NONLINEAR PHENOMENA IN BIOLOGY

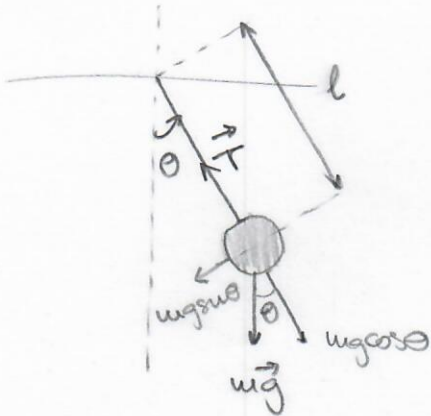## 0.- INTRODUCTION

Biological systems are highly nonlinear → SEVERAL COMPONENTS INTERACTING IN A COMPLEX WAY

What is a nonlinear system?

We can start from a system that we all know well:

PENDULUM

Dynamical equation

$$\vec{F} = m\vec{a}$$

$$\begin{cases} \\ -mg\sin\theta = m|\vec{a}| \end{cases}$$

Where we have applied the 2nd law of Newton only to the tangential plane because the movement of the pendulum is constrained to a circle. This means that the tension of the cord balances out the other component of the acceleration

Writing the linear acceleration in terms of the angle, we get:

$$S = l\theta \qquad (S \text{ is arc of length})$$

Then $v = \dfrac{ds}{dt} = l\dfrac{d\theta}{dt}$ and the linear acc. $a = l\dfrac{d^2\theta}{dt^2}$

↑
linear velocity

We finally get

$$ml \frac{d^2\theta}{dt^2} = -mg\sin\theta \implies \boxed{\ddot\theta = -\frac{g}{l}\sin\theta} \quad (2)$$

(2) is a classical example of a nonlinear system whose solution is not easily obtained. You probably are familiar with the "small angle" approximation in which $\theta \ll 1$ and thus $\sin\theta \approx \theta$

Then Eq. (2) becomes $\ddot\theta = -\frac{g}{l}\theta$ that can be easily solved by direct integration $\ddot\theta = -\frac{g}{l}\theta \implies$

$$\implies \theta(t) = \theta_0 \cos\left(\sqrt{g/l}\, t\right) \qquad \theta \ll 1.$$

Even what seems to be a very simple system, like the pendulum is analytically intractable for any θ. How can we deal with these systems when they appear and gain some analytical intuition?

<u>PENDULUM</u>

1 particle $\longrightarrow$

Deterministic
dynamics

<u>BIOLOGICAL SYSTEMS</u>

- Many entities "particles"
- Interacting in complex ways with each other.
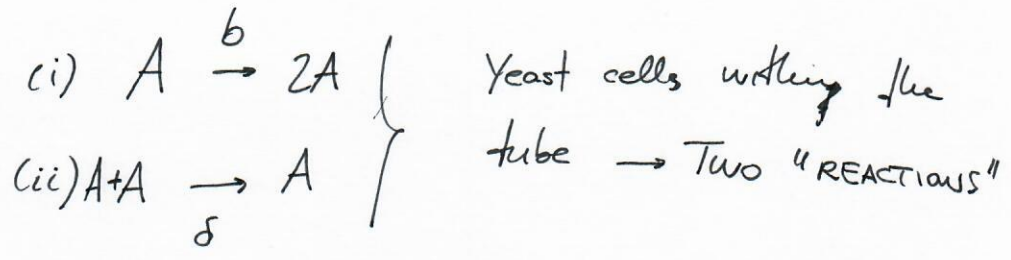- Stochastic dynamics.
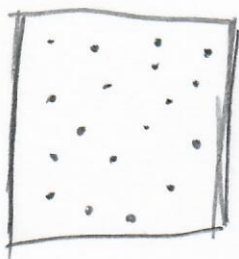
HOW DO NONLINEARITIES ARISE IN BIOLOGY?
WHAT ARE THE PROCESSES OF INTEREST?
WHAT ARE THE VARIABLES USEFUL TO DESCRIBE THEM?

(Explanation of experimental results. Gause 1932)

1. ONE SPECIES MODELS. NO SPACE
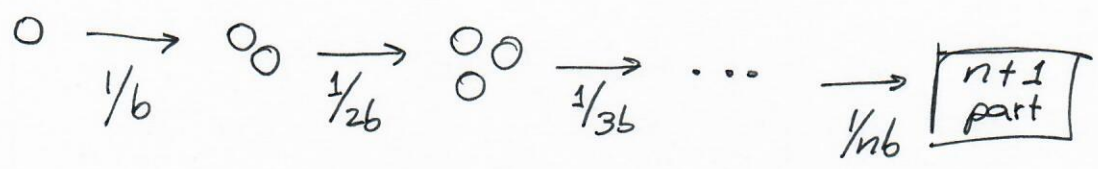
Logistic growth from microscopic dynamics.

(i) $A \xrightarrow{b} 2A$

(ii) $A+A \xrightarrow{\delta} A$

Yeast cells within the tube → Two "REACTIONS"

Assumption: cells move "∞" fast inside the tube and thus they are "well-mixed". ⟹ SPACE IS NOT IMPORTANT !!

We will consider spatial effects later.

* What do these "reactions" mean?

(i) $b →$ birth rate per capita → "BIRTH"

Consider we start with one particle:

$O \xrightarrow{1/b} {}^{O}O \xrightarrow{1/2b} {}^{O}_{O}{}^{O} \xrightarrow{1/3b} \cdots \xrightarrow{1/nb} \boxed{\begin{array}{c} n+1 \\ part \end{array}}$

Therefore, if we have n particles, the total birth rate is → $\boxed{nb}$

(ii) Second term. → "DEATH"

Again, for each particle → δ

So, for n particles → $n\delta$ ** BUT ** Now the process needs an encounter between two particles

Hence, the total rate is proportional to all other particle density $\longrightarrow \dfrac{n-1}{V}$ Total rate $\dfrac{\delta n(n-1)}{V}$

. We redefine δ such that $\tilde{\delta} = \dfrac{\delta}{V}$ and drop the tilde for simplicity

·) If $n \gg 1 \longrightarrow n-1 \approx n$

Finally transition rates are:

$$\begin{array}{|l|} \hline \Omega(n \rightarrow n+1) = nb \\ \Omega(n \rightarrow n-1) = \delta n^2 \\ \hline \end{array}$$

Given these transition rates, what is the probability of having n "particles" (cells) at time t?

$$P(n, t+dt) = P(n-1, t)\,\Omega(n-1 \rightarrow n)\,dt \qquad + \qquad (\text{DEATH})$$

$$+ P(n+1, t)\,\Omega(n+1 \rightarrow n)\,dt + b \qquad (\text{BIRTH})$$

$$+ P(n,t)\left[1 - \Omega(n \rightarrow n-1)\,dt - \Omega(n \rightarrow n+1)\,dt\right]$$

$$(\text{NOTHING})$$

$$\dfrac{P(n, t+dt) - P(n,t)}{dt} \equiv \dfrac{\partial P(n,t)}{\partial t} = P(n-1,t)(n-1)b +$$
$$+ \delta(n+1)^2\,P(n+1, t) -$$
$$- (\delta n^2 + nb)\,P(n,t)$$

MASTER EQUATION

In principle, if we know $P(n, t=0)$, we can integrate the master equation to obtain $P(n,t)$ $\forall t$ and hence the stochastic dynamics of the system. However, M. Eqs are in general hard to solve (see generating function for example).

•) Here we will pursue a less ambitious goal and obtain equations for the moments of the distribution

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

We will focus on the first moment $(k=1:$ mean value$)$

So, working with the master equation,

$$\sum_{n=0}^{\infty} n \frac{\partial P(n,t)}{\partial t} = \sum_{n=0}^{\infty} n b (n-1) P(n-1,t) + \sum_{n=0}^{\infty} n \delta(n+1)^2 P(n+1,t)$$

$$\overset{(*)}{} \qquad\qquad \overset{(**)}{}$$

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

Notice that $(*)$ and $(**)$ depend on $P(n-1)$ and $P(n+1)$ respectively. We define:

$(*)$ $n-1 \to m$
If $n=0 \to m=-1$ $\Big\}$ $\sum_{m=-1}^{\hat{}} (m+1) b m \, P(m,t)$.

$(**)$ $n+1 \to m$
If $n=0 \to m=1$ $\Big\}$ $\sum_{m=1}^{\hat{}} (m-1) \delta m^2 \, P(m,t)$

Because m is an index $\Rightarrow$ $\underline{m \to n}$

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

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

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

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

$\blacktriangleright$ The equation for the first moment appears coupled to the equation for the second moment !!

$\underline{\text{INDEED}}$, if we derive equations for the moments, we would obtain an ∞ system of coupled differential equations $\to$

$\to$ How can we truncate such hierarchy?

MEAN FIELD APPROXIMATION $\Rightarrow$ NEGLECT FLUCTUATIONS.

$$\Downarrow \langle n^2 \rangle = \langle n \rangle^2 \quad (\langle n^2 \rangle - \langle n \rangle^2 = 0)$$

Thus (dropping $\langle \rangle$ from the notation)

$$\boxed{\dot{n} = bn - \delta n^2 = bn\left(1 - \frac{\delta n}{b}\right)}$$ LOGISTIC GROWTH

$$\dot{n} = bn\left(1 - \frac{\delta n}{b}\right)$$

How can we deal with these equations?

① Analytical solution

② Numerical integration

③ Qualitative analysis of its behavior

① Usually hard for nonlinear equations $n(t) = \dfrac{K}{1 + Ae^{-bt}}$

② Numerical integration → hard to gain general solution   with $A = \dfrac{k - n_0}{n_0}$

$$K = b/\delta$$

③ **Focus of these mini-course.**

·) Steady states

$$\dot{n} = 0 \implies \begin{cases} n^* = 0 \longrightarrow \text{TRIVIAL STEADY STATE} \\ n^* = b/\delta \equiv k \to \text{NONTRIVIAL "CARRYING CAPACITY"} \end{cases}$$

·) Stability of these points. We assume that the population is at that value, n^*, and suffers a small perturbation ϵx $(\epsilon \ll 1)$. <u>How does the system respond?</u>

$$n = n^* + \epsilon X$$

Plugging this ansatz into the equation

$$\dot{n} = f(n) \implies \frac{d}{dt}(n^* + \epsilon X) = f(n^* + \epsilon X) =$$

$$= f(n^*) + f'(n^*)\epsilon X$$

(with $f(n^*) = 0$)

$$\implies \epsilon \dot{X} = f'(n^*)\epsilon X \implies$$

$$\implies X(t) = e^{f'(n^*)t} \quad \begin{cases} \text{If } f'(n^*) > 0 \text{ then} \\ \quad X(t) \text{ GROWS.} \\ \text{If } f'(n^*) < 0 \implies X(t) \text{ DIES OUT.} \end{cases}$$

Then, the steady state is

STABLE IF $f'(n^*) < 0$
UNSTABLE IF $f'(n^*) > 0$

For this particular case: $\quad f(n) = bn\left(1 - \frac{n}{k}\right) \implies$

$$\implies f'(n) = b - \delta 2n$$

$f'(0) = b \implies$ UNSTABLE
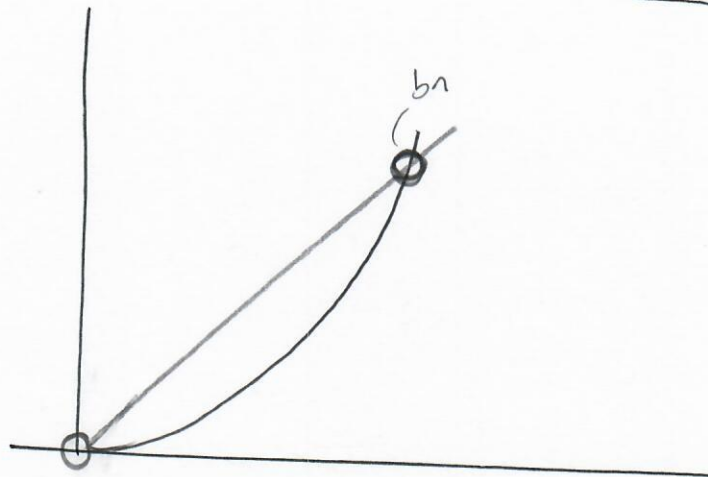
$f'(b/\delta) = b - 2b = -b \implies$ STABLE.

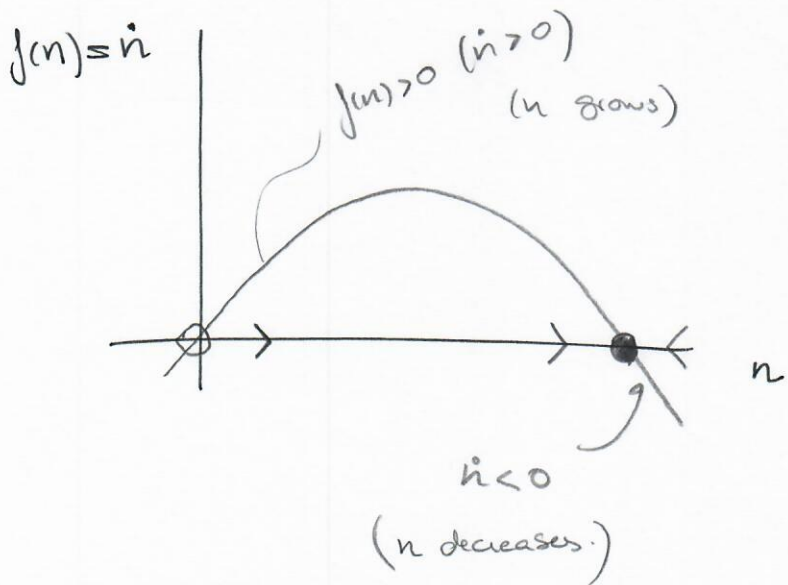$\boxed{\text{IMPORTANT}}$ Sometimes we won't be able to obtain the fixed points analytically $\rightarrow$ WHAT CAN WE DO?

$$\dot{n} = bn\left(1 - \frac{\delta n}{b}\right) \equiv f(n)$$

Steady states $\Rightarrow$ $f(n^*) = 0$ $\Rightarrow$ $\boxed{bn = \delta n^2.}$

bn

Alternatively $\rightarrow$ $f(n) = 0$

$f(n) = \dot{n}$

$f(n) > 0$ $(\dot{n} > 0)$
(n grows)

n

$\dot{n} < 0$
(n decreases.)

Notation

⬤ $\rightarrow$ STABLE

O $\rightarrow$ UNSTABLE.

2.- MULTIPLE SPECIES MODELS. NO SPACE.

So far we have consider that populations of 1 species live isolated from other species.

In this lecture, we will extend that situation to case in which several species interact with each other.

OVERVIEW OF BIOLOGICAL INTERACTIONS.

Let's consider that we have two species interacting with each other. (Experimental result Gause 1932)

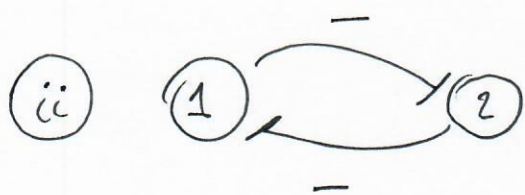Species can affect each other's growth in various ways. The main ones are three:

(i)

$$1 \overset{-}{\underset{+}{\rightleftarrows}} 2$$
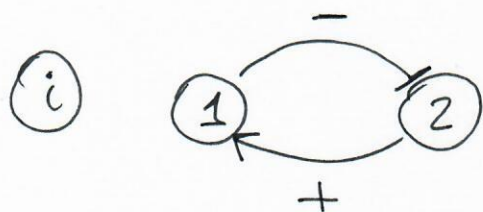
PREY - PREDATOR
HOST - PARASITE

① PREDAT. PARASITE
② PREY / HOST.

Examples: Fox and rabbit
Virus and bacteria they infect.
Ticks and zebras / dogs.
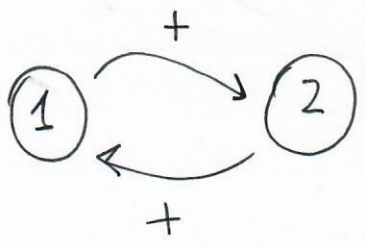
(ii)

$$1 \overset{-}{\underset{-}{\rightleftarrows}} 2$$

COMPETITION

Example: 2 carnivores feeding on the same herbivore. // 2 species sharing space.

(ii)

$$1 \xrightarrow{+} 2$$
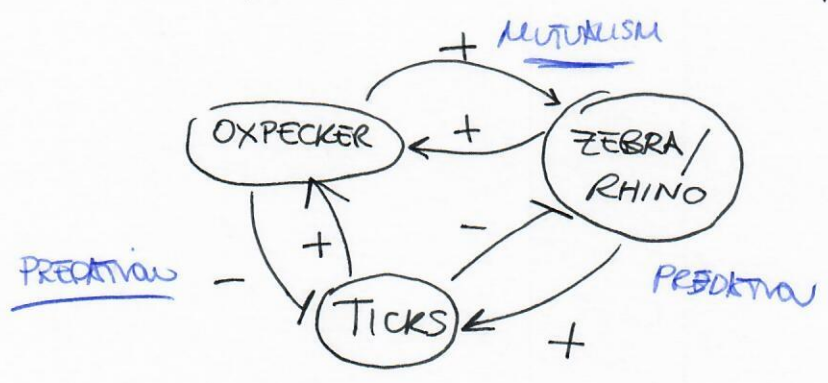$$1 \xleftarrow{+} 2$$

MUTUALISM.

Example: plants and bees.

<u>Interesting</u> case: Oxpecker (type of bird) that eats the ~~the~~ ticks from zebras / rhinos.

<u>Remark</u> although we here consider only two species, interactions often occur b/w more than two species

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HOW CAN WE MODEL THIS RICHNESS OF INTERACTIONS AND INCORPORATE THEM INTO A MATHEMATICAL FRAMEWORK?

$$\frac{dn_1}{dt} = b_1 n_1 \left[1 - \frac{n_1}{K_1} \pm \alpha_{12} \frac{n_1}{K_1} \right]$$

$$\frac{dn_2}{dt} = b_2 n_2 \left[1 - \frac{n_2}{K_2} \pm \alpha_{21} \frac{n_2}{K_2} \right]$$

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

These signs define the nature of the interaction

	PP	C	M
Eq. 1	+	−	+
Eq. 2	−	−	+

Introducing a new species and the interaction has increased the number of parameters. We can reduce it nondimensionalizing the system

$$M_1 = \frac{n_1}{k_1} \quad ; \quad M_2 = \frac{n_2}{k_2} \qquad \tau = b_1 t$$

$$\rho = b_2 / b_1 \qquad a_{12} = \alpha_{12} \frac{k_2}{k_1} \quad ; \quad a_{21} = \alpha_{21} \frac{k_1}{k_2}$$

Using these, the eqs. become:

$$\frac{du_1}{d\tau} = M_1 \left(1 - M_1 \pm a_{12} M_2 \right) = f_1(u_1, u_2)$$

$$\frac{du_2}{d\tau} = \rho M_2 \left(1 - M_2 \pm a_{21} M_1 \right) = f_2(u_1, u_2)$$

parameter :   6 $\longrightarrow$ $\cancel{6}$ 3

NONDIMENSIONAL.

Among all possible interactions, let's assume **competition**

What are the fixed points now?

$$(0,0) \quad ; \quad (1,0) \quad ; \quad (0,1) \rightsquigarrow$$ These don't explain experimental result.!!

and sometimes a fourth one

Forth one:

$$\left(1 - \mu_1 - a_{12}\mu_2\right) = 0$$
$$\left(1 - \mu_2 - a_{21}\mu_1\right) = 0$$
$\Rightarrow$

$\Rightarrow \mu_1 = 1 - a_{12}\mu_2$ and then $1 - \mu_2 - a_{21}\left(1 - a_{12}\mu_2\right) = 0$

$$\boxed{\mu_2^* = \frac{1 - a_{21}}{1 - a_{21}a_{12}}}$$

and (using the symmetry of eqs. or repeating the calculation)

$$\boxed{\mu_1^* = \frac{1 - a_{12}}{1 - a_{21}a_{12}}}$$

Notice that we need
$$a_{12}a_{21} \neq 1.$$

This forth point implies that both species <u>coexist</u>, but

<u>WHEN IS IT RELEVANT?</u>
$$\begin{cases} \mu_1^* > 0 \\ \mu_2^* > 0 \end{cases}$$

$\ast$ How can we unveil the conditions for the existence of 4th FP?

$\ast\ast$ If it exists, when is it stable?

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

- <u>GRAPHICAL ANALYSIS</u> $\rightarrow$ qualitative (often quantitative) intuition.

Nullclins → curves such that $\dot{u}_1 = 0$ | when they
$\qquad\qquad\qquad\qquad\qquad\qquad\quad \dot{u}_2 = 0$ |

intersect $\Rightarrow \dot{u}_1 = \dot{u}_2 = 0 \Rightarrow$ $\underline{STEADY\ POINT}$.

$\underline{u_1 - nullclines}$:

$\qquad \hookrightarrow \boxed{u_1 = 0}$

$\qquad \hookrightarrow 1 - u_1 - a_{12}u_2 = 0 \Rightarrow \boxed{u_2 = \dfrac{1 - u_1}{a_{12}}}$

$\underline{u_2 - nullclines}$:

$\qquad \hookrightarrow \boxed{u_2 = 0}$

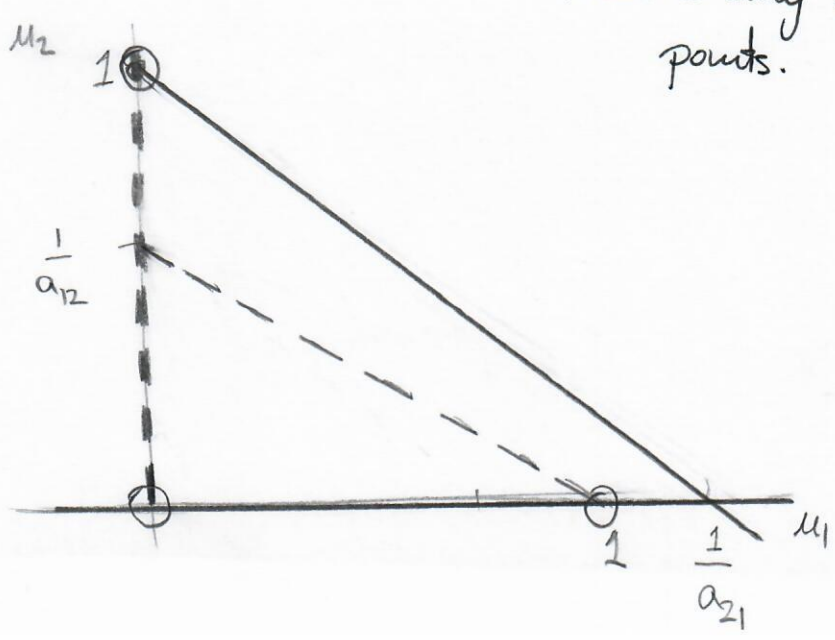$\qquad\quad 1 - u_2 - a_{21}u_1 = 0 \Rightarrow \boxed{u_2 = 1 - a_{21}u_1}$

We have 4 different cases that we need to analyze separately.

(i) $\begin{array}{l} a_{12} > 1 \\ a_{21} < 1 \end{array}$; (ii) $\begin{array}{l} a_{12} < 1 \\ a_{21} > 1 \end{array}$; (iii) $\begin{array}{l} a_{12} > 1 \\ a_{21} > 1 \end{array}$ (iv) $\begin{array}{l} a_{12} < 1 \\ a_{21} < 1. \end{array}$

(i) $\begin{array}{l} a_{12} > 1 \\ a_{21} < 1 \end{array}$

There is only 3 fixed points.

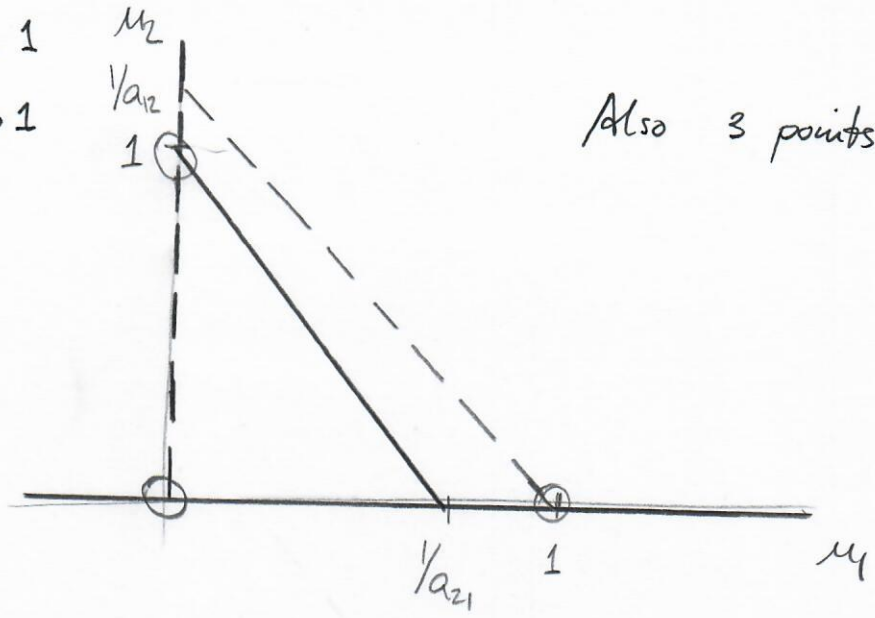Case (ii) $a_{12} < 1$
$\qquad\quad$ $a_{21} > 1$

Also 3 points

(iii) $a_{12} > 1$
$\qquad$ $a_{21} > 1$
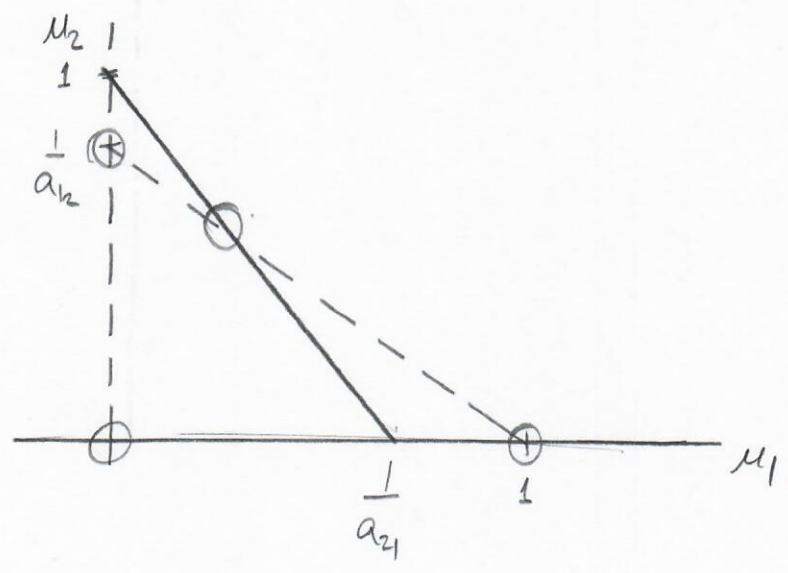
(iv) $a_{12} < 1$
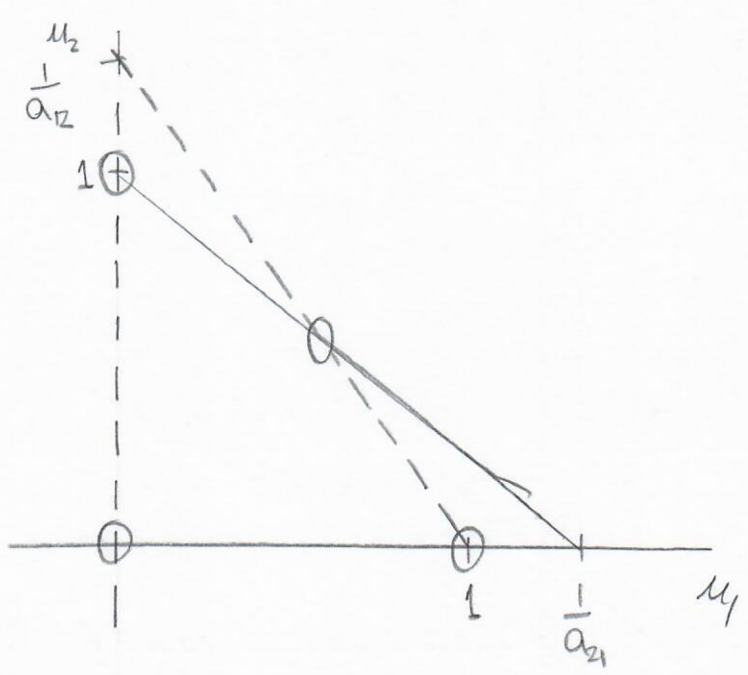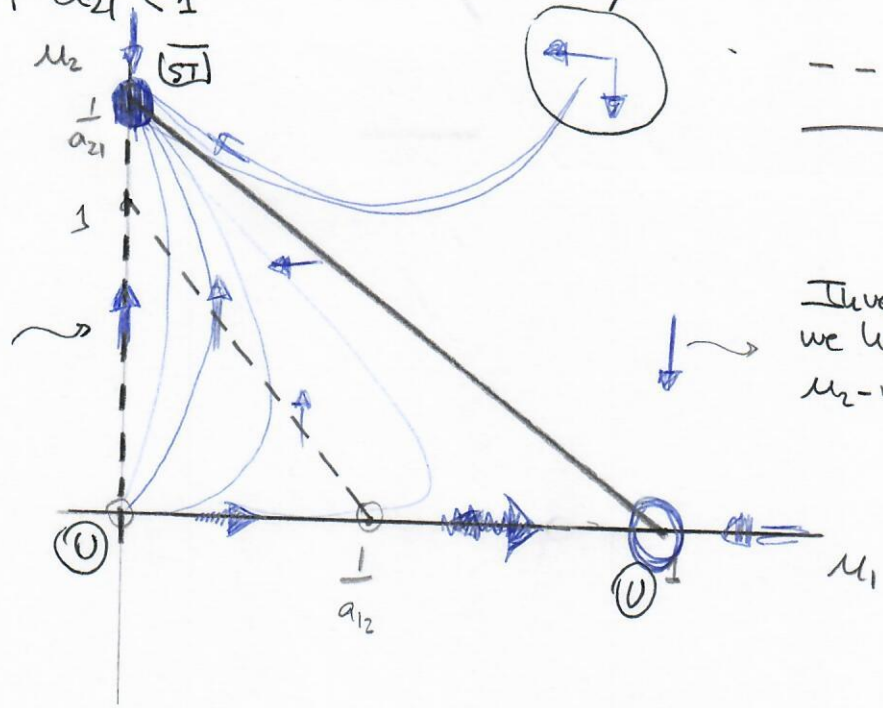$\qquad$ $a_{21} < 1$

What is the stability of these points (ESPECIALLY THE 4th !!) in each case?

Example:

Case ⓘ $\begin{cases} a_{12} > 1 \\ a_{21} < 1 \end{cases}$

The system is globally stable.

- - - - u_1-nullcline

———— u_2-nullcline.

There is only one species that grows until the carrying capacity

Inversion because we have crossed a u_2-nullcline.

How can we study the stability?

$$(\dot{u}_1 , \dot{u}_2) = (f_1(u_1, u_2) , f_2(u_1, u_2))$$ for each point (u_1, u_2)

So there is a VECTOR FIELD. ⟶ How will the dynamics evolve?

a) In the u_1-nullcline, $\dot{u}_1 = 0$ and thus the flow goes in the direction of u_2. (blue arrows.

b) When we cross u_1 - nullcline the direction of u_1 vector flips.
$\quad\quad\quad u_2 \quad\quad '' \quad\quad '' \quad\quad '' \quad\quad '' \quad u_2 \quad '' \quad '' .$

<u>Biological meaning?</u>

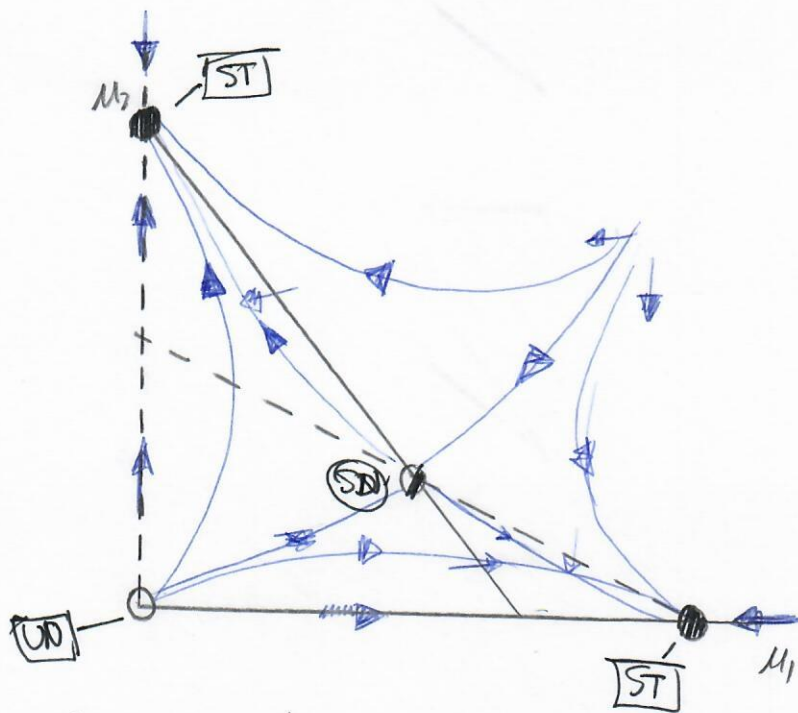$a_{12} > 1 \implies a_{12} = \alpha_{12} \dfrac{K_2}{K_1} > 1 \implies \boxed{\dfrac{\alpha_{12}}{K_1} > \dfrac{1}{K_2}}$ Species 2 inhibits the growth of species 1 <u>more</u> strongly than itself's

$a_{21} < 1 \implies a_{21} = \alpha_{21} \dfrac{K_1}{K_2} < 1 \implies \boxed{\dfrac{\alpha_{21}}{K_2} < \dfrac{1}{K}}$ Sp. 1 inhibits its own growth more strongly than species 2.
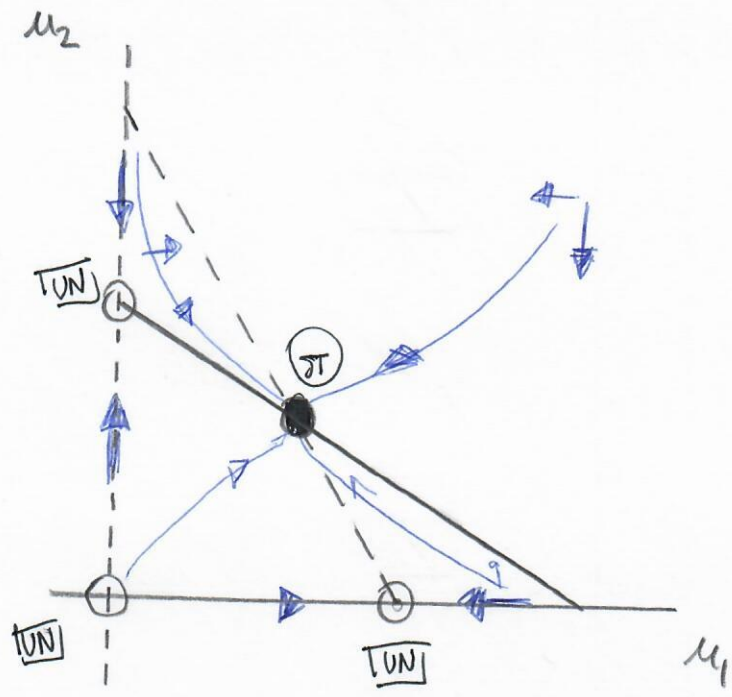
Case iii)

The coexistence point is STABLE only in one direction.
This point is called SADDLE POINT.

$$\text{If} \quad a_{12} = \alpha_{12} \frac{K_2}{K_1} > 1 \quad \Rightarrow \quad \boxed{\frac{\alpha_{12}}{K_1} > \frac{1}{K_2}}$$

$$a_{21} = \alpha_{21} \frac{K_1}{K_2} > 1 \quad \Rightarrow \quad \boxed{\frac{\alpha_{21}}{K_2} > \frac{1}{K_1}}$$

- Both species inhibit the growth of its partner more strongly than its own.

- Then, one species outcompetes the other depending on the initial condition.

Case (iv)

u_2

UN

ST

UN

UN

u_1

STABLE
COEXISTENCE

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

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

Species inhibit their own growth stronger than the growth
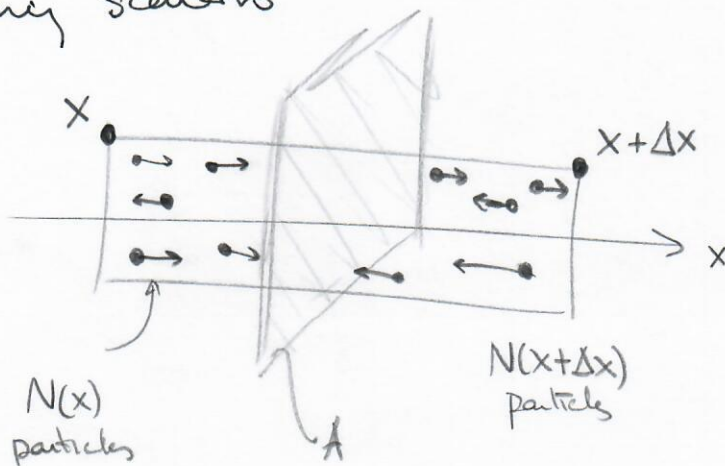of their partner, which makes coexistence stable.

Two competing species do not coexist stably unless
the intensity of interspecific competition is stronger
than intraspecific competition

3. SPATIAL MODELS: WAVES AND PATTERNS

So far, we have assumed that individuals move "∞" fast and thus well-mixed → "everyone is likely to interact with everyone".

This is, of course, not true for most natural setups, and spatial degrees of freedom are important. In the next lectures, we will study how previous models change when space is considered and introduce the interesting phenomena that arises due to such spatial structure.

Relaxing the "everyone is everywhere" hypothesis, let's consider the following scenario

$N(x)$ particles

$N(x+\Delta x)$ particles

If particles move randomly $\begin{cases} \dfrac{N(x)}{2} & \text{move} \rightarrow \\[2mm] \dfrac{N(x)}{2} & \text{move} \leftarrow \end{cases}$

(and the same for $N(x+\Delta x)$).

Therefore, the net number of particle ~~closing~~ crossing from LEFT to the right, is:

$$\frac{N(x)}{2} - \frac{N(x+\Delta x)}{2}$$

And, in an interval Δt, the flux a through A,

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

In terms of the concentration of particle, $C(x) = \frac{N(x)}{A\Delta x}$,

$$J = \frac{1}{2A\Delta t} A\Delta x \left[C(x) - C(x+\Delta x)\right] =$$

$$= \frac{\Delta x}{2\Delta t}\left[C(x) - \left(C(x) + \frac{\partial C(x)}{\partial x}\Delta x + \frac{\partial^2 C(x)}{\partial x^2}\Delta x^2 + \ldots\right)\right]$$

If $\Delta x \to 0$, then

$$\boxed{J = -\frac{(\Delta x)^2}{2\Delta t}\frac{\partial C}{\partial x} = -D\frac{\partial C}{\partial x}} \quad \text{with} \quad D = \lim_{\substack{\Delta x \to 0 \\ \Delta t \to 0}} \frac{(\Delta x)^2}{2\Delta t}.$$
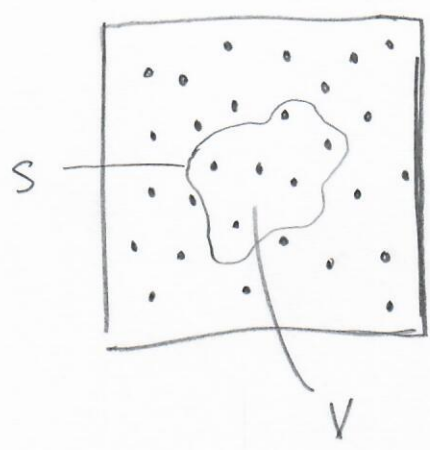
NOTE Notice the sign $(-)$, which ~~sa~~ tells us that the direction of the flux goes against the __gradient of concentration__

Let's now move to a more general case $\longrightarrow$

$\to$ we merge the scenarios studied in the first classes with the movement of individuals as described above

$C(x,t) \equiv$ concentration of individuals at a given position

within our system, we define an arbitrary volume, V, → HOW DOES THE TOTAL BIOMASS CHANGE INSIDE THE VOLUME?

Total amount of biomass inside V → $\int_V c(x,t) dV$

$$\frac{\partial}{\partial t} \int_V c(x,t) dV = - \int_S \vec{J} \cdot \vec{dS} + \int_V f \, dV$$

Flux of ind. acc through S.

Material created/destroyed in V.

(NOTE) By convention $\vec{dS}$ points outwards. we're interested in the flow inwards. so we need the minus sign.

Using the theorem of the divergence.

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

and since V is an arbitrary volume,

In 1D

$$\frac{\partial c(x,t)}{\partial t} + \frac{\partial J}{\partial x} - f(c) = 0 \qquad \text{if} \quad J = -D\frac{\partial c}{\partial x}, \text{ then}$$

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

If $D \equiv$ constant

This type of equations are called reaction-diffusion equations

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| WHAT TYPE OF NEW PHENOMENA SHOULD WE EXPECT FROM THEM? |

To keep our line of discussion, let's use $f(c) = c(1-c)$

and for simplicity $D \equiv$ constant

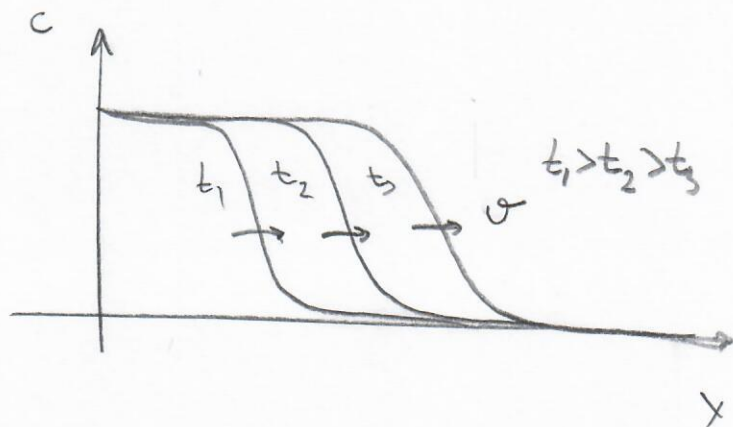$$\hookrightarrow D = D(c) \quad \text{(?)}$$
$$D = D(x,t)$$

We have
$$\boxed{\frac{\partial c}{\partial t} = c(1-c) + D\frac{\partial^2 c}{\partial x^2}} \qquad \text{FISHER-KOLMOGOROV EQ.}$$

$(**)$

- Decribes a population that grows and disperses.
- Introduced first in 1937 to describe α β the spreading of a favored gene in a population.

A) TRAVELLING WAVES.

Fixed points $\quad c = 0$
$$c = 1$$

This means that

$$c(x,t) = c(x - \sigma t) = c(z)$$

$\times$

$$\frac{\partial c}{\partial t} = c(1-c) +$$

Does this solution meet Eq. $(**)$?

$$\frac{\partial c}{\partial t} = \frac{dc}{dz}\frac{\partial z}{\partial t}$$

$$\frac{\partial^2 c}{\partial x^2} = \frac{d^2 c}{dz^2}$$

$$-\sigma\frac{dc}{dz} = c(1-c) + D\frac{d^2 c}{dz^2}$$

$$+ \quad \lim_{x \to +\infty} c(x) = 0$$

$$\lim_{x \to -\infty} c(x) = 1$$

This an eigenvalue problem

For certain σ's FK admits solutions in

What is the biological implication of these waves?

Lets compare them with typical diffusion. (without reaction)

$$\frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial x^2} \longrightarrow \text{Does it admit wave solutions ?}$$

Lets make the same change of variables:

$$c(x,t) = c(x - \sigma t) = c(z)$$

This gives,
$$D \left\{ \frac{d^2 c}{dz^2} = -\sigma \frac{dc}{dz} \right. \Rightarrow \boxed{\sigma c'(z) + D c''(z) = 0} \quad (\Delta\Delta)$$

with $\quad c(z \to \infty) = 0$
$\qquad c(z \to -\infty) = 1 .$

Eq. $(\Delta\Delta)$ is solvable:

- Change $\quad c'(z) = f(z)$ gives

$$\sigma f(z) + D f'(z) = 0 \Rightarrow \frac{df}{f} = -\frac{\sigma}{D} dz \Rightarrow \ln f = -\frac{\sigma}{D} z + K_1$$

$$f = k_1 e^{-\sigma/D \, z} \quad \text{and} \quad \text{undoing the change of variables,}$$

$$c'(z) = k_1 e^{-\sigma/D z} \Rightarrow c(z) = \int k_1 e^{-\sigma/D z} \Rightarrow c(z) = \tilde{K_1} e^{-\sigma/D z} + k_2$$

which can be constant at $\pm \infty$ only if $\tilde{K_1} = 0 .$

Actually the solution for the diffusion equation can be obtained.
If $c(x, t=0)$ is a punctual source:

Then $c(x,t) = \dfrac{c_0 \, e^{-x^2/4Dt}}{\sqrt{4\pi D t}}$

$D \equiv$ diffusion coefficient

$$\boxed{D \sim \dfrac{L^2}{T}}$$ (how fast individuals disperse)

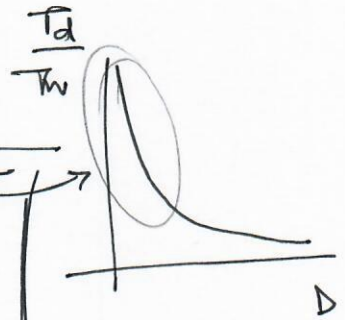For ~~the~~ travelling waves $\rightarrow$ $\boxed{\sigma \sim \dfrac{L}{T}}$

So, $T_d \sim \dfrac{L^2}{D}$

$T_w \sim \dfrac{L}{\sigma}$

$\dfrac{T_d}{T_w} \sim \dfrac{L^2}{D}\dfrac{\sigma}{L} = \dfrac{L\sigma}{D} = \dfrac{L\sqrt{Dk}}{D} \underset{\nearrow}{=}$ birth rate.

$= L\sqrt{\dfrac{k}{D}} \underset{\underset{k\sim 1}{\uparrow}}{\sim} \quad \dfrac{T_d}{T_w}$

For low diffusivity problems, the creation of mess promotes transport (for instance inside cells)!

B.— REGULAR PATTERNS. (periodic distributions of individuals).

Let's consider our RD equation:

$$\dfrac{\partial c}{\partial t} = bc - \mu c^2 + D\dfrac{\partial^2 c}{\partial x} \quad, \text{ again in the absence}$$

of spatial heterogeneities, it has two steady states $\begin{cases} c^* = 0 \\ c^* = b/\mu. \end{cases}$

$c^* = 0 \rightarrow$ UNSTABLE

$c^* = b/\mu \rightarrow$ STABLE

$\begin{cases} * \underline{\underline{BUT}} * \text{ what happens against} \\ \text{perturbations that depend on} \\ \text{the space ??} \end{cases}$

Now, we write $\quad C = C^* + \underbrace{\epsilon \psi(x,t)}$

$\epsilon \ll 1$, SMALL, SPATIAL PERTURBATION.

$$\frac{\partial(c^* + \epsilon\psi)}{\partial t} = f(c^* + \epsilon\psi(x)) + D\frac{\partial(c^* + \epsilon\psi(x))}{\partial x}$$

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

This a linear equation that we can solve using Fourier

$\longrightarrow \left[\hat{\psi}(k) = \mathcal{F}[\psi(x)] = \int e^{ikx}\psi(x,t)\,dx \right]$

$$\frac{\partial\hat{\psi}(k,t)}{\partial t} = \epsilon\hat{\psi} f'(c^*) \mp \underbrace{D\epsilon k^2 \hat{\psi}(k,t)}$$

EXPLAIN PROPERTY OF
FOURIER TRANSFORM!!

To solve the transformed equation, we assume $\hat{\psi}(k,t) \propto e^{\lambda(k)t}$.

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

$\lambda(k) = -k^2 D + f'(c^*) < 0 \qquad \underline{ALWAYS}$ because

$D > 0$
$f'(c^*) < 0$ (STABILITY.)

So, if $\lambda(k) < 0 \quad \forall k \Rightarrow$ The spatial perturbation dies out and there are no patterns. $\rightarrow$ WHAT MECHANISM CAN LEAD TO PATTERNS?

•) Non-local couplings
$\hookrightarrow$ long-range interactions

Linear stability analysis of the nonlocal FK:

$$\frac{\partial \rho}{\partial t} = b\rho - \mu\rho\tilde{\rho} + D\frac{\partial^2 \rho}{\partial x^2}$$

with $\tilde{\rho} = \int G(|x-x'|)\rho(x',t)\,dx'$

First we obtain the homogeneous solution $\rho(x,t) = \rho_0$, thus

$$\frac{\partial \rho_0}{\partial t} = \frac{\partial \rho_0}{\partial x} = 0.$$

And

$$b\rho - \mu\rho^2 = 0. \implies \begin{array}{l} \rho_0^* = 0 \quad \longrightarrow \text{ UNSTABLE} \\ \rho_0^{**} = b/\mu \longrightarrow \text{STABLE}. \end{array}$$

Now we investigate whether the stable solution ρ_2 is stable or unstable against spatial perturbations. $\longrightarrow \rho = \rho_0 + \epsilon\psi(x,t)$

$$\epsilon \ll 1$$

We obtain

$$\frac{\partial(\rho_0 + \epsilon\psi)}{\partial t} = b(\rho_0 + \epsilon\psi) - \mu(\rho_0 + \epsilon\psi)\int G(|x-x'|)(\rho_0 + \epsilon\psi)\,dx' +$$

$$+ D\frac{\partial^2(\rho_0 + \epsilon\psi)}{\partial x^2}$$

$$\epsilon\frac{\partial\psi}{\partial t} = D\epsilon\frac{\partial^2\psi}{\partial x^2} + b\rho_0 + \epsilon b\psi - \left(\mu\rho_0 + \mu\epsilon\psi\right)\left[\int G\rho_0\,dx' + \epsilon\int G\psi\,dx'\right] =$$

$$= D\epsilon \frac{\partial^2 \psi}{\partial x^2} + \left(b\rho_0 + \epsilon b\psi\right) - \left(\mu\rho_0 + \mu\epsilon\psi\right)\left[\rho_0 + \epsilon \int G\psi \, dx'\right] =$$

$$= D\epsilon \frac{\partial^2 \psi}{\partial x^2} + \underbrace{b\rho_0 - \mu\rho_0^2}_{\substack{\shortparallel \\ 0}} + \epsilon b\psi \circledast \mu\epsilon\psi\rho_0 - \mu\epsilon\rho_0 \int G\psi \, dx' + \mathcal{O}(\epsilon^2)$$

$$\Rightarrow \frac{\partial \psi}{\partial t} = D \frac{\partial^2 \psi}{\partial x^2} + \psi\left(b \oplus \mu\rho_0\right) - \mu\rho_0 \int G(|x-x'|)\, \psi(x,t)\, dx'$$

Linear equation in the perturbation (integro-differential content coeff).

we use FT: $\left[\hat{\psi}(k,t) = \int e^{ikx}\, \psi(x,t)\, dx\right]$

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

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

To solve this equation, we assume $\hat{\psi}(k,t) \propto e^{\lambda(k)t}$

$$\lambda(k)\, \hat{\psi}(k,t) = - k^2 D\, \hat{\psi}(k,t) + 2b\, \hat{\psi}(k,t) - b\, \hat{G}(k)\, \hat{\psi}(k,t)$$

$$\boxed{\lambda(k) = 2b - \left[D k^2 + b\, \hat{G}(k)\right]}$$

$$\frac{\lambda(k)}{b} = - \left[\frac{D}{b} k^2 + \hat{G}(k)\right]_{>0}$$

$$|\hat{g}(k)| = \frac{2J_1(kR)}{kR} \qquad \hat{G}(k) = \frac{\sin(kR)}{kR}$$

$$\lambda'(k_c) = - \frac{2k_c D}{b} - G'(k) = 0.$$

$$\boxed{PATTERNS} \leftarrow \boxed{\frac{D}{b} < \alpha_c}$$