Institute of Theoretical Physics
São Paulo State University

Nonlinear Phenomena in Biology

IV Journeys Into Theoretical Physics

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July 6-12, 2019

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Nonlinear Phenomena in Biology

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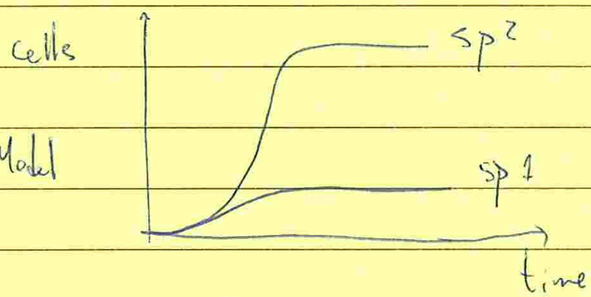
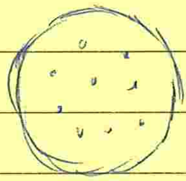
Biodiversity: how can so many species coexist in so little space

① One Species Model
No Space



probability / rate → reproduction is stochastic



Process of reproduction: $A \xrightarrow{b} A + A$

Too little food: $A + A \xrightarrow{d} A$ → cells fight and one dies

separate processes because we suppose small time

$$\begin{cases} n \to n+1 & \Omega(n \to n+1) = bn \\ n \to n-1, & \Omega(n \to n-1) = \dfrac{dn(n-1)}{V} = \delta n(n-1) \end{cases}$$

→ two cells need to find each other

→ more space, less problems $\delta = \dfrac{d}{V}$

Probability distribution $P(n,t)$

$$P(n, t+dt) = P(n-1,t)\,\Omega(n-1 \to n)\,dt + P(n+1,t)\,\Omega(n+1 \to n)\,dt + P(n,t)\left(1 - \Omega(n \to n+1)dt - \Omega(n \to n-1)\,dt\right)$$

$$\frac{\partial P(n,t)}{\partial t} = \frac{P(n,t+dt) - P(n,t)}{dt} = P(n-1,t)\,\Omega_+(n-1) + P(n+1,t)\,\Omega_-(n+1) - \left(\Omega_+(n) + \Omega_-(n)\right)P(n,t)$$

→ Master Equation

$$\langle n^k \rangle \equiv \sum_{n=0}^{+\infty} n^k P(n,t)$$

$$\sum_{n=0}^{+\infty} n \frac{\partial P(n,t)}{\partial t} = \sum_{n=0}^{+\infty} n P(n-1,t)\,\Omega_+(n-1) + \sum_{n=0}^{+\infty} n P(n+1,t)\,\Omega_-(n+1) - \sum_{n=0}^{+\infty} n P(n,t)\left[\Omega_-(n) + \Omega_+(n)\right]$$

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$$n-1 \to m \quad , \quad n \to m+1$$

$\delta n(n-1) \approx \delta n^2$

$$\frac{d\langle n\rangle}{dt} = \sum_{n=0}^{+\infty} bn(n+1)P(n,t) + \sum_{n=0}^{+\infty} \delta n^2(n-1)P(n,t) - \sum_{n=0}^{+\infty} n(\delta n^2 - bn)P(n,t)$$

$$= \sum_{n=0}^{+\infty} bn\,P(n,t) - \sum_{n=0}^{+\infty} \delta n^2 P(n,t)$$

$$\langle \dot{n}\rangle = b\langle n\rangle - \delta\langle n^2\rangle$$

the ODE for $\langle n^2\rangle$ is coupled to $\langle n^3\rangle$ and so on

Mean Field Approximation: $\langle n^2\rangle = \langle n\rangle^2$ → neglect the fluctuations

$$\langle \dot{n}\rangle = b\langle n\rangle - \delta\langle n\rangle^2 \longrightarrow \langle \dot{n}\rangle = 0 \text{ for } \begin{cases} \langle n\rangle = 0 \\ b - \delta\langle n\rangle = 0 \end{cases}$$

trivial fixed point

$\hookrightarrow \langle n\rangle = \frac{b}{\delta} \equiv K$

non-trivial fixed point

carrying capacity

Let n^* be ~~the~~ a fixed point.

Linearization: $n = n^* + \epsilon\psi$, $\epsilon \ll 1$

$$\frac{d(n^*+\epsilon\psi)}{dt} = p(n^*+\epsilon\psi) \approx \cancelto{0}{p(n^*)} + \epsilon\psi p'(n^*) + \mathcal{O}(\epsilon^2)$$

$$\epsilon\frac{d\psi}{dt} = \epsilon p'(n^*)\psi \Rightarrow \psi = c \cdot e^{p'(n^*)t}$$

$p'(n^*) \neq 0$

population growth rate

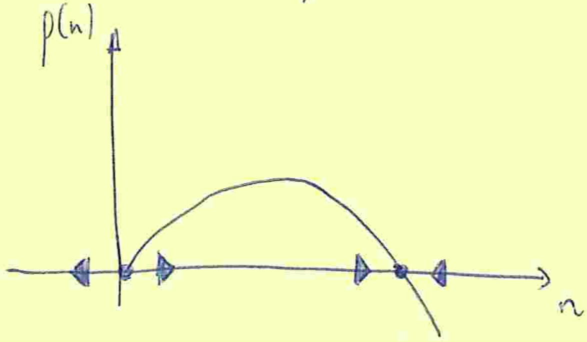
$$p(n) = bn - \delta n^2$$

$$p'(n) = b - 2\delta n$$

$n^* = 0$: $p'(n^*) = b$ → unstable

$n^* = \frac{b}{\delta}$: $p'(n^*) = -b$ → stable

What if the system was too complicated?



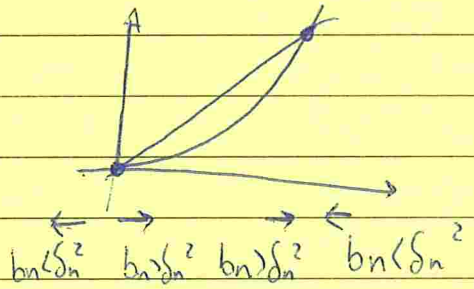
If $p(n) = 0$: fixed point

$p'(n) > 0$: unstable

$p'(n) < 0$: stable

02

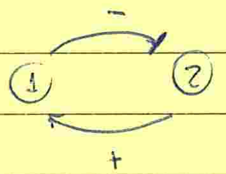
$bn - \delta n^2 = 0 \Rightarrow bn = \delta n^2$



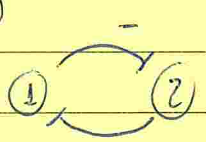
② Multiple Species Models. No Space

Overview of Biological Interactions

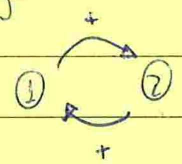
Species can affect each other's growth in various ways. The main ones are

i)  ~~prey-predator~~ ~~host-parasite~~ ① predator/parasite ② prey/host

e.g.: fox and rabbit, virus and dog, etc...

ii)  competition.

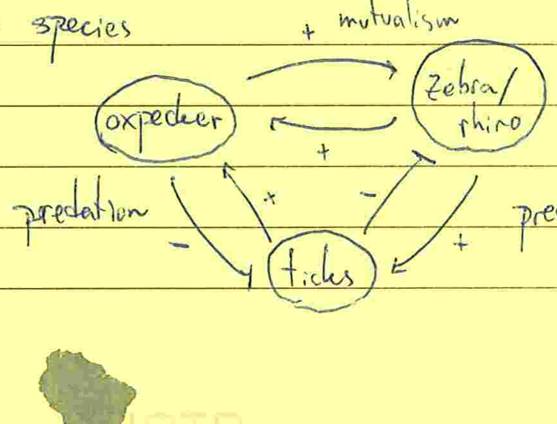
e.g.: 2 carnivores feed on the same herbivore or 2 species share space

iii)  mutualism

type of bird

e.g.: plants and bees, oxpecker that eats ticks from zebras/rhinos

Remark: we will consider 1-1, but interactions often occur between more than two species



How can we model this richness of interactions and incorporate them into a mathematical framework?

García

$$\begin{cases} \dfrac{dn_1}{dt} = b_1 n_1 \left[1 - \dfrac{n_1}{k_1} \pm \alpha_{12} \dfrac{n_2}{k_2}\right] \\ \dfrac{dn_2}{dt} = b_2 n_2 \left[1 - \dfrac{n_2}{k_2} \pm \alpha_{21} \dfrac{n_1}{k_1}\right] \end{cases}$$

In general, $\alpha_{12} \neq \alpha_{21}$

The sign in front of α_{ij} defines the character of the interaction

	PP	C	M
Eq 1	+	−	+
Eq 2	−	−	+

The interaction increased the number of parameters, but we might reduce it by using non-dimensional parameters → not unique, depends on our interest

$$u_1 = \frac{n_1}{k_1},\ u_2 = \frac{n_2}{k_2},\ \tau = b_1 t,\ \rho = \frac{b_2}{b_1},\ a_{ij} = \alpha_{ij}\frac{k_j}{k_i}$$

params: $6 \downarrow 3$

The system becomes

$$\begin{cases} \dfrac{du_1}{d\tau} = u_1(1 - u_1 \pm a_{12} u_2) = f_1(u_1, u_2) \\ \dfrac{du_2}{d\tau} = u_2(1 - u_2 \pm a_{21} u_1) = f_2(u_1, u_2) \end{cases}$$

both negative

Among all possible interactions, let's assume competition

Fixed points:

$(0,0)$; $(1,0)$; $(0,1)$ → don't explain experimental result!
→ and sometimes a fourth one

$$\left.\begin{array}{l}(1 - u_1 - a_{12}u_2) = 0 \\ (1 - u_2 - a_{21}u_1) = 0\end{array}\right\} \Rightarrow \begin{array}{l} u_1 = 1 - a_{12}u_2 \Downarrow \\ 1 - u_2 - a_{21}(1 - a_{12}u_2) = 0 \\ \Downarrow \end{array}$$

u_1^* follows by symmetry of eqs or recalculating

$$u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}} \qquad u_2^* = \frac{1 - a_{21}}{1 - a_{21}a_{12}}$$

Obs: we need $a_{12}a_{21} \neq 1$

This fourth point implies that both species coexist, but when is it relevant? → $u_1^* > 0$
$u_2^* > 0$

- What are the conditions for the existence of the fourth fixed point?
- If it exists, is it stable? ↳ remember this is a toy model, we should think of a general method

→ Analytical treatment: extension to 2D of the 1D analysis explained before (not always solvable)

→ Graphical analysis: qualitative intuition (often quantitative)

Nullclines: curves such that $\left.\begin{array}{l}\dot{u}_1 = 0 \\ \dot{u}_2 = 0\end{array}\right\}$ intersection is a steady point

For u_1: $u_1 = 0$

$1 - u_1 - a_{12} u_2 = 0 \Rightarrow u_2 = \frac{1-u_1}{a_{12}}$

For u_2: $u_2 = 0$

$1 - u_2 - a_{21} u_1 = 0 \Rightarrow u_2 = 1 - a_{21} u_1$

Four separate cases

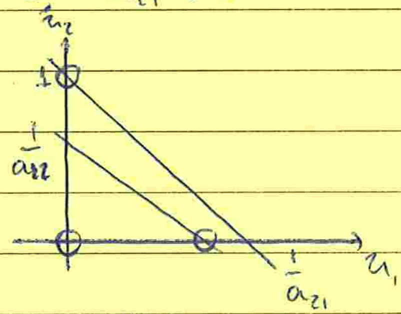
i) $a_{12} > 1$, $a_{21} < 1$

ii) $a_{12} < 1$, $a_{21} > 1$

iii) $a_{12} > 1$, $a_{21} > 1$

iv) $a_{12} < 1$, $a_{21} < 1$

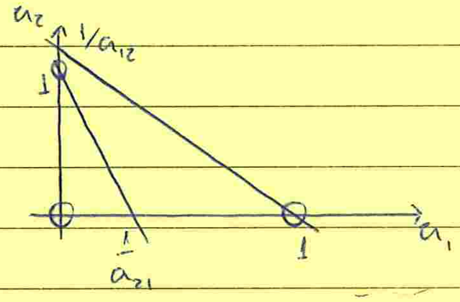
Case i). $a_{12} > 1$ $a_{21} < 1$



Only 3 fixed points

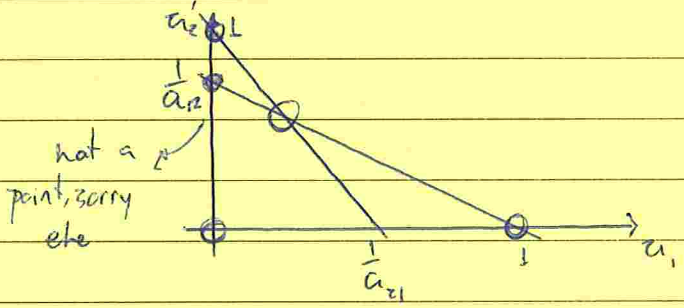
~~unstable~~ ~~stable~~ not yet

Case ii): $a_{12} < 1$, $a_{21} > 1$

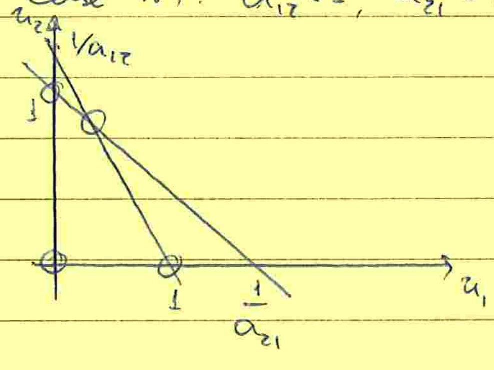


Also 3 points

Case iii): $a_{12} > 1$ $a_{21} > 1$



Case iv): $a_{12} < 1$, $a_{21} < 1$



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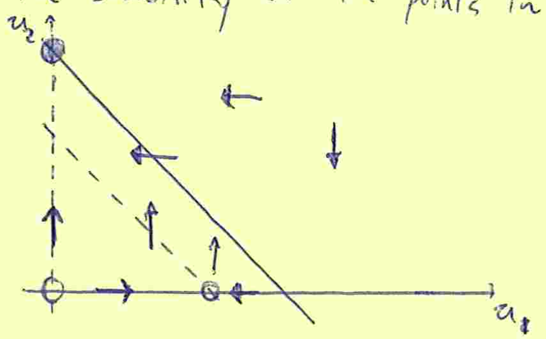
What is the stability of the points in each case?

Case ii)



u_1-nullcline ----

u_2-nullcline ——

for arrows, check first (0,0)

$\dot{u}_i$ (arrow) changes sign (direction) when I cross a u_i nullcline

(0,0) - unstable
(1,0) - saddle
(0,1) - stable

only one species grows to carrying capacity

$$(\dot{u}_1, \dot{u}_2) = (f_1(u_1,u_2), f_2(u_1,u_2)) \quad \forall (u_1,u_2)$$

↳ there is a vector field describing the dynamical evolution

a) in a u_1-nullcline, $\dot{u}_1 = 0$ and the flow goes in the direction of u_2

b) if we cross a u_i-nullcline, the direction of u_i vector flips

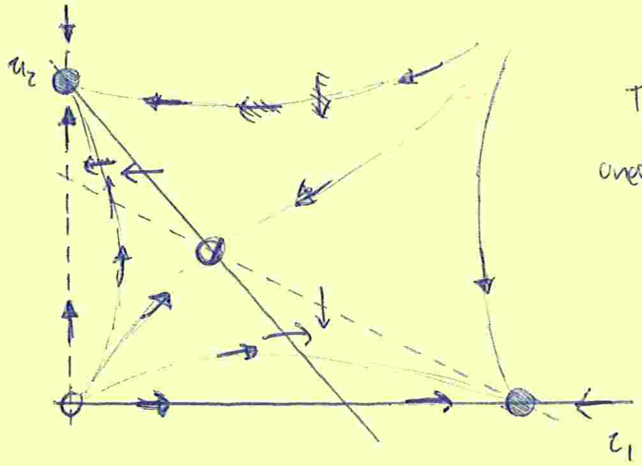
What does these results mean?

$a_{12} > 1 \Rightarrow a_{12} = \alpha_{12}\frac{k_2}{k_1} > 1 \Rightarrow \frac{\alpha_{12}}{k_1} > \frac{1}{k_2}$

$a_{21} < 1 \Rightarrow a_{21} = \alpha_{21}\frac{k_1}{k_2} < 1 \Rightarrow \frac{\alpha_{21}}{k_2} < \frac{1}{k_1}$

Species 2 inhibits the growth of species 1 more strongly than itselfs. Species 1 inhibits its own growth more strongly than species 2's.

Case iii)



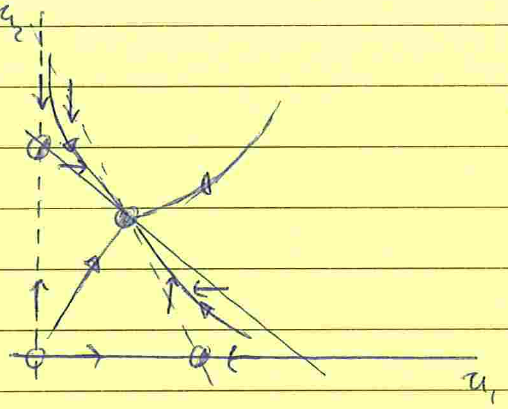
The coexistence point is stable in only one direction, i.e., it is a saddle point

$a_{12} = \alpha_{12}\frac{k_2}{k_1} > 1 \Rightarrow \frac{\alpha_{12}}{k_1} > \frac{1}{k_2}$

$a_{21} = \alpha_{21}\frac{k_1}{k_2} > 1 \Rightarrow \frac{\alpha_{21}}{k_2} > \frac{1}{k_1}$

- Both species inhibit the growth of the other more strongly than its own
- One species outcompetes the other depending on initial conditions

Case iv)



stable coexistence

$a_{12} = \alpha_{12} \frac{k_2}{k_1} < 1 \Rightarrow \frac{\alpha_{12}}{k_1} < \frac{1}{k_2}$

$a_{21} = \alpha_{21} \frac{k_1}{k_2} < 1 \Rightarrow \frac{\alpha_{21}}{k_2} < \frac{1}{k_1}$

Species inhibit their own growth more strongly than their partner's, and thus they have a stable coexistence.

Species grow to a population size smaller than if they were alone.

Another analysis method

$$\begin{cases} \dot{u}_1 = f_1(u_1, u_2) \\ \dot{u}_2 = f_2(u_1, u_2) \end{cases}, \quad \begin{cases} u_1 = u_1^* + \epsilon \psi_1 \\ u_2 = u_2^* + \epsilon \psi_2 \end{cases}$$

Then

$$\begin{cases} \epsilon \dot{\psi}_1 = \underbrace{\cancel{f(u_1^*, u_2^*)}}_{0 \text{ by def of } u_1^*, u_2^*} + \epsilon \psi_1 \left.\frac{\partial f_1}{\partial u_1}\right|_{(u_1^*, u_2^*)} + \epsilon \psi_2 \left.\frac{\partial f_1}{\partial u_2}\right|_{(u_1^*, u_2^*)} + \mathcal{O}(\epsilon^2) \\ \epsilon \dot{\psi}_2 = f(u_1^*, u_2^*) + \epsilon \psi_1 \left.\frac{\partial f_2}{\partial u_1}\right|_{(u_1^*, u_2^*)} + \epsilon \psi_2 \left.\frac{\partial f_2}{\partial u_2}\right|_{(u_1^*, u_2^*)} + \mathcal{O}(\epsilon^2) \end{cases}$$

$$\dot{\vec{\psi}} = A \vec{\psi}, \quad A = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix} \Rightarrow \vec{\psi} = \vec{v} e^{\lambda t}$$

↳ reduced to an eigenvalue problem

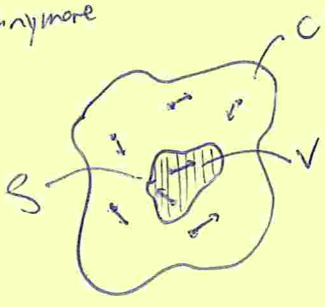
If $\lambda_1, \lambda_2 > 0$: ~~explode~~ unstable
$\lambda_1, \lambda_2 < 0$: ~~de~~ stable
$\lambda_i > 0, \lambda_j < 0$: saddle

For $\lambda \in \mathbb{C}$:
$Re(\lambda) = 0$: oscillates around point
$Re(\lambda) > 0$: $Re(\lambda) = 0$ + explodes
$Re(\lambda) < 0$: $Re(\lambda) = 0$ + decays

García

③ Spatial Models: Waves and Patterns

↳ space is now relevant. Before, cells were in a liquid and could interact with everyone, but not anymore

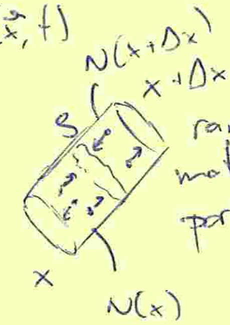


$$\frac{\partial}{\partial t}\int_V c(\vec{x},t)\,dV = \underbrace{\int_V p(c)\,dV}_{\text{death and reproduction}} - \underbrace{\int_S \vec{J}\cdot d\vec{S}}_{\text{migration}}$$

$$\int_V \frac{\partial}{\partial t} c(\vec{x},t)\,dV = \int_V p(c)\,dV - \int_V \nabla\cdot\vec{J}\,dV$$

$$\frac{\partial c}{\partial t}(\vec{x},t) = p(c) - \nabla\cdot\vec{J}$$

we need to write $\vec{J}$ in terms of $c(\vec{x},t)$



random motion of particles → half going in each direction

$$J = \frac{1}{A\Delta t}\,\frac{\left(N(\vec{x}) - N(\vec{x}+\Delta\vec{x})\right)}{2}$$

$$= \frac{1}{A\Delta t}\left[\frac{N(x) - N(x) - N'(x)\Delta x - \Theta(\Delta x^2)}{2}\right]$$

$$= \frac{\Delta x}{2A\Delta t}\left(-N'(x)\right) \qquad c(x) = \frac{N(x)}{A\,\Delta x}$$

$$= -\frac{(\Delta x)^2}{2\Delta t}\frac{\partial c}{\partial x} \qquad D = \lim_{\substack{\Delta x\to 0\\ \Delta t\to 0}} \frac{\Delta x^2}{2\Delta t}$$

$$= -D\frac{\partial c}{\partial x}$$

↳ the flux goes <u>against</u> the gradient of concentration

$$\frac{\partial c}{\partial t} = p(c) + \frac{\partial}{\partial x}\left(D\frac{\partial c}{\partial x}\right)$$

↓ constant D

$$p(c) + D\frac{\partial^2 c}{\partial x^2} = \frac{\partial c}{\partial t}$$

↓ adding the scenarios we studied and setting the carrying capacity to 1

$$\frac{\partial c}{\partial t} = b\,c(1-c) + D\frac{\partial^2 c}{\partial x^2}$$ ↝ Fisher-Kolmogorov Eq.

Travelling Waves

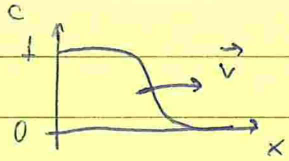
$$c(x,t) = c(x-vt) = c(z)$$ ⤵ substitute into FKE

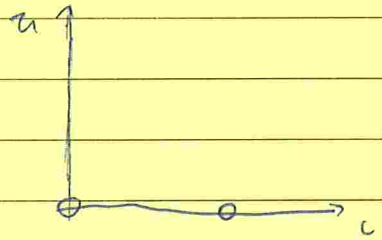
$$-vc'(z) = b\,c(1-c) + D''(z)$$

$$\begin{cases} Dc''(z) + vc'(z) + b\,c(1-c) = 0 \\ c(x\to+\infty) = 0 \\ c(x\to-\infty) = 1 \end{cases}$$

García

$$\begin{cases} c'(z) = u \\ u'(z) = -\frac{b}{D}\,c(1-c) - \frac{v}{D}\,u \end{cases}$$





two fixed point

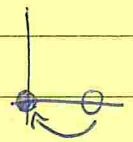
$$J = \begin{pmatrix} 0 & 1 \\ -\frac{b}{D}(1-2c^*) & -\frac{v}{D} \end{pmatrix}$$

$$\begin{vmatrix} -\lambda & 1 \\ -\frac{b}{D}(1-2c^*) & -\frac{v}{D}-\lambda \end{vmatrix} = 0 \Rightarrow \lambda\left(\frac{v}{D}+\lambda\right) + \frac{b}{D}(1-2c^*) = 0$$

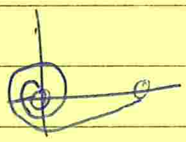
$$\lambda^2 + \frac{v}{D}\lambda + \frac{b}{D}(1-2c^*) = 0$$

$$\lambda_\pm = \frac{-\frac{v}{D} \pm \sqrt{\frac{v^2}{D^2} - 4\frac{b}{D}(1-2c^*)}}{2}$$

$\left(\frac{v}{D}\right)^2 > \frac{4b}{D} \Rightarrow v > 2\sqrt{bD}$



$\left(\frac{v}{D}\right)^2 < \frac{4b}{D} \Rightarrow v < 2\sqrt{bD}$



non-biological $(c<0)$

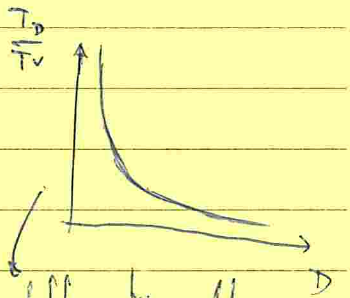
$\int_{all} c(x,t)\,dx = cte$ → no mass creation

What is the difference between Fisher-Kolmogorov and the Heat Equation? $\frac{\partial c}{\partial t} = D\frac{\partial^2 c}{\partial x^2}$ does not admit wave solutions

$D \sim \frac{L^2}{T} \rightarrow T_D \sim \frac{L^2}{D}$

$v \sim \frac{L}{T} \rightarrow T_v \sim \frac{L}{v} = \frac{L}{\sqrt{bD}}$ ↳ $O(1)$

$\Rightarrow \frac{T_D}{T_v} \sim \frac{L^2}{D}\frac{\sqrt{D}}{L} \propto \frac{1}{\sqrt{D}}$



for low diffusivity problems, the creation of mass promotes transport

④ Regular Patterns

what if our perturbations were also spece-dependent?

Garcia

$$\frac{\partial \rho}{\partial t} = f(\rho) + D \frac{\partial^2 \rho}{\partial x^2}, \quad \rho^* \Rightarrow f(\rho^*) = 0$$

$$\rho = \rho^* + \epsilon \psi(x,t)$$

$$\epsilon \frac{\partial \psi}{\partial t} = \cancel{f(\rho^*)}^{0} + \epsilon \psi(x,t) f'(\rho^*) + \epsilon D \frac{\partial^2 \psi}{\partial x^2}$$

Assuming $\hat{\psi}(k,t) \propto e^{\lambda(k)t}$, for $\hat{\psi}(k,t) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{+\infty} \psi(x,t) e^{-ikx} dx$,

$$\frac{\partial \hat{\psi}}{\partial t} = \hat{\psi}(k,t) f'(\rho^*) - k^2 D \hat{\psi}(k,t)$$

$$\lambda(k) \hat{\psi}(k,t) = \hat{\psi}(k,t) f'(\rho^*) - k^2 D \hat{\psi}(k,t)$$

$$\lambda(k) = f'(\rho^*) - k^2 D < 0$$ always because $D > 0$, $f'(\rho^*) < 0$ (stability)

If $\lambda(k) < 0$, the spatial perturbation dies out and there are no patterns

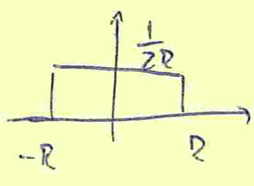
↳ what mechanism leads to patterns?

·) Non-local couplings → long-range interactions

Linear Stability Analysis of the Non-local Fisher-Kolmogorov Equation

$$\frac{\partial \rho}{\partial t} = b\rho - \mu \rho \tilde{\rho} + D \frac{\partial^2 \rho}{\partial x^2}, \quad \text{with } \tilde{\rho} = \int \rho(x',t)\, G(|x-x'|)\, dx'$$

Kernel function: G



other kernels might give a weight to the distances and so on

Homogeneous solution:

$$\frac{\partial \rho^*}{\partial t} = \frac{\partial \rho^*}{\partial x} = 0 \quad \& \quad b\rho - \mu \rho^2 = 0 \Rightarrow \begin{cases} \rho^* = 0 \rightarrow \text{unstable} \\ \rho^* = b/\mu \rightarrow \text{stable} \end{cases}$$

Is the stable solution still stable for space perturbations?

García

$$\frac{\partial(\rho^* + \epsilon\psi)}{\partial t} = b(\rho^* + \epsilon\psi) - \mu(\rho^* + \epsilon\psi)\int G(|x-x'|)(\rho^* + \epsilon\psi)\,dx' + D^2\frac{\partial^2(\rho^* + \epsilon\psi)}{\partial x^2}$$

$$\epsilon\frac{\partial\psi}{\partial t} = D\epsilon\frac{\partial^2\psi}{\partial x^2} + b\rho^* + \epsilon b\psi - (\mu\rho^* + \mu\epsilon\psi)\left[\int G\rho^* dx' + \epsilon\int G\psi\,dx'\right]$$

$$= D\epsilon\frac{\partial^2\psi}{\partial x^2} + \underbrace{(b\rho^* - \mu\rho^{*2})}_{0} + \epsilon b\psi - \mu\epsilon\psi\rho^* - \mu\epsilon\rho^*\int G\psi\,dx' + \Theta(\epsilon^2)$$

$$\frac{\partial\psi}{\partial t} = D\frac{\partial^2\psi}{\partial x^2} + \psi(b - \mu\rho^*) - \mu\rho^*\int G(|x-x'|)\,\psi(x',t)\,dx'$$

Linear Equation in Perturbation: Fourier Transform

$$\frac{\partial\hat\psi}{\partial t} = -k^2 D\hat\psi + \hat\psi(b - \mu\rho^*) - \mu\rho^*\,\hat G(k)\,\hat\psi(k,t)$$

$$\frac{\partial}{\partial t}\hat\psi(k,t) = -k^2 D\hat\psi(k,t) + \hat\psi(k,t)\left(b - \mu\frac{b}{\mu}\right) - \mu\frac{b}{\mu}\hat G(k)\,\hat\psi(k,t)$$

$$\frac{\partial}{\partial t}\hat\psi(k,t) = -\left(k^2 D + b\,\hat G(k)\right)\hat\psi(k,t)$$

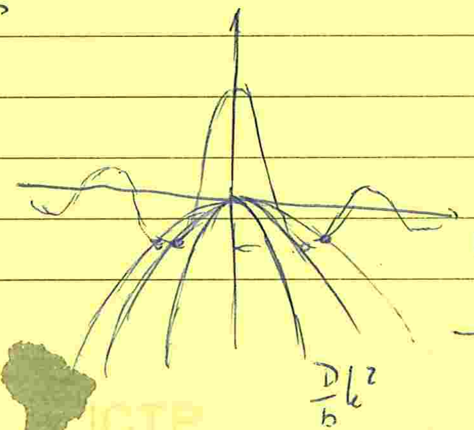
Assuming $\hat\psi(k,t) \propto e^{\lambda(k)t}$

$$\lambda(k) = -\left(Dk^2 + b\,\hat G(k)\right)$$

$$\frac{\lambda(k)}{b} = -\left(\frac{D}{b}k^2 + \hat G(k)\right)$$

we want $\frac{\lambda(k)}{b} > 0$ to obtain patterns → we need $\hat G(k) < 0$ for some value of k

$$\hat G(k) = \frac{\sin Rk}{kR}$$



by changing $\frac{D}{b}$, we change the slope of the parabola and can get pattern formation

García

By numerical integration, we can set some values for the constants and see pattern formation

↳ we can also plot $\lambda(k)$ and predict whether given parameters will yield patterns

Not every wave number is unstable: only some wave numbers appear in pattern → yields wavelenght of pattern

Vegetation Patterns

Appear all over the world, usually where there is few water

amount of water → Deblauwe et al. 2011 → Martinez-García et al. 2013

Vegetation Patterns: A Minimalistic Model

Main assumption: competition for water is the main competition for plants and this competition is mediated by roots

Mechanisms

A. Death at a constant rate: $\frac{\partial \rho}{\partial t} = -\alpha\rho$ $\boxed{2D}$

B. Population growth in three steps $\rightarrow \frac{\partial \rho}{\partial t} = P_c b\rho(1-\rho) - \alpha\rho$

1. Seed production
2. <u>Local</u> seed dispersion (space limitation)
3. Seed establishment with probability P_c (overcoming competition)

Model summary:

$$\frac{\partial \rho}{\partial t} = P_c(\tilde{\rho}, \delta)\,\beta\,\rho(x,t)\left[1-\rho(x,t)\right] - \alpha\,\rho(x,t)$$

↳ non-local terms → roots mediate competition

With P_c such that

$P_c(\tilde{\rho}, \delta=0) = 1$ } δ: competition

$P_c(\tilde{\rho}, \delta\to+\infty) \to 0$

No comp. will establish

Much comp. won't establish

more plants around me ⇓ I'm less likely to germinate ← $\left(\frac{\partial P_c}{\partial \tilde{\rho}}\right)_\delta < 0$

Example: $P_c(\tilde{\rho}, \delta) = e^{-\delta\tilde{\rho}}$ → delta modulates decay

Linear stability analysis:

$$\lambda(k) = -\alpha\rho_0\left[\frac{1}{1-\rho_0} - \frac{P_c'(\rho_0;\delta)}{P_c(\rho_0;\delta)}\hat{G}(k)\right]$$

Particular case:

$$P_c(\tilde{\rho};\delta) = \frac{1}{1+\delta\tilde{\rho}} \rightarrow \rho_0 = \frac{\beta-\alpha}{\beta+\alpha\delta}$$

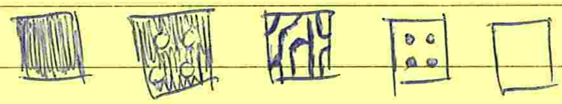
$$G(|\vec{x}-\vec{x}'|) = \begin{cases} \frac{1}{\pi R^2} & \text{if } |\vec{x}-\vec{x}'| < R \\ 0 & \text{if } |\vec{x}-\vec{x}'| \geq R \end{cases} \rightarrow \hat{G}(\vec{k}) = 2\,\frac{J_1(|\vec{k}|R)}{|\vec{k}|R}$$

$$\lambda(\vec{k}) = \frac{(\alpha-\beta)(\beta+\alpha\delta\hat{G}(\vec{k}))}{\beta(1+\delta)}$$

→ larger δ makes $\lambda(\vec{k})$ start having positive values

Numerical integration of the model

periodic boundary conditions

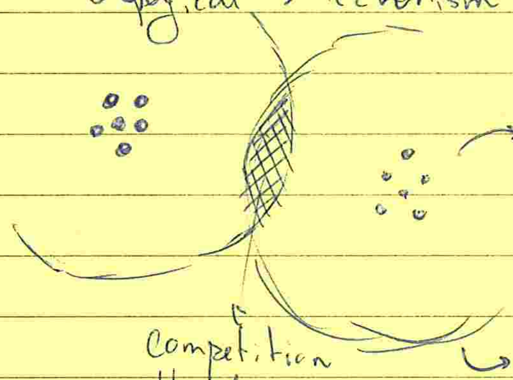


Increasing δ

Decreasing water

remember: this is a toy model

Biological Mechanism: Exclusion Areas



Obs.: this is only one way of obtaining patterns, but there are more!

Proposal by Alan Turing

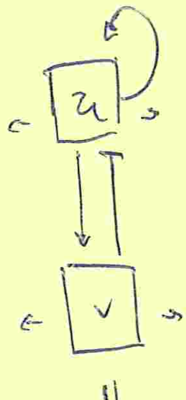
$$\begin{cases} \frac{\partial u}{\partial t} = F(u,v) + D_u \frac{\partial^2 u}{\partial x^2} \\ \frac{\partial v}{\partial t} = G(u,v) + D_v \frac{\partial^2 v}{\partial x^2} \end{cases}$$

→ two coupled reaction-diffusion equations

u: activator

v: inhibitor

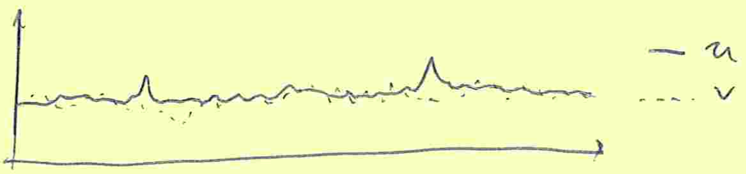
Garcia

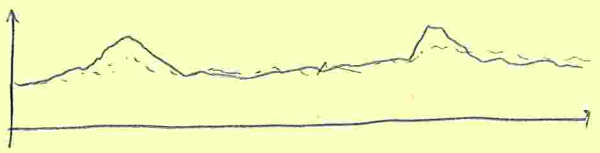


$\Downarrow$

constraints on $F(u,v)$ and $G(u,v)$

u: activates u and v } both
v: inhibits u } diffuse

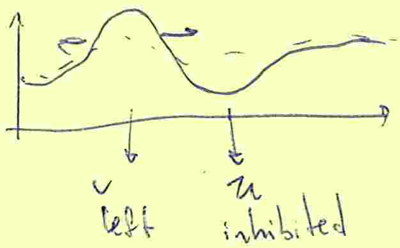




To get patterns: $D_v \gg D_u$

↳ v leaves places where u is high fastly

↳ u can grow in some places, but not in others



Due to the behavior of u and v (in qualitative sense), we know the signs of the derivatives of F and G

Plants: activator
Water: inhibitor