

chapter 1: Linear Difference Model

Difference Equations

Let N_t be a quantity at time t . Then:

$$N_{t+1} = F(N_t, N_{t-1}, \dots, N_0)$$

Malthusian Model

In the form of $N_{t+1} = R N_t$

• Solution to the model equation is

$$N_t = R^t N_0$$

Fibonacci Sequence

$$N_{t+2} = N_{t+1} + N_t$$

• Golden ratio $\varphi = \lim_{n \rightarrow \infty} \frac{N_{n+1}}{N_n} \approx 1.618033 \dots$

Solving Linear Difference Equations

• Linear difference equation is in the form of:

$$N_{t+1} = a_k N_k + a_{k-1} N_{k-1} + \dots + a_0 N_0$$

• The order is the difference between the highest & lowest term.

↳ ex: $P_{t+2} = a P_{t+1} + b P_t$ is 2nd order

• Single first order:

equation: $x_{n+1} = a x_n$

solution: $x_n = a^n x_0$

• Single 2nd order:

Model: $x_{n+1} = ax_n + bx_{n-1}$

Solution: $x_n = C_1 \lambda_1^n + C_2 \lambda_2^n$

where: $\lambda^2 - a\lambda - b = 0$

C_1 & C_2 are constants based on initial conditions

• Two first order equations:

Model:
$$\begin{cases} x_{n+1} = a_{11}x_n + a_{12}y_n \\ y_{n+1} = a_{21}x_n + a_{22}y_n \end{cases}$$

Solution:
$$\begin{pmatrix} x_{n+1} \\ y_{n+1} \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \begin{pmatrix} x_n \\ y_n \end{pmatrix}$$

$$\vec{v}_{n+1} = M \vec{v}_n$$

$$\Rightarrow \vec{v}_{n+1} = \lambda \begin{pmatrix} C_1 \lambda^n \\ C_2 \lambda^n \end{pmatrix}$$

$$\lambda \vec{v}_n = M \vec{v}_n$$

$$0 = (M - \lambda I) \vec{v}_n$$

$$0 = \begin{pmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{pmatrix} \begin{pmatrix} C_1 \\ C_2 \end{pmatrix}$$

∴ $\det \begin{pmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{pmatrix} = 0$

$\lambda^2 - \beta\lambda + \gamma = 0$

where: $\beta = \text{tr}(M)$ and $\gamma = \det(M)$

$$\Rightarrow \begin{cases} x_n = A_1 \lambda_1^n + A_2 \lambda_2^n \\ y_n = B_1 \lambda_1^n + B_2 \lambda_2^n \end{cases}$$

Behaviour of m^{th} -order Linear Difference Equations

Form: $a_0 x_n + a_1 x_{n+1} + \dots + a_m x_{n+m} = b_n$

If $b_n = 0$, then the solution is:

$$x_n = C_1 \lambda_1^n + C_2 \lambda_2^n + \dots + C_m \lambda_m^n$$

Where the eigenvalues satisfy:

$$a_0 \lambda^m + a_1 \lambda^{m-1} + \dots + a_m = 0$$

$\hookrightarrow m^{\text{th}}$ order will have m eigenvalues

Dominant Eigenvalue

\hookrightarrow Eigenvalue with the largest $|\lambda|$

\hookrightarrow determines asymptotic behaviour (long term)

$\hookrightarrow \boxed{x_{n+1} \approx \lambda_0 x_n}$ for large n .

\hookrightarrow If $|\lambda| < 1 \rightarrow$ approaches 0

If $|\lambda| > 1 \rightarrow$ grow unboundedly

Complex Eigenvalues

\hookrightarrow oscillating behaviour

$\hookrightarrow x_n = r^n (C_1 \cos(n\psi) + C_2 \sin(n\psi))$

where $r^2 = a^2 + b^2$ and $\psi = \arctan(b/a)$

for $\lambda_{1,2} = a \pm bi$

} behaviour depends on r

$\Rightarrow r > 1$: amplitude grows

$r < 1$: amplitude shrinks

$r = 1$: constant amplitude

Chapter 2: Non-linear Difference Equation

Often cannot have a neat solution

Logistic Model

$$x_{n+1} = r x_n \left(1 - \frac{x_n}{k}\right)$$

↳ k does not affect the qualitative behaviour

↳ one degree of freedom.

Non-linear difference equation

General: $x_{n+1} = f(x_n, x_{n-1}, \dots, x_0)$

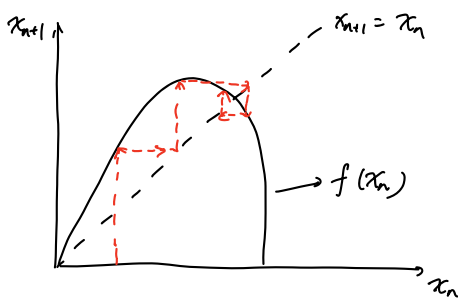
First order: $x_{n+1} = f(x_n)$, $f(x_n)$ is non-linear

Steady-state

\bar{x} such that $x_{n+1} = x_n = \bar{x}$

↳ For linear: only if $\lambda_0 = 1$ for non-trivial S.S.

Cobwebbing



• 2 cycle: if solution converges to 2 values

• Can lead to deterministic chaos as it can be very sensitive to initial conditions

↳ connected to fractals

Stability of Steady States

Two types:

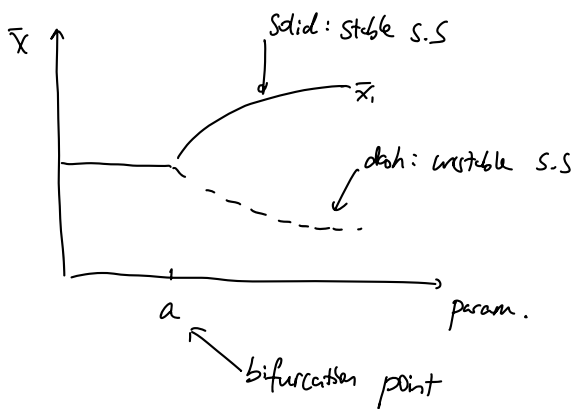
• Stable: attract nearby states

• unstable: repel nearby states

• A steady state \bar{x} of $x_{n+1} = f(x_n)$ is stable if:

$$\left| a | < 1 \iff \left| \frac{df}{dx} \Big|_{\bar{x}} \right| < 1$$

Bifurcation Diagram



Stability of 2-cycle

$$x_{n+2} = x_n \implies f(f(x_n)) = x_n$$

If $g(x) = f(f(x))$ and $k = n/2$, n even,

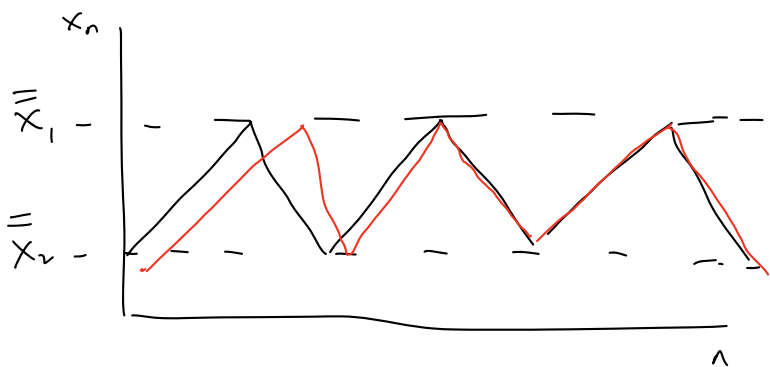
$$\implies x_{k+1} = g(x_k)$$

$$\boxed{\bar{x} = g(\bar{x})}$$

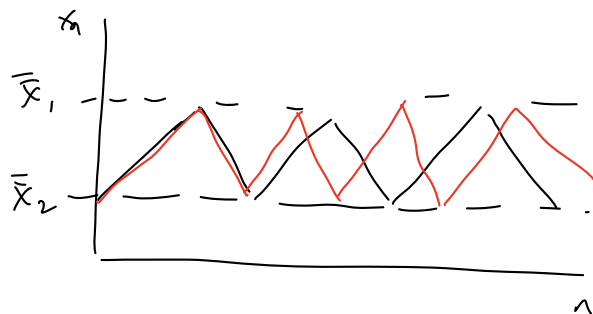
$$\implies \left| \frac{dg}{dx} \Big|_{\bar{x}_i} \right| < 1$$

$$\text{or } \left| \frac{df}{dx} \Big|_{\bar{x}_1}, \frac{df}{dx} \Big|_{\bar{x}_2} \right| < 1$$

Stable:



Unstable:



For logistic model: as $r \uparrow$, new stable branches, but old unstable branches are still there



Systems of Non-linear Difference Equations

$$\text{Model: } \begin{cases} x_{n+1} = f(x_n, y_n) \\ y_{n+1} = g(x_n, y_n) \end{cases} \Rightarrow \text{S.S: } \begin{cases} \bar{x} = f(\bar{x}, \bar{y}) \\ \bar{y} = g(\bar{x}, \bar{y}) \end{cases}$$

∴ For $x_n = \bar{x} + x'_n$, $y_n = \bar{y} + y'_n$

$$\Rightarrow \begin{cases} x_{n+1} = a_{11} x'_n + a_{12} y'_n \\ y_{n+1} = a_{21} x'_n + a_{22} y'_n \end{cases} \Rightarrow \vec{x}'_{n+1} = A \vec{x}'_n$$

where:

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial x} |_{\bar{x}, \bar{y}} & \frac{\partial f}{\partial y} |_{\bar{x}, \bar{y}} \\ \frac{\partial g}{\partial x} |_{\bar{x}, \bar{y}} & \frac{\partial g}{\partial y} |_{\bar{x}, \bar{y}} \end{pmatrix}$$

$$\vec{x}'_n = \begin{pmatrix} x'_n \\ y'_n \end{pmatrix}$$

⇒ stability requires $|\lambda_{1,2}| < 1$

$$\Rightarrow |\beta| < 1 + \gamma < 2$$

$$\beta = \text{tr}(A) \quad \text{and} \quad \gamma = \det(A)$$

Chapter 3: Application of Non-linear difference equations

Other models for population growth

$$\textcircled{1} N_{t+1} = N_t \left[e^{r(1 - N_t/k)} \right] \rightarrow \text{density dependence}$$

$$\textcircled{2} N_{t+1} = RN_t (1 + aN_t)^{-b}$$

Holt-Rosenfield Model

- Use Nicholson-Bailey Equation

$$N_{t+1} = RN_t e^{-aP_t}$$

$$P_{t+1} = cN_t (1 - e^{-aP_t})$$

$$\Rightarrow \underline{S-S}: \bar{N} = \frac{R \ln(R)}{a c (R-1)}$$

$$\bar{P} = \frac{\ln(R)}{a}$$

- With density dependent growth

$$N_{t+1} = e^{-cP_t} e^{r(1 - N_t/k)} N_t$$

$$P_{t+1} = cN_t (1 - e^{-aP_t})$$

N_t } Stable non-trivial S.S.
for some parameter, and produce
sustained oscillation for others

- With refuges \Rightarrow spatial heterogeneity

$$N_{t+1} = R(N_{ref} + (N_t - N_{ref}) e^{-aP_t})$$

$$P_{t+1} = c(N_t - N_{ref}) (1 - e^{-cP_t})$$

• Plotting:

Phase plane: variable vs. variable

parameter plane: parameter vs. parameter

• Competitive Model

$$x_{t+1} = R_1 x_t \left(1 - \frac{x_t + y_t}{K} \right)$$

$$y_{t+1} = R_2 y_t \left(1 - \frac{x_t + y_t}{K} \right)$$

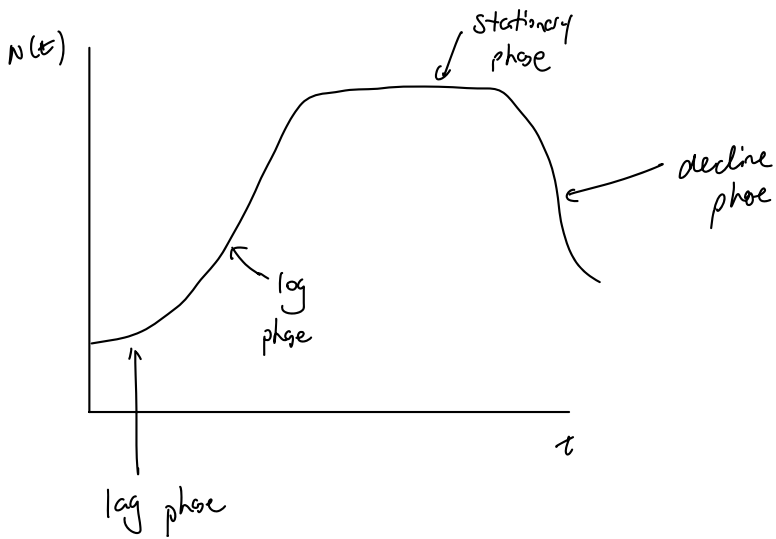
} Same carrying capacity for both

⇒ Result 4: The species with larger R wins

Chapter 4: Continuous Time (ODE) Models

⇒ If population generation overlaps, ODE models are good.

Microorganism Growth



$$N(t+\Delta t) = N(t) + kN(t)\Delta t$$

$$\frac{N(t+\Delta t) - N(t)}{\Delta t} = kN(t)$$

lim
 $\Delta t \rightarrow 0$:

$$\frac{dN(t)}{dt} = kN(t)$$

$$N(t) = N_0 e^{kt}$$

Dimension analysis

- reducing dimensionality of the parameter space via substitution

↳ if we can reduce to n parameters

↳ n degrees of freedom

- Break-down variables into dimensional & non-dimensional parts

ex: $N = N^* \hat{N}$, where

• N^* : dimensionless variable

• \hat{N} : dimension-bearing variable

- Combine constants and simplify equations

• ex: if $\frac{dc}{dt} = \frac{\alpha F}{V} C^*$, let $q = \frac{V}{F} \Rightarrow \frac{dc}{dt} = C^*$

Chemostat Model

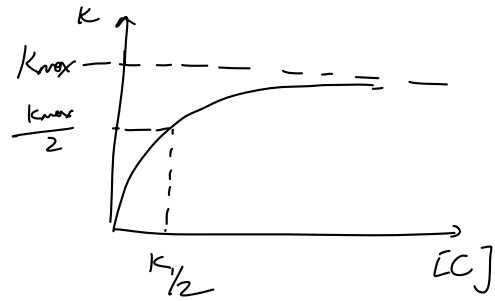
For nutrient and population:

$$\frac{dN}{dt} = \overbrace{K(c)N}^{\text{grow}} - \overbrace{F \frac{N}{V}}^{\text{flushed out}}$$

$$\frac{dc}{dt} = \underbrace{-\alpha K(c)N}_{\text{consumption}} - \underbrace{F \frac{c}{V}}_{\text{flush out}} + \underbrace{F \frac{C_0}{V}}_{\text{come in}}$$

where $K(C)$ can be described via a Michaelis-Menten Curve

$$K(C) = \frac{K_{max} C}{K_{1/2} + C}$$



After dimension analysis:

↳ 2 degrees of freedom

$$\frac{dN}{dt} = \alpha_1 \left(\frac{C}{1+C} \right) N - N, \quad \alpha_1 = \frac{V_{max}}{F}$$

$$\frac{dC}{dt} = - \left(\frac{C}{1+C} \right) N - C + \alpha_2, \quad \alpha_2 = \frac{C_0}{K_{1/2}}$$

↳ α_1 : emptying time (V/F) × max growth rate (K_{max})

α_2 : $[C_0] / K_{1/2} \Rightarrow$ larger means more nutrients needed for half maximal growth rate.

Steady State Analysis

$$\text{Requirement: } \begin{cases} \frac{dx}{dt} = 0 = F(\bar{x}, \bar{y}) \\ \frac{dy}{dt} = 0 = G(\bar{x}, \bar{y}) \end{cases}$$

≠ note different from

Stability :

$$N_{t+1} = N_t = \bar{N}$$

determined from the Jacobian:

$$J = \begin{bmatrix} \frac{\partial F}{\partial x} & \frac{\partial F}{\partial y} \\ \frac{\partial G}{\partial x} & \frac{\partial G}{\partial y} \end{bmatrix}$$

For a particular steady state, stable if:

$$\begin{aligned} \beta &= \text{Tr}(J|_{\bar{x}, \bar{y}}) < 0 \\ \gamma &= \det(J|_{\bar{x}, \bar{y}}) > 0 \end{aligned}$$

Approaching S.S

Compute $\beta^2 - 4\gamma$

↳ if $\beta^2 - 4\gamma > 0 \Rightarrow$ real eigenvalue, no oscillatory

if $\beta^2 - 4\gamma < 0 \Rightarrow$ imaginary eigenvalue, oscillatory

Chapter 5: phase plane & Qualitative solutions

Nullcline

For a system of first order DE:

$$\begin{cases} \dot{x} = F(x, y) \\ \dot{y} = G(x, y) \end{cases}$$

Phase portrait is the sketch of a family of solutions in the x-y space

↳ use nullclines to sketch them

↳ x-nullcline: set of points such that $\dot{x} = 0$

y-nullcline: set of points such that $\dot{y} = 0$

⇒ where x-nullcline & y-nullcline intersects

↳ $(\dot{x}=0, \dot{y}=0) \Rightarrow$ steady states

Flow through Nullclines

• for x-nullcline:

↳ determine values s.t. $\dot{y} > 0$ (down \rightarrow up) and $\dot{y} < 0$ (up \rightarrow down)

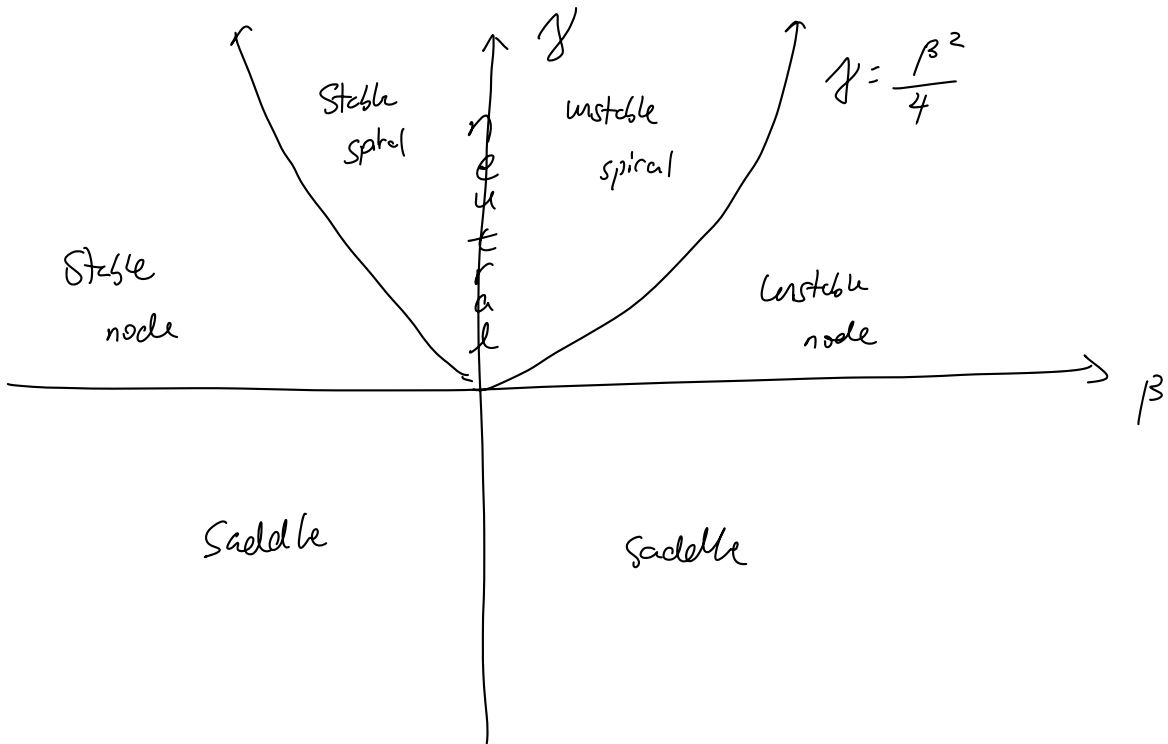
• for y-nullcline:

↳ determine values s.t. $\dot{x} > 0$ (left \rightarrow right) and $\dot{x} < 0$ (right \rightarrow left)

⇒ Flow only changes direction at steady-state (if $J \neq 0$ at that s.s.)

Stability Around S.S

Determine from $\beta = \text{tr}(J|_{\bar{x}, \bar{y}})$ and $\gamma = \det(J|_{\bar{x}, \bar{y}})$



	<u>Stable</u>	<u>Saddle/neutral</u>	<u>unstable</u>
<u>node</u>			
<u>Spiral</u>			

Limit sets

The set of points which are approached asymptotically along a solution curve

• $\lim_{t \rightarrow +\infty}$: ω -limit set \Rightarrow for stable spiral/node

• $\lim_{t \rightarrow -\infty}$: α -limit set \Rightarrow for unstable spiral/node

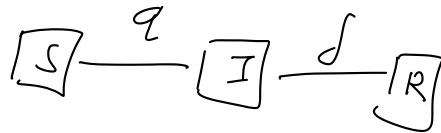
Chapter 6: Application in Population Biology

• Models for microparasite (Infection Model)

↳ Compartmental model

↳ SIR model

$$\begin{cases} \dot{S} = -\alpha IS \\ \dot{I} = \underbrace{\alpha IS}_{\text{force of infection}} - \beta I \\ \dot{R} = \beta I \\ N = S + I + R \end{cases}$$



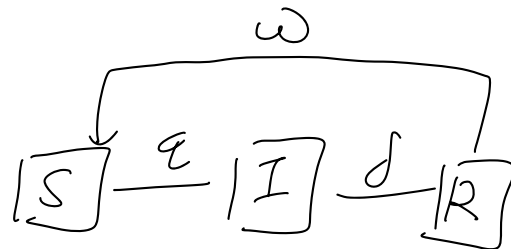
$$\Rightarrow \dot{N} = \dot{S} + \dot{I} + \dot{R} = 0$$

* Assumes mass-action mixing

* Duration of the infection: $1/\beta$

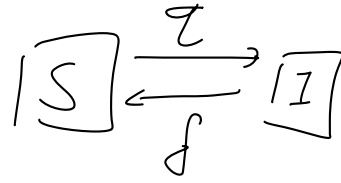
↳ SIRS Model

$$\begin{cases} \dot{S} = -\alpha IR + \omega R \\ \dot{I} = \alpha IS - \beta I \\ \dot{R} = \beta I - \omega R \end{cases}$$



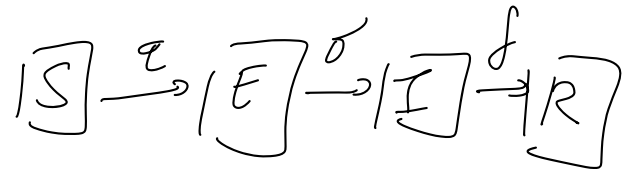
↳ SIS Model

$$\begin{cases} \dot{S} = -\alpha IS + \beta I \\ \dot{I} = \alpha IS - \beta I \end{cases}$$



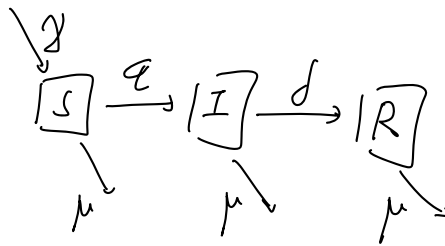
↳ SEIR Model

$$\begin{cases} \dot{S} = -\alpha IS \\ \dot{E} = \alpha IS - \sigma E \\ \dot{I} = \sigma E - \beta I \\ \dot{R} = \beta I \end{cases}$$



↳ SIR with demographic

$$\begin{cases} \dot{S} = -\alpha IS + \gamma N - \mu S \\ \dot{I} = \alpha IS - \beta I - \mu I \\ \dot{R} = \beta I - \mu R \end{cases}$$



$$\gamma N = S + I + R$$

⇒ If we set $N=1$ and $\gamma=\mu$:

$$\begin{cases} \dot{S} = \mu - \alpha IS - \mu S \\ \dot{I} = \alpha IS - \beta I - \mu I \end{cases}$$

Steady state

For non-trivial: $\boxed{\frac{\alpha}{\mu + \delta} > 1}$ \rightarrow Endemic conditions

$\hookrightarrow R_0 = \frac{\alpha}{\mu + \delta} \xrightarrow{\mu \ll \delta} \boxed{R_0 \approx \frac{\alpha}{\delta}} = \underbrace{\alpha}_{\substack{\# \text{ of} \\ \text{infections per} \\ \text{day per} \\ \text{individual}}} \cdot \underbrace{\frac{1}{\delta}}_{\substack{\text{duration of} \\ \text{infection}}}$

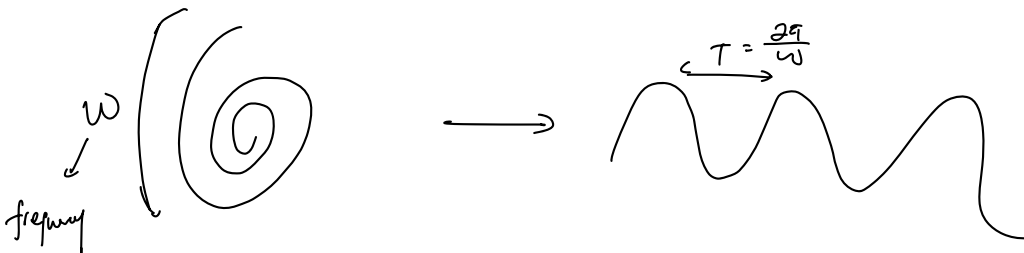
Demographic Stochasticity

Real population is discrete units \Rightarrow not continuous

\hookrightarrow discreteness is associated with randomness

\Rightarrow Demographic stochasticity is the randomness inherent in real populations due to noise in the demographic process

Period of Resurgence



Seasonality

Difference equation model:

$$\begin{cases} I_{t+1} = I_S S_t \mathcal{Q}_t \\ S_{t+1} = S_t + B_t - I_{t+1} \end{cases}$$

, $\mathcal{Q}_t(t)$ can be a periodic function that captures the period of high infectivity and period of low infectivity

Final Demographic Model

$$\begin{cases} \dot{S} = \mu N - \mu S - \mathcal{Q}(t) I S \\ \dot{I} = \mathcal{Q}(t) I S - \delta I - \mu I \\ \dot{R} = \delta I - \mu R \end{cases}$$

$\mathcal{Q}(t)$ captures 2 periods

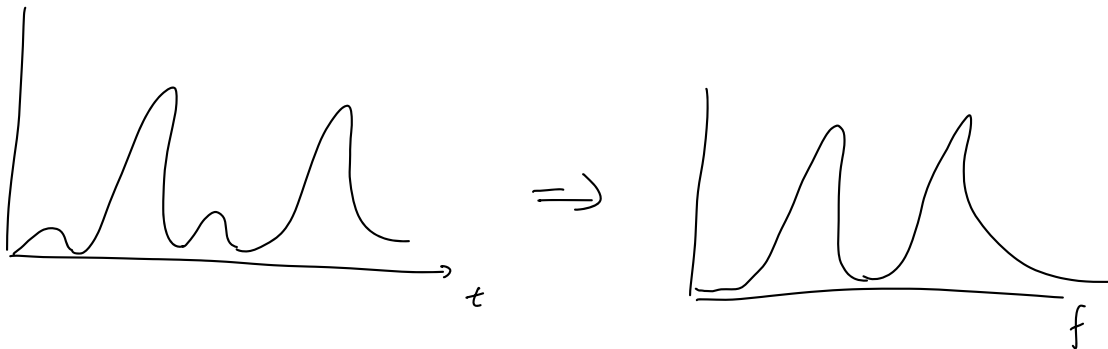
① demographic stochasticity (Real number T)

② Seasonality (integer T)

Power Spectra

Show a peak at a frequency if the time series has a strong contribution to the frequency

↳ Fourier Transform of the time series



Herd Immunity

- If a proportion (p) is big enough ($p = p_{crit} < 1$) $\Rightarrow R_0 < 1$

↳ via natural immunity or vaccination

- $R_0' = (1-p) R_0 < 1$

$$p > 1 - \frac{1}{R_0}$$

Mean Age of Infection

$$A \approx \frac{1}{\lambda}, \text{ where } \lambda = \alpha I = \text{force of infection}$$

↳ Vaccination $\downarrow I \Rightarrow \lambda \downarrow \Rightarrow A \uparrow$

Predator-Prey Model

$$\begin{cases} \dot{x} = ax - bxy \end{cases} \rightarrow \text{prey}$$

$$\begin{cases} \dot{y} = dxy - cy \end{cases} \rightarrow \text{predator}$$

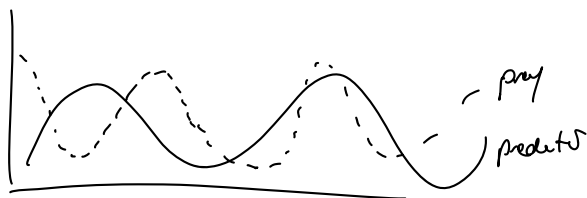
$$d = b \times \alpha$$

= encounter rate

\times yield per prey

(usually $|\alpha| < 1$)

Steady state: neutral centre



$$f = \sqrt{ca}$$

↳ $c \uparrow$ or $a \uparrow = \uparrow$ population turnover

• If there is fishing:

$$\begin{cases} \dot{x} = ax - bxy - \psi x \\ \dot{y} = -cy + dxy - \frac{\psi y}{\gamma} \end{cases} \Rightarrow \text{same dynamic, different equilibrium}$$

↳ As $\psi \rightarrow 0$, $\bar{x} \downarrow$, $\bar{y} \uparrow$

• Density dependence

$$\begin{cases} \dot{x} = ax \left(1 - \frac{x}{K}\right) - bxy \\ \dot{y} = -cy + dxy \end{cases}$$

→ carrying capacity

↳ Now, no neutral centre \Rightarrow stable S.S.

↳ This model is not robust

↳ with fishing \Rightarrow when $\psi \rightarrow 0$, $\bar{x} \downarrow$ & $\bar{y} \uparrow$

Competition Model

$$\dot{N}_1 = \underbrace{r_1 N_1 \left(1 - \frac{N_1}{K_1}\right)}_{\text{logistic growth}} - \underbrace{a_{12} N_1 N_2}_{\text{Competition}}$$

$$\dot{N}_2 = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right) - a_{21} N_1 N_2$$

} Capture competition
phenomenologically

Stability:

depends on $\frac{r_2}{a_{21}} > K_1$ & $\frac{r_1}{a_{12}} > K_2$

→ growth rate
→ carrying capacity
→ competitiveness

$$\underline{\text{If } r_2 = r_1 = K_2 = K_1 = 1}$$

I: Species 2 is an aggressive competitor ($a_{12} > 1$ and $a_{21} < 1$)

↳ species 2 wins (stable node)

II: Species 1 is an aggressive competitor ($a_{12} < 1$ and $a_{21} > 1$)

↳ species 1 wins (stable node)

III: Both species are competitive ($a_{12} > 1$ & $a_{21} > 1$)

↳ the most abundant species wins (stable node)

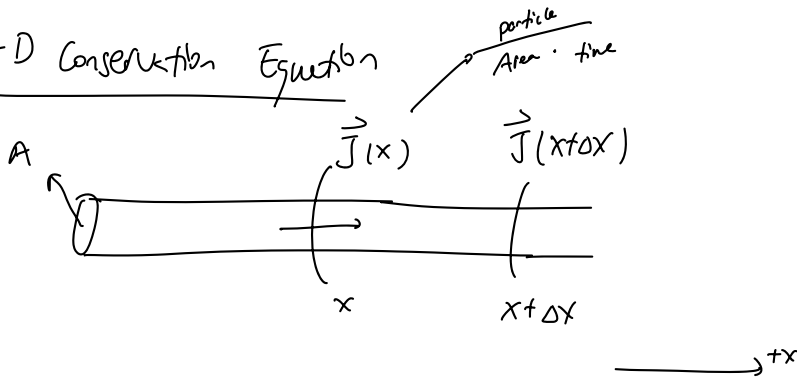
IV: Both species are not competitive ($a_{12} < 1$ & $a_{21} < 1$)

↳ Both coexist \Rightarrow neutral centre.

\Rightarrow Principle of competitive exclusion holds as long as one or both species are strongly competitive.

Chapter 7: PDE Models in Biology

1-D Conservation Equation



def:

$C(x, t)$: particle density (scalar function)

$J(x, t)$: particle flux (vector function)

$\sigma(x, t)$: rate of creation (scalar function)

$$\Rightarrow \frac{\partial}{\partial t} C(x, t) = \frac{J(x, t) - J(x + \Delta x, t)}{\Delta x} \pm \sigma(x, t)$$

$$\lim_{\Delta x \rightarrow 0} : \frac{\partial}{\partial t} C(x, t) = -\frac{\partial}{\partial x} J(x, t) \pm \sigma(x, t) \quad \text{1D balance/conservation Equation}$$

More generally:

$$\frac{\partial}{\partial t} C(x, t) = -\nabla \cdot \vec{J} \pm \sigma = -\left(\frac{\partial J_x}{\partial x} + \frac{\partial J_y}{\partial y} + \dots\right) + \sigma$$

divergence of J

If $\vec{v}(\vec{x}, t)$ is the velocity field & $C(\vec{x})$ is the concentration

$$\vec{J} = C \vec{v}$$

$$\Rightarrow \frac{\partial C}{\partial t} = -\nabla \cdot (C \vec{v}) \pm \sigma$$

If $\psi(\vec{x}, t)$ is a scalar field that attracts / repels particle, then the direction of motion is

$$\vec{J} = C \vec{v} = C (\alpha \nabla \psi)$$

gradient of $\psi = \begin{bmatrix} \frac{\partial \psi}{\partial x} \\ \frac{\partial \psi}{\partial y} \\ \frac{\partial \psi}{\partial z} \end{bmatrix}$

$$\Rightarrow \frac{\partial C}{\partial t} = -\alpha \nabla \cdot (C \nabla \psi) \pm \sigma$$

Diffusion

Fick's Law:

$$\vec{J} = -D \underbrace{\nabla C}_{\text{Concentration gradient}}$$

↓
moving down the gradient.

$$\therefore \frac{\partial C}{\partial t} = -\nabla \cdot \vec{J}$$

$$\frac{\partial C}{\partial t} = -\nabla \cdot (-D \nabla C)$$

$$\boxed{\frac{\partial C}{\partial t} = -D \nabla^2 C} = -D \frac{\partial^2 C}{\partial x^2} \text{ in 1D}$$

$$\Rightarrow \text{Average diffusion distance } \boxed{d \approx \sqrt{Dt}} \quad \text{and } t \propto \frac{d^2}{D}$$

↳ reason why cells cannot get too big via simple diffusion

⇒ The size of the cell:

$$\frac{\text{rate of supply via diffusion}}{\text{rate of metabolism}} \geq 1$$

$$\frac{J_S}{V/Q} = \frac{-D \frac{C_0}{r} 4\pi r^2}{\frac{4}{3} \pi r^3 \frac{Q}{V}} = 3DC_0 \frac{a}{r^2} \geq 1$$

$$\therefore r \leq \sqrt{3DC_0 \frac{a}{r^2}}$$

Population Diffusion - Based Model

Let $P(x,t)$ be the population size at (x,t)

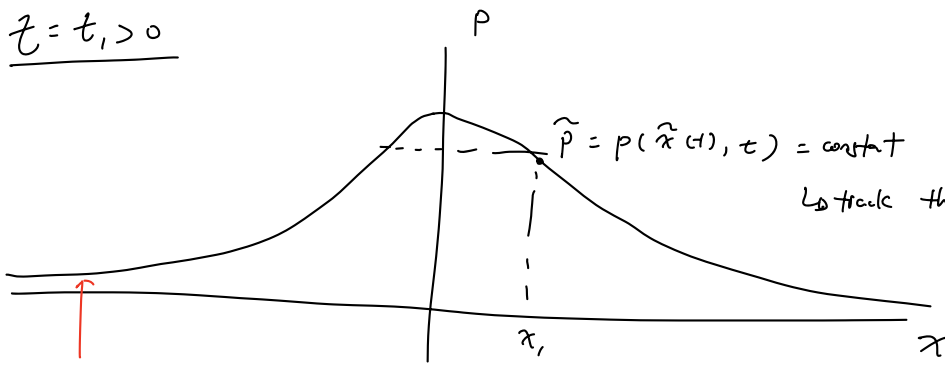
$$\frac{\partial P}{\partial t} = D \underbrace{\frac{\partial^2 P}{\partial x^2}}_{\text{dispersal across space}} + \underbrace{\alpha P}_{\text{exponential growth}}$$

(Compare with $\frac{\partial c(x,t)}{\partial t} = -D \nabla^2 c + \sigma$)

With an initial condition $\tilde{P} = P(0,0)$, the solution is:

$$P(x,t) = \frac{\tilde{P}}{2\sqrt{\alpha D t}} e^{\alpha t - \frac{x^2}{4Dt}}$$

$t = t, > 0$



atto-fires

↳ solution exhibits infinite propagation (nonzero everywhere for $t > 0$)

↳ track this point to study the rate of propagation

↳ here: $\tilde{x}_0 = 2\sqrt{\alpha D} t$

rate of prop = $\frac{\tilde{x}}{t} = 2\sqrt{\alpha D}$

In 2D: (area)^{1/2} = $2\sqrt{\alpha D} t$

↳ area = eq. population constant

Random Motion of microorganisms

$$\frac{\partial}{\partial t} b(x,t) = \mu \frac{\partial^2}{\partial x^2} b(x,t) + r b(x,t)$$

↓ population
↓ dispersal constant
↓ reproduction

If we let nutrient density to determine growth:

Lawfrenberger Model

$$\begin{cases} \frac{\partial}{\partial t} b(x,t) = \mu \frac{\partial^2 b}{\partial x^2} + [f(s) - K_e] b & \rightarrow \text{bacteria diffusion} \\ \frac{\partial}{\partial t} s(x,t) = D \frac{\partial^2 s}{\partial x^2} - \frac{1}{Y} f(s) b & \rightarrow \text{nutrient diffusion} \end{cases}$$

↓ substrate-dependent growth
↗ bacteria death rate

↓ yield output
 (mass of bacteria grown per mass of nutrient consumed)

Now we might want to move towards a source \rightarrow chemotaxis

1D:

$$J_{\text{chem}} = \chi b(x,t) \nabla c = \chi b(x,t) \frac{\partial}{\partial x} c$$

↓ chemotactic flux of bacteria
↓ chemotactic constant
↓ chemical concentration gradient

Also:

$$J_{\text{random}} = -\mu \frac{\partial}{\partial x} b(x,t)$$

↓ random diffusion of bacteria
↓ dispersal constant

Hence:

$$\frac{\partial}{\partial t} b(x,t) = -\frac{\partial}{\partial x} J = -\frac{\partial}{\partial x} (J_{\text{chem}} + J_{\text{random}})$$

$$\Rightarrow \frac{\partial}{\partial t} b(x,t) = -\chi \frac{\partial}{\partial x} (b \frac{\partial}{\partial x} c) + \mu \frac{\partial^2}{\partial x^2} b$$

Density-Dependent Dispersal

Let $D = D(p)$ s.t.

$$\frac{\partial p}{\partial t} = \underbrace{\nabla(D(p) \nabla p)}_{\text{flux}} + \underbrace{\alpha p}_{\text{growth}}$$

Let $D(p) = k p^m \rightarrow$ as $p \uparrow$, $D \uparrow$

$$\therefore \boxed{\frac{\partial}{\partial t} p(x,t) = k \nabla(p^m \nabla p) + \alpha p}$$

Pros:

- no attrition \Rightarrow occupy a finite region
- If $\alpha < 0$ (ie: mortality dominates)

\hookrightarrow region will not expand past certain boundary.

Applied to two populations:

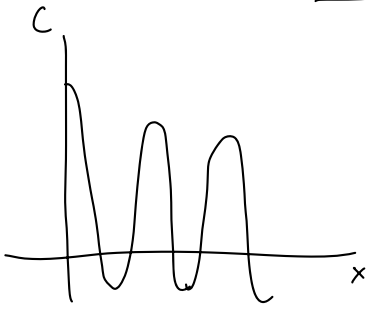
$$\frac{\partial}{\partial t} u \quad \downarrow \quad \text{population 1 density}$$
$$= -\nabla \cdot J_1 = -\nabla \cdot (u \vec{q}) \quad \downarrow \quad \begin{array}{l} \text{movement speed} \\ \text{of } u \end{array}$$
$$= k_1 \nabla \cdot (u \nabla (u+v)) \quad \nearrow \quad \text{population 2 density}$$
$$\vec{q} = -k_1 \nabla (u+v)$$

$$\therefore \left\{ \begin{array}{l} \frac{\partial}{\partial t} u = k_1 \frac{\partial}{\partial x} \left(u \frac{\partial}{\partial x} (u+v) \right) \\ \frac{\partial}{\partial t} v = k_2 \frac{\partial}{\partial x} \left(v \frac{\partial}{\partial x} (u+v) \right) \end{array} \right.$$

Result: If initial populations occupy distinct regions, they will remain distinct.

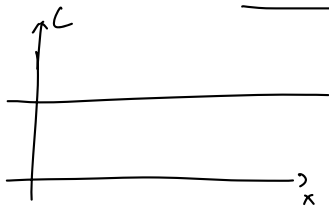
Steady State of PDEs

The non-homogeneous steady state satisfies:



$$\boxed{\frac{\partial}{\partial t} C = 0} \rightarrow \text{S.S. w.r.t. time}$$

The homogeneous steady-state satisfies:



$$\boxed{\frac{\partial}{\partial t} C = \frac{\partial}{\partial x} C = 0} \rightarrow \text{uniform in space \& time}$$

Example: Chemotaxis of bacteria ($-\frac{\partial}{\partial t} b = -\frac{\partial}{\partial x} J$)

$$\Rightarrow 0 = -\frac{\partial}{\partial x} J \quad \text{for non-homogeneous S.S.}$$

$$\int 0 = \int \frac{\partial}{\partial x} J$$

$$\boxed{\text{constant} = J}$$

Boundary condition



for $x=0$ & $x=L \Rightarrow J=0$ at $x=0$

$$\therefore \frac{\partial}{\partial x} J = 0$$

$$-\chi b \frac{\partial}{\partial x} C + \mu \frac{\partial}{\partial x} b = 0$$

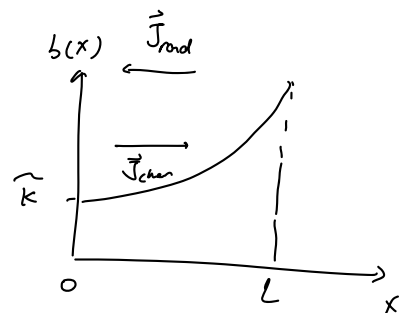
$$\mu \frac{\partial}{\partial x} b = \chi b \frac{\partial}{\partial x} C$$

$$\int \frac{\mu}{b} \frac{\partial}{\partial x} b = \int \chi \frac{\partial}{\partial x} C$$

$$\mu \ln(b) = \chi C(x) + K$$

$$\boxed{b(x) = \hat{k} \exp\left(\frac{\chi C(x)}{\mu}\right)}$$

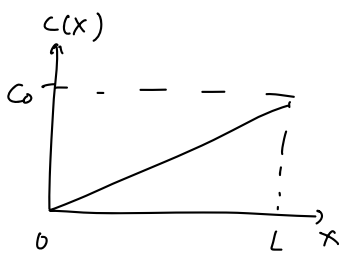
where $\hat{k} = \exp(K)$



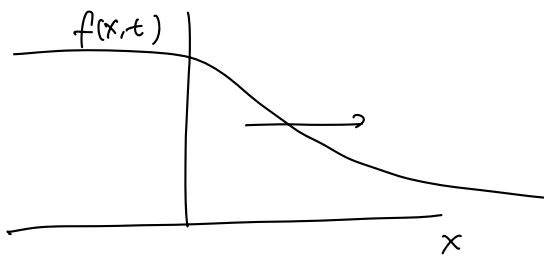
At S.S.: $\vec{J}_{chem} = -\vec{J}_{rad}$

For $C(x) \rightarrow \frac{\partial}{\partial t} C = D \frac{\partial^2}{\partial x^2} C$ and $C(0) = 0$, $C(L) = C_0$

$\Rightarrow C(x) = C_0 \frac{x}{L}$



Travelling Wave Solutions



- Stationary frame: $f(x,t) \rightarrow$ travelling wave profile
- moving frame: $F(z)$

$\hookrightarrow f(x,t) = F(z)$ if $z = x - vt$

$\underbrace{\hspace{2cm}}_{2 \text{ variables}}$
 $\underbrace{\hspace{2cm}}_{1 \text{ variable}}$

$\rightarrow \frac{\partial}{\partial x} \& \frac{\partial}{\partial t}$
 $\rightarrow \frac{d}{dz} \Rightarrow$ ODE!

By chain rule:

$$\begin{cases} \frac{\partial f}{\partial x} = \frac{\partial F}{\partial z} \\ \frac{\partial f}{\partial t} = -v \frac{\partial F}{\partial z} \end{cases}$$

\rightarrow substitute $F(z)$ for $f(x,t)$ & the corresponding derivatives to find the solution for PDEs

Fisher's Equation

Let $p(x,t)$ be the frequency of allele A (dominant)

Let $q(x,t) = 1 - p(x,t)$ be the frequency of allele a

$$\frac{\partial}{\partial t} p(x,t) = D \frac{\partial^2}{\partial x^2} p(x,t) + \alpha p(x,t)(1 - p(x,t))$$

Let $p(x,t) = P(z)$

$$\Rightarrow -v \frac{\partial}{\partial z} P(z) = D \frac{\partial^2}{\partial z^2} P(z) + \alpha P(z)(1 - P(z))$$

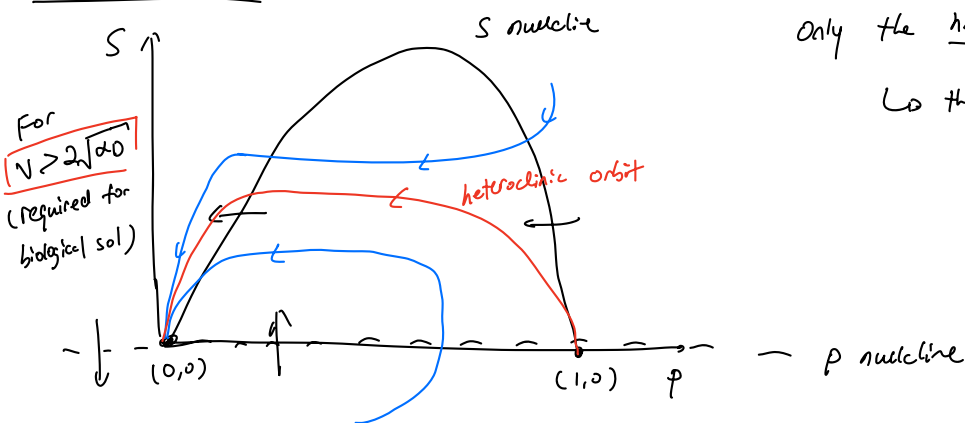
\hookrightarrow 2nd order ODE

$$\text{Let } S = \frac{\partial}{\partial z} P(z)$$

$$\Rightarrow \begin{cases} S = \frac{\partial}{\partial z} P(z) \\ VS = -D \frac{\partial}{\partial z} S(z) + \alpha P(z)(1-P(z)) \end{cases}$$

$$\Rightarrow \begin{cases} \frac{d}{dz} P(z) = -S \\ \frac{d}{dz} S(z) = \frac{\alpha}{D} P(1-P) - \frac{V}{D} S \end{cases} \Rightarrow \text{perform phase plane analysis}$$

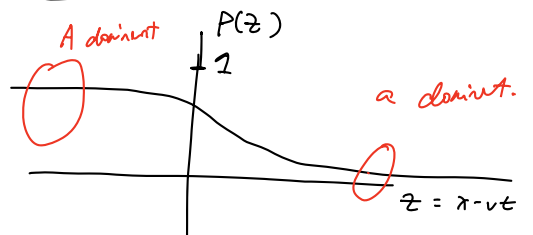
Phase portrait



only the heteroclinic orbit is a possible solution

↳ the other results in $P < 0$ or $P \rightarrow \infty$

↳ note: $0 \leq P \leq 1$



• as $z \rightarrow \infty$: $P(z) = 0$

↳ when $t \rightarrow -\infty$, A diminishes

as $z \rightarrow -\infty$: $P(z) = 1$

↳ when $t \rightarrow \infty$, A dominates

Spread of Microorganism

$$\begin{cases} \frac{\partial}{\partial t} n = D_n \frac{\partial^2}{\partial x^2} n + k n (g - g_0) \\ \frac{\partial}{\partial t} g = D \frac{\partial^2}{\partial x^2} g - c k n (g - g_0) \end{cases}$$

\swarrow min glucose required for growth.
 \uparrow yield.

Let $\hat{g} = g - g_0$ & $D_n \approx 0$ as glucose diffuses much faster

$$\begin{cases} \frac{\partial}{\partial t} n = k n \hat{g} \\ \frac{\partial}{\partial t} g = D \frac{\partial^2 \hat{g}}{\partial x^2} - c k n \hat{g} \end{cases}$$

Let $N(z) = n(x, t)$
 $G(z) = \hat{g}(x, t)$
 $z = x - vt$

$$\Rightarrow \begin{cases} -v \frac{dN}{dz} = k N G & \text{①} \\ -v \frac{dG}{dz} = D \frac{d^2 G}{dz^2} - c k N G & \text{②} \end{cases}$$

① × c + ②

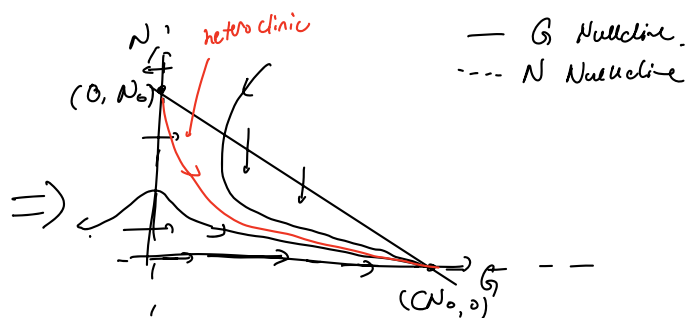
$$\int -v c \frac{dN}{dz} - v \frac{dG}{dz} = \int D \frac{d^2 G}{dz^2}$$

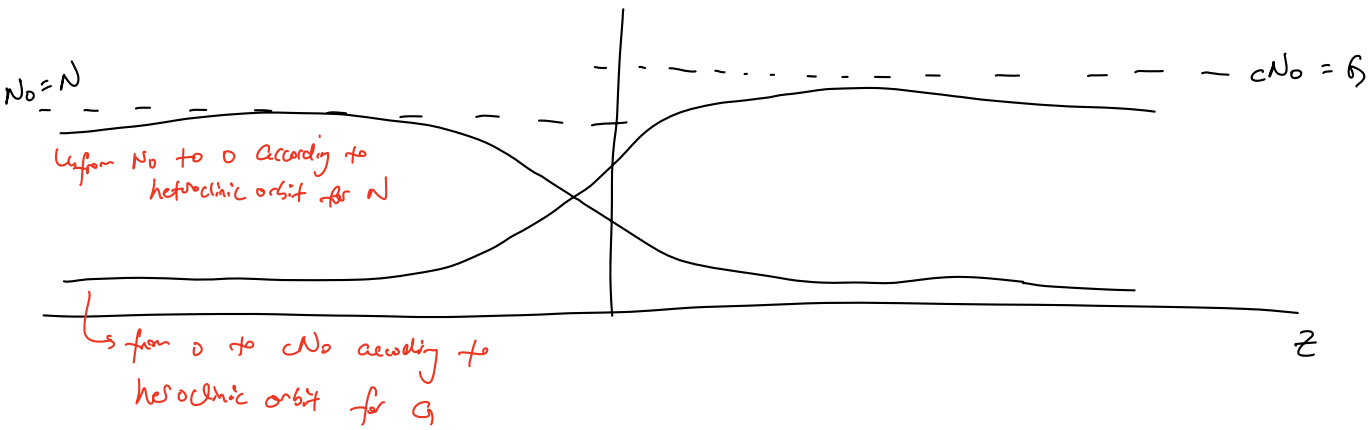
$$\Rightarrow c_0 - v c N - v G = D \frac{dG}{dz}$$

For c_0 : let $z \rightarrow -\infty$ ($t \rightarrow \infty$)

$$\hookrightarrow G = 0 \quad \& \quad \left. \frac{dG}{dz} \right|_{z=-\infty} = 0$$

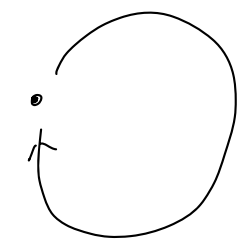
$$\Rightarrow \begin{cases} \frac{dG}{dz} = -\frac{v}{D} G - \frac{N c v}{D} + \frac{v c_0}{D} \\ \frac{dN}{dz} = -\frac{k N G}{v} \end{cases}$$



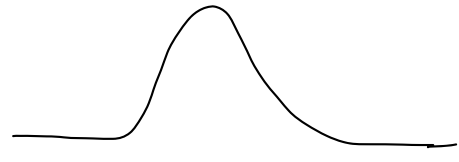
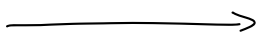


Other types of waves in PDE

①

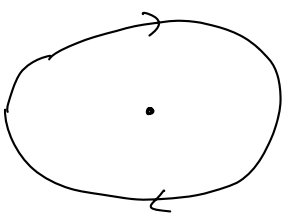


homoclinic



wave profile

②



limit cycle

