Theoretical Community Ecology

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1 Models for a single population

Lesson plan:

1. We start by discussing what it means to solve an initial-value problem: the solution is an expression that allows us to calculate $x(t)$ for any t. A few ecologically-relevant models can be solved explicitly, for example the exponential and logistic growth models.
2. Because solving differential equations is a laborious process, and in many cases writing the solution is impossible, or does not give us any insight on the dynamics, we introduce a graphical method that allows us to effortlessly sketch the dynamics of any ODE (i.e., models with a single equation).
3. This allows us to introduce essential concepts such as the notion of an equilibrium and its stability.
4. We show that determining stability using this graphical method is equivalent to performing stability analysis via linearization around an equilibrium, a method that will be extended to systems of multiple ODEs in the next chapter.
5. We briefly discuss the idea of bifurcation points — i.e., particular choices of parameters for which the dynamics of the system changes qualitatively.
6. We conclude by introducing the idea of Lyapunov functions, allowing us to determine global stability of an equilibrium without the need to explicitly solve the model. We will see several of these functions when we study larger systems.

1.1 Types of dynamical systems

Dynamical systems describe the change of certain variables, typically in time, space or a combination of the two. They have found applications in all scientific disciplines, and were introduced in ecology and evolutionary biology at the beginning of the twentieth century.

Broadly, dynamical systems can be divided into **continuous** (described by differential equations), and **discrete** (described by maps, or difference equations) models. Many models for

population dynamics can be written as (systems of) first-order ordinary differential equations, i.e., equations containing functions of one (or more) independent variables and their first derivative (typically, with respect to time).

Ordinary means we are not dealing with partial differential equations (PDEs, used in ecology for example for reaction-diffusion equations, or spatial models). **First-order**, means that they contain only the first derivative with respect to time. Here we will concentrate on **autonomous** systems, meaning that they are time-invariant (i.e., the coefficients do not change in time). We can write these systems as:

$$\frac{dx(t)}{dt} = \dot{x}(t) = f(x(t))$$

In general, we will examine cases in which $f(x(t))$ is a nonlinear function of $x(t)$. We typically deal with **deterministic** systems, in which randomness plays no role in determining future states. Stochastic differential equations (SDEs), on the other hand, include random components.

Higher-order ODEs

Differential equations containing higher-order derivatives can be re-written as a system of first-order differential equations.

For example, consider:

$$\frac{d^2 x(t)}{dt^2} = \alpha + \beta x(t) + \gamma \frac{dx(t)}{dt}$$

which we can rewrite more compactly as:

$$\ddot{x} = \alpha + \beta x + \gamma \dot{x}$$

define the variables:

$$y_1 = x$$
$$y_2 = \dot{x}$$

thus, $\dot{y}_1 = \dot{x} = y_2$, and $\dot{y}_2 = \ddot{x}$; we obtain:

$$\begin{cases} \dot{y}_1 = y_2 \\ \dot{y}_2 = \alpha + \beta y_1 + \gamma y_2 \end{cases}$$

which is equivalent to the original equation.

1.2 Initial-value problems

Typically, we would like to track the dynamics of a population in time, starting from known initial conditions. For example,

$$\frac{dx(t)}{dt} = f(x(t)), \;\; x(0) = x_0$$

where the independent variable t denotes time, and is considered non-negative. The vector $x(t)$ tracks the abundance or density of the populations at time t, $x(t) \in \mathbb{R}^n$, and the function f models the evolution of the system, mapping $\mathbb{R}^n \to \mathbb{R}^n$. The vector $x_0 = x(0) \in \mathbb{R}^n$ marks the *initial condition* of the system.

The simplest and most common case in ecology is that in which f is (infinitely) many times continuously differentiable, a.k.a. *smooth*. If this is the case, then **the solution $x(t)$ exists and is unique**.

In ecological models, dynamics are invariant with respect to the non-negative orthant $\mathbb{R}^n_{0+}$, i.e., the vector $x(t)$ remains non-negative whenever initialized at non-negative initial conditions $x_0 \in \mathbb{R}^n_{0+}$.

We can solve the (system of) ODE(s) if we can write an explicit equation for $x(t)$ given the parameters and the initial conditions.

In practice, we rarely can solve the equations we're interested in. We can however prove that, if $f(x(t))$ is sufficiently well-behaved (technically, if $f(x)$ is Lipschitz continuous, for example, if it has bounded derivatives), then the initial-value problem above has a solution, the solution is unique, and depends continuously on the initial conditions and the parameters. This means that if we start the system at any point $x(t) = x_t$, we cannot have multiple trajectories intersecting.

1.3 Solvable model: Exponential growth

History: Pierre-François Verhulst (1804-1849)

Pierre-François Verhulst was born in 1804 in Brussels, Belgium. In 1835, he became professor of mathematics at the newly-instituted Free University of Brussels.

In 1838, inspired by the work of Malthus and Quetelet, he wrote a *Note on the law of population growth*, where he argued that the geometric progression imagined by Malthus would be unfeasible to sustain. He therefore introduced an *unknown function* that would slow down growth for large populations: *"The simplest hypothesis one can make on the form of this function is to suppose that"* the unknown function would be quadratic in the size of the population. He went on to solve what is now known as the *logistic growth* model, and contrasted it with data for the growth of populations in various countries.

A model of ecological interest that has an explicit solution is that for the exponential growth:

$$\frac{dx(t)}{dt} = \rho\, x(t), \quad x(0) = x_0$$

This is a **separable** differential equation, meaning that we can formally write:

$$\frac{1}{x(t)} dx(t) = \rho\, dt$$

Integrate both sides (the left hand side in $dx(t)$, the r.h.s. in dt):

$$\int \frac{1}{x(t)} dx(t) = \rho \int dt$$

Obtaining (C_i are constants of integration):

$$\log x(t) + C_1 = \rho\, t + C_2$$
$$\log x(t) = \rho\, t + C_3$$
$$x(t) = e^{\rho\, t + C_3}$$
$$x(t) = C_4 e^{\rho\, t}$$

Substituting the initial condition $x(0) = x_0$ we find that $C_4 = x_0$:

$$x(t) = x_0 e^{\rho\, t}$$

which is our solution. If we know the value of ρ and the initial density x_0, we can compute the population density $x(t)$ for any t.

1.4 Solvable model: Logistic growth

Another model that can be solved explicitly is that of the logistic growth:

$$\frac{dx(t)}{dt} = \rho\, x(t)(1 - \alpha\, x(t)), \quad x(0) = x_0$$

again, we can separate the equation:

$$\frac{1}{x(t)(1 - \alpha\, x(t))} dx(t) = \rho\, dt$$

the r.h.s. is trivial to integrate, but the l.h.s. is trickier. We can transform it into a simpler expression by using partial fractions. We want to write:

$$\frac{1}{x(t)(1 - \alpha\,x(t))} = \frac{A}{x(t)} + \frac{B}{1 - \alpha\,x(t)}$$

where A and B are appropriate constants. Multiplying both sides by $x(t)(1 - \alpha\,x(t))$, we obtain:

$$1 = A(1 - \alpha\,x(t)) + B\,x(t) = A + x(t)\,(B - A\,\alpha)$$

The l.h.s. does not contain $x(t)$, and therefore we want to set $x(t)\,(B - A\,\alpha) = 0$, choosing $B = A\,\alpha$, and therefore $A = 1$. We can integrate the simpler form:

$$\int \frac{1}{x(t)}\,dx(t) + \int \frac{\alpha}{(1 - \alpha\,x(t))}\,dx(t) = \rho\,dt$$

obtaining:

$$\log x(t) - \log(1 - \alpha\,x(t)) = \rho\,t + C_1$$
$$\log \frac{x(t)}{1 - \alpha\,x(t)} = \rho\,t + C_1$$
$$\frac{x(t)}{1 - \alpha\,x(t)} = e^{\rho\,t + C_1}$$
$$x(t) = \frac{e^{\rho\,t + C_1}}{1 + \alpha\,e^{\rho\,t + C_1}}$$
$$x(t) = \frac{1}{\alpha + e^{-(\rho\,t + C_1)}}$$

To find the value of C_1, substitute the initial condition $x(0) = x_0$, and solve for C_1:

$$x_0 = \frac{1}{\alpha + e^{-C_1}}$$
$$C_1 = \log \frac{x_0}{1 - \alpha\,x_0}$$

Finally, substituting, we find:

$$x(t) = \frac{x_0\,e^{\rho\,t}}{1 + \alpha\,x_0\,(e^{\rho\,t} - 1)}$$

which provides an explicit solution for this (very simple) model.

Homework 1a

Sometimes the growth of bacteria is modeled using the Gompertz model:

$$\frac{dx(t)}{dt} = \alpha\, x(t) \log\left(\frac{\kappa}{x(t)}\right)$$

where α and κ are positive parameters. Solve the model for initial condition $x(0) = x_0$.

Simulate the growth when $\kappa = 10$ and $\alpha = 1$, with starting conditions $x(0) = 20$ and $x(0) = 0.1$.

1.5 Qualitative analysis of models for a single population

Because in general we cannot write an explicit solution for our models of interest, we attempt a qualitative analysis by: a) finding fixed points (**equilibria**); b) providing a qualitative description of the dynamics; c) probing the stability of fixed points; d) gaining an understanding of the system (nature of attractors, changes of behavior for different parameters) without deriving an explicit solution.

When we are dealing with a single population, we can use a graphical method. Simply, plot $dx(t)/dt$ against $x(t)$. We think of $x(t)$ as moving along the x axis, at a velocity determined by the y coordinate. For the exponential growth function:

$$\frac{dx(t)}{dt} = \rho\, x(t)$$

the graph becomes:

The only point where the curve intercepts the x axis is $x^\star = 0$. A point $x^\star$ for which $\left.\dfrac{dx(t)}{dt}\right|_{x^\star} = 0$ is an **equilibrium** (or fixed-point) for the system, meaning that if we initialize the system at $x^\star$, it will remain there unless perturbed. Whenever we apply a (small) perturbation to a **stable equilibrium**, the system returns to it; when we perturb an **unstable equilibrium**, on the other hand, the system moves away from it.

Now think of a perturbation: if we were to perturb $x^\star = 0$ by introducing a few individuals, we would find that the population starts growing (i.e., $dx(t)/dt > 0$), meaning that the equilibrium is unstable. Thus, using the graphical method introduced above, we can easily identify equilibria (i.e., points where the curve intercepts the x-axis), and their stability (i.e., by determining whether the curve around the equilibrium is above or below $dx(t)/dt = 0$).

Next, let's consider the logistic growth equation:

$$\frac{dx(t)}{dt} = \rho\,x(t)(1 - \alpha\,x(t)) = \rho\,x(t) - \rho\,\alpha\,x(t)^2$$

We can draw the graph (note the quadratic term—we're describing a parabola):

Now we have two equilibria, at $x^\star = 0$ and $x^\star = 1/\alpha$. If we perturb $x^\star = 0$, the system moves away from it (unstable), while if we perturb $x^\star = 1/\alpha$ the system goes back to it (stable).

History: Warder Clyde Allee (1885-1955)

Born in Indiana, Allee received his PhD in 1912 from the University of Chicago, where he returned in 1921. He was the Dean in the College of Arts, Literature, and Science (1924-1926) and Secretary of the Department of Zoology (1927-1934). In 1935, a spinal tumor left him paralyzed from the waist down. This did not slow down his hectic schedule of teaching, researching and writing. He stayed at U. Chicago until his retirement (1950). Allee is also remembered as a pacifist (he was raised a Quaker) and an activist.

He performed a series of studies on animal aggregation, finding that goldfish growing in a tank laced with colloidal silver would grow faster when more individuals were present. Today, the **Allee effect** applies to any population that grows faster when a certain threshold population is surpassed.

Now a more complex model, in which the population experiences an Allee effect:

$$\frac{dx(t)}{dt} = \rho\,x(t)(x(t) - \gamma)(1 - \alpha\,x(t))$$

where $0 < \gamma < 1/\alpha$. Plotting,

In this model, there are two stable equilibria ($x^\star = 0$ and $x^\star = 1/\alpha$), separated by an unstable equilibrium ($x^\star = \gamma$). Depending on the initial conditions, we might end up in either of the stable equilibria—we call this situation bistability.

Note that bistability makes it clear that we can only apply small perturbations to the equilibrium to probe its "local" stability—for example, imagine being at $x^\star = 1/\alpha$ and perturbing the population by bringing it below γ; then we would find that the population goes extinct, suggesting that $x^\star = 1/\alpha$ is "somewhat unstable".

Stability using derivatives

You might have noticed in the previous graphs that whenever the curve $dx(t)/dt$ is negative on the left of a point and positive on its right we find that the point is unstable, while, conversely, a point for which $dx(t)/dt$ is positive on the left and negative on the right is stable. We can formalize this by taking the derivative of $dx(t)/dt$ with respect to $x(t)$, and evaluating this function at different equilibria.

For example, for the exponential growth model, we have:

$$\frac{\partial}{\partial x}\frac{dx}{dt} = \frac{\partial f(x)}{\partial x} = \frac{\partial(\rho x)}{\partial x} = \rho$$

This is always positive when $\rho > 0$, and as such the only equilibrium ($x^\star = 0$) is unstable.

For the logistic growth, we find:

$$\frac{\partial f(x)}{\partial x} = \frac{\partial(\rho\,x - \rho\,\alpha\,x^2)}{\partial x} = \rho - 2\rho\,\alpha\,x$$

When we evaluate this function at the equilibrium $x^\star = 0$, we obtain $\rho > 0$, and as such the equilibrium is unstable. Conversely, when we evaluate the function at $x^\star = 1/\alpha$, we obtain $\rho - 2\rho = -\rho$, and therefore the equilibrium is stable.

Finally, for the model with Allee effect, we have:

$$\frac{\partial(\rho\,x(x - \gamma)(1 - \alpha\,x))}{\partial x} = -\rho\,\gamma + 2\rho\,x(1 + \alpha) - 3\rho\,\alpha\,x^2$$

At $x^\star = 0$, we find $-\rho\,\gamma$ which is always negative, and as such $x^\star = 0$ is stable. At $x^\star = \gamma$ we have $\rho\,\gamma\,(1 - \gamma\,\alpha)$ which is positive (as $\gamma\,\alpha < 1$) and as such is an unstable equilibrium. Finally, for $x^\star = 1/\alpha$, we have $\rho(\gamma - 1/\alpha)$ which is always negative.

What are we doing when probing stability using derivatives?

More formally, we can think of describing the dynamics of a perturbation around the equilibrium. Write $\Delta x(t) = x(t) - x^\star$ for the perturbation, and approximate its dynamics around the equilibrium. We want to write the dynamics of $\Delta x(t)$. By chain rule, $\frac{d\Delta x(t)}{dt} = \frac{d\Delta x(t)}{dx(t)}\frac{dx(t)}{dt}$, and as such

$$\frac{d\Delta x(t)}{dt} = f(x(t)) = f(\Delta x(t) + x^\star)$$

In general, we are left with a problem that is as difficult as the one we had originally; however, if we are willing to consider infinitesimally small perturbations, we can Taylor expand around $x^\star$, and approximate the dynamics of the perturbation:

$$f(\Delta x(t) + x^\star) = f(x^\star) + \left.\frac{df(x)}{dx}\right|_{x^\star}\Delta x(t) + \frac{1}{2}\left.\frac{d^2 f(x)}{dx^2}\right|_{x^\star}(\Delta x(t))^2 + \dots$$

Taking only the linear term, and noticing that $f(x^\star) = 0$ by definition, we have:

$$\frac{d\Delta x(t)}{dt} \approx \left.\frac{df(x)}{dx}\right|_{x^\star} \Delta x(t) = \rho\,\Delta x(t)$$

which is the equation for the exponential growth we have seen above. If $\left.\frac{df(x)}{dx}\right|_{x^\star} < 0$ the perturbation $\Delta x(t)$ will die out, while if it is positive it will increase quickly. Note that the analysis is valid only in the immediate surroundings of $x^\star$—i.e., only where the terms we have neglected are indeed negligible.

1.6 Bifurcations

The shape of the graphs above might depend on the value of parameters. Whenever a small change in one or several parameters causes a qualitative change in the behavior of the system, we speak of a **bifurcation** point (the term "bifurcation" was introduced by Henri Poincaré in 1885). At a bifurcation point, equilibria could disappear or be created, change their stability, the system could start cycling, etc.

In low-dimensional system, there are a variety of different behaviors, each of which has its own name (e.g., saddle-node, pitchfork, transcritical, Hopf, period-doubling, …, bifurcation). The **codimension** of a bifurcation is the number of parameters we need to change to alter the behavior of the system. Clearly, codimension-1 and -2 bifurcations are the simplest and most studied.

Here we just show the main idea using a simple example. For a detailed and accessible introduction, see @strogatz2018nonlinear and @seydel2009practical.

Consider the model:

$$\frac{dx}{dt} = \rho + x^2$$

The equilibria of the system, when they exist, are given by $x^\star = \pm\sqrt{-\rho}$. It is clear that, when $\rho < 0$ we will have two equilibria, when $\rho = 0$ a single equilibrium $x^\star = 0$, and that when $\rho > 0$ no (real) equilibrium exists. As such, the shape of the diagrams we have sketched above depend on ρ. For example, when $\rho = -4$, we have:

The equilibrium on the left is stable, while the one on the right is unstable. The graph is qualitatively the same for any $\rho < 0$. When $\rho = 0$, however, the two equilibria "collide", and merge into the single "half-stable" equilibrium:

The equilibrium $x^\star = 0$ is stable if we approach it from the left, while unstable if we are reaching it from the right. When we cross the bifurcation $\rho_c = 0$, the equilibrium disappears altogether, leading to unbounded growth:

We can summarize the behavior of the system for different values of ρ in a **bifurcation diagram**: on the x-axis we have the parameter we are varying (in this case, ρ), and on the y-axis we report $x(t)$, marking the position of all the equilibria, with a solid line indicating stable equilibria and a dashed line the unstable ones:

Note that the rate at which the system approaches (moves away from) the stable (unstable) equilibrium depends on ρ. When $\rho \ll 0$ the system moves fast, while when $\rho \to \rho_c = 0$ the system moves more slowly. This phenomenon is called "critical slowing down" and has been proposed as a generic indicator that a system is approaching a bifurcation point.

Key paper: @ludwig1978qualitative

Models for population dynamics have been used to understand insect outbreaks, for example the eastern spruce budworm (*Choristoneura fumiferana*), which is responsible for defoliation of forests in North America.

Ludwig *et al.* developed a model for the dynamics of the insect population, and performed a bifurcation analysis to understand the two regimes of either low-abundance of the insect, or massive outbreaks.

Homework 1b

The goal is to produce a bifurcation diagram for the dynamics of the spruce budworm, as detailed in the paper by Ludwig *et al.*. A nondimensional version of the model can be written as:

$$\frac{dx}{dt} = \rho x \left(1 - \frac{x}{\mu}\right) - \frac{x^2}{1 + x^2}$$

where ρ and μ are positive parameters. Depending on the values of the parameters, the model can have between one and three equilibria. The value of ρ is equivalent to a growth rate, and measures how favorable is the environment for the growth of the insect population; the parameter μ limits the population size.

To find the equilibria, you need to find values of $x > 0$ such that:

$$\rho \left(1 - \frac{x}{\mu}\right) = \frac{x}{1 + x^2}$$

or, equivalently,

$$-\frac{\rho}{\mu}x^3 + \rho x^2 - \left(1 + \frac{\rho}{\mu}\right)x + \rho = 0$$

The goal is to produce a bifurcation for the budworm model: assume that $\mu = 10$, and vary ρ between 0.3 and 0.6 in steps of 10^{-3}. For each value of ρ, solve the equation above to find the equilibria; an equilibrium is feasible only if it is real (consider values for which the imaginary

part is less than 10^{-6} to be real, to account for the numerical error when computing the roots) and positive.

To compute the roots in R, you can use the function `polyroot`; for example:

```
get_roots <- function(rho, mu) {
  # roots of the polynomial
  # c0 + c1 x + c2 x^2 + c3 x^3 = 0
  c3 <- -rho / mu
  c2 <- rho
  c1 <- -1 - rho / mu
  c0 <- rho
  polyroot(c(c0, c1, c2, c3))
}
```

Plot ρ on the x-axis and on the y-axis the value of the roots (use a different color for each of the three possible roots). You should observe three regimes: when ρ is small (for example, at $\rho = 0.35$) there is only an equilibrium, in which the population is at low abundance; for intermediate values (for example, $\rho = 0.45$), you should find three equilibria; finally, for large values of ρ (e.g., $\rho = 0.6$), you should find a single equilibrium in which the population is at high abundance ("outbreak").

Next, set $\mu = 10$ and $\rho = 0.45$. Plot dx/dt against x and classify the stability of the three equilibria.

A few interesting references on detecting the approaching of a bifurcation in experimental systems:

Key paper: @scheffer2009early

Starting in the early 2000s, much work went into trying to anticipate dramatic changes in natural and man-made systems (e.g., lakes turning eutrophic, fisheries collapsing, desertification). In this review, Scheffer *et al.* summarize previous work and present an accessible introduction to the problem.

Key paper: @dai2012generic

Dai *et al.* grew populations of *Saccharomyces cerevisiae* on sucrose. Because sucrose is split outside the cell, it creates an Allee effect: when the population density is high, it is energetically convenient to produce the enzyme to spit the sucrose, as the different cells pool their efforts; when population density is low, the gain is not sufficient to balance the cost. By tuning the mortality (dilution), they were able to experimentally recreate the bifurcation diagram of the exercise above. The data from the experiments are here.

1.7 Long term behavior of 1-D systems

First-order, single-equation ODEs can produce a very limited variety of long-terms behaviors: for $t \to \infty$ we can only have $x(t) \to \pm\infty$ or $x(t) \to x^\star$. For population models, this means that either growth is unbounded (e.g., exponential growth model), or the population will reach an equilibrium point (possibly, out of many).

This is a direct consequence of the uniqueness of trajectories: because we are moving in a 1-dimensional space, the fact that trajectories cannot cross means that if we are at a certain point $x(t) = x_t$, then either $dx(t)/dt > 0$, $dx(t)/dt < 0$, or $dx(t)/dt = 0$, but can take only one value, preventing more complex behaviors such as cycles or chaos.

For smooth functions and autonomous systems, one needs at least two equations to produce cycles and three equations to produce chaos. This is in stark contrast with difference equations—a single, innocent-looking difference equation can give rise to all sorts of dynamics.

Key paper: @may1976simple

May took a possible model for the logistic growth in discrete time, and showed how this very simple model can give rise to equilibria, cycles and chaos. This is one of the papers that launched an all-out effort to explore chaotic dynamics that lasted for the best part of the 1980s.

1.8 Lyapunov functions

While in many cases we cannot write an explicit solution for a (system of) differential equation(s), we might be able to determine the stability of equilibria and their basin of attraction (i.e., the set of initial conditions eventually leading to the equilibrium $x^\star$) by considering functions that change monotonically through the dynamics.

Suppose that $\dfrac{dx(t)}{dt} = f(x(t))$, and that $x^\star$ is an equilibrium. Let $V(x)$ be a function defined in an open set $\mathcal{O}$ containing $x^\star$, such that a) $V(x^\star) = 0$ and $V(x) > 0$ for any $x \in \mathcal{O}, x \neq x^\star$, and b) $dV/dt \leq 0$ for all $x \in \mathcal{O} \neq x^\star$. Then V is a *Lyapunov function* for the model, and $x^\star$ is stable. The Lyapunov function is called *strict*, and the equilibrium $x^\star$ *asymptotically stable* if $dV/dt < 0$ for all $x \neq x^\star$ (i.e., all trajectories starting in $\mathcal{O}$ will eventually reach $x^\star$).

While Lyapunov functions are great, because we can prove stability without the need to solve the system, there is no general rule to construct them. Often, "candidate" Lyapunov functions are available, but the process of finding the right function typically requires a lot of ingenuity and trial and errors.

Fortunately, for system with a single state a quadratic function is guaranteed to solve the problem. Take the model for logistic growth (with $\rho > 0$ and $\alpha > 0$), and the candidate Lyapunov function:

$$V(x(t)) = (x(t) - x^\star)^2$$

with $x^\star = 1/\alpha$. The function is positive for any $x(t) \neq x^\star$. Next, we derive with respect to t:

$$\frac{dV(x(t))}{dt} = \frac{dV(x(t))}{dx(t)} \frac{dx(t)}{dt} = 2\left(x(t) - \frac{1}{\alpha}\right) \rho\, x(t)(1 - \alpha\, x(t))$$

The derivative is negative whenever $x(t) > 0$ and $x(t) \neq x^\star$:

$$\frac{dV(x(t))}{dt} = 2\rho\, x(t)\left(x(t) - \frac{1}{\alpha}\right)(1 - \alpha\, x(t)) = -\frac{\rho\, x(t)}{\alpha}\left(x(t) - \frac{1}{\alpha}\right)^2$$

and as such $x^\star$ is asymptotically stable. The basin of attraction (i.e., where the Lyapunov function has the desired properties) is $x \in \mathbb{R}_+$. There can be several alternative Lyapunov functions.

A classic candidate Lyapunov function for the Lotka-Volterra model we are going to see many times in the lecture notes starts from a logarithmic inequality: if $y > 0$, then $\log y \leq y - 1$, and thus $y - 1 - \log y \geq 0$. Take $y = \frac{x}{x^\star}$, with x and $x^\star$ positive. Then,

$$\frac{x}{x^\star} - 1 - \log \frac{x}{x^\star} \geq 0$$

Now multiply by $x^\star$, obtaining:

$$x - x^\star - \log x^\star \frac{x}{x^\star} \geq 0$$

We can use this as our Lyapunov function for the logistic growth model:

$$V(x(t)) = x(t) - x^\star - x^\star \log \frac{x(t)}{x^\star}$$

which is positive for $x(t) > 0$ and $x(t) \neq x^\star$, taking the derivative w.r.t. time, we find:

$$\frac{dV(x(t))}{dt} = \left(1 - \frac{x^\star}{x(t)}\right) \rho\, x(t)(1 - \alpha\, x(t)) = -\rho\, x^\star (x(t) - x^\star)^2$$

which again is negative whenever $x^\star > 0$, $\rho > 0$ and $x(t) \neq x^\star$.

2 Models for two populations

Lesson plan:

1. We discuss the concepts introduced in the previous chapter in the context of two-dimensional ("planar") systems of differential equation.
2. We summarize important concepts from linear algebra: eigenvalues and eigenvectors, the matrix exponential.
3. We show how these concepts can be used to solve linear systems of differential equations.
4. We introduce the "community matrix", allowing us to determine the local asymptotic stability of equilibria.
5. We analyze in detail the classic Lotka-Volterra predator-prey model, and a version of the model in which the prey grows logistically.

2.1 Qualitative analysis of models for two populations

In this section, we extend the qualitative analysis we've performed for a single populations to models with two populations. Many of the methods introduced below extend to the case of an arbitrary number of populations.

Isoclines of null growth

Take a two-dimensional model, with variables x and y. For each equation, we can write the solution of $dx/dt = 0$ as a function of y, thereby defining the curve in the (x, y) plane (the "phase plane") for which the growth of species x is zero. For a concrete example, take the classic predator-prey Lotka-Volterra system:

$$\begin{cases} \dfrac{dx(t)}{dt} = \rho\, x(t) - \alpha\, x(t)\, y(t) \\ \dfrac{dy(t)}{dt} = -\delta\, y(t) + \beta\, x(t)\, y(t) \end{cases}$$

where $x(t)$ is the density of the prey species at time t and $y(t)$ that of the predator. We can interpret ρ as the intrinsic growth rate of the prey (i.e., the growth when the predator is absent), δ as the death rate of the predator, and α and β as the loss of (gain in) growth due to predation.

History: Alfred J. Lotka (1880-1949)

Alfred Lotka was born to French-speaking American parents in Lemberg (then part of the Hapsburg empire, now Lviv, Ukraine). He studied in France, Germany and England, receiving a BSc in 1901 and a DSc in 1912 from Birmingham university. He moved to the US in 1902, and worked at the US Patent office, as an editor of Scientific American, and as a statistician

at the Metropolitan Life Insurance Company in NYC. He wrote more than a hundred papers and five books, spanning a large range of topics. He's best known for the book *Elements of Physical Biology*, his contributions to demography, and one of the first studies dealing with bibliometrics [@lotka1926frequency].

Starting in 1910 (reprinted as @lotka2002contribution) he investigated coupled differential equations relating to chemical as well as ecological dynamics. In @lotka1920analytical he studied a system of two ODEs that gave rise to perpetual oscillations: *"It was, therefore, with considerable surprise that the writer, on applying his method to certain special cases, found these to lead to undamped, and hence indefinitely continued, oscillations."* He went on to describe *"1. A species of organism S_1, a plant species, say, deriving its nourishment from a source presented in such large excess that the mass of the source may be considered constant during the period of time with which we are concerned. 2. A species S_2, for example a herbivorous animal species, feeding on S_1."*

The equations he had derived (and then studied later in more detail) are now termed Lotka-Volterra equations.

Let's look at a possible trajectory for the system, to gain an intuition of what can happen:

You can see that the population densities, when drawn in the "phase plane" cycle counter-clockwise. Let's try to understand why.

The equation for the prey is zero either when $x(t) = 0$ or when $\rho - \alpha\, y(t) = 0$, yielding $y(t) = \rho/\alpha$. Whenever the density of the predator $y(t) < \rho/\alpha$, the prey will grow; conversely, whenever $y(t) > \rho/\alpha$, the prey will decline.

Graphically:

Similarly, the equation for the predator is zero either when $y(t) = 0$ or when $-\delta + \beta\, x(t) = 0$, yielding $x(t) = \delta/\beta$. Whenever the density of the prey $x(t) < \delta/\beta$, predators will decline; conversely, whenever $x(t) > x(t) = \delta/\beta$, predators will grow.

Graphically:

Now let's put the two graphs together:

Clearly, a possible equilibrium of the system is $(x^\star, y^\star)^T = (0,0)^T$ (often called the "trivial" equilibrium). You can see that there is another equilibrium where the two isoclines meet $(x^\star, y^\star)^T = (\delta/\beta, \rho/\alpha)^T$, and that the dynamics will tend to cycle around the equilibrium.

But how do we know whether dynamics will cycle toward the equilibrium, spiral away from it, or describe closed orbits? To answer this question, we can try to extend our linear analysis by Taylor-expanding the dynamics around the equilibrium.

2.2 Local stability analysis

Suppose that a feasible (i.e., positive) equilibrium $x^\star$ exists for a given model. Then we can ask whether it is **attractive** (stable), i.e., if trajectories started at initial condition $x(0)$ will eventually reach $x^\star$. This problem is in general difficult to solve (but see below); as an alternative, we can test for **local asymptotic stability**, i.e., ask whether **the system will return to the equilibrium if perturbed infinitesimally away from it**. In general, whenever we describe an ecological community as a system of nonlinear, autonomous ODEs:

$$\frac{dx_i(t)}{dt} = f_i(x(t)) \ ,$$

we define an equilibrium $x^\star$ as a vector of densities such that:

$$\left.\frac{dx_i}{dt}\right|_{x^\star} = f_i(x^\star) = 0 \quad \forall i$$

A given system might have a multitude of equilibria. When the system is resting at an equilibrium point, it will remain there unless it is perturbed away from it. Local stability analysis is a method to probe whether a system that is perturbed infinitesimally away from an equilibrium will eventually return to it, or rather move away from it.

Taylor series

Single-variable: suppose function f infinitely differentiable around a point $x = a$. Then

$$f(x) = \sum_{k=0}^{\infty} \frac{D^k f(a)}{k!} (x-a)^k = f(a) + \left.\frac{df}{dx}\right|_a (x-a) + \frac{1}{2} \left.\frac{d^2 f}{dx^2}\right|_a (x-a)^2 + \cdots$$

where $D^k f(a)$ is the k-th derivative of $f(x)$ w.r.t. x, evaluated at a.

Vector-valued functions: now $f(x)$ is a vector-valued function, and x a vector. To expand around the point a, we need to define the Jacobian matrix

$$J = Df(x)$$

with elements:

$$J_{ij} = \frac{\partial f_i(x)}{\partial x_j}$$

Next, we define the Hessian tensor (in this case, a three-dimensional tensor):

$$H_{ijk} = \frac{\partial^2 f_i(x)}{\partial x_j \, \partial x_k}$$

It is convenient to write the Taylor expansion in component form:

$$f_i(x) \approx f_i(a) + \sum_j J_{ij}\big|_a (x_j - a_j) + \frac{1}{2} \sum_j \sum_k H_{ijk}\big|_a (x_j - a_j)(x_k - a_k)$$

Example

Consider the predator-prey model with Type II functional response:

$$\begin{cases} \dfrac{dx(t)}{dt} = f_x = x(t)\left(1 - x(t) - \alpha \, \frac{y(t)}{1+x(t)}\right) \\ \dfrac{dy(t)}{dt} = f_y = y(t)\left(-1 + \alpha \, \frac{x(t)}{1+x(t)}\right) \end{cases}$$

The system has up to three equilibria: $(x^\star, y^\star) = (0,0)$, $(x^\star, y^\star) = (1,0)$, and, whenever $\alpha > 2$, $\left(\frac{1}{\alpha-1}, \frac{\alpha-2}{(\alpha-1)^2}\right)$. The Jacobian for this system is:

$$J = \begin{pmatrix} \frac{\partial f_x}{\partial x} & \frac{\partial f_x}{\partial y} \\ \frac{\partial f_y}{\partial x} & \frac{\partial f_y}{\partial y} \end{pmatrix} = \begin{pmatrix} 1 - 2x - \frac{\alpha y}{(x+1)^2} & -\frac{\alpha x}{(x+1)} \\ \frac{\alpha y}{(x+1)^2} & -1 + \frac{\alpha x}{(x+1)} \end{pmatrix}$$

The Hessian has two slices:

$$H_x = \begin{pmatrix} \frac{\partial^2 f_x}{\partial x^2} & \frac{\partial^2 f_x}{\partial x \partial y} \\ \frac{\partial^2 f_x}{\partial x \partial y} & \frac{\partial^2 f_x}{\partial x^2} \end{pmatrix} = \begin{pmatrix} 2\left(-1 + \frac{\alpha y}{(x+1)^3}\right) & -\frac{\alpha}{(x+1)^2} \\ -\frac{\alpha}{(x+1)^2} & 0 \end{pmatrix}$$

Similarly,

$$H_y = \begin{pmatrix} -2\frac{\alpha y}{(x+1)^3} & \frac{\alpha}{(x+1)^2} \\ \frac{\alpha}{(x+1)^2} & 0 \end{pmatrix}$$

Note that each slice of the Hessian is necessarily symmetric.

Now we can approximate the dynamics at any point; for example, around the equilibrium with the prey alone:

$$\frac{dx(t)}{dt} \approx J_{11}\big|_{x^\star} \Delta x + J_{12}\big|_{x^\star} \Delta y + \frac{1}{2} H_{x,1,1}\big|_{x^\star} \Delta x^2 + \frac{1}{2} H_{x,2,2}\big|_{x^\star} \Delta y^2 + H_{x,1,2}\big|_{x^\star} \Delta x \Delta y$$

with some calculations, we obtain:

$$\frac{dx(t)}{dt} \approx -\Delta x(1 + 2\Delta x) - \frac{1}{2}\alpha(1 + \Delta x)\Delta y$$

and similarly,

$$\frac{dy(t)}{dt} \approx \frac{1}{2}(\alpha - 2 + \alpha\Delta x)\Delta y$$

We can see already that, when $\Delta y > 0$ (the only sensible case), and $\Delta x = 0$, the predator can invade (at least initially) whenever $\alpha > 2$.

By considering higher and higher order terms, we can have an increasingly good approximation of the system—always obtaining a polynomial system of differential equations.

Suppose that a system is resting at an equilibrium $x^\star$, and that it is slightly perturbed away from it. $x(t) = \Delta x(t) + x^\star$ is the state of the system immediately after the perturbation. Taylor-expanding around $x^\star$ and taking only the linear term, we have:

$$f(x(t)) = f(x^\star) + J\big|_{x^\star}\Delta x(t) = J\big|_{x^\star}\Delta x(t)$$

Where J is the Jacobian matrix of the system, whose elements are defined as:

$$J_{ij} = \frac{\partial f_i(x)}{\partial x_j}$$

Each element of this matrix is therefore a function, whose value depends on x. When we evaluate the Jacobian matrix at an equilibrium point $x^\star$, we obtain the so-called "community matrix" M:

$$M = J\big|_{x^\star}$$

Note that, although each system has a unique Jacobian matrix, there are as many community matrices as there are equilibria. The community matrix details the effect of increasing the density of one species on any other species around the equilibrium point.

We can therefore write the differential equation:

$$\frac{d\Delta x(t)}{dt} \approx M\Delta x(t)$$

which is a system of linear differential equations—i.e., the simplest system of ODEs, which can be solved in full generality.

To solve the system, we need to recap a few important concepts from linear algebra.

Eigenvalues and eigenvectors

For a matrix M, we have that if $Mv = \lambda v$ with v different from the zero vector, then λ is an eigenvalue and v the corresponding eigenvector. Practically, you can think of a matrix as an operator that turns a vector into another vector. If the resulting vector is a rescaled version of the initial vector, then you've found an eigenvector of the matrix, and the rescaling factor is the associated eigenvalue.

For example, show that $(1, 1)^T$ is an eigenvector of the matrix:

$$A = \begin{pmatrix} 1 + a & 1 - a \\ 2a + 2 & -2a \end{pmatrix}$$

We have:

$$Av = \begin{pmatrix} (1 + a)v_1 + (1 - a)v_2 \\ (2a + 2)v_1 - 2av_2 \end{pmatrix}$$

if $v = (1, 1)^T$, we have:

$$Av = \begin{pmatrix} 2 \\ 2 \end{pmatrix} = 2\,v$$

and as such v is an eigenvector of M, with associated eigenvalue $\lambda = 2$.

Finding eigenvalues

The eigenvalues of a matrix M are the roots (zeros) of the chacteristic polynomial:

$$p(\lambda) = \det(\lambda I - M) = 0$$

Where does this equation come from? We write:

$$Av = \lambda v$$
$$\lambda v - Av = 0$$
$$(\lambda I - A)v = 0$$

if v is nonzero, then the matrix $\lambda I - A$ must be singular (i.e., have at least one eigenvalue equal to zero), and v should be the eigenvector of $\lambda I - A$ corresponding to a zero eigenvalue. Because the determinant is the product of the eigenvalues, then the determinant must also be zero.

For a 2×2 matrix, we have:

$$\det \begin{pmatrix} \lambda - a_{11} & -a_{12} \\ -a_{21} & \lambda - a_{22} \end{pmatrix} = (\lambda - a_{11})(\lambda - a_{22}) - a_{12}a_{21}$$
$$= \lambda^2 - \lambda(a_{11} + a_{22}) + a_{11}a_{22} - a_{12}a_{21}$$

More compactly,

$$p(\lambda) = \lambda^2 - \lambda \operatorname{tr}(A) + \det(A)$$

where $\operatorname{tr}(M) = \sum_i M_{ii} = \sum_i \lambda_i$, and $\det(M) = \prod_i \lambda_i$. We therefore find:

$$\lambda = \frac{\operatorname{tr}(M) \pm \sqrt{(\operatorname{tr}(M))^2 - 4\det(M)}}{2}$$

Find the eigenvalues for the matrix A above:

$$\lambda = \frac{1 - a \pm \sqrt{(1-a)^2 + 8(1+a)}}{2}$$
$$= \frac{1 - a \pm \sqrt{(1 + a^2 - 2a + 8a + 8)}}{2}$$
$$= \frac{1 - a \pm (a+3)}{2}$$

The eigenvalues are therefore $\lambda_1 = 2$ and $\lambda_2 = -(1+a)$.

Facts about eigenvalues and eigenvectors

Given a matrix A, of size $n \times n$, a complex number λ is an eigenvalue of A if there is a nonzero (complex) vector v such that $Av = \lambda v$. The vector v is called the (right) eigenvector of A associated with λ. Note that eigenvectors are defined up to multiplication: if v is an eigenvector, then αv, with α real is also an eigenvector. Often, we choose v such that its norm $\sqrt{\sum_i v_i^2} = 1$ (called "unit" eigenvector).

A matrix of size n has at most n distinct eigenvalues. If all eigenvalues are distinct, then the eigenvectors are linearly independent. This means that if we build the matrix $V = (v_1, v_2, \dots, v_n)$, then V is invertible.

Because of the fact above, if a matrix is diagonalizable (e.g., a sufficient condition is to have all eigenvalues distinct), then we can write:

$$A = V\Lambda V^{-1}$$

where V is the matrix of eigenvectors, and Λ a diagonal matrix with the eigenvalues of A on the diagonal. As such, $V^{-1}AV = \Lambda$. This is a "similarity transformation", meaning that the eigenvalues of A and Λ are (obviously) the same.

If the matrix A contains only real numbers (as it is always the case in population models), then the eigenvalues of A are either real, or form pairs of complex conjugate eigenvalues of form $\alpha \pm i\,\beta$. This means for example that all odd-sized real matrices have at least one real eigenvalue. If A is real and symmetric, all eigenvalues are real, and all eigenvectors are orthogonal, and if it is diagonalizable we can write $A = V\Lambda V^T$. A diagonal matrix A has eigenvalues $\lambda_i = A_{ii}$.

If A has eigenvalues λ, $B = \beta A$ has eigenvalues $\beta\,\lambda$, and $C = A + \gamma I$ has eigenvalues $\lambda + \gamma$. The eigenvalues of $A^2 = A \times A$ are λ^2, and the eigenvalues of A^{-1} are λ^{-1}. The eigenvalues of A^T are the same as those of A (but the eigenvectors are not the same in general). $A + A^T$ (this matrix is symmetric) has only real eigenvalues, and $A - A^T$ (this matrix is skew-symmetric) has purely imaginary eigenvalues.

A symmetric matrix is positive definite if all its eigenvalues are real and positive. If a matrix A is positive definite, then $\sum_j A_{ij}x_i x_j = x^T A x \geq 0$ for all x, and it is exactly zero only if $x = 0$. A matrix is positive semi-definite if eigenvalues can be zero. The matrices AA^T and $A^T A$ are positive semi-definite, and have the same eigenvalues up to some zeros (used in SVD and PCA). Correlation and covariance matrices have these form.

Provided that some mild conditions are satisfied, a matrix with non-negative entries has a unique largest real eigenvalue with a corresponding eigenvector that can be chosen to have strictly positive components (Perron-Frobenius theorem). A matrix with constant row sums θ has θ as an eigenvalue, and $v = 1$ as the corresponding eigenvector (e.g., Markov Chains).

Descartes' rule of signs

Take α_i to be the coefficients of the polynomial in standard form:

$$P(\lambda) = \sum_{i=0}^{n} \alpha_i \lambda^i$$

then the number of *real positive roots* of the polynomial is at most the number of sign changes in the sequence $\alpha_0, \dots, \alpha_n$, omitting the zeros. As a corollary, the number of *real negative roots* is at most the number of sign changes when we write $P(-\lambda)$. In particular, to have no real positive roots, we need all the α_i to have the same sign (omitting the zeros). The difference between the number of sign changes and the number of positive roots is always even.

Example:

$$P(\lambda) = 1 + 4\lambda - 5\lambda^2 + \lambda^3$$

we have two sign changes (the signs are $++-+$), and therefore the polynomial has at most two positive real roots (i.e., either two positive roots, or zero). Taking:

$$P(-\lambda) = 1 - 4\lambda - 5\lambda^2 - \lambda^3$$

we find a single change in signs, meaning that the polynomial has a negative real root. This polynomial has indeed one negative and two positive real roots.

Routh-Hurwitz criterion

The Routh-Hurwitz criterion allows to determine whether all the roots of a polynomial lie in the left half-plane (i.e., have negative real part). These polynomials are called stable, for reasons that will be obvious in a moment. It is easily stated for second and third-degree polynomials.

The polynomial:

$$P(\lambda) = \alpha_0 + \alpha_1\lambda + \lambda^2$$

is stable if and only if $\alpha_0 > 0$ and $\alpha_1 > 0$.

The polynomial:

$$P(\lambda) = \alpha_0 + \alpha_1\lambda + \alpha_2\lambda^2 + \lambda^3$$

is stable if and only if $\alpha_i > 0 \quad \forall i$ and $\alpha_2\alpha_1 > \alpha_0$.

Homework 2a

Show that a matrix A with sign-pattern:

$$S(A) = \begin{pmatrix} - & + \\ - & 0 \end{pmatrix}$$

has eigenvalues with negative real part. When a matrix is stable due to its sign-pattern (rather than specific values of the coefficients), it is called *qualitatively stable* or *sign-stable*.

A matrix A is sign-semistable if any matrix with signs $S(A)$ has eigenvalues with non-positive real parts. A matrix is sign-semistable if and only if:

- $A_{ii} \leq 0$ for all i
- $A_{ii} < 0$ for at least one i
- $A_{ij}A_{ji} \leq 0$ for all $i \neq j$
- All cyclic sequences of length ≥ 3, for example $A_{ij}A_{jk}A_{ki}$, with $i \neq j \neq k$ are equal to zero (i.e., the graph associated with the matrix has no cycles of length three or more)

- $\det(A) \neq 0$

Find all 3×3 signed matrices $S(A)$ that are sign-semistable.

Key paper: @may1973qualitative

The idea of "sign-stability" was first introduced in economics. May borrowed the idea to analyze simple food webs. Analysis of ecological models based on sign (rather than magnitude) of coefficients was further developed by Richard Levins and collaborators. A good modern summary, along with a few new results, are provided by @dambacher2003qualitative.

We can now analyze systems of linear ODEs.

Solution of linear systems of ODEs

Matrix exponential

In analogy with the power series

$$e^x = \sum_{n=0}^{\infty} \frac{x^n}{n!} = 1 + x + \frac{x^2}{2} + \frac{x^3}{6} + \frac{x^4}{24} + ...$$

we define the matrix exponential

$$e^X = \sum_{n=0}^{\infty} \frac{1}{n!} X^n = I + X + \frac{1}{2}X^2 + \frac{1}{6}X^3 + \frac{1}{24}X^4 + ...$$

where $X^2 = X \times X$ and so on.

Solution of systems of linear ODEs

This allows us to solve the system of linear differential equations

$$\frac{dx(t)}{dt} = Ax(t)$$

with $x(0) = x_0$. When the determinant of A, $\det A \neq 0$, the only equilibrium of the system is $x^\star = 0$. If $\det A = 0$ (and $A \neq 0$), on the other hand, there are infinitely many equilibria, all belonging to the same line (in 2-d). By writing the solution we can determine whether trajectories will approach or move away from an equilibrium. We write the solution as:

$$x(t) = e^{At} x_0$$

Importantly, we have that, if A is diagonalizable,

$$e^{At} = Ve^{\Lambda t}V^{-1}$$

where Λ is the diagonal matrix containing the eigenvalues of A. Because Λ is diagonal, we can solve the exponential explicitly:

$$e^{\Lambda t} = \begin{pmatrix} e^{\lambda_1 t} & 0 & \dots & 0 \\ 0 & e^{\lambda_2 t} & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & e^{\lambda_n t} \end{pmatrix}$$

Now we want to study the dynamics of the system. To keep the complexity to a minimum, we define $y(t) = V^{-1}x(t)$, meaning that we are choosing the most appropriate coordinates to study our trajectories. Our equation becomes:

$$x(t) = Ve^{\Lambda t}V^{-1}x_0$$
$$V^{-1}x(t) = V^{-1}Ve^{\Lambda t}V^{-1}x_0$$
$$y(t) = e^{\Lambda t}y_0$$

And therefore $y_j(t) = e^{(\lambda_j)t}y_j(0)$. Clearly, if all λ_j are real and negative, the trajectories will die out, and the origin $y^\star = 0$ is stable. Similarly, if any eigenvalue is real and positive, then the perturbation will amplify in at least one direction. Next, we consider λ_j to be complex. In this case, $\lambda_j = \alpha + i\,\beta$. Using Euler's formula, we have

$$y_j(t) = y_j(0)\,e^{(\alpha + i\,\beta)t} = y_j(0)\,e^{\alpha t}(\cos(\beta\,t) + i\sin(\beta\,t))$$

As such, the solution will oscillate, with damped oscillations whenever $\alpha < 0$ and increasing oscillations when $\alpha > 0$. For example, a case of damped oscillations:

and of increasing oscillations:

In fact, all the possible trajectories in planar systems can be classified using only the determinant (product of eigenvalues) and the trace (sum of the eigenvalues) of the matrix A:

Now we can solve the system of ODEs:

$$\frac{d\Delta x(t)}{dt} \approx M\Delta x(t)$$

obtaining:

$$\Delta x(t) = e^{Mt}\Delta x(0) = Qe^{\Lambda t}Q^{-1}\Delta x(0)$$

Where Q is the matrix containing the (unit) eigenvectors of M, and Λ is a diagonal matrix containing the eigenvalues of M. As such, the eigenvalues of M determine the stability of the equilibrium $x^\star$: if all the eigenvalues have negative real part, then the system will eventually return to the equilibrium after sufficiently small perturbations; conversely, if any of the eigenvalues have positive real part, the system will move away from the equilibrium whenever perturbed. Therefore, depending on the sign of the "rightmost" eigenvalue of M, λ_1, we can determine the stability of $x^\star$:

$$\text{Re}(\lambda_1) \begin{cases} < 0 \to x^\star & \text{is stable} \\ > 0 \to x^\star & \text{is unstable} \end{cases}$$

Key paper: @neubert1997alternatives

As we have seen, some simple linear algebra can be used to determine the long-term behavior of an ecological system. As Neubert & Caswell show in this masterful paper, similar techniques can be used to determine the *transient* behavior of these systems: will perturbations amplify before subsiding? How far from the equilibrium can the system move?

2.3 Stability analysis of the Lotka-Volterra Predator-Prey model

We still haven't figured out whether the coexistence equilibrium for the model

$$\begin{cases} \dfrac{dx(t)}{dt} = \rho\, x(t) - \alpha\, x(t)\, y(t) \\ \dfrac{dy(t)}{dt} = -\delta\, y(t) + \beta\, x(t)\, y(t) \end{cases}$$

is stable or not. The Jacobian becomes:

$$J = \begin{pmatrix} \rho - \alpha\, y & -\alpha\, x \\ \beta\, y & -\delta + \beta\, x \end{pmatrix}$$

The community matrix for the equilibrium $(x^\star, y^\star)^T = (0, 0)^T$ is:

$$M_0 = J|_{(0,0)^T} = \begin{pmatrix} \rho & 0 \\ 0 & -\delta \end{pmatrix}$$

which has eigenvalues $\rho > 0$ and $-\delta < 0$ — the equilibrium is unstable. The coexistence equilibrium $(x^\star, y^\star)^T = (\delta/\beta, \rho/\alpha)^T$ yields the community matrix:

$$M_c = J|_{(\delta/\beta, \rho/\alpha)^T} = \begin{pmatrix} 0 & -\dfrac{\alpha\,\delta}{\beta} \\ \dfrac{\beta\,\rho}{\alpha} & 0 \end{pmatrix}$$

which has purely imaginary eigenvalues $\lambda = \pm i\sqrt{\rho\,\delta}$. As such the equilibrium is not attractive nor unstable. In fact, both Lotka and Volterra were (independently) able to prove that the system cycles neutrally around the equilibrium.

Vito Volterra (1860-1940)

Vito Volterra was born in Ancona (then part of the Papal State) in a poor Jewish family. The financial situation precipitated with the death of his father, when Vito was two. Vito and his mother went to live with relatives in Turin and then Florence. Volterra showed amazing mathematical talent at a very young age. Antonio Roiti, professor of physics in Florence, noticed the budding mathematician and hired him as his assistant, so that he could continue his studies. He went on to enroll at the Scuola Normale in Pisa, receiving a degree in Physics in 1882. At age 23 he was made full professor of Rational Mechanics in Pisa, and then in 1900 of Mathematical Physics in Rome. For thirty years, he contributed important studies in mathematics, and enriched academic life in Italy (for example, he was the first director of the National Center for Research). In 1931 he refused to take an oath of loyalty to the fascist regime (only 12 professors out of 1250 refused), and was therefore forced to resign (his take on the fascist enterprise: *"Empires die, but Euclid's theorems keep their youth forever"*).

His interest in mathematical ecology is due to Umberto D'Ancona (his son-in-law), who had studied the trends in fisheries in the Adriatic sea before and immediately after WWI. In 1914-1918 fisheries in the Adriatic had stopped completely because of the conflict. D'Ancona had noticed that, while herbivorous fish had remained about constant, the piscivorous fish had increased dramatically in numbers. The problem piqued Volterra who immediately published a sophisticated study, proposing the same equations studied by Lotka. In a short letter to Nature [@volterra1926fluctuations], he stated the so-called "Volterra's Effect" (which he termed "Law III"): *"a complete closure of the fishery was a form of 'protection' under which the voracious fishes were much the better and prospered accordingly, but the ordinary food-fishes, on which these are accustomed to prey, were worse off than before."* This brief paper was a summary of a much more extensive article [@volterra1926variazioni].

Lotka-Volterra interactions

In 1927, Lotka wrote to Nature to raise the issue that the equations studied by Volterra and the figures presented in Volterra's brief article were identical to those found in *Elements of Physical Biology* (published in 1925). He concluded: *"It would be gratifying if Prof. Volterra's publication should direct attention to a field and method of inquiry which apparently has hitherto passed almost unnoticed."*

Volterra graciously conceded *"I recognize his priority, and am sorry not to have known his work, and therefore not have been able to mention it."* He however listed a few points in which the two authors had pursued different directions, and concluded *"Working independently the one from the other, we have found some common results, and this confirms the exactitude and the interest in the position of the problem. I agree with him in his conclusions that these studies and these methods of research deserve to receive greated attention from scholars, and should give rise to important applications."*

Constant of motion for Lotka-Volterra Predator-Prey

Write:

$$\frac{dx(t)}{dy(t)} = \frac{\rho\, x(t) - \alpha\, x(t)\, y(t)}{-\delta\, y(t) + \beta\, x(t)\, y(t)}$$

As such:

$$(-\delta\, y + \beta\, x\, y)\, dx = (\rho\, x - \alpha\, x\, y)\, dy$$

dividing both sides by $x\, y$, we obtain:

$$\left(-\frac{\delta}{x} + \beta\right) dx = \left(\frac{\rho}{y} - \alpha\right) dy$$

Integrating both sides:

$$\beta\, x - \delta\, \log x = -\alpha\, y + \rho\, \log y + C$$

where C is a constant of integration. Rearranging, and substituting $x^\star = \delta/\beta$ and $y^\star = \rho/\alpha$, we obtain:

$$\beta(x - x^\star \log x) + \alpha(y - y^\star \log y) = C$$

This means that the system has a constant of motion (a.k.a. "first integral"): the value of C depends on the initial conditions, and then the system will cycle around the equilibrium in closed orbits. Note that a) $C > 0$ if the initial conditions are different from the equilibrium; b) $C = C_m > 0$ if we are at equilibrium; and therefore c) $C \geq C_m$ for all (positive) initial conditions.

We can use C as a Lyapunov function:

$$V(x, y) = \beta(x - x^\star \log x) + \alpha(y - y^\star \log y)$$

$$\frac{dV(x, y)}{dt} = \left(\beta - \frac{\delta}{x}\right)\frac{dx}{dt} + \left(\alpha - \frac{\rho}{y}\right)\frac{dy}{dt} = 0$$

Therefore, the dynamics are such that $V(x, y)$ remains constant.

Analysis of Predator-Prey model with logistic growth for the prey

In the classic Lotka-Volterra model, the local stability analysis of the coexistence equilibrium is inconclusive. When however the prey grows logistically it is easy to show that the equilibrium is now stable. For example, consider the system

$$\begin{cases} \dfrac{dx}{dt} = x(1 - x/2 - y) \\ \dfrac{dy}{dt} = y(x - 1) \end{cases}$$

First, we find the equilibria. From the first equation, we have $x^\star = 0$, or $y^\star = 1 - x^\star/2$; from the second equation, we have $y^\star = 0$ or $x^\star = 1$. Combining them, we find that either $(x^\star, y^\star)^T = (0, 0)^T$ (trivial), $(x^\star, y^\star)^T = (2, 0)^T$ (boundary), or $(x^\star, y^\star)^T = (1, 1/2)^T$ (coexistence).

The isoclines of zero growth are $y = 1 - x/2$ for the prey, and $x = 1$ for the predator. The Jacobian for the system is

$$J = \begin{pmatrix} 1 - x - y & -x \\ y & x - 1 \end{pmatrix}$$

At the equilibrium $(x^\star, y^\star)^T = (1, 1/2)^T$, we have:

$$M = \begin{pmatrix} -\frac{1}{2} & -1 \\ \frac{1}{2} & 0 \end{pmatrix}$$

The trace is $-1/2$ and the determinant $1/2$, as such the equilibrium is stable. The eigenvalues are given by:

$$p(\lambda) = \lambda^2 + \frac{1}{2}\lambda + \frac{1}{2}$$

Obtaining:

$$\lambda = \frac{-\frac{1}{2} \pm \sqrt{\frac{1}{4} - 2}}{2} = \frac{-1 \pm i\sqrt{7}}{4}$$

Therefore small perturbations will oscillate back to equilibrium. Numerically:

Global stability

We can write a Lyapunov function for the system above. Take:

$$V(x, y) = \left(x - x^\star - x^\star \log \frac{x}{x^\star}\right) + \left(y - y^\star - y^\star \log \frac{y}{y^\star}\right) = (x - 1 - \log x) + \left(y - \frac{1}{2} - \frac{1}{2} \log 2y\right)$$

Derive with respect to time to obtain:

$$\frac{dV(x, y)}{dt} = -\frac{1}{2}(1 - x)^2 < 0$$

As such, the equilibrium $(x^\star, y^\star)^T = (1, 1/2)^T$ is globally stable.

Homework 2b

Take the competitive Lotka-Volterra model:

$$\frac{dx}{dt} = D(x)(r - Ax)$$

with positive growth rates $r = (1, \rho)^T$, and

$$A = \begin{pmatrix} \alpha & \beta \\ \beta & \alpha \end{pmatrix}$$

.

Discuss the existence of a coexistence equilibrium and its stability. Write a Lyapunov function to prove global stability of the feasible equilibrium.

3 Generalized Lotka-Volterra model

Lesson plan:

1. We start by discussing the Generalized Lotka-Volterra model, which we are going to see over and over again in the remainder of the lectures.
2. We discuss the existence of equilibria in the case of n populations.
3. We show that the GLV model can give rise to all sort of dynamics, including limit cycles and chaos.
4. We show that a positive equilibrium is necessary for coexistence, and that, when populations coexist, the equilibrium is the time-average of the trajectories.
5. We show how to perform local stability analysis for GLV.
6. We introduce D-stability, allowing us to write a Lyapunov function to determine global stability in GLV models.
7. We conclude by analyzing the MacArthur's consumer-resource model, highlighting its deep connection to GLV.

3.1 Formulation

We can write the Generalized Lotka-Volterra model as:

$$\frac{dx(t)}{dt} = D(x(t))(r + Ax(t))$$

where $x(t)$ is a (column) vector of length n containing the densities of all populations $1, \ldots, n$ at time t, r is a vector of "intrinsic growth rates" (or death rates, when negative), measuring the growth (decline) of population i when grown alone at low density, and A is a $n \times n$ matrix of interaction coefficients. We use $D(x)$ to denote the diagonal matrix with x on the diagonal.

In component form, we have (dropping the dependence on t):

$$\dot{x}_i = x_i \left(r_i + \sum_j A_{ij} x_j \right)$$

Sometimes the model is written in a slightly different way, by bringing the vector r outside the parenthesis:

$$\dot{x}_i = x_i \left(r_i + \sum_j A_{ij} x_j \right)$$

$$= r_i x_i \left(1 + \frac{1}{r_i} \sum_j A_{ij} x_j \right)$$

$$= r_i x_i \left(1 + \sum_j B_{ij} x_j \right)$$

where we have defined $B_{ij} = A_{ij}/r_i$. In matrix form, we obtain:

$$\dot{x} = D(x \circ r)\,(1_n + Bx)$$

where $\circ$ is the Hadamard (element by element) product. This notation is convenient when computing the equilibria of the system; the previous notation is more convenient when investigating their stability. We will alternate between the two notations, using A and $B = D(r)^{-1}A$ for the two matrices.

3.2 A single population

The simplest case to study is that of a single population, in which case the equation becomes that of the logistic growth:

$$\frac{dx(t)}{dt} = x(t)(\rho + \alpha x(t))$$

Note that whenever $\rho > 0$ and $\alpha < 0$ there exists a feasible equilibrium $x^\star = \rho/\alpha$. The equilibrium is globally stable (as shown using either a quadratic Lyapunov function, or the $V = x - x^\star - x^\star \log(x/x^\star)$). As we've seen before, this is a separable ODE, with solution:

$$x(t) = \frac{\rho\, x_0\, e^{\rho t}}{\rho - \alpha\, x_0\, (e^{\rho t} - 1)}$$

Metapopulation dynamics

Consider a fragmented landscape in which habitable patches are connected by dispersal (for simplicity, suppose that all patches are reachable from any other). Call $p(t)$ the proportion of patches occupied by the species of interest at time t, and assume that a) an empty patch (the proportion of empty patches is $1 - p(t)$) is colonized by the populations in other patches with rate $\gamma\, p(t)$, where γ is the "colonization rate", and b) that occupied patches become empty at

rate $\epsilon\, p(t)$ ("extinction rate"). We want to model the proportion of patches occupied by the population at time t [@levins1969some]:

$$\frac{dp(t)}{dt} = \gamma\, p(t)(1 - p(t)) - \epsilon\, p(t) = p(t)((\gamma - \epsilon) - \gamma\, p(t))$$

which is equivalent to the logistic equation above with $\rho = \gamma - \epsilon$ and $\alpha = -\gamma$. As such, asymptotically the proportion of patches occupied by the population will be $-\rho/\alpha = (\gamma - \epsilon)/\gamma = 1 - \epsilon/\gamma$.

S-I-S model

Consider a population of individuals, each of which can be in one of two states: susceptible to a disease, or infective/infected. Call $S(t)$ the proportion of susceptible individuals at time t, and $I(t)$ the proportion of infected individuals, with $S(t) + I(t) = 1$. When individuals meet, an infected individual can transmit the disease to susceptibles with rate β; infected individuals recover from the disease with rate γ, and return susceptible. We can write the system of equations:

$$\begin{cases} \dfrac{dS(t)}{dt} = -\beta S(t)I(t) + \gamma I(t) \\ \dfrac{dI(t)}{dt} = \beta S(t)I(t) - \gamma I(t) \end{cases}$$

Note that the equations sum to zero, because the quantity $S(t) + I(t) = 1$ is conserved through the dynamics. Take the second equation, and substitute $S(t) = 1 - I(t)$; rearranging:

$$\frac{dI(t)}{dt} = \beta(1 - I(t))I(t) - \gamma I(t) = I(t)(\beta - \gamma - \beta I(t))$$

which is again the equation for the logistic growth with $\rho = \beta - \gamma$ and $\alpha = -\beta$. As such, provided that $\beta - \gamma > 0$, asymptotically a fraction $(\beta - \gamma)/\beta$ of individuals will be infected. The condition $\beta - \gamma > 0 \rightarrow \beta > \gamma \rightarrow \beta/\gamma > 1$ is often written as $\mathcal{R}_0 = \beta/\gamma > 1$.

3.3 Multi-species dynamics

Existence of an equilibrium

Returning to the multi-species system, and in analogy with the single species model, we can look for stationary points (fixed points, equilibria).

If an equilibrium $x^\star$ in which all populations are present exists, it must be the solution of

$$1_n + Bx^\star = 0_n$$
$$Bx^\star = -1_n$$
$$x^\star = -B^{-1}1_n$$

when the matrix B is invertible. Naturally, the equilibrium must be positive (called *feasible*) to be biologically attainable.

For example, consider:

$$A = \begin{pmatrix} -4 & -1 & -3 \\ -14 & -8 & -10 \\ -6 & -15 & -13 \end{pmatrix} \quad r = \begin{pmatrix} 8 \\ 32 \\ 34 \end{pmatrix} \quad B = D(r)^{-1}A = \begin{pmatrix} -\frac{1}{2} & -\frac{1}{8} & -\frac{3}{8} \\ -\frac{7}{16} & -\frac{1}{4} & -\frac{5}{16} \\ -\frac{3}{17} & -\frac{15}{34} & -\frac{13}{34} \end{pmatrix}$$

There is an equilibrium when at which all populations are present:

$$x^\star = -A^{-1}r = -B^{-1}1_n = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

If the matrix B is rank-deficient (and thus singular) there are infinitely many equilibria; for example, if the rank of B is $n-1$ there are infinitely many equilibria belonging to a line in $\mathbb{R}^n$.

When B is nonsingular, the model admits at most one positive equilibrium in which all populations are present. However, there can be up to $2^n - 1$ equilibria in which *one or more populations are absent/extinct*. Call $B^{(k,k)}$ the submatrix of B obtained by retaining the rows and columns indexed by the set k. Then by solving

$$B^{(k,k)}x^{(k)\star} = -1_{\|k\|}$$

we obtain an equilibrium for the subcommunity where only the populations in k are present (provided that the equilibrium is feasibile).

For the example above, we have:

$$B^{(\{1,2\},\{1,2\})} = \begin{pmatrix} -\frac{1}{2} & -\frac{1}{8} \\ -\frac{7}{16} & -\frac{1}{4} \end{pmatrix}$$

and

$$x^{(\{1,2\})\star} = -(B^{(\{1,2\},\{1,2\})})^{-1}1_2 = \begin{pmatrix} \frac{16}{9} \\ \frac{8}{9} \end{pmatrix}$$

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Therefore, the subsystem in which only the first two populations are present yields a feasible equilibrium.

Similarly,

$$x^{(\{1,3\})\star} = \begin{pmatrix} \frac{1}{17} \\ \frac{44}{17} \end{pmatrix} \quad x^{(\{1\})\star} = \begin{pmatrix} 2 \end{pmatrix} \quad x^{(\{2\})\star} = \begin{pmatrix} 4 \end{pmatrix} \quad x^{(\{3\})\star} = \begin{pmatrix} \frac{34}{13} \end{pmatrix}$$

The subsystem in which only populations 2 and 3 are present does not yield a feasible equilibrium.

Types of dynamics

For a single population, the GLV model can yield only two outcomes: unbounded growth, or convergence to an equilibrium; if the equilibrium is $x^\star = 0$, we say that the population is extinct at the equilibrium.

When we have two populations, we can also observe neutral cycles (as in the classic LV predator-prey system), and bistability (i.e., one population survives, while the other goes extinct; the identity of the population going extinct depends on the initial conditions).

For three populations we can observe limit cycles.

For three or more populations (in the general case), or four or more populations (in competitive systems), we can have chaos (i.e., non-periodic oscillations).

Equilibrium as time-average

Suppose that $x(t)$ has a periodic orbit, of period T (i.e., we assume $x(0) = x(T)$). Further, assume that the GLV has a feasible, interior equilibrium $x^\star$. We want to calculate the average density for each population:

$$\frac{1}{T} \int_0^T x(t) dt$$

First, we assume that $x(t) > 0$ and write the dynamics of its logarithm:

$$\frac{d \log(x_i(t))}{dt} = \frac{1}{x_i(t)} \frac{dx_i(t)}{dt} = r_i + \sum_j A_{ij} x_j(t)$$

In vector form:

$$\frac{d \log x(t)}{dt} = r + Ax(t)$$

Compute the average on both sides:

$$\frac{1}{T} \int_0^T \frac{d \log(x(t))}{dt} dt = \frac{1}{T} \int_0^T (r + Ax(t)) \, dt$$

yielding:

$$\frac{1}{T} (\log(x(T)) - \log(x(0))) = 0_n = r + A \left(\frac{1}{T} \int_0^T x(t) dt \right)$$

Note that the l.h.s. is zero because $x(0) = x(T)$. Now rearrange:

$$-r = A \left(\frac{1}{T} \int_0^T x(t) dt \right)$$

Multiplying by the matrix inverse:

$$-A^{-1} r = x^\star = \frac{1}{T} \int_0^T x(t) dt$$

showing that *the average density is* in fact *the equilibrium.* With a similar argument, one can prove that if the trajectory stays in a compact space (i.e., in case of chaotic attractors), then the long-time average is still $x^\star$.

Coexistence requires a feasible equilibrium

A necessary condition for the coexistence of populations is the existence of a positive (feasible) equilibrium.

Farkas' lemma

Consider matrix A, of size $n \times n$, and the vector b, of length n.

Then either:

$$\exists x \geq 0_n \quad | \quad Ax = b$$

or:

$$\exists y \in \mathbb{R}^n \quad | \quad A^T y \geq 0_n \text{ and } b^T y < 0$$

Suppose that the system does not have a feasible equilibrium, i.e., an $x^\star > 0_n$ such that $Ax^\star = -r$. Then, there must exist a y such that $A^T y \geq 0_n$ and $r^T y > 0$.

But then, consider the function:

$$P = \prod_i x_i^{y_i}$$

The function is positive when all $x_i > 0$. Differentiating with respect to time, we find:

$$
\begin{aligned}
\dot{P} &= \sum_i \left(y_i \dot{x}_i x_i^{y_i - 1} \prod_{j \neq i} x_j^{y_j} \right) \\
&= \sum_i \left(y_i \frac{\dot{x}_i}{x_i} \prod_j x_j^{y_j} \right) \\
&= P \sum_i y_i \left(r_i + \sum_j A_{ij} x_j \right) \\
&= P(y^T r + y^T A x)
\end{aligned}
$$

but by Farkas' lemma, we have that $y^T r > 0$ and $y^T A \geq 0_n^T$; then P always grows in time, and eventually diverges to ∞.

Note that $P(t) \to \infty$ requires some $x_i^{y_i}(t) \to \infty$, which happens when either $x_i(t) \to \infty$ and $y_i > 0$ (i.e., a population grows without bound), or $x_i(t) \to 0$ and $y_i < 0$ (i.e., a population goes extinct). Thus, in the absence of an equilibrium, trajectories can either diverge to infinity, or one or more populations can go extinct.

A feasible equilibrium is therefore a necessary condition for coexistence.

Local stability of the coexistence equilibrium

Suppose that a feasible equilibrium $x^\star$ exists: $x^\star = -A^{-1} r > 0_n$. We have:

$$J_{ii} = \frac{\partial (r_i x_i + \sum_j A_{ij} x_i x_j)}{\partial x_i} = r_i + \sum_j A_{ij} x_j + A_{ii} x_i$$

At equilibrium, we have:

$$r_i + \sum_j A_{ij} x_j^\star = 0$$

and therefore

$$M_{ii} = \left. J_{ii} \right|_{x^\star} = A_{ii} x_i^\star$$

Similarly,

$$J_{ii} = \frac{\partial(r_i x_i + \sum_j A_{ij} x_i x_j)}{\partial x_j} = A_{ij} x_i$$

and thus

$$M_{ij} = \left. J_{ij} \right|_{x^\star} = A_{ij} x_i^\star$$

Putting them together, we obtain:

$$M = \left. J \right|_{x^\star} = D(x^\star) A$$

and thus the equilibrium is l.a.s. if and only if all of the eigenvalues of $D(x^\star)A$ have negative real part.

Matrix similarity

Two square matrices A and B are called **similar** if there exists an invertible matrix P such that:

$$B = PAP^{-1}$$

The two matrices A and B share many properties; notably, they have the same eigenvalues.

Matrix congruence

Two square matrices A and B are called **congruent** if there exists an invertible matrix P such that:

$$B = PAP^T$$

Further, if A and B are real and symmetric, then the number of positive, negative and zero eigenvalues in the two matrices are the same (Sylvester's law of inertia).

If the matrix A is symmetric, any feasible equilibrium is stable if and only if the eigenvalues of A are all negative (i.e., A is negative definite). To prove this, take $A = A^T$ and consider the similarity transformation

$$D(x^\star)^{-\frac{1}{2}} D(x^\star) A D(x^\star)^{\frac{1}{2}}$$
$$D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$$

The matrices $D(x^\star)A$ and $D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$ are *similar*, and thus have the same eigenvalues; the matrices A and $D(x^\star)^{\frac{1}{2}} A D(x^\star)^{\frac{1}{2}}$ are *congruent*, and thus have the same number of positive, negative and zero eigenvalues by Sylvester's law of inertia.

A symmetric matrix is negative definite if all its submatrices obtained by deleting a set of rows and the corresponding columns are negative definite as well. Then, if $A = A^T$ is negative definite, a) a feasible equilibrium is locally stable, and b) for any subsystem, feasibility implies local stability.

Note that this is generally not the case for nonsymmetric matrices A, in which case we could have that A has all eigenvalues with a negative real part, while $D(x^\star)A$ has some eigenvalues with positive real part (or viceversa). For example, take

$$A = \begin{pmatrix} -3 & 4 & 0 \\ 5 & -2 & -2 \\ 5 & 5 & -3 \end{pmatrix} \quad \lambda(A) = \{-7, \frac{1}{2}(-1 \pm i\sqrt{15})\}$$

and the equilibrium $x^\star = (1, 1, 1/2)^T$ (obtained for $r = (-1, -2, -17/2)$); we obtain:

$$M = D(x^\star)A = \begin{pmatrix} -3 & 4 & 0 \\ 5 & -2 & -2 \\ \frac{5}{2} & \frac{5}{2} & -\frac{3}{2} \end{pmatrix} \quad \lambda(B) = \{-7, \frac{1}{4}(1 \pm i\sqrt{31})\}$$

Thus, the equilibrium is not locally asymptotically stable.

D-stability and Lyapunov-Diagonal Stability

A matrix A is called *stable* if all its eigenvalues have negative real part. A matrix A is called *D-stable* if $D(x)A$ is stable for every choice of x such $x_i > 0 \ \forall i$. While conditions for *D-stability* are not known for matrices of size greater than 3, a **sufficient** condition for *D-stability* is that there exists a diagonal matrix D with positive elements on the diagonal such that $DA + A^T D$ is negative definite (i.e., has negative eigenvalues).

Consequences for Lotka-Volterra dynamics

- If a matrix A is stable and symmetric, it is *D-stable* (just take $D = I$).

- Take a GLV system with a stable, non symmetric matrix A such that $A + A^T$ is negative definite. Then any feasible equilibrium is locally stable: we have $M = D(x^\star)A$, but if A is *D-stable* then M is stable.

Lyapunov diagonal stability and global stability

A candidate Lyapunov function for GLV is due to Goh, and shows that, whenever there exists a positive diagonal matrix $D(w)$ such that $D(w)A^T + AD(w)$ is negative definite, then the equilibrium $x^\star > 0_n$ is globally stable. A matrix with this property is called **Lyapunov diagonally stable**.

We start with the simplest case in which $w = 1_n$ and thus $D(w) = I$. Take the function

$$V(x(t)) = \sum_i \left(x_i - x_i^\star - x_i^\star \log \frac{x_i}{x_i^\star} \right)$$

The function is positive for every $x \in \mathbb{R}_+^n$, because $z - 1 - \log z \geq 0$ whenever $z > 0$; take $z = x_i/x_i^\star$ and then multiply by $x_i^\star$ to prove that the function is nonnegative.

Differentiating with respect to time, we find:

$$
\begin{aligned}
\dot{V}(x(t)) &= \sum_i \left(\dot{x}_i - x_i^\star \frac{\dot{x}_i}{x_i} \right) \\
&= \sum_i \left(x_i(r_i + (Ax)_i) - x_i^\star(r_i + (Ax)_i) \right) \\
&= \sum_i \Delta x_i(-(Ax^\star)_i + (Ax)_i) \\
&= \sum_{i,j} \Delta x_i A_{ij} \Delta x_j \\
&= \Delta x^T A \Delta x \\
&= \frac{1}{2} \Delta x^T (A + A^T) \Delta x
\end{aligned}
$$

Thus, if the symmetric part of A, $H(A) = \frac{1}{2}(A + A^T)$ is negative definite, then $\dot{V}(x(t)) < 0$ for every $\Delta x \neq 0$ and the equilibrium is stable.

To extend the reach of the candidate function, consider the change of variables:

$$z_i = x_i/w_i \quad x_i = w_i z_i$$

with $w_i > 0$. This change of variables cannot impact the existence or stability of equilibria (we are simply changing the units of measure we are using to measure the density of each population). Then,

$$\dot{z}_i = \frac{\dot{x}_i}{w_i} = \frac{x_i}{w_i}(r_i + (Ax)_i) = z_i(r_i + (AD(w)z)_i) = z_i(r_i + (\tilde{A}z)_i)$$

Thus, if $H(\tilde{A}) = \frac{1}{2}(AD(w) + D(w)A^T)$ is negative definite, the equilibrium is stable.

Saturated equilibria

We say that an equilibrium $\bar{x}$ is saturated if we have that some populations (say y) are coexisting at a stable equilibrium, while the rest of the populations (say z) are extinct and **cannot reinvade the system from low abundance**. As such, saturated equilibria are **locally stable** with respect to the reintroduction of the extinct populations.

When Goh's function holds, we can prove that dynamics starting from positive conditions $x(t) > 0_n$ will converge to a *saturated equilibrium* $\tilde{x}$ characterized by two conditions. We have n populations, and at the saturated equilibrium the populations in set k coexist at a globally stable equilibrium, and the remaining populations, belonging to set $n - k$ are extinct, and cannot re-invade the system starting from low abundance.

Without loss of generality, we can order the populations such that the first $\|k\|$ populations are those that coexist at the saturated equilibrium, and the remaining $\|n - k\|$ are those extinct at the saturated equilibrium. We partition all variables according to the two sets:

$$x = \begin{pmatrix} y \\ z \end{pmatrix} \quad \tilde{x} = \begin{pmatrix} y^\star \\ 0_{n-k} \end{pmatrix} \quad A = \begin{pmatrix} \mathfrak{A} & \mathfrak{B} \\ \mathfrak{C} & \mathfrak{D} \end{pmatrix} \quad r = \begin{pmatrix} \mathfrak{r} \\ \mathfrak{s} \end{pmatrix}$$

We consider a minor modification of Goh's function:

$$V(x(t)) = \sum_{i \in k} \left(y_i - y_i^\star - y_i^\star \log \frac{y_i}{y_i^\star} \right) + \sum_{i \in n-k} z_i$$

Differentiating with respect to time, we obtain:

$$\dot{V}(x(t)) = \sum_{i \in k} \left(\dot{y}_i - y_i^\star \frac{\dot{y}_i}{y_i} \right) + \sum_{i \in n-k} \dot{z}_i$$
$$= \Delta y^T(\mathfrak{r} + \mathfrak{A}y + \mathfrak{B}z) + z^T(\mathfrak{s} + \mathfrak{C}y + \mathfrak{D}z)$$

Now we substitute $\mathfrak{r} = -\mathfrak{A}y^\star$, and add and subtract $z^T \mathfrak{C}y^\star$:

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$$\dot{V}(x(t)) = \Delta y^T(-\mathfrak{A}y^\star + \mathfrak{A}y + \mathfrak{B}z) + z^T(\mathfrak{s} + \mathfrak{C}y + \mathfrak{D}z + \mathfrak{C}y^\star - \mathfrak{C}y^\star)$$
$$= \Delta y^T(\mathfrak{A}\Delta y + \mathfrak{B}z) + z^T(\mathfrak{s} + \mathfrak{C}\Delta y + \mathfrak{D}z + \mathfrak{C}y^\star)$$

Now we write the function as the sum of two parts:

$$\dot{V}(x(t)) = (\Delta y^T\mathfrak{A}\Delta y + \Delta y^T\mathfrak{B}z + z^T\mathfrak{C}\Delta y + z^T\mathfrak{D}z) + z^T(s + \mathfrak{C}y^\star)$$
$$= \begin{pmatrix}\Delta y \\ z\end{pmatrix}^T \begin{pmatrix}\mathfrak{A} & \mathfrak{B} \\ \mathfrak{C} & \mathfrak{D}\end{pmatrix} \begin{pmatrix}\Delta y \\ z\end{pmatrix} + z^T(s + \mathfrak{C}y^\star)$$
$$= \begin{pmatrix}\Delta y \\ z\end{pmatrix}^T A \begin{pmatrix}\Delta y \\ z\end{pmatrix} + z^T(s + \mathfrak{C}y^\star)$$

Whenever $H(A) = \frac{1}{2}(A + A^T)$ is negative definite, then the first term is negative for any choice of y and z. Examining the second term, we see that $\mathfrak{s} + \mathfrak{C}y^\star$ measures the invasion growth rate of the populations in the set $n - k$ when they are attempting to invade the community that is resting at $y^\star$. Thus, if we can find a saturated equilibrium, it is globally stable and will be reached for any $x(0) > 0_n$.

This derivation can be extended by considering a diagonal matrix $D(w)$ with $w > 0_n$, as done above.

3.4 MacArthur's consumer-resource model

History: Robert H. MacArthur (1930-1972)

Robert MacArthur was born in Toronto, and moved to Vermont when his father (a geneticist) became a professor at Marlboro College.

He studied mathematics first at Marlboro College and then at Brown University. He enrolled as a PhD student in mathematics at Yale, but quickly switched to studying ecology with George Evelyn Hutchinson.

He was a professor first at the University of Pennsylvania and then at Princeton University. In his brief career (he died at age 42) he revolutionized ecology, by making it into a rigorous, predictive science based on general principles.

He is recognized for developing the *Theory of Island Biogeography* (with E. O. Wilson, @macarthur2001theory), the investigation of limiting similarity (with R. Levins, @macarthur1967limiting), the contributions to the complexity-stability debate (@macarthur1955fluctuations, see next lecture). The consumer-resource model he proposed in 1969 now bears his name

(published also in @macarthur1970species in a longer form—the first paper in the journal Theoretical Population Biology!).

MacArthur considered a system with two classes of equations: those describing the dynamics of consumers (x_i) and resources (y_i). Resources do not interact with each other (only with themselves), and consumers interact only through the sharing of resources. Several parameterizations are possible—here we choose a simple formulation that retains the main features of the model (see @case1979global for a slightly more general model):

$$
\begin{cases}
\dfrac{dy_i}{dt} = y_i \left(r_i - b_i\, y_i - \sum_j P_{ij}\, x_j \right) \\
\dfrac{dx_j}{dt} = x_j \left(-m_j + \sum_i v_j\, P_{ij}\, y_i \right)
\end{cases}
$$

In the absence of consumers, each resource grows logistically. In the absence of resources, consumers go extinct. In the model, all parameters are taken to be positive: r_i is the growth rate for resource i, b_i models its self-regulation; m_j is the death rate of consumer j, and v_j models the efficiency of transformation of resources into consumers. The matrix P is in general rectangular ($n \times k$, where n is the number of resources and k that of consumers).

Block matrices

Any matrix can be rewritten as a series of smaller matrices stitched together. For square matrices, it is often convenient to partition a matrix into blocks such that diagonal blocks are square matrices and off-diagonal blocks are (in general) rectangular.

For example:

$$
M = \begin{pmatrix}
1 & 2 & 3 & 4 & 5 \\
6 & 7 & 8 & 9 & 10 \\
11 & 12 & 13 & 14 & 15 \\
16 & 17 & 18 & 19 & 20 \\
21 & 22 & 23 & 24 & 25
\end{pmatrix}
$$

Can be written as:

$$
M = \begin{pmatrix} M_{11} & M_{12} \\ M_{21} & M_{22} \end{pmatrix}
$$

with:

$$
M_{11} = \begin{pmatrix} 1 & 2 \\ 6 & 7 \end{pmatrix} \quad M_{21} = \begin{pmatrix} 3 & 4 & 5 \\ 8 & 9 & 10 \end{pmatrix} \quad \dots
$$

Multiplication of block matrices

The multiplication of two block matrices with square diagonal blocks is very easy:

$$\begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} \begin{pmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{pmatrix} = \begin{pmatrix} A_{11}B_{11} + A_{12}B_{21} & A_{11}B_{12} + A_{12}B_{22} \\ A_{21}B_{11} + A_{22}B_{21} & A_{21}B_{12} + A_{22}B_{22} \end{pmatrix}$$

Determinant of block matrices

Take

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix}$$

and assume that A_{22} is invertible. Then $\det(A) = \det(A_{22})\det(A_{11} - A_{12}A_{22}^{-1}A_{21})$

Inverse of block matrix

Similarly, if A_{22} is invertible, and $\det(A) \neq 0$ (and hence the Schur complement $A_{11} - A_{12}A_{22}^{-1}A_{21}$ is nonsingular) then

$$A^{-1} = \begin{pmatrix} S & -SA_{12}A_{22}^{-1} \\ -A_{22}^{-1}A_{21}S & A_{22}^{-1} + A_{22}^{-1}A_{21}SA_{21}A_{22}^{-1} \end{pmatrix}$$

where $S = (A_{11} - A_{12}A_{22}^{-1}A_{21})^{-1}$

We can rewrite the system as a generalized Lotka-Volterra model (see @case1979global). We define:

$$z = (y, x)^T \quad s = (r, -m)^T$$

And the block structured matrix A:

$$A = \begin{pmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{pmatrix} \text{ with } A_{11} = -D(b), \ A_{12} = -P, \ A_{21} = D(v)P^T, A_{22} = 0_{k,k}$$

where $0_{k,k}$ is a $k \times k$ matrix of zeros. Now the system becomes:

$$\frac{dz}{dt} = D(z)(s + Az)$$

Existence of an equilibrium

For simplicity, we concentrate on the study of the feasibility and stability of the coexistence equilibrium. If an equilibrium $z^\star \neq 0$ exists, it is the solution of $Az^\star = -s$, which requires matrix A to be non-singular. Matrix A is non-singular only if $w = 0$ is the only solution of $Aw = 0$. We prove that A is non-singular whenever A_{12} is of rank k, and A_{11} is negative definite. We do so by contradiction. First, because the matrix A has a special structure, we can split w into $(w_1, w_2)^T$, and write:

$$A \begin{pmatrix} w_1 \\ w_2 \end{pmatrix} = \begin{pmatrix} A_{11}w_1 + A_{12}w_2 \\ A_{21}w_1 \end{pmatrix} = \begin{pmatrix} 0_n \\ 0_k \end{pmatrix}$$

We therefore have $A_{21}w_1 = 0$ and $A_{11}w_1 + A_{12}w_2 = 0$.

- Suppose that $w_1 = 0$ and $w_2 \neq 0$; then we find $A_{12}w_2 = 0$ with $w_2 \neq 0$, which is not possible when A_{12} has rank k.
- Now suppose that $w_1 \neq 0$ and $w_2 = 0$, but this implies $A_{11}w_1 = 0$ with $w_1 \neq 0$, which is impossible given that A_{11} is clearly of full rank (rank n).
- We are left with the case in which both $w_1 \neq 0$ and $w_2 \neq 0$. We have $A_{21}w_1 = 0$, but $A_{21}w_1 = D(v)P^T w_1 = 0$, which implies $P^T w_1 = 0$ because all $v_i > 0$. Then, multiply the first set of equations by w_1^T and the second by w_2^T. We obtain $w_1^T A_{11}w_1 - w_1^T P w_2 = 0$ and $w_2^T D(v)P^T w_1 = 0 = w_2^T P^T w_1$. But then $w_1^T P w_2 = 0$, leaving us with $w_1^T A_{11}w_1 = 0$ with $w_1 \neq 0$, which is again a contradiction because A_{11} is clearly negative definite (and as such $w_1^T A_{11}w_1 \leq 0$, with equality implying $w_1 = 0$).

We have proven that A is non-singular, and therefore a unique equilibrium point for the system exists (the equilibrium for the moment needs not to be feasible) whenever $A_{11} = -D(b)$ is negative definite (which is always the case whenever resources are self-regulating) and, importantly, A_{12} has rank k (the number of consumers). This in turn implies that **the number of resources must be larger (or equal) than the number of consumers**. A similar argument is developed in the classic @levin1970community.

Key paper: @levin1970community

Starting from fairly generic assumptions, the principle of competitive exclusion is generalized: *No stable equilibrium can be attained in an ecological community in which some r components are limited by less than r limiting factors. In particular, no stable equilibrium is possible if some r species are limited by less than r factors.*

Global stability

Next, we prove that if a feasible equilibrium for the system exists, it is globally stable. First, we choose a diagonal matrix G

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$$G = \begin{pmatrix} I_n & 0_{n,k} \\ 0_{k,n} & D(v)^{-1} \end{pmatrix}$$

We have:

$$B = GA = \begin{pmatrix} -D(b) & -P \\ P^T & 0_{k,k} \end{pmatrix}$$

B is therefore negative semi-definite:

$$\frac{1}{2}(B + B^T) = \begin{pmatrix} -D(b) & 0_{n,k} \\ 0_{k,n} & 0_{k,k} \end{pmatrix}$$

with eigenvalues $-b$ and 0 (with multiplicity k). Therefore,

$$\begin{aligned}
\frac{dV(z(t))}{dt} &= 1^T G \left(\frac{dz(t)}{dt} - D(z^\star)\frac{d \log z(t)}{dt} \right) \\
&= \frac{1}{2}(z - z^\star)^T (GA + A^T G)(z - z^\star) \\
&= \frac{1}{2}(z - z^\star)^T (B + B^T)(z - z^\star) \\
&= (y - y^\star)^T (-D(b))(y - y^\star)
\end{aligned}$$

which is zero only when the resources are at equilibrium. We can invoke LaSalle's invariance principle to prove that any feasible equilibrium is stable.

Homework 3a

Prove the local stability of the feasible coexistence equilibrium.

Hint: if we have a (not necessarily symmetric) matrix A such that $x^T A x < 0$ for every $x \in \mathbb{R}^n$, with $x \neq 0$, then the eigenvalues of A have negative real part. To prove this, consider a generic eigenvector/eigenvalue of A:

$$\begin{aligned}
Av &= \lambda v \\
A(u + iw) &= (\alpha + i\beta)(u + iw) \\
Au + iAw &= \alpha u - \beta w + i(\alpha w + \beta u)
\end{aligned}$$

Write two systems of equations, one for the real parts, and one for the imaginary parts:

$$\begin{cases} Au = \alpha u - \beta w \\ Aw = \alpha w + \beta u \end{cases}$$

Multiply the first set of equations by u^T, and the second by w^T:

$$\begin{cases} u^T A u = \alpha u^T u - \beta u^T w \\ w^T A w = \alpha w^T w + \beta w^T u \end{cases}$$

Sum the two equations:

$$u^T A u + v^T A v = \alpha(u^T u + w^T w)$$

If we have that $x^T A x < 0$ for any $x \neq 0$, then the left-hand side is negative whenever either $u \neq 0$, $v \neq 0$, or both are nonzero. In the right-hand side, we have that $u^T u = \sum_i u_i^2 \geq 0$, and $v^T v \geq 0$. Moreover if $x = u + iv$ is an eigenvector, necessarily at least one of u and v is nonzero. Thus the left-hand side is negative, and the part in parenthesis in the right-hand side is positive. Then, $\alpha < 0$, proving that all eigenvalues have a negative real part.

Use this argument to prove local stability of the consumer-resource model.

Separation of time-scales

In the original article, @macarthur1970species takes an interesting shortcut, which can shed light on the behavior of the GLV when the matrix of interactions is symmetric (i.e., $A = A^T$). Consider the Consumer-Resource model above, and assume that resources equilibrate quickly compared to the dynamics of the consumers. In practice, this means that the system operates on two different time scales, such that the consumers perceive resources to be constantly at equilibrium.

We solve the equations for the resources:

$$r - D(b)\, y - P\, x = 0$$
$$y = D(b)^{-1}(r - P\, x)$$

Substituting in the equations for the consumers, we obtain:

$$\begin{aligned} \frac{dx}{dt} &= D(x)\left(-m + D(v)P^T y\right) \\ &= D(x)\left(-m + D(v)P^T D(b)^{-1}(r - P\,x)\right) \\ &= D(x)\left([D(v)P^T D(b)^{-1}r - m] - [D(v)P^T D(b)^{-1}P]\,x\right) \\ &= D(x)D(v)\left([P^T D(b)^{-1}r - D(v)^{-1}m] - [P^T D(b)^{-1}P]\,x\right) \\ &= D(x)D(v)\left(s - B\,x\right) \end{aligned}$$

Which is again GLV, with growth rates $s = P^T D(b)^{-1} r - D(v)^{-1} m$ and interaction matrix $B = P^T D(b)^{-1} P$, which, importantly, is symmetric (note also that if P is of rank k and $b > 0$, then B is of full rank).

Lyapunov function for symmetric Lotka-Volterra

We have the equations:

$$\frac{dx_i}{dt} = x_i v_i \left(s_i - \sum_j B_{ij} x_j \right)$$

At equilibrium, we have $x^\star = B^{-1} s$. Consider the function:

$$V(x(t)) = 2 \sum_i s_i x_i - \sum_{ij} B_{ij} x_i x_j$$

Note that $\sum_i s_i x_i > 0$ and that whenever B is stable (and because it's symmetric, negative definite), $-\sum_{ij} B_{ij} x_i x_j > 0$. At equilibrium, we have:

$$V(x^\star) = \sum_i \left(s_i x_i^\star + \left(s_i x_i^\star - \sum_j B_{ij} x_j^\star \right) \right) = \sum_i s_i x_i^\star$$

It is of particular interest the case in which $s_i = 1$ for all i and $V(x^\star)$ is simply the total biomass of the system at equilibrium.

Now, let's take the derivative of $V(x(t))$ with respect to x_i:

$$\frac{\partial V}{\partial x_i} = 2 s_i - 2 \sum_j B_{ij} x_j$$

The 2 in front of the B_{ij} stems from the fact that we are summing over both $B_{ij} x_i x_j$ and $B_{ji} x_j x_i$. But then:

$$\frac{dx_i}{dt} = x_i v_i \left(s_i - \sum_j B_{ij} x_j \right) = x_i v_i \frac{1}{2} \frac{\partial V}{\partial x_i}$$

And therefore, by chain rule:

$$\frac{dV}{dt} = \sum_i \frac{\partial V}{\partial x_i} \frac{dx_i}{dt} = \sum_i x_i v_i \frac{1}{2} \left(\frac{\partial V}{\partial x_i} \right)^2$$

which is always non-negative, and is zero at equilibrium. Therefore, $V(x(t))$ is maximized through the dynamics. This holds even more generally, as we will see in the lecture on assembly and in the following homework. In a way, symmetric, competitive dynamics are "optimizing" V, by following a gradient. This argument can be further expanded, showing that many ecological models can be interpreted as optimization processes (@marsland2019minimum).

Homework 3b

Consider a five-species system with symmetric, stable B (with all positive coefficients) and positive s, yielding the feasible equilibrium $x^\star$.

- Find random parameters satisfying 1) $B_{ij} = B_{ji} > 0 \ \forall i, j$; 2) B is stable; 3) $s_i > 0 \ \forall i$; 4) $B^{-1}s = x^\star > 0$. These parameters define your pool of species.
- For each possible subset of species in the pool, (i.e., for all combinations ranging from a single species [5 cases], to two species [10 cases], ..., to all species together [1 case]), compute the corresponding equilibrium. Is it feasible? Is it stable?
- Take two subset of species such that a) both are feasible and stable; b) subset 1 contains subset 2 (i.e., all species in 2 are in 1, but not the converse); c) the value of $V(x^\star)$ for subset 1 is larger than that for subset 2. Try invading subset 2 with the species by introducing at the equilibrium of subset 2 the species that are in subset 1 but not in 2—starting all of them at low density. What happens?

3.5 Further readings

On the theory of GLV:

- @hofbauer1998evolutionary is a wonderful introduction to dynamical systems in ecology and population genetics, with a nice introduction to evolutionary game theory.

- @hadeler2017topics contains a more mathematically-oriented treatment of the material covered in the first part of this lecture.

- @baigent2016lotka is a mathematical introduction to Lotka-Volterra dynamics.

4 Stability of large ecological communities

Lesson plan:

1. We introduce the so-called diversity-stability debate, by discussing the seminal contributions of MacArthur (1955) and May (1972).
2. We show how the celebrated May's stability criterion can be derived using elementary results from random matrix theory.
3. We extend May's results to the case in which interactions between the species are correlated.
4. We discuss a few tools from random matrix theory that are useful for ecology.

4.1 Complexity and stability

Key paper: @macarthur1955fluctuations

In 1955, MacArthur used an information-theoretic argument to suggest more speciose communities would be more "stable": having a food web with many species would open several "channels" for energy to flow from resources to consumers, such that if a channel were to go dry, another channel could take its place.

Key paper: @may1972will

This idea was challenged by May, who showed that, all other things being equal, larger communities would be less likely to be *dynamically stable*. This paper started the so-called "diversity-stability" debate that populates the literature to this day.

Key paper: @mccann2000diversity

In this review, McCann summarizes the development of the diversity-stability debate over the span of three decades.

As we have seen before, an equilibrium $x^\star$ is stable if the community matrix for the equilibrium has all eigenvalues with negative real part. For a Generalized Lotka-Volterra model, to determine the equilibrium and its stability, we would need to specify all the growth rates (r, n values), as well as the matrix of interactions (A, n^2 values). This is impractical to do for large systems (though we will try this out later). But can something quite general be said about the limit in which many species are in the community?

4.2 The stability of random ecosystems

History: Robert M. May (1936-2020)

Born and educated in Sidney, May received a PhD in theoretical physics from the University of Sidney in 1959. Having started his career in the physics of super-conductivity, May became interested in ecology. When visiting Princeton during his stay at the Institute for Advanced Studies, he met MacArthur, and decided to change fields.

He ended up changing the field of ecology, with an incredible number of contributions on population dynamics and chaos (see key papers in preceding lectures), the dynamics of infectious diseases (with Roy Anderson, @anderson1992infectious), evolutionary game theory (@nowak1992evolutionary), the estimation of the number of species on Earth (@may1988many), bibliometrics (@may1997scientific), and even banking (by modeling systemic risks, @haldane2011systemic). He succeeded MacArthur at Princeton, and concluded his career in England (University of Oxford).

He won a large number of prizes, and was created a life peer (Lord May, Baron of Oxford). He served as president of the Royal Society and as Chief Scientific Adviser to the government.

@may1972will attempted to answer this question by considering a **random community matrix**. In a GLV system, the diagonal elements $M_{ii} = A_{ii}x_i^\star$ are influenced by self-regulation (i.e., as in a carrying capacity), while the off-diagonal elements $M_{ij} = A_{ij}x_i^\star$ model the effect of species j on the equilibrium of species i. May considered the following algorithm to build a random community matrix. Take a large community, resting at an unspecified, feasible equilibrium; we build the community matrix by setting:

- $M_{ij} = 0$ with probability $(1 - C)$; with probability C we draw M_{ij} from a distribution with mean zero and variance σ^2. C is the proportion of realized connections, termed the "connectance" of the system.
- the diagonal elements are set to $-d$, modeling self-regulation.

May did not specify the distribution from which one would draw the nonzero interactions (more on this later). For the moment, let's assume it's a Normal distribution with mean zero and variance σ^2.

Note that the average of the eigenvalues of a matrix A is given by the average of its diagonal elements $\frac{1}{n}\sum_i \lambda_i = \frac{1}{n}\mathrm{Tr}(A) = \frac{1}{n}\sum_i A_{ii}$. As such, if $A = dI + B$, the eigenvalues of A will be those of B shifted by d.

We want to determine whether the equilibrium will be stable, given n, C, d and σ^2. To do so, we need to find the location of the "rightmost" eigenvalue of M. For example, let's plot the eigenvalues of a large matrix (500×500, the red-dashed line marks the location of zero on the x axis):

The eigenvalues fall into an almost perfect circle! Turns out, that this is the behavior we should expect, as stated by the so-called "Circular Law", one of the most beautiful results in random matrix theory.

Circular law: Take a non-symmetric, $n \times n$ random matrix in which all coefficients X_{ij} are i.i.d. random variables with $\mathbb{E}[X_{ij}] = 0$ and $\mathbb{E}[X_{ij}^2] = 1$. Then, as $n \to \infty$, the e.s.d. of $X/\sqrt{n}$ converges to the circular law:

$$\mu(\lambda) = \begin{cases} \frac{1}{\pi} & \text{if } (\mathrm{Re}(\lambda))^2 + (\mathrm{Im}(\lambda))^2 \leq 1 \\ 0 & \text{otherwise.} \end{cases}$$

This result can be used to calculate the radius of the eigenvalue distribution of the matrices studied by May: when the off-diagonal coefficients M_{ij} are 0 with probability $1 - C$ and are sampled independently from a distribution with mean 0 and variance σ^2 with probability C, we have that $\mathbb{E}[M_{ij}] = 0$ and $\mathbb{E}[M_{ij}^2] = C\sigma^2$. This means that if we were to divide the coefficients of M by $\sqrt{C\sigma^2}$ we would recover the unit variance, and the matrix would follow the circular law when S is large. Armed with this, we can calculate the radius: if the radius of $M/\sqrt{nC\sigma^2}$ converges to 1 when the matrix is large, then the radius of M is approximately $\sqrt{nC\sigma^2}$. For stability, we need a sufficiently negative diagonal (setting the center of the circle), yielding May's stability criterion:

$$\sqrt{nC\sigma^2} < d$$

We can try this on our matrix (black dashed line):

Showing that we accurately approximate the location of the rightmost eigenvalue. Note that, in the case of large n, whenever the circle crosses zero, some eigenvalues will be positive, determining the instability of the equilibrium.

Importantly, the distribution from which the coefficients are sampled does not matter—only that the mean is zero and that the variance is σ^2. For example, build the matrix using coefficients from a uniform distribution:

This property is called **universality** in random matrix theory.

Homework 4a

The probability that a matrix is stable, given C, σ and n is close to 1 when the stability criterion is satisfied, and close to 0 when it is not. Matrices satisfying $\sqrt{nC\sigma^2} = d$ are at the critical point. In theory, the results only hold in the limit $n \to \infty$ (to be accurate, $nC \to \infty$), as eigenvalues can fall outside the circle with small probability.

- Write code to compute the real part for the "rightmost" eigenvalue of a random matrix (Note: computing eigenvalues is fairly expensive in terms of computing time. Use `eigen(M, only.values = TRUE)$values` to speed up calculations).
- Write code to build matrices like those studied by May (nonzero elements sampled from a normal distribution).
- Set $d = 10$ and choose parameters n, C and σ^2 such that you are close to the critical point (make sure n and C are large enough, for example $nC > 10$). Draw 1000 random matrices and compute the probability drawing a stable matrix.
- Vary n, C and σ^2 in turn, making them cross the critical point. Draw a graph where the probability of stability is on the y axis, the x axis measures $\sqrt{nC\sigma^2}$. The graph should look like the one reported below:

4.3 Accounting for interaction types

In ecological communities, the effect of species i on j and that of j on i are typically not independent (as assumed above): in the case of competition between species, we expect them both to be negative; for consumption, if one is positive, the other is negative, and so forth. A more refined model of a random matrix would therefore sample interactions in pairs from a bivariate distribution. The elliptic law can deal with this case:

Elliptic law: Take a non-symmetric, $n \times n$ random matrix in which the pairs of coefficients (X_{ij}, X_{ji}) are sampled independently from a bivariate distribution defined by a vector of means $m = (0,0)^T$ and a covariance matrix $\Sigma = \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix}$. Then, as $n \to \infty$, the e.s.d. of $X/\sqrt{n}$ converges to the elliptic law:

$$\mu(\lambda) = \begin{cases} \frac{1}{\pi(1-\rho^2)} & \text{if } \frac{(\text{Re}(\lambda))^2}{(1+\rho)^2} + \frac{(\text{Im}(\lambda))^2}{(1-\rho)^2} \leq 1 \\ 0 & \text{otherwise} \end{cases}$$

Note that when $\rho = 0$, the elliptic law reduces to the circular law. Using the elliptic law, @allesina2012stability were able to extend May's criterion to ecological networks with different mixtures of interaction types.

Build a matrix M by sampling the entries in pairs: (M_{ij}, M_{ji}) are zero with probability $(1 - C)$, and with probability C sampled independently from a bivariate distribution with mean $\nu = (0,0)^T$, and covariance matrix $\Sigma = \sigma^2 \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix}$. Then $\mathbb{E}[M_{ij}] = 0$, $\mathbb{E}[M_{ij}^2] = C\sigma^2$, and $\mathbb{E}[M_{ij}M_{ji}] = C\sigma^2\rho$. By dividing the entries M by $\sqrt{nC\sigma^2}$, we obtain a matrix following the elliptic law. As such, the stability criterion becomes:

$$\sqrt{nC\sigma^2}(1 + \rho) < d$$

To see the elliptic law in action, we can build matrices in which we sample the coefficients in pairs from a bivariate normal distribution. If we sample the entries from a distribution with a positive correlation, we obtain a horizontally-stretched ellipse (and hence, more difficult to stabilize than the circle):

Similarly, a negative correlation (e.g., as in predator-prey) would make the system easier to stabilize:

Allesina and Tang therefore concluded that, all other things being equal, ecological communities in which predator-prey interactions are prevalent (and as such $\mathbb{E}[M_{ij}M_{ji}] < 0$) are easier to stabilize than those dominated by competition/mutualism ($\mathbb{E}[M_{ij}M_{ji}] > 0$).

4.4 Symmetric matrices

Build a random symmetric matrix X by sampling the coefficients X_{ij} in the upper-triangular part (i.e., $i < j$) independently from a distribution such that $\mathbb{E}[X_{ij}] = 0$ and $\mathbb{E}[X_{ij}^2] = 1$. Set $X_{ji} = X_{ij}$, thereby building a symmetric matrix. The diagonal elements are sampled from a distribution with mean zero and finite variance. Then, as $n \to \infty$, the empirical spectral distribution of $X/\sqrt{n}$ (i.e., of the matrix in which all the coefficients have been divided by the $\sqrt{n}$) converges almost surely to the Wigner's semicirle distribution:

$$\mu(\lambda) = \begin{cases} \frac{1}{2\pi}\sqrt{4 - \lambda^2} & \text{if } \lambda \in [-2, 2] \\ 0 & \text{otherwise.} \end{cases} \tag{1}$$

Importantly, we have not defined the distribution of the X_{ij}: as long as the coefficients have mean zero, and unit variance, the result holds (universality).

4.5 Covariance matrices

Take a $p \times n$ rectangular matrix X, with $p < n$ and i.i.d. coefficients with $\mathbb{E}[X_{ij}] = 0$ and $\mathbb{E}[X_{ij}^2] = 1$. When $n \to \infty$, the ratio $p/n \to y$ (i.e., the number of rows and columns grow proportionally). Then the eigenvalue distribution of the scaled covariance matrix $S = \frac{1}{n}XX^T$ converges to the Marchenko-Pastur distribution:

$$\mu(\lambda) = \begin{cases} \frac{1}{2\pi\lambda y}\sqrt{((1 + \sqrt{y})^2 - \lambda)(\lambda - (1 - \sqrt{y})^2)} & \text{if } (1 - \sqrt{y})^2 \leq \lambda \leq (1 + \sqrt{y})^2 \\ 0 & \text{otherwise.} \end{cases} \tag{2}$$

4.6 Small-rank perturbations

The basic results listed above consider matrices whose coefficients have mean zero. Clearly, this is rarely the case in ecological systems, and therefore for applications we need to incorporate the possibility of nonzero means. While in general one cannot compute the distribution of the eigenvalues of a sum of two matrices $M = A + B$ from the eigenvalues of the two matrices, this calculation is possible whenever A has small-rank (i.e., few nonzero eigenvalues, or a finite amount in the limit of infinitely large sizes) and B is a large random matrix. In this case, the distribution of the eigenvalues of M will be composed by a bulk, defined by the spectrum of B, and (possibly) a few outlier eigenvalues, matching closely the nonzero eigenvalues of A (a correction is needed when the coefficients of B are correlated, @o2014low).

For example, let's add a matrix with three nonzero eigenvalues to a large random matrix of the type studied by May:

4.7 Structured matrices

Some special matrices with few nonzero eigenvalues are of the form:

$$M = \begin{pmatrix} \alpha_{k,k} & \beta_{k,n-k} \\ \gamma_{n-k,k} & \delta_{n-k,n-k} \end{pmatrix}$$

where for example $\alpha_{k,k}$ is a $k \times k$ matrix with α in all entries.

The eigenvalues of this matrix (or more complicated block-structured matrices with constants in every block) are easy to compute. Take:

$$M' = \begin{pmatrix} \frac{k}{n}\alpha & \frac{k}{n}\beta \\ \frac{n-k}{n}\gamma & \frac{n-k}{n}\delta \end{pmatrix}$$

and call λ' the eigenvalues of M'. Then the eigenvalues of M are $\lambda = n\lambda' \cup 0_{n-2}$.

Homework 4b

Study the spectrum of the community matrix of a competitive community in which species are divided into two groups (e.g., benthic, pelagic), and interactions are as follow:

- $M_{ii} = -5 \; \forall i$
- $M_{ij} \sim \mathcal{N}(\mu_1, \sigma^2)$ when i and j belong to the same group, and $M_{ij} \sim \mathcal{N}(\mu_2, \sigma^2)$ when they belong to different groups. Use $\mu_1 = -1, \mu_2 = -1/2, \sigma^2 = 1/4$ and assume the two groups have equal sizes.

4.8 Further readings

On random matrices and stability:

- @allesina2015stability is an opinionated review on applications of random matrices in ecology.
- The lecture follows @theorecolrandom quite closely. The online version of the book is available through the library.

5 Predicting coexistence in ecological communities

Lesson plan:

1. We consider the problem of co-culturing several species taken from a pool in all possible combinations.
2. This type of experiments has been conducted to test hypotheses on the relationship between diversity and ecosystem functioning.

3. The number of combinations grows quickly with the size of the pool, making experiments difficult.
4. The difficulty is compounded by the fact that not all combinations are expected to lead to coexistence.
5. We parameterize a simple statistical model, and draw a connection with GLV dynamics.
6. We test whether our model is able to predict the outcomes of experiments out-of-fit.

5.1 Background: Diversity and Ecosystem Functioning

Key paper: @tilman2001diversity

This paper present the results of the biodiversity-ecosystem functioning experiments carried out at Cedar Creek, Minnesota, by Dave Tilman and collaborators. These multi-year experiments are among the largest ever carried out in ecology, and have been hugely influential. The same type of experiments have been performed with different organisms, in the lab, and in mesocosms.

Ecologists have performed large experiments in which different assemblages of species are co-cultured. These experiments have been conducted with plants (for example, Biodiversity Ecosystem Functioning experiments e.g., @hector1999plant @tilman2001diversity, @cadotte2013experimental) and in the laboratory using protozoan, algae or bacteria. Two commonly-encountered problems in this type of experiments have to to with the scaling of the number of experiments with the number of species, and with the probability of coexistence.

Scale: How many communities can we form from a pool of n species? We can culture a single species in isolation (n possibilities), two species in pair ($n(n-1)/2$ possibilities), and so on. The total is therefore:

$$\sum_{j=1}^{n} \binom{n}{j} = 2^n - 1$$

And this is only considering the presence/absence of each species! Moreover, we might want to vary the initial conditions (e.g., starting two species at low/high abundance, equal abundance, high/low abundance), etc. Clearly, this makes trying all possible combinations unfeasible when n is large enough. For example, for 10 species we can form 1023 assemblages, while with 20 more than a million!

Coexistence: even if we could try all possible experiments, many assemblages would collapse to smaller communities because of extinctions. For example, pairs could become monocultures, triplets become pairs or monocultures, etc. As such, even if we were to try all possible combinations, we would end up observing a smaller set of "final communities".

To guide experimentation, we need a way to be able to predict the (probable) outcome of experiments without having to run them all. Here we attempt to do so by examining a handful

of experimental results, and using these data to parametrize a statistical model. The model provides a way to navigate the enormous space of possibilities, thereby suggesting "good" experiments that yield a large probability of coexistence.

5.2 Example data

For our explorations, we are going to use recent data from Ishizawa and colleagues, which you can find here:

H. Ishizawa, Y. Tashiro, D. Inoue, M. Ike, H. Futamata. *Learning beyond-pairwise interactions enables the bottom–up prediction of microbial community structure* PNAS 121 (7) e2312396121 (2024).

The Authors inoculated duckweed (*Lemna minor*) with synthetic bacterial communities formed by all possible combinations of seven strains. To this end, they cultured the infected duckweed in flasks for 10 days. At the end of the experiment, they plated the communities on agar plates containing antibiotics that would allow the growth only of a particular strain. In this way, they were able to measure the final density of each of the seven strains in each of the $2^7 - 1 = 127$ possible communities, and conducted each experiment in replicate. The full data set reports the outcome of 692 separate experiments!

More modestly, here we are going to focus on a smaller pool of three strains taken from the seven available. We therefore have 7 possible communities, ranging from a single strain growing in isolation to the three strains growing together. For example, a few of the measurements are:

DW067	DW102	DW145	community	replicate
		0.8	1	1
		0.812	1	2
	0.529		2	1
	0.356		2	2
	0.703	0.909	3	1
	0.395	0.661	3	2
0.386	0.602	0.563	4	1
0.379	0.774	0.293	4	2

We can therefore associate each measurement with a) the strain being measured, i; b) the community in which i was grown, k; and c) the (biological) replicate experiment, r.

5.3 A simple statistical framework

The simplest model we can write for this type of data is one in which the outcomes of replicate experiments are independent samples from a distribution:

$$\tilde{x}_i^{(k,r)} \sim Q_i \left(x_i^{(k)}, \gamma_i^{(k)} \right)$$

where $\tilde{x}_i^{(k,r)}$ is the *observed* density of population i for the r replicate in which population i is grown in community k. The value $x_i^{(k)}$ represents the *true* mean of the distribution (i.e., the average if we were to conduct many replicates—hence it does not depend on r), and $\gamma_i^{(k)}$ is a parameter (or several parameters) controlling the shape of the distribution Q_i.

Implicitly, we are making a very strong assumption: if we observe the community k, it is always found around $x^{(k)}$—i.e., we cannot have *true multistability*, in which, depending on initial conditions, we end up with different outcomes in which all populations are present (we can still have that, depending on initial condition, the system ends up at different points/attractors, as long as they have different compositions).

This model requires estimating all the $x_i^{(k)}$ and $\gamma_i^{(k)}$, and is therefore not very useful. To make the model applicable to real data, we make another strong assumption:

$$x_i^{(k)} = \alpha_i - \sum_{j \in k;\, j \neq i} \beta_{ij} x_j^{(k)}$$

The interpretation is simple: if population i is grown by itself, it will reach the carrying capacity α_i; if other species are co-cultured along with i, they will change the final density of i according to their density $(x_j^{(k)})$ and an interaction term β_{ij}.

We perform some manipulations:

$$\sum_{j \in k;\, j \neq i} \beta_{ij} x_j^{(k)} + x_i^{(k)} = \alpha_i$$

$$\sum_{j \in k;\, j \neq i} \frac{\beta_{ij}}{\alpha_i} x_j^{(k)} + \frac{1}{\alpha_i} x_i^{(k)} = 1$$

$$\sum_{j \in k;\, j \neq i} B_{ij} x_j^{(k)} + B_{ii} x_i^{(k)} = 1$$

$$\sum_{j \in k} B_{ij} x_j^{(k)} = 1$$

$$\left(B^{(k,k)} x^{(k)} \right)_i = 1$$

$$B^{(k,k)} x^{(k)} = 1_{\|k\|}$$

But this is exactly the structure of the equilibria for a GLV model, which we have introduced before.

5.4 The structure of equilibria in GLV

Take the model:

$$\dot{x} = D(x \circ r)(1_n - Bx)$$

with $r > 0_n$; compute all the feasible equilibria and collect them into a matrix E. For example:

$$B = \begin{pmatrix} 2 & -3 & 3 \\ -2 & 7 & -3 \\ 2 & -2 & 2 \end{pmatrix} \qquad E = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{7} & 0 \\ 0 & 0 & \frac{1}{2} \\ \frac{5}{4} & \frac{1}{2} & 0 \\ 0 & \frac{5}{8} & \frac{9}{8} \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

where each row contains a feasible equilibrium (if it exists) corresponding to a given composition.

Key paper: @tilman1997plant

We are not the first people to consider "in-silico" biodiversity experiments. Tilman and collaborators were doing the same more than twenty years ago! For a more sophisticated model, see @loreau1998biodiversity.

Consider the matrix:

$$1_m 1_n^T - E B^T = \begin{pmatrix} 0 & 2 & 0 \\ \frac{10}{7} & 0 & \frac{9}{7} \\ -\frac{1}{2} & \frac{5}{2} & 0 \\ 0 & 0 & -\frac{1}{2} \\ -\frac{1}{2} & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

For each row, we find 0 for the corresponding population at equilibrium (in red), and the remaining values express $(1_n - Bx^{(k)})_j$, which has the same sign as the invasion growth rates for population j, when $r > 0_n$. Hence, a saturated equilibrium will correspond to a row with non positive values (e.g., the community $k = \{1, 2\}$ is saturated, because population 3 cannot invade when rare).

Next, call E_i the sub matrix obtained selecting only rows for which $x_i^{(k)} > 0$. For example, for population 1:

$$E_1 = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

We have that:

$$E_i B_i = 1_l$$

Where B_i is the ith row of B, and l is the number of experiments in which i is present:

$$E_1 B_1 = \begin{pmatrix} \frac{1}{2} & 0 & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix} \begin{pmatrix} 2 \\ -3 \\ 3 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Practically, this means that all the ith component of all the equilibria $x^{(k)}$ of a GLV model belong to a *hyperplane* in $\mathbb{R}^n$ defined by $\sum_j B_{ij} x_j^{(k)} = 1$.

This also means that we can recover the values of B_i from the equilibria:

$$B_i = E_i^{-1} 1_n$$

which can be computed when E_i is square.

Moore-Penrose pseudoinverses

For a $n \times n$ matrix A, the inverse is determined (when it exists), as a matrix A^{-1} such that $AA^{-1} = A^{-1}A = I$. A square matrix is invertible if its determinant (remember, the product of its eigenvalues) is nonzero. A matrix with determinant zero is called *singular* or *degenerate* and has no inverse. Singular matrices are rare, in the sense that a random matrix is "almost never" singular (this can be stated in a precise mathematical way). An invertible matrix has *full rank* (i.e., the rows [columns] are all linearly independent).

Can we find a matrix that "works like" an inverse when A is singular (or not square)? Turns out, we can find a matrix A^+ that satisfies these four criteria:

$$AA^+A = A$$
$$A^+AA^+ = A^+$$

$$AA^+ = (AA^+)^T$$

$$A^+A = (A^+A)^T$$

Suppose that A has linearly independent columns (i.e., it is of full column rank), then $A^T A$ has full rank and is therefore invertible. In this case, we can compute the *left* pseudo-inverse as

$$A^+ = (A^T A)^{-1} A^T$$

This is called the left inverse because $A^+A = (A^T A)^{-1} A^T A = I$. When A has independent rows, one can compute the *right inverse*. Note that a generalized inverse A^+ exists even if A is not of full column nor full row rank, but in this case it is not unique.

Application: least squares

The pseudo-inverse can be used to find the *least-squares solution* of a system of linear equations. For example, in linear regression, we want to model a set of n observations, y, as a linear function of measured predictors X (for example, a matrix with n rows [one for each observation], and k columns [the number of measured predictors for each observation, typically with $k \ll n$]) and some parameters b. The linear system

$$Xb = y$$

has no solution (for example, because X is rectangular). If X were to be invertible, finding the parameters would be easy:

$$\widehat{b} = X^{-1}y$$

we can attempt the same approach using the pseudo-inverse:

$$\widehat{b} = X^+ y$$

in particular, it can be proven that the solution $\widehat{b}$ minimizes the sum of squared deviations (SSQ): call $\widehat{y} = X\widehat{b}$, then the solution $\widehat{b}$ is the parameter choice minimizing $SSQ = \sum_i (y_i - \widehat{y}_i)^2$.

If E_i is rectangular, we can use the Moore-Penrose pseudo-inverse. For example:

$$E_2 = \begin{pmatrix} 0 & \frac{1}{7} & 0 \\ \frac{5}{4} & \frac{1}{2} & 0 \\ 0 & \frac{5}{8} & \frac{9}{8} \\ \frac{1}{2} & \frac{1}{2} & \frac{1}{2} \end{pmatrix}$$

$$(E_2^T E_2)^{-1} E_2^T 1_4 = \begin{pmatrix} -2 \\ 7 \\ -3 \end{pmatrix} = B_2$$

This also provides a naive method to get a draft of B when only the equilibrium values are available.

The method is going to return a unique solution provided that each matrix E_i has rank n. In practice, this means that, for each population i, a) E_i has at least n rows (i.e., population i is present at n distinct equilibria), and b) each species j is present in at least one equilibrium with i, i.e., each pair of populations is found in at least one equilibrium.

This might be a tall order when n is large, and we will see how to circumvent this issue below.

5.5 Predicting coexistence

Suppose that we have estimated the matrix B, and that we want to determine whether a certain combination of populations can or cannot coexist. This is useful when we have sufficient data to estimate B, but we have not carried out all the possible experiments—we want to predict the outcome of further experiments in advance.

Then, according to our statistical model, we can take $B^{(k,k)}$ for the desired community k, and take the row sums of the inverse:

$$x^{(k)} = \left(B^{(k,k)} \right)^{-1} 1_{\|k\|}$$

If all the components of $x^{(k)}$ are positive, we assume that this will be the outcome of the experiment. If *any* of the components is negative, on the other hand, we conclude that the populations cannot coexist.

Homework 6a

As seen above, for GLV, the matrix $B = D(r)^{-1} A$ encodes all the equilibria (feasible or unfeasible) for the model. Knowing B is therefore all we need to determine the existence of a feasible equilibrium for any community we can form from the pool.

1. Does the matrix B informs us on invasibility? Take a sub-community k resting at its feasible equilibrium point. Can one determine whether a species $i \notin k$ can invade when rare by inspecting the matrix B?

2. When can the matrix B be used to determine the stability of the feasible equilibrium for a subset k?

5.6 Scoring matrices B

The paragraph above suggests a good way to score matrices in practice (i.e., when the empirically-observed matrix $\tilde{E}$ is a noisy estimate of a true matrix E):

- Propose a matrix B
- Compute $x^{(k)}$ for each observed $\tilde{x}^{(k,r)}$
- Try to minimize the *distance* between the predicted and observed

Naturally, this algorithm relies on a notion of distance. The simplest choice would be to choose B such that the sum of squared deviations is minimized:

$$SSQ(B) = \sum_r \sum_k \sum_i \left(\tilde{x}_i^{(k,r)} - x_i^{(k)} \right)^2$$

When the values of $\tilde{x}_i^{(k)}$ vary considerably (as expected when populations interact), minimizing the SSQ will favor matrices that match closely the rows of $\tilde{E}$ containing large values, such that a 10% error on a small value of $\tilde{x}_i^{(k)}$ "counts" less than a 1% error for a large value.

If we want to put all rows on the same footing, we can implement a Weighted Least Squares scheme, in which

$$WLS(B) = \sum_r \sum_k \sum_i \left(\frac{\tilde{x}_i^{(k,r)} - x_i^{(k)}}{\sigma_i^{(k)}} \right)^2$$

where deviations are weighted by the respective standard deviation (for simplicity, we can take $\sigma_i^{(k)} = \sqrt{\mathbb{E}\left((\tilde{x}_i^{(k,r)})^2 \right) - \left(\mathbb{E}\left(\tilde{x}_i^{(k,r)} \right) \right)^2}$.

Finally, we can have a likelihood-based approach in which we are trying to maximize the sum of log-likelihoods:

$$\mathcal{L}(B) = \sum_r \sum_k \sum_i \log P\left(\tilde{x}_i^{(k,r)} | x_i^{(k)}, \gamma_i^{(k)} \right)$$

where $P(x|\mu, \gamma)$ is the density of a probability distribution function whose shape is controlled by parameters μ and γ.

Key paper: @loreau2001partitioning

Ecologists are fond of the idea of partitioning effects into (hopefully) orthogonal components that have a clear biological interpretation. In this influential paper, Loreau and Hector show how the effect of diversity on functioning can be partitioned into "selection" (dominance of species with particular traits) vs. "complementarity" (increased resource use due

to niche partitioning). As for any interesting idea, critics abound—and some are over the top (@pillai2019not), leading to rebuttals of rebuttals (@loreau2019not, @wagg2019not, @pillai2019not3, @pillai2019not2)...

5.7 Example

We are going to use the code accompanying the paper

- Skwara, A., Lemos-Costa, P., Miller, Z.R. and Allesina, S., 2023. Modelling ecological communities when composition is manipulated experimentally. Methods in Ecology and Evolution, 14(2), pp.696-707.

which you can find here

https://github.com/StefanoAllesina/skwara_et_al_2022/

we have slightly massaged the code for this tutorial.

Sum of squares

First, we are going to use all the data to find a matrix B that best encodes the density of the populations. To this end, we try to minimize the SSQ

$$SSQ(B) = \sum_r \sum_k \sum_i \left(\tilde{x}_i^{(k,r)} - x_i^{(k)} \right)^2$$

This can be accomplished by calling:

```
full_SSQ <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "full", # estimate B allowing each coefficient to take the best value
  goalf = "SSQ", # minimize Sum of Squared Deviations
  pars = NULL, # start from Identity matrix
  skipEM = TRUE # go directly to numerical optimization
)
```

The values being printed are the SSQ after each round of numerical optimization (in this case, the calculation converges immediately to the solution).

```
plot_results_boxplot(full_SSQ$observed, full_SSQ$predicted)
```

The boxplots show the data (points), as well as the corresponding boxplots, with the horizontal line being the median value of $\tilde{x}_i^{(k,r)}$ across r, the triangle shows the location of the empirical mean. The circle marks the fitted mean value for the combination of strain/community, obtained computing $\left(B^{(k,k)}\right)^{-1} 1_{\|k\|}$. As you can see, we can find a matrix B that recapitulates the observed means quite well.

Let's plot the predicted vs. observed values:

```
plot_pred_obs(full_SSQ)
```

Where the points mark the predicted vs observed means, and the crosses the full data. The dashed line is the 1:1 line.

Weighted leas squares

We can repeat the calculation, but this time trying to minimize

$$WLS(B) = \sum_r \sum_k \sum_i \left(\frac{\tilde{x}_i^{(k,r)} - x_i^{(k)}}{\sigma_i^{(k)}} \right)^2$$

by calling:

```
full_WLS <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "full", # estimate B allowing each coefficient to take the best value
  goalf = "WLS",
  pars = NULL, # start from Identity matrix
  skipEM = TRUE, # go directly to numerical optimization
)
```

Plotting:

```
plot_results_boxplot(full_WLS$observed, full_WLS$predicted)
plot_pred_obs(full_WLS)
```

Notice that the points have moved slightly—this is because we are penalizing deviations differently depending on the measured variance (and thus points with a higher variance can depart more strongly from the 1:1 line).

Maximum likelihood

Now we take a different approach, and take the observations to be independent samples from a log-normal distribution:

$$\tilde{x}_i^{(k,r)} \sim LN(x_i^{(k)}, \sigma_i)$$

i.e., we take each variable to have a mean determined by the corresponding $x_i^{(k)}$, and a variance parameter that depends only on strain identity.

```
full_LN <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "full", # estimate B allowing each coefficient to take the best value
  goalf = "LikLN",
  pars = NULL, # start from Identity matrix
  skipEM = TRUE # go directly to numerical optimization
)
```

```
plot_results_boxplot(full_LN$observed, full_LN$predicted)
plot_pred_obs(full_LN)
```

Also in this case, we obtain a good fit.

Leave-one-out cross validation

The ultimate test for this type of model is to be able to predict experimental results before running the experiment.

In our case, we can try to leave out one of the 7 communities:

```
dt <- read_csv("dat/Ishizawa_3_strains.csv")
```

```
LOO_LN <- run_model_LOO(datafile = "dat/Ishizawa_3_strains.csv",
                        model = "full", goalf = "LikLN",
                        pars = NULL, skipEM = TRUE, plot_results = TRUE,
                        LOO_row_num =  40 # exclude all experiments with this community
)
```

The model is quite successful at recovering the observed means for the community we left out.

```
plot_results_boxplot(LOO_LN$observed, LOO_LN$predicted, LOO_LN$infit)
```

Simplified models

We have seen in the lecture that this approach estimates all n^2 coefficients of the matrix B. For the approach to be successful, we need to have observed enough combinations of populations growing together (each population must be present in at least n experiments with distinct compositions, each pair of populations must appear in at least one final community). When the number of populations in the pool is large, and experiments are few, this approach is unfeasible. We can therefore try to simplify the model to reduce the number of parameters.

The idea brought forward by Skwara *et al.* is to approximate the matrix B as the sum of a diagonal matrix and a low-rank matrix. For example, a version of the model with only $n + 1$ parameters reads:

$$B = D(s) + \alpha 1_n 1_n^T$$

i.e., a model in which each diagonal element $B_{ii} = s_i + \alpha$ has its own parameter (and thus can take arbitrary values), while the off-diagonals are all the same (i.e., each population has the same "mean-field" effect on all others).

A more general model using $3n - 1$ parameters reads:

$$B = D(s) + uv^T$$

in which the diagonal coefficients $B_{ii} = s_i + u_i v_i$ can take arbitrary values, while the off-diagonal elements $B_{ij} = u_i v_j$ are constrained; the effect of species j on i depends on two values: v_i that measures how strongly species i respond to the presence of other species, and v_j that measures the magnitude of the typical effect of species j. Either u or v can be taken as unitary (i.e., $\sum_i v_i^2 = 1$) without loss of generality, thereby bringing the total number of parameters to $3n - 1$. When the number of populations is small, this approach does not lead to big gains (e.g., for $n = 3$ we have 8 parameters instead of 9), but the reduction in parameters is substantial when n becomes larger (e.g., for the whole data set, $n = 7$, and thus we would use 20 parameters instead of 49).

Another advantage of this approach is that we can write the inverse in linear time, thereby removing the only big computational hurdle of the approach:

$$B^{-1}1_n = (D(s) + uv^T)^{-1}1_n$$
$$= \left(D(s)^{-1} - \frac{1}{1 + v^T D(s)^{-1}u}D(s)^{-1}uv^T D(s)^{-1}\right)1_n$$
$$= D(s)^{-1}\left(1_n - \frac{v^T D(s)^{-1}1_n}{1 + v^T D(s)^{-1}u}u\right)$$

These models can be derived from the consumer-resource framework that you have seen in class.

We can test different versions of the simplified model. A model with only the diagonal and an extra parameter performs very poorly:

```
diag_a11 <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "diag_a11t",
  goalf = "LikLN",
  pars = NULL, # start from Identity matrix
  skipEM = TRUE
)
```

```
plot_pred_obs(diag_a11)
```

A model with symmetric interactions, $B = D(s) + vv^T$ does slightly better:

```
diag_vvt <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "diag_vvt",
  goalf = "LikLN",
  pars = NULL, # start from Identity matrix
  skipEM = TRUE
)
```

```
plot_pred_obs(diag_vvt)
```

And, finally, the model with 8 parameters, $B = D(s) + vw^T$:

A model with symmetric interactions, $B = D(s) + vv^T$ does slightly better:

```
diag_vwt <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
```

```
  model = "diag_vwt",
  goalf = "LikLN",
  pars = NULL, # start from Identity matrix
  skipEM = TRUE
)


plot_pred_obs(diag_vwt)
```

5.8 Further readings

The backbone of the statistical model can be found in numerous articles, which converged to the same solution starting from different angles:

- Xiao, Y., Angulo, M. T., Friedman, J., Waldor, M. K., Weiss, S. T., & Liu, Y.-Y. (2017). Mapping the ecological networks of microbial communities. Nature Communications, 8(1), 1–12.

- Fort, H. (2018). On predicting species yields in multispecies communities: Quantifying the accuracy of the linear Lotka-Volterra generalized model. Ecological Modelling, 387, 154–162.

- Maynard, D. S., Miller, Z. R., & Allesina, S. (2020). Predicting coexistence in experimental ecological communities. Nature Ecology & Evolution, 4(1), 91–100.

- Ansari, A. F., Reddy, Y., Raut, J., & Dixit, N. M. (2021). An efficient and scalable top-down method for predicting structures of microbial communities. Nature Computational Science, 1(9), 619–628.

- Davis, J.D., Olivença, D.V., Brown, S.P. and Voit, E.O., (2022). Methods of quantifying interactions among populations using Lotka-Volterra models. Frontiers in Systems Biology, 2, p.1021897.

For the tutorial, we are going to closely follow:

- Skwara, A., Lemos-Costa, P., Miller, Z.R. and Allesina, S., 2023. Modelling ecological communities when composition is manipulated experimentally. Methods in Ecology and Evolution, 14(2), pp.696-707.

The same method can be extended to provide a simple test for phylogenetic effects on competition/growth:

- Lemos-Costa, P., Miller, Z.R. and Allesina, S., 2024. Phylogeny structures species' interactions in experimental ecological communities. Ecology Letters, 27(8), p.e14490.