\gamma}{\delta}g'(K^*)}_{\substack{\text{slope of C-iso.}\\ \text{at equilibrium}}} - \underbrace{\Big(\frac{f(K^*)}{g(K^*)}\Big)'}_{\substack{\text{slope of K-isocline}\\ \text{at equilibrium}}}\Big) > 0$$

$$\operatorname{tr} A = \frac{\delta}{\gamma}C^*\Big(\Big(\frac{f(K^*)}{g(K^*)}\Big)' - \gamma\Big) < 0$$

For local stability we require:

① $\begin{pmatrix}\text{slope of C-isocline}\\ \text{at equilibrium}\end{pmatrix} > \begin{pmatrix}\text{slope of K-isocline}\\ \text{at equilibrium}\end{pmatrix}$

② $\begin{pmatrix}\text{slope of K-isocline}\\ \text{at equilibrium}\end{pmatrix} < \gamma$

Diffusive instability

Necessarily (but not sufficient)

③ $\begin{pmatrix}\text{slope of K-isocline}\\ \text{at equilibrium}\end{pmatrix} > 0$

This would then give

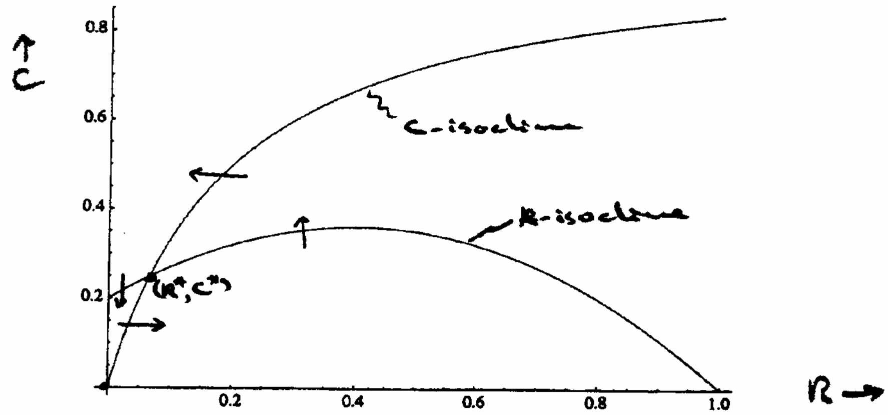
$$A = \begin{pmatrix} + & - \\ + & - \end{pmatrix}$$

activator-inhibitor system with the resource as activator and the consumer as inhibitor.

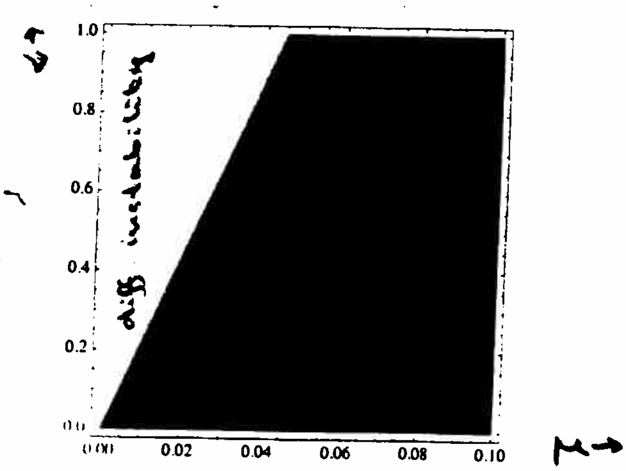
Specific example

$$\begin{cases} f(R) = R(1-R) & \text{(logistic)} \\ g(R) = \dfrac{\beta R}{1+\beta T R} & \text{(Holling-II)}. \end{cases}$$

E.g., For $\beta=5,\ \gamma=1,\ \delta=1,\ T=1$ there exists a unique positive equilibrium (R^*, C^*), which is stable



Diffusion instab occurs for diff coeffs μ (resource) and ν (consumer) in the light region:



The eigenvalues of the spatial system are calculated as

$$\lambda_{1,2} = \frac{1}{2}\left[-p \pm \sqrt{p^2 - 4pq}\right]$$

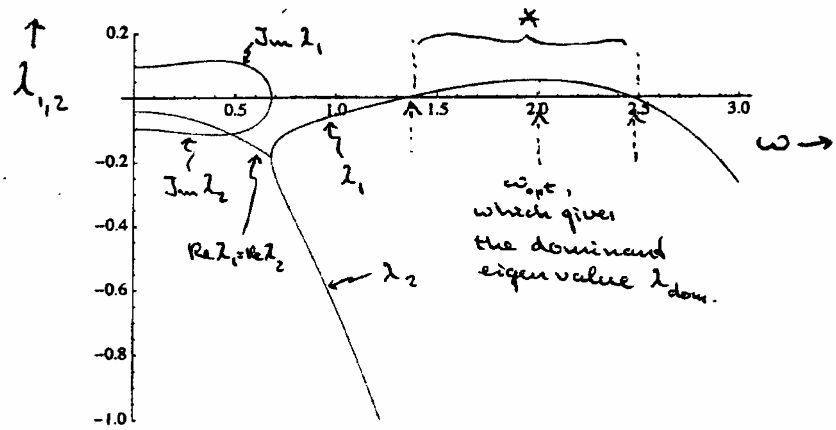
where

$$\begin{cases} p = \omega^2(\mu+\nu) - \mathrm{tr}A \\ q = \omega^2\left[\omega^2\mu\nu - \mu a_{22} - \nu a_{11}\right] + \det A. \end{cases}$$

where

$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$ is the Jacobian at (R^*, C^*).

As a function of ω this gives



- Frequencies in the interval (*) are amplified; other frequencies are dampened
- The emerging pattern has a frequency ω_{opt}, which correspond to the dominant eigenvalue.

(not necessarily final pattern)