Lecture 2

Single species population models

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1 Insect outbreak: spruce budworm

Spruce budworm is a moth whose caterpillars eat the foliage on trees, leading to tree death; this constitutes a big problem for the timber business in Canada. Curiously, the damage caused can vary greatly year on year.

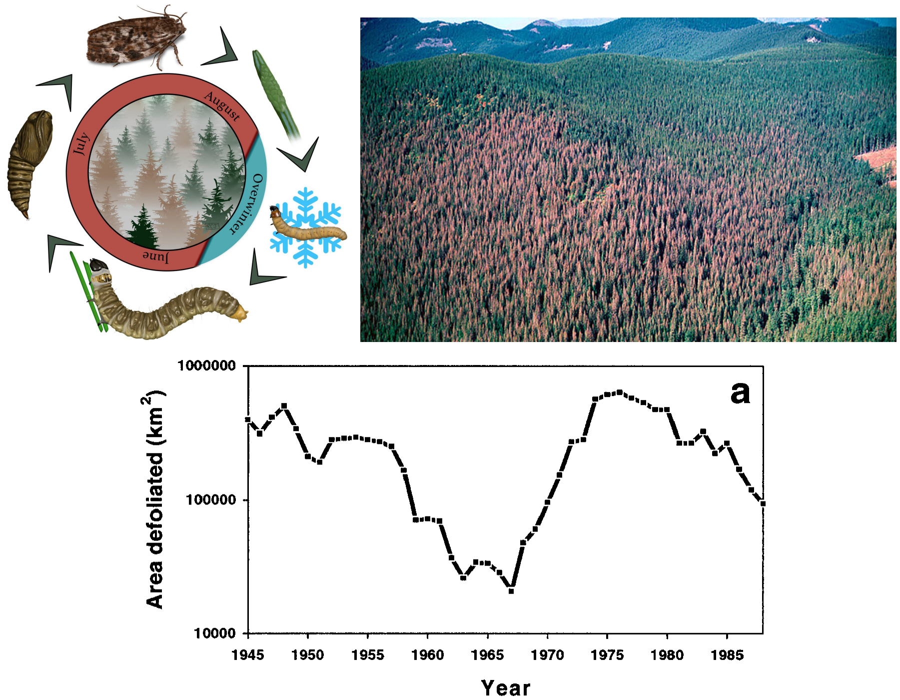


Figure 1: (Left) Life cycle of Spruce Budworm (*Choristoneura fumiferanae*); credit: Rob Johns, @robcjohns. (Right) Aerial photograph of western spruce budworm outbreak at Mount Hood National Forest, Oregon; credit: William M. Ciesla, Forest Health Management International, Bugwood.org. (Bottom) Time series of total area defoliated by eastern spruce budworm in eastern North America from 1945 to 1988 [Williams & Liebhold, *Oecologia* **124**, 544 (2000)].

The peaks in damage largely corresponds to outbreaks in the budworm population.

Question: why do outbreaks occur and can they be controlled?

Ludwig *et al.* (1978) proposed a simple model that does not explicitly model the outbreak phenomenon, but does indicate why they occur.

Assumptions: Let $N(t)$ be the budworm population density. In addition to natural birth and death processes, the are also eaten by birds (predators which will not be explicitly modelled). The key assumptions are:

(1) $N(t)$ grows logistically in absence of predation.

(2) Predation by birds. The population of birds is assumed constant and we denote the predation rate $P(N)$. The functional form of $P(N)$ will have properties that reflect the following:

i) $N(t)$ is "small", the birds look elsewhere for food.

ii) $N(t)$ is "large", the birds can only eat so much in a day.

Since no budworm can be eaten when $N = 0$, then $P(0) = 0$. So we can write

$$P(N) = NE(N)$$

where $E(N)$ is the amount of effort per unit time per predator.

(2.1) Statement i) suggests that $E'(N) > 0$ when N is small, i.e. the birds put more effort in the more budworm there are. The simplest choice is to assume $E(N) \propto N$, hence

$$P(N) \propto N^2 \,, \quad \text{when } N^2 \text{ is small}$$

(2.2) Statement ii) implies that $P(N) \to$ const. as $N \to \infty$. Given the form of $P(N)$ for small N from (2.1), we can choose, for example

$$P(N) = \frac{AN^2}{B^2 + N^2} \tag{1}$$

so $P(N)$ acts like a switch (sometimes called "Type III" predation).

The model: combining the above assumptions, Ludwig *et al.* (1978) proposed the following model

$$\frac{dN}{dt} = r_b N \left(1 - \frac{N}{K_b}\right) - \frac{A\,N^2}{B^2 + N^2},$$

with $N(0) = N_0$. The model has 5 parameters r_b, K_b, A, B and N_0 and we **non-dimensionalise** the system following the 3 steps of Lecture 1, Sec. 4.1.

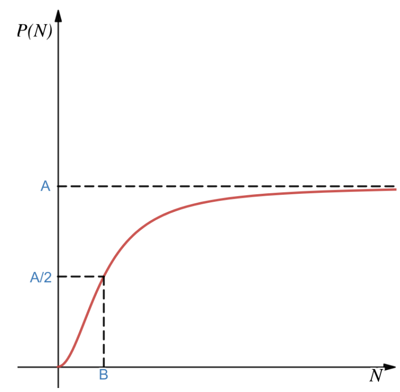


Figure 2: Sketch of predation rate function in Eq. (1).

1. **Rescale all variables:** write $N = n_0 u$ and $t = t_0 \tau$, hence

$$\frac{n_0}{t_0}\frac{du}{d\tau} = r_b n_0 u \left(1 - \frac{n_0 u}{K_b}\right) - \frac{A\,n_0^2 u^2}{B^2 + n_0^2 u^2}$$

and $N(0) = N_0 = n_0 u(0)$.

2. **Grouping the constants so that all expressions either side of "=", "+" and "-" are dimensionless quantities**: here, we multiply through by t_0/n_0 and manipulate to get

$$\frac{du}{d\tau} = r_b t_0 u \left(1 - \frac{n_0 u}{K_b}\right) - \frac{t_0 A}{n_0}\frac{u^2}{(B^2/n_0^2 + u^2)}$$

and $u(0) = N_0/n_0$.

3. **Choose rescaling constants**: although, it is usual to eliminate r_b and K_b (as with the logistic model), it is more convenient to eliminate A and B in the predation term (see why later). Choosing
$$n_0 = B\,, \quad t_0 = \frac{n_0}{A} = \frac{B}{A}$$
we obtain
$$\frac{du}{d\tau} \;=\; ru\left(1 - \frac{u}{K}\right) - \frac{u^2}{1+u^2} \;\equiv\; f(u) \tag{2}$$
and $u(0) = u_0$, where $r = t_0 r_b = \dfrac{B r_b}{A}$, $K = \dfrac{K_b}{B}$ and $u_0 = \dfrac{N_0}{B}$.

The dimensionless model has only 3 parameters r, K and u_0.
This budworm ODE is not solvable in explicit form (category 2 in Lecture 1 Appendix) for general parameters, so will have to use qualitative methods described in the Appendix to study the model.

1.1 Steady-states analysis

Finding the steady-states. The steady-states $u = u^*$ satisfy $f(u^*) = 0$, i.e.
$$f(u^*) = u^*\left[r\left(1 - \frac{u^*}{K}\right) - \frac{u^*}{1+u^{*2}}\right] = 0 \tag{3}$$
so

1) $u^* = 0$. Can show $f'(0) > 0$ and therefore unstable. [Exercise!]

2) Up to 3 non-zero steady-states satisfying
$$r\left(1 - \frac{u^*}{K}\right) - \frac{u^*}{1+u^{*2}} = 0 \quad\Rightarrow\quad r\left(1 - \frac{u^*}{K}\right)\left(1+u^{*2}\right) - u^* = 0$$
which leads to a cubic in u^*. Cubics are notoriously awkward and the solutions unwieldy (see **Maple file M1.2**). We seek an alternative approach.

A graphical analysis of the non-zero steady-sates. We rewrite the formula for the non-zero steady-states,
$$r\left(1 - \frac{u^*}{K}\right) = \frac{u^*}{1+u^{*2}}\,. \tag{4}$$
Plotting the left and right hand-sides, we find the picture shown in Fig. 4.
Here the non-dimensionalisation means that the "complicated bit", i.e. $u^{*2}/(1+u^{*2})$, is fixed on the graph and by simply manoeuvring a straight line with negative gradient we can identify the three important cases.
Generally speaking, we find three cases as the growth rate r is varied. For each of the 3 cases we can sketch "accurate enough" phase-lines to deduce the **biologically relevant**, positive steady-states and their stability.

1. "Small r_1" $\Rightarrow$ small u^*, let us call it $u = u_1^*$.
2. "Intermediate r_2" $\Rightarrow$ three positive u^*s: $u = u_1^*, u_2^*$ and u_3^* say.
3. "Large r_3" $\Rightarrow$ large u^*, let us call it $u = u_3^*$.

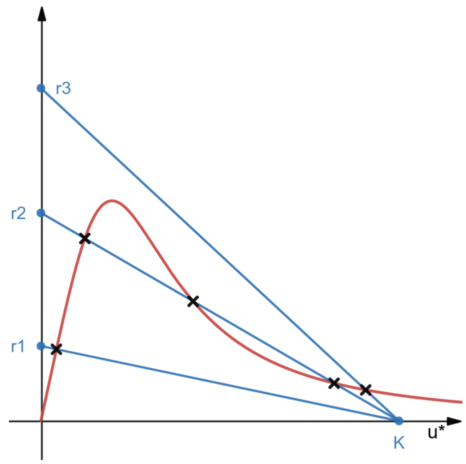


Figure 3: Three general cases of solutions of Eq. (4) as the parameter r is varied $r = r_1,\, r_2,\, r_3$.

Definition 1.4A: a **bifurcation** is a point at which the qualitative behaviour of the solutions of a model changes as a parameter changes.

Figure 4 shows each of the three cases identified above with the corresponding phase-line plot. By remembering the definition of $f(u)$ in Eq. (3) we can deduce the sign of $f(u)$ and hence the behaviour of the steady states.

1. "Small r_1": $u = u_1^*$ is a *stable* steady state
2. "Intermediate r_2": $u = u_1^*$ is a *stable* steady state; $u = u_2^*$ is an *unstable* steady state; $u = u_3^*$ is a *stable* steady state.
3. "Large r_3": $u = u_3^*$ is a *stable* steady state.

See Fig. 4 for more details.

Note 1.4A: The transition between Cases 1 & 2 and Cases 2 & 3, i.e. are examples of "tangent bifurcations".

Very Big Note 1.4B: The situation in Note 1.4A requires very specific parameter sets, which means that are very unlikely to be observed in reality. These "in between" cases **will not be discussed in this module.** For example, suppose we have a parameter α in a model and there is a bifurcation at $\alpha = 1$, then we will consider cases $0 < \alpha < 1$ and $\alpha > 1$ in detail, but will never discuss $\alpha = 1$. (Though a Hopf bifurcation discussed in Section 2 will be an exception of this).

Using numerical methods (see **Maple file M1.2** on Learn), we can summarise the three cases in a $K - r$ "parameter space" diagram:

There's a problem. We have learnt a lot about the solutions of the model just by sketching a few graphs, but there is no indication from the model as to why outbreaks occur. In fact, the model suggests the opposite, as it predicts $u(t) \to u^*$, a constant, as $t \to \infty$.

What's wrong? The main problem is that in practice r and K are not fixed, e.g. outbreaks of diseases/parasites in budworm and birds, localised environmental or climate changes will effect these parameters.

Consider a fixed $K = K^*$ as shown above, then the dependence of the steady states on r can be summarised in the **bifurcation diagram** below.

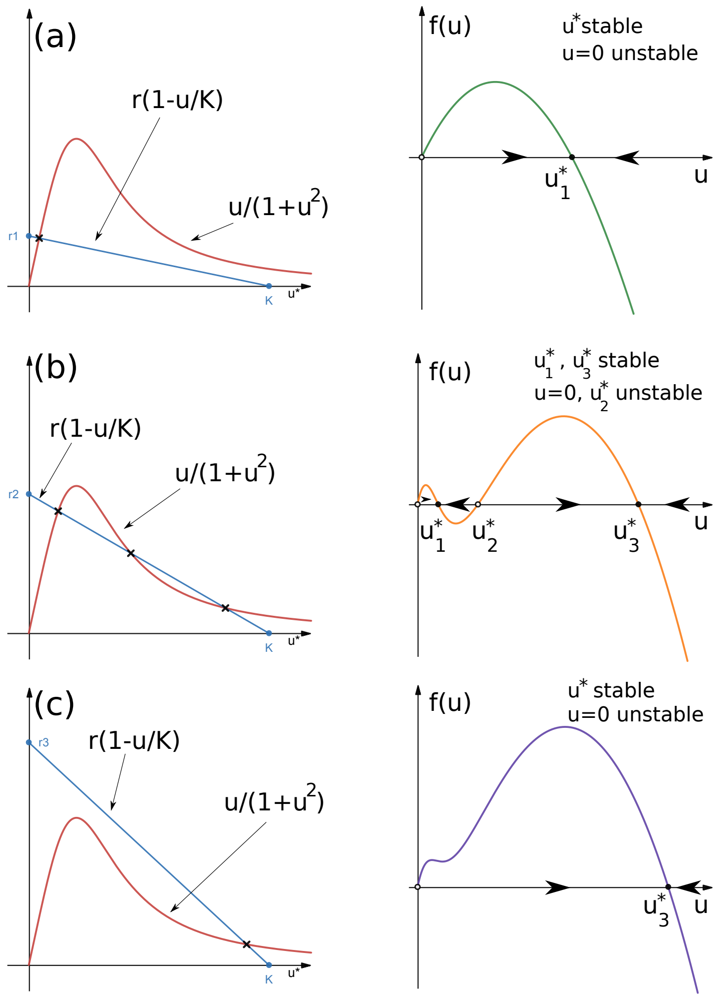


Figure 4: Solution of the budworm model. Each row shows one case in the solution parametrised by the value of r for $r_1 < r_2 < r_3$. The left column shows the left and right-hand side of Eq. (4); the intersection of the two curves gives the steady states of the model. The right column shows $f(u)$ [Eq. (3)] for the same value of r, K as on the left column. The zeros of $f(u)$ correspond to stable and unstable steady states.

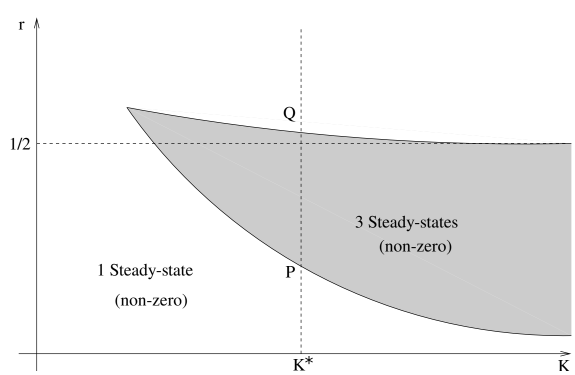
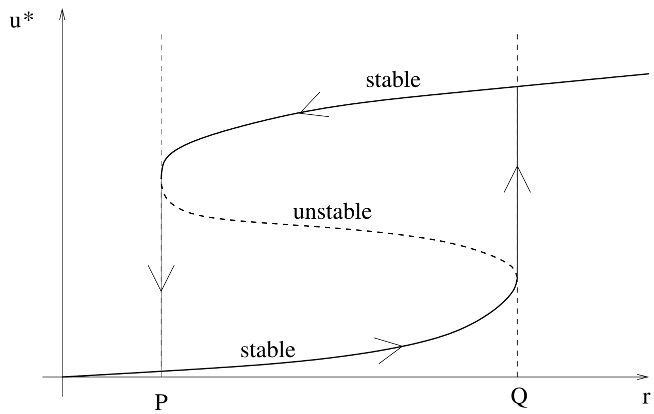


Figure 5: Phase diagram of the steady states of the budworm model.

This bifurcation diagram shows the steady-states and their stability as a function r along $K = K^*$.

- Suppose we increase r from 0, then u^* will move along the **lower branch**, until it reaches



point Q, where u^* jumps to the **upper branch**, i.e. $u_1^* \to u_3^*$, as r increases.

- If we now decrease r then u^* will move back along the **upper branch**, until P where u^* will drop down to the **lower branch**, i.e. $u_3^* \to u_1^*$, as r decreases.
- As r changes the current population depends on past values, a phenomenon known as **hysteresis**. Hysteresis is often an outcome from models with bistability, such as the current one.

Summarizing, in models exhibiting hysteresis, such as this, we find that:

- current state depends on history of the population;
- shifts in the growth rate r provides a simple mechanism to describe large jumps in observed budworm population.

To control population explosions of budworm we need to somehow influence the internal parameters K and r:

- Reduce $K = K_b/B$ - could be done by spraying foliage ($K_b \searrow$).
- Reduce $r = Br_b/A$ - increase predation with a new predator ($B \nearrow$).

Although these conclusions are perhaps obvious the model provides a means of quantifying what measures are needed (whether they are environmentally sound or not). However, later it will be found that spatial effects (dispersal) is very important.

The upshot: The budworm population can be effected by a number of factors, but the model predicts that there is an underlying hysteresis in the dynamics that leads to dramatic (or **catastrophic** = mathematical term) changes in population $\implies$ population outbreaks.

This behaviour is demonstrated in a stochastic simulation in **Maple file M1.2**.

Appendix

A Phase-plane analysis

Note: You will not be required to derive the theory in the exam, but proficiency in its application is expected.

Consider the system

$$\frac{dN}{dt} = f(N,M), \tag{5}$$

$$\frac{dM}{dt} = g(N,M). \tag{6}$$

The second-order ODE equivalent of the phase-line diagram (see the Appendix in Lecture 1) is called the **phase-plane** and the aim is to display qualitatively the direction (or *flow*) of **trajectories** in $N-M$ space. It is a useful tool to establish relatively quickly the qualitative behaviour of the solutions of (5) and (6).

Defintions:

- **Trajectory** = the curve tracked by vector $(N(t), M(t))$ parametrised by t.
- **Phase Plane** = plots of the trajectories in $N-M$ space.

A.1 Trajectories

Let a trajectory follow the path $\boldsymbol{N(t)} = (N(t), M(t))$ and let $\boldsymbol{\delta N}$ be the vector displacement from time t to $t+\delta t$, then

$$\begin{aligned}
\boldsymbol{\delta N} &= \boldsymbol{N(t+\delta t) - N(t)} \\
&= (N(t+\delta t), M(t+\delta t)) \; - \; (N(t), M(t)) \\
&\approx \left(N(t) + \delta t \,\frac{dN}{dt}, \quad M(t) + \delta t\, \frac{dM}{dt} \right) \; - \; (N(t), M(t)) \\
&= \delta t \left(\frac{dN}{dt}, \frac{dM}{dt} \right) \\
&= \delta t \, (f(N,M), g(N,M))
\end{aligned}$$

using linearisation to get from lines 2 to 3. Hence,

- a trajectory at a point (N,M) flows parallel to the vector function $(f(N,M),\, g(N,M))$.

These ideas form the basis of phase-plane construction (see A.2).

Very Big Note: for sufficiently smooth functions $f(N,M)$ and $g(N,M)$:

$$\boxed{\textbf{Trajectories never cross}}$$

Technically, $f(N,M)$ and $g(N,M)$ need to be "Lipschitz continuous" to ensure this; this will be the case in all examples in this module. (See, for example, the Wikipedia article on Lipschitz continuity).

A.2 Drawing phase-planes - a rough guide

The aim of this is to get an **idea of what the global behaviour of the solutions** of the ODE system (rather than local to the steady-state that would have been the focus in Math Methods 3). For this, a key step in constructing the phase-plane is to establish

Where in the phase-plane $\boldsymbol{f(N,M)}$ and $\boldsymbol{g(N,M)}$ are positive or negative?

The boundaries where $f(N,M)$ and $g(N,M)$ change sign are lines called **null-clines**, and they satisfy $\boldsymbol{f(N,M)=0}$ and $\boldsymbol{g(N,M)=0}$, whereby

- On $f(N,M)=0 \;\Rightarrow\; \frac{dN}{dt}=0 \;\Rightarrow\;$ the trajectories are *perpendicular* to the N-axis.
- On $g(N,M)=0 \;\Rightarrow\; \frac{dM}{dt}=0 \;\Rightarrow\;$ the trajectories are *perpendicular* to the M-axis.

Furthermore,

- **Steady-states** are always where the $f(N,M)=0$ and $g(N,M)=0$ null-clines cross.

A.2.1 A recipe for drawing phase-planes:

1. Draw the N and M axes for the region of interest. (Here $N \geq 0$ and $M \geq 0$).
   (*For part 4, let the "x-axis" and "y-axis" be the N and M axes, respectively*).
2. Sketch Null clines: i.e. plot $f(N,M)=0$ and $g(N,M)=0$.
   (*Usually you will be able to express $f(N,M)$ and $g(N,M)$ in the form of $M=h(N)$ and/or $N=H(M)$ and they should then be relatively easy to draw).*
3. Highlight steady-states.
   (*They are always where the $f(N,M)=0$ and $g(N,M)=0$ null-clines cross).*
4. **Key step:** Indicate within each of the regions bordered by the null-clines whether $f(N,M)$ and $g(N,M)$ are positive or negative. (*This is the trickiest part - needs practice*).
   - *One way is to start on a null-cline, say $f(N,M)=0$, and increase (or decrease) either N or M deciding whether $f(N,M)$ is increasing ($\therefore f>0$) or decreasing ($\therefore f<0$) in the region you are moving into. Repeat for $g(N,M)=0$.*
   - *This will tell us the general direction of a trajectory. Suppose in a region:*
     - *if $f>0$, $g>0$ then, from (5)-(6), $\frac{dN}{dt}>0$ and $\frac{dM}{dt}>0$, i.e. N and M are both increasing, hence trajectories will be pointing "north-east".*
     - *if $f>0$, $g<0$ then $\frac{dN}{dt}>0$ and $\frac{dM}{dt}<0$, i.e. N is increasing and M is decreasing $\Rightarrow$ trajectories are pointing "south-east".*

- *if $f < 0$, $g < 0$ then $\frac{dN}{dt} < 0$ and $\frac{dM}{dt} < 0$, i.e. N and M are both decreasing $\Rightarrow$ trajectories are pointing "south-west".*
- *if $f < 0$, $g > 0$ then $\frac{dN}{dt} < 0$ and $\frac{dM}{dt} > 0$, i.e. N is decreasing and M is increasing $\Rightarrow$ trajectories are pointing "north-west'.*

5. Draw the vertical and horizontal arrows on the null-clines as appropriate to indicate the direction of the trajectories as they cross the null-clines. **(This step is often forgotten by students and absence of these arrows in a phase-plane will lose marks).**

6. Draw a few representative trajectories, typically between 2-6, making sure that they **do not contradict your findings in parts 4 and 5** and that they **do not cross**. Indicate stability/instability of steady-states if possible.