Integrodifference equations in spatial ecology

Lecture 15: Pattern formation

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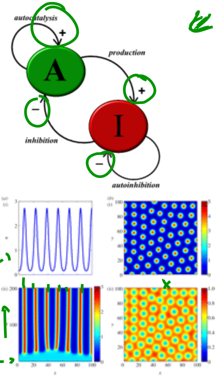
Turing's discovery

$$\frac{\partial A}{\partial t} = F(A, I) + dA_{xx}$$

$$\frac{\partial I}{\partial t} = G(A, I) + DI_{xx}$$

$$d \ll D$$

- chemical reaction
- well-mixed system is stable
- spatial diffusion can lead to instability
- requirement I: activator and inhibitor
- requirement II: difference in diffusion rates



A(x)

time

x

x

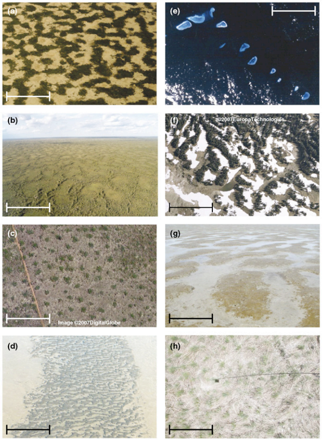
y

y

Applications

- morphogenesis
- animal coat pattern
- developmental patterning
- ecology? 1970s

Hard: $d \ll D$



TRENDS in Ecology & Evolution

Rietkerk et al 20?

Pattern formation in IDEs?

Start with

$$N_{t+1} = F(N_t, P_t), \qquad P_{t+1} = G(N_t, P_t)$$

with coexistence state

$$N^* = F(N^*, P^*) > 0, \quad P^* = G(N^*, P^*) > 0,$$

that is locally asymptotically stable, i.e.

$$J = \begin{bmatrix} F_N^* & F_P^* \\ G_N^* & G_P^* \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix},$$

has

1) $$1 - (a_{11} + a_{22}) + (a_{11}a_{22} - a_{12}a_{21}) > 0, \qquad +1$$

2) $$1 + a_{11} + a_{22} + (a_{11}a_{22} - a_{12}a_{21}) > 0, \qquad -1$$

3) $$1 - (a_{11}a_{22} - a_{12}a_{21}) > 0. \qquad |\lambda| < 1$$

Pattern formation in IDEs?

N^*, P^*

Analyze the stability of N^*, P^* in $N^*(x) \equiv N^*$, $P^*(x) \equiv P^*$

$$\left.\begin{aligned} N_{t+1}(x) &= \int_{\mathbb{R}} K_N(x,y)F(N_t(y), P_t(y))dy, \\ P_{t+1}(x) &= \int_{\mathbb{R}} K_P(x,y)G(N_t(y), P_t(y))dy, \end{aligned}\right\}$$

Linearize: $\hat{n}(\omega)$ $\quad a_{11}\hat{k}_N(\omega)\cdot\hat{n}_t(\omega)\ \cdot\ \ \cdots$

$$\left.\begin{aligned} n_{t+1}(x) &= \int K_N(x-y)[a_{11}n_t(y) + a_{12}p_t(y)]dy, \\ p_{t+1}(x) &= \int K_P(x-y)[a_{21}n_t(y) + a_{22}p_t(y)]dy. \end{aligned}\right\} *$$

$$J = \begin{bmatrix} a_{11} & \cdot \\ \cdot & \cdot \end{bmatrix}$$

Fourier transform

$\hat{n}(\omega) = \int n(x) e^{i\omega x}\, dx$ s

$\cos(\omega x) + i \sin(\omega x)$

$\hat{K}$

$$\begin{bmatrix}\widehat{n}(\omega)\\ \widehat{p}(\omega)\end{bmatrix}_{t+1} = \begin{bmatrix}\widehat{K}_N(\omega) & 0\\ 0 & \widehat{K}_P(\omega)\end{bmatrix}\begin{bmatrix}a_{11} & a_{12}\\ a_{21} & a_{22}\end{bmatrix}\begin{bmatrix}\widehat{n}(\omega)\\ \widehat{p}(\omega)\end{bmatrix}_t = \widehat{\mathbf{K}}J\begin{bmatrix}\widehat{n}(\omega)\\ \widehat{p}(\omega)\end{bmatrix}_t$$

- Difference equation with parameter ω – wavelength
- Jury conditions:

$\hat{K}_N(\omega) = M_N(r\omega)$ $\qquad \hat{K}(0) = 1$

$\hat{k}(0) = 1$

$$\begin{aligned}1 - (\widehat{K}_N a_{11} + \widehat{K}_P a_{22}) + \widehat{K}_N\widehat{K}_P(a_{11}a_{22} - a_{12}a_{21}) &> 0, \quad +1\\ 1 + (\widehat{K}_N a_{11} + \widehat{K}_P a_{22}) + \widehat{K}_N\widehat{K}_P(a_{11}a_{22} - a_{12}a_{21}) &> 0, \quad -1\\ 1 - \widehat{K}_N\widehat{K}_P(a_{11}a_{22} - a_{12}a_{21}) &> 0, \quad |\lambda| < 1\end{aligned}$$

- Stability conditions satisfied for small $|\omega|$

Pattern formation?

Either $a_{11}, a_{12} \le 1$

or if $a_{11} > 1$ then $a_{22} < 1$

and vice versa.

- stability conditions satisfied for $\omega = 0$.
- at least one condition violated for $\omega > 0$.

some

Pattern formation

Dispersal kernels

- K symmetric implies $\widehat{K}$ is real
- K a pdf implies that $-1 \le \widehat{K} \le 1$.

$$|\hat{k}(\omega)| = \left|\int k(x) e^{i\omega x} dx\right|$$

$$\le \int k(x) \underbrace{|e^{i\omega x}|}_{=1} dx \le 1$$

$\Rightarrow -1 \le \hat{k} \le 0$

$\rightarrow 0 \le \hat{k} \le 1$

First observation:

$$\boxed{a_{11} + a_{22} < 1 + \det J < 2}$$

$1 - (a_{11} + a_{22}) + \det] > 0$

$a_{11} + a_{22} < 1 + \det] < 2$

A 'plus-one' instability

First condition violated:

$$\boxed{1-(\widehat{K}_N a_{11}+\widehat{K}_P a_{22})+\widehat{K}_N\widehat{K}_P(a_{11}a_{22}-a_{12}a_{21})<0}$$

Proposition:
If $0<\widehat{K}_N,\widehat{K}_P\le 1$ then a necessary condition for a 'plus-one' bifurcation is

$$a_{12}\,a_{21}<0 \quad\text{and}\quad (a_{11}-1)(a_{22}-1)<0.$$

$\Downarrow$ have to be pred & prey

$\Downarrow$ $\boxed{a_{11}>1}$ and $a_{22}<1$

or reverse

$\Rightarrow$ parallel to RDE

Proof

Assume: $1 - \hat{K}_N a_{11} - \hat{K}_p a_{22} + \hat{K}_N \hat{K}_p \underbrace{(a_{11}a_{22} - a_{12}a_{21})} < 0$

We know: $\underbrace{a_{11}a_{22} - a_{12}a_{21}} > a_{11} + a_{22} - 1 \quad \leftarrow$

$$\Rightarrow \quad 1 - \hat{K}_N a_{11} - \hat{K}_p a_{22} + \hat{K}_N \hat{K}_p (a_{11} + a_{22} - 1) < 0$$

$$1 - \hat{K}_N \hat{K}_p + \hat{K}_N a_{11} \underbrace{(\hat{K}_p - 1)} + \hat{K}_p a_{22} \underbrace{(\hat{K}_N - 1)} < 0$$

<u>If this holds for some $a_{11}, a_{22} \le 1$</u> then it holds for $a_{11} = a_{22} = 1$

So $\quad 1 - \hat{K}_N \hat{K}_p + \hat{K}_N (\hat{K}_p - 1) + \hat{K}_p (\hat{K}_N - 1) < 0$

$$1 + \hat{K}_N \hat{K}_p - \hat{K}_N - \hat{K}_p < 0$$

Proof

$$1 + \hat{k}_N \hat{k}_p - \hat{k}_N - \hat{k}_p < 0$$

$$1 - \hat{k}_N + \hat{k}_p (\hat{k}_N - 1) < 0$$

$$\hat{k}_p \underbrace{(\hat{k}_N - 1)} < \underbrace{\hat{k}_N - 1}$$

$$\hat{k}_p (1 - \hat{k}_N) > 1 - \hat{k}_N$$

But $\hat{k}_p \le 1$ Contradiction.

$\Rightarrow a_{11} > 1$ and $a_{22} < 1$ or vice versa

$\Rightarrow$ $\boxed{(a_{11} - 1)(a_{22} - 1) < 0}$ First condition.

$$a_{11} a_{22} - a_{11} - a_{22} + 1 < 0$$

$$1 - (a_{11} + a_{22}) + \underbrace{a_{11} a_{22} - a_{12} a_{11}} + a_{12} a_{21} < 0$$

$$\underbrace{1 - (a_{11} + a_{22}) + (a_{11} a_{22} - a_{12} a_{21})}_{>0} + a_{12} a_{21} < 0$$

by assumption

$\Downarrow$

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

A '~~plus~~-one' instability

Third condition violated:

$$\underline{1 - \widehat{K}_N \widehat{K}_P (a_{11}a_{22} - a_{12}a_{21}) \not< 0}$$

Proposition:
This condition cannot be violated.

Proof: • $1 - \det J \geq 0$

• $|\hat{K}_N \hat{K}_P| < 1$

$\Rightarrow \quad 1 - \hat{K}_N \hat{K}_P \det J > 0$

A ‘plus-one’ instability

First condition violated:

$$1 - (\widehat{K}_N a_{11} + \widehat{K}_P a_{22}) + \widehat{K}_N \widehat{K}_P (a_{11}a_{22} - a_{12}a_{21}) < 0 \quad !$$

Proposition:
If $\boxed{0 < \widehat{K}_N \leq 1}$ and $\boxed{-1 \leq \widehat{K}_P < 0}$ then a necessary condition for a ‘plus-one’ bifurcation is

$$\underbrace{a_{12}\, a_{21} < 0}_{\text{pred/prey}} \quad \text{and} \quad \underbrace{(a_{11} > 1 \text{ or } a_{22} < 1)}_{\text{much weaker than before.}}.$$

Show now

Proof 1) Show: $\underline{\hat{K}_N a_{11} + \hat{K}_P a_{22} > \hat{K}_N} + \hat{K}_P$

Assume not:

$$(1-\hat{K}_N)(1-\hat{K}_P) = 1-(\hat{K}_N+\hat{K}_P)+\hat{K}_N\hat{K}_P$$

<0

$$\le 1-(\hat{K}_N a_{11}+\hat{K}_P a_{22})+\hat{K}_N\hat{K}_P$$

$$< 1-(\hat{K}_N a_{11}+\hat{K}_P a_{11})+\hat{K}_N\hat{K}_P \det] < 0$$

by assumption

However: >0 contradiction

Have: $\hat{K}_N a_{11} + \hat{K}_P a_{22} > \hat{K}_N + \hat{K}_P$

$\boxed{a_{11}>0 \text{ or } a_{22}<1 \text{ is necessary}}$

$$\overset{>0}{\underbrace{\hat{K}_N(a_{11}-1)}_{<0}} + \overset{<0}{\underbrace{\hat{K}_P(a_{22}-1)}_{<0}} > 0$$

If $a_{11}<1$ and $a_{22}>1$ then >0 is not possible

Proof

$a_{12}a_{21} < 0$

Want.

$$I(a_{11},a_{22}) := 1 - (\hat{k}_N a_{11} + \hat{k}_p a_{22}) + \hat{k}_N \hat{k}_p \det] \quad < 0$$

$a_{11}a_{22} - a_{12}a_{21}$

$$\frac{\partial I}{\partial a_{11}} = -\hat{k}_N + \hat{k}_N \hat{k}_p a_{22} \stackrel{!}{=} 0 \qquad a_{22} = \frac{1}{\hat{k}_p}$$

$$\hat{k}_N, \hat{k}_p \neq 0$$

$$\frac{\partial I}{\partial a_{22}} = -\hat{k}_p + \hat{k}_N \hat{k}_p a_{11} \stackrel{!}{=} 0 \qquad a_{11} = \frac{1}{\hat{k}_N}$$

at this point, the Hessian

$$\underbrace{\begin{bmatrix} 0 & \hat{k}_N \hat{k}_p \\ \hat{k}_N \hat{k}_p & 0 \end{bmatrix}}_{H}$$

$$(a_{11}, a_{22})\, H \begin{pmatrix} a_{11} \\ a_{22} \end{pmatrix} = \dots = 2 > 0$$

pos. definit

$\Rightarrow$ extremum is min.

Proof substitute

$$I\left(\frac{1}{\hat{K}_N}, \frac{1}{\hat{K}_p}\right) = 1 - (1+1) + \hat{K}_N \hat{K}_p \left(\frac{1}{\hat{K}_N}\cdot\frac{1}{\hat{K}_p} - a_{12}a_{21}\right)$$

$$= \overset{0}{\cancel{1 - 2 + 1}} - \hat{K}_N \hat{K}_p a_{12} a_{21} < 0$$

by assumption: $\hat{K}_N \hat{K}_p < 0$

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

Proof