Mathematical Biology

Mathematical modelling is the art of turning stories into simple equations.

§1 Population Dynamics (and other stories)

We will describe systems that can be modelled by first order ODEs.

1.1 Birth and Death

Describe a population size by $N(t) \in \mathbb{R}$. Take time $t \in \mathbb{R}$.

let $b =$ no. of offspring $\underbrace{\text{per individual}}_{\text{per capita}}$ $\underbrace{\text{per unit time}}_{\text{rate}}$,

$d =$ death rate per capita.

Then

$$N(t+\Delta t) = N(t) + (b-d)N(t)\,\Delta t.$$

Taylor expand LHS, take $\Delta t \to 0$ to get

$$\frac{dN}{dt} = (b-d)N,$$

b, d const. $\Rightarrow$ $N(t) = N_0 e^{rt}$, $r = b-d$.

- $r > 0 \Rightarrow$ exponential growth (Malthus 1798)
- $r < 0 \Rightarrow$ exponential decay.

Exercise For $r<0$. what is half-life of population?

Exercise A new disease has 1500 cases this week and 1000 last week. When did first case appear?

The logistic equation

More generally, we could have

$$\frac{dN}{dt} = [\underset{\uparrow}{b(N)} - \underset{\uparrow}{d(N)}]\, N.$$

b, d depend on N.

The logistic equation (Velhurst 1838) is

$$\frac{dN}{dt} = rN - \lambda N^2 \longleftarrow$$

growth rate gets smaller as population grows due to lack of resources

$$= r\left(1 - \frac{N}{k}\right) N,$$

with $k = r/\lambda$ the carrying capacity.

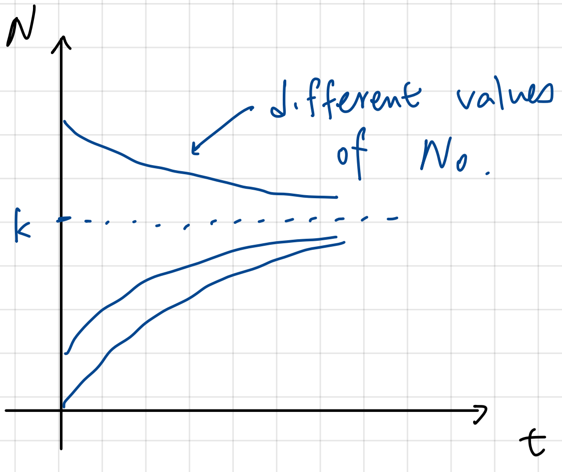
Typically, $r, \lambda > 0$. Solve

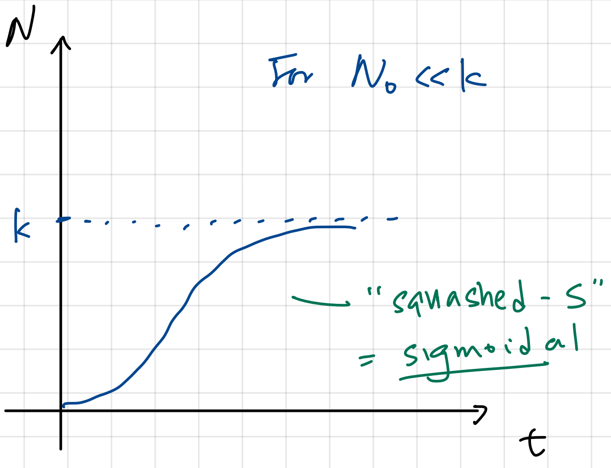
$$\int dN \, \frac{k}{(k-N)N} = \int dN \left(\frac{1}{N} - \frac{1}{k-N}\right) = \log\left|\frac{N}{k-N}\right| + \log\left|\frac{N_0}{k-N_0}\right| = rt.$$

Rearrange,

$$N = \frac{N_0 k e^{rt}}{k + N_0(e^{rt} - 1)}$$

This is the logistic function. Characteristic time is $1/r$.





The shape arises whenever there is a natural ceiling, e.g. fraction of a population adapting in some way.

For $N<k$, can write (for some t_0)

$$N = \frac{1}{2}k\left(1+\tanh\left(\frac{r}{2}(t-t_0)\right)\right)$$

For $N>k$,

$$N = \frac{1}{2}k\left(1+\coth\left(\frac{r}{2}(t-t_0)\right)\right)$$

Spread of beneficial mutation

let $p(t)$ = fraction of population that carries a beneficial mutation.

$$N_{\text{mutant}}(t) = p(t)\,N(t)$$
$$N_{\text{normal}}(t) = (1-p(t))\,N(t).$$

Suppose N_{normal} grows at rate r and N_{mutant} at rate $r+s$, $s>0$,

$$N_{\text{mutant}}(t+\delta t) = (1+(r+s)\delta t)\,pN$$
$$N_{\text{normal}}(t+\delta t) = (1+r\,\delta t)(1-p)N.$$

$$\Rightarrow \quad N(t+\delta t) = (1+r\delta t+sp\,\delta t)\,N(t)$$

Fraction of mutant at $t+\delta t$

$$\begin{aligned}
p(t+\delta t) &= \frac{N_{\text{mutant}}(t+\delta t)}{N(t+\delta t)}\\
&= \frac{1+(r+s)\delta t}{1+r\delta t+sp(t)\delta t}\,p(t) \qquad \Big)\ \text{Taylor}.\\
&= (1+(r+s)\delta t)(1-r\delta t-sp(t)\delta t)\,p(t)\\
&= (1+s(1-p(t))\delta t)\,p(t) + O(\delta t^2)
\end{aligned}$$

So $$\frac{dp}{dt} = \lim_{\delta t\to 0}\frac{p(t+\delta t)-p(t)}{\delta t} = sp(t)(1-p(t)).$$

This is the logistic equation.

Nondimensionalisation.

We will often declutter our eqns by working in rescaled, dimensionless variables.

e.g. $X = N/k$ and $\tau = rt$, then the logistic eqn becomes

$$\frac{dx}{d\tau} = x(1-x).$$

and sol^n is $$x = \frac{x_0 e^{\tau}}{1+x_0(e^{\tau}-1)}$$

Fixed points

Consider a 1D eqn of the form $\dot{x} = f(x)$. The FP $x = x_*$. are const. sol^{n}s, i.e.

$$f(x_*) = 0.$$

To understand stability, we perturb:

$$x(t) = x_* + \quad (t)$$

small

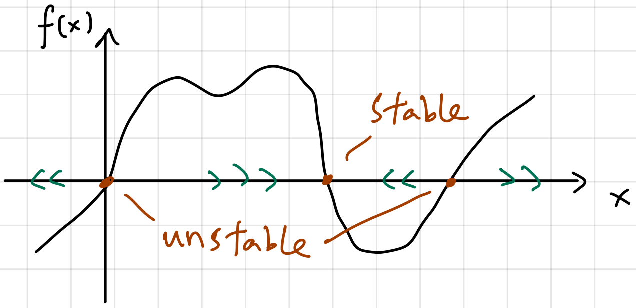
Taylor expand:

$$\frac{d\varepsilon}{dt} = f(x_* + \varepsilon) \approx f'(x_*)\,\varepsilon + \ldots$$

$$\Rightarrow \varepsilon(t) = \varepsilon_0 \, e^{f'(x_*)\,t}$$

So FP stable if $f'(x_*) < 0$, unstable if $f'(x_*) > 0$.

Graphically,



Exercise Check stability of FP for logistic eqn.

1.2 Delay Models

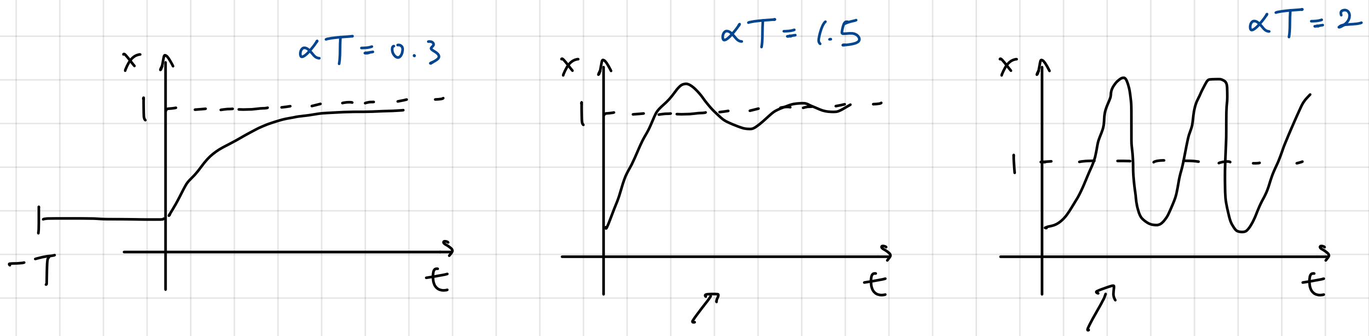
The <u>Hutchinson-Wright</u> model is a delayed logistic equation.

$$\frac{dx(t)}{dt} = \alpha x(t)\left[1 - x(t-\underset{\nwarrow \text{delay.}}{T})\right].$$

These kind of eqns are hard to solve.

<u>Note</u>: Need I.C. $x(t)$ for $-T \leq t \leq 0$ to get a sol^n $\forall t > 0$.

<u>Numerical sol^{n}s</u>



Population $x(t)$ exceeds $x=1$ ceiling since $x(t-T) < 1$.

We can linearise about $x = 1$ FP.

$$x(t) = 1 + \varepsilon(t), \qquad \varepsilon \ll 1$$

$$\Rightarrow \frac{d\varepsilon}{dt} =^{?} \pm \alpha\, \varepsilon(t-T) + \mathcal{O}(\varepsilon^2).$$

We solve with ansatz $\varepsilon(t) = e^{st}$ with $s \in \mathbb{C}$.

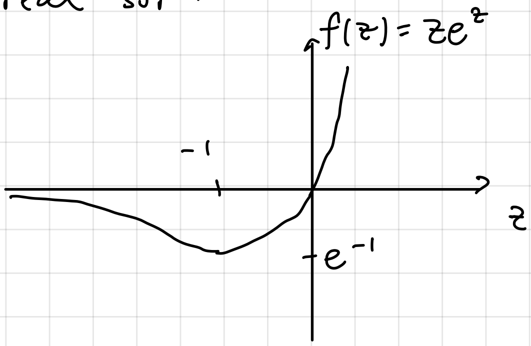
- $\text{Re}(s) < 0 \Rightarrow$ converge to $x=1$
- $\text{Re}(s) > 0 \Rightarrow$ move away from $x = 1$
- $\text{Im}(s) \neq 0 \Rightarrow$ oscillate.

Substitute.

$$se^{sT} = -\alpha,$$

$$\Rightarrow ze^{z} = -\alpha T, \qquad z = sT.$$

First look for real sol^n.



- Only sol^n if $\alpha T \leq \frac{1}{e} \approx 0.37$. These are stable as $z<0$.
- For $\alpha T \ll 1$, $ze^z \approx z$, and sol^n is $s = -\alpha$, which is behaviour of original logistic eqn.

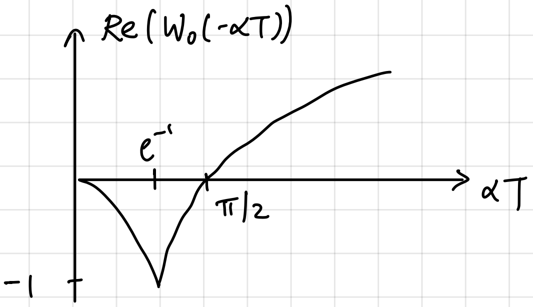
For $\alpha T > e^{-1}$, there are only complex sol^n to $ze^z = -\alpha T$.

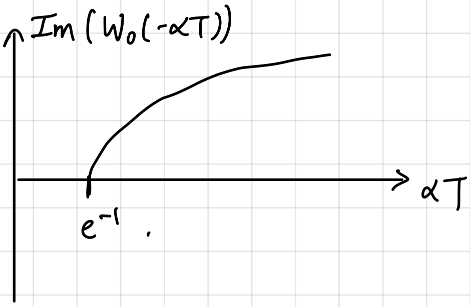
These are Lambert W f^{n}s.

$$z = W_k(-\alpha T).$$

$\nwarrow$ $k \in \mathbb{Z}$. reflects the branch of $\log z$.

The $z \in \mathbb{R}$ sol^n are part of $W_0(-\alpha T)$ which looks like.





Claim $Re(W_0(-\alpha T)) < 0$ when $\alpha T < \pi/2$.

Pf: First note $z = i\pi/2 \Rightarrow ze^z = -\pi/2$.

Next, write $z = \sigma + i\omega$, then $z = -\alpha T e^{-z}$

$$\Rightarrow \sigma + i\omega = -\alpha T e^{-\sigma}(\cos\omega - i\sin\omega)$$

$$\Rightarrow \sigma = -\alpha T e^{-\sigma}\cos\omega, \quad \omega = \alpha T e^{-\sigma}\sin\omega$$

- $|\omega| > \alpha T$, then $\sigma < 0$
- $|\omega| < \alpha T < \pi/2$, then $\cos\omega > 0 \Rightarrow \sigma < 0$. $\square$

Note For $\alpha T = \frac{\pi}{2}$ + little bit, $Im(z) \approx \frac{\pi}{2} \Rightarrow$ oscillates as $e^{i\pi t/2T}$, period $2T/\pi$.

Note The are other values of z s.t. $\mathrm{Re}(z)=0$,

$$z = (2k+1)\frac{\pi i}{2} \Rightarrow ze^{z} = -(2k+1)\frac{\pi}{2}$$

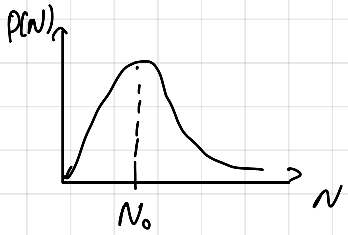
This is where $\mathrm{Re}[W_k(-z)]=0$; and this branch goes from stable to unstable. In general, sol^n is

$$x(t) = \sum_{k\in\mathbb{Z}} A_k e^{z_k t/T},$$

where $z_k = W_k(-\alpha T)$ and A_k determined by ICs. If $A_0 = 0$, then $x=1$ fixed pt. is unstable only for $\alpha T > \frac{5\pi}{2}$.
If $A_0 = A_1 = 0$, instability kicks in at $\alpha T = 9\pi/2$, and so on.

Blowflies

$N(t)$ = population of blowflies



Total egg production is $P(N) = P_0 N e^{-N/N_0}$.

The population is described by

$$\frac{dN(t)}{dt} = P(t-\underset{\text{delay for eggs to hatch}}{T}) - \overset{\text{const. death rate.}}{\mu} N(t)$$

Rescale $x = N/N_0$, $\tau = \mu t$, $a = \mu T$, $b = P_0 T$.

$$\frac{dx}{dt} = \frac{b}{a}\, x(\tau-a)\, e^{-x(\tau-a)} - x(\tau)$$

The eqm points $x = x_*$ obeys

$$\frac{b}{a} x_* e^{-x_*} = x_* \Rightarrow x_* = \log(b/a).$$

Assume $b>a$, so $x_*>0$. For stability, look at

$$x(\tau) = x_* + \varepsilon(\tau)$$

$$\Rightarrow \quad \frac{d\varepsilon(\tau)}{d\tau} = \frac{b}{a}\left(x_* + \varepsilon(\tau-a)\right) e^{-x_*} e^{-\varepsilon(\tau-a)} - x_* - \varepsilon(\tau)$$

$$= \left(x_* + \varepsilon(\tau-a)\right)\left(1 - \varepsilon(\tau-a) + \dots\right) - x_* - \varepsilon(\tau) + O(\varepsilon^2)$$

$$= (1-x_*)\,\varepsilon(\tau-a) - \varepsilon(\tau) + O(\varepsilon^2)$$

Anstaz $\varepsilon(\tau) = e^{s\tau}$ $\Rightarrow$ $s = (1-x_*)\,e^{-sa} - 1$

<u>Claim</u>: $x_* = \log(b/a)$ is stable if $b/a < e^2$.

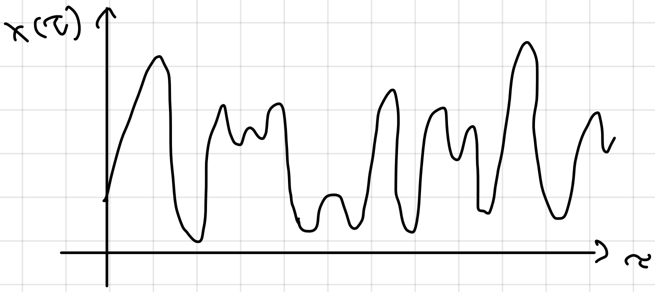
Pf: Write $s = \sigma + i\omega$, then

$$\sigma = (1-x_*)\,e^{-\sigma a}\cos(\omega a) - 1$$

$$\omega = -(1-x_*)\,e^{-\sigma a}\sin(\omega a)$$

If $b/a < e^2$, then $|1-x_*| < 1$. If $\sigma > 0$, then $(1-x_*)\,e^{-\sigma a}\cos(\omega a) < 1 \Rightarrow \sigma < 0$ $\#$. So must have $\sigma < 0$. □

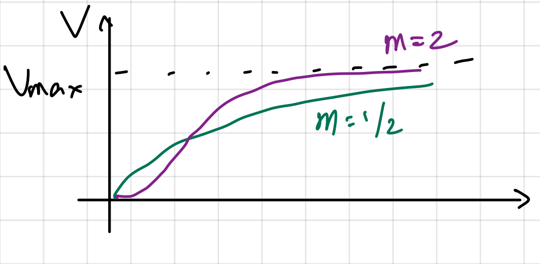
Numerical simulations show wild oscillations for $b \gg a$



Breathing

The volume of breath, V, depends on the concentration c of CO_2 in blood. Can model as a <u>Hill f^n</u>.

$$V(c) = V_{max}\frac{c^m}{A^m + c^m}.$$



for some constant A, m.

We model CO_2 in blood by

$$\frac{dc(t)}{dt} = \underset{\text{const. absorption}}{p} - \overset{\text{const.}}{b}\,\underbrace{c(t)\ V(t)}_{\text{amount expanded} \sim c \times V}$$

but feedback means $V(t)$ depends on $c(t-T)$

$$\frac{dc(t)}{dt} = p - bc(t)\ V(c(t-T))$$

$$= p - b V_{max}\ c(t)\ \frac{c(t-T)}{A^m + c(t-T)^m}$$

Rescale $c' = c/A$, $t' = \frac{pt}{A}$ and $\beta = \frac{AbV_{max}}{p}$, $T' = \frac{pT}{A}$

and relabel $c' \to c$, $t' \to t$, $T' \to t$,

$$\Rightarrow \quad \frac{dc(t)}{dt} = 1 - \beta c(t)\ \frac{c(t-T)^m}{1 + c(t-T)^m}$$

FP $c = C_*$ obeys $\frac{C_*^{m+1}}{1+C_*} = \frac{1}{\beta}$

<u>Question</u> : Is this stable (good) or unstable (very bad) ?

look at $c(t) = c_* + \varepsilon(t)$, then

$$\frac{d\varepsilon(t)}{dt} = -p\,\varepsilon(t) - q\,\varepsilon(t-T)$$

with $p = 1/c_*$, $q = m/c_*(1+c_*)$

Work with $\varepsilon(t) = e^{st}$, then $s = -p - q e^{-sT}$.

Write $s = \sigma + i\omega$, then

$$\sigma = -p - q e^{-\sigma T} \cos(\omega T)$$

$$\omega = q e^{-\sigma T} \sin(\omega T).$$

- when $T = 0$, $\sigma = -(p+q) < 0$. so stable.
- $\omega = 0$ is always a sol^n. but a second sol^n when $qe^{-\sigma t} > 1$.

- Stable when $p > q$. This follows from

$$(\sigma + p)^2 + \omega^2 = q^2 e^{-2\sigma T}$$

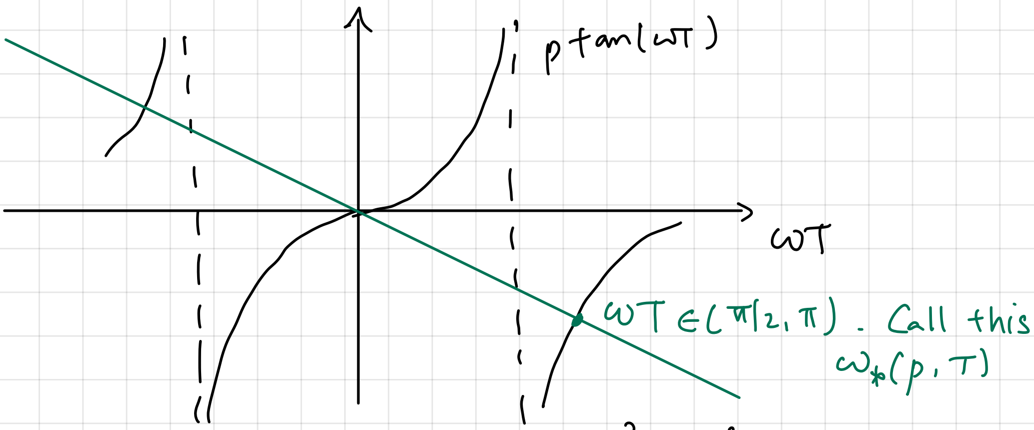
$$\Rightarrow \quad q e^{-\sigma T} > |\sigma + p|$$

If $\sigma > 0$ (unstable), then $q > q e^{-\sigma T} > |\sigma + p| > p$,

so unstable $\Rightarrow$ $q > p$. , so $p > q \Rightarrow$ stable

To find the onset of instab., look for sol^n with $\sigma = 0$.

$$\begin{aligned} p &= -q\cos(\omega T) \\ \omega &= q\sin(\omega T). \end{aligned} \quad \Rightarrow \quad \begin{aligned} p\tan(\omega T) &= -\omega \\ p^2 + \omega^2 &= q^2 \end{aligned}$$



$\omega T \in (\pi/2, \pi)$. Call this $\omega_*(p, T)$

Then at marginal instability, $p^2 + \omega_*^2 = q^2$

<u>Exercise</u> Show that for critical m,

$$1 + \frac{c_* \pi^2}{4T^2} < \frac{m^2}{(1 + c_*^m)^2} < 1 + \frac{c_*^2 \pi^2}{T^2}$$

hence, critical $m > 1$

1.3 Populations with age structure

Let $n(a,t)$ be the density of a population with age a at time t, i.e. $n(a,t)$ = # people between a and a+da.

$$N(t) = \int_0^{\infty} n(a,t)\, da. \quad \leftarrow \text{optimistic}$$

Expect birth rate $b(a)$ and death rate $\mu(a)$ depend on a.,

e.g.

The population ages as

$$n(a+\delta t,\ t+\delta t) = n(a,t) - \underbrace{\mu(a)\, n(a,t)\, \delta t}_{\text{those who die in the time}}$$

Taylor expand in δt, get the <u>von Foerster eqn</u>

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)\, n(a,t).$$

Babies are born at age $a=0$. so birthrate gives a b.c.

$$n(0,t) = \int_0^\infty b(a)\, n(a,t)\, da \qquad (*)$$

Look for separable sol^n $n(a,t) = \tilde{n}(a) e^{rt}$, $r \in \mathbb{R}$.

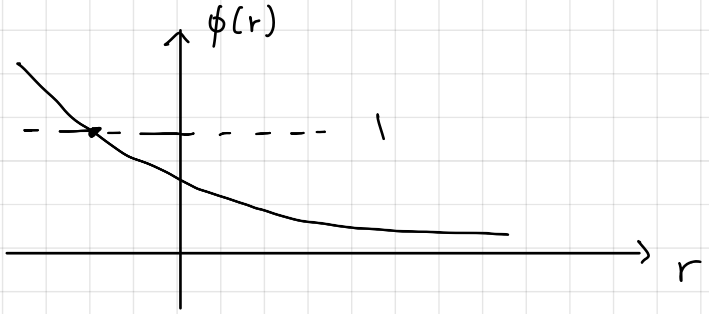
Age profile remains the same, but grows or shrinks with time.

$$\Rightarrow \frac{\partial \tilde{n}}{\partial a} = -\left(r + \mu(a)\right) \tilde{n}(a)$$

$$\Rightarrow \tilde{n} = n_0 e^{-ra} \exp\left(-\int_0^a \mu(s)\, ds\right).$$

Substituting into $(*)$ to get

$$\phi(r) := \int_0^\infty da\ b(a) e^{-ra} \exp\left(-\int_0^a ds\, \mu(s)\right) = 1$$



- $\phi(0) > 1 \Rightarrow r > 0$, and population grows
- $\phi(0) < 1 \Rightarrow r < 0$, and population shrinks.

Can think of $\phi(0)$ as avg offspring per individual.

Exercise If $b(a) = b$ and $\mu(a) = d$ are const.

- Compute $\phi(r)$
- does $\phi(0)$ make sense?
- Solve $\phi(r) = 1$
- What are the conditions on b, d for growth?

1.4 Interacting Species

We'll look at models of two populations, described by

$$\frac{du}{dt} = f(u,v), \qquad \frac{dv}{dt} = g(u,v)$$

The fixed pt. obeys $f(u^*, v^*) = g(u^*, v^*) = 0$. To determine the stability, we perturb

$$u(t) = u^* + \xi(t) \qquad v(t) = v^* + \eta(t)$$

To linear order,

$$\begin{pmatrix} \dot{\xi} \\ \dot{\eta} \end{pmatrix} = J \begin{pmatrix} \xi \\ \eta \end{pmatrix}$$

with $J = \begin{pmatrix} \partial f/\partial u & \partial f/\partial v \\ \partial g/\partial u & \partial g/\partial v \end{pmatrix}_{(u^*, v^*)}$.

Look for evals λ_1, λ_2 of J, which obey $\det(J - \lambda I) = 0$.

$$\Rightarrow \lambda^2 - \mathrm{Tr}(J) + \det(J) = 0.$$

$$\Rightarrow \mathrm{Tr}\, J = \lambda_1 + \lambda_2, \quad \det J = \lambda_1 \lambda_2.$$

In particular, if $\mathrm{Tr}\, J < 0$, and $\det J > 0$, then $\lambda_1, \lambda_2 < 0$.

and FP is stable.

Predator-prey models

The simplest (and most famous) model is the Lotka-Volterra eqn.

$N(t)$ = population of prey

$P(t)$ = population of predators.

with
$$\frac{dN}{dt} = N(a - bP), \qquad \frac{dP}{dt} = P(dN - c),$$

with $a, b, c, d > 0$.

prey thrive on their own

but not with P around

die out when $N = 0$.

We rescale $u = \frac{d}{c}N$, $v = \frac{b}{a}P$, $t \mapsto at$.

$$\frac{du}{dt} = u(1-v), \qquad \frac{dv}{dt} = \alpha v(u-1).$$

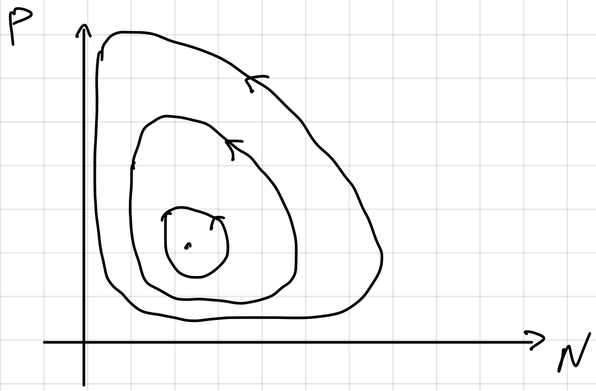
where $\alpha = c/a > 0$.

Unusually, there is an exact soln. Think of $v = v(u)$, then

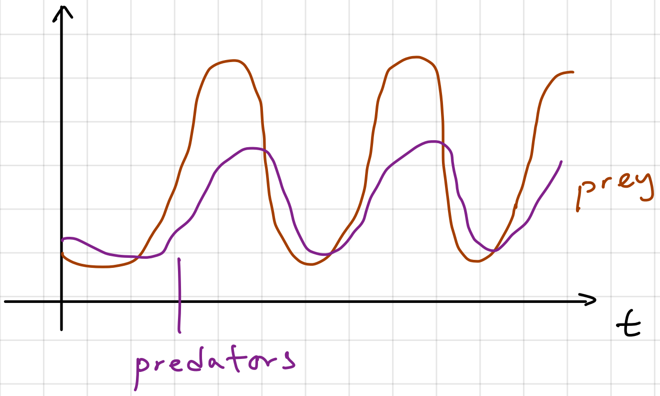
$$\frac{dv}{du} = \frac{\alpha v(u-1)}{u(1-v)}$$

$$\Rightarrow \int dv \, \frac{1-v}{v} = \alpha \int du \, \frac{u-1}{u}.$$

$$\Rightarrow \log v - v + \alpha(\log u - u) = \text{const}.$$



FP at $(u^*, v^*) = (1, 1)$



Claim : The avg is $\langle u \rangle = \langle v \rangle = 1$

Pf : $\dot{u} = u(1-v) \Rightarrow \int_0^T dt \, \frac{\dot{u}}{u} = \int_{u_{start}}^{u_{finish}} du \, \frac{1}{u} = [\log u]_{start}^{finish} = 0$

Meanwhile

$$0 = \int_0^T dt \, \frac{\dot{u}}{u} = \int_0^T dt \, (1-u) = T - T\langle u \rangle \Rightarrow \langle v \rangle = 1.$$

Similarly, $\langle v \rangle = 1$ □

To prepare us for more complicated models, we use other techniques to determine phase plane orbits.

First, stability : FP are $(u^*, v^*) = (0,0), (1,1)$.

Jacobian $J = \begin{pmatrix} 1-v & -u \\ \alpha v & \alpha(u-1) \end{pmatrix}$.

- $(u^*, v^*) = (0,0) \Rightarrow \lambda = 1, -\alpha$ → saddle

  (prey flourish, predators go extinct)

- $(u^*, v^*) = (1,1) \Rightarrow \lambda = \pm i\sqrt{\alpha}$ ⇒ oscillations at linear level.

The general linearised sol^n is

$$(u,v) = (1,1) + A_+ \underline{x}_+ e^{i\sqrt{\alpha} t} + A_- \underline{x}_- e^{-i\sqrt{\alpha} t}.$$

with $\underline{x}_\pm = (\pm i, \sqrt{\alpha})$ s.t. $J \underline{x}_\pm = \pm i\sqrt{\alpha} \, \underline{x}_\pm$. with $A_\pm$ const.

Here, the full sol^n do oscillate, but in general, the linearised analysis is not sufficient to determine this — could be stabalised by higher order terms.

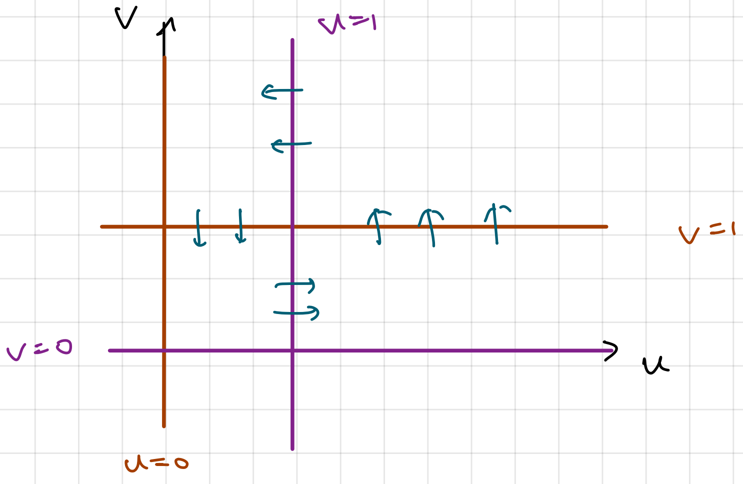
Next, nullclines are sol^n to

$$\dot{u} = 0 \Rightarrow u = 0, \; v = 1$$

$$\dot{v} = 0 \Rightarrow v = 0, \; u = 1$$

- Plot nullclines
- Work out direction of flow on nullclines

Again, this suggests orbits.



Hunting / Fishing

We can include an additional term to account for hunting (or fishing) of prey.

$$\frac{dN}{dt} = N(a-bP) - hN$$

h>0 for hunting

$$\frac{dP}{dt} = P(dN-c)$$

This doesn't change the structure of eqn if h<a. FP (or avg) is

$$(N,P) = \left(\frac{c}{d}, \frac{a-h}{b}\right).$$

This is counter-intuitive: hunting prey doesn't change no. of prey, it changes the no. of predators.

A Logistic Twist

The Lotka-Volterra orbits do not survive most changes to the eqns. e.g.

$$\dot{u} = u(1-v-\mu_1 u)$$

$$\dot{v} = \alpha v(u-1-\mu_2 v)$$

$\mu_1, \mu_2 > 0$ are logistic-like terms

need $\mu_1 < 0$ so $v^* > 0$

Exercise Show that FPs are $(0,0)$, $\left(\frac{1}{\mu_1}, 0\right)$, $\frac{1}{1+\mu_1\mu_2}(1+\mu_2, 1-\mu_1)$

Note : $u^* > 1$ and $v^* < 1$, so prey benefits, predators do not.

For stability, look at $J = \begin{pmatrix} 1 - v^* - 2\mu_1 u^* & -u^* \\ \alpha v^* & \alpha(u^* - 1 - 2\mu_2 v^*) \end{pmatrix}$

using e.g. $1 - v^* - \mu_1 u^* = 0$,

$$J = \begin{pmatrix} -\mu_1 u^* & -u^* \\ \alpha v^* & -\alpha \mu_2 v^* \end{pmatrix} = \begin{pmatrix} - & - \\ + & - \end{pmatrix}$$

$\Rightarrow$ $\mathrm{Tr}\, J < 0$, $\det J > 0$ $\Rightarrow$ two evals with $\mathrm{Re}(\lambda) < 0$.

$\Rightarrow$ stable FP no matter how small μ_1, μ_2.

Exercise Draw nullclines and sketch the flows in phase space.

Dengue Fever

Dengue is a virus transmitted by mosquitoes. Wolbachia is a bacteria which can infect mosquitoes and block transmission.

We have the following facts.

- All mosquitoes carry dengue, but those infected are harmless
- Only "verticle" transmission to offspring
- Female infected, then all her eggs will be too, but she lays fewer eggs than the uninfected.
- If an uninfected female + infected male $\Rightarrow$ no viable eggs
- Infected mosquitoes die sooner.

Let x = # uninfected female mosquitoes,

y = # infected female mosquitoes

Assume proportion of males tracks females, e.g. fraction of uninfected males is $x/(x+y)$.

Cross	frequency	egg rate	State
$f \times m$	$x \cdot \frac{x}{x+y}$	r	uninfected
$f \times ⓜ$	$x \cdot \frac{y}{x+y}$	0	—
$ⓕ \times m$	$y \cdot \frac{x}{x+y}$	λr	infected
$ⓕ \times ⓜ$	$y \cdot \frac{y}{x+y}$	λr ↑ $\lambda < 1$	infected

$\bigcirc$ = infected

death rate

$$\frac{dx}{dt} = x\left(r\frac{x}{x+y} - d - \varepsilon(x+y)\right)$$

logistic-style competition

$$\frac{dy}{dt} = y\left(\lambda r - \mu d - \varepsilon(x+y)\right)$$

$\mu > 1$ as die sooner

Rescaling $t \to rt$, $x \to \varepsilon x/r$, $y \to \varepsilon y/r$, then

$$\frac{dx}{dt} = x\left(x_0 - \frac{y}{x+y} - (x+y)\right)$$

$$\frac{dy}{dt} = y\left(y_0 - (x+y)\right)$$

with $x_0 = 1 - \frac{d}{r}$, $y_0 = \lambda - \frac{\mu d}{r}$.

Assume:
- $r > d$ (uninfected breed more than they die)

  $\Rightarrow x_0 > 0$
- $y_0 > 0$, then $\lambda < 1$ and $\mu > 1 \Rightarrow 0 < y_0 < x_0 < 1$.

FPs: $(0,0)$, $(x_0, 0)$, $(0, y_0)$, and

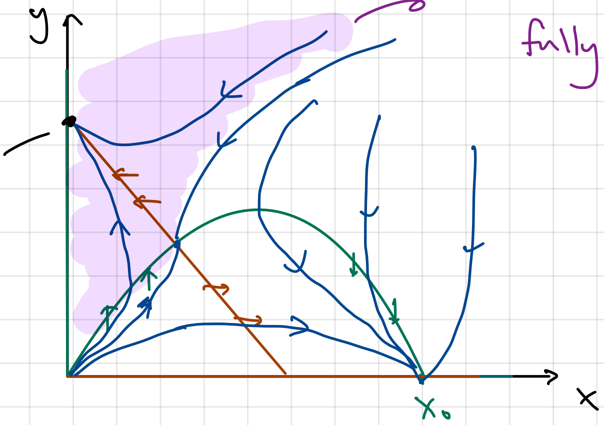
$$(x^*, y^*) = y_0\left(1 - x_0 + y_0,\ x_0 - y_0\right)$$

Exercise Check (x^*, y^*) is saddle.

Draw phase plane. First look at null clines

$$\dot{x} = 0 \Rightarrow x = 0, \quad y = x_0(x+y) - (x+y)^2$$

$$\dot{y} = 0 \Rightarrow y = 0, \quad x + y = y_0$$



basin of attraction fully infected mosquitoes.

want to be here

1.5 Epidemiology

Focus on SIR model.

S = # suspects. I = # infected, R = # recovered / dead (removed)

with
$$\frac{dS}{dt} = -\beta IS$$
$$\frac{dI}{dt} = +\beta IS - \nu I \quad , \quad \beta, \nu > 0$$
$$\frac{dR}{dt} = \nu I$$

rate at which people recover. (for ν)

rate at which people get infected (for β)

Note $N = S + I + R$ = const. $\Rightarrow$ $\dot{R}$ eqn not needed.

- $\dot{I}(0) > 0 \Leftrightarrow \beta S(0) > \nu$. Usually $S(0) \simeq N$.

Define reproductive ratio $R_0 = \beta N / \nu$. Disease spreads if $R_0 > 1$.

- $\frac{1}{\nu} \approx$ transmission period
- β = transmission rate per contact
- N = # contacts.

Some numbers.

- Original covid strain $R_0 \approx 2\text{-}5$
- Polio $R_0 \approx 4-6$
- Mumps $R_0 \approx 10-12$
- Measles $R_0 \approx 16-18$.

Suppose we vaccinate a fraction p of population.

$$\Rightarrow \quad S(0) = (1-p)N.$$

$$\Rightarrow \quad R_{eff} = (1-p)R_0.$$

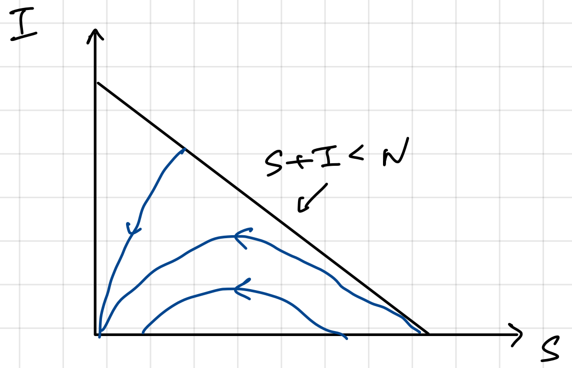
We can stop the spread if $R_{eff} < 1$ or $p > \frac{R_0 - 1}{R_0}$.

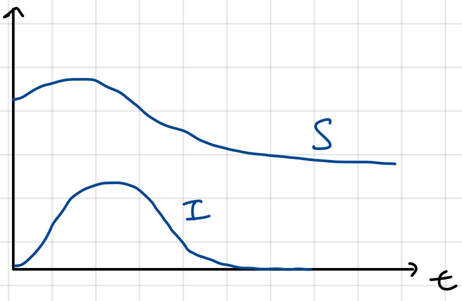
e.g. Covid $p_{needed} \approx 0.5 - 0.8$.

We can solve for trajectories in phase plane by viewing $I(S)$ with

$$\frac{dI}{dS} = \frac{\nu}{\beta S} - 1 = \frac{N}{R_0 S} - 1$$

$$\Rightarrow I(S) = \frac{N}{R_0} \log S - S + \text{const}.$$





Exercise Show that max I at $S = N/R_0$. Explain why this is the case in terms of a suitable R_{eff}.

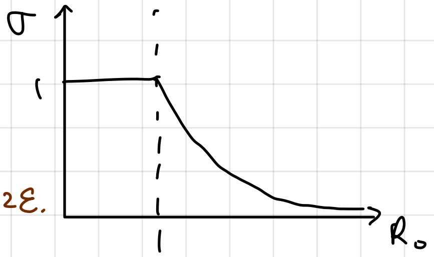
Not everyone becomes infected. As $t \to \infty$, $S \to S_\infty \neq 0$. There are two values of S s.t.

$$I(S_0) = I(S_\infty) = 0.$$

$$\Rightarrow \quad \frac{N}{R_0}\log S_0 - S_0 = \frac{N}{R}\log S_\infty - S_\infty .$$

Typically, start with $S_0 \approx N$. Let $S_\infty = \sigma N$, then

$$\log \sigma = R_0(\sigma - 1)$$



Note: $\sigma \ll 1 \Rightarrow \sigma \approx e^{-R_0}$

Exercise Show that $R_0 \approx 1+\epsilon$, $\epsilon \ll 1$, then $\sigma \approx 1-2\epsilon$.

A generalisation: include birth rate b and death rate μ.

$$\frac{dS}{dt} = -\beta I S + bN - \mu S$$

$$\frac{dI}{dt} = \beta I S - \nu I - \mu I$$

$$\frac{dR}{dt} = \nu I - \mu R .$$

Note: • everyone give birth, so disease doesn't kill.

- babies are born susceptible.
- constant death rate μ for all groups.
- $S+I+R = N$ obeys $\frac{dN}{dt} = (b-\mu)N$.

Assume (unrealistically) $b=\mu \Rightarrow N = \text{const}$.

When $S \approx N$, $\dot{I} = (\beta S - \mu - \nu) I > 0$ if

$$R_0 = \frac{\beta N}{\mu + \nu} > 1 .$$

Typically, recovery time $\frac{1}{\nu} \ll$ lifetime $\frac{1}{\mu} \Rightarrow \nu \gg \mu$.

Eqn for R decouples, we have a FP at (S^*, I^*) with

$$S^* = \frac{\nu+\mu}{\beta} = \frac{N}{R_0}$$

and

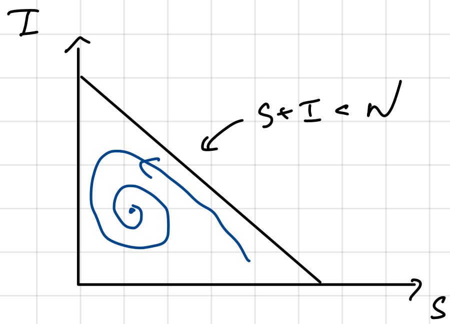
$$I^* = \mu \frac{N - S^*}{\beta S^*} = \frac{\mu}{\beta}(R_0 - 1)$$

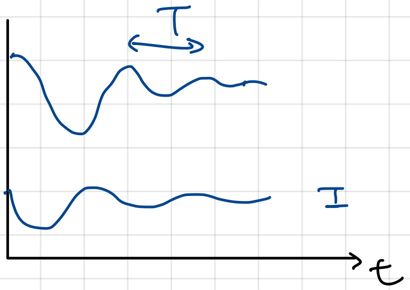
Jacobian $$J = \begin{pmatrix} -\mu R_0 & -(\nu+\mu) \\ \mu(R_0-1) & 0 \end{pmatrix}$$

evals $$\lambda = -\tfrac{1}{2}\mu R_0 \pm \tfrac{1}{2}\sqrt{\mu^2(R_0-2)^2 - 4\mu\nu(R_0-1)}$$

$$\underset{\nu \gg \mu.}{\approx} \tfrac{1}{2}\mu R_0 \pm i\omega, \qquad \omega = \sqrt{\mu\nu(R_0-1)}$$

This suggests transient oscillations with period $T = \frac{2\pi}{\omega} = \frac{2\pi}{\sqrt{\mu\nu(R_0-1)}}$.





e.g. measles $\frac{1}{\nu} \approx 12$ days, $\frac{1}{\mu} \approx 70$ years $\Rightarrow T \approx 2.2$ yrs.

1.6 Chemical Reactions

A reaction $A + B \xrightarrow{\overset{\text{rate}}{k}} C$ is described by

$$\frac{dA}{dt} = -k\underbrace{AB}_{\substack{A * B \text{ is the} \\ \text{law of mass action}}}, \qquad \frac{dB}{dt} = -kAB, \qquad \frac{dC}{dt} = kAB$$

Michaelis-Menten Enzyme Kinetics

Enzymes help speed up a chemical reaction.

$$\underset{\text{substrate}}{S} + \underset{\text{enzymes}}{E} \underset{k_2}{\overset{k_1}{\rightleftharpoons}} \underset{\text{complex}}{C} \xrightarrow{k_3} E + \underset{\text{product}}{P}$$

$$\frac{dS}{dt} = -k_1 SE + k_2 C \qquad \frac{dC}{dt} = k_1 SE - (k_2+k_3)C$$

$$\frac{dE}{dt} = -k_1 SE + (k_2+k_3)C \qquad \frac{dP}{dt} = k_3 C.$$

Assume $S(0) = S_0$, $E(0) = E_0$, $C(0) = P(0) = 0$.

Two conservation laws: $E + C = E_0$, $S + C + P = S_0$.

$$\Rightarrow \quad \frac{dS}{dt} = -k_1 E S + (k_1 S + k_2) C$$

$$\frac{dC}{dt} = k_1 E_0 S - (k_1 S + k_2 + k_3) C$$

Let $s = S/S_0$, $c = C/E_0$, so $s(0) = 1$, $c(0) = 0$, and $\tau = k_1 E_0 t$.

$$\Rightarrow \frac{ds}{d\tau} = -s + (s + \mu - \lambda) c, \quad \frac{dc}{d\tau} = \frac{1}{\varepsilon}(s - (s+\mu)c)$$

with $\lambda = \dfrac{k_2}{k_1 S_0}$, $\mu = \dfrac{k_2 + k_3}{k_1 S_0}$, $\varepsilon = E_0/S_0$.

Assume $\varepsilon \ll 1$. Solve numerically

All trajectories lead to a common curve which they follow to the origin.

This happens because there are 2 timescales in the system when $\varepsilon \ll 1$. $c(t)$ changes much faster than $s(t)$.

Roughly, the system quickly relaxes to $\dot{c} = 0$ curve

$$c = \frac{s}{s+\mu}.$$

There's a much slower progression along the curve

$$\frac{ds}{d\tau} = -s + (s + \mu - \lambda) c = -\frac{\lambda s}{s+\mu}.$$

This tells us how fast the substrate is depleted.

1.7 Neuron Excitations

Excitable systems can "spike". Here we look at a simplified model for neuron signalling.

Fitzhugh - Nagumo Model

$$\frac{du}{dt} = \frac{1}{\varepsilon}\left(u+v-\frac{1}{3}u^3 - Z(t)\right)$$

$$\frac{dv}{dt} = -(u-a+bv)$$

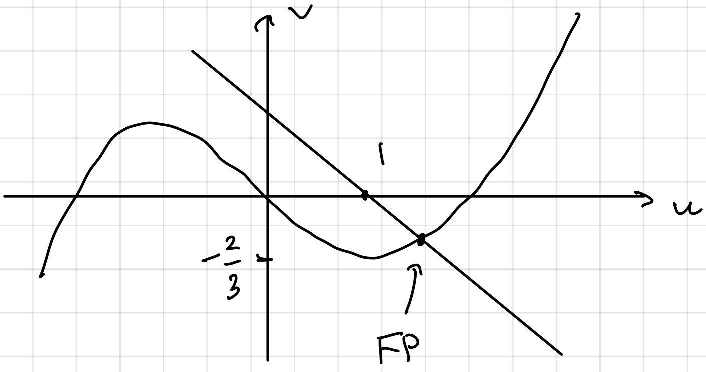
- $u(t) \approx$ voltage across membrane
- $v(t) \approx$ ease with which ions can cross

a, b, ε s.t $0<b\leq 1.$, $1-\frac{2b}{3}<a<1$ $(*)$,

$Z(t)$ an external input f^n. Take $\varepsilon \ll 1$.

To start, set $Z(t)=0$

Nullclines : $v = u\left(\frac{1}{3}u^2-1\right)$, $v = \frac{a-u}{b}$.



Note: • slope of cubic at origin $= -1$

slope of line $= -\frac{1}{b}$ ⇒ line steeper ⇒ only 1 FP

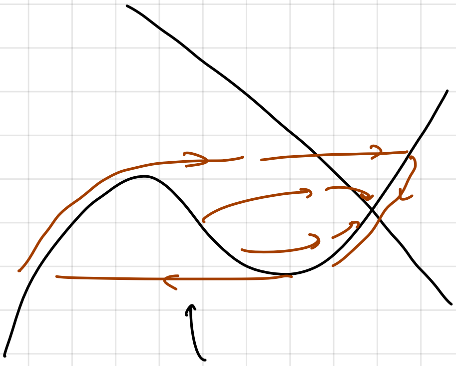
- Roots of cubic at $u=0$, $\pm 1/\sqrt{3}$. Minimum at $u_{min}=1$.

Inequality $(*)$ ⇒ FP $u_* > 1$

At FP, $J = \begin{pmatrix} (1-u^{*2})/\varepsilon & 1/\varepsilon \\ -1 & -b \end{pmatrix} \Rightarrow \mathrm{Tr}\,J < 0,\ \det J > 0$

$\Rightarrow$ stable FP

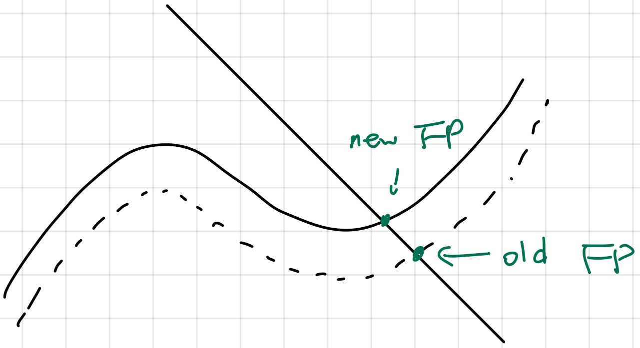
For $\varepsilon \ll 1$,



This trajectory goes the long way round.

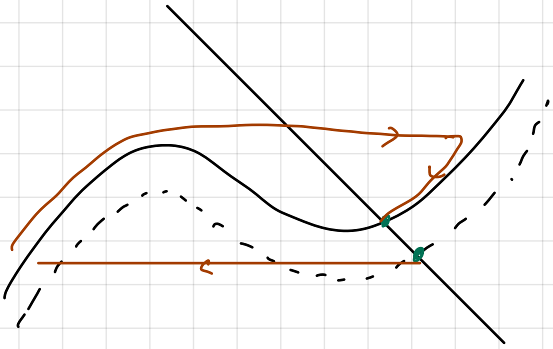
Now we perturb the system $z(t) = \begin{cases} 0 & t<0 \\ V_0 = \text{const.} & t>0 \end{cases}$.

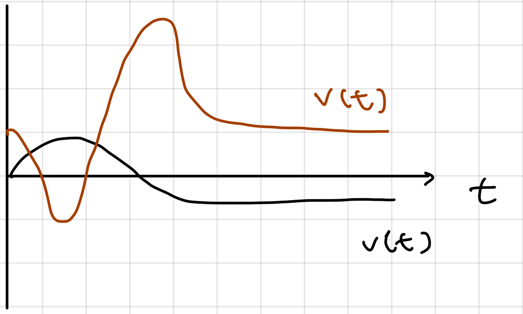
This shifts the nullclines upward.



Can check FP remains stable if $V_0 < V_{crit} = \frac{2}{3} + \frac{a-1}{b}$.

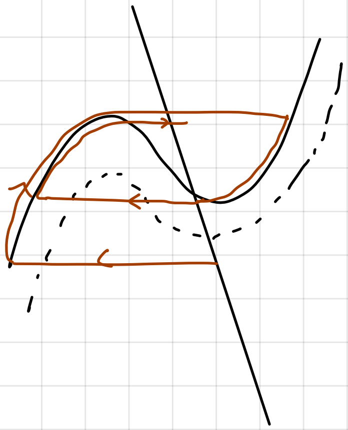
Suppose that the old FP sits below the minimum of the new cubic. Then, for $V_0 < V_{crit}$, the system makes a huge diversion in phase plane.

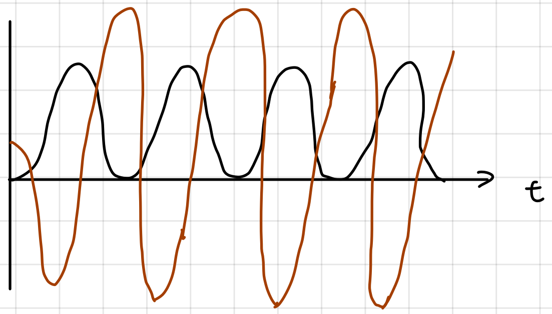




Small perturbation $\Rightarrow$ large spike.

For $V_0 > V_{crit}$. the new FP unstable.





Now we're in a limit cycle and perturbation ⇒ spike train.

1.8 Discrete Time

Sometimes it is better to measure time in discrete intervals, $n \in \mathbb{Z}$ (e.g. Seasons / generations). In the simplest cases, we get difference eqn like

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

Poppies

Let x_n = no. of annual plants in year n

- γ = no. of seeds per plant
- σ = prob. of germination after one year.
- τ = prob. of germinating in second year.

Assume all seeds die after 2 years

$$x_n = \sigma\gamma x_{n-1} + \tau(1-\sigma)\gamma x_{n-2}.$$

Only steady state is $x_n = 0$.

For linear eqn, sol^n of the form $x_n = p^n$.

$$\Rightarrow p^2 = \sigma\gamma p + \tau(1-\sigma)\gamma$$

$$\Rightarrow p = p_\pm = \frac{1}{2}\sigma\gamma \pm \frac{1}{2}\sqrt{\sigma^2\gamma^2 + 4\tau(1-\sigma)\gamma}$$

Note $p_- < 0 < p_+$, $|p_-| < |p_+|$

The general sol^n is $x_n = A p_-^n + B p_+^n$.

Since $|p_+| > |p_-|$, second term dominates at large n.

- $p_+ > 1 \Rightarrow$ population grows.
- $p_+ < 1 \Rightarrow$ population shrinks

We have $p_+ = 1 \Rightarrow$ $\gamma \underbrace{|\sigma + \tau(1-\sigma)|}_{\text{prob. that seed germinates}} = 1$

Breathing

Return to breathing model.

$\swarrow$ CO$_2$ conc.

$$V_{n+1} = \alpha C_{n-k}.$$

and vol. of breath

$$C_{n+1} - C_n = M - \beta V_{n+1}$$

with $\alpha, \beta, M > 0$. Eliminate V_{n+1} to get

$$C_{n+1} = M + C_n - \alpha\beta C_{n-k}.$$

Steady state $C^* = M/\alpha\beta$. Look at perturbation.

<u>$k=0$:</u> $C_n = C^* + \varepsilon_n$, $\varepsilon_n \ll 1$, then

$$\varepsilon_{n+1} = (1-\alpha\beta)\varepsilon_n$$

Steady state is stable for $\alpha\beta < 2$.

unstable for $\alpha\beta > 2$.

<u>$k=1$:</u> Now

$$\varepsilon_{n+1} = \varepsilon_n - \alpha\beta\varepsilon_{n-1}$$

Look for sol^n $\varepsilon_n = p^n$ to get $p^2 - p + \alpha\beta = 0$

$$\Rightarrow p = p_\pm = \frac{1}{2}\left(-1 \pm \sqrt{1-4\alpha\beta}\right)$$

If $\alpha\beta < \frac{1}{4}$, then $p_\pm \in \mathbb{R}$, $|p_\pm| < 1$. so $\varepsilon_n = A p_+^n + B p_-^n \to 0$ as $n \to \infty$

So stable.

If $\alpha\beta > \frac{1}{4}$, then $p_\pm \in \mathbb{C}$. So system oscillates. We have

$$|p_\pm|^2 = \frac{1}{4} + (\alpha\beta - \frac{1}{4}) = \alpha\beta$$

Stability requires $|p_\pm| < 1$, so stable if $\alpha\beta < 1$. Unstable o/w.

Logistic Map

This is the most famous of all discrete maps.

$$x_{n+1} = f(x_n) = r\, x_n (1 - x_n).$$

It's like the logistic eqn. but we can't absorb r by rescaling time.

Take $x_n \in [0,1]$. Then $x_{n+1} \in [0,1]$ provided $0 \leq r \leq 4$.

The map has 2 FP at $x = 0$ and $x^* = 1 - \frac{1}{r}$ (if $r > 1$).

Near the origin, write $x_n = \varepsilon_n \ll 1$, then

$$\varepsilon_{n+1} = r\,\varepsilon_n (1 - \varepsilon_n) \approx r\,\varepsilon_n$$

Stable for $r < 1$, unstable for $r > 1$.

For the other FP, write $x_n = x^* + \varepsilon_n$,

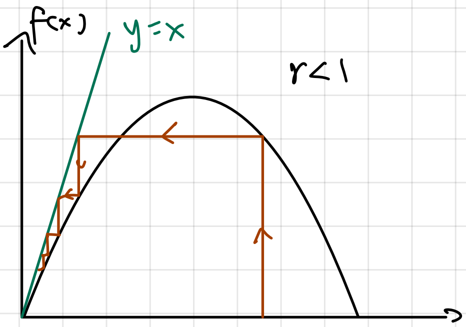
$$x_{n+1} = x^* + f'(x^*)\varepsilon_n + \dots$$

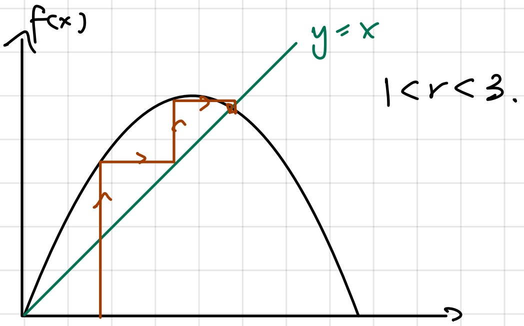
$f'(x^*) = 2 - r$.

FP stable if $1 < r < 3$. Unstable if $r > 3$.

Note that $f'(x^*) < 0$ for $2 < r < 3$, so successive terms jump about x^*.

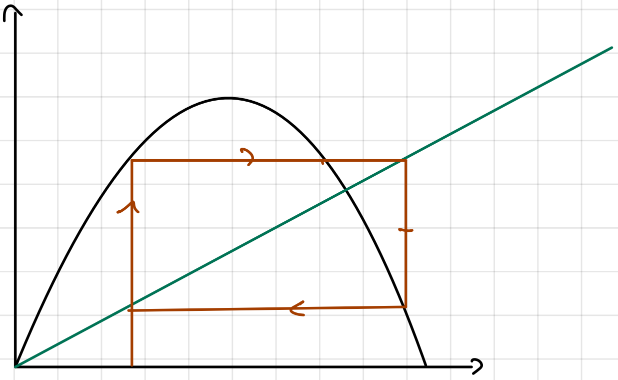
We see this in <u>Cobweb diagrams</u>. Plot $f(x)$ and $y = x$.





Repeated iterations zooms in on FP.

What happens for $r > 3$?



Find that it settles down to a periodic pattern. A trajectory that orbits p successive points is called a p-cycle. Here we find a 2 cycle.

Look at $f^2(x) = f(f(x)) = rf(x)(1-f(x)) = r^2 x(1-x)(1-rx(1-x))$.

This has FP $x = f^2(x)$.

$$\Rightarrow \underbrace{x(1-r+rx)}_{\text{FP of } f(x).}\underbrace{(1+r-r(1+r)x+r^2x^2)}_{\text{new}} = 0$$

$$\Rightarrow x_I = \frac{1}{2r}\left(1+r \pm \sqrt{(r-3)(r-1)}\right) \in \mathbb{R} \text{ if } r > 3.$$

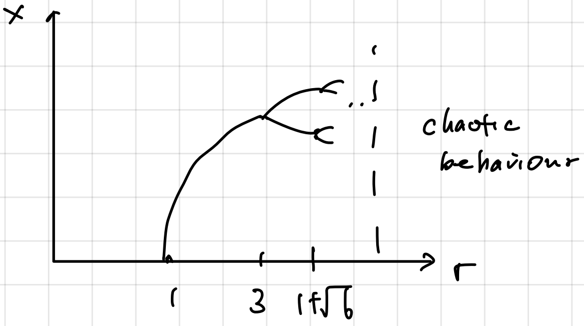
We can check stability of FP. Look at

$$\frac{df^2}{dx} = f'(f(x))\,f'(x).$$

$$\Rightarrow \left.\frac{df^2}{dx}\right|_{x_+} = f'(x_-)\,f'(x_+) = \left.\frac{df^2}{dx}\right|_{x_-} = -r^2+2r+4.$$

Ex. Show that the 2-cycle stable for $r < 1+\sqrt{6} \approx 3.45\ldots$

At this pt. interesting things happen. Long term behaviour.



The r-value at which 2^n-cycle become unstable is r_n.

n	period	r_n
0	1	3
1	2	3.449
2	4	3.544
3	8	3.564

Claim: $\lim_{n\to\infty} \frac{r_n - r_{n-1}}{r_{n+1} - r_n} = 4.669\ldots$ a universal const. called Feigenbaum const.

Bifurcations asymptote to $r \approx 3.5699\ldots$, after this, chaos.

In 1970s, suggested that based on logistic map, that chaos is common in ecology. Seen in controlled experiments on flour beetles, but difficult to detect in nature.

§2 Spatial Variations

Consider a population density $n(\underline{x}, t)$, so the population in a region V is

$$N(t) = \int_V n(\underline{x}, t)\, d^3x .$$

If a density $n(\underline{x}, t)$ conserved, then there exists a current, or flux $\underline{J}(\underline{x}, t)$ obeying

$$\frac{\partial n}{\partial t} + \nabla \cdot \underline{J} = 0$$

Then

$$\frac{dN}{dt} = \int_V d^3x\, \frac{\partial n}{\partial t}$$

$$= -\int_V d^3x\, \nabla \cdot \underline{J} = -\int_{S=\partial V} \underline{J} \cdot d\underline{S}$$

ie. stuff in V can change only if there is a flow in/at the boundary of V.

Things we care about (population, chemical conc.) are conserved except when they're not. More generally,

$$\frac{\partial u}{\partial t} + \nabla \cdot \underset{\sim}{J} = F(n, \underset{\sim}{x}, t)$$

↖ captures birth / death / competition.

Typically, $\underset{\sim}{J}$ takes one of two forms.

- Advection: the stuff $n(\underset{\sim}{x},t)$ is dragged along by some underlying flow $\underset{\sim}{u}(\underset{\sim}{x},t)$.

$$\underset{\sim}{J}(\underset{\sim}{x},t) = n(\underset{\sim}{x},t)\, \underset{\sim}{u}(\underset{\sim}{x},t).$$

- Diffusion:

$$\underset{\sim}{J}(\underset{\sim}{x},t) = -\underset{\uparrow \text{ diffusivity}}{D}\, \nabla n(\underset{\sim}{x},t) \qquad \text{(Fick's law)}$$

Typically arises when there is underlying randomness.

The cty eqn becomes the heat eqn

$$\frac{\partial n}{\partial t} = D \nabla^2 n.$$

Note: $[D] = L^2/T$.

Could have both advection and diffusion. An interesting class of eqns takes the general form

$$\frac{\partial n}{\partial t} - D \nabla^2 n = F(n)$$

These are reaction-diffusion eqns.

2.1 Diffusion

In 1D, heat eqn is

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 x}{\partial t^2}$$

Diffusion on a finite interval

Consider $x \in [0, L]$ with BC

$$n(0,t) = n_0, \quad n(L,t) = n_1$$

e.g. n = temp. of rod, population of bacteria in a tube.

Steady state sol^n

$$\frac{\partial^2 n}{\partial x^2} = 0 \quad \Rightarrow \quad n(x,t) = n^*(x,t) = n_0 + (n_1 - n_0)\, x/L$$

The flux is

$$J = -D\, \partial n/\partial x = D\,(n_0 - n_1)/L\,.$$

Flux is from high density to low density.

Now write $n(x,t) = n^*(x) + c(x,t)$

$$\Rightarrow \quad \frac{\partial c}{\partial t} - D\frac{\partial^2 c}{\partial x^2} = 0\,, \quad \text{with} \quad c(0,t) = c(L,t) = 0$$

Look for sol^n $c(x,t) = f(x)\,g(t)$

$$\Rightarrow \quad f\dot{g} = D g f''$$

$$\Rightarrow \quad \dot{g}/g = D f''/f$$

depends only on t

only on x $\Rightarrow$ so both const.

We have $f(0) = f(L) = 0$, so

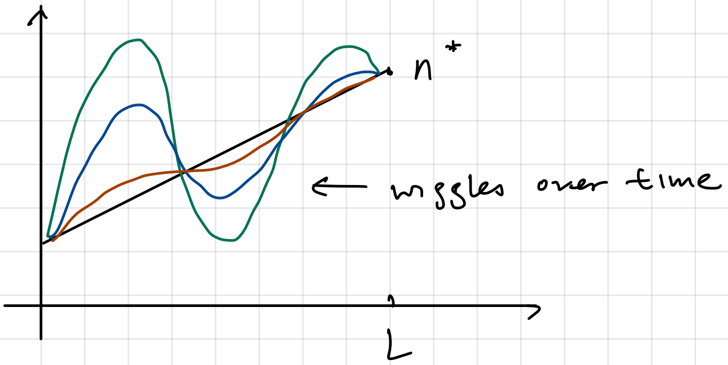
$$f(x) = \sin\left(\frac{n\pi x}{L}\right) \qquad , n = 1, 2, \ldots$$

Then

$$\dot{g} = -\lambda_n g \quad \Rightarrow \quad g(t) = e^{-\lambda_n t} \quad . \text{ with } \lambda_n = D\frac{\pi^2 n^2}{L^2}\,.$$

General sol^n:

$$c(x,t) = \sum_{n=1}^{\infty} c_n\, e^{-\lambda_n t} \sin\left(\frac{n\pi x}{L}\right).$$



Note: faster wiggles decay more quickly. Diffusion smooths things.

Exercise Change BC to $n(0,t) = n_0$, but $J(L,t) = -D \left.\frac{\partial u}{\partial x}\right|_{x=L} = 0$.

What is the slowest mode?

tube is blocked

Example (Cooking a Turkey)

Claim: time τ to cook a turkey scales as $\tau \sim M^{2/3}$.

Temp. obeys heat eqn

$$\frac{\partial T}{\partial t} = D \nabla^2 T$$

for turkey. $D \approx 2 \times 10^{-3}\ \text{cm}^2\ \text{s}^{-1}$

Assume spherical turkey in spherical oven, so $T(r,t)$.

$$\Rightarrow \nabla^2 T = \frac{1}{r^2} \frac{\partial}{\partial r}\left(r^2 \frac{\partial T}{\partial r}\right).$$

Let $V(r,t) = rT(x,t)$

$$\Rightarrow \frac{\partial V}{\partial t} = D \frac{\partial^2 V}{\partial r^2}.$$

Separable sol^n:

$$V(r,t) = e^{-\lambda D t}\left[A \cos(\sqrt{\lambda} r) + B \sin(\sqrt{\lambda} r)\right)$$

But $T = V/r$ finite at $r=0 \Rightarrow A = 0$

Outside, $T(r,t) = T_{hot}\ \forall\ r > R$, where R = radius of turkey.

temp. of oven

Then $\sqrt{\lambda} = \frac{n\pi}{R}$, $n = 1, 2, \ldots$ and

$$T(r,t) = T_{hot} + \frac{1}{r} \sum_{n=1}^{\infty} V_n \sin\left(\frac{n\pi r}{R}\right) e^{-n^2\pi^2 D t / R}$$

for $0 \leq r \leq R$. The V_n are set by $T(r,0) = T_0 \ll T_{hot}$ for $0 \leq r \leq R$

i.e. pick V_n to cancel $1/r$ term. Check that

$$T(r,t) = T_{hot} - \frac{2R}{\pi^2} \frac{(T_{hot} - T_0)}{r} \sum_{n=1}^{\infty} \frac{(-1)^n}{n} \sin\left(\frac{n\pi r}{R}\right).$$

Initial conditions decay away in time

$$\tau = R^2/n\pi^2 D,$$

where $n=1$ mode has decayed, the turkey is cooked.

Note: $\tau \sim R^2 \propto M^{2/3}$. For $R = 10\,\text{cm} \Rightarrow \tau \approx 5000\,\text{s}$

Diffusion with growth

We will study the 1D eqn

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + \lambda n \quad . \qquad \leftarrow \lambda = \text{const.}$$

Like Malthusian population model, but with diffusion.

Take $x \in [0, L]$ and $n(0,t) = n(L,t) = 0$.

Note: no growth $(\lambda = 0) \Rightarrow n = 0$

no diffusion $(D = 0) \Rightarrow n \sim e^{\lambda t}$.

Let $\tilde{n}(x,t) = e^{\lambda t} n(x,t)$

$$\Rightarrow \quad \frac{\partial \tilde{n}}{\partial t} = D\frac{\partial^2 \tilde{n}}{\partial x^2}$$

Now we can solve as before.

Exercise Show that population dies out if $L < L_c$ but grows for $L > L_c$ for some critical length L_c.

Diffusion on line

Now we solve $\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2}$ with $x \in \mathbb{R}$.

We require $J \sim \frac{\partial n}{\partial x} \rightarrow 0$ as $x \rightarrow \pm\infty$. so

$$N = \int_{-\infty}^{\infty} dx \; n(x,t)$$

is conserved.

$$\frac{dN}{dt} = \int dx\, \dot{n} = -D\int dx\, \frac{\partial^2 n}{\partial x^2} = -D\left[\frac{\partial n}{\partial x}\right]_{-\infty}^{\infty} = 0.$$

We will look for self-similar sol^{n}s (not the most general sol^{n}s).

We do some dimensional analysis $[D] = L^2 T^{-1}$. Introduce dimensionless combination

$$\xi = x/\sqrt{Dt}.$$

In addition, $[N] = L[n]$, so look for sol^n of the form

$$n(x,t) = \frac{N}{\sqrt{Dt}} f(\xi)$$

Algebra: $\frac{\partial \xi}{\partial t} = -\frac{1}{2}\xi/t$, $\frac{\partial \xi}{\partial x} = \xi/x$

$$\Rightarrow \frac{\partial n}{\partial t} = -\frac{1}{2t}\frac{N}{\sqrt{Dt}} f + \frac{N}{\sqrt{Dt}} f'(\xi)\frac{\partial \xi}{\partial t} = -\frac{1}{2t}\frac{N}{\sqrt{Dt}}\frac{\partial}{\partial \xi}(\xi f).$$

and

$$\frac{\partial^2}{\partial x^2} = \frac{1}{2t}\frac{\partial^2}{\partial \xi^2}.$$

Heat eqn become ODE.

$$\frac{d^2 f}{d\xi^2} + \frac{1}{2}\frac{d}{d\xi}(\xi f) = 0$$

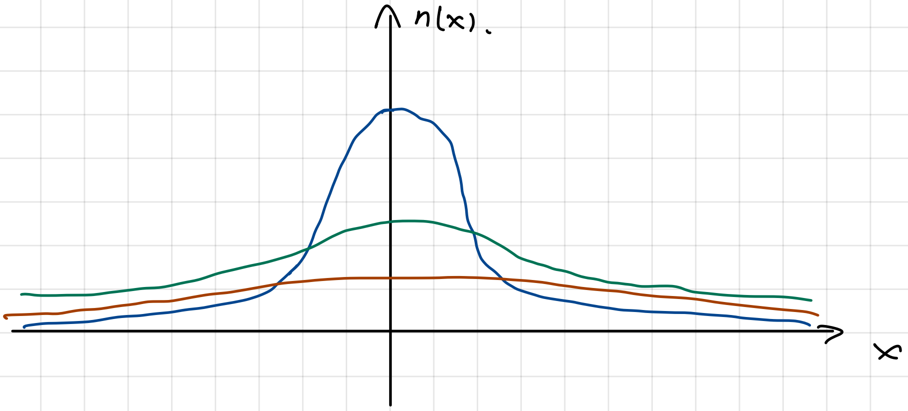
$$\Rightarrow \frac{df}{d\xi} + \frac{1}{2}\xi f = \text{const.}$$

We want a localised sol^n with $f, f' \to 0$ as $x \to \pm\infty$, so const. $= 0$.

$$\Rightarrow f(\xi) = A e^{-\xi^2/4}$$

Normalise by $\int_{-\infty}^{\infty} d\xi \, f(\xi) = 1 \Rightarrow A = \frac{1}{\sqrt{4\pi}}$ and

$$n(x,t) = \frac{N}{\sqrt{4\pi D t}} e^{-x^2/4t}.$$



Gaussian, with width that spreads as $\Delta x \sim \sqrt{Dt}$ and a height that gets smaller.

$\uparrow$ Characteristic behaviour of diffusion

A second approach

Try $n(x,t) = t^\alpha g(x/t^\beta)$, i.e. $\xi = x/t^\beta$, then

$$\frac{\partial n}{\partial t} = \alpha t^{\alpha-1} g - \beta t^\alpha \frac{x}{t^{\beta+1}} g' = t^{\alpha-1}(\alpha g - \beta \xi g')$$

$$D\frac{\partial^2 n}{\partial x^2} = Dt^{\alpha}\frac{1}{t^{2\beta}}g''$$

$$\Rightarrow t^{\alpha-1}(\alpha g - \beta\xi g') = Dt^{\alpha-2\beta}g''$$

$$\Rightarrow \alpha g - \beta\xi g' = Dt^{1-2\beta}g''$$

Similarity sol^n requires $\beta = 1/2$.

Use conservation law to determine α.

$$N = \int n\,dx = \int t^{\alpha} g(\xi)\,dx = \int t^{\alpha+\beta} g(\xi)\,d\xi.$$

This is indpt. of time only if $\alpha = -\beta = -1/2$.

Exercise For d dimension, $\frac{\partial n}{\partial t} = D\nabla^2 n$. $N = \int_{\mathbb{R}^d} d^d x\, n$.

Let $n(\underline{x},t) = t^{\alpha} g(r/t^{\beta})$, $r = |\underline{x}|$, what α,β work?

Different BCs

Look for sol^{n}s with $n(x,t) \to \begin{cases} 1 & x \to +\infty \\ -1 & x \to -\infty \end{cases}$.

We no longer have conserved N. since $\int n\,dx$ ill defined.

Try

$$n(x,t) = t^{\alpha} g(\xi), \quad \xi = x/\sqrt{Dt}.$$

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} \Rightarrow \alpha - \frac{1}{2}\xi g = g''$$

Require $n(x,t) \to \pm 1$ indpt of time, as $x \to \pm\infty \Rightarrow \alpha \to 0$.

$$\Rightarrow g'' + \frac{1}{2}\xi g' = 0$$

Integrate

$$\Rightarrow g'(\xi) = Ae^{-\xi^2/4}$$

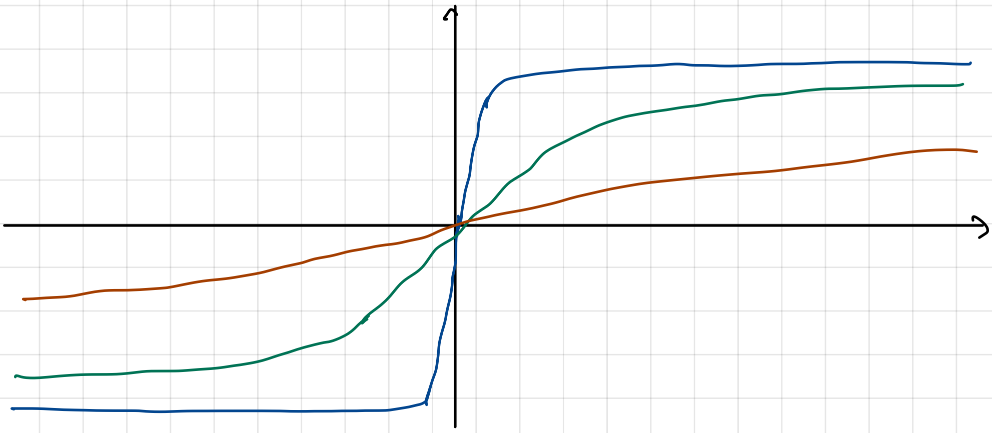
$$\Rightarrow g(\xi) = B + A\underbrace{\int_0^{\xi} d\eta\, e^{-\eta^2/4}}_{\text{This is the error f}^n}$$

$\text{Erf}(x) = \frac{2}{\sqrt{\pi}}\int_0^x dy\, e^{-y^2}$.

So that $\mathrm{Erf}(x) \approx \frac{2x}{\sqrt{\pi}}$ for $x \ll 1$. $\mathrm{Erf}(x) \approx \pm 1$ as $x \to \pm\infty$.

Fix A, B by BC

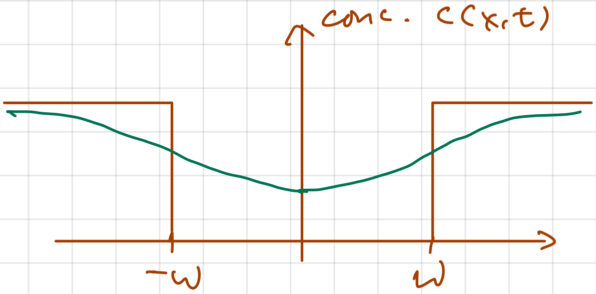
$$n(x,t) = \mathrm{Erf}\left(\frac{x}{\sqrt{4Dt}}\right).$$



Again, the sharp kink gets smoothed at with width $\Delta x \sim \sqrt{Dt}$.

Example FRAP (Fluoresence recovery after photobleaching).

This is an experiment to measure D in cells. Add fluorescence, zap it, watch it recover.



$$c(x,t) = 1 - \frac{1}{2}\mathrm{Erf}\left(\frac{x+\omega}{\sqrt{4Dt}}\right) + \frac{1}{2}\mathrm{Erf}\left(\frac{x-\omega}{\sqrt{4Dt}}\right).$$

Exercise For $\omega = 10^{-6}$ m, the flourescence is half recovered after 1s. Estimate D.

Diffusion with growth

We can solve $\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + \lambda n$

by $n(x,t) = \frac{N}{\sqrt{4\pi Dt}} e^{\lambda t} e^{-x^2/4t}$

For any fixed x, we have $t \to \infty$,

$$n(x,t) \to \begin{cases} 0 & \lambda < 0 \\ \infty & \lambda > 0 \end{cases}$$

So growth beats diffusion (less interesting than on an interval.)

Note: No similarity sol^n $n(x,t) = t^\alpha g(x/t^\beta)$ in this case. Find

$$t^{\alpha-1}(\alpha g - \beta \xi g') = t^{\alpha-2\beta} D g'' + \lambda t^\alpha g$$

$\xi = x/t^\beta$

Different t scalings → no sol^n. Typically, no similarity sol^n when we have ≥ 3 terms.

Non-linear diffusion

A more complicated and interesting set of problems arise when

$$D = D(n(x,t)).$$

For example, $D = kn$, k const. so

$$\frac{\partial n}{\partial t} = k \frac{\partial}{\partial x}\left(\underbrace{n \frac{\partial n}{\partial x}}\right).$$

$J = D \frac{\partial n}{\partial x}$ so still cty eqn.

For $J \to 0$ at $x \to \pm\infty$,

$$N = \int_{-\infty}^{\infty} dx \; n(x,t).$$

We'll look for sim. sol^{n}s. Need some dim. analysis.

$$[k] = L^2 T^{-1} n^{-1}, \quad [N] = Ln.$$

Construct dimensionless variable.

$$\xi = \frac{x}{(NkT)^{1/3}}$$

and ansatz

$$n(x,t) = \frac{N}{(NkT)^{1/3}} f(\xi)$$

Exercise Find suitable ansatz when $D = kn^2$.

Can check that $\int_{-\infty}^{\infty} dx\, n = N$ becomes

$$\int_{-\infty}^{\infty} d\xi\, f = 1 .$$

Now do the algebra

$$\frac{\partial \xi}{\partial t} = -\frac{1}{3}\xi/t, \qquad \frac{\partial \xi}{\partial x} = \frac{1}{(NkT)^{1/3}} = \xi/x.$$

$$\Rightarrow \quad \frac{\partial x}{\partial t} = \frac{1}{3t}\frac{N}{(NkT)^{1/3}} f + \frac{N}{(NkT)^{1/3}} f' \frac{\partial \xi}{\partial t} = -\frac{1}{3t}\frac{N}{(NkT)^{1/3}}\frac{d}{d\xi}(\xi f).$$

Meanwhile,

$$\frac{\partial}{\partial x}\left(n\frac{\partial n}{\partial x}\right) = \frac{1}{(NkT)^{1/3}}\frac{\partial}{\partial \xi}\left(\frac{Nf}{kt}\frac{df}{d\xi}\right) = \frac{1}{kt}\frac{N}{(Nkt)^{1/3}}\frac{d}{d\xi}(ff')$$

Non-linear diffusion becomes

$$\frac{d}{d\xi}(ff') = -\frac{1}{3}\frac{d}{d\xi}(\xi f).$$

with $f, f' \to 0$ as $x \to \pm\infty$.

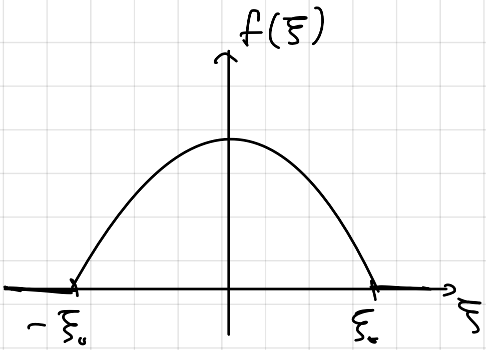
$$\Rightarrow \quad ff' = -\frac{1}{3}\xi f.$$

Two sol^n:

- $f = 0$ (boring)
- $f' = -\frac{1}{3}\xi \quad \Rightarrow \quad f = -\frac{1}{6}\xi^2 + \text{const}.$ ← doesn't obey BC.

Splice the two sol^n together.

$$f(\xi) = \begin{cases} A - \frac{1}{6}\xi^2 & |\xi| < \xi_0 = \sqrt{6A}. \\ 0 & |\xi| > \xi_0 \end{cases}$$



The sol^n is cts. but f' discts at $\xi = \pm\xi_0$

Why is this allowed? Roughly because eqn is

$$f(f' + \tfrac{1}{3}\xi) = 0$$

and the $f=0$ beats the discty in f' at $\xi = \pm\xi_0$.

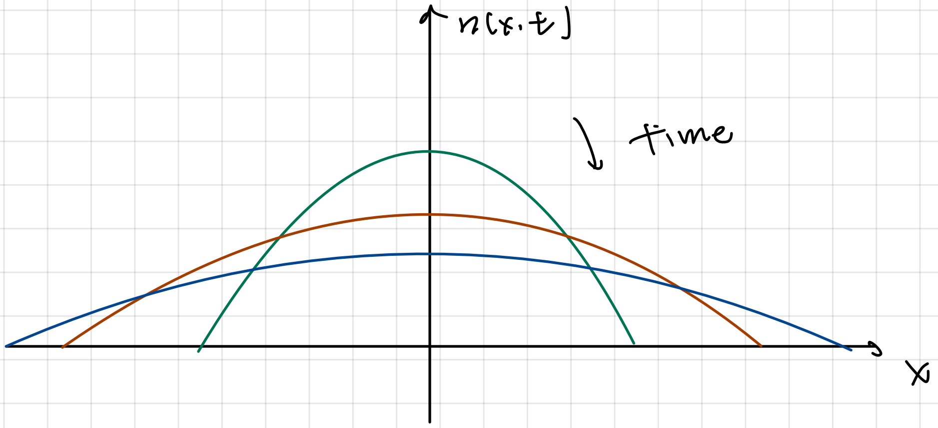
We fix the const. by normalisation condition

$$1 = \int_{-\xi_0}^{\xi_0} d\xi \, f(\xi) = 2A\xi_0 - \frac{1}{9}\xi_0^3 = \frac{4\sqrt{6}}{3} A^{3/2}$$

$$\Rightarrow A = \left(\frac{3}{32}\right)^{1/3}, \quad \xi_0 = \left(\frac{9}{2}\right)^{1/3}$$

$$\Rightarrow n(x,t) = \frac{1}{6}\frac{N^{2/3}}{(kt)^{1/3}}\left(\left(\frac{9}{2}\right)^{1/3} - \frac{x^2}{(Nkt)^{2/3}}\right) = \frac{1}{6kt}(x_0^2 - x^2)$$

With $x_0 = \left(\frac{9}{2}Nkt\right)^{1/3}$ for $x < x_0$, and $n(x,t) = 0$ o/w



2.2 Travelling Waves

Consider 1D reaction-diffusion eqn.

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + F(n) \leftarrow \text{forcing term / "reaction"}$$

For spatially homogeneous sol^n with $\partial n/\partial x = 0$, have dyn. sys.

$$\frac{\partial n}{\partial t} = F(n).$$

At a FP n^* obeys $F(n^*) = 0$. Then look at perturbation

$$n(x,t) = n^* + \varepsilon(x,t), \quad \varepsilon \ll 1.$$

which obeys

$$\frac{\partial \varepsilon}{\partial t} = D \frac{\partial^2 \varepsilon}{\partial x^2} + \lambda \varepsilon + \dots \, , \qquad \lambda = \left.\frac{\partial F}{\partial n}\right|_{n^*} .$$

This is linear diffusion + linear growth. As we've seen

- $\lambda < 0 \Rightarrow$ stable
- $\lambda > 0 \Rightarrow$ unstable.

The instability is the interesting case. What happens as the perturbation grows?

The Fisher equation

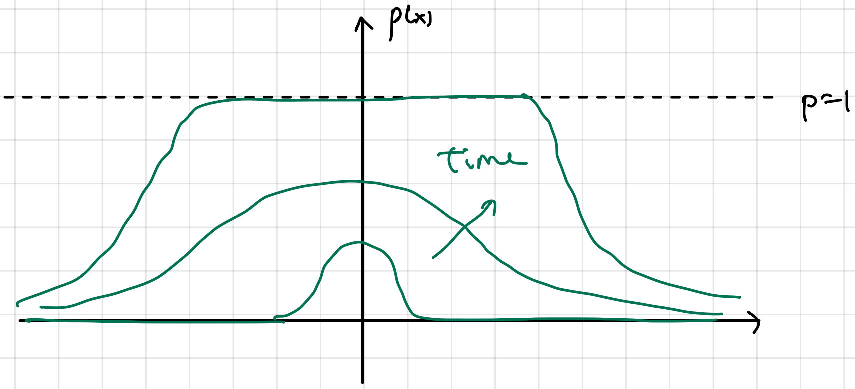
Consider a dimensionless dynamical variable $p(x,t)$, obeying

$$\frac{\partial p}{\partial t} = \underset{\text{diffusion}}{\frac{\partial^2 p}{\partial x^2}} + \underset{\text{logistic}}{p(1-p)}$$

This is the Fisher equation (or KPP - Fisher eqn)

This is used to model spread of advantageous genes (Fisher 1937).

or other "beneficial" mutation.



Intuitively, we expect some spatially localised perturbation.

Expect perturbation to grow and spread.

We will focus on the leading edge of the solⁿ.

Rather surprisingly, this is described by a wave-like solⁿ.

$$p(x,t) = f(\xi), \qquad \xi = x - ct.$$

with $c>0$ is some unknown wave speed.

With the ansatz, the Fisher eqn becomes

$$-cf' = f'' + f(1-f) \qquad , \quad f \in [0,1]$$

We'll look at this in various ways

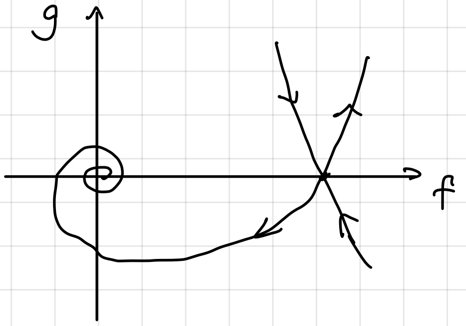
First, we write $g = f'$. and $g' = -cg - f(1-f)$. This is now the kind of dynamical systems.

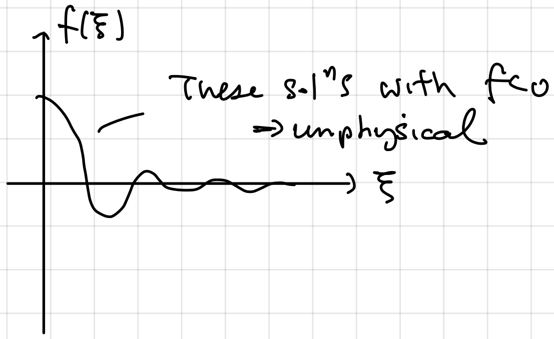
Exercise Show that the FP are at $(f,g) = (0,0)$ $(1,0)$.

Compute Jacobians J at each FP to show

- $(1,0)$ saddle
- $(0,0)$ stable focus / spiral for $c<2$. (evals $\lambda \pm i\omega$)
- $(0,0)$ Stable for $c \geq 2$.

ie. $c<2$

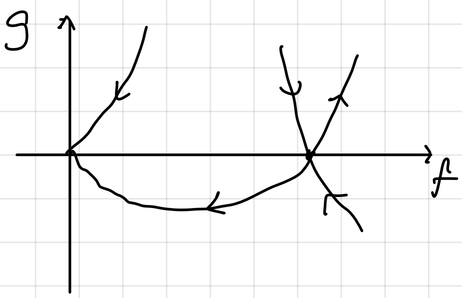


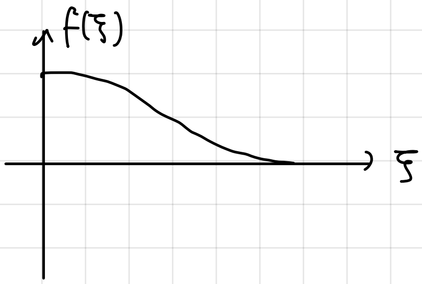


This means that physical sol^n must have $c \geq 2$.

The sol^{n}s that start near $(f,g) = (1,0)$. look like

$c \geq 2$





These are sol^n that we want. They seem to exist $\forall\, c \geq 2$.

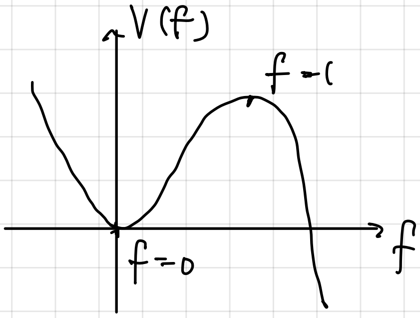
We will revisit this soon.

Note Sol^{n}s go from $f=1 \to f=0$. But we expect $p=0 \to p=1$. This is because $\xi = x - ct$ measures time with a minus sign.

A different method: A mechanical analogy

Write $f'' = f(f-1) - cf' = \frac{\partial V}{\partial f} - cf'$ with $V = \frac{1}{2}f^2 - \frac{1}{3}f^3$.

This looks like a problem with f the position of a particle, and $-cf'$ due to friction.

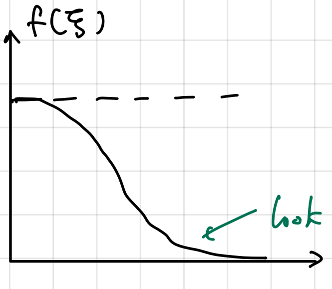


$f=1$ unstable

$f=0$ stable

The situation with $c<2$ has little friction (under-damped) so we go to $f<0$. Meanwhile, $c>2$ is over-damped, and $c=2$ is critical damping.

Linearised Analysis



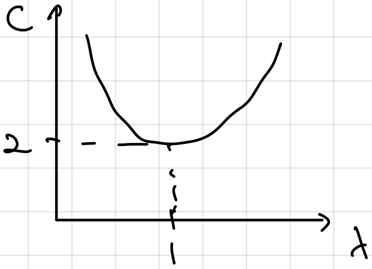
look at where $f \ll 1$.

Look at leading edge of wave where $f \ll 1$ and linearise

$$-cf' = f'' + f$$

Solve by $f(\xi) = e^{-\lambda\xi}$, $\lambda > 0$.

$$\Rightarrow \lambda^2 - c\lambda + 1 = 0 \Rightarrow c = \lambda + \frac{1}{\lambda}.$$



We learn that the speed and the shape of the (leading edge of the) wave are related.

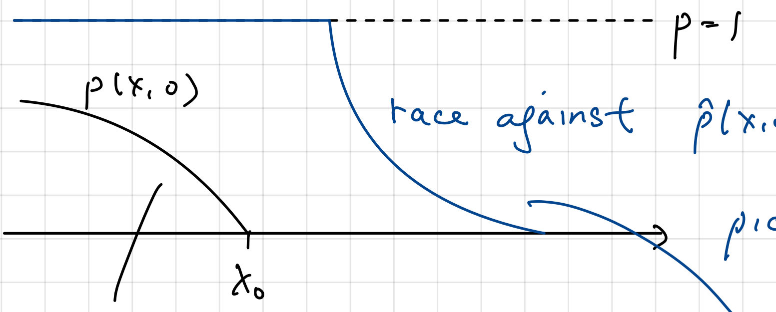
Non-linear Wave

Claim With IC $\rho(x,0) = 0 \;\forall\; |x| \geq X_0$. the system will ultimately settle down to a wave with $c=2$.

Argument: • Non-linear wave must have speed $c \geq 2$.

• We will show that non-linear speed $\leq$ each possible speed of linear wave

Consider localised IC $p(x,0)=0$ for $|x| \geq X_0$.



race against $\hat{p}(x,0) = \begin{cases} Ae^{-\lambda x} & 0<p<1 \\ 1 & \text{o/w} \end{cases}$

pick A s.t. $p(x,0) < \hat{p}(x,0)$

evolve by $\dfrac{\partial p}{\partial t} = \dfrac{\partial^2 p}{\partial x^2} + p(1-p)$

evolve by

$$\frac{\partial \hat{p}}{\partial t} = \frac{\partial^2 \hat{p}}{\partial x^2} + \hat{p}$$

travels with $c = \lambda + \frac{1}{\lambda}$.

We will show that for any λ, $p(x,t)$ can never overtake $\hat{p}(x,t)$ (The $-p^2$ term only delays things).

Define $g(x,t) = \hat{p}(x,t) - p(x,t)$, then

$$\frac{\partial g}{\partial t} = \frac{\partial \hat{p}}{\partial t} - \frac{\partial p}{\partial t} = \frac{\partial^2 g}{\partial x^2} + g + p^2 \geq \frac{\partial^2 g}{\partial x^2} + g$$

i.e. $\partial g/\partial t$ at least as fast as diffusion with linear growth

If $g(x,0)>0$, then $g(x,t)>0 \;\forall t$, i.e. $\hat{p}(x,t) \geq p(x,t) \;\forall t$ and non-linear speed $\leq$ linear speed $\forall t$, i.e. non-linear speed is $c=2$.

Front Propagation in a Bistable system

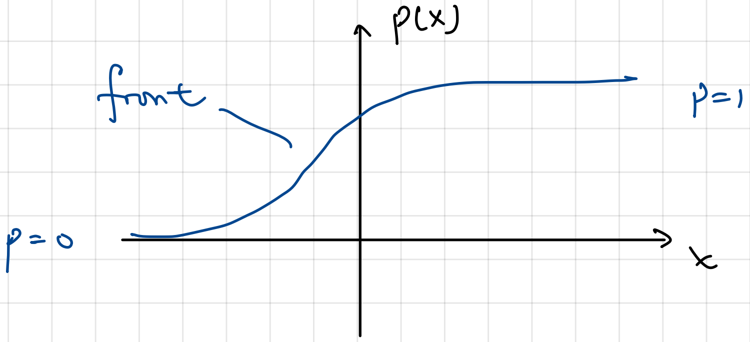
Consider $$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial x^2} - p(p-r)(p-1)$$

with $0<r<1$.

When $\partial p/\partial x = 0$, FP are $p=0,1$ (stable), $p=r$ (unstable).

This is a bistable system.

Suppose that we have IC $p(x,0)$



Does the front move left or right?

We might view this as a model for disease propagation, or for how chemicals spread.

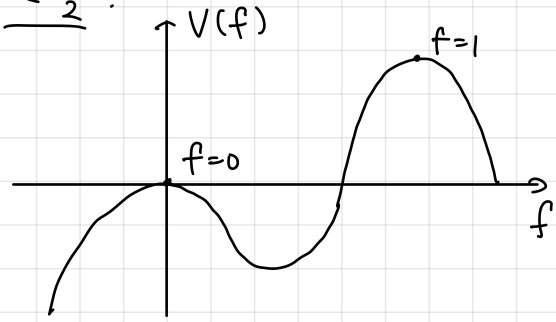
Again, look for a wave sol^n $p(x,t)=f(\xi)$, $\xi = x - \overset{\text{unknown}}{c}t$.

We get $$-cf' = f'' - f(f-r)(f-1)$$

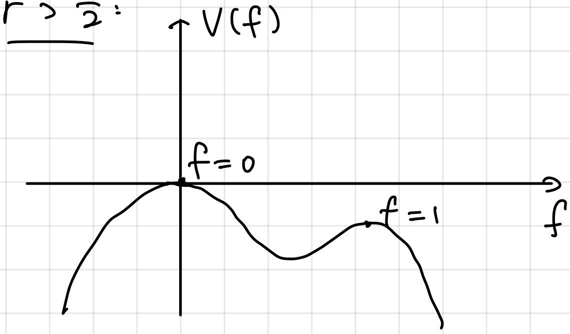
Write this as $$f'' = -\frac{\partial V}{\partial f} - cf',$$

with $V(f) = -\frac{1}{4}f^4 + \frac{1}{3}(1+r)f^3 - \frac{1}{2}rf^2$.

$r<\frac{1}{2}$:



$r>\frac{1}{2}$:



- c large ⇒ friction large and settle in minimum.
- c small ⇒ overshoots
- c critical s.t. $f=1 \to f=0$ is a sol^n. This is the value of c we want.

There are only sol^{n}s that interpolate between $f=0$ and $f=1$ for specific value of c.

recall $\xi = x - ct$

For $r < \frac{1}{2}$, interpolate from $f=1$ to $f=0$. ⇒ $p(x,t) \to 1$ as $t \to \infty$

⇒ front moves left

For $r > \frac{1}{2}$, from $f=0$ to $f=1$ ⇒ $p(x,t) \to 0$ as $t \to \infty$

⇒ front moves right.

This time, the mechanical analogy fixes the speed c.

To determine c, consider

$$\int_{-\infty}^{\infty} d\xi \, \underbrace{f'f''}_{\frac{1}{2}\frac{d}{d\xi}(f')^2} = \int_{-\infty}^{\infty} d\xi \left(-f'\frac{dV}{df} - cf'^2\right) = \int_{-\infty}^{\infty} d\xi \left(-\frac{dV}{d\xi} - cf'^2\right.$$

but $f' \to 0$ as $\xi \to \pm\infty$

$$\Rightarrow \quad c = \frac{\Delta V}{\int_{-\infty}^{\infty} d\xi (f')^2} = \frac{\frac{1}{6}\left(\frac{1}{2} - r\right)}{\int_{-\infty}^{\infty} d\xi (f')^2}$$

using $\Delta V = V(f=1) - V(f=0)$

We need to compute $\int d\xi (f')^2$, and for this, we usually need $f(\xi)$.

We can compute $f(\xi)$ when $r = \frac{1}{2}$, so $c = 0$. Check that

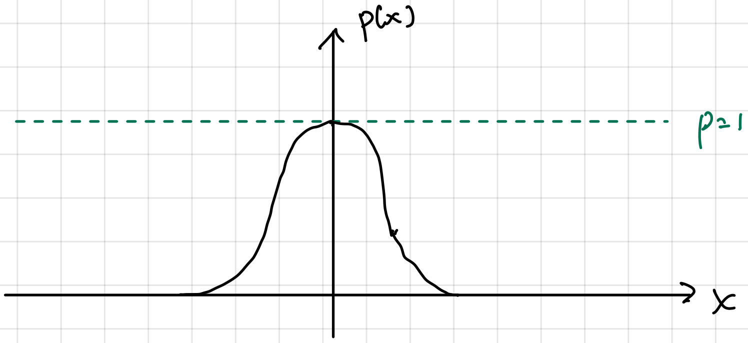
$$f(\xi) = \frac{1}{2}\left(1 - \tanh(\xi/2\sqrt{2})\right)$$

For $r \approx \frac{1}{2}$, we could do an expansion in $(r-\frac{1}{2})$. To leading order, use $f(\xi)$ above in the integral. We get

$$C = 2(r-\tfrac{1}{2}) + O((r-\tfrac{1}{2})^2)$$

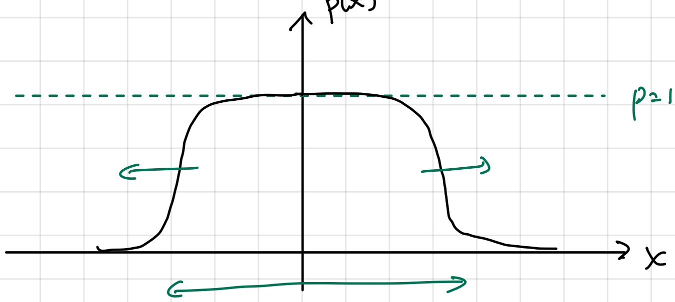
Localised Perturbations

Consider

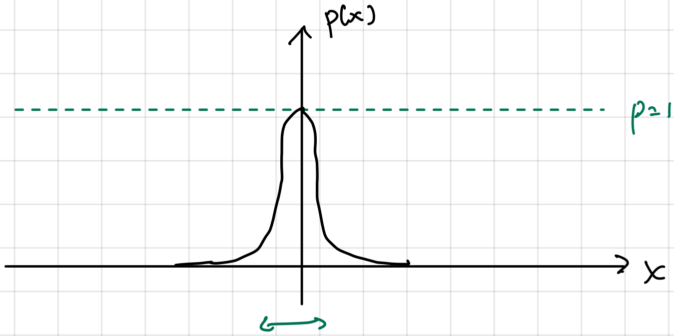


Does this shrink or grow?

- $r > \frac{1}{2} \Rightarrow$ shrinks to $p=0$
- $r < \frac{1}{2} \Rightarrow$ more complicated and depends on width of perturbation.



large width will grow



Small width, shrinks to $p=0$ state

Dengue Revisited

Recall our Walbachia vs mosquitoes from §1.4. This was a 2D sys.

$$\overset{\text{uninfected}}{\frac{du}{dt}} = u\left(u_0 - \frac{v}{u+v} - (u+v)\right)$$

$$\overset{\text{infected}}{\frac{dv}{dt}} = v(v_0 - (u+v))$$

Exercise Show that $p = \frac{v}{u+v}$ (i.e. prop. of infected) obeys

$$\frac{dp}{dt} = -p(p-r)(p-1), \quad r = u_0 - v_0 \in (0,1)$$

Now add diffusion to capture spread of infected mosquitos, with $\rho = \rho(t,x)$.

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

ie. localised region of infected mosquitos spreads only if $r < \frac{1}{2}$.

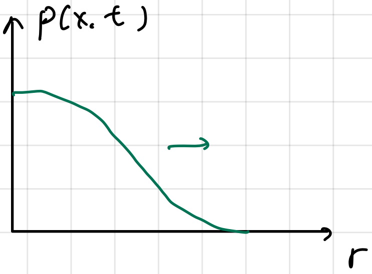
Exercise Suppose insecticide kills mosquitos at const. per capita rate (same for u, v). How will this change the required introduction width?

Note Mosquitos definitely move in 2D, not 1D, with circular symmetry.

We have

$$\frac{\partial p}{\partial t} = \frac{\partial^2 p}{\partial r^2} + \frac{1}{r}\frac{\partial p}{\partial r} - p(p-r)(p-1)$$

$r > 0$, $dp/dr < 0$, so $\frac{1}{r}\frac{dp}{dr}$ slows down propagation of the wave. But as $r \to \infty$, it becomes less important, and so we reduce to the 1D sol^n.



2.3 Turing Instability

The surprising result is that homogeneous stable sol^n and diffusion

$\Rightarrow$ unstable and inhomogeneous.

Consider the 2-variable reaction diffusion eqns.

$$\frac{\partial u}{\partial t} = f(u,v) + D_1 \nabla^2 u$$

$$\frac{\partial v}{\partial t} = g(u,v) + D_2 \nabla^2 v.$$

with $D_1, D_2 > 0$.

Assume $\exists$ homogeneous stable FP (u^*, v^*), i.e.

$$f(u^*, v^*) = g(u^*, v^*) = 0$$

Jacobian is $J = \begin{pmatrix} f_u & f_v \\ g_u & g_v \end{pmatrix}_{(u^*, v^*)}$,

Stability means $\mathrm{Tr}\, J = f_u + g_v < 0$

$$\det J = f_u g_v - f_v g_u > 0.$$

Now perturbations can vary in space

$$u(\underline{x}, t) = u^* + \hat{u}(t)\, e^{i\underline{k}\cdot\underline{x}}$$

$$v(\underline{x}, t) = v^* + \hat{v}(t)\, e^{i\underline{k}\cdot\underline{x}}$$

linearise eqn $\Rightarrow$ can take Re, Im

Taylor expand and keep linear terms

$$\frac{d\hat{u}}{dt} = f_u \hat{u} + f_v \hat{v} - D_1 k^2 \hat{u}$$

$$\frac{d\hat{v}}{dt} = g_u \hat{u} + g_v \hat{v} - D_2 k^2 \hat{v}. \qquad , \quad k^2 = \underline{k}\cdot\underline{k}$$

evaluated at (u^*, v^*)

Is the FP stable against inhomogeneous perturbations?

$$J_{new} = \begin{pmatrix} f_u - D_1 k^2 & f_v \\ g_u & g_v - D_2 k^2 \end{pmatrix}$$

We have $\mathrm{Tr}\, J_{new} = \mathrm{Tr}\, J - (D_1 + D_2) k^2 < 0$

$$\det J_{new} = (f_u - D_1 k^2)(g_v - D_2 k^2) - f_v g_u$$

$$= \det J - k^2 (D_1 g_v - D_2 f_u) + D_1 D_2 k^4$$

Stability requires $\det J_{new} > 0$, but not generalised.

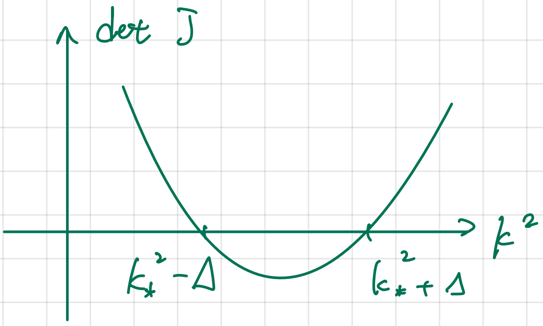
Write $\det J_{new} = A k^4 - B k^2 + C$.

We have $\det J_{new} < 0$ if $B > 0$, $B^2 - 4AC > 0$

$$\Rightarrow \boxed{D_1 g_v + D_2 f_u > \sqrt{4D_1D_2(f_u g_v - f_v g_u)}}$$

This is the condition for Turing instability.

Note The sys. is stable for long wavelength ($k \ll 1$) pert. and short wavelengths ($k \gg 1$). Instability arises in an intermediate regime



with $k_* = \sqrt{\frac{B}{2A}}$, $\Delta = \frac{\sqrt{B^2-4AC}}{2A}$.

The system borders on instablity when $B^2 = 4AC$. At this point the first mode become unstable is

$$k_* = \left(\frac{C}{A}\right)^{1/4} = \left(\frac{\det J}{D_1 D_2}\right)^{1/4}$$

This corresponds to a wavelength $\lambda_* = 2\pi/k_*$.

The end point of the instability is typically a pretty pattern depending on $f(u,v)$ and $g(u,v)$.

The patterns on animal's coat are conjectured to arise from Turing instability.

The Turing instability requires $D_1 \neq D_2$. If $D_1 = D_2$, then $J_{new} = J - k^2 D_1 I$, and Re(evals) of J_{new} are -ve $\Rightarrow$ stable

Define $d = D_1/D_2$, then Turing instability requires

$$f_u + d g_v > 0 .$$

But we know $\operatorname{Tr} J = f_u + g_v < 0$, so clearly $d \neq 1$.

Note: For instability, need f_u, g_v opposite sign.

Suppose $f_u > 0 \Rightarrow u$ is activator

$g_v < 0 \Rightarrow v$ is inhibitor

In finite domain, we typically impose BC that make $\underline{k}$ discrete.

The minimum k is $k_0 = 2\pi / L$.

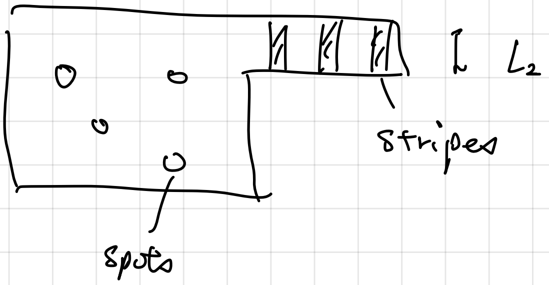
$\uparrow$ size of sys.

For small sys, $k_0^2 > k_*^2 + \Delta \Rightarrow$ no instability

Consider a rectangle, $L_1 \times L_2$, BCs s.t. $k_1 = \frac{2\pi n_1}{L_1}$, $k_2 = \frac{2\pi n_2}{L_2}$

Suppose L_1, L_2 suitably large, instability gives rise to spots

When $L_2 \ll L_1$, we could have no instability in y-dir, but still unstable in x-dir.



e.g. animal tails.

Example Consider
$$\frac{\partial u}{\partial t} = -u + u^2 v + \nabla^2 u$$
$$\frac{\partial v}{\partial t} = b - u^2 v + d \nabla^2 v \quad . \qquad b > 0$$

ratio of diffusivities

FP $(u^*, v^*) = (b, 1/b)$ with $J = \begin{pmatrix} 1 & b^2 \\ -2 & -b^2 \end{pmatrix}$

$\operatorname{tr} J = 1 - b^2$

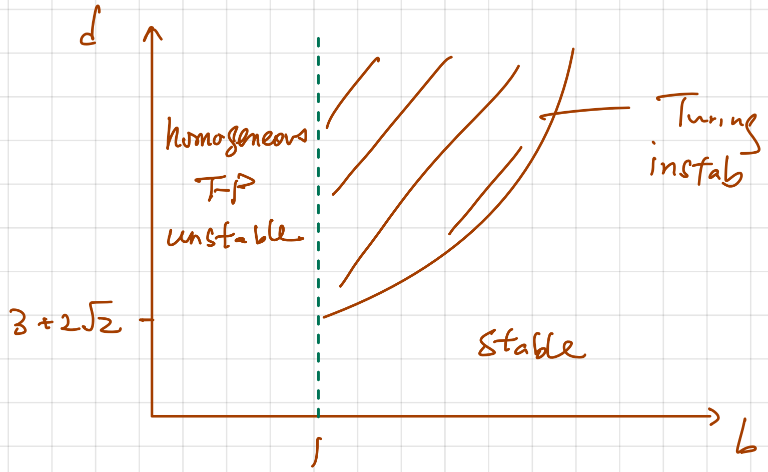
$\det J = b^2 > 0$

$\Rightarrow$ stability if $b > 1$

With diffusion. $J_{new} = \begin{pmatrix} 1-h^2 & b^2 \\ -2 & -b^2-dh^2 \end{pmatrix}$.

$$\det J_{new} = dh^4 - (d-b^2)h^2 + b^2$$

This has roots provided that $d - b^2 \geq 4b\sqrt{d} \Rightarrow d > (3+2\sqrt{2})\, b^2$.



3.2 Chemotaxis

This means movement (typically of bacteria or single celled organisms) due to background chemicals.

- $n(\underline{x},t)$ = density of bacteria
- $c(x,t)$ = density of a chemical that they like.

The chemical diffuses

$$\frac{\partial c}{\partial t} - D_c \nabla^2 c = G(n,c)$$

Some f^n that specifies the dynamics

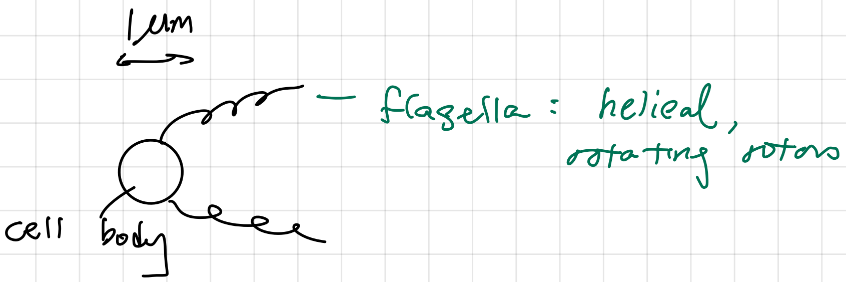
Bacteria diffuses <u>and</u> swims

$$\frac{\partial n}{\partial t} + \nabla \cdot \underline{J} = F(n,c)$$

with $\underline{J} = -D_n \nabla n + n \underline{V}$, $\underline{v} = \chi \nabla c$

diffusion swimming $\chi > 0$ fondness of c

How do bacteria know to swim in direction ∇c?



Two modes of motion

- run = straight line motion at speed ~10 – 50 μm/s.
- tumble = random reorientation every second or so.

Random walk = diffusion. Change in tumbling rate less frequent in higher conc. ⇒ spend longer time where c bigger ⇒ swimming

chemotaxis term

$$\frac{\partial n}{\partial t} = D_n \nabla^2 n - \chi \nabla\cdot(n\nabla c) + F(n,c)$$

$$\frac{\partial c}{\partial t} = D_c \nabla^2 c + G(n,c)$$

Example $F(n,c) = \gamma - \delta n$, $G(n,c) = \alpha n - \beta c$.

const. injection of bacteria · death · production of chemical by bacteria · decay

Homogeneous FP $(n^*, c^*) = \left(\frac{\gamma}{\delta}, \frac{\alpha\gamma}{\beta\delta}\right)$, $J = \begin{pmatrix} -\delta & 0 \\ \alpha & -\beta \end{pmatrix}$

→ evals : $-\delta, -\beta$ ⇒ stable

Now perturb. $n(\underline{x},t) = n^* + u(t) e^{i\underline{k}\cdot\underline{x}}$

$c(\underline{x},t) = c^* + v(t) e^{i\underline{k}\cdot\underline{x}}$

Linearise ⇒

$$\frac{\partial u}{\partial t} = -D_n{}^2 k^2 u + \chi n^* k^2 v - \delta u$$

$$\frac{\partial v}{\partial t} = -D_c{}^2 k^2 v + \alpha u - \beta v.$$

Note if $\chi = 0$ ⇒ stable (ie. no Turing instab)

We have $\operatorname{Tr} J_{new} = -(\alpha+\beta) - k^2(D_n^2 + D_c^2) < 0$

$$\det J_{new} = (\alpha^2 + k^2 D_n)(\alpha + k^2 D_c) - \frac{\alpha r \chi}{\delta} k^2 .$$

Stability requires $\det J_{new} > 0$ but this breaks down if χ big enough

Exercise Show that the first unstable mode as you increase χ is

$$k_* = (\beta\delta / D_n D_c)^{1/4} , \quad \chi = \frac{\delta}{\alpha\beta}\left(\sqrt{\delta D_c} + \sqrt{\beta D_n}\right)^2 .$$

§ 3 Random Variations

We would like to incorporate random fluctuations in our analysis. For this, look at stochastic systems

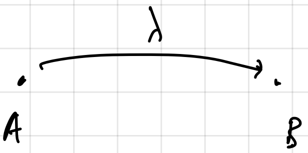
5.1 Discrete Outcomes

Consider a sys. with two states A and B.

$$P(A,t) = \text{prob. in state } A \text{ at time } t.$$

$$P(B,t) = 1 - P(A,t)$$

Transition from $A \to B$ with rate λ, meaning prob. to transition in time δt is $\lambda \delta t$.



$$P(A, t+\delta t) = P(A,t)\,(1-\lambda\delta t)$$

Taylor expand

$$\Rightarrow P(A,t) + \frac{dP(A,t)}{dt}\delta t + O(\delta t^2) = P(A,t)(1-\lambda\delta t)$$

$$\Rightarrow \frac{dP(A,t)}{dt} = -\lambda P(A,t)$$

$$\Rightarrow P(A,t) = e^{-\lambda t}. \quad (\text{assuming } P(A,0)=1)$$

Can we ask for prob. dist^n $f(t)$ to make the jump at time t?

First compute

$$P[t<T] = \int_0^T f(t)\,dt$$

prob. to make the jump $A \to B$ before T.

But $P(t<T) = P(B,T) = 1-e^{-\lambda T}$.

$$\Rightarrow f(t) = \frac{dP(B,t)}{dt} = \lambda e^{-\lambda t}. \quad (\text{relabel } T \to t).$$

This obeys $\int_0^\infty f(t)\,dt = 1$.

The expected time to make the jump is

$$\langle t \rangle = \int_0^\infty t f(t)\,dt = \frac{1}{\lambda}.$$

The variance is

$$\mathrm{Var}(t) = \langle t^2 \rangle - \langle t \rangle^2 = \frac{1}{\lambda^2}$$

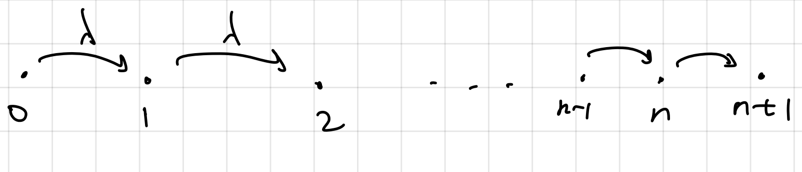
So S.D. is

$$\sigma(t) = \sqrt{\mathrm{Var}(t)} = 1/\lambda.$$

Discrete population size

$P(n,t)$ = prob. population has size $n \in \{0,1,2,\dots\}$ at time t.

Prob. rate λ to add 1 population.



Start at $n=0$,
immigration rather than births

In eqn, for $n \gg 1$,

$$P(n, t+\delta t) = P(n,t)\,(1-\lambda\,\delta(t)) + P(n-1,t)\cdot\lambda\,\delta t.$$

Taylor expand

$$\Rightarrow \quad \frac{dP(n,t)}{dt} = \lambda\left(P(n-1,t) - P(n,t)\right) \qquad (*).$$

This is an example of a master eqn, here for discrete n and cts t.

Exercise Set $P(0,0)=1$, $P(n,0)=0$ for $n\geq 1$. Solve $(*)$ inductively to get

$$P(n,t) = \frac{(\lambda t)^n e^{-\lambda t}}{n!}$$

We solve $(*)$ by introducing generating f^n.

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

Pick $s \in [0,1]$ for convergence.

This encodes lots of useful info, e.g.

$$\langle n(t) \rangle = \sum_{n=0}^{\infty} n\, P(n,t) = \left.\frac{\partial \phi(s,t)}{\partial s}\right|_{s=1}$$

and

$$\langle n^2(t) \rangle = \sum_{n=0}^{\infty} n^2 P(n,t)$$

$$= \sum_{n=0}^{\infty} n(n-1) P(n,t) + \sum_{n=0}^{\infty} nP(n,t)$$

$$= \left.\frac{\partial^2 \phi}{\partial s^2}\right|_{s=1} + \left.\frac{\partial \phi}{\partial s}\right|_{s=1}$$

We can also invert

$$P(n,t) = \frac{1}{n!} \left.\frac{\partial^n \phi(s,t)}{\partial s^n}\right|_{s=0} \qquad (\ddagger)$$

Note We must have $\phi(1,t) = \sum_n P(n,t) = 1$ as a b.c. Other b.c. usually come from $\phi(s,0)$ as i.c.

We can convert master eqn (*) into a DE for $\phi(s,t)$

$$\frac{\partial \phi}{\partial t} = \sum_{n=0}^{\infty} s^n \frac{\partial P(n,t)}{\partial t}$$

$P(-1,t)=0$.

$$= \lambda \sum_{n=0}^{\infty} s^n \left(P(n-1,t) - P(n,t) \right).$$

$$= \lambda \sum_{n=0}^{\infty} \left(s^{n+1} P(n,t) - s^n P(n,t) \right) = \lambda s(s-1)\, \phi(s,t).$$

Integrate

$$\Rightarrow \phi(s,t) = \phi(s,0)\, e^{\lambda(s-1)t}.$$

Pick i.c. $P(n,0) = \delta_{n,0} \Rightarrow \phi(s,0) = 1$.

Then $\phi(s,t) = e^{\lambda(s-1)t}$. From (‡),

$$P(n,t) = \frac{(\lambda t)^n e^{-\lambda t}}{n!}$$

Can compute $\langle n(t) \rangle = \lambda t$ and $\sigma = \sqrt{\lambda t}$.. Importantly,

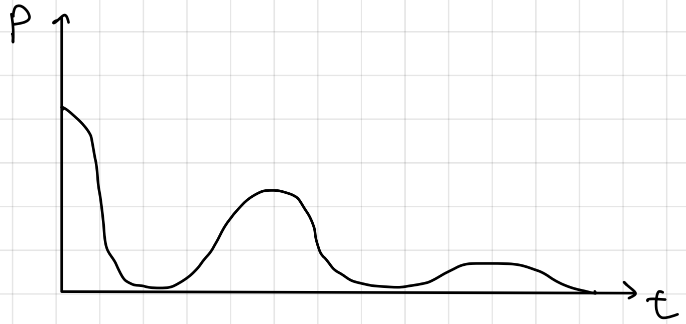
$$\frac{\sigma}{\langle n(t) \rangle} \sim \frac{1}{\sqrt{\lambda t}},$$

i.e. fluctuations are less important over time. The general result

$$\frac{\sigma}{\langle n \rangle} \sim \frac{1}{\sqrt{n}}$$

is very common.

Prob. distⁿ.



ie peak moves and spreads. Using Stirling's. $n! \approx \sqrt{2\pi n}\, n^n e^{-n}$

$$\Rightarrow P(n,t) \approx \frac{1}{\sqrt{2\pi}} e^{-\lambda t} e^{g(n,t)},$$

with $g(n,t) = n + \log(nt) - n \log n - \frac{1}{2} \log n$,

max at $n = n^* \approx \lambda t$

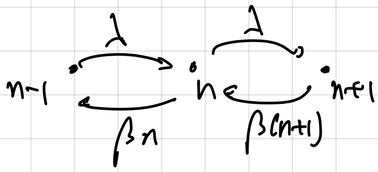
Write $g(n,t) \approx g(n^*) + \frac{1}{2}(n-n^*)^2 \frac{\partial^2 g}{\partial n^2} = \lambda t - \frac{(n-n^*)^2}{2\lambda t} - \frac{1}{2}\log(\lambda t)$.

$$\Rightarrow \quad P(n,t) \approx \frac{1}{\sqrt{2\pi\lambda t}} e^{-(n-\lambda t)^2/2\lambda t}$$

ie. Gaussian marching forward in time with $\langle n \rangle = \lambda t$.

Birth and Death

- const growth rate λ for $n \mapsto n+1$
- const. death rate per capita β for $n \mapsto n+1$



The master eqn is

$$\frac{dP(n,t)}{dt} = -(\lambda+\beta n)P(n,t) + \lambda P(n-1,t) + \beta(n+1)P(n+1,t).$$

The generating f^n $\phi(s,t) = \sum_{n=0}^{\infty} s^n P(n,t)$. obeys

$$\frac{\partial \phi}{\partial t} = \sum_{n=0}^{\infty} s^n \frac{\partial P}{\partial t}$$

$P_n = P(n,t)$

$$= \sum_{n=0}^{\infty} s^n \left[-\lambda P_n + \lambda P_{n-1} - \beta n P_n + \beta(n+1) P_{n+1}\right].$$

$$= \sum_{n=0}^{\infty} \left[-s^n\lambda + s^{n+1}\lambda - s^n\beta n + s^{n-1}\beta n\right] P_n.$$

Use $\frac{\partial \phi}{\partial s} = \sum_{n=0}^{\infty} n s^{n-1} P_n$ to write

$$\frac{\partial \phi}{\partial t} = (s-1)\left(\lambda\phi - \beta\frac{\partial \phi}{\partial s}\right).$$

Note $\phi(1,t) = 1 \Rightarrow \frac{\partial \phi}{\partial t}(1,t) = 0$.

Use ansatz $\phi(s,t) = e^{(s-1)f(t)}$ (obeys $\phi(1,t) = 1$)

$$\Rightarrow \frac{df}{dt} = \lambda - \beta f(t).$$

$$\Rightarrow f(t) = \frac{\lambda}{\beta}(1-e^{-\beta t})$$

assuming $P(n,t) = \delta_{n,0} \Rightarrow \phi(s,0) = 1.$

$$\Rightarrow \phi(s,t) = \exp\left(\frac{\lambda}{\beta}(s-1)(1-e^{-\beta t})\right).$$

Exercise Use ϕ to show that $\langle n\rangle = \mathrm{Var}(n) = \frac{\lambda}{\beta}(1-e^{-\beta t})$.

As $t\to\infty$, we settle down to a steady state $\phi = e^{\frac{\lambda}{\beta}(s-1)}$.

In more complicated situations, we can only compute steady state by setting $\frac{\partial\phi}{\partial t} = 0 \Rightarrow \frac{\partial\phi}{\partial s} = \frac{\lambda}{\beta}\phi$

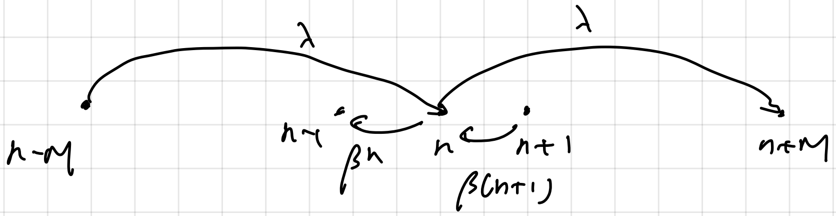
$$\Rightarrow \phi(s) = e^{\frac{\lambda}{\beta}(s-1)}, \text{ using } \phi(1)=1.$$

This translates to the steady state prob. distⁿ.

$$P(n) = \frac{1}{n!}\left(\frac{\lambda}{\beta}\right)^n e^{-\lambda/\beta}.$$

More offspring

Consider the following situation



Then $$\frac{dP_n}{dt} = -(\lambda+\beta n)P_n + \lambda P_{n-M} + \beta(n+1)P_{n+1}.$$

Exercise Show $\frac{\partial\phi}{\partial t} = \lambda(s^M-1)\phi - \beta(s-1)\frac{\partial\phi}{\partial s}$.

This is hard to solve, but steady state solⁿ is

$$\frac{\partial\phi}{\partial s} = \frac{\lambda(s^M-1)}{s-1}\phi.$$

e.g. $M=2 \rightarrow \phi(s) = \exp\left(\frac{\lambda}{\beta}(s+\frac{1}{2}s^2-\frac{3}{2})\right).$

We can also use master eqn to calculate moments directly.

Example
$$\frac{d\langle n(t)\rangle}{dt} = \sum_{n=0}^{\infty} n \frac{dP_n}{dt}$$

$$= \sum_{n=0}^{\infty} n \left[-(\lambda+\beta n) P_n + \lambda P_{n-M} + \beta(n+1) P_{n+1} \right]$$

$$= \sum_{n=0}^{\infty} \left(-\lambda n - \beta n^2 + \lambda(n+M) - \beta(n-1)n \right) P_n .$$

$$= \sum_{n=0}^{\infty} (\lambda M - \beta n) P_n = \lambda M - \beta \langle n(t)\rangle .$$

Solve to get $\langle n(t)\rangle = \frac{\lambda M}{\beta}(1-e^{-\beta t})$.

Also
$$\frac{d\langle n^2(t)\rangle}{dt} = \sum_{n=0}^{\infty} n^2 \frac{dP_n}{dt}$$

$$= \sum_{n=0}^{\infty} n^2 \left[-(\lambda+\beta n) P_n + \lambda P_{n-M} + \beta(n+1) P_{n+1} \right]$$

$$= \sum_{n=0}^{\infty} \left(-\lambda n^2 - \beta n^3 + \lambda(n+M)^2 - \beta n(n-1)^2 \right) P_n$$

$$= \lambda M^2 + (2\lambda M + \beta)\langle n(t)\rangle - 2\beta \langle n^2(t)\rangle .$$

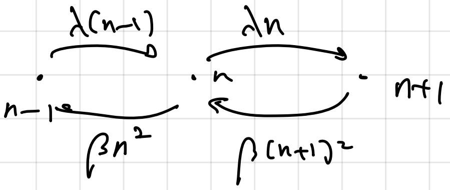
Exercise Show that in steady state,
$$\langle n^2\rangle = \frac{1}{2\beta}\left(\lambda M^2 + \frac{\lambda M}{\beta}(2\lambda M + \beta) \right)$$

and for $M \gg 1$,
$$\mathrm{Var}(n) \approx \frac{\lambda}{2\beta} M^2 ,$$

ie. more offspring ⇒ more variance.

Non-linear growth rates

Above, we found a nice DE for $\langle n(t)\rangle$, but this is because rates were linear. Consider



$$\frac{dP(n,t)}{dt} = -(\lambda n+\beta n^2)\,P(n,t) + \lambda(n-1)\,P(n-1,t) + \beta(n+1)^2 P(n+1,t)$$

Now $$\frac{d\langle n(t)\rangle}{dt} = \sum_{n=0}^{\infty} n\,\frac{dP_n}{dt}$$

$$= \sum_{n=0}^{\infty}\left(-\lambda n^2-\beta n^3+\lambda n(n+1)+\beta(n-1)n^2\right)P(n,t)$$

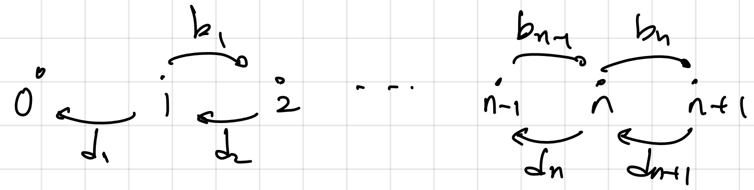
$$= \sum_{n=0}^{\infty}\left(\lambda n-\beta n^2\right)P(n,t) = \lambda\langle n(t)\rangle - \beta\langle n^2(t)\rangle$$

To compute $\langle n(t)\rangle$, need to know $\langle n^2(t)\rangle$. Then for $\langle n^2(t)\rangle$ depends on $\langle n^3(t)\rangle$ and so on.

Extinction

For a closed population, with a birth rate b_n and a death rate d_n.

with



No births when $n=0$, ie. $b_0=0$.

Question: What's prob. of extinction?

Let Q_n = prob. of extinction if start at n. Clearly $Q_0=1$.

Use recurrence relation:

$$Q_n = \frac{b_n}{b_n+d_n}Q_{n+1} + \frac{d_n}{b_n+d_n}Q_{n-1}$$

$$\Rightarrow Q_{n+1}-Q_n = \frac{d_n}{b_n}\left(Q_n-Q_{n-1}\right)$$

$$= \prod_{i=1}^{n}\frac{d_i}{b_i}\left(Q_1-Q_0\right)$$

But relistically, expect that death wins at large n, ie.

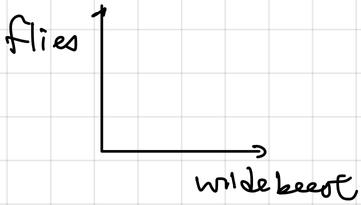
$\exists R>1$ and N s.t. $\frac{d_n}{b_n} > R$ $\forall n>N$.

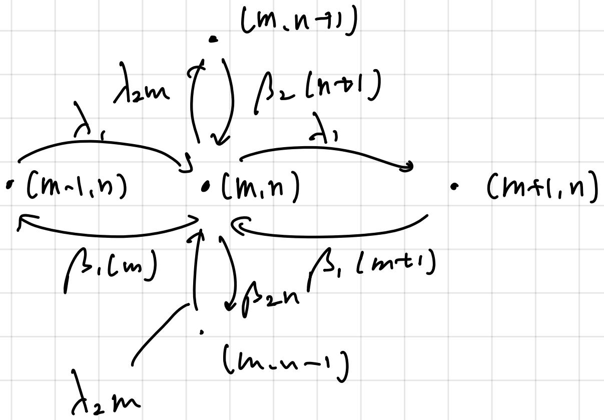
This means that $\prod_{i=1}^{n} d_i/b_i$ gets arbitrarily large for $n \gg N$.

But $Q_i \in [0,1]$, so we must have $Q_{n-1} - Q_n = Q_1 - Q_0 = 0$, but $Q_0 = 1 \Rightarrow Q_n = 1 \ \forall n$, so extinction inevitable, but may take very long time.

Multiple Populations

	Wildebeest : m	Flies : n
Birth rate	λ_1	$\lambda_2 m$ ← Wildebeest attract flies
Death rate	$\beta_1 m$	$\beta_2 n$





$$\frac{dP_{m,n}}{dt} = \lambda_1\left(P_{m-1,n} - P_{m,n}\right) + \beta_1\left((m+1)P_{m+1,n} - mP_{m,n}\right) + \lambda_2\left(mP_{m,n-1} - mP_{m,n}\right) + \beta_2\left((n+1)P_{m,n+1} - nP_{m,n}\right)$$

For wilderbeest.

$$\frac{d\langle m\rangle}{dt} = \lambda_1\left(\langle m+1\rangle - \langle m\rangle\right) + \beta_n\left(\langle (m-1)(m)\rangle - \langle m^2\rangle\right) + \lambda_2\left(\langle m^2\rangle - \langle m^2\rangle\right) + \beta_2\left(\langle mn\rangle - \langle mn\rangle\right).$$

$$= \lambda_1 - \beta_1\langle m\rangle$$

Exercise Show $\frac{d\langle n\rangle}{dt} = \lambda_2\langle m\rangle - \beta_2\langle n\rangle$.

$$\frac{d\langle m^2\rangle}{dt} = \lambda_1 + (2\lambda_1 + 1)\langle m\rangle - 2\beta n\langle m^2\rangle$$

$$\frac{d^2\langle n^2\rangle}{dt} = \lambda_2\langle m\rangle + \beta_2\langle n\rangle + 2\lambda_2\langle mn\rangle - 2\beta_2\langle n^2\rangle$$

$$\frac{d\langle mn\rangle}{dt} = \lambda_1\langle n\rangle + \lambda_2\langle m^2\rangle - (\beta_1+\beta_2)\langle mn\rangle .$$

In steady state, $\langle m\rangle = \lambda_1/\beta_1$, $\langle n\rangle = \frac{\lambda_2}{\beta_2}\langle m\rangle = \lambda_1\lambda_2/\beta_1\beta_2$.

The variance of flies is

$$\mathrm{Var}(n) = \langle n^2\rangle - \langle n\rangle^2 = \frac{\lambda_2}{\beta_2}\langle mn\rangle + \langle n\rangle - \overset{\frac{\lambda_2}{\beta_2}\langle m\rangle\langle n\rangle}{\langle n\rangle^2}$$

$$\Rightarrow \mathrm{Var}(n) = \underbrace{\langle n\rangle}_{\substack{\text{intrinsic variation}\\ \text{of flies}}} + \frac{\lambda_2}{\beta_2}\Big(\underbrace{\langle mn\rangle - \langle m\rangle\langle n\rangle}_{\substack{\text{covariance } \mathrm{Cov}(m,n)\\ \text{extrinsic variability}}}\Big)$$

3.2 The Fokker-Planck Equation

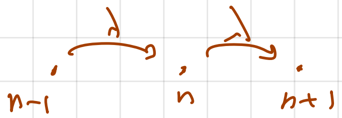
Previously, we derived master eqn for $P(n,t)$ with n discrete.
Now we want to extend this to $P(x,t)$ with $\underline{x} \in \mathbb{R}^d$.

First, we rewrite our previous results

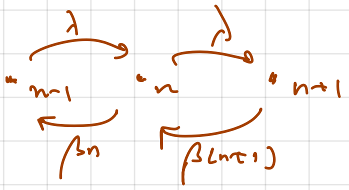
$$W(n,r) = \text{jump rate from } n \text{ to } n+r \quad (n,r\in\mathbb{Z})$$

i.e. r is jump size. Typically $W(n,r)\neq 0$ only for small subset of small values of r.

Example



$$W(n,r) = \begin{cases} \lambda & r=1 \\ 0 & \text{o/w}. \end{cases}$$



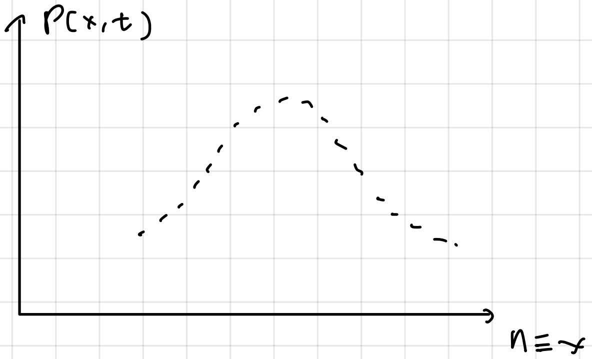
$$W(n,r) = \begin{cases} \lambda & r=1 \\ \beta n & r=-1 \\ 0 & \text{o/w}. \end{cases}$$

Master eqn is

relabel n as x (still think as discrete)

$$\frac{dP(n,t)}{dt} = \sum_{r\in\mathbb{Z}}\left[W(n-r,r)\,P(n-r,t) - W(n,r)\,P(n,t)\right].$$

The key idea is that for $x \gg r$ (with $W(x,r) \neq 0$), the distⁿ $P(x,t)$ looks cts.



RHS of master eqn looks like $f(x-r) - f(x)$ with $f(x) = W(x,r)\,P(x,t)$

Write

$$f(x-r) \approx f(x) - r\frac{df}{dx} + \frac{1}{2}r^2\frac{d^2f}{dx^2} + \underbrace{\dots}_{\text{drop these}}$$

Then

$$\frac{\partial P}{\partial t}(x,t) = \sum_{r\in\mathbb{Z}}\left(-r\frac{\partial}{\partial x}\big(W(x,r)\,P(x,t)\big) + \frac{1}{2}r^2\frac{\partial^2}{\partial x^2}\big(W(x,r)\,P(x,t)\big)\right)$$

Write this as

$$\frac{\partial P(x,t)}{\partial t} = -\frac{\partial}{\partial x}\big(u(x)\,P(x,t)\big) + \frac{\partial^2}{\partial x^2}\big(D(x)\,P(x,t)\big).$$

with $u(x) = \sum_{r\in\mathbb{Z}} r\,W(x,r)$, $D(x) = \frac{1}{2}\sum_{r\in\mathbb{Z}} r^2 W(x,r)$.

This is the Fokker-Planck eqn.

Comment Often write $\frac{\partial P}{\partial t} = -\frac{\partial}{\partial x}(AP) + \frac{1}{2}\frac{\partial^2}{\partial x^2}(BP)$, with $A = u$, and $B = 2D$.

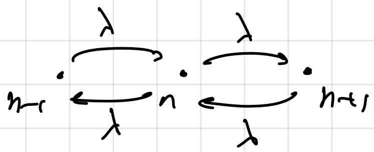
Probability conserved, with $\int dx\, P(x,t) = 1$, and the FP eqn is a cty eqn

$$\frac{\partial P}{\partial x} + \frac{\partial J}{\partial x} = 0$$

with $J = \underbrace{uP}_{\text{advection/drift}} + \underbrace{\frac{\partial}{\partial x}(DP)}_{\text{diffuse}}$

Diffusion Revisited

Consider the process



We have $W(n,1) = W(n,-1) = \lambda$.

$$\Rightarrow u = 0, \qquad D = \lambda.$$

In this case, FP is diffusion eqn

$$\frac{\partial P}{\partial t} = D \frac{\partial^2 P}{\partial x^2}$$

This kind of randomness underlies all diffusion, e.g. Brownian motion, spread of ink in water. The diffusion eqn captures microscopic random walk.

Note Previously, we thought of population densities $n(x,t)$ or chemical concentrations $c(x,t)$ diffusing. Closely related to probabilities as $n(x,t) = N P(x,t)$, with N = total population.

Moments

We can use FP eqn to see how moments of x evolve, e.g. $x, x^2, \dots$

$$\frac{d\langle x\rangle}{dt} = \int dx\, x \frac{\partial P}{\partial t} = \int dx\, x\left(-\frac{\partial}{\partial x}(uP) + \underbrace{\frac{\partial^2}{\partial x^2}(DP)}_{}\right)$$

IBP twice.

and use $P(x,t) \to 0$ as $|x| \to \infty$

$$= \int dx\, uP$$

$$= \langle u(x)\rangle$$

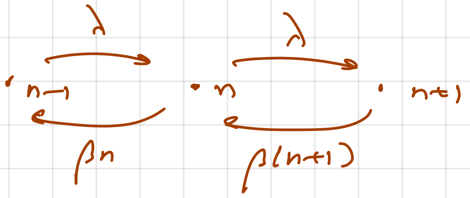
The f^n $u(x)$ governs drift of distribution.

$$\frac{d\langle x^2\rangle}{dt} = \int dx\, x^2\left(-\frac{\partial}{\partial x}(uP) + \frac{\partial^2}{\partial x^2}(DP)\right) = 2\langle x u(x)\rangle + 2\langle D(x)\rangle.$$

For $\mathrm{Var}(x) = \langle x^2\rangle - \langle x\rangle^2$, we get

$$\frac{d\,\mathrm{Var}(x)}{dt} = 2\langle D(x)\rangle + 2\,\underbrace{\mathrm{Cov}(x, u(x))}_{= \langle x u(x)\rangle - \langle x\rangle\langle u(x)\rangle.}$$

Example



with $W(n,r) = \begin{cases} \lambda & r=1 \\ \beta n & r=-1 \\ 0 & \text{o/w} \end{cases}$

FP eqn has $u(x) = W(x,1) - W(x,-1) = \lambda - \beta n$

$$D(x) = \tfrac{1}{2}\left(W(x,1) + W(x,-1)\right) = \tfrac{1}{2}(\lambda + \beta n)$$

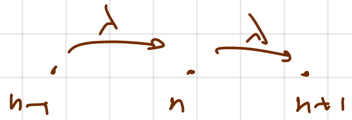
We have $\dfrac{d\langle x\rangle}{dt} = \lambda - \beta\langle x\rangle \Rightarrow \langle x\rangle = \dfrac{\lambda}{\beta}\left(1 - e^{-\beta t}\right)$

$$\frac{d\langle x^2\rangle}{dt} = \lambda + (2\lambda + \beta)\langle x\rangle - 2\beta\langle x^2\rangle$$

So steady state has $\langle x\rangle = \mathrm{Var}(x) = \lambda/\beta$.

Both the first two moments agree with discrete case. This is because we truncate the Taylor expansion to 2nd order.

Exercise For



s.t. $W(n,1) = \lambda$. Compute $\langle x\rangle, \langle x^2\rangle$, and show that $\langle x^3\rangle = (\lambda t)^3 + 3(\lambda t)^2$. Now return to discrete model and compute $\langle n\rangle, \langle n^2\rangle, \langle n^3\rangle$.

For this example, FP is $\dfrac{\partial p}{\partial t} = -\lambda\dfrac{\partial p}{\partial x} + \dfrac{1}{2}\lambda\dfrac{\partial^2 p}{\partial x^2}$. We can solve by introducing $\xi = x - \lambda t$, reflecting const. drift. Then we write $P(x,t) = G(\xi, t)$ and

$$\rightarrow \frac{\partial G}{\partial t} = \frac{1}{2}\lambda\frac{\partial^2 G}{\partial \xi^2}$$

Which we know how to solve.

If i.c. is delta f^n, then

$$P(x,t) = \frac{1}{\sqrt{2\pi\lambda t}} \exp\left(-\frac{(x-\lambda t)^2}{2\lambda t}\right).$$

i.e. even-spreading Gaussian + const. drift.

Multivariable F-P eqn

The master eqn for discrete outcome $\underline{x} \in \mathbb{Z}^d$ is

$$\frac{\partial P}{\partial t}(\underline{x},t) = \sum_{\underline{r}\in\mathbb{Z}^d} \left(W(\underline{x}-\underline{r}, \underline{r})\, P(\underline{x}-\underline{r},t) - W(\underline{x},\underline{r})\, P(\underline{x},t)\right)$$

Repeat previous steps and Taylor expand

$$f(\underline{x}-\underline{r}) = f(\underline{x}) + r_i \frac{\partial f}{\partial x_i} + \frac{1}{2} r_i r_j \frac{\partial^2 f}{\partial x_i \partial x_j} + \dots$$

with $f(\underline{x}) = W(\underline{x},\underline{r})\, P(\underline{x},t)$. This gives multidimensional FP

$$\frac{\partial P(\underline{x},t)}{\partial t} = -\frac{\partial}{\partial x_i}\left(u_i(\underline{x})\, P(\underline{x},t)\right) + \frac{\partial^2}{\partial x_i \partial x_j}\left(\overset{\text{sym.}}{D_{ij}}(\underline{x})\, P(\underline{x},t)\right)$$

where $u_i(\underline{x}) = \sum_{\underline{r}\in\mathbb{Z}^d} r_i W(\underline{x},\underline{r})$, and $D_{ij} = \frac{1}{2}\sum_{\underline{r}\in\mathbb{Z}^d} r_i r_j W(\underline{x},\underline{r})$

$$\frac{d}{dt}\langle x_i\rangle = \int d^dx\; x_i \frac{\partial P}{\partial t} = \int d^dx\; x_i\left(-\partial_j(u_j P) + \partial_i\partial_j(D_{ij} P)\right)$$

$$= \int d^dx\; u_i P \qquad (\text{IBP})$$

$$\Rightarrow \quad \frac{d\langle \underline{x}\rangle}{dt} = \overset{\text{avg. drift}}{\langle \underline{u}\rangle}$$

$$\frac{d}{dt}\langle x_i x_j\rangle = \int d^dx\; x_i x_j\left(-\partial_k(u_k P) + \partial_k\partial_l(D_{kl} P)\right).$$

$$= \langle x_i u_j\rangle + \langle u_i x_j\rangle + \langle D_{ij}\rangle.$$

Define symmetric covariance matrix

$$C_{ij} = \mathrm{cov}(x_i, x_j) = \langle x_i x_j\rangle - \langle x_i\rangle\langle x_j\rangle$$

Then

$$\frac{dC_{ij}}{dt} = \mathrm{cov}(x_i, u_j) + \mathrm{cov}(x_j, u_i) + 2\langle D_{ij}\rangle \qquad (*).$$

Wildebeest and Flies revisited

Recall m: population of wildebeest

n: flies

$$\frac{dp_{mn}}{dt} = \lambda_1 \left(p_{m-1,n} - p_{m,n}\right) + \beta_1 \left((m+1)\, p_{m+1,n} - m p_{m,n}\right)$$
$$+ \lambda_2 \left(m\, p_{m,n-1} - m p_{m,n}\right) + \beta_2 \left((n+1)\, p_{m,n+1} - n p_{m,n}\right)$$

Exercise Show that $\underline{u} = \begin{pmatrix} \lambda_1 - \beta_1 m \\ \lambda_2 - \beta_2 n \end{pmatrix}$ and find D_{ij}.

Since $\frac{d\langle \underline{x}\rangle}{dt} = \langle \underline{u}\rangle$, any steady state prob. distⁿ must have $\langle \underline{u}\rangle = 0$. For us, this means

$$\langle m\rangle = \lambda_1/\beta_1 , \quad \langle n\rangle = \lambda_1\lambda_2/\beta_1\beta_2$$

in agreement with earlier discrete analysis. What about fluctuations?

Recall : $C_{ij} = \mathrm{cov}(x_i, x_j) = \langle x_i x_j\rangle - \langle x_i\rangle\langle x_j\rangle$.

In steady state, want

$$\frac{dC_{ij}}{dt} = \mathrm{cov}(x_i, u_j) + \mathrm{cov}(x_j, u_i) + 2\langle D_{ij}\rangle = 0$$

Write $\underline{u} = \underline{\lambda} + a\underline{x}$, with $\underline{\lambda} = \begin{pmatrix} \lambda_1 \\ 0 \end{pmatrix}$, $a = \begin{pmatrix} -\beta_1 & 0 \\ \lambda_2 & \beta_2 \end{pmatrix}$, $\underline{x} = \begin{pmatrix} m \\ n \end{pmatrix}$.

$$\Rightarrow \mathrm{cov}(x_i, v_j) = a_{jk}\, \mathrm{cov}(x_i, x_k) = a_{ij}\, C_{ik}$$

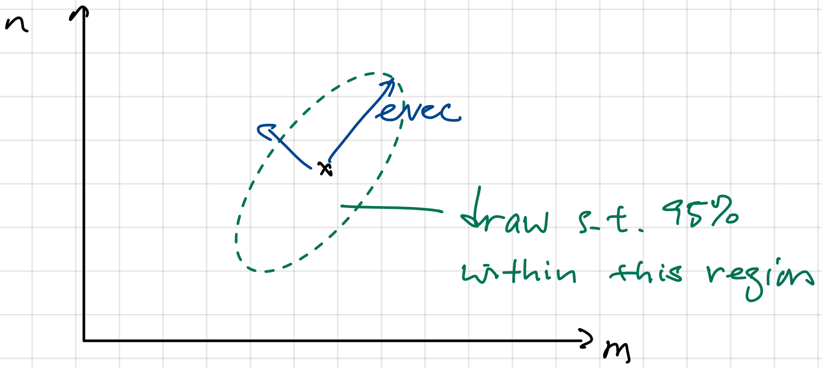
Then $(*)$ becomes

$$\frac{dC}{dt} = aC + Ca^T + 2\langle D\rangle = 0$$

This is a <u>Lyapunov eqn</u> for C.

Exercise Show that $C_{11} = Var(m) = \lambda_1/\beta_1$, $C_{12} = C_{21} = \lambda_1\lambda_2/\beta_1(\beta_1+\beta_2)$ and $C_{22} = Var(n) = \frac{\lambda_1\lambda_2}{\beta_1\beta_2}\left(1 + \frac{\lambda_2}{\beta_1+\beta_2}\right)$

The evals and evecs of C_{ij} give info about the population



4.3 The Fluctuation-Dissipation theorem.

Consider N2 for a particle immersed in liquid

$$m\ddot{\underline{x}} = -\gamma\dot{\underline{x}} - \nabla V + \underline{f}(t)$$

friction

random force due to bombardment by molecules of liquid, e.g. Brownian motion

Idea: draw $\underline{f}(t)$ from some prob. distⁿ. and try to construct prob. dist. $p(\underline{x}, t)$ for $\underline{x}$.

This is an example of a stochastic DE, or Langain eqn.

It turns out that $P(\underline{x}, t)$ obeys FP eqn.

Suppose that motion is friction dominated, so we can ignore the $\ddot{\underline{x}}$ term. Assume $\langle \underline{f}(t) \rangle = 0$. Then average velocity is

$$\langle \dot{\underline{x}} \rangle = -\frac{1}{\gamma} \langle \nabla V \rangle .$$

Compare this to FP where $\langle \dot{\underline{x}} \rangle = \langle \underline{u} \rangle$, suggests that the FP eqn should be

$$\frac{\partial P}{\partial t} = \frac{1}{\gamma} \nabla \cdot (P \nabla V) + D \nabla^2 P .$$

for some $D_{ij} = D\,\delta_{ij}$, assuming D const, and rotational symmetry

The eqm dist^n then obeys

$$\nabla \cdot \left(\frac{1}{\gamma} P \nabla V + D \nabla P \right) = 0$$

$$\Rightarrow \quad P(\underline{x}) \sim e^{-\gamma V(\underline{x}) / D}$$

normalisation

Suppose that the surrounding liquid is at temp. T. From Stat phys., the eqm prob. dist^n must be Boltzmann dist^n.

$$P(\underline{x}) = e^{-E/k_B T} = e^{-V(\underline{x})/k_B T}$$

Equating,

$$\boxed{D = \frac{k_B T}{\gamma}}$$

This is Einstein eqn.