

3 Interacting species (Murray, Chapter 3)

Interactions between species may affect their growth rates. Here we will focus on two interacting species (while in nature often many species interact). The interaction is commonly divided into three categories depending on how it affects the populations:

- **Predator-prey** if interaction increases growth rate of one species and decreases it for the other.
- **Competition** if interaction decreases growth rates of both populations.
- **Symbiosis** if interaction increases growth rates of both populations.

The general growth equations of two interacting species take the form

$$\begin{aligned}\dot{u} &= f(u, v) \\ \dot{v} &= g(u, v),\end{aligned}$$

where f and g depend on the sizes of the two populations u and v . Here these equations describe the interactions between two species, but they can also describe more general interactions, such as the kinetics of biochemical reactions (Lecture 4).

3.1 Predator-prey models

Predation or parasitism are examples of ecological interactions between species. While predators use their prey as a source of food, parasites use their hosts both as food and habitat. For many species, predation or parasitism dominate the size evolution. It is therefore of great interest to model predator-prey interactions.

3.1.1 Lotka-Volterra systems (M3.1)

We want to construct a model for predator-prey interactions between a prey population of size N and a predator population of size P . To this end, make the following assumptions:

- In absence of predation, prey has unbounded Malthusian growth $\dot{N} = aN$ with per capita growth rate $a > 0$.
- Prey population decays proportionally to the interaction rate with predator population. We often model the interaction rate as proportional to the product of population sizes, NP (rate of encounters between randomly moving individuals in homogeneous environment). We assume limitless appetite: interactions have the same outcome independent from the population sizes. This results in the following contribution to \dot{N} : $-bNP$ with constant $b > 0$.
- In absence of prey, predators have Malthusian decay $\dot{P} = -dP$ with per capita decay rate $d > 0$.
- Predator population increases proportional to their interaction rate with prey population (limitless appetite).

Combining these assumptions gives the simplest predator-prey model:

$$\begin{aligned}\dot{N} &= N(a - bP) \\ \dot{P} &= P(cN - d),\end{aligned}$$

All parameters a , b , c , d are positive. This model was proposed independently by Lotka (1920, chemical reactions) and Volterra (1926, populations).

These equations can be solved analytically. First, change to dimensionless units

$$\tau = at, \quad u(\tau) = \frac{c}{d}N(t), \quad v(\tau) = \frac{b}{a}P(t)$$

and let $\alpha = d/a$ to get:

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

Divide the equations:

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

These equations are separable:

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

Integrate:

$$[\log v - v]_{v_0}^v = \alpha [u - \log u]_{u_0}^u.$$

\Rightarrow the quantity

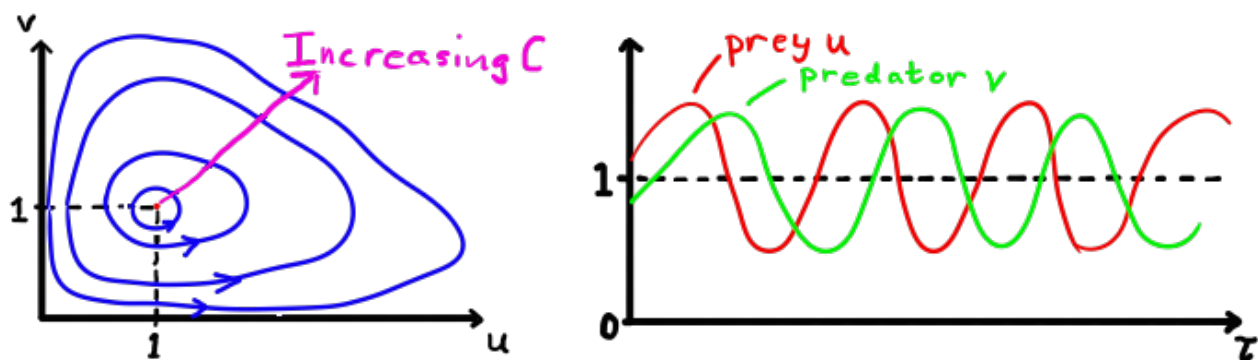
$$v + \alpha u - \log(vu^\alpha) = \underbrace{v_0 + \alpha u_0 - \log(v_0 u_0^\alpha)}_{\text{Const. } C} \quad (2)$$

is a conserved quantity (each trajectory has specific value of C that is determined by the initial condition v_0 and u_0).

- The minimal value $C_{\min} = 1 + \alpha$ for positive u and v is obtained at $u = v = 1$.
- $(u^*, v^*) = (1, 1)$ is also an isolated fixed point of Eq. (1).

That C has a local minimum at the fixed point implies that trajectories must orbit the fixed point, a ‘nonlinear center’ (Strogatz 6.5). The argument for this is as follows: different values of C correspond to different contour lines of Eq. (2). Since C increases in all directions around the isolated fixed point (where C is minimal), level curves for C slightly above C_{\min} must enclose the fixed point, forming closed orbits.

Since this is the only fixed point with $u > 0$ and $v > 0$, all solutions (with $C > C_{\min}$) are closed orbits in the u - v -plane (phase plane):



The system shows out-of phase oscillations between predator and prey populations. Note that the direction of curves is such that prey grows if predator population is low and predators grow if prey population is high.

The closed orbits are not structurally stable (i.e. a small perturbation may change the character of the solution), for example a small higher-order perturbation to the flow

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

implies that the equations are no longer separable \Rightarrow no conserved quantity $C \Rightarrow$ the center becomes a spiral (the formerly closed orbits either spiral into, or out from the fixed point).

Since the solution is structurally unstable, the Lotka-Volterra predator-prey equations should not be used as a model for interacting species. A refined model is needed.

3.1.2 More realistic predator-prey models (M3.3, 3.4)

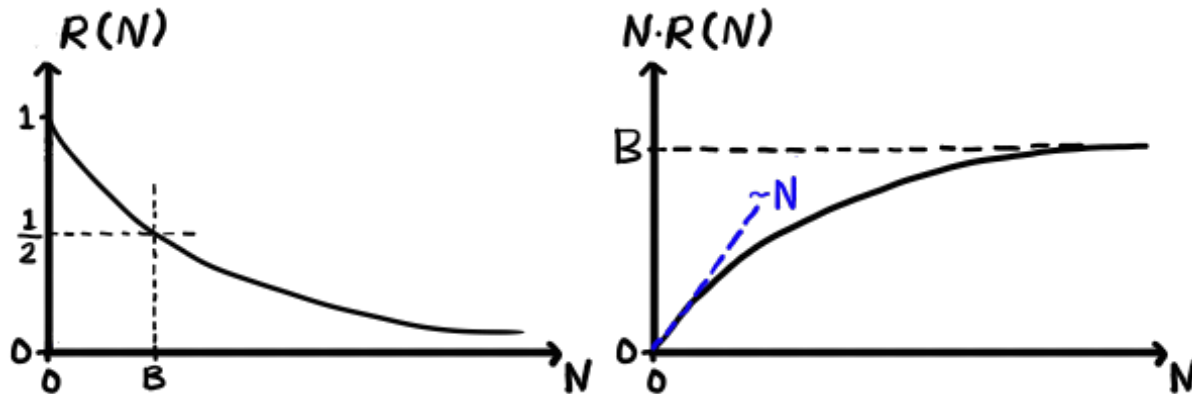
Two of the unrealistic assumptions of the Lotka-Volterra model is that the prey growth is unbounded in the absence of predation and that the predator appetite is unbounded. We therefore introduce a more realistic model. For the prey population, use logistic growth in absence of predators and modify the interaction rate:

$$\dot{N} = N \left[a \left(1 - \frac{N}{K} \right) - bPR(N) \right] \quad \text{[3]}$$

with $R(N)$ a decreasing function, for example:

$$R(N) = \frac{1}{1 + N/B}.$$

with saturation scale B :



The function $R(N)$ reduces the interaction rate in a way that models limited predator appetite: if N is small (compared to the parameter B), most encounters lead to reduction of prey, if N is large, only a few encounters lead to reduction of prey population. Larger values of B means larger appetite, as $B \rightarrow \infty$ the interaction of the Lotka-Volterra model is reobtained.

One possibility to model the predator growth is to replace the interaction cNP by $cNPR(N)$. An alternative which we consider below, is to replace the Lotka-Volterra interaction for P by a logistic growth with carrying capacity that is proportional to the prey population N :

$$\dot{P} = sP \left(1 - h \frac{P}{N} \right).$$

This model has 6 parameters a, b, K, B, s, h . Introduce dimensionless units

$$\tau = at, \quad u(\tau) = \frac{N(t)}{K}, \quad v(\tau) = \frac{h}{K}P(t)$$

and let

$$\alpha = \frac{bB}{ah}, \quad \beta = \frac{s}{a}, \quad \gamma = \frac{B}{K}$$

to get

$$\begin{aligned}\frac{du}{d\tau} &= u(1-u) - \alpha \frac{uv}{u+\gamma} \equiv f(u, v) \\ \frac{dv}{d\tau} &= \beta v \left(1 - \frac{v}{u}\right) \equiv g(u, v).\end{aligned}\tag{3}$$

The system has three positive dimensionless parameters α, β, γ . Fixed points are solutions to

$$f(u^*, v^*) = 0 \text{ and } g(u^*, v^*) = 0.$$

The only positive solution is

$$\begin{aligned}u^* &= \frac{1}{2} \left(1 - \alpha - \gamma + \sqrt{(1 - \alpha - \gamma)^2 + 4\gamma}\right) \\ v^* &= u^*.\end{aligned}$$

As in one dimension we classify the dynamics in the vicinity of the fixed point using linear stability analysis:

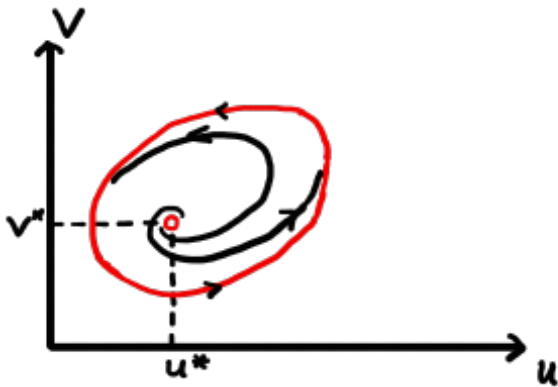
$$\begin{pmatrix} \frac{du}{d\tau} \\ \frac{dv}{d\tau} \end{pmatrix} \approx \underbrace{\begin{pmatrix} f(u^*, v^*) \\ g(u^*, v^*) \end{pmatrix}}_{=0} + \underbrace{\begin{pmatrix} \frac{\partial f}{\partial u}(u^*, v^*) & \frac{\partial f}{\partial v}(u^*, v^*) \\ \frac{\partial g}{\partial u}(u^*, v^*) & \frac{\partial g}{\partial v}(u^*, v^*) \end{pmatrix}}_{\mathbb{J}(u^*, v^*)} \begin{pmatrix} u - u^* \\ v - v^* \end{pmatrix} + \dots$$

The local dynamics around (u^*, v^*) is determined by the eigensystem of the stability matrix $\mathbb{J}(u^*, v^*)$ (denoted community matrix in population context).

The fixed point can be classified into different types depending on the eigenvalues λ_1 and λ_2 of $\mathbb{J}(u^*, v^*)$ (Murray, Appendix A).

The fixed point is stable if both $\mathcal{Re}[\lambda_1] < 0$ and $\mathcal{Re}[\lambda_2] < 0$. and if either $\mathcal{Re}[\lambda_1] > 0$ or $\mathcal{Re}[\lambda_2] > 0$ the fixed point is unstable. An analysis (Murray 3.4) shows that there exists a volume in parameter space (α, β, γ space) for which the fixed point is stable and a complementary volume for which it is unstable. When the fixed point is stable, the system eventually settles at a constant population (u^*, v^*) . When the fixed point is unstable, it is possible to show (by constructing a

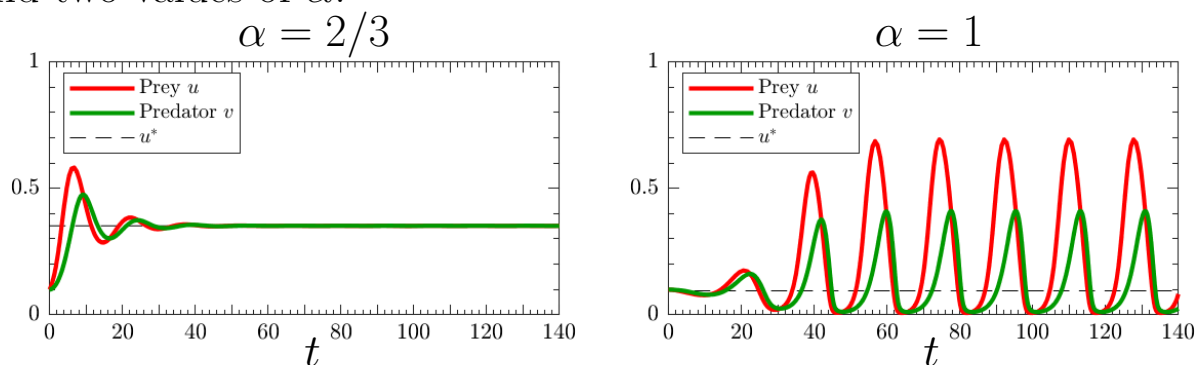
trapping region around the fixed point, see Murray 3.4 for details) that the system forms a limit cycle:



The population densities show oscillations with a phase lag, similar to the behaviour observed for the Lotka-Volterra model in Section 3.1.1 (the difference now is that the system has one single attracting periodic solution which is structurally stable).

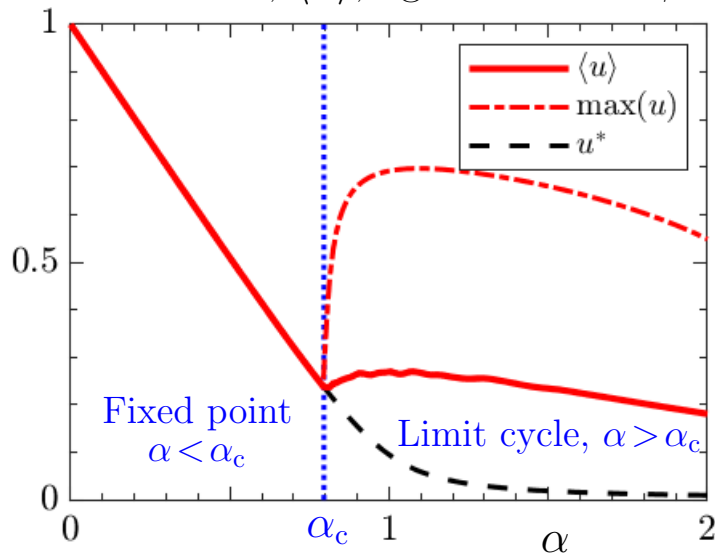


Pest control The model described above can be used to model biological pest control which aims at controlling a pest population using its natural enemies. Assume that prey corresponds to pest and predators to a natural enemy. Simulations for $\beta = 0.5$, $\gamma = 0.01$ and two values of α :



In the absence of predators we have one stable steady state $u^* = 1$. When the natural enemy is present (with $\alpha = 2/3$) we obtain a steady state with reduced pest population $u^* \approx 0.3$. One might expect that a more effective predator [larger α , see Eq. (3)] gives more efficient pest control. This is not always so ($\alpha = 1$ in Figure above). Even though u^* decreases monotonously with increasing α , when α passes a bifurcation point the system shows high oscillations (limit cycle surrounding the fixed point). This is illustrated by plotting the average prey population

on the attractor, $\langle u \rangle$, against α with $\beta = 0.5$, $\gamma = 0.01$:



At $\alpha = \alpha_c \approx 0.8$ the system bifurcates from stable steady state ($\alpha < \alpha_c$) to stable limit cycle ($\alpha > \alpha_c$). The figure shows that the average prey population has a local minimum at the bifurcation point α_c .

3.2 Competing species (M3.5)

A simple model for competition for resources (e.g. nutrients, water, or territory) is to use logistic growth where a fraction b_{ij} of the other species contribute to the reduction of per capita growth rate (intrusion) due to finite carrying capacity:

$$\begin{aligned}\dot{N}_1 &= r_1 N_1 \left(1 - \frac{N_1 + b_{12} N_2}{K_1} \right) \\ \dot{N}_2 &= r_2 N_2 \left(1 - \frac{N_2 + b_{21} N_1}{K_2} \right),\end{aligned}$$

with growth rates $r_i > 0$, carrying capacities $K_i > 0$ and interactions $b_{ij} > 0$ (positive \Rightarrow competition). In dimensionless units

$$\tau = r_1 t, \quad u_1(\tau) = \frac{N_1(t)}{K_1}, \quad u_2(\tau) = \frac{N_2(t)}{K_2}$$

we have three dimensionless parameters

$$\rho = \frac{r_2}{r_1}, \quad a_{12} = b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2}$$

and the dimensionless dynamics:

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1 (1 - u_1 - a_{12}u_2) \\ \frac{du_2}{d\tau} &= \rho u_2 (1 - u_2 - a_{21}u_1) .\end{aligned}$$

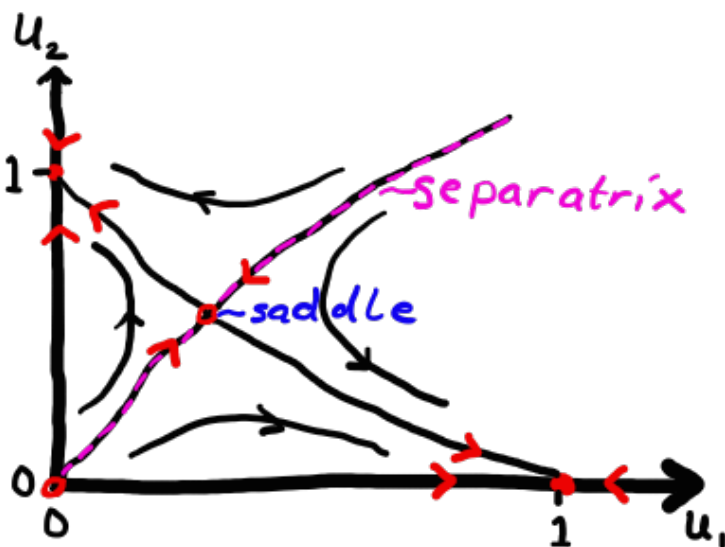
No interaction In the absence of the other species (or in the absence of competition, $a_{12} = a_{21} = 0$), the dynamics is one-dimensional along an axis and the population eventually reaches it's carrying capacity ($u_1 = 1$ for species 1 or $u_2 = 1$ for species 2).

Weak interaction If both a_{12} and a_{21} are positive but smaller than unity the competition is weak and the populations reach a stationary state (stable node) with both population sizes below their carrying capacities.

Strong interaction If both a_{12} and a_{21} are larger than unity the competition is aggressive. Linear stability analysis for this case gives:

Fixed points	$(0, 0)$	$(1, 0)$	$(0, 1)$	$\frac{(a_{12}-1, a_{21}-1)}{a_{12}a_{21}-1}$
Sign of eigenvalues (eigenvalues real)	$[+, +]$	$[-, -]$	$[-, -]$	$[+, -]$
Type	Unstable node	Stable node	Stable node	Saddle

The flow follows the coordinate axes, connecting the origin to the stable nodes $(0, 1)$ and $(1, 0)$. Due to topological constraints (no crossing of trajectories along axes and negative flow for large u_1 or u_2) the saddle must connect to the other fixed points (heteroclinic orbits):



The separatrix separates regions of initial conditions ending up at a particular fixed point. For initial conditions below the separatrix, the population u_2 eventually get locally extinct (in the modelled ecosystem). Initial conditions above the separatrix implies local extinction of u_1 .

In general, if one or both of a_{12} and a_{21} are larger than unity, eventually one species dies out. **This is the principle of competitive exclusion: if one species has the slightest advantage over another, it will dominate in the long term.** This leads either to local extinction of the disadvantageous species, or to an evolutionary or behavioural adjustment to a different ecological niche [Gause (1934)] (reduction of a_{ij}). As a consequence, to avoid competition many species find their own niche, for example different species of birds foraging for insects in the same type of tree, with each species focusing on a different part of the tree.

The principle of competitive exclusion has been used to successfully treat infections of harmful bacteria by introducing a less harmful but more advantageous bacteria of the same strand. However, this method may backfire: if the target evolves to become more efficient when the competitor is introduced, it may make more damage (genetic evolution of one species to become better is not included in the competitive models).

3.3 Population dynamics of more species (M3.7)

The models for interacting species above can be extended to include additional species. The behaviours observed for two species (periodic oscillations of predator prey populations and extinction of competing species) are common, but there are also cases where more complex dynamics arise (limit tori, or strange attractors and chaos).

In conclusion, the study of interacting populations highlights the sensitivity of many ecosystems upon introduction of new species. One important example (among many) is the catastrophic consequences of implanting the Nile perch in Lake Victoria (Murray 3.7).