Year 3 — Mathematical Biology and Ecology

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Contents

1 Continuous Models for a single species

We are going to model simply how we model population dynamics for a single species. We are going to call $N(t)$ our population size at a certain time. We are going to say that $N(t)$ is continuous. We also say $N \in \mathbb{R}$ and so it's going to be a density measure. We are going to constrain this $N \geq 0$, $\forall\, t$. We can measure this and create a model, *Lecture 2*

$$\frac{dN}{dt} = f(N, t, \boldsymbol{\mu})$$

We call N the variable, then $\boldsymbol{\mu}$ the parameter. We let $t \in \mathbb{R}$ and $t > 0$.

Let's start off by thinking about an actual population of individuals, we have observed that there is some sort of growth dynamics. We can write a mechanistic model, by including mechanisms that affect the population.

$$\frac{dN}{dt} = +\text{births} + \text{resources} + \text{net migration} - \text{deaths}$$

If the positive things are greater, the population will grow, otherwise if they are smaller they decline, or they stay equal.

Now we make some assumptions, so we can write down a mathematical model.

1. Births and deaths predominate:
$$\frac{dN}{dt} = \text{births} - \text{deaths}$$
2. Births and deaths are proportional to N:
$$\frac{dN}{dt} = \alpha N - \beta N \qquad \alpha, \beta \in \mathbb{R}^+$$
where we call α the birthrate and β the deathrate and $\boldsymbol{\mu} = (\alpha, \beta)$.

If we consider, as an aside,

$$\frac{dN}{dt} = \alpha N - \beta N + \gamma \qquad \gamma \in \mathbb{R}$$

this adds something like independent migration, where we assume migration is constant, this could be γN if it's proportional to N.

We can solve this equation nicely,

$$\begin{aligned} \frac{dN}{dt} &= N(\alpha - \beta) \\ \int \frac{1}{N}\frac{dN}{dt}\, dt &= \int (\alpha - \beta) dt \\ \ln N &= (\alpha - \beta)t + C \\ N(t) &= Ae^{(\alpha-\beta)t} \end{aligned}$$

Now assume this is an initial value problem, $N_0 = A$ and so,

$$N(t) = N_0 e^{(\alpha-\beta)t}$$

We are also interested in the long term dynamics of these models, the asymptotic dynamics. Hence, we consider $t \to \infty$.

$$\lim_{t\to\infty} N(t) = \begin{cases} \infty & \text{if } \alpha > \beta \\ 0 & \text{if } \alpha < \beta \\ N_0 & \text{if } \alpha = \beta \end{cases}$$

We call the case where $\alpha = \beta$ a steady state solution.

You don't usually see just a t in the equation, but we may want to use a forcing term, i.e. periodic migration in Cornwall.

$$\frac{dN}{dt} = \alpha N - \beta N + \cos(t)$$

We are not going to consider these non-autonomous systems. Hence we can write,

$$\frac{dN}{dt} = f(N, \boldsymbol{\mu})$$

We have a nice thing to make sure our growth doesn't go exponential. It's the logistic map,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) \qquad r, k > 0 \quad N \geq 0$$

where $f(N) = rN\left(1 - \frac{N}{k}\right)$ is called the logistic model. This model has a level of self regulation, so if N is high, then it will decrease later. Firstly, look at $f(N)$,

$$f(N) = rN\left(1 - \frac{N}{k}\right)$$

We start by graphing it,

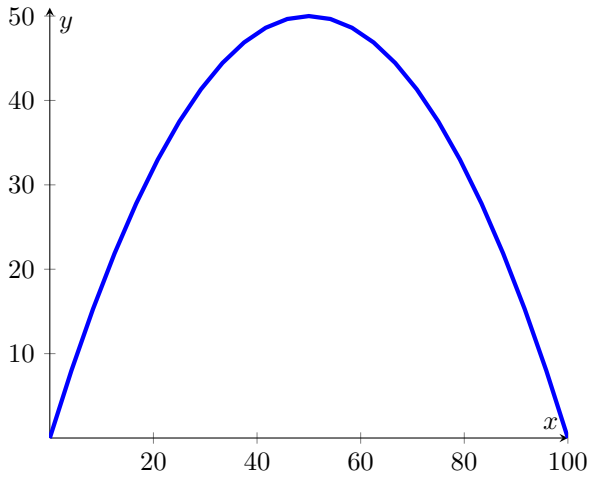


Figure 1: $y = 2x\left(1 - \frac{x}{100}\right)$

Exercise. Solve $\frac{dN}{dt} = rN(1 - \frac{N}{k})$

The solution to this equation is,

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

As $t \to \infty$, we can consider it and see that it will depend on N_0. If $N_0 = 0$, then we get that $N(t) = 0, \forall\, t$. If we then take $N_0 > 0$, then we get,

$$\begin{aligned} N(t) &= \frac{N_0 k}{\frac{k - N_0}{e^{kt}} + N_0} \\ &= k \qquad\qquad\qquad\qquad\qquad\qquad t \to \infty \end{aligned}$$

lets try and formalise some of these ideas. So consider, *Lecture 3*

$$\frac{dN}{dt} = f(N)$$

where $N \in \mathbb{R}, t \in \mathbb{R}, f : \mathbb{R} \to \mathbb{R}$. Then we define steady states as, where $f(N^*) = 0$. These are also reffered to as fixed points or equilibrium. When a system in the first place depends on whether the state is attracting.

Definition 1.1 (Attrracting)**.** A steady state N^* is attracting if all trajectories that start close to N^* approach it as $t \to \infty$.

We consider $N = N^* + n$, recall the taylor series is an approximation to a function at a point,

$$f(x) \approx f(a) + f'(a)(x-a) + \frac{f''(a)(x-a)^2}{2!} + \dots$$

as we consider small values of n we can throw away higher terms. Hence, we can linearise it.

$$\begin{aligned}
\frac{dN}{dt} &= f(N) \\
\frac{dN^* + n}{dt} &= f(N^* + n) \\
\frac{dn}{dt} &= f(N^* + n) \\
\frac{dn}{dt} &\approx f(N^*) + f'(N^*)(N^* + n - N^*) + f''(a)\frac{(N^* + n - N^*)}{2!} + \dots \\
\frac{dn}{dt} &\approx 0 + f'(N^*)n + \frac{f''(N^*)}{2!}n^2 + \dots \\
\frac{dn}{dt} &\approx f'(N^*)n
\end{aligned}$$

and so we can model it by,

$$\frac{dn}{dt} = f'(N^*)n$$

which can be solved as,

$$n(t) \approx n_0 e^{f'(N^* t}$$

If $f'(N^*) > 0$, then we just have an exponential (unstable), but if $f'(N^*) < 0$ then we have a decaying exponential (stable).

Example. We shall consider,

$$\frac{dx}{dt} = rN\left(1 - \frac{N}{k}\right)$$

and so we want $f(N^*) = 0$ and hence we get that $N^* = 0$ and $N^{**} = k$. Then we find $f'(N) = r\left(1 - \frac{2N}{K}\right)$. Hence we can find $f'(0) = r$ and $r'(k) = -r$ and as $r > 0$, $f'(N^*) > 0$ hence N^* is unstable and as $f(N^{**}) < 0$ then N^{**} is stable.

We are going to recap last lectures, and study, *Lecture 4*

$$\frac{dN}{dt} = N(N - \alpha)(N - \beta)$$

where $N \in \mathbb{R}^+$ and $0 < \alpha < \beta$. We are going to focus on long term dynamics, i.e. $t \to \infty$. The steady state will give us information about that, once we know what they are and their stability, we know everything. Steady states are going to be where, $\frac{dN}{dt} = f(N) = 0$, then we can see that this is just $N^* = 0$, $N^{**}\alpha$, $N^{***} = \beta$.

Definition 1.2 (Trajectory)**.** From an initial N_0, a trajectory is how $N(t)$ evolves.

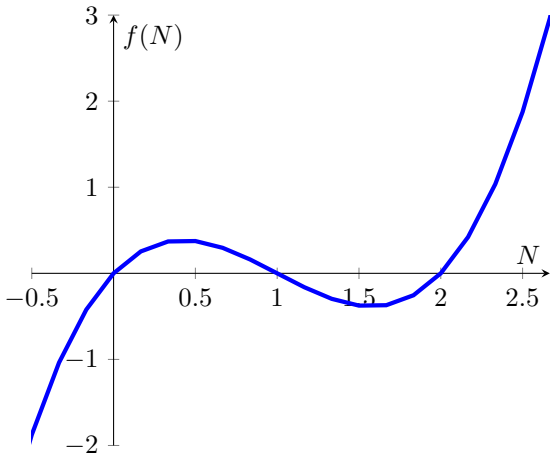


Figure 2: $y = N(N - \alpha)(N - \beta)$

Then we consider the small perturbations around the steady states and it was a linear ODE that resulted in exponential decay or just an exponential. We don't need to do this though, as we can look at the phase space as it has split up the graph into regions. These regions are $(-\infty, 0]$, $[0, \alpha]$, $[\alpha, \beta]$.

- For $(-\infty, 0]$ the system declines and so we draw arrows going away from 0 to the left.
- Then it's going to move towards α from 0 where it stops at the steady state α.
- From α to β, the particle is going to move from β to α.
- Anything larger than β, it shoots off to infinity.

From this, we can talk about the stability of the stable states. We can call 0 and β unstable and we can say α is a stable fixed point. So now we ask how do we describe $N(t)$ from this information?

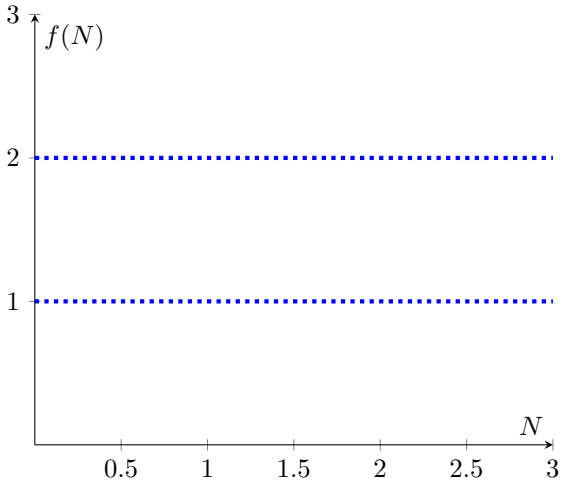


Figure 3: Steady States of the system

2 Modelling Spruce Budworm

Spruce Budworm eats spruce trees and populations have been watched and there exists some oscillatory behavior. Let's formulate some sort of model, firstly with a cartoon and then the assumptions to create a mathematical model. We consider $N =$ population density $\in \mathbb{R}$. We assume that;

- bounded growth, the logistic growth model (e.g. limited resources)
- predation (by birds)

and so we can write,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - p(N)$$

and now a few assumptions for p,

- no predation if no prey, $p(0) = 0$
- predator population is not infinite, this means the rate of predation saturates as $n \to \infty$.
- If n is small, $p(N)$ is small.

We want a sigmoidal form of function so we can encode these assumptions.

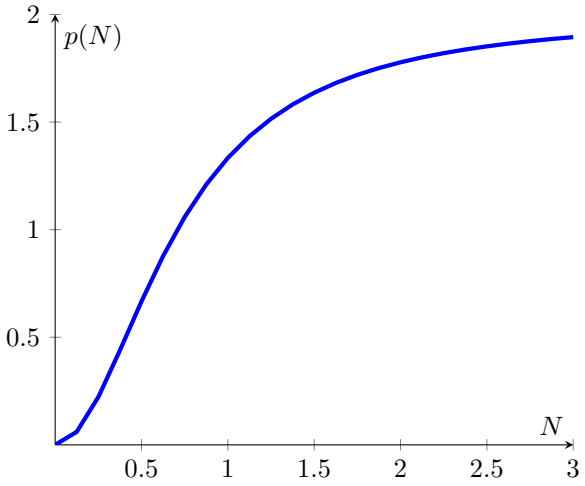


Figure 4: Sigmoidal Function, $p(N)$

We will let $p(N) = \frac{BN^2}{A^2+N^2}$, which will work quite nicely. This is a function seen all over Maths Biology. Hence, we write,

$$\frac{dN}{dt} = r_B N\left(1 - \frac{N}{k_B}\right) - \frac{BN^2}{A^2 + N^2}$$

where $r_B, k_B, B, A > 0$ and $N \geq 0$. In mathematical Biology we don't really have any big ideas about what our parameters are, we talk more generally about what our parameters actually mean. This makes it harder to know what's going on with multiple parameters.

2.1 Scaling and Non-dimensionalisation

The goal is to scale variables and time such that we get an equivalent system with fewer parameters, equivalent is in relation to the steady states and their stabilities.

Our stategy is to find constants α and β so that $u = \alpha$ and $\tau = \beta t$ yields a simpler system. The first thing we do is write down a new system, $\frac{du}{d\tau}$.

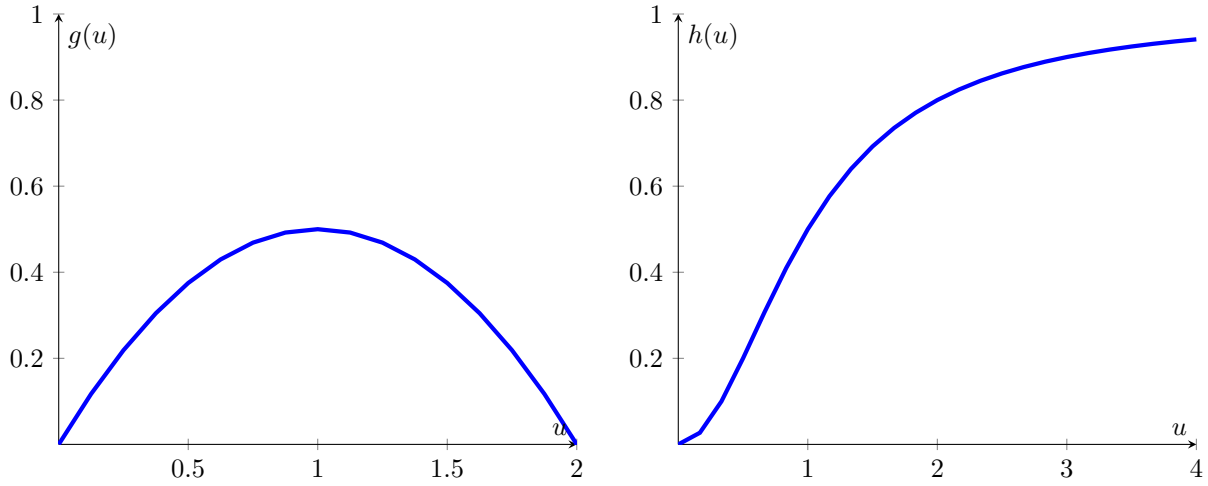
$$\frac{du}{d\tau} = \frac{dN}{dt}\frac{dt}{d\tau}\frac{du}{dN}$$

and so we can do some algebra (ommited), then we get to a point where we want to choose some values for our placeholders of α and β, given the form of the system, we choose that $\alpha = \frac{1}{A}$ and $\beta = B\alpha = \frac{B}{A}$ and hence the system simplifies to,

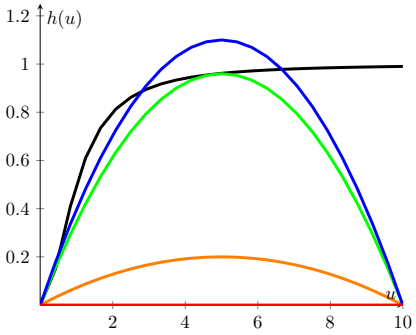
$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2}$$

We are now going to look at our non-dimensionalised system by looking at the steady states and look at the stability. *Lecture 5*

Previously we just plotted the functions. However, this is slightly harder to do, but we write out, $f(u) = g(u) + h(u)$ and then plot them individually



and now we can consider them on the same axis,



Where we can say that there is an equilibrium when $g(u) = 0$ and this is a unstable equilibrium. Now for a $r \neq 0$, then we have the orange curve, then we have that the equilibrium at 0 is still unstable and there is a new steady state which we find to be stable. We have a third value (green), where we have u^{**}, where we have another unstable fixed point. Finally, when we move our function higher again, (blue) and we get a u^{***} that's stable. There is another interesting point, where there is a tangent between the two graphs above this

one $u^{**} = u^{***}$ and hence we have three steady states.

We shall note the geometric approach, we can graph the functions and consider the derivatives around critical points. We can summarise this in a bifurcation diagram.

2.2 Bifurcation Diagram

Imagine we have those snapshots and put them on a diagram. where a filled dot is stable and unfilled is

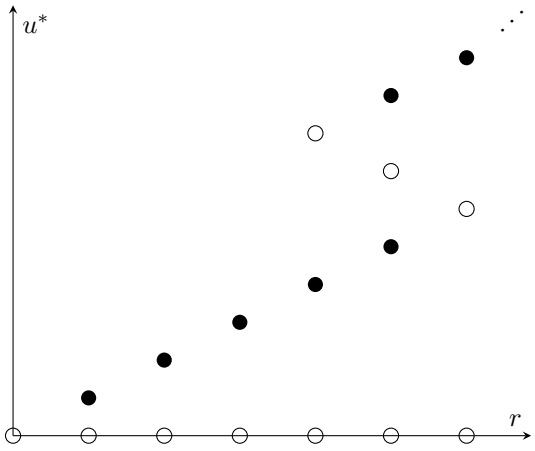


Figure 5: Bifuration Diagram for our system

unstable. We can further this by drawing smooth curves along where we have placed the dots and produce said bifurcation diagram.

Hence, let us think about trajectories of the system. The bifurcation diagram has split us into three different areas. From an initial condition, in a region one (before the unstable area) we have an unstable fixed point and an unstable fixed point. Hence, aslong as you start with a positive initial condition we converge to u^*. Moreover, Region 2 is even more interesting, in the unstable area.

We can move back to our model. Let B be the population dynamics of predators, and consider $r = \frac{r_B A}{B}$ *Lecture 6* and consider a slow change in B. Consider a decrease in B, hence an increase in r and u. As soon as you

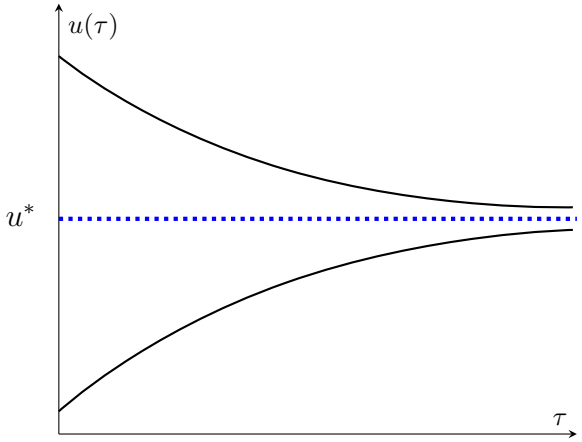


Figure 6: Steady States of the R_1

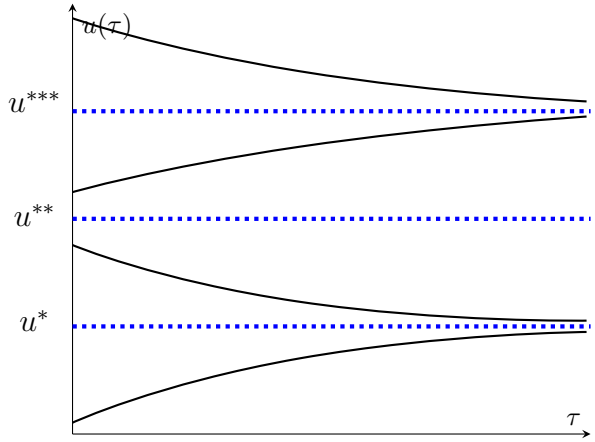


Figure 7: Steady States of the R_1

reach an unstable steady state, you jump up to the higher state and carries on as usual.

Now we are at a higher level, we have depopulation. So, what happens now as B increases, well then r and u decrease and we follow the branch back down.

This phenomena is called Hysteresis. This occurs when the bifurcation diagram has a sudden jump and then a 'reason' for the population to decrease again. We also introduced a potential way that oscillatory behavior can occur.

If we have a stable and an unstable fixed point and as you increase r, you must reach one of them eventually, as the two stable states get closer and closer they must collide, when you get a tangency. Our case is a saddle-node bifurcation.

Definition 2.1 (Saddle-node bifurcation)**.** Consider $\frac{dN}{dt} = f(N, k)$ where k is a parameter and there is a critical value of k, k_c. So that when $k = k_c$, $f'(N^*) = 0$ for an equilibrium N^*.

Then the bifurcation at $k = k_c$ is a saddle-node bifurcation if a stable-unstable pair of equilibrium are either created or destroyed.

Our system is $f = g - h$ and so, $f' = g' - h'$ is our condition for the Budworm equations.

2.3 Bistability

If we cosider our bifurcation diagram and when r is in Region 2, we have two steady states, and they coexist. If we draw the trajectories of the system; with stable, unstable, stable, unstable.

Consider some unmodeled factors, so some noise. We may use a stochastic differential equation to model. Then the noise may be enough for it to jump to the other stable steady state and so converge there.

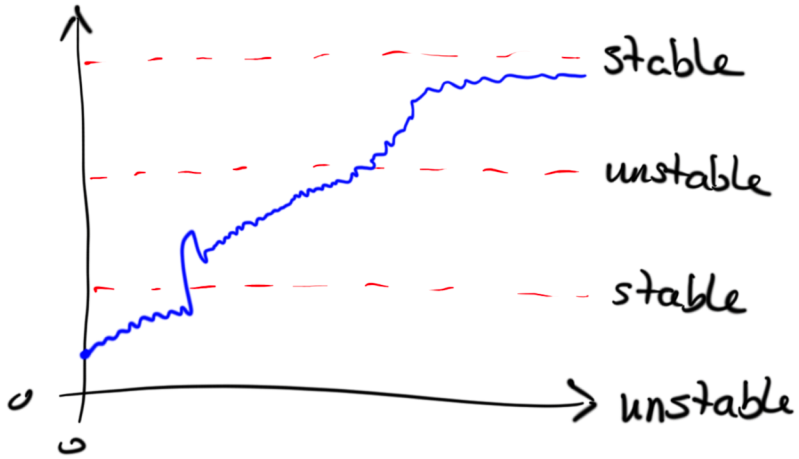


Figure 8: Noise on a trajectory

3 Harvesting a single natural population

We are now going to move into another example and consider different types of bifurcation. We are going to now consider a harvesting, *Lecture 7*

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - h(N)$$

where $h(N)$ is our harvesting rate. Initially we are going to keep it simple and let h be our harvesting rate, $h(N) = hN$. Now look for steady states,

$$rN\left(1 - \frac{N}{k}\right) - hN = 0$$

which has solutions, $N^* = 0$ and $r - \frac{rN^{**w}}{k} - h = 0$, hence, $N^{**} = k\left(1 - \frac{h}{r}\right)$.
We can consider $f(N) = F(N) - G(N)$ where $F(N) = rN\left(1 - \frac{N}{k}\right)$ and $G(N) = hN$ and then plot them.

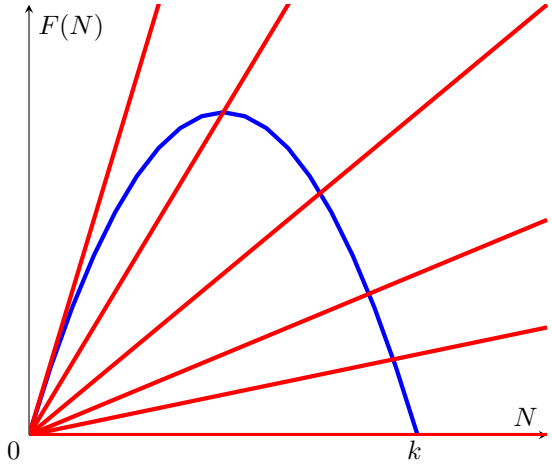


Figure 9

We can find the stability, firstly consider $f'(N) = r - h - \frac{2t}{k}N$ and see $f'(0) = r - h$ and $f'(N^*) = h - r$. We notice that for a positive steady state at N^{**} we need $h < r$. So assume that $h < r$, then we can see that we have $f'(0) > 0$ and $f'(N^*) < 0$ and so we call the $h < r$ sustainable harvesting.
In actuality, we want some yield. We denote yield, $Y(h) = nN_h$ where $N_h = N^{**}$. Hence we write $y(h)$,

$$y(h) = hk\left(1 - \frac{h}{r}\right)$$

this is a quadratic and so we have a control parameter h. Given it's a parabola we can find a maximum yield bt finding the maxima of the parabola. This occurs at $h = \frac{r}{2}$ and the yield is, $\frac{rk}{4}$. We can also find the value of N_h, which is $N_h = \frac{k}{2}$. These are the two values we expect for the logistic curve.

We can vary h and when $h = 0$ we can just see that they intersect at $(0, k)$ and it's not that interesting. Then as h increases it heads towards the $\frac{k}{2}$ and this is a critical value, as we see in Figure 9. Now imagine we increase the slope further then we reach the point where they are tangential. Over the varying of h we can see that the stability changes, after the tangential behavior they meet again for negative N and creates a new saddle point.

3.1 Transcritical Bifurcation

Before, we reached a point where the steady states absorb eachother. Here we have places where they meet and then don't absorb eachother. Here is the diagram;

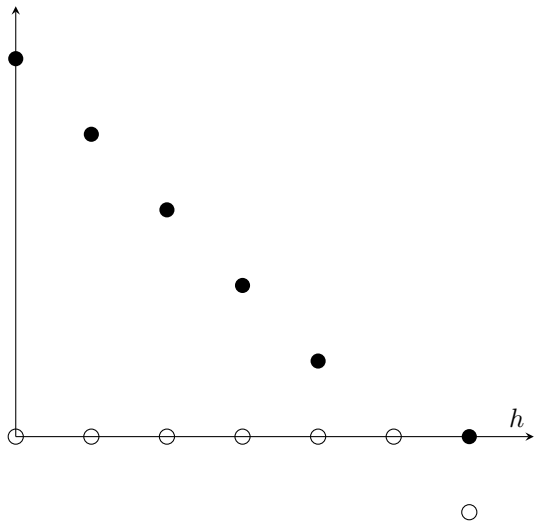


Figure 10: Bifuration Diagram for our system

Consider $\frac{dN}{dt} = f(N,k)$ where k is a parameter. There is a critical value of k, k_c such that when $k = k_c$ then $f'(N^*) = 0$ for some N^*.

Definition 3.1 (Transcritical Bifurcation)**.** Then the bifurcation at k_c is transcritical if as k passes through the stable-unstable pair of equilibria collide and exchange stability.

Whenever $k < k_c$ we have stable node and an unstable node. We go from harvesting state was supporting the population to depletion at $k = k_c$.

We now consider another factor, the time response. We define this as $T_R = \frac{1}{|f'(N^*)|}$. We say that the sign of the derivative denotes the stability of the point but the inverse maginitude is the time it takes the perturbation to return to normal. If we remove something from the population, will it take ages to get back to normal? Firslt consider the non-zer steady state. We saw that $f'(N_h) = h - r$, and we know that $h < r$ and so, $T_R(h) = \frac{1}{r-h}$ and when $h = 0$, $T_r(h = 0) = \frac{1}{r}$.

Definition 3.2 (Relative Recovery Time)**.** We define simply the relative recovery time as,

$$\frac{T_R(h)}{T_R(h=0)}$$

and s the relative recovery time for our system at N_h is simply,

$$RRT = \frac{r}{r-h}$$

We can now start to look at the relation between yield and the relative recovery time and yield.

3.2 RRT and yield

We remember that $y(t) = hk\left(1 - \frac{h}{r}\right)$ and we can then write $h^2 - rh + \frac{rY}{k} = 0$. Hence by the quadratic formula, $h = \frac{r}{2}\left(1 + \sqrt{1 - \frac{4Y}{rK}}\right)$ and now as we know our maximum yield is simply just $\frac{rk}{4}$, then we can say,

$h = \frac{r}{2}\left(1 + \sqrt{1 - \frac{Y}{Y_{max}}}\right)$. Hence, now we go to recovery time.

$$T_R(h) = \frac{1}{r-h} = \frac{1}{r - \frac{r}{2}\left(1 \pm \sqrt{1 - \frac{Y}{Y_{max}}}\right)}$$

and now the relative recovery time.

$$RRT(Y) = \frac{2}{1 \pm \sqrt{1 - \frac{Y}{Y_{max}}}}$$

We split our RRT into two branches, L_+ and L_-. We also note that $0 \leq \frac{Y}{Y_{max}} \leq 1$. If $\frac{Y}{Y_{max}} = 1$, then, *Lecture 7* $L_+ = 1$. Hence, we can plot this RRT function.

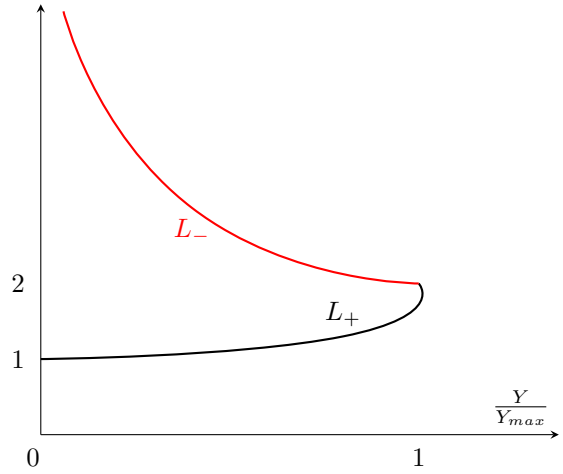


Figure 11: RRT for different values of $\frac{Y}{Y_{max}}$

This relates to as you go further and further towards the $(0, 0)$ steady state you go off to infinity.

3.3 Constant Yield Harvesting

We use the same model as before, but now we let $f(N) = N_0$. Then we can find the steady states and we get a quadratic which we can them solve and get our steady states $N = \frac{1}{2}\left(k \pm \sqrt{k^2 - \frac{4kY_0}{r}}\right) = \frac{k}{2}\left(1 \pm \sqrt{1 - \frac{4Y_0}{kr}}\right)$ and now again we consider $f(N) = g(N) - Y_0$.

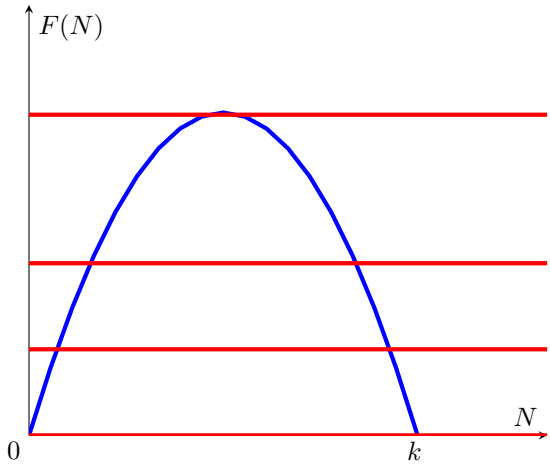


Figure 12

When $Y_0 = 0$, we get two steady states, one saddle point at 0 and a stable node at N^*. When we have a tangent line, then $f'(N) = 0$ at that point and we have a bifurcation there. We notice here, again, we have a saddle node bifurcation.

Now we consider the time response, we can see that $f'(N) = r - \frac{2rN}{k}$ and so,

$$T_R(N_+) = \frac{1}{r\sqrt{1 - \frac{Y_0}{Y_{max}}}}$$

$$RRT = \frac{1}{\sqrt{1 - \frac{Y_0}{Y_{max}}}}$$

and then we get an asymptote and so RRT goes to infinity. However there are several problems to what we are going here, as we head towards the tangential line, there may be a point where it jumps from one point to another. At other points, it can't jump as it's further apart.

4 Interactive Populations

We are now going to jump to 2D,

Example. Let's model the density of $N(t)$ which is our population of prey and $P(t)$ be the population of predators.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - NPR(N)$$
$$\frac{dP}{dt} = sN\left(1 - \frac{P}{hN}\right)$$

We know need to choose $R(N)$, so we want a curve where we start at $(0,0)$ and asymptotes for large N. We let it be a $R(N) = \frac{k}{N+D}$, hence our system is:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{kNP}{N+D}$$
$$\frac{dP}{dt} = sN\left(1 - \frac{P}{hN}\right)$$

We can now consider the steady states of $\frac{dN}{dt}$ and so we can seek to non-dimensionalise it.

We will let $u = \frac{N}{K}$, $v = \frac{P}{hk}$ and $\tau = rt$. Then we substitute in, *Lecture 8*

$$\begin{aligned}\frac{du}{d\tau} &= \frac{dN}{dt}\frac{du}{dN}\frac{dt}{d\tau} \\ &= u - u^2 - \frac{uKkuhK}{K^2ru + KrD} \\ &= u - u^2 - \frac{hK}{r}\frac{uv}{u + \frac{D}{k}} \\ &= u - u^2 - \frac{auv}{u+d}\end{aligned}$$

that's the first equation dealt with, so we consider the other.

$$\begin{aligned}\frac{dv}{d\tau} &= \frac{dv}{dP}\frac{dP}{dt}\frac{dt}{d\tau} \\ &= \frac{1}{hKr}\left[sP - \frac{sP}{hN}\right] \\ &= \frac{s}{r}v\left(1 - \frac{v}{u}\right) \\ &= bv\left(1 - \frac{v}{u}\right)\end{aligned}$$

We are now going to consider the steady states of this system, we can't solve it as nicely using a graph. Our system is now going to live in $\mathbb{R}^2$. The part of the plane where both of them live is called the phase space. We will find trajectories that are tangents to these vector fields.

4.1 Steady States

The definition is still the same,

Definition 4.1 (Steady State)**.** A point $\mathbf{u}^*$ is a steady state if $\mathbf{F}(\mathbf{u}^*) = \mathbf{0}$.

What if only one component is zero? These are called the nullclines.

Definition 4.2 (Nullclines)**.** The u_n nucline contains points (u_1, u_2) such that $f_n(u_1, u_2) = 0$.

Let's consider our system, we have,

$$f_1(u, v) = u(1-u) - \frac{auv}{u+d}$$
$$f_2(u, v) = bv\left(1 - \frac{v}{u}\right)$$

and we find the nuclines are,

$$v = \frac{u(1-u)(u+d)}{au} = 0$$
$$u = v \qquad \text{or} v = 0$$

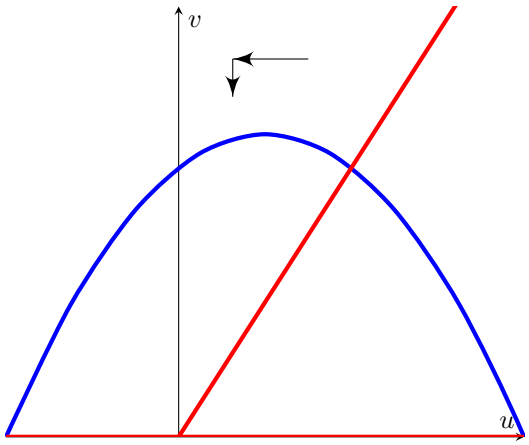


Figure 13

We can now find the direction of the vector field using some quick calculation

5 Discrete Time Systems in 1D

Consider,

$$N_{t+1} = f(N_t)$$

and $t \in \mathbb{Z}$. We can say that N_t is the population size at time step t, and we now have an evolution function $f : \mathbb{R} \to \mathbb{R}$. Starting at N_0, we can generate a trajectory by just recursively applying our map.

$$N_0 \xrightarrow{f} N_1 \xrightarrow{f} N_2 \xrightarrow{f} \dots$$

Here is an example, $f(N) = rN$ where $r > 0$ is just our birth rate. We get that $N_t = r^t N_0$. So there are three things that can happen,

1. $N_t \to 0$ as $t \to \infty$ if $r < 1$ (extinction)
2. $N_t \to \infty$ as $t \to \infty$ if $r > 1$ (survival)
3. $N_t \to N_0$ as $t \to \infty$ if $r = 1$ (survival)

We will be considering maps with a single maximum in $(0, \infty)$, so something like an inverted quadratic. Again we will loop at the logistic map,

$$f(N) = rN\left(1 - \frac{N}{k}\right)$$

5.1 Equilibria, Stability and Cobwebbing

Recall that for a continuous time system, $N(t) = N_*$ if $\forall\, t \geq 0$ if $f(N_*) = 0$. For discrete systems,

$$N_t = N_*$$

$$\implies N_{t+1} = N_t = N_* \,\forall\, t \geq 0$$

and so we just want $f(N_*) = N_*$. We call N_* as fixed point for the function f.

We can consider cobwebbing to find these Equilibria, we take a initial condition, then draw up to f, then project to $f(N) = N$, then project down again to N_1. We then repeat this.

If we can converge on a fixed point we can think of it as stable, but some fixed points can't be converged upon and so they are unstable. Again, we see that $f'(N_*)$ defined the dynamics. There are four possibilities.

1. $0 \leq f'(N_*) < 1$, we converge onto a fixed point wherever we start from. So $N_t \to N_0$ and so N_0 is stable.
2. $f'(N_*) > 1$ and so our cobweb just diverges to positive or negative infinity. It diverges monotonically in each direction.
3. $-1 < f'(N_*)$, here we get a spiral inwards. Here N_* is oscillatory stable. This a non-monotonic convergence.
4. $f'(N_*) < -1$, here we get an unstable spiral. It diverges to infinity. We say N_* is oscillatory unstable.

To see this formally, we write $N_t = N_* + n_t$ and take some sort of Taylor expansion. Then,

$$\begin{aligned} N_* + n_t &= f(N_* + n_t) \\ &= f(N_*) + f'(n_t)n_t + hot. \\ &= f'(N_*)n_t \end{aligned}$$

Ignoring the higher order terms we can write,

$$n_{t+1} = f'(N_*)n_t$$

and so now we can consider the assymptotic dynamics and we see that all we need to consider is $f'(N_*)$. Hence we see,

1. If $|f'(N_*)| < 1$, then $n_t \to 0$ and $N_t \to N_*$ as $t \to \infty$. Hence N_* is a stable fixed point
2. If $|f'(N_*)| > 1$ and so $n_t \to \infty$ and $N_t \to \infty$. Hence N_* is an unstable fixed point.
3. If $|f'(N_*)| = 1$, there is a change in stability, called a bifurcation.

If we are interested in the types of bifurcation and the characteristics of each bifurcation, we will consider solutions of different periods. For the bifurcation of the logistic map at $r = 3$, we consider period 2 solutions. If we consider these maps, we can find a different type of bifurcation called a period-doubling bifurcation. For each bifurcation we see period 2^n solutions. This is where the 'classic' bifurcations come from. This is what we call a period-doubling cascade. An interesting thing is when $r = 3.57$, we get 2^n-period solutions for all n, but they are all unstable. This is deterministic chaos.

6 Reaction Kinetics

We will consider the Michaelis-Menten Scheme, we will consider an enzyme, E, that binds to a substrate S in order to catalyse S into a product P.

$$\mathrm{S} + \mathrm{E} \underset{\mathrm{k_{-1}}}{\overset{\mathrm{k_1}}{\rightleftharpoons}} \mathrm{C} \xrightarrow{\mathrm{k_2}} \mathrm{P} + \mathrm{E}$$

We want to know that happens as we increase time. So we want to create systems of differential equations. We use the Law of Mass Action, this states that the rate of a reaction is proportional to the concetration of the reactants. Our reaction scheme has m reactions, $\{R_1, \ldots, R_m\}$ and n reactants $\{X_1, \ldots, X_n\}$. We denote the concentration of $x_i = [X_i]$. We then define,

1. Chemical species vector, $x = \begin{pmatrix} x_1 & \ldots & x_n \end{pmatrix}^T$
2. Reaction vector, $\mathbf{v}(\mathbf{x}) = \begin{pmatrix} \mathbf{v}_1(\mathbf{x}) & \ldots & \mathbf{v}_m(\mathbf{x}) \end{pmatrix}^T$ where $\mathbf{v}_j(\mathbf{x})$ is the rate of R_j.
3. Stoichiometry Matrix, $N = (N_{ij})$ where N_{ij} is the number of molecules of the X_i produced/consumed in R_j.

We then obtain the equations for $\mathbf{x}(t)$,

$$\dot{\mathbf{x}} = N\mathbf{v}(\mathbf{x})$$

Hence we just decompose our equations,

$$\mathrm{S} + \mathrm{E} \xrightarrow{\mathrm{k_1}} \mathrm{C} \tag{$R1$}$$

$$\mathrm{C} \xrightarrow{\mathrm{k_{-1}}} \mathrm{S} + \mathrm{E} \tag{$R2$}$$

$$\mathrm{C} \xrightarrow{\mathrm{k_2}} \mathrm{P} + \mathrm{E} \tag{$R3$}$$

and we write $[S] = s$, $[E] = e$ and so on. We want to write,

$$\mathbf{x} = \begin{pmatrix} s \\ e \\ c \\ p \end{pmatrix}, \ \mathbf{v}(\mathbf{x}) = \begin{pmatrix} k_1 se \\ k_{-1}c \\ k_2 c \end{pmatrix}, \ N = \begin{pmatrix} -1 & 1 & 0 \\ -1 & 1 & 1 \\ 1 & -1 & -1 \\ 0 & 0 & 1 \end{pmatrix}$$

Now we can say,

$$\frac{d}{dt}\begin{pmatrix} s \\ e \\ c \\ p \end{pmatrix} = \begin{pmatrix} -1 & 1 & 0 \\ -1 & 1 & 1 \\ 1 & -1 & -1 \\ 0 & 0 & 1 \end{pmatrix}\begin{pmatrix} k_1 se \\ k_{-1}c \\ k_2 c \end{pmatrix}$$

and so we want write,

$$\begin{aligned} \frac{d}{dt}s &= -k_1 se + k_{-1}c \\ \frac{d}{dt}e &= -k_1 se + k_{-1}c + k_2 c \\ \frac{d}{dt}c &= k_1 se - k_{-1}c - k_2 c \\ \frac{d}{dt}p &= k_2 c \end{aligned}$$

Now we choose suitable intial conditions, say $s(0) = s_0$, $e(0) = e_0$, $c(0) = p(0) = 0$. Now we can deduce that the last equation can jusr be solved, it doesn't depend on any other equation. Hence we can write,

$$p(t) = k_2 \int_0^t c(s)\, ds$$

and also we can say that $\dot{e} + \dot{c} = 0$ and the amount of enzyme is conserved. Hence,

$$e(t) + c(t) = k \,\forall\, t$$

and hence, $e(0) + c(0) = e_0 = k$ and so $e(t) = e_0 - c(t)$ and we can compute the enzyme concentration from c. Now we can reduce our equations using this,

$$\begin{aligned}\dot{s} &= -k_1 e_0 s + (k_1 s + k_{-1} c)\\ \dot{c} &= k_1 e_0 s - (k_1 s + k_{-1} + k_2)c\end{aligned}$$

Now we can now simplify these further by non-dimensionalise them. We let $\tau = k_1 e_0 t$ and then via chain rule,

$$\begin{aligned}\frac{ds}{d\tau} &= \frac{ds}{dt}\frac{dt}{d\tau}\\ &= \frac{1}{k_1 e_0}\dot{s}\\ &= -s + (s + \frac{k_{-1}}{k_1})\frac{c}{e}\end{aligned}$$

and so the second we get that,

$$\frac{dc}{d\tau} = s - (s + \frac{k_{-1} + k_2}{k_1})\frac{c}{e}$$

and we let $v = \frac{c}{e_0}$,

$$\begin{aligned}\frac{ds}{d\tau} &= -s + (s + \frac{k_{-1}}{k_1})v\\ \frac{dv}{d\tau} &= \frac{s}{e_0}u + (\frac{s}{e_0} - \frac{k_{-1} + k_2}{e_0 k_1})v\end{aligned}$$

Now we let $u = \frac{s}{e_0}$

$$\begin{aligned}\frac{du}{d\tau} &= -u + (u + \frac{k_{-1}}{k_1 s_0})v\\ \frac{e_0}{s_0}\frac{dv}{d\tau} &= u - (u + \frac{k_{-1} + k_2}{s_0 k_1})v\end{aligned}$$

Now let $\varepsilon = \frac{e_0}{s_0}$ and $k = \frac{k_{-1}+k_2}{k_1 s_0}$ and $\lambda = \frac{k_2}{k_1 s_0}$ and we get,

$$\begin{aligned}\frac{du}{d\tau} &= -u + (u + k - \lambda)v\\ \varepsilon\frac{dv}{d\tau} &= u - (u + k)v\end{aligned}$$

with initial conditions of $u(0) = 1$ and $v(0) = 0$. In general we have $e_0 << s_0$ and so $\varepsilon << 1$. Hence, let $\varepsilon = 0$ (the rate of the complex formation is very fast), following $\frac{dv}{d\tau} \approx 0$, the complex is essentally at equilibrium. This is referred to as the **Quasi-Stable State Assumption**, and implies,

$$v = \frac{u}{u + k}$$

and so,

$$\frac{du}{d\tau} = -u + (u + k - \lambda)\frac{u}{u+k} = -\lambda\frac{u}{u+k}$$

and in dimensionalised form,

$$\frac{ds}{dt} = \frac{V_{max}s}{s + k_m}$$

where $V_{max} = k_2 e_0$ and $k_m = \frac{k_{-1}+k_2}{k_1}$. Hence if follows that,

$$\frac{dp}{dt} = \frac{V_{max}s}{s + k_m}$$

this is the Michaelis-Menten equation for product formation. We call the k_m the Michaelis Constant, it is a threshold value.

6.1 Two Binding States - Cooperative Binding

Now we consider there are two binding states for the substrate and the binding of one substrate molecule fascilitates the binding of the other. Then we can show that,

$$\frac{dp}{d\tau} = \frac{v_{max}s^2}{s^2 + k_m^2}$$

This is the hill function and for n binding sites,

$$\frac{dp}{dt} = \frac{v_{max}s^n}{s^n + k_m^n}$$

The hill functions are used as a template for modelling gene expression.

6.2 Autocatalysts

Consider the following reaction,

$$\mathrm{A} + \mathrm{X} \xrightarrow{\mathrm{k_1}} 2\,\mathrm{X} \qquad \mathrm{x} + \mathrm{Y} \xrightarrow{\mathrm{k_2}} 2\,\mathrm{Y} \qquad \mathrm{Y} \xrightarrow{\mathrm{k_3}} \mathrm{B}$$

where we fix $[A] = a_0$ and the usual setup applies. This scheme is an example of autocatalysis, X and Y are involved in the their own production. We convert the scheme to ODEs as before,

$$\mathbf{x} = \begin{pmatrix} x \\ y \\ b \end{pmatrix} \; \mathbf{v}(\mathbf{x}) = \begin{pmatrix} k_1 a_0 x \\ k_2 xy \\ k_3 y \end{pmatrix}, \; N = \begin{pmatrix} 1 & -1 & 0 \\ 0 & 1 & -1 \\ 0 & 0 & 1 \end{pmatrix}$$

and now we get the following,

$$\begin{aligned} \dot{x} &= k_1 a_0 x - k_2 xy \\ \dot{y} &= k_2 xy - k_3 y \\ \dot{b} &= k_3 y \end{aligned}$$

and again we see that $b(t) = k_3 \int_0^t y(s)\,ds$. So we now non-dimensionalise this system, define $\tau = k_1 a_0 t$ and then,

$$\begin{aligned} \frac{dx}{d\tau} &= \frac{dx}{dt}\frac{dt}{d\tau} \\ &= x - \frac{k_2}{k_1 a_0} xy \end{aligned}$$

similarly,

$$\frac{dy}{d\tau} = \frac{k_2}{k_1 a_0} xy - \frac{k_3}{k_1 a_0} y$$

now let $v = \frac{k_2}{k_1 a_0}$ and so,

$$\begin{aligned} \frac{dx}{d\tau} &= x - xv \\ \frac{dv}{d\tau} &= \frac{k_2}{k_1 a_0}(\frac{k_2}{k_3} x - v) \end{aligned}$$

Now finally, we let $u = \frac{k_2}{k_3} x$ and let $\alpha = \frac{k_3}{k_1 a_0}$. Then,

$$\begin{aligned} \frac{du}{d\tau} &= u(1 - v) \\ \frac{dv}{d\tau} &= \alpha v(u - 1) \end{aligned}$$

This is just the Lotka-Volterra Predator-Prey system. We can write,

$$\begin{aligned} \frac{du}{dv} &= \frac{du}{d\tau}\frac{d\tau}{dv} \\ &= \frac{u(1-u)}{\alpha v(u-1)} \\ \alpha \frac{u-1}{u} du &= \frac{1-v}{v} dv \\ C &= \alpha u + v + \ln(u^\alpha v) \end{aligned}$$

We see that for $C \geq 1 + \alpha$, the solutions are closed curves over (u, v) plane. We get this oscillatory behaviour as both u and v feed into eachother.

7 Stage Structured Population Models- PPMs

We start by considering classification by age, here we have one class per year of their life cycle and the discrete time steps are in years. We can represent our population as a population vector

$$\mathbf{x}(t) = \begin{pmatrix} x_1(t) & x_2(t) & \dots & x_n(t) \end{pmatrix}^T$$

where $x_i(t)$ is population at life cycle i. A simple age-based odel is the following,

$$\begin{aligned} x_1(t+1) &= f_1 x_1(t) + \cdots + f_n x_n(t) \\ x_2(t+1) &= p_1 x_1(t) \\ x_3(t+1) &= p_2 x_2(t) \\ &\vdots \\ x_n(t+1) &= p_{n-1} x_{n-1}(t) \end{aligned}$$

If wr let f_i be the fecundities in each age class and the p_i's the survival probabilities of each age class. We note that $0 \leq p_i \leq 1$ and usually the first couple of f_i's are zero ($f_i \geq 0$). We can write the following in vector form,

$$\mathbf{x}(t+1) = \begin{pmatrix} f_1 & f_2 & f_3 & \dots & f_n \\ p_1 & 0 & 0 & \dots & 0 \\ 0 & p_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \dots & p_n \end{pmatrix} \mathbf{x}(t)$$

We denote this middle matrix as L as it's a Leslie matrix. We are now going to generalise this model to be a stage structured model. This has the form,

$$\begin{aligned} x_1(t+1) &= f_1 x_1(t) + \cdots + f_n x_n(t) \\ x_2(t+1) &= g_1 x_1(t) + p_2 x_2(t) \\ x_3(t+1) &= g_2 x_2(t) + p_3 x_3(t) \\ &\vdots \\ x_n(t+1) &= g_{n-1} x_{n-1}(t) + p_n(t) x_n(t) \end{aligned}$$

Again f_i's are the fecundities of each stage class, the g_i's are the growth probability and p_i''s as the stasis probability of each stage class. Again $0 \leq p_i, g_i \leq 1$ and $f_i \geq 0$. Now we see,

$$\mathbf{x}(t+1) = \begin{pmatrix} f_1 & f_2 & f_3 & \dots & 0 & f_n \\ g_1 & p_2 & 0 & \dots & 0 & 0 \\ 0 & g_2 & p_3 & \dots & 0 & 0 \\ 0 & 0 & g_3 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \dots & g_{n-1} & p_n \end{pmatrix} \mathbf{x}(t)$$

These are examples of the PPM models, these have the general form:

$$\mathbf{x}(t+1) = A\mathbf{x}(t) \qquad \mathbf{x}(0) = \mathbf{x}_0$$

Example. Tulip PPM
Assume three stage classes: Seeds, Bulbs and Flowers. We assume that seeds can become bulbs and bulbs can become flowers. Bulbs can stay as bulbs and flowers as flowers. Finally flowers produce bulbs and seeds. Hence our PPM is,

$$A = \begin{pmatrix} 0 & 0 & A_{13} \\ A_{21} & A_{22} & A_{23} \\ 0 & A_{32} & A_{33} \end{pmatrix}$$

7.1 Assymptotic Dynamics

We are really interested in assymptotic dynamics, so we consider $\mathbf{x}(t+1) = A\mathbf{x}(t)$ and we can see that $x(t) = A^t\mathbf{x}_0$. Hence we are really interested in what A^t looks like. So we want the eigenvalue decomposition of A. Assume that A has eigenvalues of $\{\lambda_1, \lambda_2, \dots, \lambda_n\}$ and eigenvectors, $\{\mathbf{w}_1, \mathbf{w}_2, \dots, \mathbf{w}_n\}$ and now we write,

$$P = \begin{pmatrix} \mathbf{w}_1 & \mathbf{w}_2 & \dots & \mathbf{w}_n \end{pmatrix}$$

and so,

$$AP = \begin{pmatrix} A\mathbf{w}_1 & A\mathbf{w}_2 & \dots & A\mathbf{w}_n \end{pmatrix} = \begin{pmatrix} \mathbf{w}_1 & \mathbf{w}_2 & \dots & \mathbf{w}_n \end{pmatrix} \begin{pmatrix} \lambda_1 & 0 & \dots & 0 \\ 0 & \lambda_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & \lambda_n \end{pmatrix}$$

and so we can write $AP = P\Lambda$ and so $A = P\Lambda P^{-1}$. Using this similarity condition, we want find that,

$$A^n = P\Lambda P^{-1} P\Lambda P^{-1} \dots P\Lambda P^{-1} = P\Lambda^n P^{-1}$$

Now we can expand $\mathbf{x}_0 = \alpha_1\mathbf{w}_1 + \alpha_2\mathbf{w}_2 \cdots + \alpha_n + \mathbf{w}_2$ and so,

$$\mathbf{x}_0 = P\boldsymbol{\alpha}, \qquad \boldsymbol{\alpha} = \begin{pmatrix} \alpha_1 \\ \vdots \\ \alpha_n \end{pmatrix}$$

and so $\mathbf{x}(t) = A^t\mathbf{x}_0 = P\Lambda^t\alpha$ and

$$\Lambda^t = \begin{pmatrix} \lambda_1^t & & 0 \\ & \ddots & \\ 0 & & \lambda_n^t \end{pmatrix}$$

and so we can now write that,

$$\begin{aligned} \mathbf{x}(t) &= \begin{pmatrix} \mathbf{w}_1 & \mathbf{w}_2 & \dots & \mathbf{w}_n \end{pmatrix} \begin{pmatrix} \lambda_1^t & & 0 \\ & \ddots & \\ 0 & & \lambda_n^t \end{pmatrix} \begin{pmatrix} \alpha_1 \\ \vdots \\ \alpha_n \end{pmatrix} \\ &= \alpha_1\lambda_1^t\mathbf{w}_1 + \alpha_2\lambda_2^t\mathbf{w}_2 + \cdots + \alpha_n\lambda_n^t\mathbf{w}_n \end{aligned}$$

This is the eigenmode expansion of a solution. We can say that as $t \to \infty$, then there will be a mode that dominates.

Theorem 7.1 (Perron-Frobenius Theorem)**.** Assume that the PPM A is primitive, ie. for some $k \geq 1$, $(A^k)_{ij} \geq 0$. Then:

1. A has a single eigenvalue λ_1 of maximum modulus.
2. λ_1 is real and positive
3. Both the right $\mathbf{w}_1$ and the left eigenvector $\mathbf{v}_1$ are both positive.

$$A\mathbf{w}_1 = \lambda_1\mathbf{w}_1 \qquad \mathbf{v}_1^T A = \lambda_1\mathbf{v}_1^T$$

4. $\mathbf{v}_1$ and $\mathbf{w}_1$ are unique left and right eigenvectors.

Thus, for a primitive A,

$$\mathbf{x}(t) \to \alpha_1 \lambda_1^t \mathbf{w}_1 \text{ as } t \to \infty$$

or more formally,

$$\lim_{t\to\infty} \lambda_1^{-t} \mathbf{x}(t) = \alpha_1 \mathbf{w}_1$$

so now only three things can happen assumptotically,

1. If $\lambda_1 > 1$, then $\|x(t)\| \to \infty$ as $t \to \infty$
2. If $\lambda_1 = 1$, then $\mathbf{x}(t) \to \alpha_1 \mathbf{w}_1$ as $t \to \infty$, so it stabilises
3. If $\lambda_1 < 1$, then $\mathbf{x}(t) \to \mathbf{0}$ as $t \to \infty$, so we have extinction

Now we can consider the fixed points, $x(t) = \hat{x}$ for all time. If $\hat{\mathbf{x}} = A\hat{\mathbf{x}}$ and no eigenvalues are equal to one we see that $|A - I| \neq 0$ so,

$$\hat{\mathbf{x}} = (A - I)\mathbf{0} = \mathbf{0}$$

then we have a unique fixed point. Hence, we have the first condition in the theorem it being unstable, the third it being stable and the second a bifurcation.

What about α_1? We know,

$$\mathbf{x}_0 = \alpha_1 \mathbf{w}_1 + \cdots + \alpha_n \mathbf{w}_n$$

for $i \neq j$, then $\mathbf{v}_i^T \mathbf{w}_j = 0$. This can be proved by considering the definitions, multiplying and then manipulating the expressions. So,

$$\begin{aligned}
\mathbf{v}_1^T \mathbf{x}_0 &= \alpha_1 \mathbf{v}_1^T \mathbf{w}_1 + \alpha_2 \mathbf{v}_2^T \mathbf{w}_2 + \cdots + \alpha_n \mathbf{v}_n^T \mathbf{w}_n \\
\mathbf{v}_1^T \mathbf{x}_0 &= \alpha_1 \mathbf{v}_1^T \mathbf{w}_1 \\
\frac{\mathbf{v}_1^T \mathbf{x}_0}{\mathbf{v}_1^T \mathbf{w}_1} &= \alpha_1
\end{aligned}$$

That is the population inertia.

In summary, when A is primitive,

$$\lim_{t\to\infty} \lambda_1^{-t} \mathbf{x}(t) = \frac{\mathbf{v}_1^T \mathbf{x}_0}{\mathbf{v}_1^T \mathbf{w}_1} \mathbf{w}_1$$

where,

$$A\mathbf{w}_1 = \lambda_1 \mathbf{w}_1, \quad \mathbf{v}_1^T A = \lambda_1 \mathbf{v}_1^T$$

and $\mathbf{w}_1$ is the stable state structure and $\mathbf{v}_1$ is the reproductive value.

7.2 Issues

We now, for simplicity, drop the subscript 1, so any v, w and λ are the first.

1. We now consider some target growth rate λ_T, and we assume that this to be one. So the question is how can be change A to make $\lambda = \lambda_T$.
2. How can be find bounds on $\frac{\mathbf{v}^T \mathbf{x}_0}{\mathbf{v}^T \mathbf{w}}$

7.2.1 Controlling $\lambda - \lambda_T$

If we are interested in an age-structured model, we have a Leslie matrix. What is the characteristic polynomial of the Leslie matrix?

$$\begin{aligned} c_A(s) &= |sI - A| \\ &= s^n - f_1 s^{n-1} - f_2 p_1 s^{n-2} + \cdots + f_n p_1 + p_{n-1} \end{aligned}$$

and we can show this has only one positive root, λ. As $s \to \infty$, $c_A(s) \to \infty$. So, for $s \geq 0$ the graph must only touch the x axis once, Thus for $s \geq 0$:

- $c(A) < 0$ if $s > \lambda$
- $c(A) > 0$ if $s < \lambda$

If follows that $\lambda > \lambda_T \iff c_A(\lambda_T) < 0$. In particular,

$$\lambda > 1 \iff c_A(1) < 0$$

This is equivilent to $R(A) > 0$, where,

$$R(A) = f_1 + f_2 p_1 + \cdots + f_n p_1 + \cdots + p_{n-1}$$

and so $\lambda > 1 \iff R(A) > 1$, growth, and $\lambda < 1 \iff R(A) < 1$, decline.

7.2.2 Determining the range of the population inertia

We know that,

$$\lim_{t \to \infty} \lambda^{-t} \mathbf{x}(t) = \frac{\mathbf{v}^T \mathbf{x}_0}{\mathbf{v}^T \mathbf{w}}$$

we define $\mathbf{x}_0 = (x_i)$, $\mathbf{v} = (v_i)$, $v_{min} = \min_i v_i$ and $v_{max} = \max_i v_i$. Assume wlog,

$$\sum_{i=1}^{n} x_{i_0} = 1$$

then,

$$\begin{aligned} \mathbf{v}^T x_0 &= \sum_{i=1}^{n} v_i x_{i_0} \\ &\leq \sum_{i=1}^{n} v_{max} x_{i_0} \\ &= v_{max} \sum_{i=1}^{n} x_{i_0} \\ &= v_{max} \end{aligned}$$

and so $\mathbf{v}^T \mathbf{x}_0 \leq v_{max}$ and we can show $v_{min} \leq \mathbf{v}^T \mathbf{x}_0$ and so,

$$\frac{v_{min}}{\mathbf{v}^T w} \leq \frac{\mathbf{v}^T \mathbf{x}_0}{\mathbf{v}^T \mathbf{w}} \leq \frac{v_{max}}{\mathbf{v}^T \mathbf{w}}$$

These bounds are sharp, these are attained for suitable choices of $\mathbf{x}_0$. We just take $\mathbf{x}_0$ to have a one where the maximum or minimum value of $\mathbf{v}$.

7.3 Sensitivity Analysis

We take A and preterb it to $A + \Delta A$ and so we want to consider $\lambda(A) \mapsto \lambda(A + \Delta A)$. We will firstly consider this through a linear approximation with sensitivity analysis and then transfer function analysis which is exact.

7.3.1 Sensitivity Analysis

We want to map $A \mapsto A + \Delta A$, we then map, each useful quantity from $f(A) \mapsto f(A + \Delta A)$. Now,

$$\lambda(A) = \lambda(a_{11}, \ldots, a_{nn})$$

and,

$$\lambda(A + \Delta A) = \lambda(a_{11} + \Delta a_{11}, \ldots, a_{nn} + \Delta a_{nn})$$

and as we have done many times before we approximate this with a Taylor expansion.

$$\lambda(A + \Delta A) = \lambda(a_{11}, \ldots, a_{nn}) + \sum_{i,j=1}^{n} \frac{\partial \lambda}{\partial a_{ij}}(A)\Delta a_{ij} + \mathcal{O}(2)$$

Thus,

$$\lambda(A + \Delta A) = \lambda(A) + \Delta\lambda + \mathcal{O}(2)$$

and similarly,

$$\mathbf{v}(A + \Delta A) = \mathbf{v}(A) + \Delta\mathbf{v} + \mathcal{O}(2)$$
$$\mathbf{w}(A + \Delta A) = \mathbf{w}(A) + \Delta\mathbf{w} + \mathcal{O}(2)$$

and now exploit that our equations will satisfy the perterbed eigenvalue eignvector equations,

$$(A + \Delta A)\mathbf{w}(A + \Delta A) = \lambda(A + \Delta A)\mathbf{w}(A + \Delta A)$$
$$(A + \Delta A + \mathcal{O}(2))(\mathbf{w} + \boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2)) = (\lambda(A) + \Delta\lambda + \mathcal{O}(2))(\mathbf{w} + \boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2))$$
$$A\mathbf{w} + A\boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2) + \Delta A\mathbf{w} + \Delta A\boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2) = \lambda(A)\mathbf{w} + \lambda(A)\boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2) + \Delta\lambda\boldsymbol{\Delta}\mathbf{w} + \mathcal{O}(2)$$
$$A\mathbf{w} + A\boldsymbol{\Delta}\mathbf{w} + \Delta A\mathbf{w} = \lambda\mathbf{w} + \lambda\boldsymbol{\Delta}\mathbf{w} + \Delta\lambda\mathbf{w} + \mathcal{O}(2)$$
$$\mathbf{v}^T A\mathbf{w} + \mathbf{v}^T A\boldsymbol{\Delta}\mathbf{w} + \mathbf{v}^T\Delta\mathbf{w} = \lambda\mathbf{v}^T\mathbf{w} + \lambda\mathbf{v}^T\boldsymbol{\Delta}\mathbf{w} + \Delta\lambda\mathbf{v}^T\mathbf{w} + \mathcal{O}(2)$$

Now $TA\mathbf{w} = \lambda\mathbf{w}$ and $\mathbf{v}^T A = \lambda\mathbf{v}^T$

$$\lambda\mathbf{v}^T\mathbf{w} + \lambda\mathbf{v}^T\Delta\mathbf{w} + \mathbf{v}^T\Delta A\mathbf{w} = \lambda\mathbf{v}^T\mathbf{w} + \lambda\mathbf{v}^T\boldsymbol{\Delta}\mathbf{w} + \Delta\lambda\mathbf{v}^T\mathbf{w} + \mathcal{O}(2)$$
$$\mathbf{v}^T\Delta A\mathbf{w} = \Delta\lambda\mathbf{v}^T\mathbf{w} + \mathcal{O}(2)$$

Thus,

$$\Delta\lambda = \frac{\mathbf{v}^T\Delta A\mathbf{w}}{\mathbf{v}^T\mathbf{w}} + \mathcal{O}(2)$$

We now assume that ΔA is obtained by perturbing one entry a_{ij} ($a_{ij} \mapsto a_{ij} + \Delta a_{ij}$). Then,

$$\Delta A = \Delta a_{ij}\mathbf{e}_i\mathbf{e}_j^T$$
$$= \begin{pmatrix} 0 & & & & 0 \\ & \ddots & & \iddots & \\ & & a_{ij} & & \\ & \iddots & & \ddots & \\ 0 & & & & 0 \end{pmatrix}$$

where it is on the i^{th} row and j^{th} column. We now substitute this back in and obtain,

$$\begin{aligned}\Delta\lambda &= \frac{\mathbf{v}^T\mathbf{e}_i\mathbf{e}_j^T\mathbf{w}}{\mathbf{v}^T\mathbf{w}}\Delta a_{ij} + \mathcal{O}(2)\\ &= \frac{v_i w_j}{\mathbf{v}^T\mathbf{w}}\Delta a_{ij} + \mathcal{O}(2)\\ \frac{\Delta\lambda}{\Delta a_{ij}} &= \frac{v_i w_j}{\mathbf{v}^T\mathbf{w}} + \mathcal{O}(1)\end{aligned}$$

Now take the limit as $\Delta a_{ij} \to 0$, we obtain,

$$\frac{\partial\lambda}{\partial a_{ij}} = \frac{v_i w_j}{\mathbf{v}^T\mathbf{w}}$$

These are our terms and so we can find the sensitivity matrix,

$$S = \left(\frac{\partial\lambda}{\partial a_{ij}}\right) = \frac{\mathbf{v}\mathbf{w}^T}{\mathbf{v}^T\mathbf{w}}$$

Summary: We mapped $A \mapsto \Delta A$ and $\lambda(A) \mapsto \lambda(A + \Delta A)$ where $\mathcal{L}(A + \Delta A) = \lambda(A) + \Delta\lambda + \mathcal{O}(2)$ and,

$$\Delta\lambda = \sum_{i=1}^{n} \frac{\partial\lambda}{\partial a_{ij}}(A)\Delta a_{ij}$$

In particular, if we only have one element being perterbed,

$$\lambda(A + \Delta A) = \lambda(A) + \frac{\partial\lambda}{\partial a_{ij}}(A)\Delta a_{ij} + \mathcal{O}(2)$$

We want $A + \Delta A$ with an eigenvalue λ_T. Then we can say that,

$$\lambda_T = \lambda + \frac{\partial\lambda}{\partial a_{ij}}\Delta a_{ij} + \mathcal{O}(2)$$

Then it follows for small pertibations,

$$\Delta a_{ij} \approx \frac{\lambda_T - \lambda}{\frac{\partial\lambda}{\partial a_{ij}}}$$

this is a linear approximation. We can choose the smallest perturbation after calculating the partial derivatives.

7.3.2 Transfer Function Analysis for PPMs

The idea here is $a_{ij} \mapsto a_{ij} + p_{ij}$ such that the perturbed eigenvalue is λ:

$$\Delta A = p_{ij}\mathbf{e}_i\mathbf{e}_j^T = \begin{pmatrix} 0 & & & & 0 \\ & \ddots & & \iddots & \\ & & p_{ij} & & \\ & \iddots & & \ddots & \\ 0 & & & & 0 \end{pmatrix}$$

and again we proceed from the perturbed eigenvalue equation.

$$\begin{aligned}(A + \Delta A)\mathbf{w} &= \lambda\mathbf{w}\\ A\mathbf{w} + p_{ij}\mathbf{e}_i\mathbf{e}_j^T\mathbf{w} &= \lambda I\mathbf{w}\\ (\lambda I - A)\mathbf{w} &= p_{ij}\mathbf{e}_i\mathbf{e}_j^T\mathbf{w}\end{aligned}$$

Now assume that $|\lambda I - A| \neq 0$ thus can multiply both sides by $e_j^T(\lambda I - A)^{-1}$

$$\begin{aligned}
\mathbf{e}_j^T(\lambda I - A)^{-1}(\lambda I - A)\mathbf{w} &= \mathbf{e}_j^T(\lambda I - A)^{-1}p_{ij}\mathbf{e}_i\mathbf{e}_j^T\mathbf{w} \\
\mathbf{e}_j^T\mathbf{w} &= p_{ij}\mathbf{e}_j^T(\lambda I - A)^{-1}\mathbf{e}_i(\mathbf{e}_j^T\mathbf{w}) \\
1 &= p_{ij}\mathbf{e}_j^T(\lambda I - A)^{-1}\mathbf{e}_i \\
p_{ij} &= \frac{1}{\mathbf{e}_j^T(\lambda I - A)^{-1}\mathbf{e}_i} \\
p_{ij} &= \frac{1}{[(\lambda I - A)^{-T}]_{ij}}
\end{aligned}$$

7.4 Transient Dynamics

7.4.1 From transient to asymptotic dynamics

For $\mathbf{x}(t+1) = A\mathbf{x}(t)$ where $\mathbf{x}(t) = (x_i(t))$ and we can write,

$$\lim_{t\to\infty} \lambda^{-t}\mathbf{x}(t) = \frac{\mathbf{v}^T\mathbf{x}(0)}{\mathbf{v}^T\mathbf{w}}\mathbf{w}. \tag{1}$$

We now introduce $N(t) = \|\mathbf{x}(t)\|_1 = \sum_{i=1}^n |x_i(t)| = \sum_{i=1}^n x_i(t) = \mathbf{1}^T\mathbf{x}(t)$. Now we consider 1 and then dot with $\mathbf{1}$.

$$\begin{aligned}
\mathbf{1}^T \lim_{t\to\infty} \lambda^{-t}\mathbf{x}(t) &= \mathbf{1}^T \frac{\mathbf{v}^T\mathbf{x}(0)}{\mathbf{v}^T\mathbf{w}}\mathbf{w} \\
\lim_{t\to\infty} \lambda^{-t}\mathbf{1}^T\mathbf{x}(t) &= \frac{\mathbf{v}^T\mathbf{x}(0)}{\mathbf{v}^T\mathbf{w}}\mathbf{1}^T\mathbf{w} \\
\lim_{t\to\infty} \lambda^{-t}N(t) &= \frac{\mathbf{v}^T\mathbf{x}(0)}{\mathbf{v}^T\mathbf{w}}\|\mathbf{w}\|_1 \\
\lim_{t\to\infty} N(t) &= \frac{\mathbf{v}^T\mathbf{x}(0)}{\mathbf{v}^T\mathbf{w}}\|\mathbf{w}\|_1 \lambda^t
\end{aligned}$$

Asymptotically, three possibilities. We have exponential growth, stasis and exponential decay. What we want to know now is what happens before the asymptotic behaviour? We want some way to bound the possibilities.

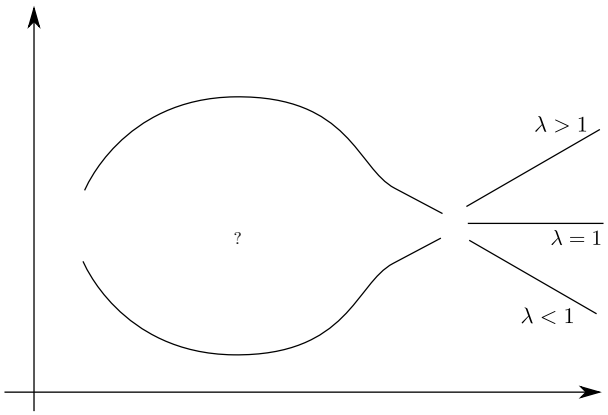


Figure 14: Transient and Asymptotic Dynamics.

7.4.2 Bound 1 - Population Amplification and Attenuation

We will consider maximum and minimum column sums. We know $\mathbf{x}(t) = A^t\mathbf{x}(0)$. Thus $N(t) = \mathbf{q}^t\mathbf{x}(t) = \mathbf{1}^T A^t\mathbf{x}(0) = \mathbf{1}^T M\mathbf{x}(0)$, where $M = A^t$ given $\mathbf{x}(0)$ such that $N(0) = \mathbf{1}^T\mathbf{x}(0) = 1$. How large or small can $N(t)$ become?

Assume that $M = (m_{ij})$ is a non-negative matrix and that $\mathbf{x} = (x_j)$ is a non-negative vector. Then,

$$\begin{aligned}\mathbf{1}^T\mathbf{M}\mathbf{x} &= \sum_{i,j=1}^{n} M_{ij}x_j = \sum_{j=1}^{n}\left(\sum_{i=1}^{n} M_{ij}\right)x_j \\ &\leq \sum_{j=1}^{n}\max_j\left(\sum_{i=1}^{n} M_{ij}\right)x_j = \max_j\left(\sum_{i=1}^{n} M_{ij}\right)\sum_{j=1}^{n} x_j = \left(\max_j\sum_{i=1}^{n} M_{ij}\right)\mathbf{1}^T\mathbf{x}\end{aligned}$$

We have to show that,

$$\mathbf{1}^T M\mathbf{x} \leq \overline{c}\mathbf{1}^T\mathbf{x}$$

where $\overline{c} = \max_j \sum_{i=1}^{n} M_{ij} = \sum_{i=1}^{n} M_{ij_M}$. Similarly we can show that,

$$\mathbf{1}^T M\mathbf{x} \geq \underline{c}\mathbf{1}^T\mathbf{x}$$

where $\underline{c} = \min_j \sum_{i=1}^{n} M_{ij} = \sum_{i=1}^{n} M_{ij_m}$. Taking these together,

$$\underline{x}\mathbf{1}^T\mathbf{x} \leq \mathbf{1}^T M\mathbf{x} \leq \overline{c}\mathbf{1}^T\mathbf{x} \qquad (*)$$

Take $M = A^t$, $\mathbf{x} = \mathbf{x}(0)$ in *, then,

$$\underline{c}\mathbf{1}^T\mathbf{x}(0) \leq \mathbf{1}^T A^t\mathbf{x}(0) \leq \overline{c}\mathbf{1}^T\mathbf{x}$$

where $\overline{c}$ is the maximum column sum of A^t, denoted ρ_t, and $\underline{c}$ is the minimum column sum of A^t, denoted, a_t. Thus,

$$a_t \leq N(t) \leq \rho_t \qquad t \geq 0.$$

This is bound 1. We call a_t the minimum attenuation and ρ_t the maximum attenuation. These bounds are

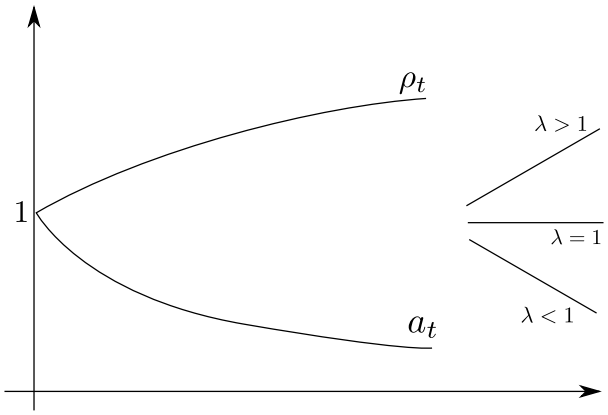


Figure 15: Bound 1.

sharp. That is, for a given t', $\mathbf{x}(0) = \mathbf{e}_{jM}$ (a basis vector), this will give $N(t') = \rho_{t'}$ and $\mathbf{x}(0) = \mathbf{e}_{jm}$ will give $N(t') = a_{t'}$. In simpler terms, they can be attained.

7.4.3 Bound 2

Now we multiply on the left by $\mathbf{v}^T$ and get, (wlog when we write $\mathbf{v}$ and λ we mean $\mathbf{v}_1$ and λ_1, the dominant eigenvector.)

$$\begin{aligned}\mathbf{v}^T\mathbf{x}(t+1) &= \mathbf{v}^T\mathbf{A}\mathbf{x}(t)\\ &= \lambda\mathbf{v}^T\mathbf{x}(t)\\ &= \sum v_i x_i(t)\end{aligned}$$

and so we can write,

$$v_{\min}N(t) \le \mathbf{v}^T\mathbf{x}(t) \le v_{\max}N(t)$$

and so we can form another bound,

$$v_{\min}N(t+1) \le \lambda v_{\max}^T N(t)$$

and the other way around and so,

$$\frac{v_{\min}}{v_{\max}}\lambda^t \le N(t) \le \frac{v_{\max}}{v_{\min}}\lambda^t$$

This is bound 2. This bound isn't sharp, but is a lot easier to calculate.

7.4.4 Bound 3

We now look at $\mathbf{x}(t) = A^t\mathbf{x}(0)$ and we write this as

$$\begin{aligned}N(t+1) &= \mathbf{1}A\mathbf{x}(t)\\ &= \begin{pmatrix}c_1(A) & \dots & c_n(A)\end{pmatrix}\mathbf{x}(t)\end{aligned}$$

Now we will get $\underline{c}(A)N(t) \le N(t+1) \le \overline{c}(A)N(t)$ and now we iterate and get that,

$$\underline{c}(A)^t N(0) \le N(t) \le (\overline{c}(A))^t N(0).$$

This is bound 3. This only contains values that can be found from A.

7.4.5 Combining Bounds

We now consider combining these bounds to create one overall bound. We consider bound 2 and 3. These say,

$$N(t) \ge \frac{v_{\min}}{v_{\max}}\lambda^t, \qquad N(t) \ge \underline{c}^t.$$

This gives,

$$N(t) \ge \max\left(\frac{v_{\min}}{v_{\max}}\lambda^t, \underline{c}^t\right)$$

Then bound 1 gives us that $N(t) \ge a_t$, with $N(t) = a_t$ for suitable $\mathbf{x}(0)$. Thus,

$$a_t \ge \max\left(\frac{v_{\min}}{v_{\max}}\lambda^t, \underline{c}^t\right).$$

Similarly, follows from bounds 2 and 3 that,

$$\rho_t \le \min\left(\frac{v_{\max}}{v_{\min}}\lambda^t, \overline{c}^t\right)$$

Where the red lines are the bounds for a_t and ρ_t. Further, these then give us bounds for any solutions for all the different initial conditions. That is, we can attain the less accurate bounds from just A. Sometimes as A gets complex A^t is very hard to calculate.

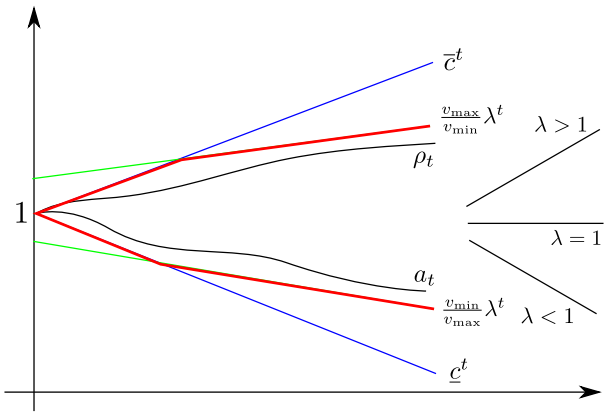


Figure 16: Combined Bounds.

8 Spatially distributed reaction-diffusion kinetics

8.1 Background

Consider the concentration $c(\mathbf{x}, t)$. This is the concentration of some chemical species at $\mathbf{x} \in \mathbb{R}^3$ at time t.

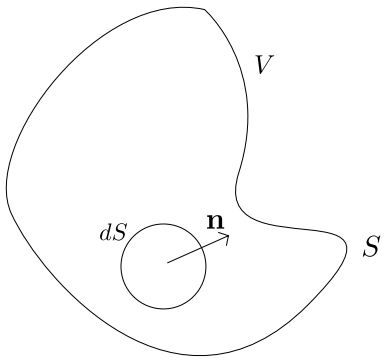


Figure 17: Model setup

Let $f = f(c, \mathbf{x}, t)$ be the source of the chemical in V. Introduce the flux vector $\mathbf{J} = J_1\mathbf{i} + J_2\mathbf{j} + J_3\mathbf{k}$. We define this as, $\mathbf{J} \cdot d\mathbf{S} = \mathbf{J} \cdot \mathbf{n}dS$. This is the rate of movement of chemical across dS per unit time. We can write the following conservation equation,

$$\frac{\partial}{\partial t}\iiint_V c(\mathbf{x}, t)dV = \iiint_V f dV - \iint_S \mathbf{J} \cdot d\mathbf{S}$$

We recall the divergence theorem,

$$\iint_S \mathbf{J} \cdot d\mathbf{S} = \iiint_V \nabla \cdot \mathbf{J} dV$$

Thus,

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

This holds for an arbitrary volume V. We can equate the integrands,

$$\frac{\partial c(\mathbf{x}, t)}{\partial t} = -\nabla \cdot \mathbf{J} + f \tag{2}$$

If transport is via diffusion, then,

$$\mathbf{J} = -D\nabla c$$

where D is the diffusion coefficient. In general $D = D(\mathbf{x}, t)$. This is referred to as Fick's law. In $1D$, then $J = -D\frac{\partial c}{\partial x}$. We now substitute into 2. We obtain,

$$\frac{\partial c}{\partial t} = f + \nabla \cdot (D\nabla c). \tag{3}$$

This is the reaction-diffusion equation. We now go further and assume that $D(\mathbf{x}, t) = D$ is constant. Then 3 simplifies to,

$$\frac{\partial c}{\partial t} = f + D\nabla \cdot \nabla c = f + D\nabla^2 c \tag{4}$$

where ∇^2 is just the Laplacian. If $f = 0$, then we obtain the diffusion equation in three dimensions. We consider m reactants, with concentration,

$$u_1(\mathbf{x}, t), \ldots, u_m(\mathbf{x}, t)$$

with diffusion constants, $D_1, \ldots, D_m$ and source terms $f_1(u_1, \ldots, u_m), \ldots, f_m(u_1, \ldots, u_m)$. We then write the equations as,

$$\frac{\partial u_i}{\partial t} = f_i(u_1, \ldots, u_m) + D_i\nabla^2 u_i \qquad 1 \leq i \leq m.$$

We can write this in vector form,

$$\frac{\partial \mathbf{u}}{\partial t} = \mathbf{f}(\mathbf{u}) + \mathbf{D}\nabla^2\mathbf{u}$$

where,

$$\mathbf{u} = (u_1, \ldots, u_m)^T \qquad \mathbf{f} = (f_1, \ldots, f_m)^T$$

and,

$$D = \begin{pmatrix} D_1 & & 0 \\ & \ddots & \\ 0 & & D_m \end{pmatrix}$$

First, we consider one reactant, $m = 1$ and $x \in \mathbb{R}$. This gives arise to,

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