

Theoretical Community Ecology

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2025-05-06

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Preliminaries

Approach and target audience

The material was prepared for the graduate class *Theoretical Community Ecology* (ECEV 43900) taught at the University of Chicago — AY 2020/2021, and revised several times (last iteration, Spring 2025). Following the material requires some familiarity with calculus (multivariable integration, derivatives, chain rule) and linear algebra (vector spaces, eigenvalues, eigenvectors). Also, a good working knowledge of R (writing functions, working with the packages `deSolve` and `tidyverse`) is needed to follow the code (all figures are generated at runtime, and therefore the source code for these lectures contains all the code/data needed to replicate the figures).

The approach taken throughout the course is to alternate between code/simulations and mathematical derivations. While several theorems are (informally) stated, proofs are included only when elementary and/or informative of the underlying biological processes.

The class builds upon material typically presented in classes on population, community and theoretical ecology. The main goal of the class is to build a toolbox for solving problems in theoretical community ecology, bridging the gap between what is typically presented in introductory classes and the primary literature.

Topics

The choice of themes is very opinionated, and heavily biased toward my own research interests. Because of this, the focus is squarely on continuous time, time-invariant models—in most cases without any consideration of space and stochasticity. Similarly, the material mostly deals with the case of multispecies dynamics, though low-dimensional models are considered when their analysis helps with the understanding of the multispecies case. Finally, much of the material is centered around the Generalized Lotka-Volterra model and its cousins (e.g., the replicator equation). This is because a) the Generalized Lotka-Volterra model for multiple interacting species is in a way the simplest nonlinear model

for population dynamics; and b) it is a “canonical” model—in the sense that many other models can be re-cast in GLV form.

Notation

Unless specified or for obvious exceptions, Greek letters stand for scalars (i.e., real or complex numbers), lower case Roman letters for vectors, and capital Roman letters for matrices (as such a_i or A_{ij} are scalars). We typically work in \mathbb{R}^n (the n -dimensional Euclidean space), \mathbb{R}_+^n (i.e., the positive orthant of \mathbb{R}^n), or \mathbb{R}_{0+}^n (non-negative orthant). $D(x)$ is a diagonal matrix with x on the diagonal. The matrix A^T is the transpose of A . Whenever it is clear what I mean, I will drop the dependency on time of certain variables. I often use \dot{x} as a shorthand for $\frac{dx(t)}{dt}$.

The Generalized Lotka-Volterra model:

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

can be written in compact form as:

$$\dot{x} = D(x)(r + Ax)$$

Grading and code of conduct

Students should follow the rules and regulations set out by University policy. I am expecting all students to a) participate in all classes (please contact me if you are going to be absent); b) actively contribute to discussions and lectures; c) be punctual (both for class and when submitting the homework); d) be professional and honest (no copying/cheating/plagiarizing).

Homework (80%)

Each lecture contains exercises that should be completed as graded homework. The homework should be submitted through Canvas as one or more `pdf` files obtained by compiling `Rmd` files. The homework should contain the derivations (you can use `LaTeX` to typeset mathematics within `Rmd`, see here for commonly used commands), and code. The code must run and be correct to get a passing grade.

Review (20%)

The remaining 20% of the grade is based on a graded review. Each student should choose an interesting (important, provocative, etc.) published paper or preprint in theoretical community ecology, and produce a review (of the kind one would submit to a journal if solicited for comments). The review must contain two sections: a) Comments to the Authors, and b) Recommendation for the Editor. Good advice on writing reviews can be found [here](#).

Accommodation for students with disabilities

University of Chicago is committed to ensuring equitable access to our academic programs and services. Students with disabilities who have been approved for the use of academic accommodations by Student Disability Services (SDS) and need a reasonable accommodation(s) to participate fully in this course should follow the procedures established by SDS for using accommodations. Timely notifications are required in order to ensure that your accommodations can be implemented. Please meet with me to discuss your access needs in this course after you have completed the SDS procedures for requesting accommodations.

A note about biographies

The lecture notes are interdispersed with short biographies of scientists who greatly contributed to the problems being studied. The attentive reader will notice that most of the photographs are depicting old white men. Their age is easy to explain: I have only included biographies of deceased scientists (so that they cannot contradict me!), and most of them enjoyed a long life (with some exceptions; for example Robert MacArthur tragically died at age 45). The impossibly skewed gender ratio, and the lack of ethnic diversity has to be explained with the tremendous homogeneity of the field—which was broken only recently. It is my hope that these lectures will engage young ecologists from different backgrounds and histories with the theory of community ecology, such that whoever will teach this type of material in a couple of decades will be able to include a more interesting and diverse gallery of portraits.

Sources

Many excellent books are available on these topics. Here are the main references I've used while preparing these lectures:

- Strogatz (2018) — a clear, concise introduction to dynamical systems.
- Ellner and Guckenheimer (2011) — an introduction to dynamical models focusing on biology.
- Hofbauer and Sigmund (1998) — a great resource for models of population dynamics and evolutionary game theory.
- Hadeler et al. (2017) — a more mathematically-focused reading.

- Hirsch et al. (2012) — an extensive, clearly written and rigorous introduction to dynamical systems.
- Szederkenyi et al. (2018) — an introduction to quasi-polynomial systems and reaction networks.

Acknowledgements

These lectures grew out of a set of four lectures I have presented at the ICTP-SAIFR/IFT-UNESP “School on Community Ecology: from patterns to principles”, held on January 20-25, 2020 in São Paulo, Brazil. Thanks to the organizers (Marcus Aguiar, Jacopo Grilli, Roberto Kraenkel, Ricardo Martinez-Garcia and Paulo Inácio Prado) for the invitation and for prompting me to start working on the material.

The lecture on assembly was test-driven at the ICTP “Winter School on Quantitative Systems Biology: Quantitative Approaches in Ecosystem Ecology”, organized by Simon Levin, Matteo Marsili, Jacopo Grilli, and Antonio Celani.

I am grateful to the students in both schools for useful feedback.

The development of this material was supported by the National Science Foundation (DEB #2022742). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation.

Chapter 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:

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

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 $\ddot{y}_2 = \ddot{x}$; 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,

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

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 $\mathbb{R}^n \rightarrow \mathbb{R}^n$. 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**.

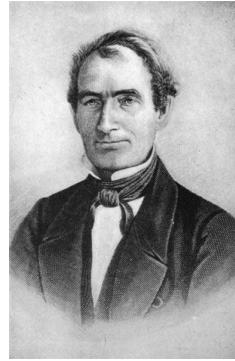
In ecological models, dynamics are invariant with respect to the non-negative orthant \mathbb{R}_{0+}^n , i.e., the vector $x(t)$ remains non-negative whenever initialized at non-negative initial conditions $x_0 \in \mathbb{R}_{0+}^n$.

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):

$$\begin{aligned}\log x(t) + C_1 &= \rho t + C_2 \\ \log x(t) &= \rho t + C_3 \\ x(t) &= e^{\rho t + C_3} \\ x(t) &= C_4 e^{\rho t}\end{aligned}$$

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:

$$\begin{aligned}
\log x(t) - \log(1 - \alpha x(t)) &= \rho t + C_1 \\
\log \frac{x(t)}{1 - \alpha x(t)} &= \rho t + C_1 \\
\frac{x(t)}{1 - \alpha x(t)} &= e^{\rho t + C_1} \\
x(t) &= \frac{e^{\rho t + C_1}}{1 + \alpha e^{\rho t + C_1}} \\
x(t) &= \frac{1}{\alpha + e^{-(\rho t + C_1)}}
\end{aligned}$$

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

$$\begin{aligned}
x_0 &= \frac{1}{\alpha + e^{-C_1}} \\
C_1 &= \log \frac{x_0}{1 - \alpha x_0}
\end{aligned}$$

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

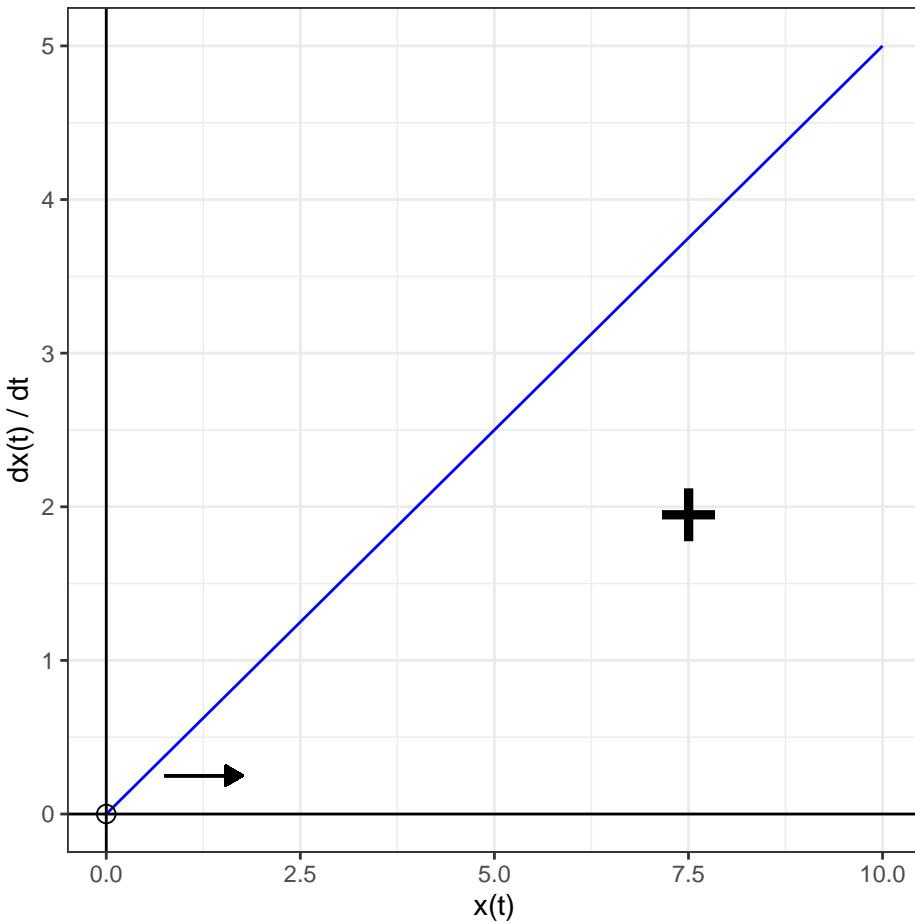
1.5. QUALITATIVE ANALYSIS OF MODELS FOR A SINGLE POPULATION15

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 $x^* = 0$. A point x^* for which $\left. \frac{dx(t)}{dt} \right|_{x^*} = 0$ is an **equilibrium** (or fixed-point) for the system, meaning

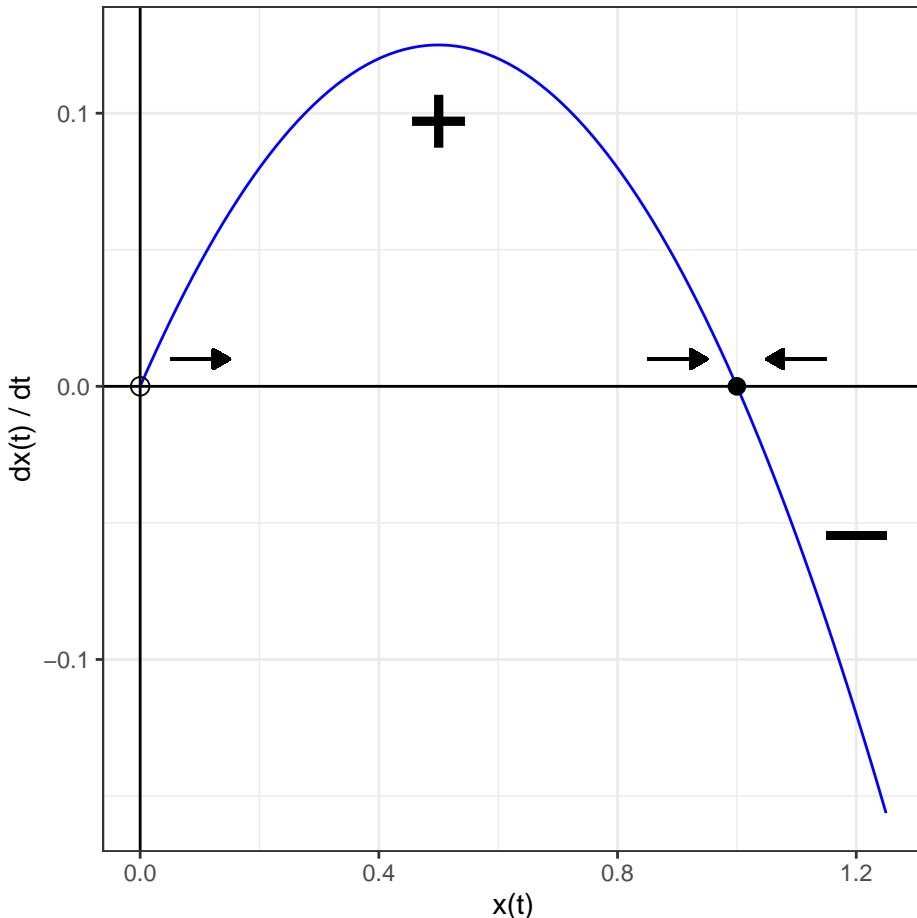
that if we initialize the system at x^* , it will remain there unless perturbed. Whenever we apply a (small) perturbation to a **stable equilibrium**, the system returns to it; when we perturb an **unstable equilibrium**, on the other hand, the system moves away from it.

Now think of a perturbation: if we were to perturb $x^* = 0$ 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 $x^* = 0$ and $x^* = 1/\alpha$. If we perturb $x^* = 0$, the system moves away from it (unstable), while if we perturb $x^* = 1/\alpha$ the system goes back to it (stable).

History: Warder Clyde Allee (1885-1955)



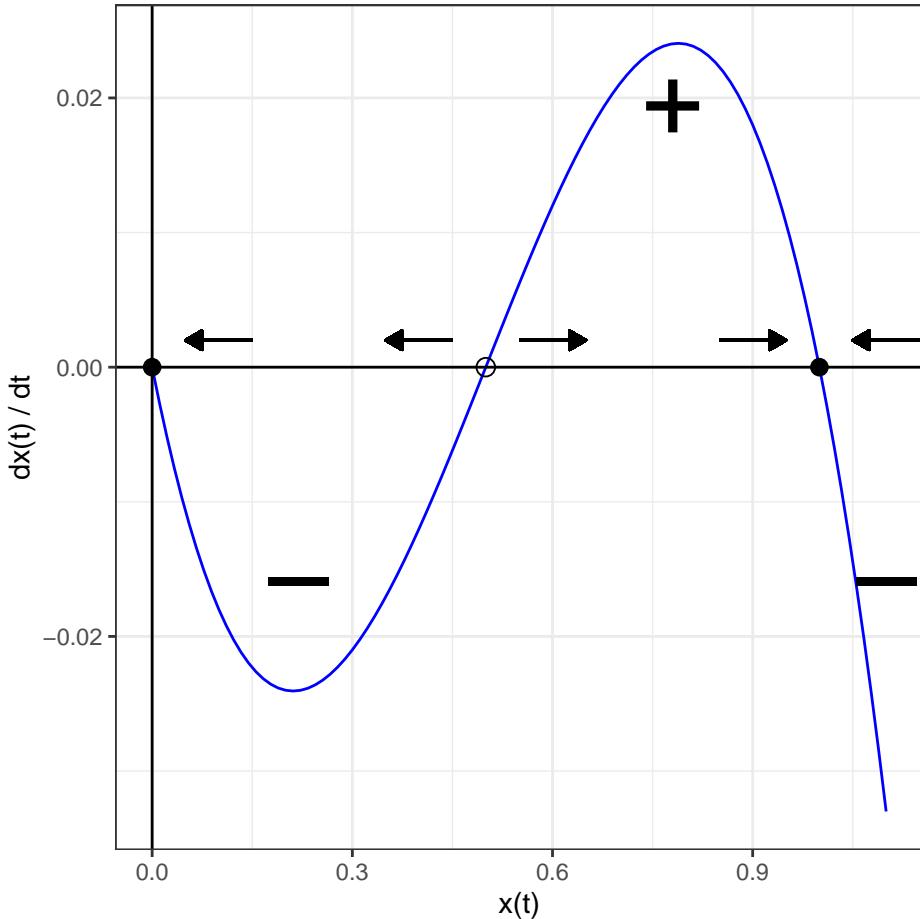
Born in Indiana, Allee received his PhD in 1912 from the University of Chicago, where he returned in 1921. He was the Dean in the College of Arts, Literature, and Science (1924-1926) and Secretary of the Department of Zoology (1927-1934). In 1935, a spinal tumor left him paralyzed from the waist down. 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 ($x^* = 0$ and $x^* = 1/\alpha$), separated by an unstable equilibrium ($x^* = \gamma$). 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 $x^* = 1/\alpha$ and perturbing the population by bringing it below γ ; then we would find that the population goes extinct, suggesting that $x^* = 1/\alpha$ is “somewhat unstable”.

1.5.1 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 ($x^* = 0$) 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 $x^* = 0$, we obtain $\rho > 0$, and as such the equilibrium is unstable. Conversely, when we evaluate the function at $x^* = 1/\alpha$, 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 $x^* = 0$, we find $-\rho \gamma$ which is always negative, and as such $x^* = 0$ is stable. At $x^* = \gamma$ we have $\rho \gamma (1 - \gamma \alpha)$ which is positive (as $\gamma \alpha < 1$) and as such is an unstable equilibrium. Finally, for $x^* = 1/\alpha$, we have $\rho(\gamma - 1/\alpha)$ which is always negative.

1.5.2 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 $\Delta x(t) = x(t) - x^*$ 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

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

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^* , and approximate the dynamics of the perturbation:

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

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

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

which is the equation for the exponential growth we have seen above. If $\left. \frac{df(x)}{dx} \right|_{x^*} < 0$ 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^* —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.

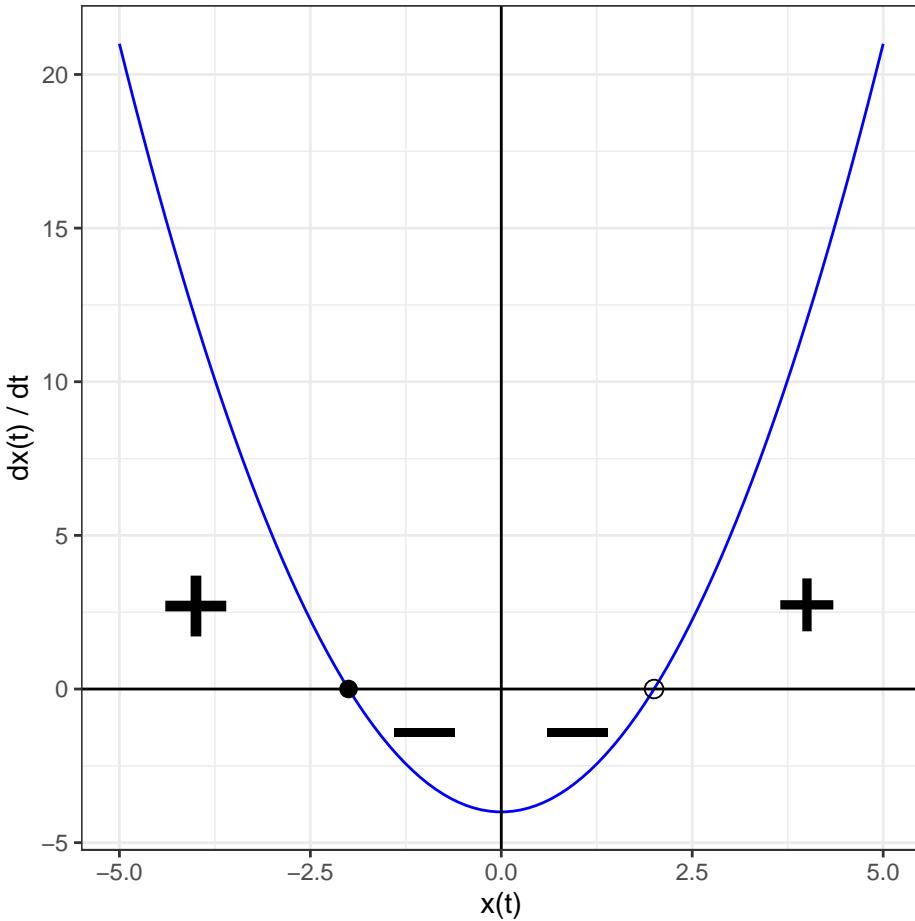
In low-dimensional system, there are a variety of different behaviors, each of which has its own name (e.g., saddle-node, pitchfork, transcritical, Hopf, period-doubling, ..., bifurcation). The **codimension** of a bifurcation is the number of parameters we need to change to alter the behavior of the 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 Strogatz (2018) and Seydel (2009).

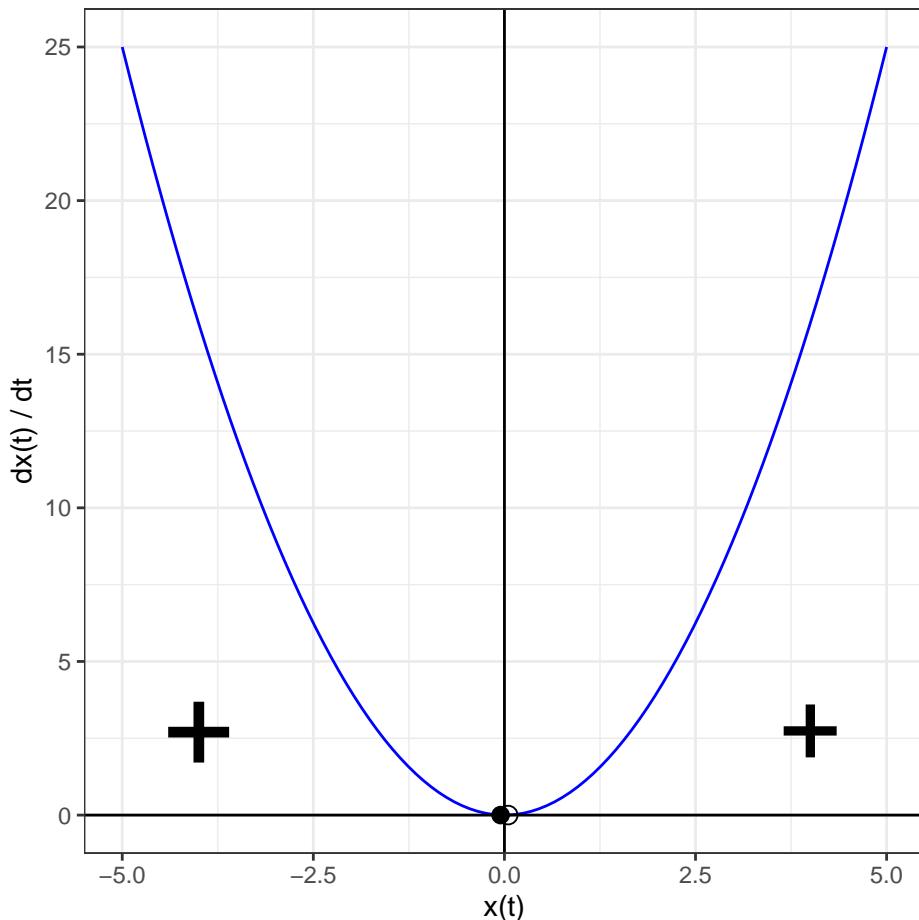
Consider the model:

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

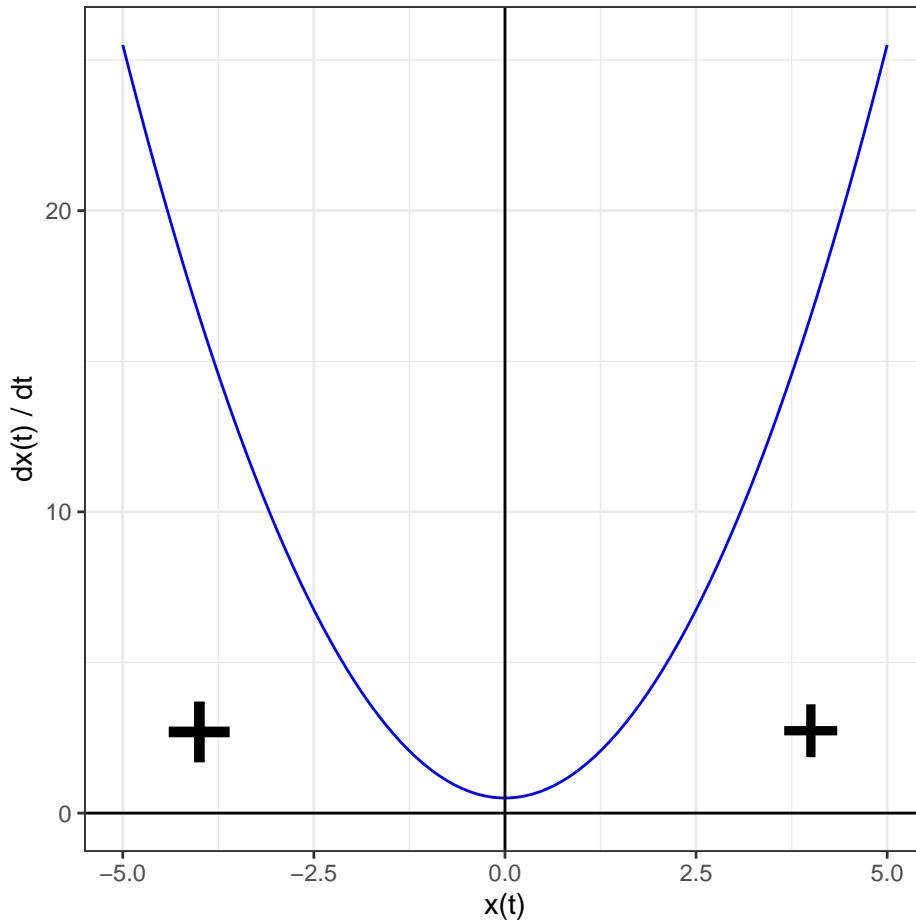
The equilibria of the system, when they exist, are given by $x^* = \pm\sqrt{-\rho}$. It is clear that, when $\rho < 0$ we will have two equilibria, when $\rho = 0$ a single equilibrium $x^* = 0$, and that when $\rho > 0$ no (real) equilibrium exists. As such, the shape of the diagrams we have sketched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



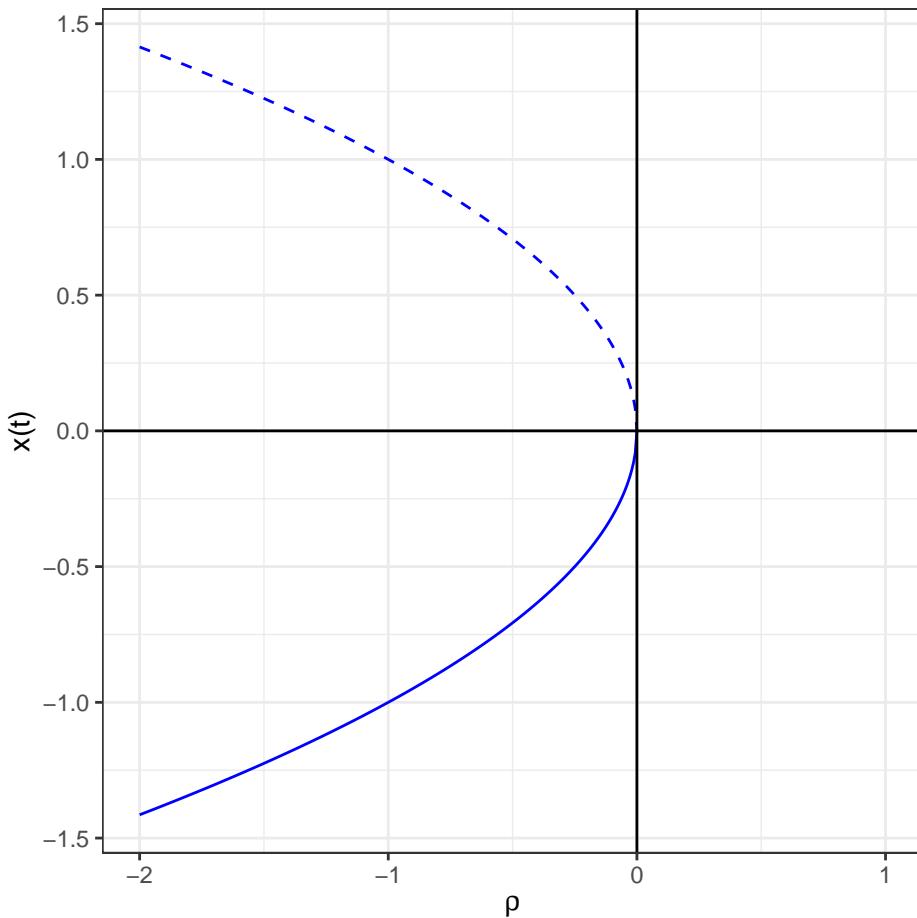
The equilibrium on the left is stable, while the one on the right is unstable. The graph is qualitatively the same for any $\rho < 0$. When $\rho = 0$, however, the two equilibria “collide”, and merge into the single “half-stable” equilibrium:



The equilibrium $x^* = 0$ 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 $\rho \rightarrow \rho_c = 0$ 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: Ludwig et al. (1978)

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: Scheffer et al. (2009)

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: Dai et al. (2012)

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-term behaviors: for $t \rightarrow \infty$ we can only have $x(t) \rightarrow \pm\infty$ or $x(t) \rightarrow x^*$. 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: May (1976)

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^*) by considering functions that change monotonically through the dynamics.

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

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:

$$V(x(t)) = (x(t) - x^*)^2$$

with $x^* = 1/\alpha$. The function is positive for any $x(t) \neq x^*$. 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 $x(t) \neq x^*$:

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

and as such x^* 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 $y = \frac{x}{x^*}$, with x and x^* positive. Then,

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

Now multiply by x^* , obtaining:

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

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

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

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

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

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

Chapter 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.

2.1.1 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:

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

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)

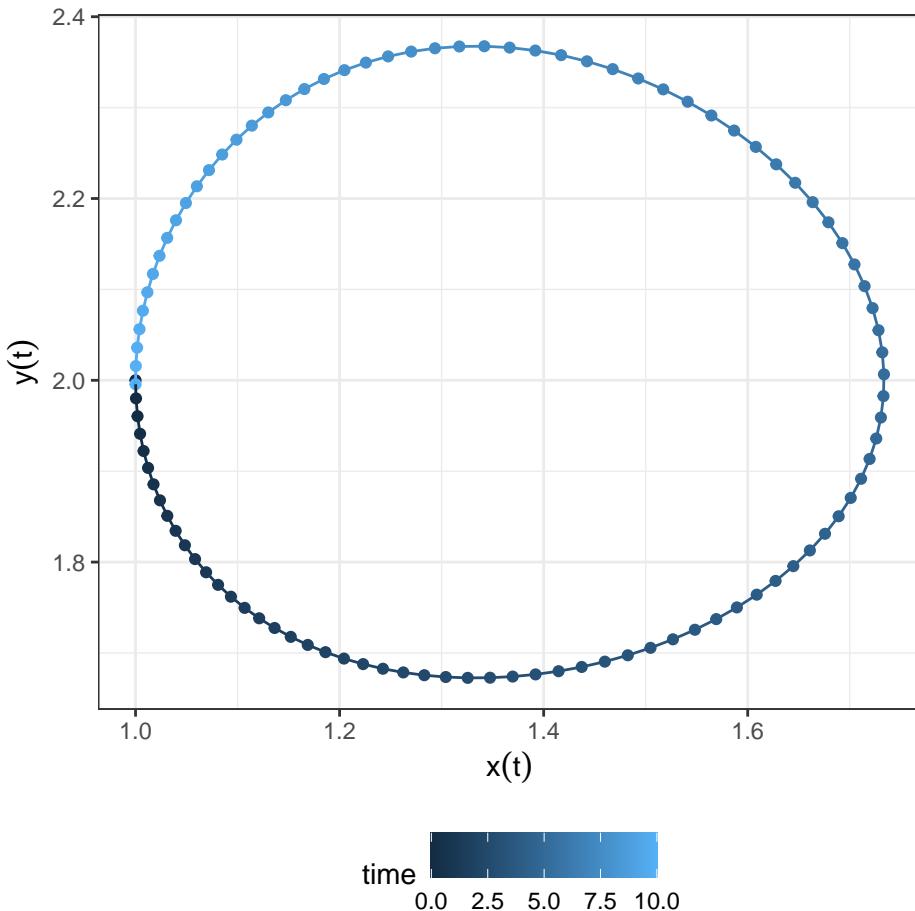


Alfred Lotka was born to French-speaking American parents in Lemberg (then part of the Hapsburg empire, now Lviv, Ukraine). He studied in France, Germany and England, receiving a BSc in 1901 and a DSc in 1912 from Birmingham university. He moved to the US in 1902, and worked at the US Patent office, 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 (Lotka 1926).

Starting in 1910 (reprinted as Lotka (2002)) he investigated coupled differential equations relating to chemical as well as ecological dynamics. In Lotka (1920) 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.

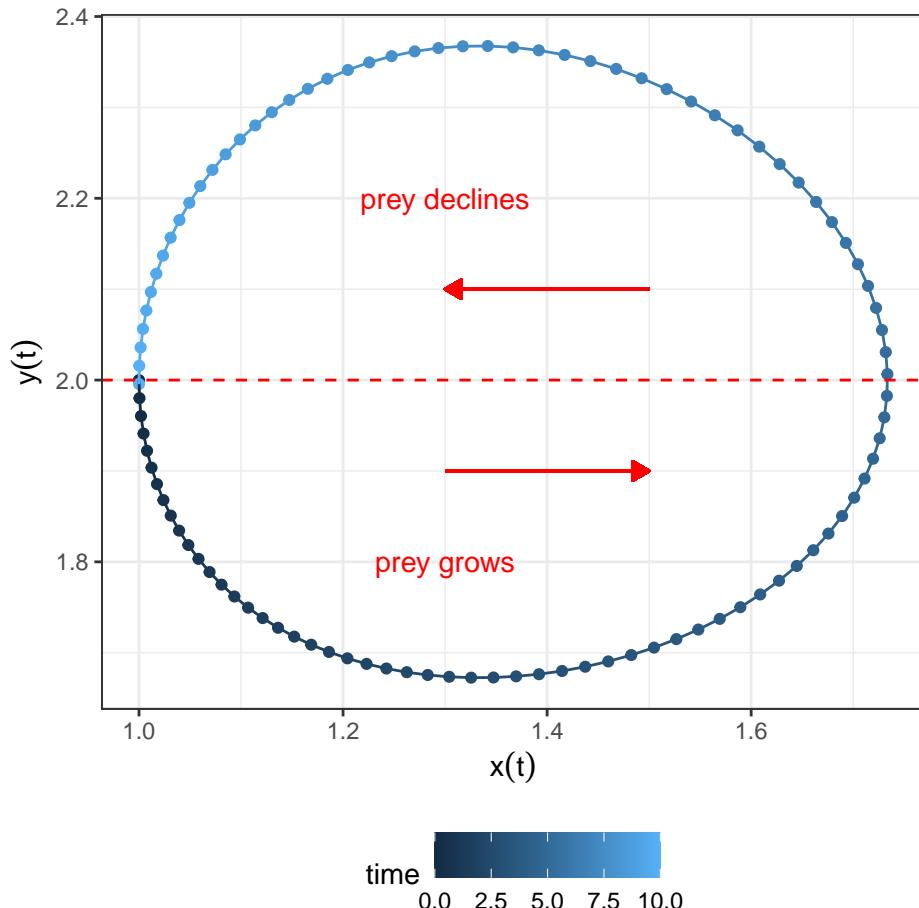
Let's look at a possible trajectory for the system, to gain an intuition of what can happen:



You can see that the population densities, when drawn in the “phase plane” cycle counterclockwise. 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.

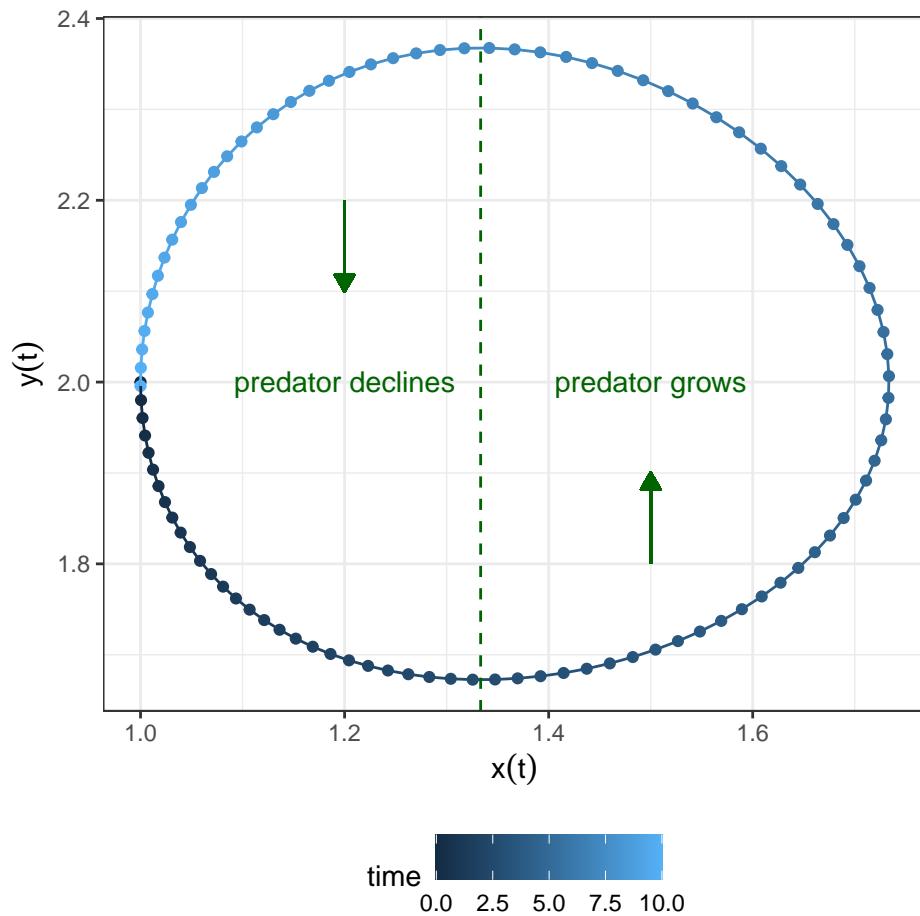
Graphically:



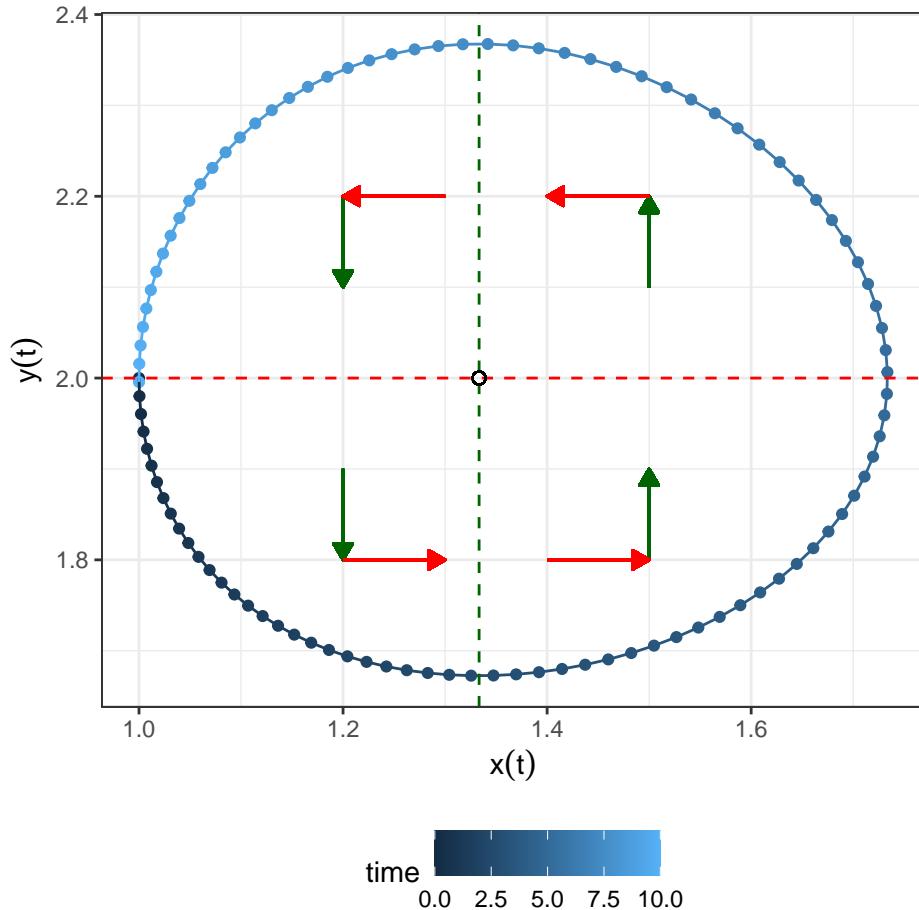
Similarly, the equation for the predator is zero either when $y(t) = 0$ or when $-\delta + \beta x(t) = 0$, yielding $x(t) = \delta/\beta$. Whenever the density of the prey $x(t) < \delta/\beta$, predators will decline; conversely, whenever $x(t) > x(t) = \delta/\beta$, predators will grow.

Graphically:

2.1. QUALITATIVE ANALYSIS OF MODELS FOR TWO POPULATIONS 33



Now let's put the two graphs together:



Clearly, a possible equilibrium of the system is $(x^*, y^*)^T = (0, 0)^T$ (often called the “trivial” equilibrium). You can see that there is another equilibrium where the two isoclines meet $(x^*, y^*)^T = (\delta/\beta, \rho/\alpha)^T$, 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^* 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^* . 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^* as a vector of densities such that:

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

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

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

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:

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

Example

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

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

The system has up to three equilibria: $(x^*, y^*) = (0, 0)$, $(x^*, y^*) = (1, 0)$, 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:

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

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:

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

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

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

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^* , we obtain the so-called “community matrix” M :

$$M = J|_{x^*}$$

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:

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

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 characteristic polynomial:

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

Where does this equation come from? We write:

$$\begin{aligned} Av &= \lambda v \\ \lambda v - Av &= 0 \\ (\lambda I - A)v &= 0 \end{aligned}$$

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:

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

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:

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

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: May (1973)

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 Dambacher et al. (2003).

We can now analyze systems of linear ODEs.

Solution of linear systems of ODEs

Matrix exponential

In analogy with the power series

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

we define the matrix exponential

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

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 $x^* = 0$. 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,

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

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

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

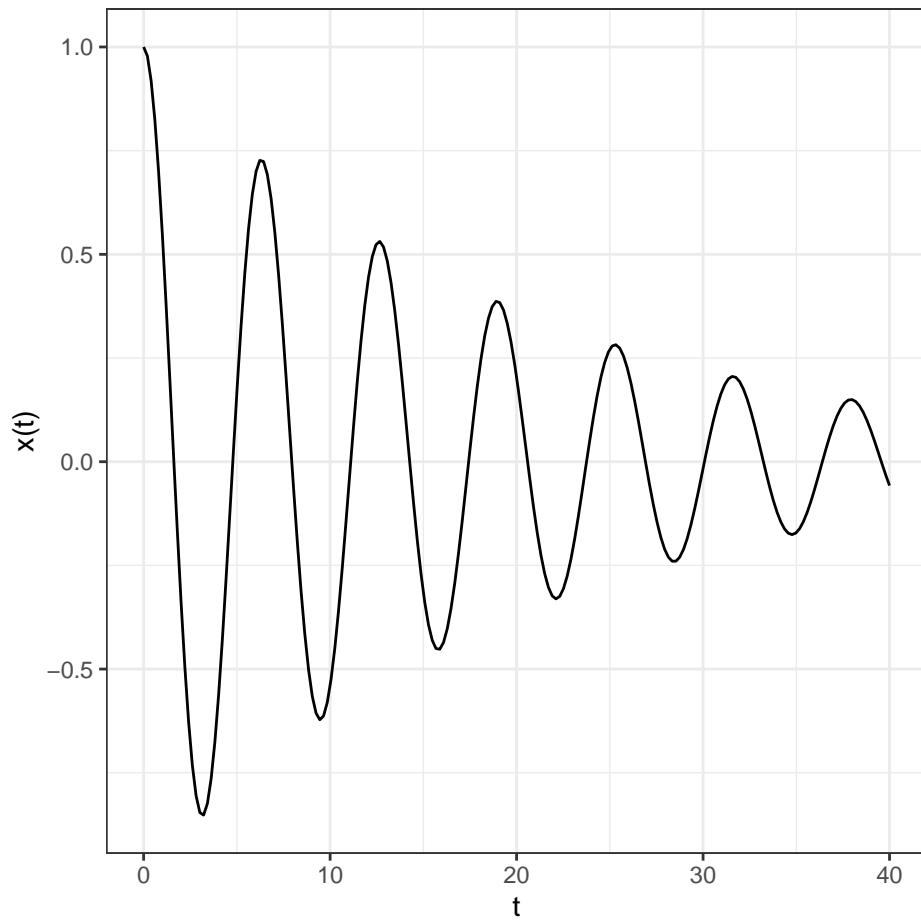
Now we want to study the dynamics of the system. To keep the complexity to a minimum, we define $y(t) = V^{-1}x(t)$, meaning that we are choosing the most appropriate coordinates to study our trajectories. Our equation becomes:

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

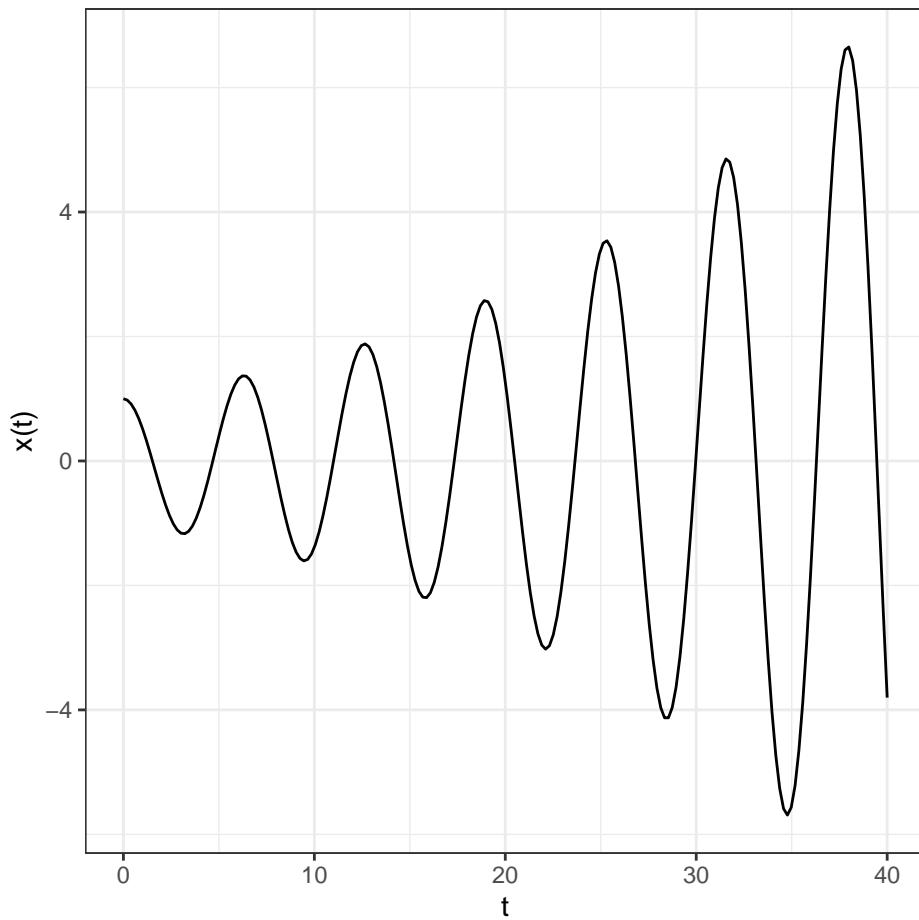
And therefore $y_j(t) = e^{(\lambda_j)t}y_j(0)$. Clearly, if all λ_j are real and negative, the trajectories will die out, and the origin $y^* = 0$ is stable. Similarly, if any eigenvalue is real and positive, then the perturbation will amplify in at least one direction. Next, we consider λ_j to be complex.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

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

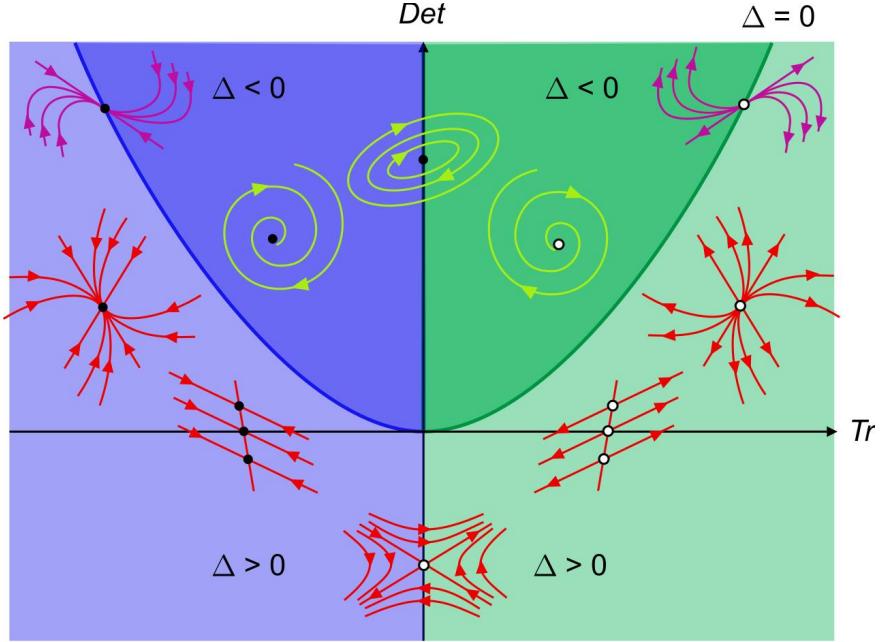
As such, the solution will oscillate, with damped oscillations whenever $\alpha < 0$ and increasing oscillations when $\alpha > 0$. For example, a case of damped oscillations:



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 :



$$\begin{aligned}\frac{dx}{dt} &= A_{11}x + A_{12}y \\ \frac{dy}{dt} &= A_{21}x + A_{22}y\end{aligned}$$

$$\begin{aligned}Tr A &= A_{11} + A_{22} \\ Det A &= A_{11}A_{22} - A_{21}A_{12} \\ \Delta &= Tr^2 - 4Det\end{aligned}$$

Now we can solve the system of ODEs:

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

obtaining:

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

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^* : 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^* :

$$\operatorname{Re}(\lambda_1) \begin{cases} < 0 \rightarrow x^* \text{ is stable} \\ > 0 \rightarrow x^* \text{ is unstable} \end{cases}$$

Key paper: Neubert and Caswell (1997)

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

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

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 $(x^*, y^*)^T = (0, 0)^T$ is:

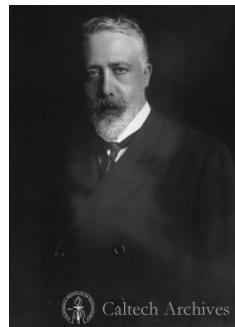
$$M_0 = J|_{(0,0)^T} = \begin{pmatrix} \rho & 0 \\ 0 & -\delta \end{pmatrix}$$

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

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

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 (Volterra 1926a), 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 (Volterra 1926b).

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 greater attention from scholars, and should give rise to important applications.*”

2.3.1 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 $x^* = \delta/\beta$ and $y^* = \rho/\alpha$, we obtain:

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

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:

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

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

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

2.3.2 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 logically it is easy to show that the equilibrium is now stable. For example, consider the system

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

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

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

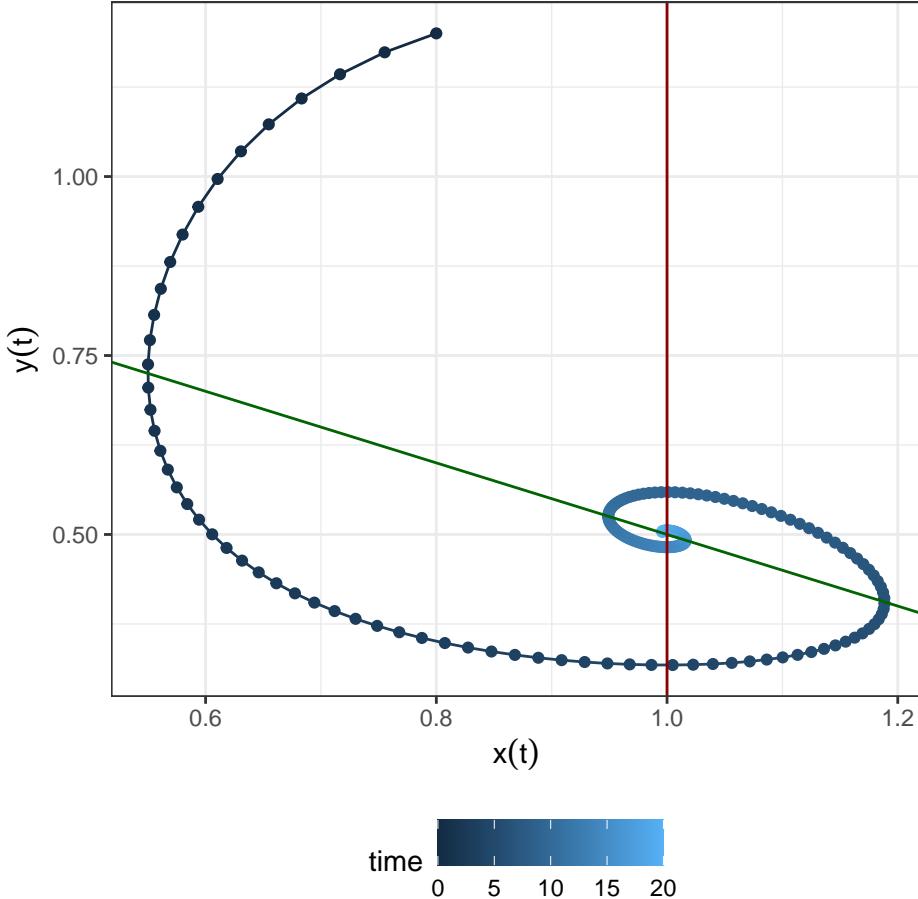
The trace is $-1/2$ and the determinant $1/2$, as such the equilibrium is stable. The eigenvalues are given by:

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

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:



2.3.2.1 Global stability

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

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

Derive with respect to time to obtain:

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

As such, the equilibrium $(x^*, y^*)^T = (1, 1/2)^T$ 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.

Chapter 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 $1, \dots, n$ 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:

$$\begin{aligned} \dot{x}_i &= x_i \left(r_i + \sum_j A_{ij} x_j \right) \\ &= r_i x_i \left(1 + \frac{1}{r_i} \sum_j A_{ij} x_j \right) \\ &= r_i x_i \left(1 + \sum_j B_{ij} x_j \right) \end{aligned}$$

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 $x^* = \rho/\alpha$. The equilibrium is globally stable (as shown using either a quadratic Lyapunov function, or the $V = x - x^* - x^* \log(x/x^*)$). As we've seen before, this is a separable ODE, with solution:

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

3.2.1 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 (Levins 1969):

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

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 $-\rho/\alpha = (\gamma - \epsilon)/\gamma = 1 - \epsilon/\gamma$.

3.2.2 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:

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

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

3.3.1 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^* in which all populations are present exists, it must be the solution of

$$\begin{aligned} 1_n + Bx^* &= 0_n \\ Bx^* &= -1_n \\ x^* &= -B^{-1}1_n \end{aligned}$$

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

For example, consider:

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

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

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

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 feasible).

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

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

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

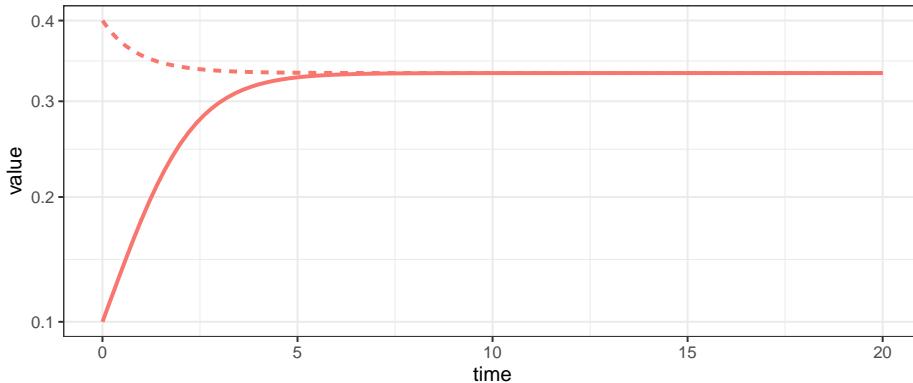
Similarly,

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

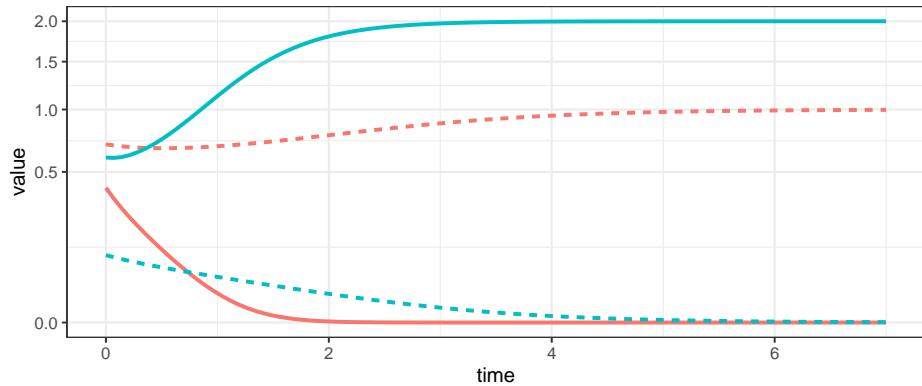
The subsystem in which only populations 2 and 3 are present does not yield a feasible equilibrium.

3.3.2 Types of dynamics

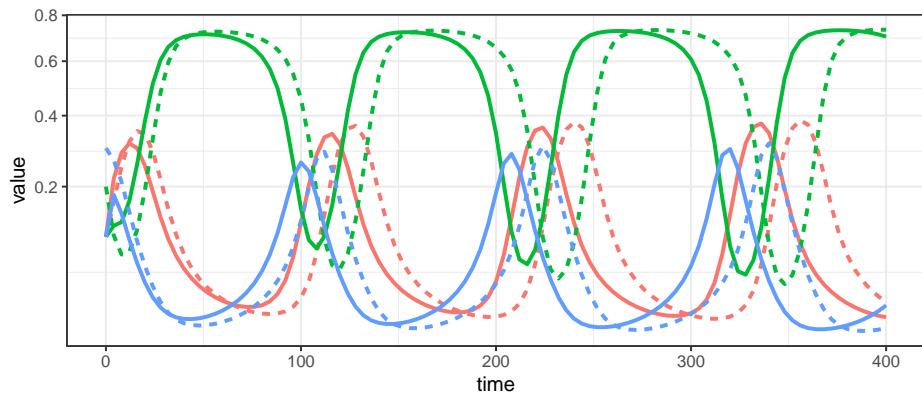
For a single population, the GLV model can yield only two outcomes: unbounded growth, or convergence to an equilibrium; if the equilibrium is $x^* = 0$, we say that the population is extinct at the equilibrium.



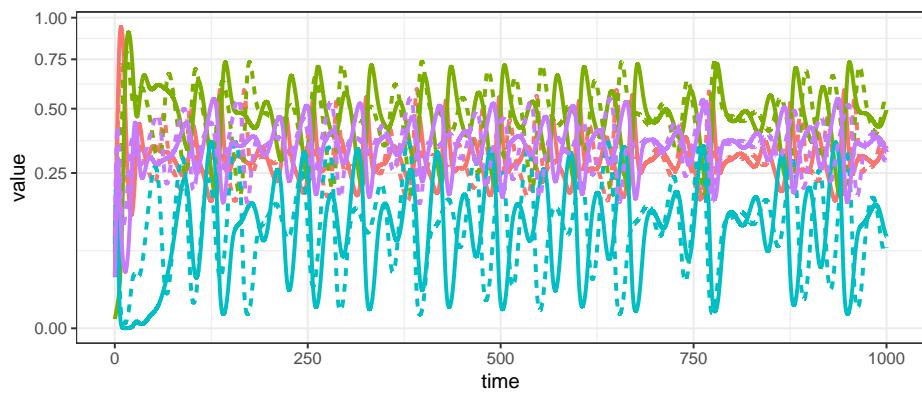
When we have two populations, we can also observe neutral cycles (as in the classic LV predator-prey system), and bistability (i.e., one population survives, while the other goes extinct; the identity of the population going extinct depends on the initial conditions).



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).



3.3.3 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^* . 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:

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

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^* .

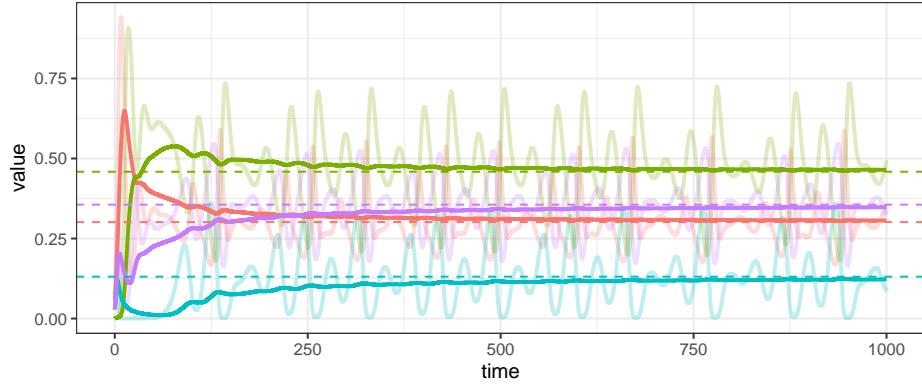


Figure 3.1: Semi-transparent lines: trajectories; dashed lines: equilibrium values; solid line: (cumulative) average of trajectory.

3.3.4 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 $x^* > 0_n$ such that $Ax^* = -r$. 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 $P(t) \rightarrow \infty$ requires some $x_i^{y_i}(t) \rightarrow \infty$, which happens when either $x_i(t) \rightarrow \infty$ and $y_i > 0$ (i.e., a population grows without bound), or $x_i(t) \rightarrow 0$ 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.

3.3.5 Local stability of the coexistence equilibrium

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

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

and therefore

$$M_{ii} = J_{ii}|_{x^*} = A_{ii} x_i^*$$

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

$$M_{ij} = J_{ij}|_{x^*} = A_{ij}x_i^*$$

Putting them together, we obtain:

$$M = J|_{x^*} = D(x^*)A$$

and thus the equilibrium is l.a.s. if and only if all of the eigenvalues of $D(x^*)A$ 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

$$\begin{aligned} &D(x^*)^{-\frac{1}{2}} D(x^*) A D(x^*)^{\frac{1}{2}} \\ &D(x^*)^{\frac{1}{2}} A D(x^*)^{\frac{1}{2}} \end{aligned}$$

The matrices $D(x^*)A$ and $D(x^*)^{\frac{1}{2}}AD(x^*)^{\frac{1}{2}}$ are *similar*, and thus have the same eigenvalues; the matrices A and $D(x^*)^{\frac{1}{2}}AD(x^*)^{\frac{1}{2}}$ 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 $D(x^*)A$ 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 $x^* = (1, 1, 1/2)^T$ (obtained for $r = (-1, -2, -17/2)$); we obtain:

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

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 $M = D(x^*)A$, but if A is *D-stable* then M is stable.

3.3.6 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 $x^* > 0_n$ 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

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

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

Differentiating with respect to time, we find:

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

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.

3.3.7 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:

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

We consider a minor modification of Goh's function:

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

Differentiating with respect to time, we obtain:

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

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

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

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

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

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 $\mathfrak{s} + \mathfrak{C}y^*$ 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^* . 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, MacArthur and Wilson (2001)), the investigation of limiting similarity (with R. Levins, MacArthur and Levins (1967)), the contributions to the complexity-stability debate (MacArthur (1955), see next lecture). The consumer-resource model he proposed in 1969 now bears his name (published also in MacArthur (1970) 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 Case and Casten (1979) for a slightly more general model):

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

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:

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

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 Case and Casten (1979)). 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:

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

3.4.1 Existence of an equilibrium

For simplicity, we concentrate on the study of the feasibility and stability of the coexistence equilibrium. If an equilibrium $z^* \neq 0$ exists, it is the solution of $Az^* = -s$, 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 Levin (1970).

Key paper: Levin (1970)

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.*

3.4.2 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

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

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,

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

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 $x^T Ax < 0$ 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 :

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

Sum the two equations:

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

If we have that $x^T Ax < 0$ 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.

3.4.3 Separation of time-scales

In the original article, MacArthur (1970) 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:

$$\begin{aligned} r - D(b)y - Px &= 0 \\ y &= D(b)^{-1}(r - Px) \end{aligned}$$

Substituting in the equations for the consumers, we obtain:

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

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).

3.4.4 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:

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

It is of particular interest the case in which $s_i = 1$ for all i and $V(x^*)$ 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 :

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

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 (Marsland III et al. (2019)).

Homework 3b

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

- Find random parameters satisfying 1) $B_{ij} = B_{ji} > 0 \forall i, j$; 2) B is stable; 3) $s_i > 0 \forall i$; 4) $B^{-1}s = x^* > 0$. 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 $V(x^*)$ 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:

- Hofbauer and Sigmund (1998) is a wonderful introduction to dynamical systems in ecology and population genetics, with a nice introduction to evolutionary game theory.
- Hadeler et al. (2017) contains a more mathematically-oriented treatment of the material covered in the first part of this lecture.
- Baigent (2016) is a mathematical introduction to Lotka-Volterra dynamics.

Chapter 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: MacArthur (1955)

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: May (1972)

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: McCann (2000)

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^* 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, Anderson and May (1992)), evolutionary game theory (Nowak and May (1992)), the estimation of the number of species on Earth (May (1988)), bibliometrics (May (1997)), and even banking (by modeling systemic risks, Haldane and May (2011)). 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.

May (1972) attempted to answer this question by considering a **random community matrix**. In a GLV system, the diagonal elements $M_{ii} = A_{ii}x_i^*$ are influenced by self-regulation (i.e., as in a carrying capacity), while the off-diagonal elements $M_{ij} = A_{ij}x_i^*$ model the effect of species j on the equilibrium of species i . May considered the following algorithm to build a random community matrix.

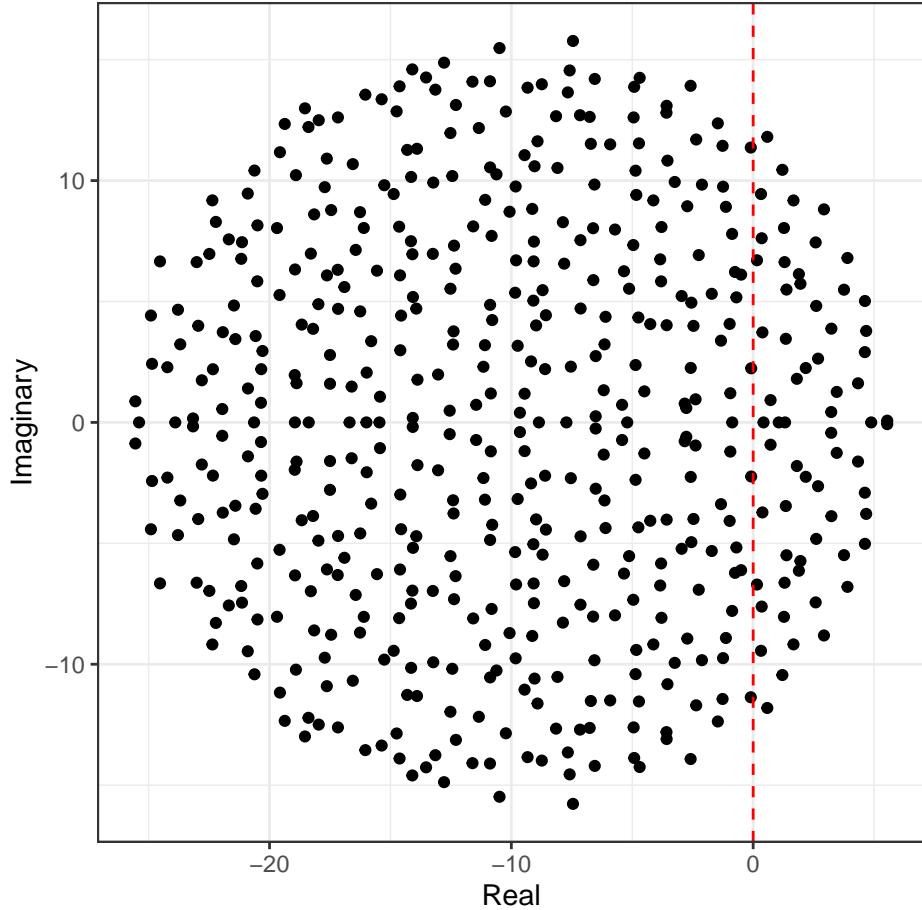
Take a large community, resting at an unspecified, feasible equilibrium; we build the community matrix by setting:

- $M_{ij} = 0$ 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 $\frac{1}{n} \sum_i \lambda_i = \frac{1}{n} \text{Tr}(A) = \frac{1}{n} \sum_i A_{ii}$. 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 $n \rightarrow \infty$, the e.s.d. of X/\sqrt{n} converges to the circular law:

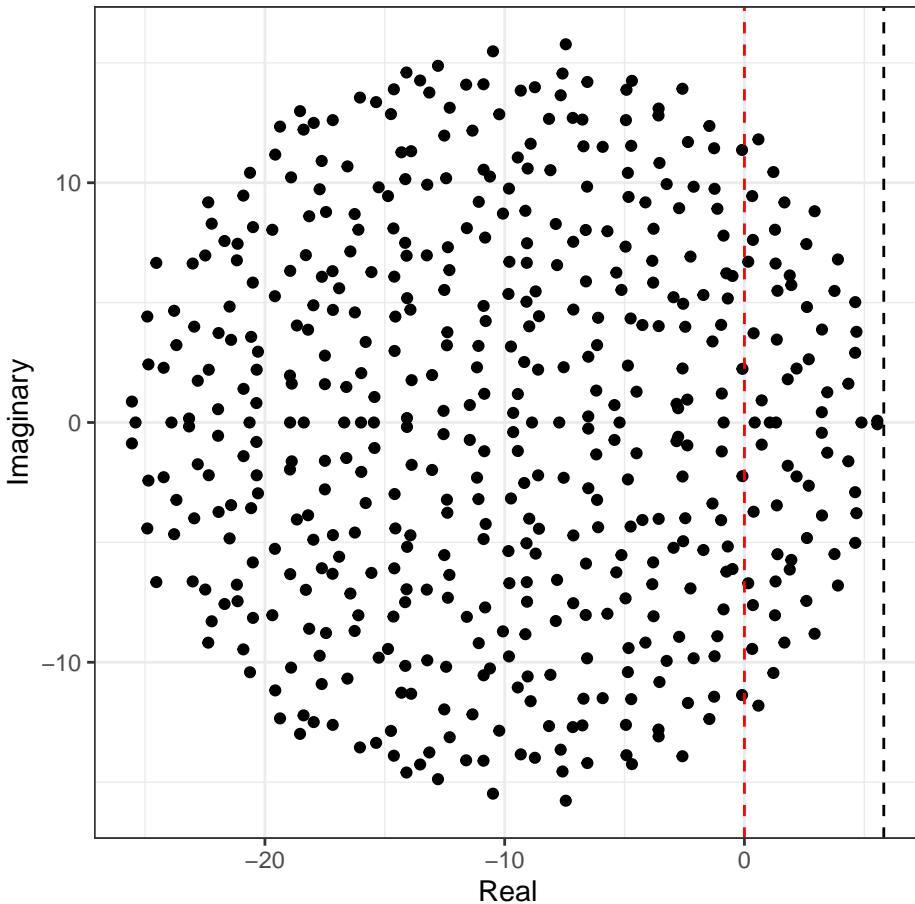
$$\mu(\lambda) = \begin{cases} \frac{1}{\pi} & \text{if } (\operatorname{Re}(\lambda))^2 + (\operatorname{Im}(\lambda))^2 \leq 1 \\ 0 & \text{otherwise.} \end{cases}$$

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:

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

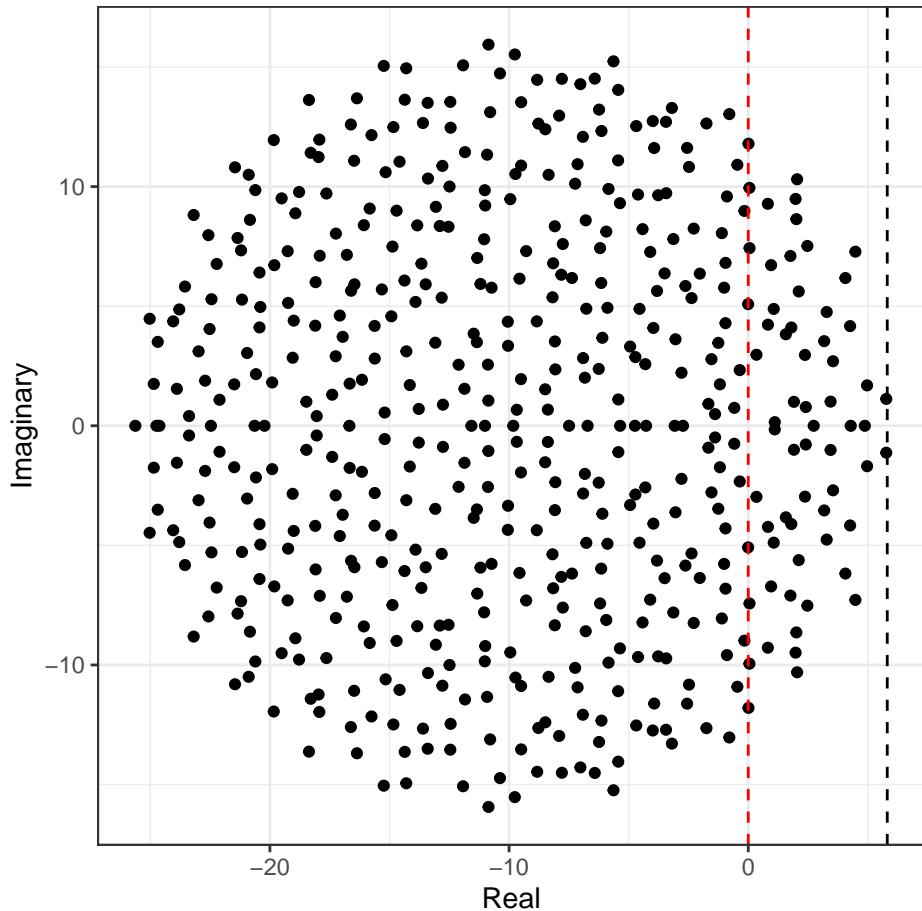
We can try this on our matrix (black dashed line):



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.

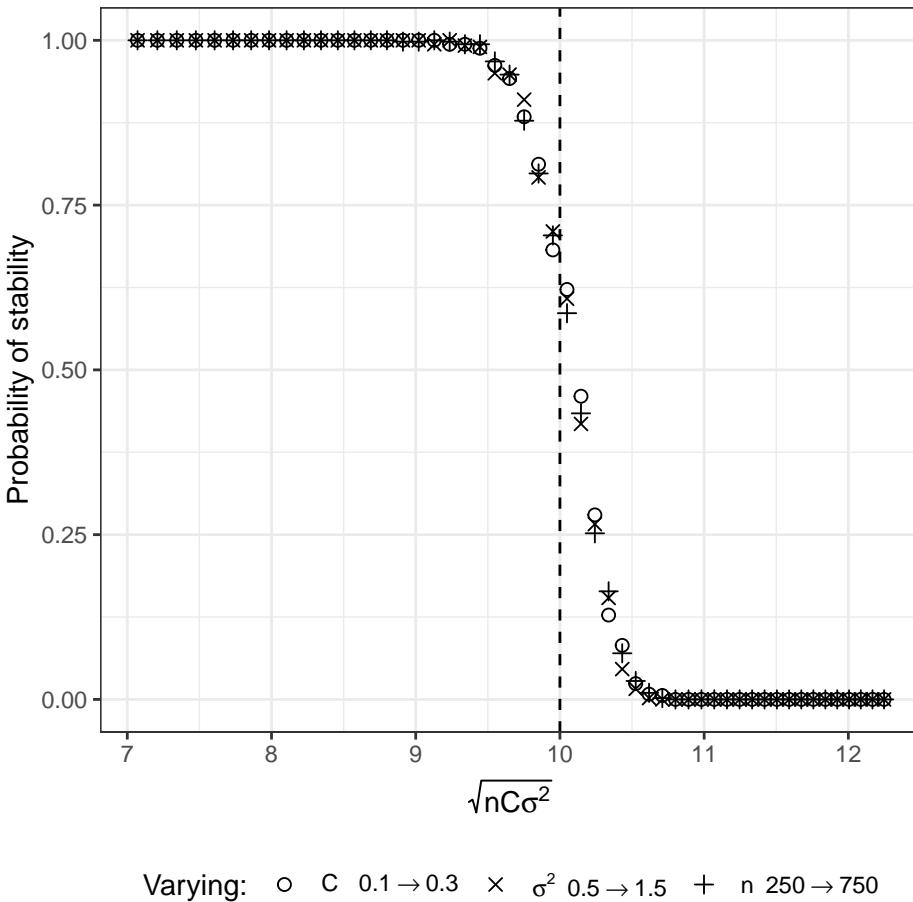
Homework 4a

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 $n \rightarrow \infty$ (to be accurate, $nC \rightarrow \infty$), 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 $n \rightarrow \infty$, the e.s.d. of X/\sqrt{n} converges to the elliptic law:

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

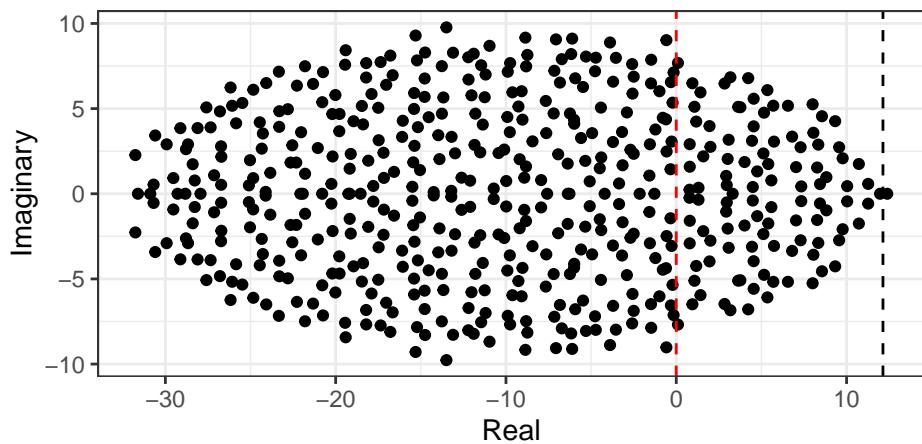
Note that when $\rho = 0$, the elliptic law reduces to the circular law. Using the elliptic law, Allesina and Tang (2012) were able to extend May's criterion to ecological networks with different mixtures of interaction types.

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 $\Sigma = \sigma^2 \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix}$.

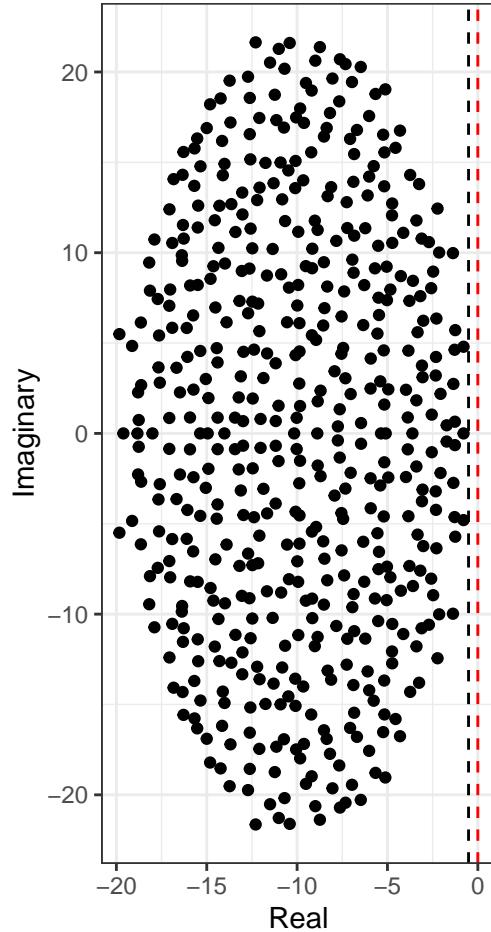
Then $\mathbb{E}[M_{ij}] = 0$, $\mathbb{E}[M_{ij}^2] = C\sigma^2$, and $\mathbb{E}[M_{ij}M_{ji}] = C\sigma^2\rho$. By dividing the entries M by $\sqrt{nC\sigma^2}$, we obtain a matrix following the elliptic law. As such, the stability criterion becomes:

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

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 ($\mathbb{E}[M_{ij}M_{ji}] > 0$).

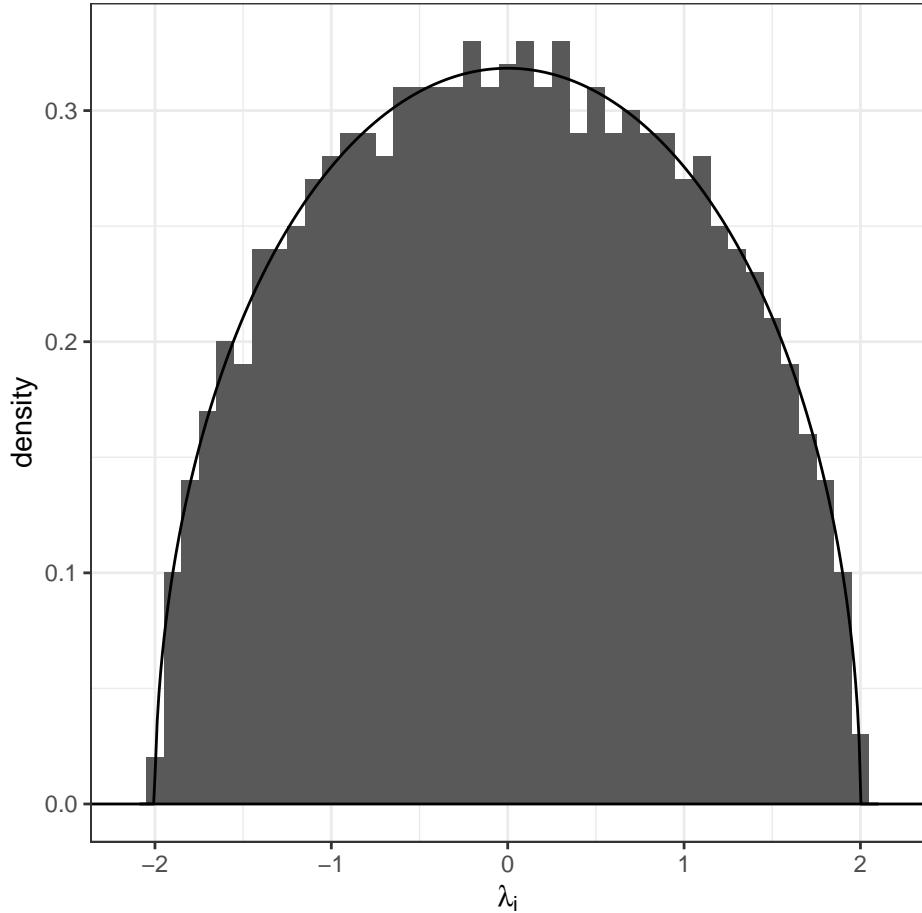
4.4 Symmetric matrices

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 $n \rightarrow \infty$, 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 semicircle distribution:

$$\mu(\lambda) = \begin{cases} \frac{1}{2\pi} \sqrt{4 - \lambda^2} & \text{if } \lambda \in [-2, 2] \\ 0 & \text{otherwise.} \end{cases} \quad (4.1)$$

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).

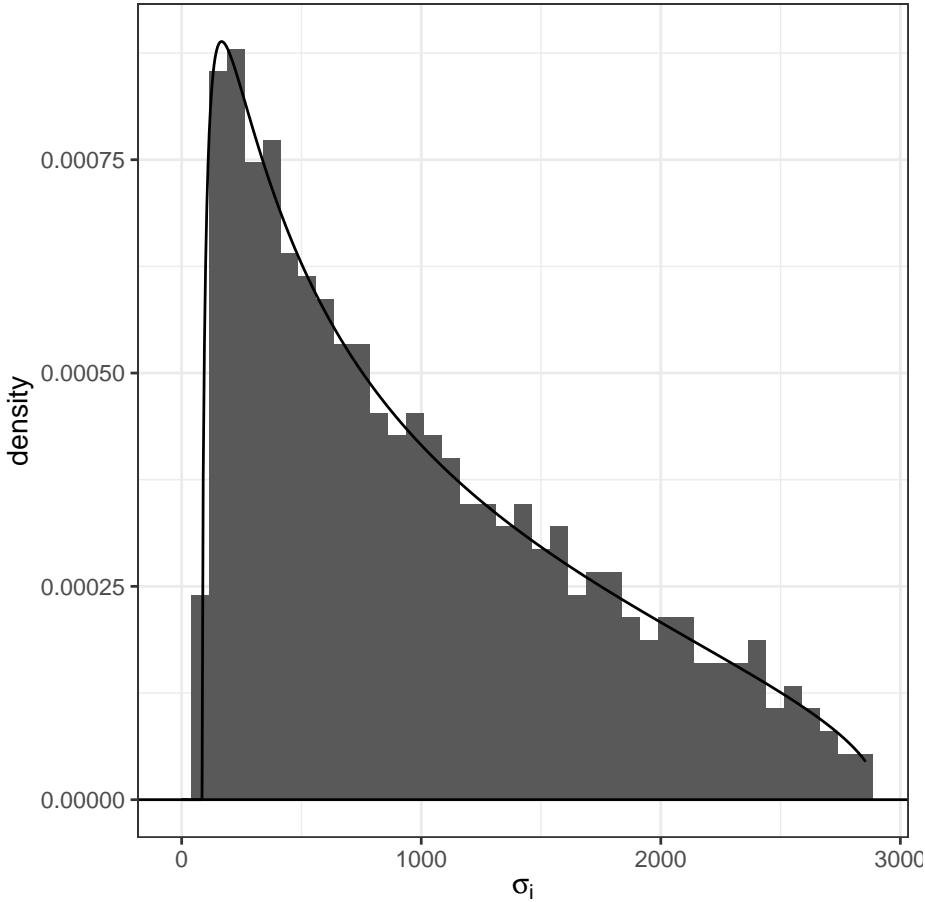


4.5 Covariance matrices

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 $n \rightarrow \infty$, the ratio $p/n \rightarrow y$ (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:

$$\mu(\lambda) = \begin{cases} \frac{1}{2\pi\lambda y} \sqrt{\left((1 + \sqrt{y})^2 - \lambda\right)\left(\lambda - (1 - \sqrt{y})^2\right)} & \text{if } (1 - \sqrt{y})^2 \leq \lambda \leq (1 + \sqrt{y})^2 \\ 0 & \text{otherwise.} \end{cases} \quad (4.2)$$

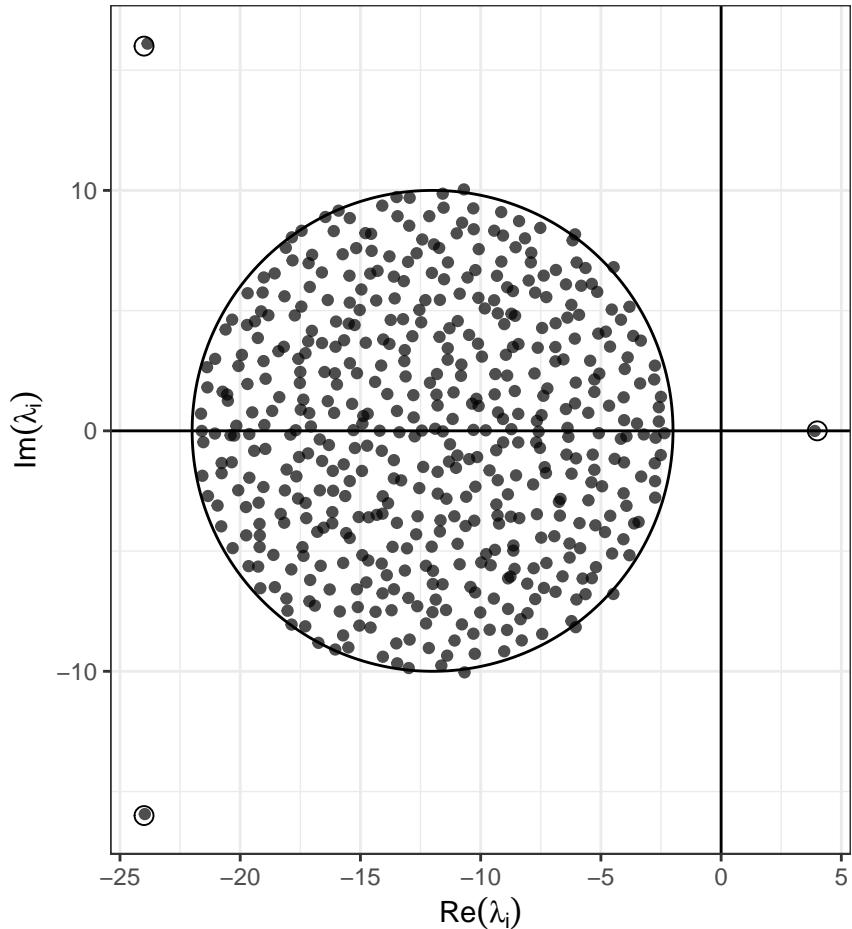


4.6 Small-rank perturbations

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, O'Rourke and Renfrew (2014)).

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:

- Allesina and Tang (2015) is an opinionated review on applications of random matrices in ecology.
- The lecture follows Allesina and Grilli (2020) quite closely. The online version of the book is available through the library.

Chapter 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: Tilman et al. (2001)

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., Hector et al. (1999) Tilman et al. (2001), Cadotte (2013)) and in the laboratory using protozoan, algae or bacteria. Two commonly-encountered problems in this type of experiments have to do 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:

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

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:

$$\begin{aligned} \sum_{j \in k; j \neq i} \beta_{ij} x_j^{(k)} + x_i^{(k)} &= \alpha_i \\ \sum_{j \in k; j \neq i} \frac{\beta_{ij}}{\alpha_i} x_j^{(k)} + \frac{1}{\alpha_i} x_i^{(k)} &= 1 \\ \sum_{j \in k; j \neq i} B_{ij} x_j^{(k)} + B_{ii} x_i^{(k)} &= 1 \\ \sum_{j \in k} B_{ij} x_j^{(k)} &= 1 \\ \left(B^{(k,k)} x^{(k)} \right)_i &= 1 \\ B^{(k,k)} x^{(k)} &= 1_{\|k\|} \end{aligned}$$

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:

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

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

Key paper: Tilman et al. (1997)

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 Loreau (1998).

Consider the matrix:

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

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 i^{th} 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 i^{th} 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:

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

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:

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

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

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

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

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

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

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

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:

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

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 5a

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 $\sigma_i^{(k)} = \sqrt{\mathbb{E}((\tilde{x}_i^{(k,r)})^2) - (\mathbb{E}(\tilde{x}_i^{(k,r)}))^2}$.

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

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

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

Key paper: Loreau and Hector (2001)

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 (Pillai and Gouhier (2019a)), leading to rebuttals of rebuttals (Loreau and Hector (2019), Wagg et al. (2019), Pillai and Gouhier (2019b), Pillai and Gouhier (2019c))...

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.

5.7.1 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

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

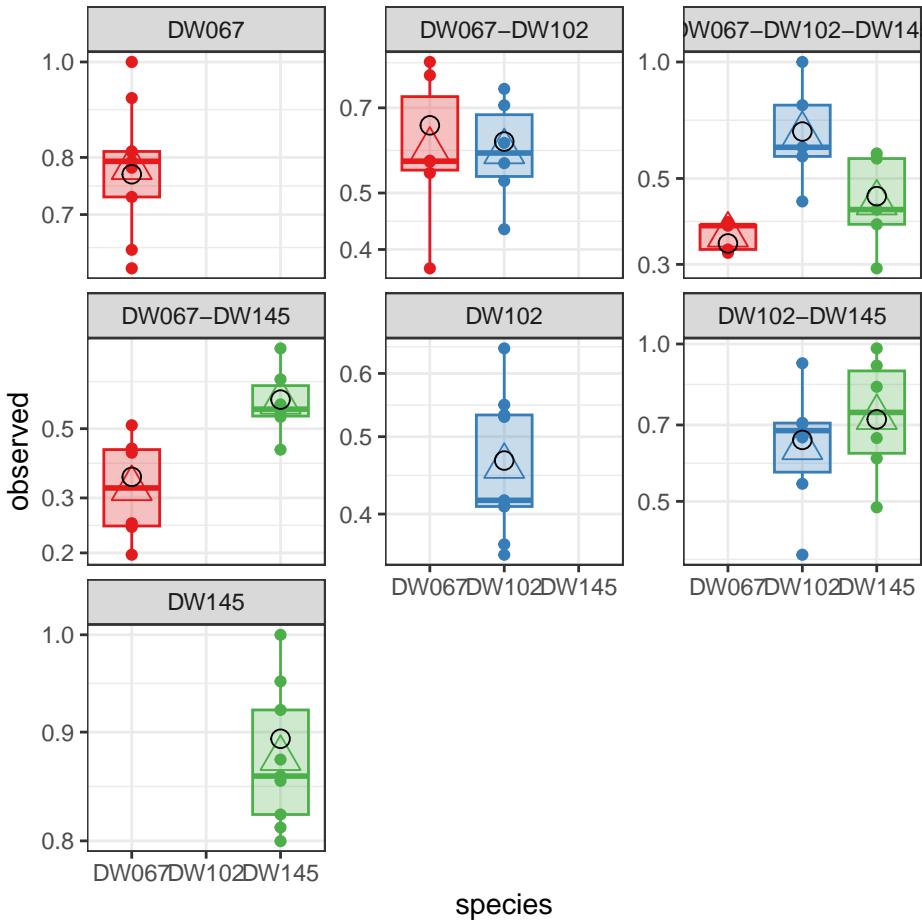
This can be accomplished by calling:

```
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
)
```

```
[1] "numerical search" [1] 1.289597 [1] 1.289597 [1] 1.289597 [1] 1.289597 [1]
1.289597 [1] 1.289597 [1] 1.289597 [1] 1.289597 [1] 1.289597 [1] 1.289597
```

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

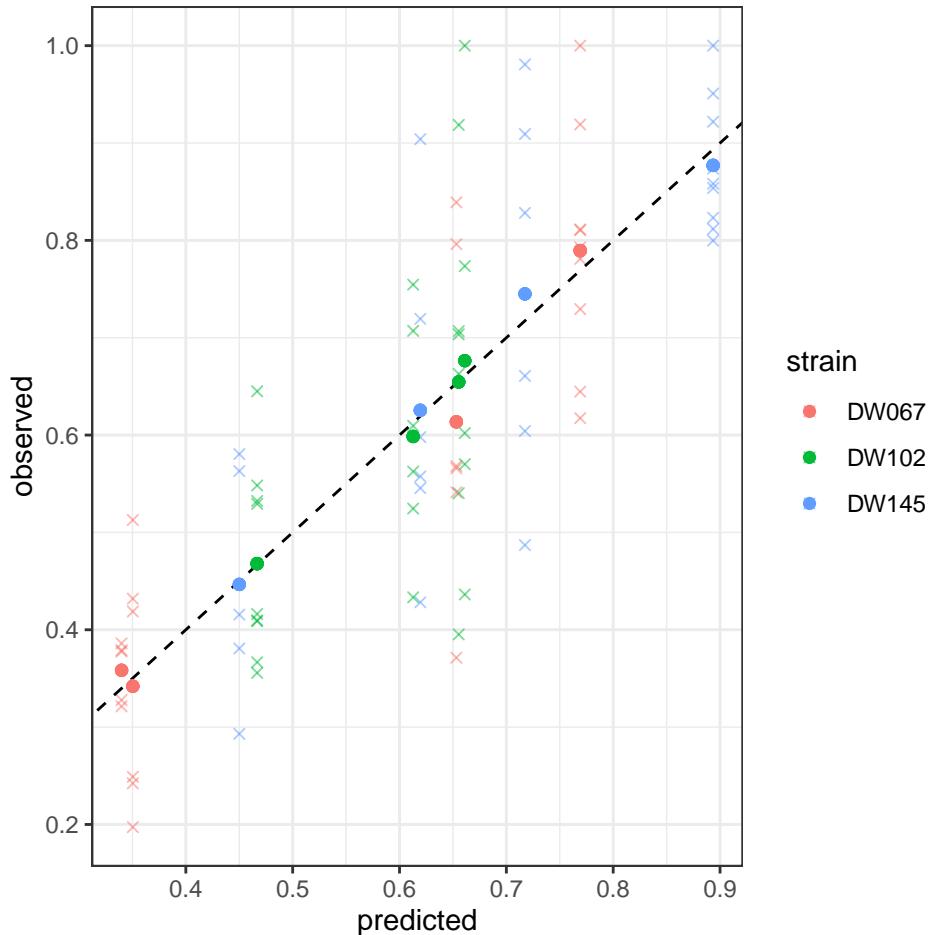
```
plot_results_boxplot(full_SSQ$observed, full_SSQ$predicted)
```



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 $(B^{(k,k)})^{-1} \mathbf{1}_{\parallel k \parallel}$. 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.

5.7.2 Weighted least 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
```

```

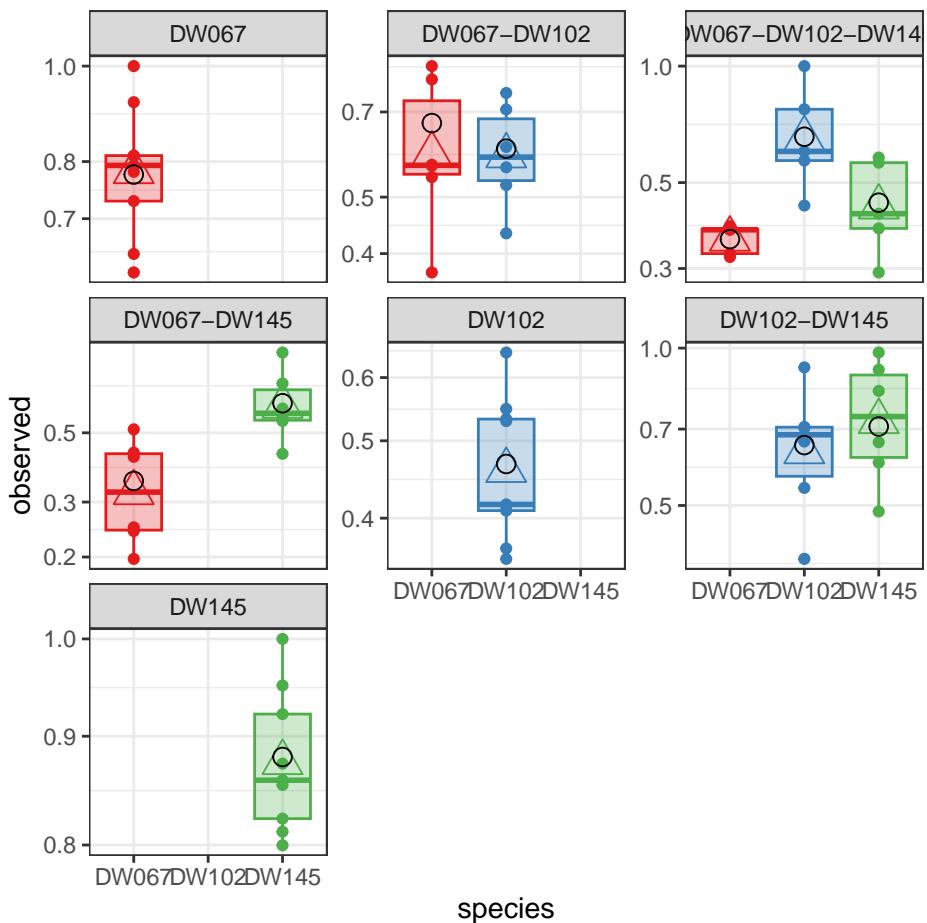
goalf = "WLS",
pars = NULL, # start from Identity matrix
skipEM = TRUE, # go directly to numerical optimization
)

```

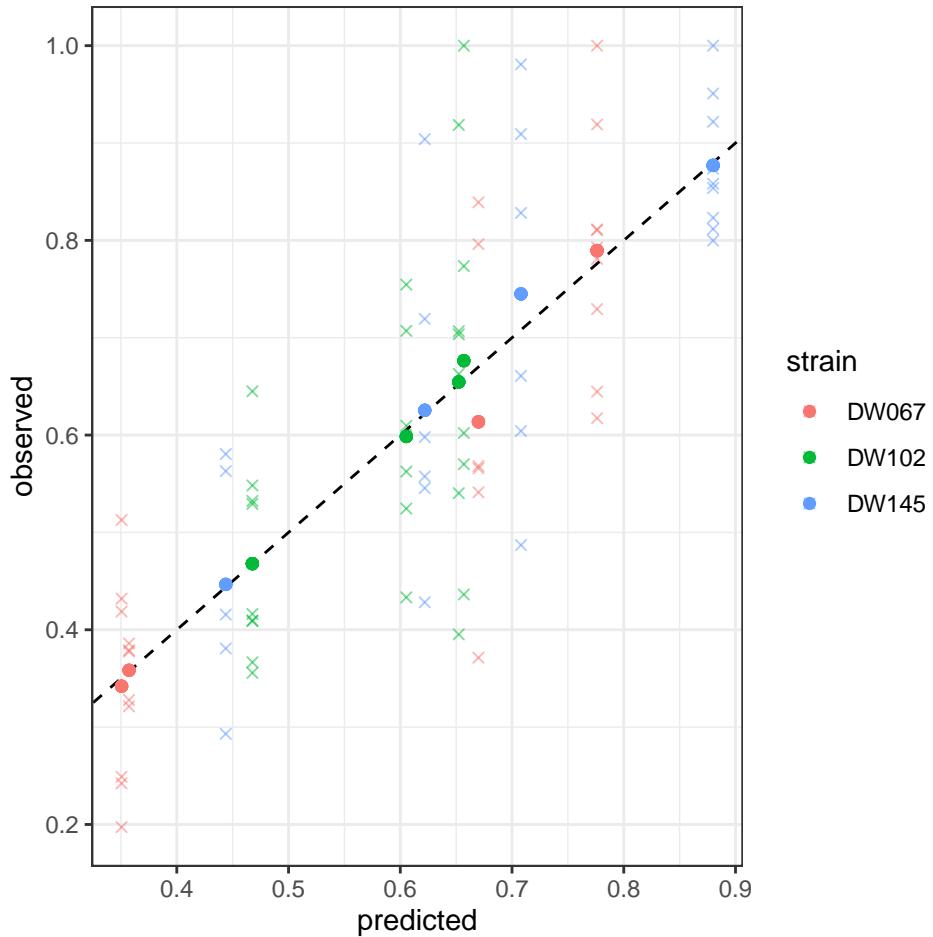
```
[1] "numerical search" [1] 67.07833 [1] 67.07833 [1] 67.07833 [1] 67.07833 [1]
67.07833 [1] 67.07833 [1] 67.07833 [1] 67.07833 [1] 67.07833 [1] 67.07833
```

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).

5.7.3 Maximum likelihood

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

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

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
```

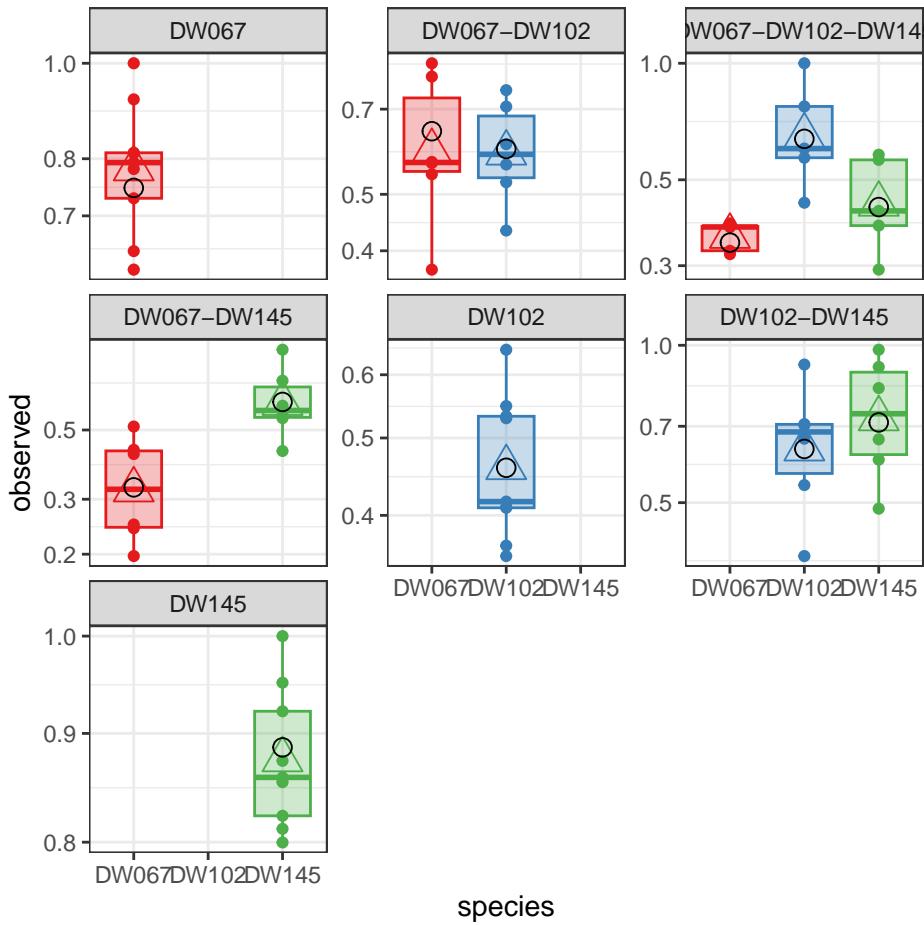
```

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
)

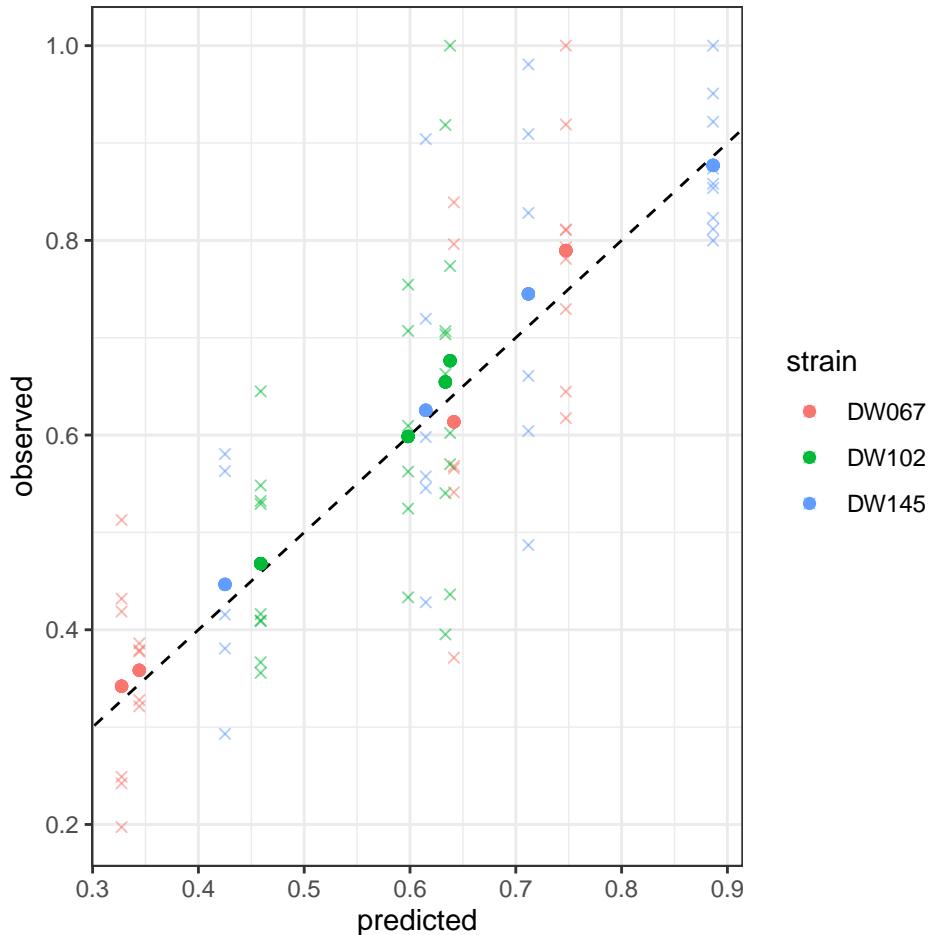
[1] "numerical search" [1] -49.19108 [1] -49.19108 [1] -49.19108 [1] -49.19108 [1]
-49.19108 [1] -49.19108 [1] -49.19108 [1] -49.19108 [1] -49.19108 [1] -49.19108

plot_results_boxplot(full_LN$observed, full_LN$predicted)

```



```
plot_pred_obs(full_LN)
```



Also in this case, we obtain a good fit.

5.7.4 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:

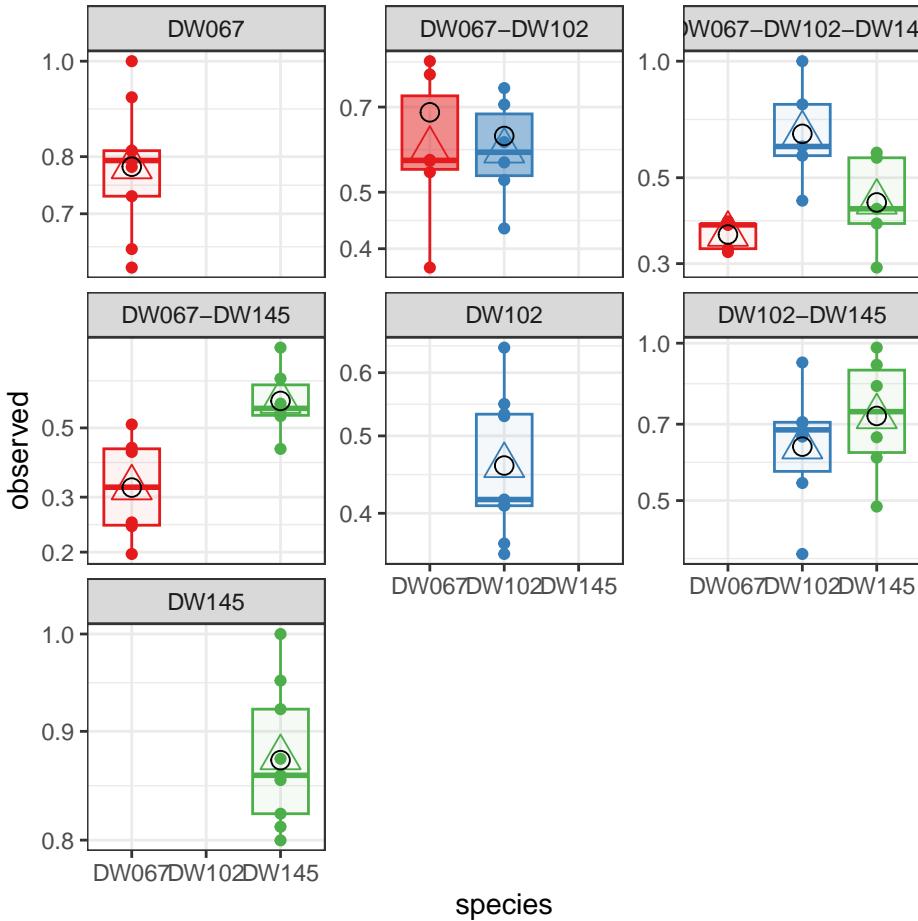
```
dt <- read_csv("dat/Ishizawa_3_strains.csv")

L00_LN <- run_model_L00(datafile = "dat/Ishizawa_3_strains.csv",
                         model = "full", goalf = "LikLN",
                         pars = NULL, skipEM = TRUE, plot_results = TRUE,
                         L00_row_num = 40 # exclude all experiments with this community
)
```

```
[1] "numerical search" [1] -43.08928 [1] -43.08928 [1] -43.08928 [1] -43.08928 [1]
-43.08928 [1] -43.08928 [1] -43.08928 [1] -43.08928 [1] -43.08928 [1] -43.08928
```

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)
```



5.7.5 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:

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

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:

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

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

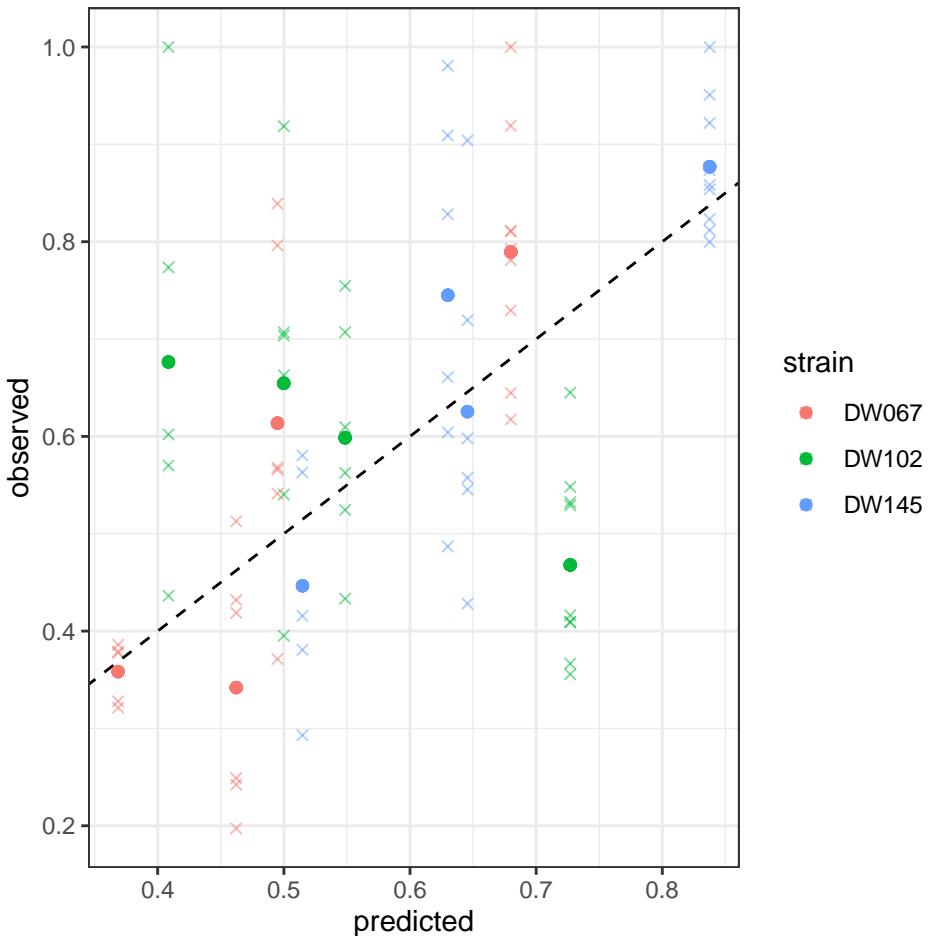
We can test different versions of the simplified model. A model with only the diagonal and an extra parameter performs very poorly:

```
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
)
[1] "numerical search" [1] -22.62175 [1] -22.62175 [1] -22.62175 [1] -22.62175 [1]
-22.62175 [1] -22.62175 [1] -22.62175 [1] -22.62175 [1] -22.62175 [1] -22.62175
plot_pred_obs(diag_a11)

```



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

```

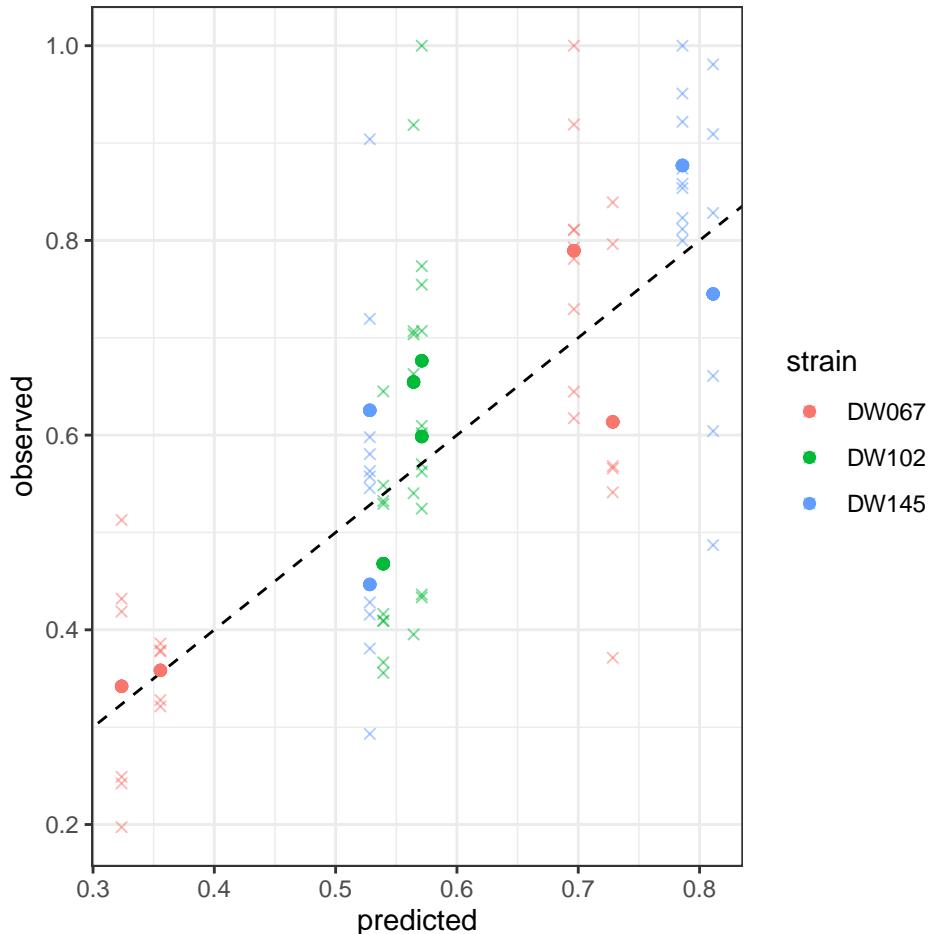
diag_vvt <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "diag_vvt",
  goalf = "LikLN",
  pars = NULL, # start from Identity matrix
)

```

```

skipEM = TRUE
)
[1] "numerical search" [1] -38.12933 [1] -38.36503 [1] -38.37226 [1] -38.38069 [1]
-38.38508 [1] -38.39331 [1] -38.39618 [1] -38.39655 [1] -38.39655 [1] -38.39655
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:

```

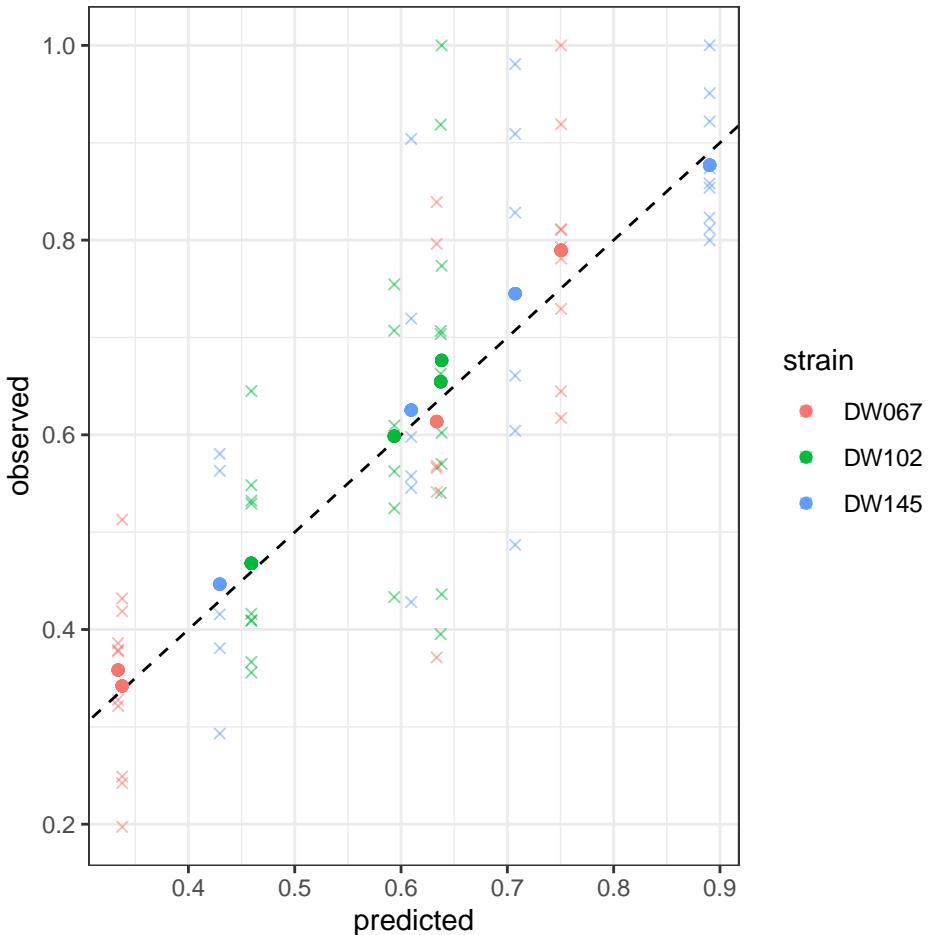
diag_vwt <- run_model(
  datafile = "dat/Ishizawa_3_strains.csv", # csv file containing the data to be fit
  model = "diag_vwt",
  goalf = "LikLN",

```

```

pars = NULL, # start from Identity matrix
skipEM = TRUE
)
[1] "numerical search" [1] -34.87107 [1] -49.06619 [1] -49.06753 [1] -49.0681 [1]
-49.0681 [1] -49.0681 [1] -49.0681 [1] -49.06811 [1] -49.06811 [1] -49.06811
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.

Chapter 6

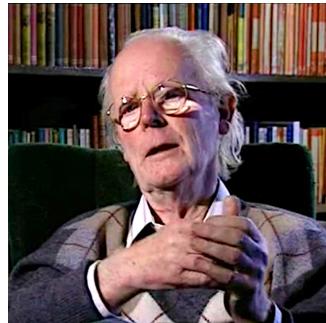
Game theory and replicator dynamics

6.1 Game theory

We briefly introduce the study of game theory, the science of strategic interactions, and its relation to the GLV model.

While the origin of the discipline can be traced back to the 1700s, modern game theory started with von Neumann's paper *On the Theory of Games of Strategy*, published in 1928, and with the subsequent 1944 book with Morgenstern *Theory of Games and Economic Behavior*. John Nash's paper (Nash 1950) introduced the notion of a **Nash Equilibrium** (NE), and proved that any non-cooperative game has at least one such equilibrium. Originally, game theory was studied by economists and mathematicians, but with a series of papers in the early 1970s, and the subsequent book *Evolution and the Theory of Games* (Maynard Smith 1982), John Maynard Smith showed how the same tools could be used to study evolutionary dynamics, introducing the influential concept of an **Evolutionary Stable Strategy** (ESS). Evolutionary game theory was greatly advanced through the introduction of the **Replicator Equation** (RE), which, as we will see later, has strong connection with the GLV model. For a detailed introduction to evolutionary game theory see Hofbauer and Sigmund (1998).

History: John Maynard Smith (1920-2004)



Born in London, when he was at Eaton he decided to study (independently) the work of JBS Haldane. He set out to Cambridge to study engineering, and subsequently worked as an engineer designing military aircrafts. In 1947, he had a change of heart and decided to study *Drosophila* genetics at U.C.L. under Haldane. In 1973, based on his interaction with George Price, he formalized the concept of “Evolutionary Stable Strategy”, which became central to evolutionary game theory. His book *Evolution and the Theory of Games* (1982) was an immediate success and contributed to the birth of the field.

History: George R. Price (1922-1975)



One of the most remarkable characters in the history of biology, he was born in New York. He studied chemistry at U. Chicago, receiving a PhD in 1946 (for work connected to the Manhattan Project). He went on to take a variety of jobs: teaching chemistry at Harvard, consulting at Argonne, researching at Bell Lab, writing popular science, working on medical research at U. Minnesota, and consulting for IBM on computer graphics.

In 1966, he was operated for a tumor, and the operation resulted in a partial paralysis. With the money from his medical insurance, he moved to the UK to start a new life.

Without any training in population genetics or statistics, he devised the Price equation, based on his readings of Hamilton’s papers on kin selection. This feat landed him a job at Galton Lab at UCL, despite his lack of credentials. His collaborations with Hamilton and Maynard-Smith led to the development of evolutionary game theory.

A strong atheist from an early age, in 1970 Price had a religious experience, con-

verted to Christianity and started (inspired by his own equation) to perform acts of random kindness to complete strangers. Having given up all his possessions, and possibly due to his stopping of thyroid treatment, Price grew depressed and committed suicide in 1975.

The book *The Price of Altruism: George Price and the Search for the Origins of Kindness* (Oren Harman, 2010) narrates the incredible story of his life.

6.2 Bimatrix games

We start by analyzing games in which two players face each other; the two players simultaneously choose a strategy out of a set. Importantly, we consider static games in which each player makes their decision without having knowledge of the decision of the other player.

Player 1 chooses a **pure strategy** s_1 from the set of pure strategies S_1 , while player 2 chooses $s_2 \in S_2$. We call $\pi_k(s_1, s_2)$ the **payoff** for player k when player 1 chooses s_1 and player 2 s_2 .

In a matrix game, we can arrange the payoffs for each player in a matrix. We call A the matrix of payoffs for player one (the row player) and B that for player two (the column player).

6.2.1 Example: the prisoner's dilemma

Two prisoners allegedly committed a crime, but the police do not have enough evidence to convict them. They therefore approach each prisoner separately, proposing a deal: if the prisoner confesses (“defects” the other prisoner), then their sentence will be reduced. In particular: i) if both confess (both “defect”), they are sentenced to 4 years in prison; ii) if one confesses (“defects”) and the other keeps quiet (“cooperates” with the other prisoner), then the one who has confessed is let free, and the other sentenced to 5 years; iii) if both keep quiet (“cooperate”), then they are both sentenced to two years of detention for some accessory crime.

In matrix form, we have (rows for pl 1 strategy C/D; cols for pl 2 strategy):

$$A = \begin{pmatrix} -2 & -5 \\ 0 & -4 \end{pmatrix} \quad B = \begin{pmatrix} -2 & -5 \\ 0 & -4 \end{pmatrix}$$

What is the best strategy player 1 can play—without knowing whether player 2 will confess or not? If player 2 were to keep quiet, player 1 should confess and be let free; if player 2 confesses, on the other hand, player 1 should also confess and get a reduced sentence. As such, each player would rationally choose to confess, thereby getting sentenced to four years in prison; note that if they could trust the other player, they could cooperate to get a much reduced sentence.

The defect/defect is called a **Nash Equilibrium**: no player can improve their payoff by changing only their own strategy.

One of the most interesting problems in this area is the study of the evolution of cooperation. Here is a very minimal bibliography:

Key paper: Axelrod and Hamilton (1981)

The seminal paper in this area. Interestingly, it details the outcome of a computer-based tournament in which several programs iteratively play the prisoner's dilemma against each other.

Key paper: Clutton-Brock (2009)

An opinionated review on cooperation between non-kin in animal societies. The opening “*As Darwin appreciated, cooperative behaviour—actions adapted to assist others that involve costs to the fitness of participants—poses a fundamental problem to the traditional theory of natural selection*”, a succinct summary of why the evolution of cooperation is such a central problem in biology.

Key paper: Nowak and May (1992)

Nowak and May examine the case in which populations of “cooperators” and “defectors” play the prisoner's dilemma in a spatial setting. Despite the simple setting and the deterministic nature of the simulation, they find long-term coexistence of the different populations, giving rise to amazing spatial patterns.

Key paper: Nowak and Sigmund (2005)

Cooperation can evolve via indirect reciprocity (I help you in the hope that someone will help me) when players have a “reputation” to defend.

6.2.2 Mixed strategies

Above, the player could choose one out of two strategies. A generalization of this situation is one in which players play **mixed strategies**, i.e., play a given strategy at random according to a set of probabilities. Call p_i the probability that player 1 plays strategy i ; then $p_i \geq 0$, and $\sum_i p_i = 1$. Similarly, q_i is the probability that player 2 plays strategy i . A natural choice for the payoff of player 1 is therefore:

$$\sum_{i=1}^m \sum_{j=1}^n p_i q_j \pi_1(s_i, s_j) = p^T A q$$

which amounts to the expected payoff for player 1. Similarly, we have $q^T B^T p$ for player 2.

6.2.3 Nash Equilibria

A pair of mixed strategies p^* and q^* is called a Nash Equilibrium for a bimatrix game if:

$$\begin{aligned} p^{*T} A q^* &\geq p^T A q^* \quad \text{for all } p \\ q^{*T} B^T p^* &\geq q^T B^T p^* \quad \text{for all } q \end{aligned}$$

John Nash proved that every non-cooperative game has at least one Nash Equilibrium.

6.2.4 Symmetric bimatrix games

The prisoner's dilemma above is an example of a symmetric bimatrix game, in which the matrix of payoffs is the same for both players ($A = B$), and the two players have access to the same set of strategies. Nash proof extends to symmetric games: every symmetric bimatrix game has at least one symmetric Nash equilibrium when considering mixed strategies (note that here “symmetry” refers to the fact that the optimal strategy is the same for all players—the matrix A needs not to be symmetric). The condition for a Nash equilibrium becomes:

$$p^{*T} A p^* \geq p^T A p^* \quad \text{for all } p$$

6.2.5 Evolutionary stable strategies

Consider a symmetric bimatrix game, defined by matrix A , and a Nash equilibrium p^* . In the context of evolution, one might imagine that “mutants” are generated, playing a variation on p^* . A Nash equilibrium is *evolutionary stable* if it yields a higher payoff than nearby mutants. The concept of an Evolutionary Stable Strategy (ESS) was introduced by Maynard-Smith and Price.

We write the mutant as p and the Nash equilibrium as p^* . When the mutant arises, the population is composed mostly of the p^* ; we model the state of the population as $q = (1 - \epsilon)p^* + \epsilon p$. The value $0 \leq \epsilon \leq 1$ determines how rare the mutant is. We want to determine whether the expected payoff for p when the population is q is lower than that of the p^* :

$$\begin{aligned} p^T A q &< p^{*T} A q \\ p^T A((1 - \epsilon)p^* + \epsilon p) &< p^{*T} A(1 - \epsilon)p^* + \epsilon p \\ (1 - \epsilon)p^T A p^* + \epsilon p^T A p &< (1 - \epsilon)p^{*T} A p^* + \epsilon p^{*T} A p \\ (1 - \epsilon)(p^{*T} A p^* - p^T A p^*) + \epsilon(p^{*T} A p - p^T A p) &> 0 \end{aligned}$$

If this inequality is met, then the mutant cannot grow when rare (i.e., invade). Note that the first term is always greater than or equal to zero when p^* is a Nash

equilibrium. Thus, for sufficiently small ϵ , as long as the first term is positive, we have evolutionary stability. However, the first term could be exactly zero (this happens when there is an alternative “best reply” to p^*), in which case we need the second term to be positive, yielding:

For $p \neq p^*$, and for p such that $p^{*T} Ap^* = p^T Ap^*$, then

$$\begin{aligned} p^{*T} Ap - p^T Ap &> 0 \\ p^{*T} Ap &> p^T Ap \end{aligned}$$

Next, we connect NE and ESS with dynamical systems.

6.3 Replicator dynamics

Consider a population composed of individuals, such that individuals of type i always play strategy i . We denote $p_i(t)$ as the frequency of individuals of type i at time t . When two individuals of type i and j meet, the individual of type i receives the payoff A_{ij} . Then the expected payoff for an individual of type i is:

$$\sum_j A_{ij} p_j(t) = (Ap(t))_i$$

We then assume that the payoff is invested in reproduction, making $(Ap)_i = f_i$ the *fitness* of type i . Because we are tracking frequencies, if a type increases in frequency, necessarily another type must decline in frequencies. A natural choice is therefore to subtract from the fitness of type i the expected fitness across all types.

$$\sum_{i,j} A_{ij} p_i(t) p_j(t) = p^T Ap = \bar{f}$$

We can write the per-capita growth rate of type i as:

$$\frac{\dot{p}_i}{p_i} = f_i - \bar{f}$$

Thus obtaining the *replicator equation*:

$$\frac{dp_i}{dt} = p_i \left(\sum_j A_{ij} p_j - \sum_{jk} p_j A_{jk} p_k \right) = p_i ((Ap)_i - p^T Ap) = p_i (f_i - \bar{f})$$

As we will see, the RE is essentially equivalent to a GLV model in which we track frequencies instead of abundances.

Importantly, we can see p as a “mixed strategy” for the symmetric game encoded in A . In this context, a **Nash Equilibrium for the game is an equilibrium of the replicator equation**; similarly, an **Evolutionary Stable Strategy for the game is a stable equilibrium for the replicator equation**. As we will see later, the converse is not true: we could have a stable equilibrium of the RE which is not an ESS.

6.3.1 Nash equilibria are equilibria of the RE

Consider an equilibrium in which all types are present: we will say that the equilibrium is in the interior of the simplex, $p^* \in \Delta_{\text{int}}$. The simplex is the space of $p_i \geq 0$, such that $\sum_j p_j = 1^T p = 1$. The interior of the simplex is the set of p such that $p_i > 0$ and $1^T p = 1$.

p^* is a Nash equilibrium iff:

$$p^{*T} Ap^* \geq p^T Ap^* \quad \forall p \in \Delta$$

$p^* \in \Delta_{\text{int}}$ is an equilibrium of the RE if:

$$Ap^* = (p^{*T} Ap^*) 1_n$$

i.e., if all types have the same fitness at p^* , we have $f_i = (Ap^*)_i = \bar{f}$. But then:

$$Ap^* = \bar{f} 1_n$$

Plugging this into the definition of Nash equilibrium, we have:

$$\begin{aligned} p^{*T} Ap^* &\geq p^T Ap^* \\ \bar{f} p^{*T} 1_n &\geq \bar{f} p^T 1_n \\ \bar{f} &\geq \bar{f} \end{aligned}$$

which is true: a Nash equilibrium in the interior of the simplex is also an equilibrium point for the replicator equation.

6.3.2 ESS are globally stable equilibria of the RE

Next, we consider the definition of an ESS in the interior of the simplex:

$$\begin{aligned} p^{*T} Ap &\geq p^T Ap \\ p^T Ap - p^{*T} Ap &\leq 0 \end{aligned}$$

together with the candidate Lyapunov function:

$$V = - \sum_j p_j^* \log \frac{p_j}{p_j^*} \geq 0$$

We differentiate with respect to time, obtaining:

$$\begin{aligned}\dot{V} &= - \sum_j p_j^* \frac{\dot{p}_j}{p_j} \\ &= - \sum_j p_j^* ((Ap)_j - p^T Ap) \\ &= \left(- \sum_j p_j^* Ap_j \right) + p^T Ap \\ &= -p^{*T} Ap + p^T Ap\end{aligned}$$

Showing that \dot{V} is decreasing in time if and only if p^* is an ESS. Hence evolutionary stability implies dynamical global stability of p^* .

6.3.3 Stability of the RE with symmetric A

We examine the special case of a symmetric matrix of payoffs $A = A^T$. In this case, the two players have exactly the same interests—this type of games is sometimes called *partnership game*. One might expect that, given that the two players have a shared interest, the average payoff would grow in time. This is indeed the case, and in fact the average payoff is a Lyapunov function for the system.

Take $A = A^T$, then the average payoff $W = p^T Ap$ can only grow in time:

$$\dot{W} = p^T A \dot{p} + \dot{p}^T A p = p^T A \dot{p} + p^T A^T \dot{p} = 2p^T A \dot{p}$$

It is convenient to write $f = Ap = A^T p$ (the fitness vector) and the average fitness $p^T Ap = p^T f = \bar{f}$. But then, $\dot{p} = D(p)(f - \bar{f}1_n)$, and

$$\begin{aligned}\dot{W} &= 2(p^T AD(p)(f - \bar{f}1_n)) \\ &= 2(f^T D(p)f - f^T p \bar{f}) \\ &= 2(p^T D(f)f - \bar{f}^2) \\ &= 2(p^T f^2 - \bar{f}^2) \\ &= 2(\mathbb{E}[f_i^2] - \mathbb{E}[f_i]^2) \geq 0\end{aligned}$$

Fisher's fundamental theorem of natural selection, which states that “The rate of increase in fitness of any organism at any time is equal to its genetic variance

in fitness at that time". What we have shown is that, for partnership games, indeed the rate of increase \dot{W} of the average fitness (W) is indeed determined by $\mathbb{E}[f_i^2] - \mathbb{E}[f_i]^2 = \mathbb{V}\mathcal{D}\setminus[f_i]$. Note the parallel with MacArthur's Lyapunov function (which was in fact suggested by Kimura, who was aware of Fisher's theorem). See Baez (2021) for a discussion of Fisher's theorem in the context of the replicator equation.

6.3.4 Invariants

Adding a constant to each column of A does not alter the dynamics. We have $B = A + 1_n b^T$; Then:

$$\begin{aligned}\dot{p}_i &= p_i((Bp)_i - p^T Bp) \\ &= p_i((Ap)_i + b^T p - p^T Ap - p^T 1_n b^T p) \\ &= p_i((Ap)_i + b^T p - p^T Ap - b^T p) \\ &= p_i((Ap)_i - p^T Ap)\end{aligned}$$

Showing that \dot{p} (and thus the dynamics) is unchanged.

Similarly, defining:

$$q_i = \frac{w_i p_i}{\sum_j w_j p_j}$$

does not alter the dynamics: we can map the trajectories of p on those of q and vice-versa. This is called the *projective transformation* in Hofbauer and Sigmund (exercise 7.1.3). We have:

$$\begin{aligned}\dot{q}_i &= \frac{w_i \dot{p}_i}{\sum_k w_k p_k} - \frac{w_i p_i}{\sum_k w_k p_k} \sum_j \frac{w_j \dot{p}_j}{\sum_k w_k p_j} \\ &= q_i ((Ap)_i - p^T Ap) - q_i \sum_j q_j ((Ap)_j - p^T Ap) \\ &= q_i ((Ap)_i - p^T Ap - q^T Ap + p^T Ap) \\ &= q_i ((Ap)_i - q^T Ap) \\ &= q_i ((AD(w)^{-1} D(w)p)_i - q^T AD(w)^{-1} D(w)p) \\ &= (\sum_j w_j p_j) q_i ((AD(w)^{-1} q)_i - q^T AD(w)^{-1} q) \\ &= (\sum_j w_j p_j) q_i ((Bq)_i - q^T Bq)\end{aligned}$$

where we have defined $B = AD(w)^{-1}$. Finally, we rescale time by $\sum_j w_j p_j > 0$, obtaining:

$$\dot{q}_i = q_i((Bq)_i - q^T Bq)$$

Thus, if we have $B = AD(w)^{-1}$, we have that the replicator equation in A, p and that in B, q are equivalent (e.g., the type of dynamics is the same, the existence/stability of equilibria is unchanged, etc.). By combining the two invariants, we find that $B = (A + 1b^T)D(w)^{-1}$, for $b \in \mathbb{R}^n$ and $w \in \mathbb{R}_+^n$ yields a RE that is equivalent to that in A .

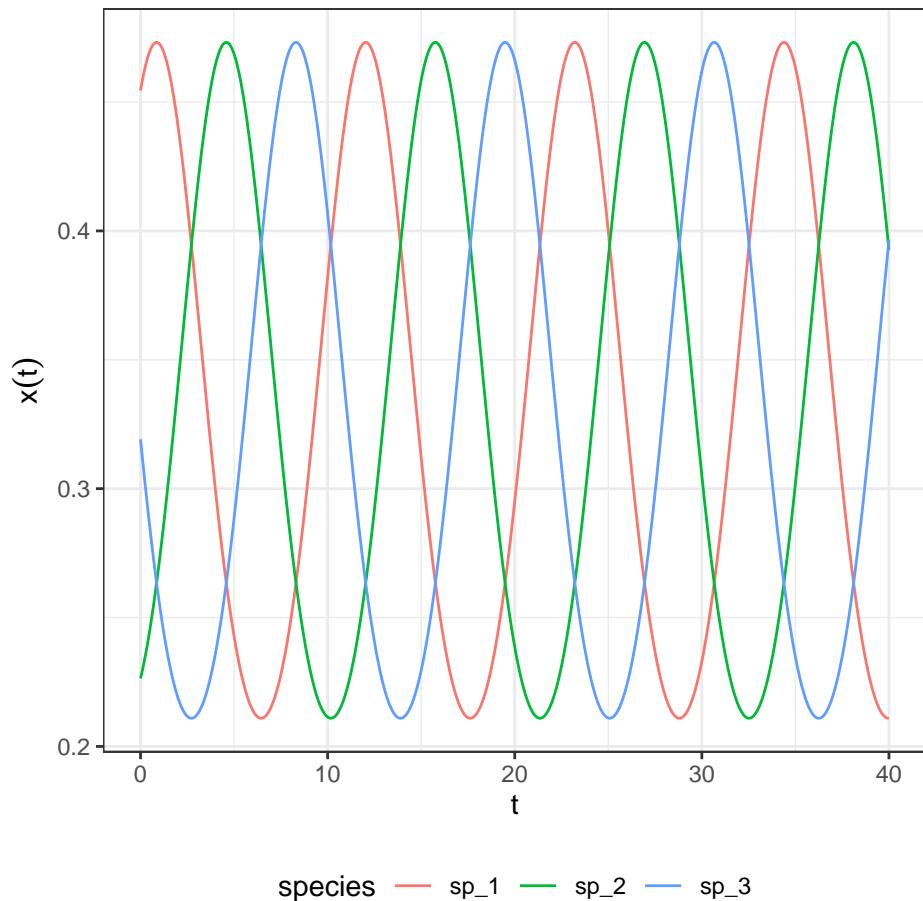
Very interestingly, the notion of ESS is not closed under the second invariant: we can have a p^* that is not an ESS, and choose $w > 0_n$ such that q^* is an ESS (and viceversa). I have recently written a paper exploiting this fact to extend the reach of the Lyapunov function above.

6.3.5 Rock-paper-scissor

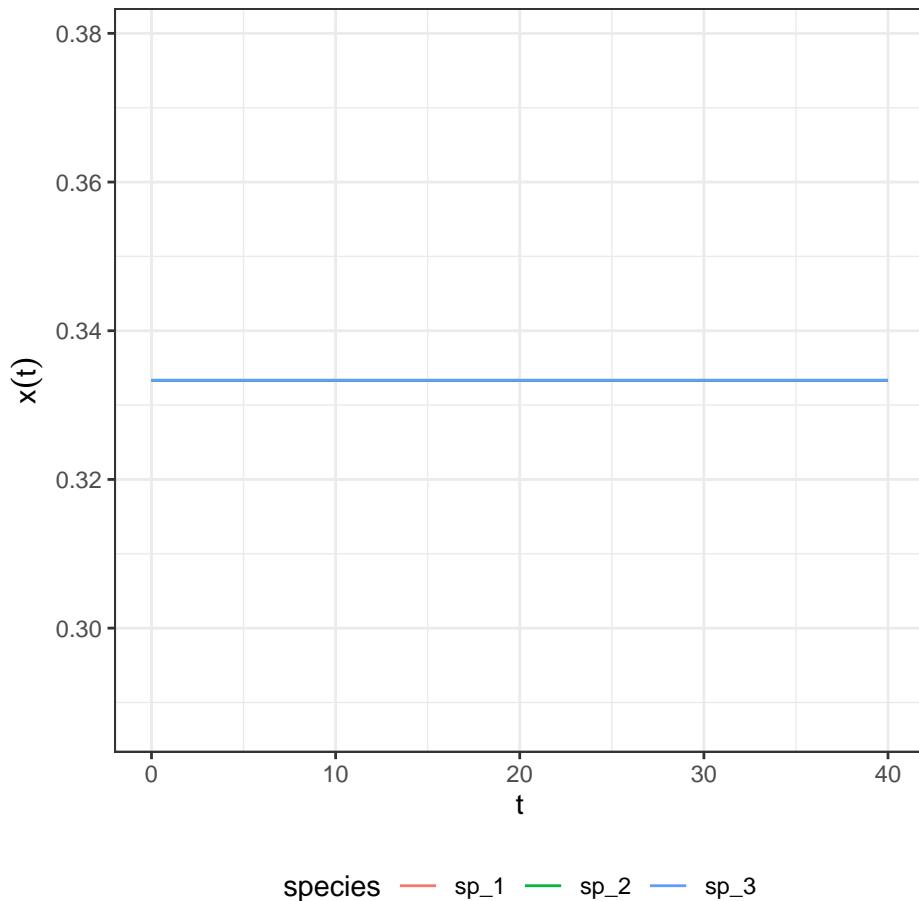
Let's try our hand at a simple zero-sum (i.e., $A = -A^T$) replicator equation. We have three populations ("rock", "paper", and "scissors") with payoff matrix:

$$A = \begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix}$$

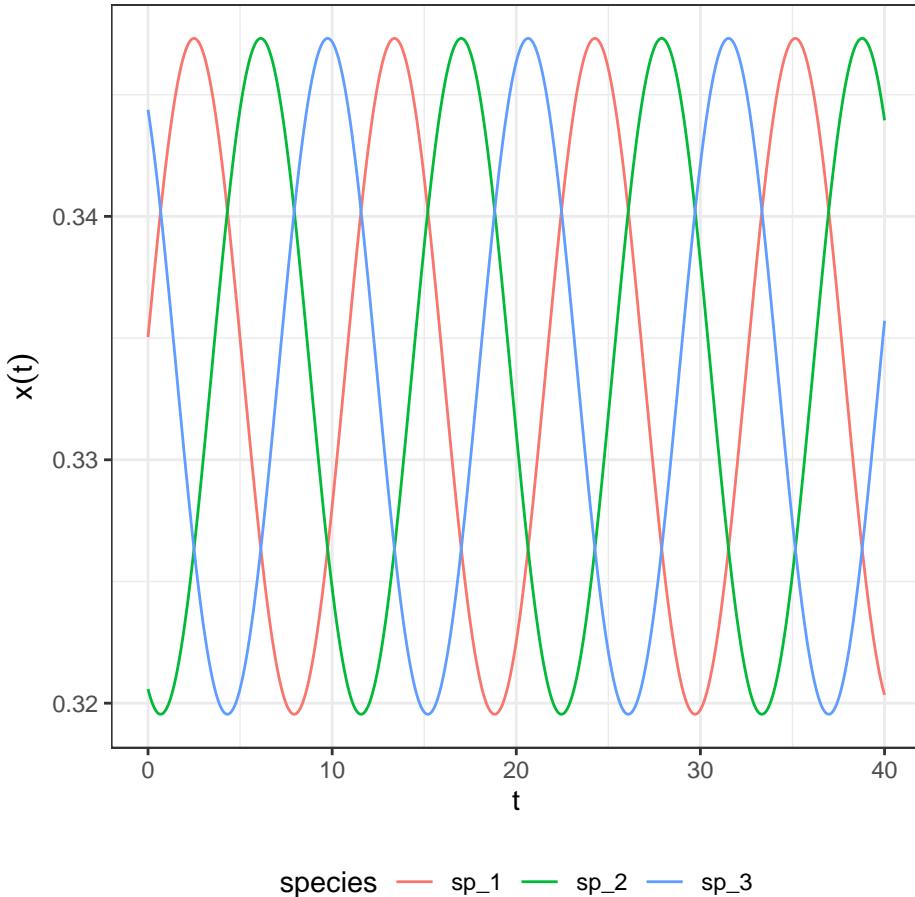
We start the population at a random initial condition, and track dynamics:



What if we start all populations at the same density?



And if they are close to $p_i = \frac{1}{3}$ for all i ?



We can try our candidate Lyapunov function to show that indeed we have neutral cycles, determined by the initial conditions.

$$V = - \sum_i p_i^* \log \frac{p_i}{p_i^*}$$

and

$$\begin{aligned} \dot{V} &= -p^{*T} A p + p^T A p \\ &= -p^T A^T p^* + 0 \\ &= p^T A p^* \\ &= 0 \end{aligned}$$

Showing that V is conserved through the dynamics (as in the classic Lotka-Volterra predator-prey system) and thus set by the initial conditions.

6.3.6 Equivalence with GLV

For a given n -species GLV system, there is an equivalent $(n+1)$ -dimensional replicator equation with zeros in the last row of the matrix.

Take the GLV model with n species:

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

and add a “new species” x_{n+1} such that $x_{n+1}(0) = 1$, and $\dot{x}_{n+1} = 0$; define $\tilde{x} = \{x, x_{n+1}\}$ and the matrix:

$$\tilde{A} = \begin{pmatrix} A & r \\ 0 & 0 \end{pmatrix}$$

we then have a new $n+1$ dimensional GLV system:

$$\frac{d\tilde{x}}{dt} = D(\tilde{x})\tilde{A}\tilde{x}$$

Now we want to move from abundances to frequencies/proportions. Note that we drop all the tilde signs for easier typing. Define:

$$y_i = \frac{x_i}{\sum_j x_j}$$

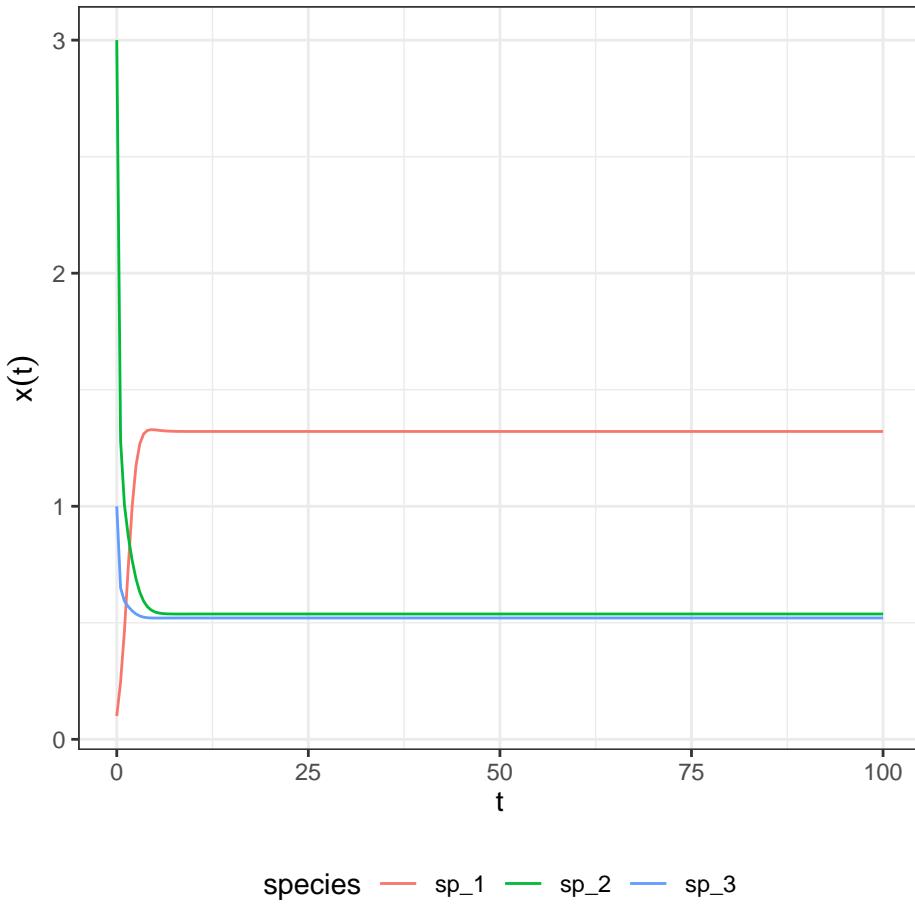
Then,

$$\begin{aligned} \frac{dy_i}{dt} &= \sum_k \frac{\partial y_i}{\partial x_k} \frac{dx_k}{dt} \\ &= \frac{1}{\sum_j x_j} \frac{dx_i}{dt} - \frac{1}{(\sum_j x_j)^2} x_i \sum_k \frac{dx_k}{dt} \\ &= \frac{1}{\sum_j x_j} x_i \sum_l A_{il} x_l - \frac{1}{(\sum_j x_j)^2} x_i \sum_k \left(x_k \sum_l A_{kl} x_l \right) \\ &= y_i \sum_l A_{il} x_l - y_i \sum_k \left(y_k \sum_l A_{kl} x_l \right) \\ &= (\sum_j x_j) y_i \left(\sum_l A_{il} y_l - \sum_{k,l} A_{kl} y_k y_l \right) \end{aligned}$$

Finally, you rescale time using $\sum_j x_j$ to obtain the replicator equation. To show this is indeed the case, let’s consider the GLV system:

$$r = \begin{pmatrix} 1 \\ 2 \\ 3 \end{pmatrix} \quad A = \begin{pmatrix} -1 & \frac{1}{2} & \frac{1}{10} \\ -\frac{7}{10} & -2 & 0 \\ -\frac{3}{10} & 0 & -5 \end{pmatrix}$$

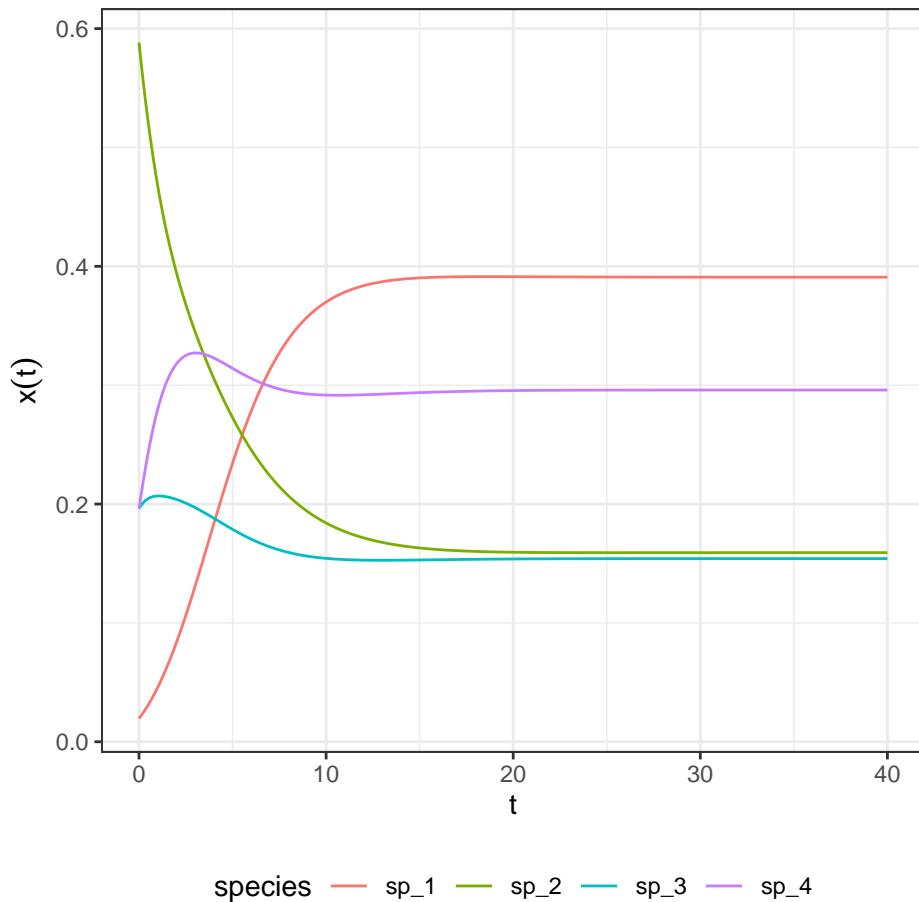
And compute the trajectory, when starting at $x(0) = (1/10, 3, 1)^T$:



Now build the corresponding replicator equation. The matrix of payoffs \tilde{A} becomes:

$$\begin{bmatrix} -1 & 0.5 & 0.1 & 1 \\ -0.7 & -2 & 0 & 2 \\ -0.3 & 0 & -5 & 3 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

Integrate the dynamics of the replicator equation:



Now let's look at the equilibrium of the GLV model:

time	species	density
100	sp_1	1.3209145
100	sp_2	0.5376799
100	sp_3	0.5207451

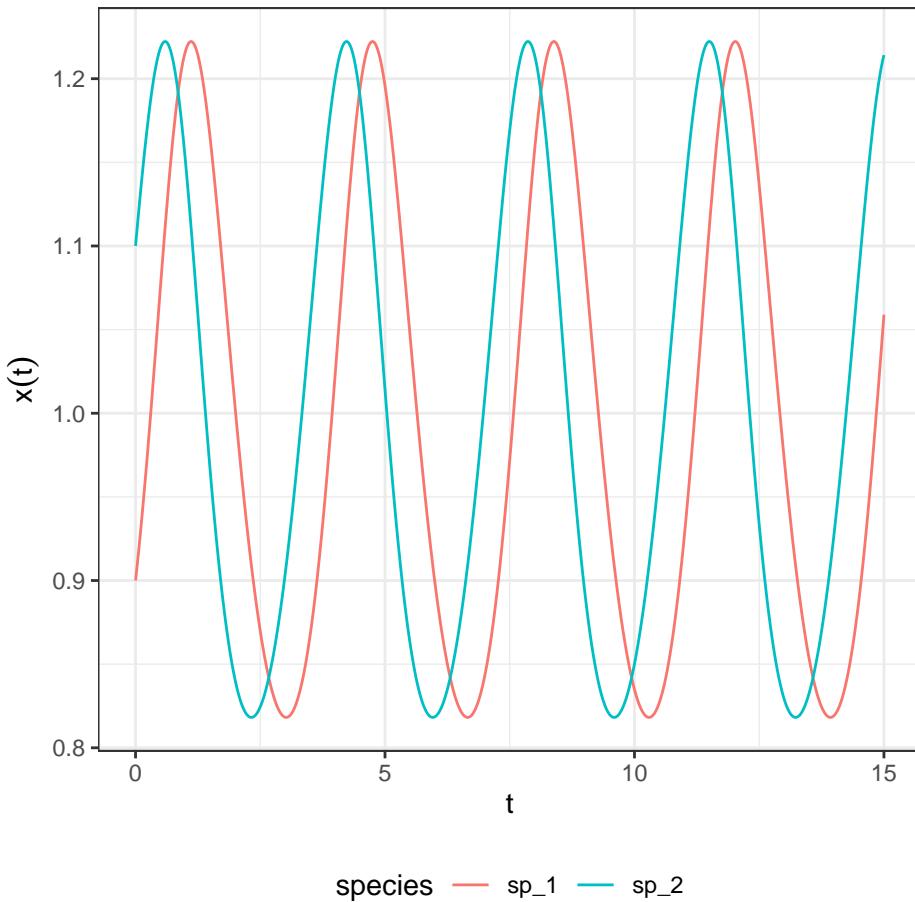
This is the final state of the RE:

time	species	density
40	sp_1	0.3908793
40	sp_2	0.1591076
40	sp_3	0.1540969
40	sp_4	0.2959162

By dividing for the value of the last “species”, we recover the equilibrium for GLV:

time	species	density
40	sp_1	1.3209123
40	sp_2	0.5376779
40	sp_3	0.5207453
40	sp_4	1.0000000

Not only the equilibria are the same, but also the trajectories are the same once time has been properly rescaled. Similarly, for each RE system we can always recover a matrix with zero in the last row by applying the transformations detailed above, and therefore recover the corresponding GLV. For example, take the matrix for the RPS above, and make each coefficient in the last row zero by adding the appropriate constant to each column. Then one recovers some sort of a predator-prey system:



in which the species oscillate around one.

Key paper: Page and Nowak (2002)

In this brief paper, Page and Nowak show that the replicator-mutator equation and the Price equation are two ways of tracking general evolutionary dynamics. They discuss the connections with GLV and adaptive dynamics.

6.4 Hypertournament games

The rock-paper-scissor game above is a simple case of a “hypertournament” game. Take the zero-sum payoff matrix $A = -A^T$. Then, we have

$$\sum_i \sum_j A_{ij} p_i p_j = 0$$

and the RE simplifies to

$$\frac{dp}{dt} = D(p)Ap$$

At equilibrium, either some elements of p are zero, or

$$Ap^* = 0$$

meaning that if an equilibrium $p^* \in \Delta_{\text{int}}$ exists, it is an eigenvector of A corresponding to a zero eigenvalue.

6.4.0.1 Number of coexisting species

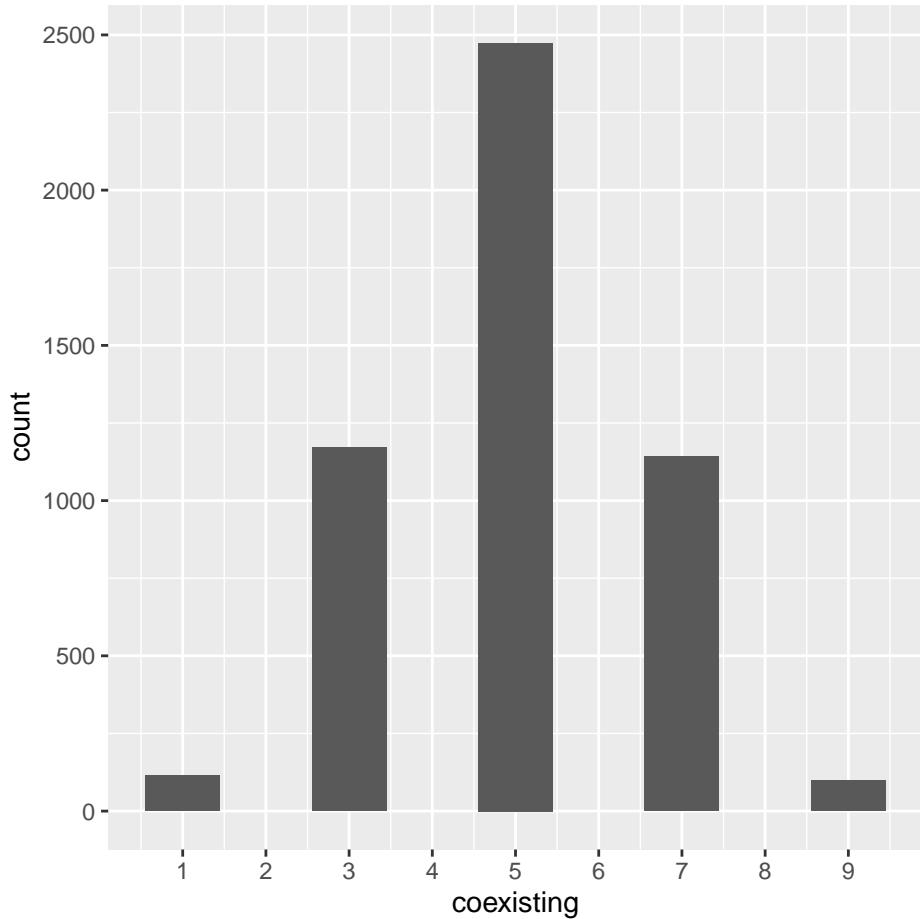
We now show how the equations above can arise when modeling ecological dynamics. Suppose that a forest is composed of a fixed number of trees. Each time a tree dies (with rate $d = 1$ for all species), a gap in the canopy opens, and species will compete to colonize it. Let's assume that two seeds (sampled with probability proportional to the density of the species) land in the empty patch, and that they compete to fill the gap. Call H_{ij} the probability that i wins when competing with j ; we have $H_{ij} + H_{ji} = 1$. We can write the dynamics (Grilli et al. 2017) as:

$$\begin{aligned}
\frac{dp_i}{dt} &= p_i \left(\sum_j 2H_{ij}p_j - 1 \right) \\
&= p_i \sum_j (2H_{ij}p_j - p_j) \\
&= p_i \sum_j (H_{ij}p_j + (1 - H_{ji})p_j - p_j) \\
&= p_i \sum_j (H_{ij} - H_{ji})p_j \\
&= p_i \sum_j A_{ij}p_j
\end{aligned}$$

I.e., we recover the RE for a zero-sum game. What happens if we draw H (and therefore A) at random? Allesina and Levine (2011) and Grilli et al. (2017) applied the results of Fisher and Reeves (1995) and Brandl (2017) to show that, when n species compete, the probability of observing k coexisting species/strategies is $p(k|n) = \binom{n}{k} 2^{1-n}$ when k is odd, and $p(k|n) = 0$ when k is even.

Importantly, to find the set of coexisting species we do not need to integrate dynamics. One can use linear programming to solve for the set of species that will coexist.

Now let's try to count how many species survive when starting with 10:



6.4.1 Lyapunov function

In the rock-paper-scissor example above, species cycled neutrally around the unique equilibrium point. To show that this is in fact the behavior of this type of RE, we write the usual Lyapunov function. By finding a constant of motion we can show that the species will follow closed orbits, exactly as found for the rock-paper-scissors game.

Suppose $p_i^* > 0$ is the equilibrium for the system. We write:

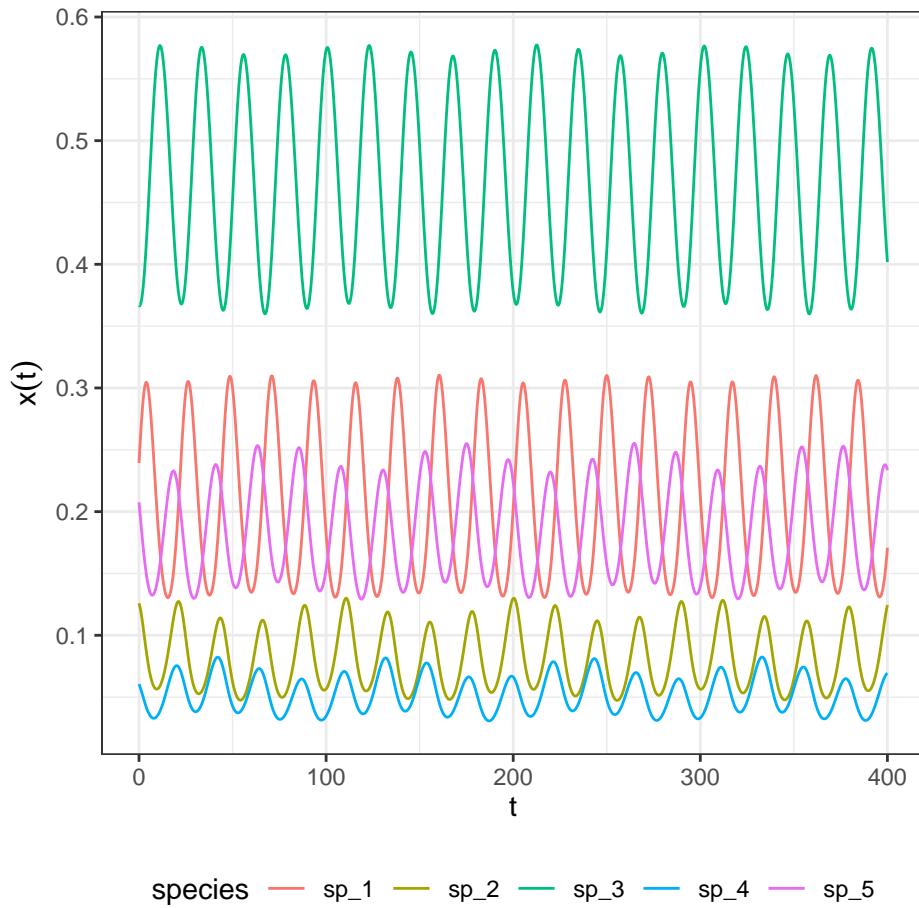
$$V(p) = - \sum_i p_i^* \log \frac{p_i}{p_i^*}.$$

Because of Gibbs' inequality, $V(p) \geq 0$ for any p , and is equal to zero only if $p = p^*$. Note also that at equilibrium $2 \sum_j H_{ij} p_j^* = 1$. We write:

$$\begin{aligned}
\frac{dV}{dt} &= \sum_i \frac{\partial V}{\partial p_i} \frac{dp_i}{dt} \\
&= - \sum_i \frac{p_i^*}{p_i} \frac{dp_i}{dt} \\
&= -2 \sum_{i,j} p_i^* H_{ij} p_j + \sum_i p_i^* \\
&= -2 \sum_{i,j} p_i^* H_{ij} p_j + 1 \\
&= \sum_j \left(-2 \sum_i H_{ij} p_i^* \right) p_j + 1 \\
&= \sum_j \left(-2 \sum_i (1 - H_{ji}) p_i^* \right) p_j + 1 \\
&= \sum_j \left(-2 \sum_i p_i^* + 2 \sum_i H_{ji} p_i^* \right) p_j + 1 \\
&= \sum_j (-2 + 1) p_j + 1 \\
&= - \sum_j p_j + 1 \\
&= 0
\end{aligned}$$

We have found a constant of motion, meaning that the system will follow closed orbits. Hence, unless we start the system precisely at p^* , the abundances will cycle neutrally around the equilibrium.

Let's try with a larger system:

**Homework 7a**

Analyze the replicator equation when the matrix A is:

$$A = \begin{pmatrix} 0 & -\alpha & 1 \\ 1 & 0 & -\alpha \\ -\alpha & 1 & 0 \end{pmatrix}$$

for the cases in which a) $\alpha > 1$, b) $\alpha < 1$. Write code to simulate the system, and prove stability/instability depending on the value of α .

Homework 7b

As seen above, generally zero-sum matrix games will lead to an odd number of species coexisting.

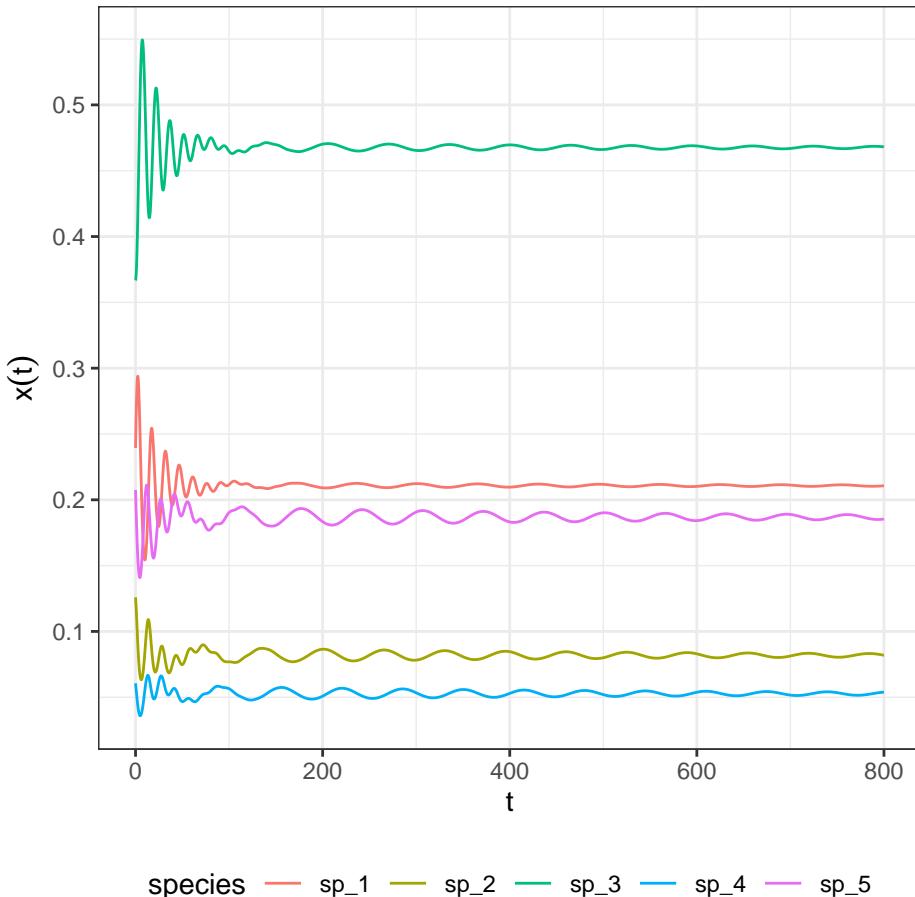
- Can you build a matrix leading to four species/strategies coexisting?
- Now simulate the dynamics several times, starting from different initial conditions—do species cycle around the same equilibrium? Why?

6.4.2 Higher-order interactions

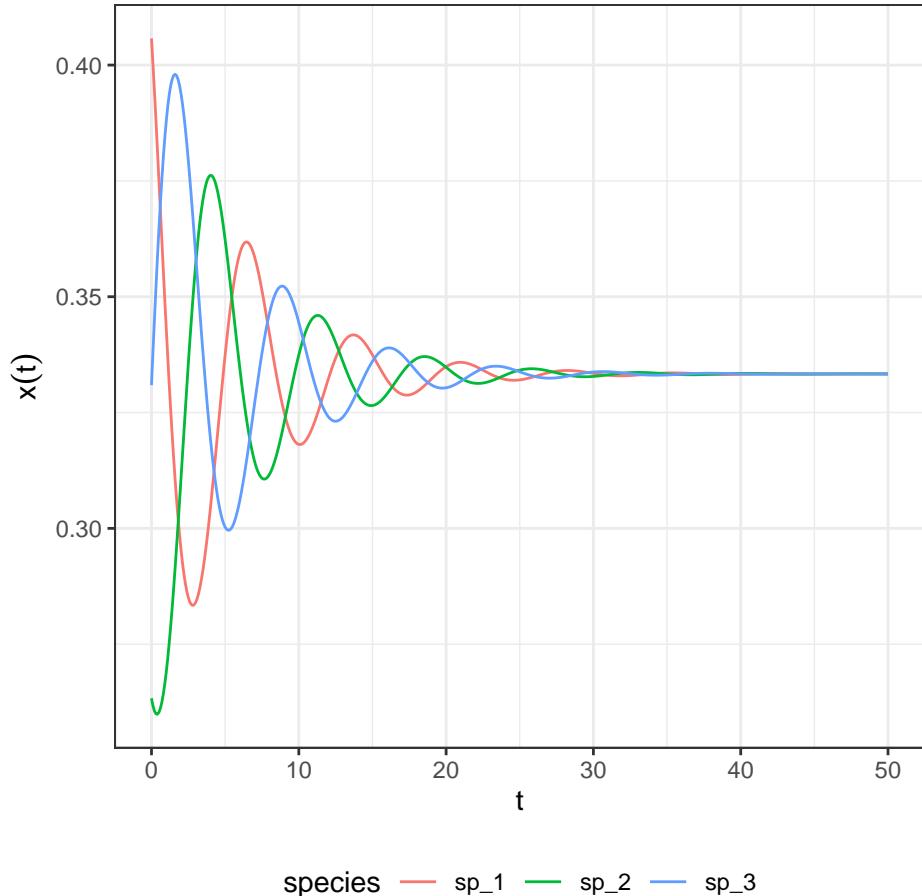
We can extend the game above to the case in which three (or more) seeds compete to fill each patch. Grilli et al. (2017) showed that in this case, one can write the replicator equation:

$$\frac{dp_i}{dt} = p_i \sum_{j,k} A_{ijk} p_j p_k$$

where the tensor A (a three-dimensional matrix) encodes the effect of a pair of species (j and k) on the density of i . Importantly, one can choose the tensor such that the equilibrium is the same as for the two-player replicator equation: take $A_{ijk} = 2H_{ij}H_{ik} - H_{ji}H_{jk} - H_{ki}H_{kj}$, which can be derived from first principles by writing the stochastic dynamics. What is surprising is that, while the equilibrium is unchanged, the dynamics are now globally stable:



And the three-player rock-paper-scissors:



When assuming the same death rates for all species/strategies, and the payoff structure is as detailed above, the usual Lyapunov function can be used to prove stability.

$$\frac{dp_i}{dt} = p_i \left(\sum_{j,k} (2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}) p_j p_k - 1 \right) = p_i \left(2 \sum_{j,k} (H_{ij}H_{ik} + H_{ij}H_{jk}) p_j p_k - 1 \right)$$

$$\frac{dp_i}{dt} = p_i \sum_{j,k} P_{ijk} p_j p_k$$

where the coefficient $P_{ijk} = 2H_{ij}H_{ik} - H_{ji}H_{jk} - H_{ki}H_{kj}$. We write:

$$\begin{aligned}
p_i \left(\sum_{j,k} (2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj}) p_j p_k - 1 \right) &= p_i \sum_{j,k} (2H_{ij}H_{ik} + H_{ij}H_{jk} + H_{ik}H_{kj} - 1) p_j p_k \\
&= p_i \sum_{j,k} (2H_{ij}H_{ik} + (1 - H_{ji})H_{jk} + (1 - H_{ki})H_{kj} - 1) p_j p_k \\
&= p_i \sum_{j,k} (2H_{ij}H_{ik} - H_{ji}H_{jk} - H_{ki}H_{kj}) p_j p_k \\
&= p_i \sum_{j,k} P_{ijk} p_j p_k
\end{aligned}$$

Now we want to show that now an equilibrium $p^* > 0$ is globally stable.

$$\begin{aligned}
\frac{dV}{dt} &= - \sum_i \frac{p_i^*}{p_i} \frac{dp_i}{dt} \\
&= -2 \sum_{i,j,k} (p_i^* H_{ij} H_{jk} p_j p_k + p_i^* H_{ij} H_{ik} p_j p_k) + \sum_i p_i^* \\
&= -2 \sum_{j,k} \left(\sum_i p_i^* H_{ij} \right) H_{jk} p_j p_k - 2 \sum_i p_i^* \left(\sum_j H_{ij} p_j \right)^2 + 1 \\
&= -2 \sum_{j,k} \frac{1}{2} H_{jk} p_j p_k - 2 \sum_i p_i^* \left(\sum_j H_{ij} p_j \right)^2 + 1 \\
&= -\frac{1}{2} - 2 \sum_i p_i^* \left(\sum_j H_{ij} p_j \right)^2 + 1 \\
&= -2 \sum_i p_i^* \left(\sum_j H_{ij} p_j \right)^2 + \frac{1}{2},
\end{aligned}$$

where we used $\sum_i p_i^* H_{ij} = \frac{1}{2}$ and $\sum_{jk} H_{jk} p_j p_k = \frac{1}{2}$. Next we introduce $\xi_j = p_j - p_j^*$ (note that $\sum_j \xi_j = 0$ by definition), obtaining

$$\begin{aligned}
\frac{dV}{dt} &= -2 \sum_i p_i^* \left(\sum_j H_{ij}(p_j^* + \xi_j) \right)^2 + \frac{1}{2} \\
&= -2 \sum_i p_i^* \left(\frac{1}{2} + \sum_j H_{ij}\xi_j \right)^2 + \frac{1}{2} \\
&= -\frac{1}{2} - 2 \sum_i p_i^* \sum_j H_{ij}\xi_j - 2 \sum_i p_i^* \left(\sum_j H_{ij}\xi_j \right)^2 + \frac{1}{2} \\
&= -2 \sum_j \left(\sum_i p_i^* H_{ij} \right) \xi_j - 2 \sum_i p_i^* \left(\sum_j H_{ij}\xi_j \right)^2 \\
&= -\sum_j \xi_j - 2 \sum_i p_i^* \left(\sum_j H_{ij}\xi_j \right)^2 \\
&= -2 \sum_i p_i^* \left(\sum_j H_{ij}\xi_j \right)^2 \leq 0
\end{aligned}$$

for any choice of ξ , and therefore, for any value of p . Assuming that the matrix \mathbf{H} is of full rank, $dV/dt = 0$ only if $\xi = 0$, i.e., only if $p = p^*$. Since $V(p) \geq 0$ for any p and $V(p) = 0$ only if $p = p^*$, $dV/dt \leq 0$ implies that $p = p^*$ is a globally stable fixed point.

Chapter 7

Ecological assembly

Lesson plan:

1. We have seen in the previous lectures that a large ecological community will almost invariably be unstable, possibly leading to extinctions. It is therefore natural to ask what happens when either a feasible equilibrium does not exist, or it is unstable. In particular, we want to know how many species can persist.
2. We discuss the problem of assembly, and why is it so challenging to study analytically.
3. We introduce a few assumptions that make the problem tractable and at the same time non trivial.
4. We compute how many species will coexist in a GLV with random parameters, and see how we can study assembly by drawing an “assembly graph”

7.1 Assembly

We call **ecological assembly** the process by which **ecological communities are built** by the interplay of invasions (increasing community “richness”) and extinctions (decreasing it). The typical setting for an assembly model is one in which a large (possibly infinite) pool of species are available (e.g., in a “mainland”), and every so often individuals from the species’ pool enter a local habitat (island, patch, etc.), at which point they might either grow (invasion, establishment, etc.), or go extinct. In either case, the local community might respond to the invader—for example, the invader could send some of the local populations extinct, or shift the community from one state to another.

Historically, this type of island-mainland models (based on species) have been contrasted with “trait-environment” models, in which species’ traits, rather than identity are the focus of the dynamics. In such models, ideas such as

“environmental filtering” (i.e., the pruning of species that cannot grow in the local environment) and “trait underdispersion” (i.e., the fact that the filtering imposed by the environment results in a convergence in traits) arise naturally. When thinking of communities of competitors (e.g., different species of plants), then we might think that species’ interactions will also play a role—because species need to be different enough to coexist, this would generate “trait overdispersion” (due to limiting similarity). For a very opinionated summary of 25 years of discussions on these themes (1975-2000), see Weiher and Keddy (2001) (but first read the review Gotelli (1999), stating that the language and tone of the introduction is “an embarrassment to the discipline”).

The idea of assembly was first introduced in ecology by the pioneers of “succession”. For example, in 1899 Henry Chandler Cowles studied the vegetation development in the Indiana Dunes—sand dunes are first colonized by “pioneer” species of plants, which are then overgrown by different vegetation in older dunes. Because dunes are regularly disrupted by wind, one could make a “space-for-time” substitution and reconstruct the development of the vegetation as a “chronosequence”. Importantly, Cowles (and then Clements) held the view that succession would be a strongly ordered, “deterministic” process by which communities tended to a certain “climax” state. In the 1920s, Henry Gleason challenged this view, advocating for a much greater role for chance.

History: Henry Chandler Cowles (1869-1939)



Born in Kensington, Connecticut, Cowles attended Oberlin College, and received a PhD from the University of Chicago in 1898. His thesis is centered on the vegetation succession of the Indiana Dunes. His main inspiration came from the work of Eugen Warming (Cowles studied Danish in order to read the original *Plantesamfund*).

He was one of the pioneers of “ecology” in the US, a term that he helped popularizing, for example writing (along with Coulter and Barnes, all at U.

Chicago) *A textbook of botany for colleges and universities*, with the second volume dedicated to the “Ecology” of plants. He was one of the founding members of the Ecological Society of America (in 1915).

Another important piece of the puzzle was provided by the work of Jared Diamond who, while studying avian assemblages in New Guinea, proposed that certain species assemblages would be “forbidden” (due to competition)—by observing several instances of assembly (in the different islands), one could guess the rules of the assembly game (Diamond (1975)). Diamond’s work sparked decades of intense debate, bringing a focus on the role of null models in ecology (are the observed patterns due to chance or necessity?), with especially cogent critiques brought forward by Simberloff, Connor and Gotelli (see for example Gotelli and Graves (1996)).

History: Evelyn Chrystalla “E.C.” Pielou (1924-2016)



Born in England, and developing her career in Canada, she was one of the first women in mathematical ecology. She studied radio-physics at the University of London, receiving her certificate at 18 years old. She went on to work in the Navy during WWII—meeting, and subsequently marrying a biologist. This fact changed the course of her career—having completed a Bachelor’s degree in Botany, she kept publishing research while raising three children and eventually earning a PhD (also from U. London). After a few years in the Canadian Dept. of Forestry (and then Agriculture), she was hired as a full professor at Queens U. (Ontario), and subsequently Dalhousie and Lethbridge.

Her books “Introduction to Mathematical Ecology” and subsequent “Mathematical Ecology” (Pielou (1977))—which starts with: “*The fact that ecology is essentially a mathematical subject is becoming even more widely accepted*”—have formed generations of (theoretical) ecologists. As stated in her obituary “*Never afraid to express an opinion, she did not suffer fools gladly*”—as shown over and again in her work.

She is well-known for her books, for the development of null models in biogeography, and her measure of “evenness” of a community.

In the early 2000s, the focus changed decisively and became centered on the difference between “neutrality” (i.e., where species distribution are driven by stochastic fluctuations, Hubbell (2001)) and “niche” (i.e., driven by species interactions—or rather their avoidance).

Finally, the budding field of “community phylogenetics” (Cadotte and Davies (2016)) is centered on relating these concepts to data stemming from phylogenetic trees.

Here, we step back and reconsider basic models of ecological assembly in the style for example of Drake (1991), Law and Morton (1996), and Morton et al. (1996).

7.1.1 What makes the study of assembly difficult?

There are three main complications that stand in the way of the development of simple theories for ecological assembly (taken from Serván and Allesina (2020)):

1. **Invasion rates.** We have a timescale for the local dynamics, and a timescale for invasions, and the time at which the first species goes extinct after an invasion influences the effect of subsequent invasions. The simplest way to think of this is to have a “rock-paper-scissors” community. Suppose that our island contains only “rock”, and that “paper” enters the system—if we wait for long enough, it will displace rock; if *before rock goes extinct*, “scissors” invades, we can recover the full three-species community; if instead scissors arrives when rock is extinct, then it will displace paper.

As such, if the speed at which the dynamics of the local community proceed are slow enough compared to the rate of invasion, we have that several species can invade before the community has reached its asymptotic configuration. At the extreme where local dynamics are fast compared to the rate of invasion, we have that each invader finds the local community at its asymptotic state; as the invasion rate increases, the system approaches a point where all the species enter the system before any extinction takes place. Increasing the invasion rate even further would result in an open system with constant immigration.

2. **Invasion size.** Consider the two-species competitive Lotka-Volterra model with preemptive competition, and suppose that initially we have species x_1 resting at its carrying capacity, i.e., the state of the system is $\{x_1\}$. If x_2 invades with sufficiently low density, we find $\{x_1, x_2\} \rightarrow \{x_1\}$; on the other hand, if x_2 has sufficiently high density, we can cross the separatrix in the phase plane, leading to $\{x_1, x_2\} \rightarrow \{x_2\}$. This simple example shows that the density at which the invader enters the system can alter the outcome of the dynamics.
3. **Invasion timing.** When the local community coexists at a non-fixed point attractor, the fate of the invader could be very different depending on when it is introduced. For example, a predator requiring its prey to

be above a certain level would not be able to invade an oscillating system whenever prey are at low abundance, but would start growing if the invasion happened at a time when prey were abundant.

7.1.2 Ecological assembly without tears

We make three main assumptions, which remove the difficulties above while leaving the model interesting to study:

1. **Invasion events are rare.** We assume that the invasion rate is low enough such that, after an invasion, the local community has sufficient time to reach its asymptotic configuration before the next invader arrives. In other words, we consider cases in which local dynamics operates at a much faster rate than invasions. Note that this choice precludes certain dynamics; for example, under these stringent conditions the rock-paper-scissors community described above would never reach the three-species configuration. While this is a strong requirement, it corresponds to assumptions routinely made in the study of population genetics, and in invasion analysis.
2. **Invaders arrive at low abundance.** We assume that the density of the invader is low enough so that intraspecific effects are negligible at the time of invasion (again, as routinely assumed in invasion analysis). Under this assumption, the assembly of the Lotka-Volterra preemptive competition model would have two possible final states, corresponding to each species in isolation. Note also that whenever the invader can enter the system only at low abundance, the local stability of an attractor (i.e. the community at the attractor is resistant to small perturbations caused by changes in abundance of any of the species in the pool) is sufficient to make it a possible outcome of the assembly process.
3. **Fixed-point dynamics.** Finally, we consider models in which the asymptotic state of the local community is a feasible, stable equilibrium, thereby sidestepping the difficulty stemming from the timing of invasion.

For example, the Generalized Lotka-Volterra model with a symmetric matrix of interaction A yields only fixed-point dynamics.

7.1.3 Top-down and bottom-up assembly

We distinguish between two extreme cases of assembly. In **top-down** assembly, all species enter the system (at arbitrary densities) **at the same time**; assembly then is simply the pruning of some of the species through the dynamics. At the other extreme, we find **bottom-up assembly**, in which species enter the system one at a time. Our second lecture will focus on top-down assembly, and the third on bottom-up assembly.

7.2 Modeling invasions

Imagine starting with a bare environment, and introducing the first species. If the species can grow in the new environment, it will establish, and if not, it will go extinct. Mathematically, we assume that **new species are introduced at very low abundance**, so that they do not experience self-limitation due to crowding, and that **invasion are spaced in time** so that the dynamics can play out before the next invasion happens. For example, consider the GLV model, and the case of the first species entering the system, and write the equation for the per-capita growth rate:

$$\frac{1}{x_i(t)} \frac{dx_i(t)}{dt} = r_i + A_{ii}x_i(t)$$

If $x_i(0) \ll 1$, we can set $A_{ii}x_i(0) \approx 0$, obtaining

$$\frac{1}{x_i(t)} \frac{dx_i(t)}{dt} \approx r_i$$

That is, the species will establish if it has a positive growth rate in the new environment. Suppose that this is the case: then species i will grow to its equilibrium abundance $x_i^* = -r_i/A_{ii}$. Now add a second species. Its initial per-capita growth rate is going to be:

$$\frac{1}{x_j(t)} \frac{dx_j(t)}{dt} = r_j + \sum_k A_{jk}x_k(t) \approx r_j + A_{ji}x_i^*$$

Species j can therefore grow when rare if $r_j + A_{ji}x_i^* > 0$, i.e., $r_j > -A_{ji}x_i^*$. We call this type of inequality an “**invasion criterion**”.

If the species j can grow when rare, in general, it could a) grow initially, but then go extinct; b) displace species i , sending it to extinction; c) coexist with species i . By reiterating invasions with different species, we can assemble a large ecological community.

7.2.1 Invasions in multispecies communities

Now consider a pool of species (e.g., a metacommunity/mainland) and an environment (e.g., a local habitat/island) in which some of the species are present, and coexisting at an equilibrium. We have n species in the pool, and k species in the habitat/island. We want to write conditions for the invasibility of the equilibrium. To this end, we can re-arrange the rows and columns of A , and the elements of r to obtain two blocks: one for the k species already in the community, and one for the $n - k$ potential invaders.

The fixed point \bar{x} can be written as:

$$\bar{x} = \begin{pmatrix} x^{(k)} \\ 0^{(n-k)} \end{pmatrix}$$

where $x^{(k)}$ contains the density of the coexisting species. Similarly, the growth rates are

$$r = \begin{pmatrix} r^{(k)} \\ r^{(n-k)} \end{pmatrix}$$

and the interaction matrix

$$A = \begin{pmatrix} A^{(k,k)} & A^{(k,n-k)} \\ A^{(n-k,k)} & A^{(n-k,n-k)} \end{pmatrix}$$

where each block $A^{(a,b)}$ contains the effects of the species in set b on the growth of the species in a . For feasibility we need:

$$x^{(k)} = -\left(A^{(k,k)}\right)^{-1} r^{(k)} > 0$$

Now we want to write the condition for the **non-invasibility** of the resident community by the other species in the metacommunity. For each species in $(n - k)$, we need to have a negative growth rate when invading:

$$r^{(n-k)} + A^{(n-k,k)} x^{(k)} < 0$$

an equilibrium \bar{x} for which a) the $x^{(k)}$ is feasible and stable (when considering only the species in k) and b) no other species can invade when rare is called the **feasible, stable, non-invasive solution** or the **saturated equilibrium**.

7.2.2 Lyapunov stability and saturated equilibria

We have seen in previous section that, whenever there exists a diagonal matrix with positive coefficients on the diagonal C such that $CA + A^T C$ is negative definite, and we have a feasible equilibrium x^* , then the equilibrium is globally stable.

Now we consider the case in which a feasible equilibrium does not exist. However, we have proven that a **saturated equilibrium** exists and is unique: we have an equilibrium \bar{x} in which some components are positive and some are zero such that k species coexist at a globally stable equilibrium, and the remaining $(n - k)$ species cannot invade it.

7.3 Top-down assembly

To begin our explorations of assembly, we consider the case in which all species are introduced in the habitat at the same time, and at arbitrary initial densities.

Here we investigate the simplest case in which dynamics are given by the GLV model, the (stable) matrix of interactions has random coefficients, and the growth rates are also random. For simplicity, we take the off-diagonal elements of A and the growth rates from a distribution centered at zero. This case was studied by Serván et al. (2018).

First, we are going to consider a trivial case, then consider a more complex one, and finally outline the proof in Serván et al. (2018).

7.3.1 A trivial case

Suppose we take n populations, each growing according to:

$$\dot{x}_i = x_i(r_i - A_{ii}x_i)$$

with $A_{ii} > 0$. We assume that the growth rates are sampled independently from a distribution: $r_i \sim Q$, a distribution with mean 0, $\mathbb{E}(r_i) = 0$ and symmetric about its mean, such that $\phi(r_i) = \phi(-r_i)$, where $\phi(\cdot)$ is the p.d.f. of distribution Q . For example, we could choose $r_i \sim \mathcal{N}(0, \sigma^2)$, or $r_i \sim \mathcal{U}[-1, 1]$. Naturally, whenever $r_i > 0$, the population will grow to $x_i^* = r_i/A_{ii}$. If $r_i < 0$, on the other hand, the population will go extinct. Because of the symmetry around zero, each population has therefore probability 1/2 of persisting. When we have n populations, the number of coexisting populations $\|k\|$ is a random variable following the binomial distribution:

$$p(\|k\||n) = \binom{n}{\|k\|} \frac{1}{2^n} \quad \|k\| \sim \mathcal{B}\left(n, \frac{1}{2}\right)$$

7.3.2 The random zoo

Now consider a GLV model with random parameters. We choose r_i from a distribution with mean zero and symmetric about the mean, and each interaction A_{ij} from a distribution with mean zero and symmetric about the mean. Moreover, we add a constant to the diagonal of the matrix such that the symmetric part of A , $H(A) = \frac{1}{2}(A + A^T)$ is positive definite. As we have seen before, this means that dynamics will always converge to a saturated equilibrium.

We now introduce a family of 2^n matrices S_i , with:

$$\begin{aligned}
S_1 &= \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & \cdots & 0 \\ 0 & 0 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} = I_n \\
S_2 &= \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & 1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \\
S_3 &= \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \\
S_4 &= \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \\
&\vdots \\
S_{2^n} &= \begin{pmatrix} -1 & 0 & 0 & \cdots & 0 \\ 0 & -1 & 0 & \cdots & 0 \\ 0 & 0 & -1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & -1 \end{pmatrix} = -I_n
\end{aligned}$$

These matrices, called *signature matrices* are their own inverse (a matrix with this property is called *involutory*), and therefore, we have that $S_i S_i = S_i^2 = I_n$. Geometrically, these matrices represent a reflection in each of the axes corresponding to the negated rows or columns.

We then consider what happens when we transform the parameters by multiplying them by S_i . Take an arbitrary GLV system, and solve for the x that makes $r - Ax = 0_n$:

$$x = A^{-1}r$$

The vector is a feasible equilibrium for the system if $x > 0_n$. Now consider the transformed system:

$$r' = S_i r \quad A' = S_i A S_i$$

Note that A' is similar to A , and therefore has the same eigenvalues; moreover, $\phi(r') = \phi(r)$ and $\phi(A') = \phi(A)$, because of symmetry. Now compute the new solution

$$\begin{aligned} x' &= (A')^{-1} r' \\ &= (S_i A S_i)^{-1} S_i r \\ &= S_i A^{-1} S_i S_i r \\ &= S_i A^{-1} r \\ &= S_i x \end{aligned}$$

That is, the transformation changes the sign of the components of x corresponding to the negative coefficients in S_i . Hence, for any possible choice of r and A , there is only one possible choice of S_i that makes the equilibrium feasible. Because all matrices A' and all vectors r' have the same probability/density, then the probability of having a positive x is exactly $1/2^n$. Thus, a system with random parameters and a strongly stable matrix of interactions has the same probability of feasibility as that of a system in which populations are not interacting!

We have seen that when A is such that $H(A)$ is negative definite, dynamics always converge to a saturated equilibrium. We want to compute the probability of finding a saturated equilibrium, in which populations belonging to set k coexist, and the remaining populations cannot invade when rare.

We thus divide x , r and A as:

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

We also divide S_i into:

$$S_i = \begin{pmatrix} S_i^{(k)} & 0_{\|k\|, \|n-k\|} \\ 0_{\|n-k\|, \|n\|} & S_i^{(n-k)} \end{pmatrix}$$

When we use the signature matrix, the vector \mathfrak{s} and the matrix \mathfrak{C} become:

$$\mathfrak{s}' = S_i^{(n-k)} \mathfrak{s} \quad \mathfrak{C}' = S_i^{(n-k)} \mathfrak{C} S_i^{(k)}$$

The feasibility and noninvadability condition, for a given choice of S_i read:

$$\begin{cases} y' = S_i^{(k)} (\mathfrak{A}^{-1} \mathfrak{r}) > 0_{\|k\|} \\ D(z)^{-1} z = S_i^{(n-k)} (\mathfrak{s} + \mathfrak{C} y') < 0_{\|n-k\|} \end{cases}$$

There is only one choice out of $2^{\|k\|}$ that makes $y' > 0_{\|k\|}$; moreover, there is only one choice of $S_i^{(n-k)}$ that fulfills the noninvasibility condition, out of $2^{\|n-k\|}$ equiprobable choices. Then, we have that the probability of finding exactly $\|k\|$ populations coexisting at the saturated equilibrium, with the remaining $\|n - k\|$ that cannot invade is exactly $1/(2^{\|k\|} \cdot 2^{\|n-k\|}) = 1/2^n$. The number of coexisting populations at the saturated equilibrium follows the binomial distribution:

$$p(\|k\||n) = \binom{n}{\|k\|} \frac{1}{2^n} \quad \|k\| \sim \mathcal{B}\left(n, \frac{1}{2}\right)$$

exactly as for the non-interacting case.

7.3.3 Simulating final composition

This section details how the problem above can be simulated efficiently. First, we load some functions to integrate GLV dynamics and plot results:

```
source("dat/general_code_assembly.R")
```

And then write functions to give us a (barely) stable, symmetric matrix A , and random growth rates:

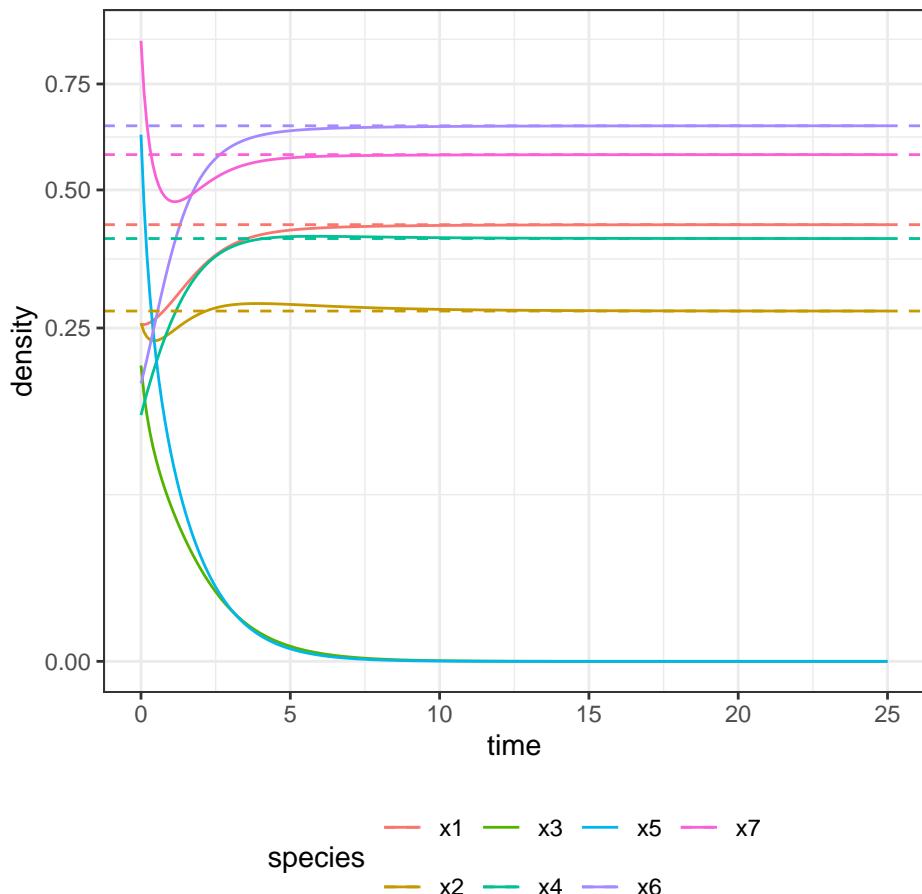
```
# function to build symmetric, Lyapunov Diagonally-stable matrix
build_LDstable <- function(n){
  A <- matrix(0, n, n)
  A[upper.tri(A)] <- rnorm(n * (n - 1) / 2)
  # make symmetric
  A <- A + t(A)
  # now find the largest eigenvalue
  l1A <- max(eigen(A, only.values = TRUE, symmetric = TRUE)$values)
  if (l1A > 0){
    # set the diagonal to make it stable
    diag(A) <- diag(A) - l1A - 0.01
  }
  return(A)
}

# function to get random growth rates
build_randomr <- function(n){
  return(rnorm(n))
}
```

Now, we build a random system with seven species, and integrate the dynamics:

```
set.seed(5) # for reproducibility
n <- 7
A <- build_LDstable(n)
r <- build_randomr(n)
```

```
x0 <- runif(n)
out <- GLV_dynamics(z0 = x0, A = A, r = r, maxtime = 25, bytime = 0.1)
show(plot_dynamics(out))
```

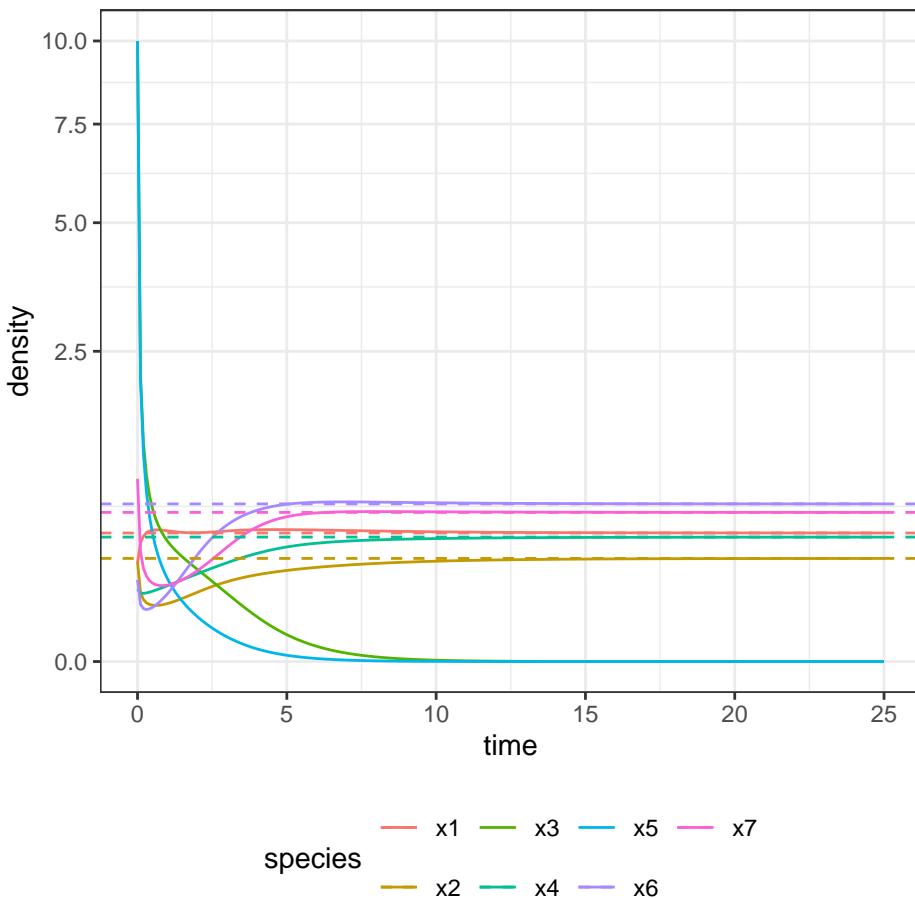


```
knitr::kable(
  out$ts %>%
    filter(out$ts$time == max(out$ts$time))
)
```

time	species	density
25	x1	0.4290121
25	x2	0.2761340
25	x3	0.0000000
25	x4	0.4021960
25	x5	0.0000000
25	x6	0.6452999
25	x7	0.5776737

As you can see, in this case, two species (3 and 5) go extinct, while the other ones reach a feasible equilibrium. Let's try to start the system with species 3 and 5 at high abundance, to show that the equilibrium is indeed globally stable:

```
x0[3] <- 10
x0[5] <- 10
out <- GLV_dynamics(z0 = x0, A = A, r = r, maxtime = 25, bytime = 0.1)
show(plot_dynamics(out))
```



```
knitr::kable(
  out$ts %>%
    filter(out$ts$time == max(out$ts$time))
)
```

time	species	density
25	x1	0.4291312
25	x2	0.2759277
25	x3	0.0000000
25	x4	0.4020638
25	x5	0.0000000
25	x6	0.6454349
25	x7	0.5777422

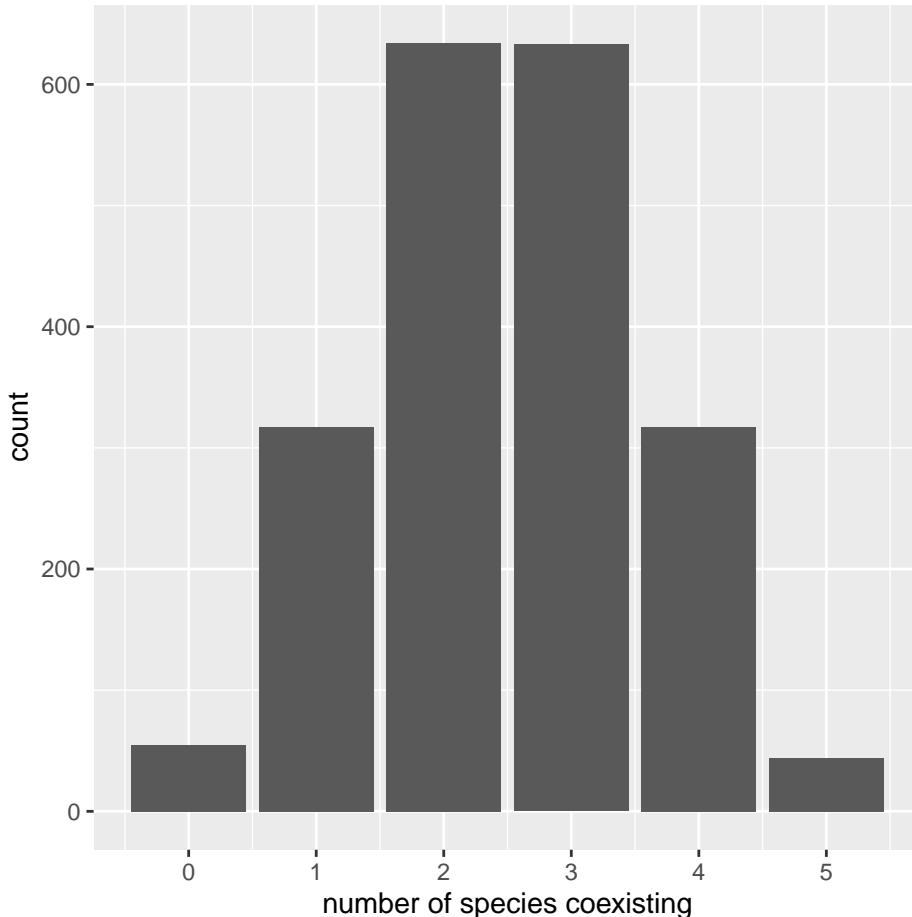
As you can see, the system still goes to the same equilibrium, with 3 and 5 extinct. Turns out, for this type of system, one does not even need to integrate dynamics: the Lemke–Howson algorithm can be adapted to solve the problem efficiently (Serván et al. 2018) (this is an efficient algorithm to find Nash equilibria in a game). I have coded up the algorithm already, and you can load the function `get_final_composition(A, r)` by typing:

```
source("dat/L-H.R")
get_final_composition(A, r) # use LH instead of integrating dynamics
```

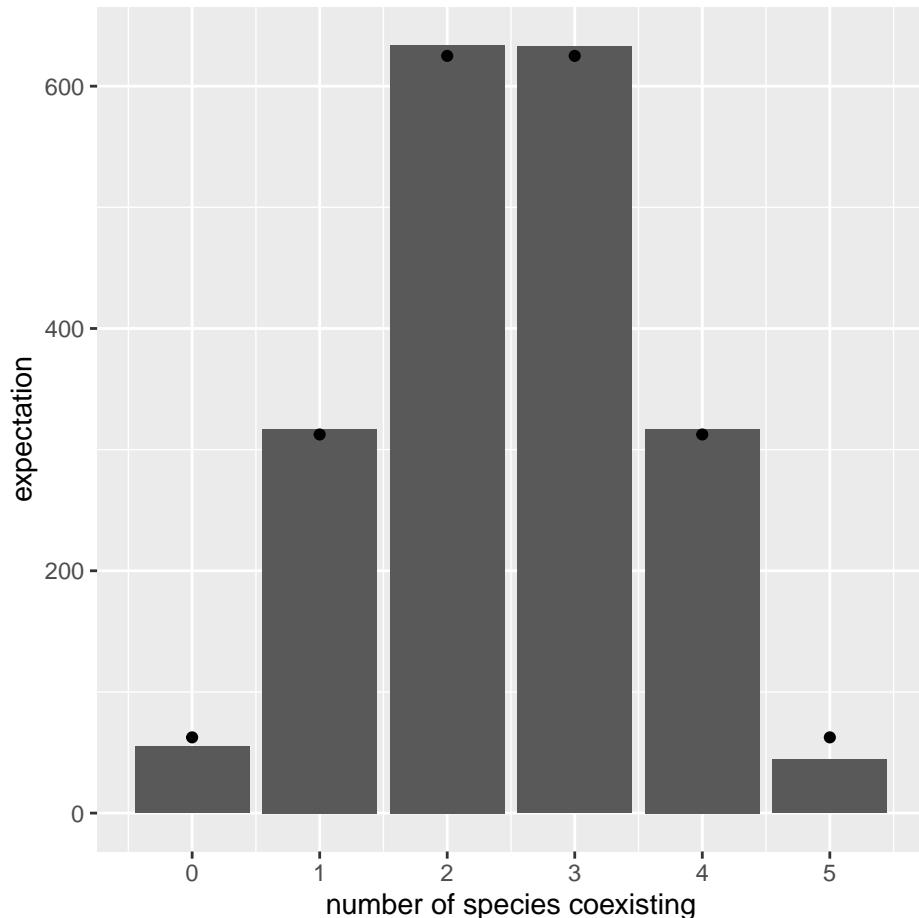
```
[1] 0.4290300 0.2761030 0.0000000 0.4021761 0.0000000 0.6453202 0.5776840
```

To simulate the random zoo, we take random matrices and random growth rates with n species, and tally the number of coexisting species over several simulations:

```
set.seed(1)
n <- 5
nsim <- 2000
results <- tibble(simulation = 1:nsim,
                   ncoexisting = rep(NA, nsim))
for (i in 1:nsim){
  # build the matrix and vector
  A <- build_LDstable(n)
  r <- build_randomr(n)
  xstar <- get_final_composition(A, r)
  results$ncoexisting[i] <- sum(xstar > 0)
}
pl <- ggplot(data = results) +
  aes(x = ncoexisting) +
  geom_bar() +
  scale_x_continuous("number of species coexisting", breaks = 0:10)
show(pl)
```



```
# add binomial distribution
tbinom <- data.frame(ncoexisting = 0:n,
                      expectation = nsim * dbinom(0:n, n, 0.5))
pl <- pl + geom_point(data = tbinom, aes(x = ncoexisting, y = expectation))
show(pl)
```



We find again that the number of coexisting species follows the binomial distribution with parameters n and $1/2$ (i.e., exactly the same result found for non interacting species).

7.3.4 A random zoo in the wild

One might object that the derivations above have no parallel in reality. However, they can be seen as a simplified version of an experiment done routinely by ecologists. Take for example the work of Bittleston et al. (2020). They sampled bacterial communities from ten different pitcher plants, and cultured them in the laboratory on a synthetic medium. They tracked the change of richness in time. This is their Figure 2 (look at panel b):

The more the species present at day 3 (i.e., once those with a negative growth rate had disappeared), the more one would find after two months—and the relationship is linear!

7.4 Bottom-up assembly

Mother Nature, of course, does not assemble her networks by throwing n species together in one go. It makes more sense to assume that she adds one species after another through successive invasions.

Sigmund (1995)

Having considered the case in which all species are thrown into the habitat at the same time (**top-down** assembly), we consider a process in which we start from the “bare ground” and build our community from the **bottom-up**.

Note that in top-down assembly, any feasible equilibrium can be achieved by starting with the appropriate initial conditions; being slightly less generous, we can think of being able to assemble from the top-down any “persistent” (e.g., stable), feasible community we can form from the pool. It makes therefore sense to ask whether these same states can or cannot be accessed when assembling the community from the ground up.

7.4.1 Simulating bottom-up assembly

Now let’s make it more complicated: we assemble an ecological community from the ground up. At each step, we introduce a species at low abundance, starting from an empty community. We then compute the new equilibrium, completing a step of the assembly:

```
assembly_one_step <- function(x, r, A){
  n <- nrow(A)
  invader <- sample(1:n, 1)
  x[invader] <- 0.001 # introduce the invader at low abundance
  present <- x > 0 # these are the species present now
  # compute new equilibrium
  y <- get_final_composition(A[present, present, drop = FALSE], r[present])
  x[present] <- y
  return(x)
}
```

Now we can take a species pool along with their parameters, and try to assemble the system until we can no longer add any more species (i.e., until we reach a saturated equilibrium):

```
set.seed(7)
n <- 10
A <- build_LDstable(n)
r <- build_randomr(n)
# start with no species
x <- rep(0, n)
# assemble for 40 steps and keep track of richness and composition
ninvasions <- 40
```

```

results <- tibble(invasion = 1:ninvasions,
                   richness = rep(NA, ninvasions),
                   composition = rep(NA, ninvasions))
for (i in 1:ninvasions){
  x <- assembly_one_step(x, r, A)
  results$richness[i] <- sum(x > 0)
  results$composition[i] <- paste((1:n)[x>0], collapse = "-"))
}
knitr::kable(head(results))

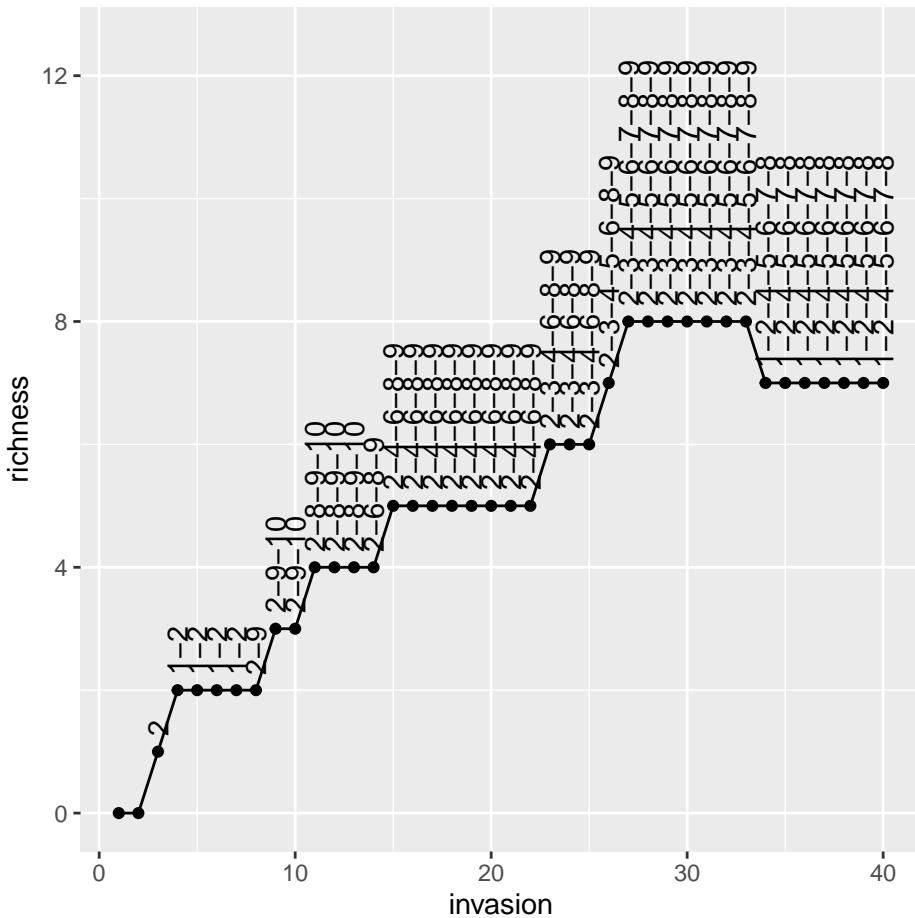
```

invasion	richness	composition
1	0	
2	0	
3	1	2
4	2	1-2
5	2	1-2
6	2	1-2

```

pl <- ggplot(results) + aes(x = invasion, y = richness, label = composition) +
  geom_point() + geom_line() + geom_text(hjust = 0, nudge_y = 0.25, angle = 90) +
  ylim(c(0, n * 1.25))
show(pl)

```

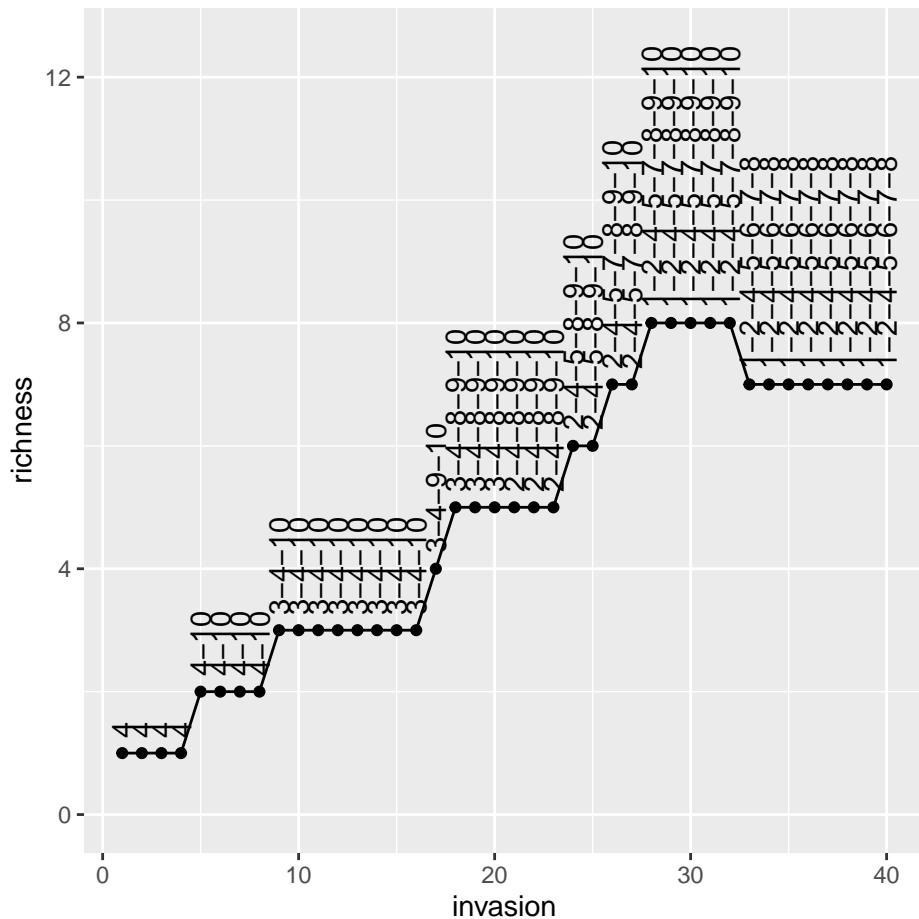


Now let's roll back history and assemble again:

```
# start with no species
x <- rep(0, n)
# assemble for 40 steps and keep track of richness
ninvasions <- 40
results <- tibble(invasion = 1:ninvasions,
                   richness = rep(NA, ninvasions),
                   composition = rep(NA, ninvasions))
for (i in 1:ninvasions){
  x <- assembly_one_step(x, r, A)
  results$richness[i] <- sum(x > 0)
  results$composition[i] <- paste((1:n)[x>0], collapse = "-"))
}
knitr::kable(head(results))
```

invasion	richness	composition
1	1	4
2	1	4
3	1	4
4	1	4
5	2	4-10
6	2	4-10

```
pl <- ggplot(results) + aes(x = invasion, y = richness, label = composition) +
  geom_point() + geom_line() + geom_text(hjust = 0, nudge_y = 0.25, angle = 90) +
  ylim(c(0, n * 1.25))
show(pl)
```



As you can see, despite taking a different assembly history, we reach the same final composition. In fact, this is exactly what we would expect if we were to throw all species in the environment at the same time:

```
get_final_composition(A, r)

[1] 1.7588344 2.5440743 0.0000000 0.7860178 1.8730535 2.5502055 0.6961259
1.6956878 0.0000000 [10] 0.0000000

x

[1] 1.7588344 2.5440743 0.0000000 0.7860178 1.8730535 2.5502055 0.6961259
1.6956878 0.0000000 [10] 0.0000000
```

In fact, given enough time, any assembly history for a symmetric, stable matrix A will eventually reach the final composition represented by the saturated equilibrium (Serván and Allesina (2020)).

Interestingly, this is not the case when the matrix is not symmetric. Serván et al. (2018) conjectured however that the probability of finding a system whose final composition cannot be assembled one species at a time decreases rapidly with the size of the pool, as long as A is Lyapunov Diagonally stable.

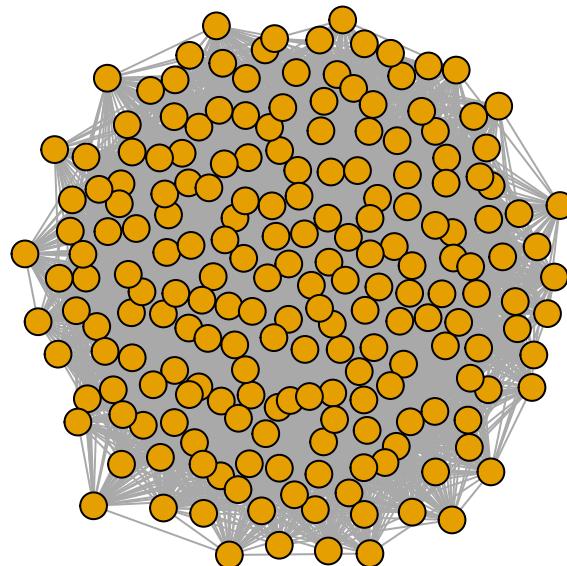
7.4.2 Network spandrels

What is the network structure of the assembled community vs. that of the initial pool? Can we detect a signature of the forces acting on the community such that some species can persist, while other go extinct? To answer these questions, we start by considering a larger pool of species:

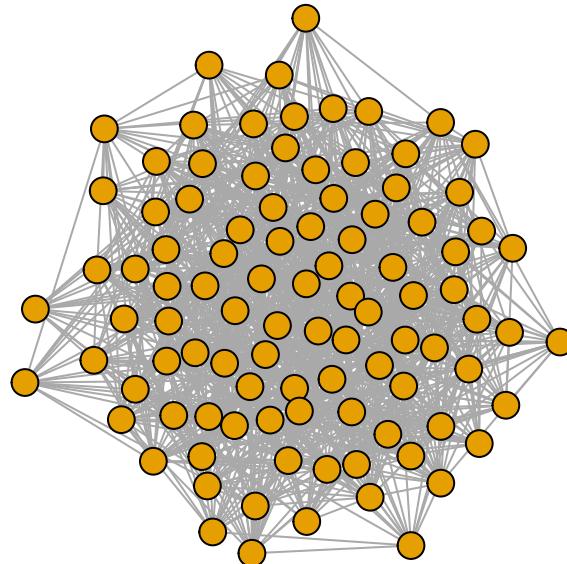
```
set.seed(1)
# initial pool
A <- build_LDstable(200)
r <- build_randomr(200)
# final composition
xstar <- get_final_composition(A, r)
A_pruned <- A[xstar > 0, xstar > 0]
r_pruned <- r[xstar > 0]
```

Are the properties of matrix A different from those of the pruned version \tilde{A} ? We probe this in two ways: first, we build a graph with the strongest interactions, and plot it.

```
# draw an edge i->j if Bij is above the 75% of strengths (in abs)
plot_graph_strong <- function(B, quantile = 0.75){
  Bstrong <- abs(B)
  diag(Bstrong) <- 0
  Bstrong[Bstrong < quantile(Bstrong, quantile)] <- 0
  gr <- graph_from_adjacency_matrix((Bstrong > 0) * 1, mode = "undirected")
  plot(gr, vertex.size=10, vertex.label=NA, layout=layout_with_fr)
}
plot_graph_strong(A)
```



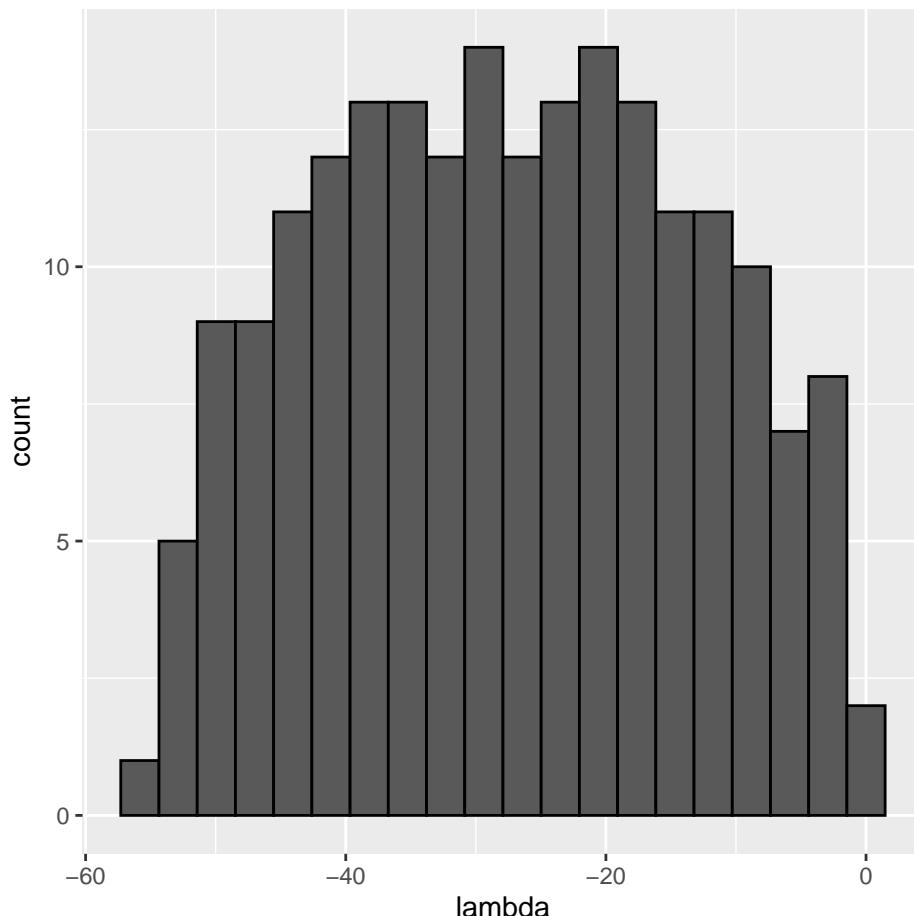
```
plot_graph_strong(A_pruned)
```



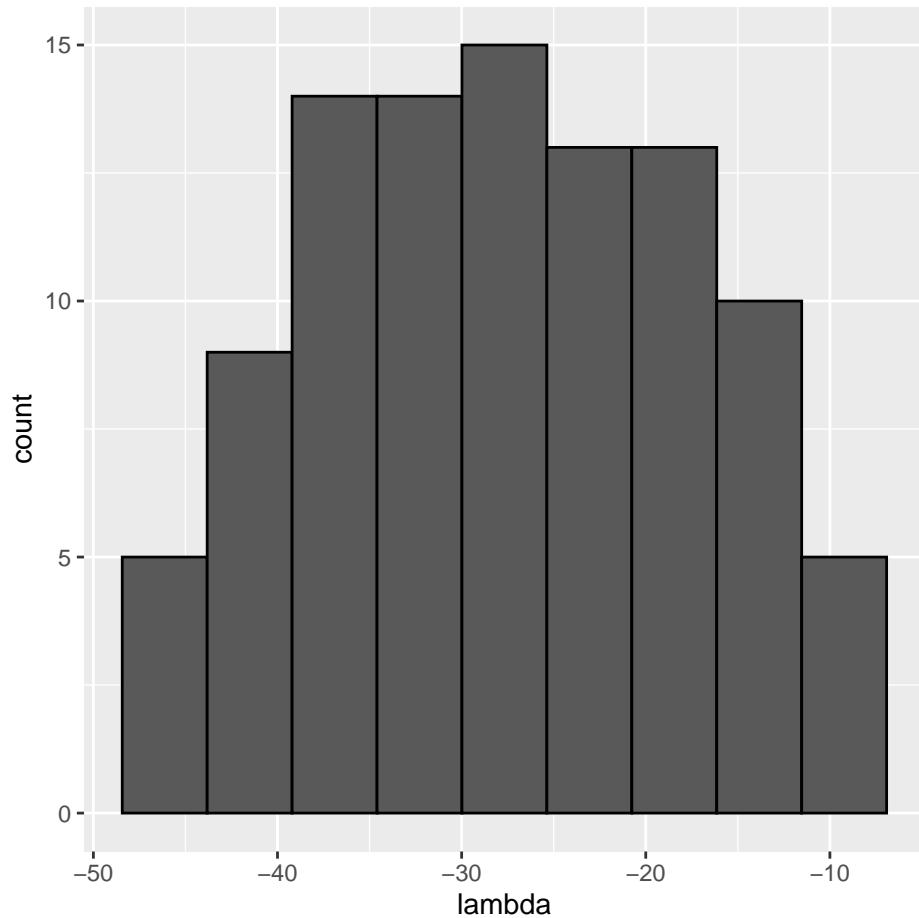
There seems to be no special structure. A more powerful way to show the same is to plot the eigenvalues of A and \tilde{A} . For a symmetric matrix with off-diagonal elements centered at zero, the eigenvalues should follow Wigner's semicircle law:

```
plot_eigen <- function(B){
  evals <- data.frame(lambda = eigen(B, only.values = TRUE, symmetric = TRUE)$values)
  ggplot(data = evals) +
```

```
aes(x = lambda) +  
  geom_histogram(bins = as.integer(nrow(evals) / 10), colour = "black")  
}  
plot_eigen(A)
```

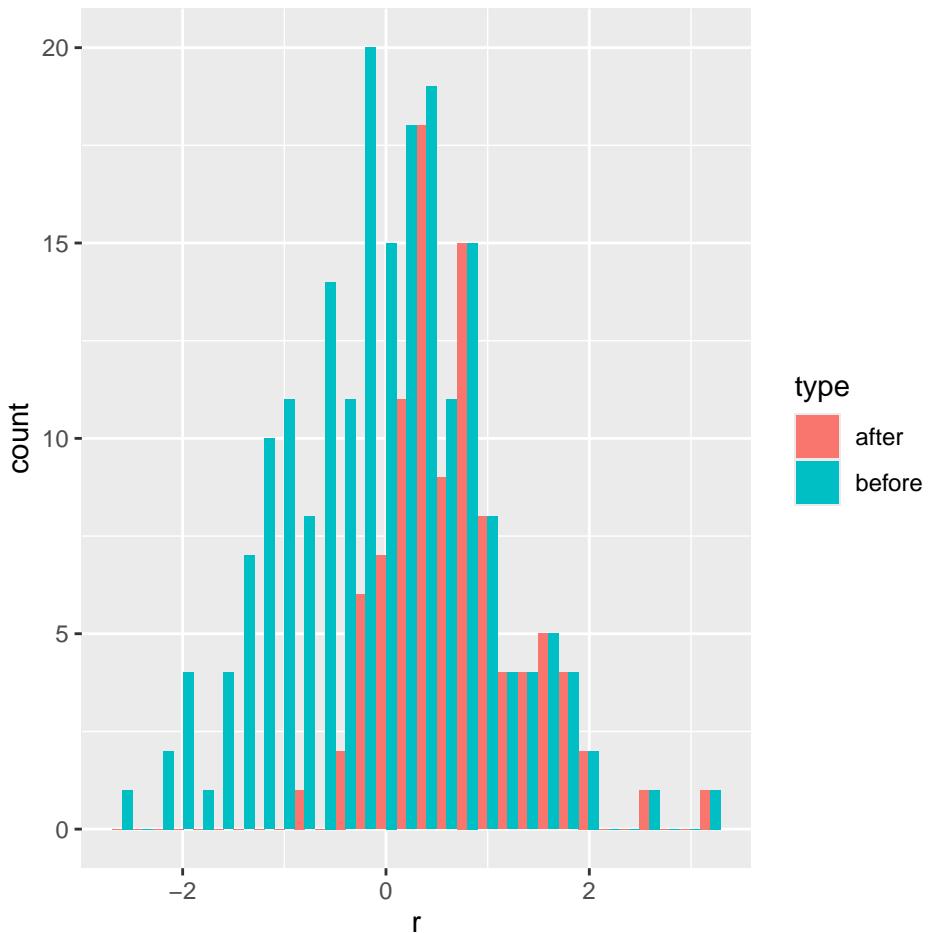


```
plot_eigen(A_pruned)
```



As such, the matrix of interactions before/after dynamics seem to have the same properties. However, as shown in Serván et al. (2018), the distribution of the growth rates changes in a non-trivial way:

```
toplot <- data.frame(r = r, type = "before")
toplot <- rbind(toplot, data.frame(r = r_pruned, type = "after"))
ggplot(toplot) + aes(x = r, fill = type) + geom_histogram(position = "dodge")
```



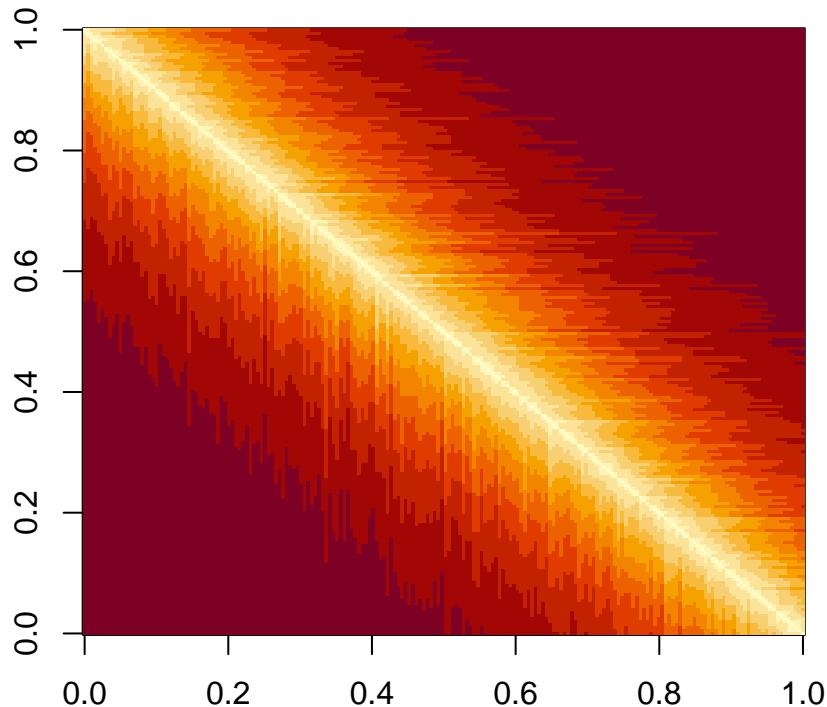
But what if species were to be related to each other? For example, suppose $r_i = 1$ for all species, and build a matrix in which the interactions of species $i + 1$ are obtained by mutating slightly those of species i :

```
n <- 200
r <- rep(1, 200)
A <- matrix(0, n, n)
# set first species
A[1, 1] <- -1
# now each species is obtained by mutating the previous one
for (i in 2:n){
  ai <- A[i -1,] * (1 - 0.05 * runif(n))
  A[i, ] <- A[i, ] + ai
  A[, i] <- A[, i] + ai
  A[i, i] <- -1
}
```

```
# make LD-stable
l1 <- max(eigen(A, only.values = TRUE, symmetric = TRUE)$values)
if (l1 > 0) diag(A) <- diag(A) - l1 * 1.01
```

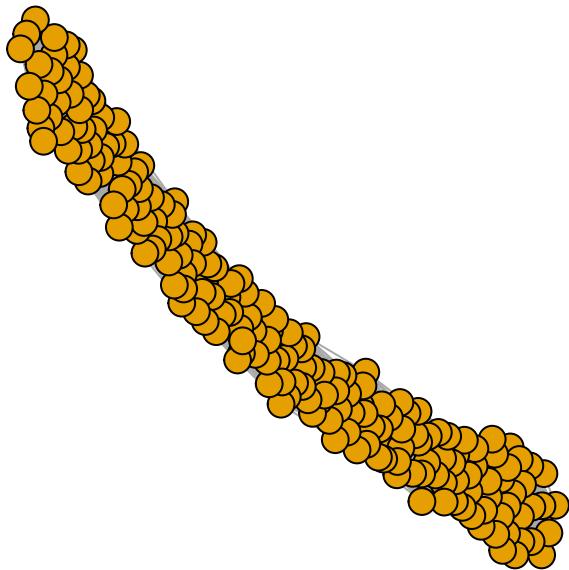
Now each species is similar to the previous one:

```
image(A[1:n, n:1])
```

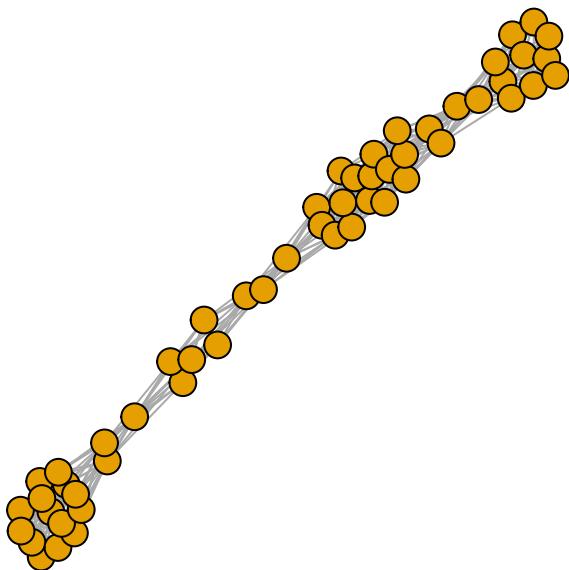


Perform the pruning, and plot networks and eigenvalues:

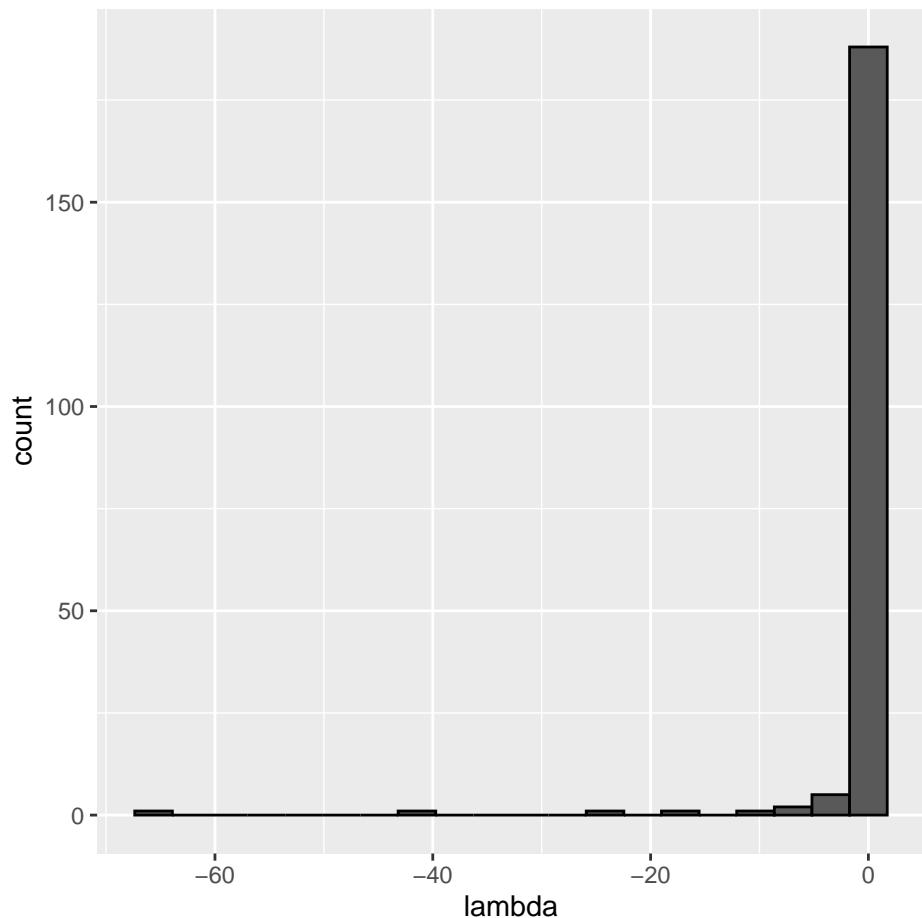
```
xstar <- get_final_composition(A, r)
A_pruned <- A[xstar > 0, xstar > 0]
r_pruned <- r[xstar > 0]
plot_graph_strong(A)
```

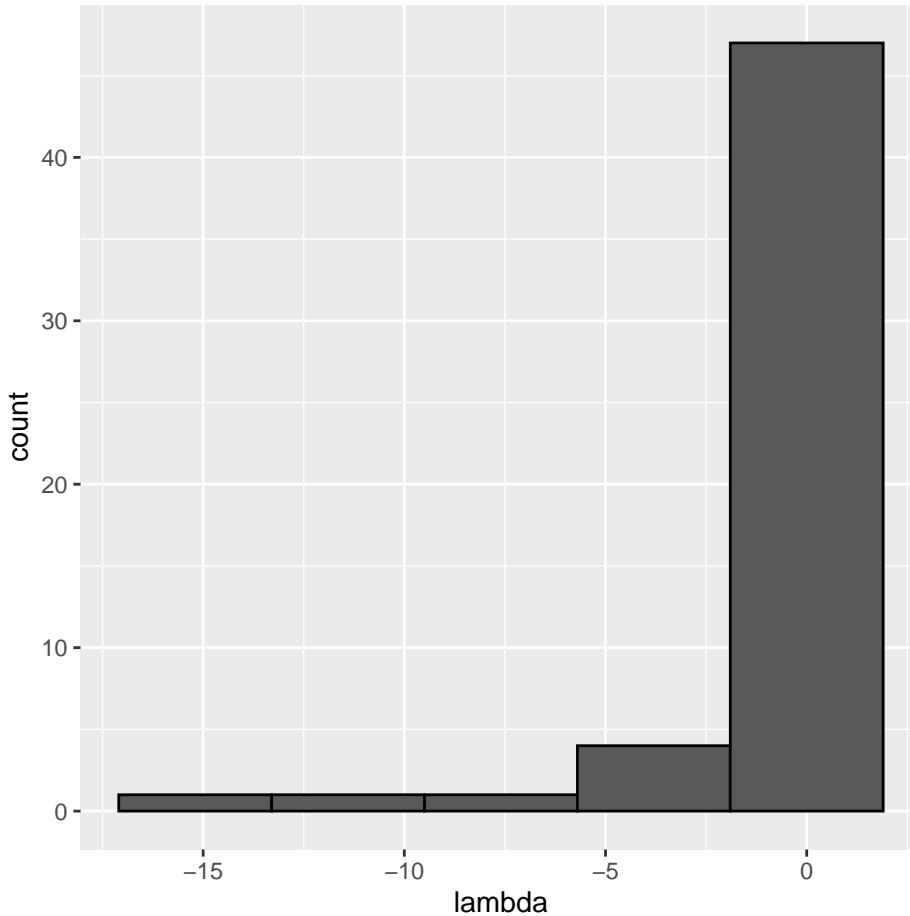


```
plot_graph_strong(A_pruned)
```



```
plot_eigen(A)
```





Meaning that if our matrix A is structured, we will recover a structured matrix after pruning, while if A is unstructured, we will recover an unstructured matrix. Maynard et al. (2018) showed that a well-defined network structure could be a “network spandrel” (cfr. Gould and Lewontin (1979) and Solé and Valverde (2006)) arising from the way new species are introduced, rather than a “signature of stability”.

7.4.3 An assembly graph

In GLV, a given (sub-)community has at most one feasible equilibrium; that is, there is **no true multi-stability in GLV**: we can find the system at different stable states, but **they have to differ in composition**. Because of this fact, we can devise a scheme to label the possible states our community can be in.

We call 0 the state in which no species are present, 1 the state in which only species 1 is present, 2 the state in which only species 2 is present, 3 the state in which species 1 and 2 are both present, and so on. Practically, we take

the community composition to be the base-2 representation of the label. For example, label 11 in a community of 6 species corresponds to 001011 (i.e., a state in which species 1, 2, and 4 are present). As this notation makes obvious, for a given pool of n species, we can have up to $2^n - 1$ feasible equilibria. As we saw in Lecture 1, the existence of a feasible equilibrium is a necessary (but not sufficient—we should require also some form of stability/permanence) condition for coexistence.

Clearly, any feasible (and persistent/stable) sub-community can be observed by initializing the system at (or, in case of locally/globally stable configurations, close to) the desired densities. On the other hand, unstable configurations will eventually collapse to some other sub-community. As such, we take the labels/states representing stable/persistent communities to be the **nodes** in a directed graph. Then, we take the **edges** of this graph to represent invasions, moving the local community from one state to another. To keep the graph simple, we only consider “successful” invasions (i.e., those for which the initial and final state differ), thereby removing the need for “self-loops”.

This **assembly graph** was considered several times in the literature (see for example Law and Morton (1993), Hang-Kwang and Pimm (1993), Schreiber and Rittenhouse (2004), Capitán et al. (2009)). Here, we follow the approach Serván and Allesina (2020), and note that the assembly graph fully describes the assembly process whenever the assumptions that we’ve made at the onset of our exploration (invasions are rare, invasions are small, dynamics converge to equilibria) are satisfied. When this is the case, we can study the assembly process in its full glory by studying a graph (which definitely sounds more fun!).

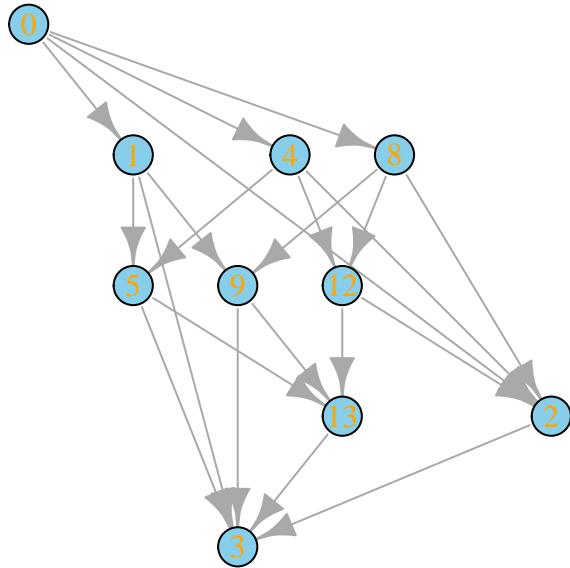
7.4.4 How many invasions?

First, we might want to think of the problem of invasion. The bottom-up assembly can be seen as a single, massive invasion. At the other extreme, we have assembly proceeding with invasions of a single species at a time. Of course, we can imagine anything in between: species invade in small groups, there is a distribution describing the number of species invading at each step, etc.

For example, let’s build the assembly graph for a given set of (random) parameters: we take A to be a symmetric, **stable** nonpositive matrix (e.g., representing competition between species), and r to be a vector of positive, random growth rates. Let’s build the assembly graph when we consider that species can enter the system only one at a time:

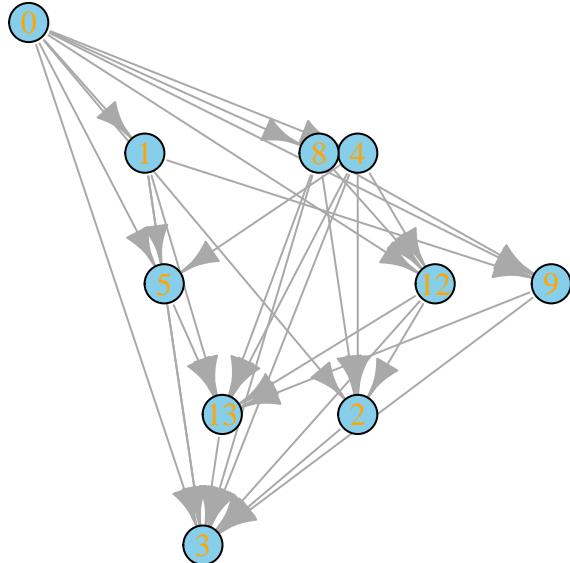
```
source("dat/general_code_assembly.R")
source("dat/L-H.R") # Lemke-Howson algorithm to get saturated equilibrium
source("dat/build_assembly_graph.R")
source("dat/build_assembly_graph_unstable.R") # code to build and draw assembly graphs
set.seed(4) # for reproducibility
A <- build_competitive_stable(4)
r <- runif(4)
```

```
assembly_invasion_1 <- build_assembly_graph_unstable(r, A)
plot_assembly_graph(assembly_invasion_1$graph, assembly_invasion_1$info)
```



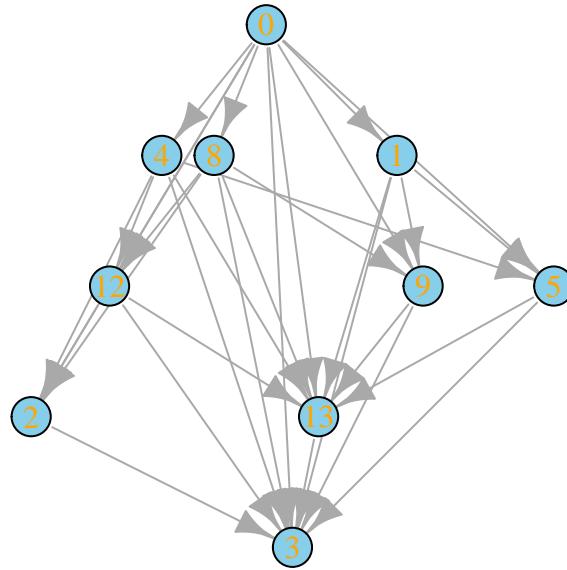
What if we allow for two invasions at a time?

```
assembly_invasion_2 <- build_assembly_graph_unstable(r, A, 2)
plot_assembly_graph(assembly_invasion_2$graph, assembly_invasion_2$info)
```



And allowing four invasions in one go (as in top-down assembly):

```
assembly_invasion_4 <- build_assembly_graph_unstable(r, A, 4)
plot_assembly_graph(assembly_invasion_4$graph, assembly_invasion_4$info)
```



For simplicity, let's stick with the case in which only a single species enter in the local community at every invasion event.

7.4.5 Properties of the assembly graph

Accessibility: which states can we reach starting from the bare ground, and performing invasions of (say) one species at a time? We call states that can be built in this way “accessible”. Translated into graph properties, we call a state accessible if there is a path leading from the state 0 to the community of interest (“an assembly path”). If all states are accessible, we call the graph itself accessible. States that are not accessible can be reached by top-down, but not bottom-up assembly.

Cycles: directed cycles in the graph translate into sub-communities for which invasions drive the system in a cyclic composition (a generalization of rock-paper-scissors!).

Assembly endpoints: if a node has no outgoing edges, assembly will stop once the corresponding state has been reached. We call this state an “assembly endpoint”. A more complex type of assembly endpoint is that in which there is a cycle connecting two or more communities, and the cycle as a whole has no outgoing edges.

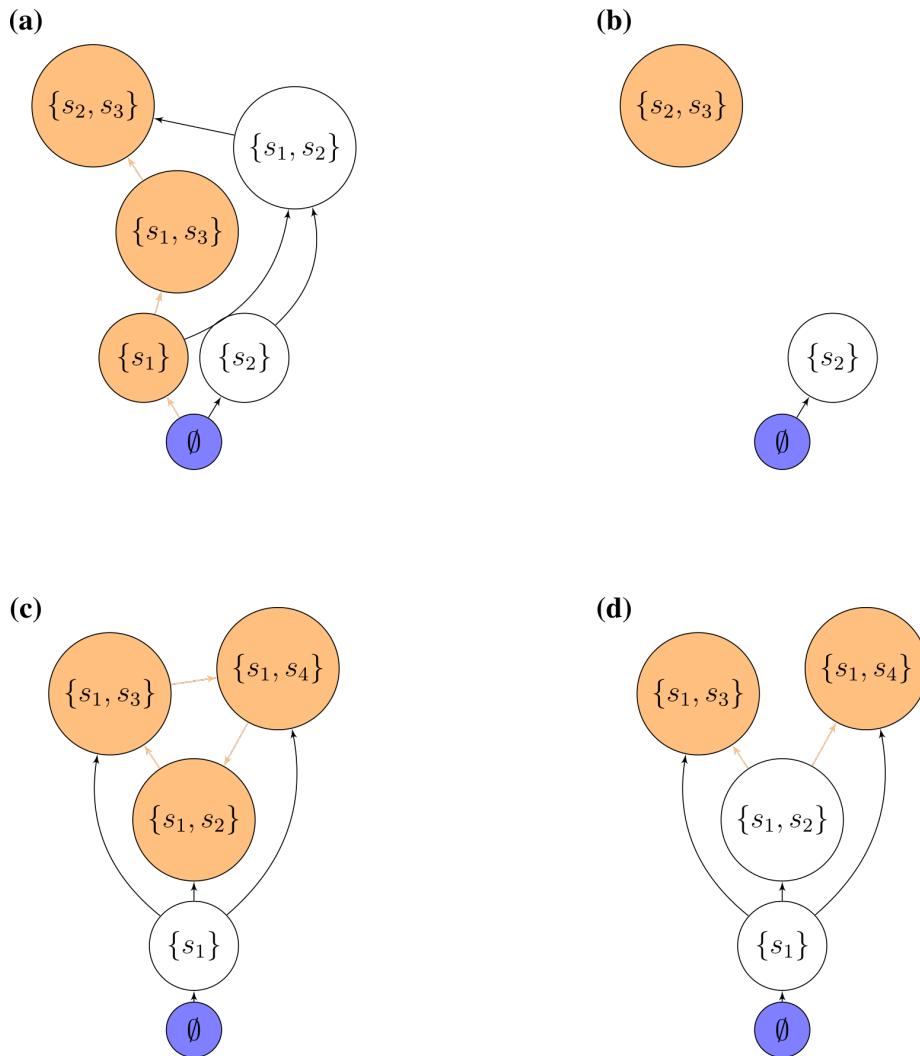


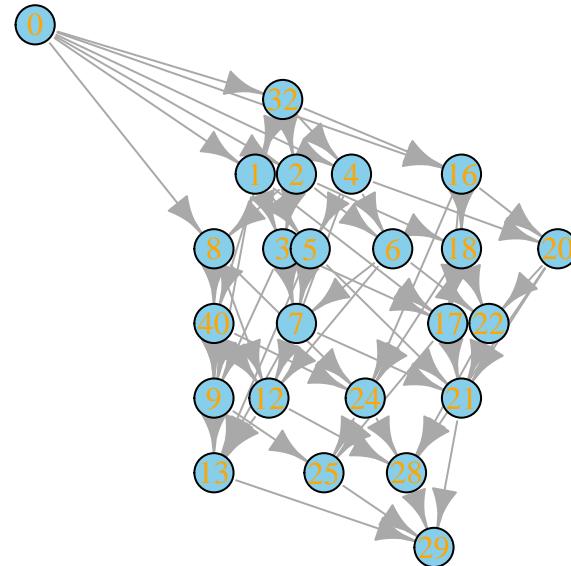
Figure 7.1: Possible assembly graphs

7.4.6 Assembly graphs for GLV

For GLV with symmetric, competitive interactions (actually, for a slightly more general case), Serván and Allesina (2020) proved that:

- For a species pool of competitors (i.e., a given $r > 0$ and a symmetric matrix $A < 0$), **the bottom-up assembly endpoints are the same as the endpoints for top-down assembly**.
- Moreover, **the assembly graph is accessible**—therefore we can build any feasible, stable sub-community from the ground up. In fact, for each sub-community we can find the “shortest” assembly path, which we can construct without any extinction.
- **The assembly graph is acyclic**, meaning that we will never observe communities with cyclic compositions.
- **Every walk on the assembly graph eventually reaches a sink**, and, when A is stable, **the sink is unique**. This means that for this type of species pool, historical contingencies (Fukami (2015)) are impossible—if we wait for long enough, the system will always reach the same state, thereby erasing any trace of the assembly history.

```
set.seed(5)
A <- build_competitive_stable(6)
r <- runif(6)
ag <- build_assembly_graph_unstable(r, A)
plot_assembly_graph(ag$graph, ag$info)
```



Community “29” is composed of species 1, 3, 4, 5. We can assemble this state

without extinctions starting from the bare ground: first invade with species 4, sending the community to state “8”; then, add species 3, moving the state to “12”; then add species 5, moving to “28”, and finally add species 1, reaching “29”.

This fact has important consequences: for example, we can assemble the final state without the need for “transient invaders” (or “stepping stone species”, i.e., species that allow the assembly to proceed, but then disappear). Recently Amor et al. (2020) demonstrated experimentally the occurrence of transient invaders: they co-cultured *Corynebacterium ammoniagenes* (Ca) and *Lactobacillus plantarum* (Lp) and showed that one species displaces the other, with the identity of the winner depending on initial conditions (bistability). When the environment is dominated by Lp, Ca cannot invade. However, if first we introduce *Pseudomonas chlororaphis* (Pc), and then invade with Ca, Lp-dominated environments can be invaded by Ca—and Pc disappears without a trace. This is their Figure 1:

7.4.7 Relationship with Lyapunov functions

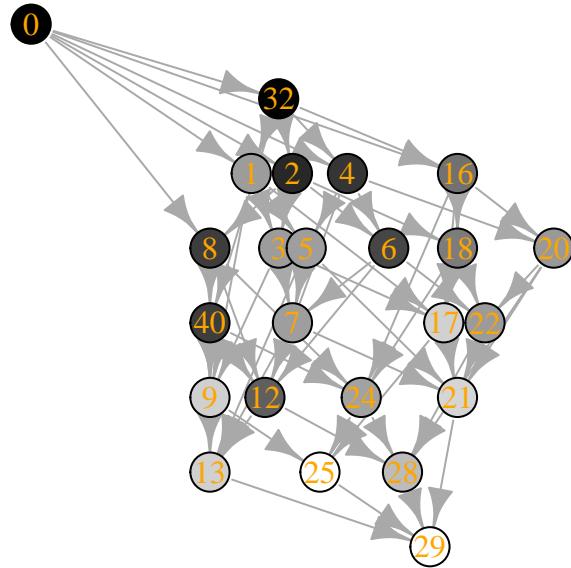
If a graph has the properties above (acyclic, single source, single sink), then there is a way to order the nodes such that all edges point in the same direction (topological sorting). In this case, we can devise an “energy” associated with each community state such that assembly “maximizes” the quantity, connecting “low-energy” states to “high-energy ones” via invasion.

In fact, we can even write down such a function—it is exactly the Lyapunov function devised by MacArthur (1970, Note: the first paper ever in Theoretical Population Biology!) for GLV with symmetric, competitive interactions:

$$V(x) = 2 \sum_i r_i x_i + \sum_{i,j} A_{ij} x_i x_j$$

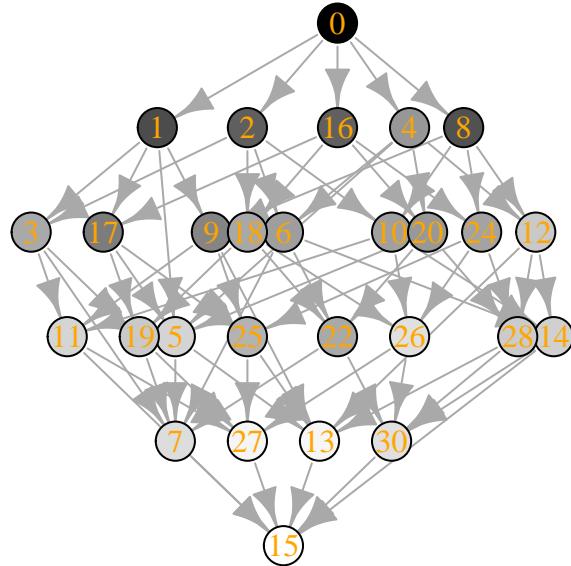
MacArthur proved that this quantity is maximized through the dynamics when the equilibrium exists and A is stable. At equilibrium, we find $V(x^*) = \sum_i r_i x_i^*$. During assembly, community composition changes such that $V(\bar{x})$ is maximized through the assembly process. Note that when $r_i = 1$ for all species, then $V(\bar{x})$ is simply the total biomass in the community. As such, through invasions the total biomass in the community is maximized.

```
plot_assembly_graph(ag$graph, ag$info, TRUE)
```



Now a case with equal growth rates:

```
set.seed(10)
A <- build_competitive_stable(5)
r <- rep(1, 5) # same growth rates!
ag2 <- build_assembly_graph(r, A)
plot_assembly_graph(ag2$graph, ag2$info, TRUE)
```



The community “15” is composed of species 1, 2, 3, and 4, while community “30” of species 2, 3, 4, and 5. Let’s compute their biomasses:

```
# community 15
biom_15 <- sum(solve(A[1:4, 1:4], -r[1:4]))
print(paste("Community 15:", biom_15))
```

```
[1] "Community 15: 0.974135821684639"
# community 30
biom_30 <- sum(solve(A[2:5, 2:5], -r[2:5]))
print(paste("Community 30:", biom_30))
```

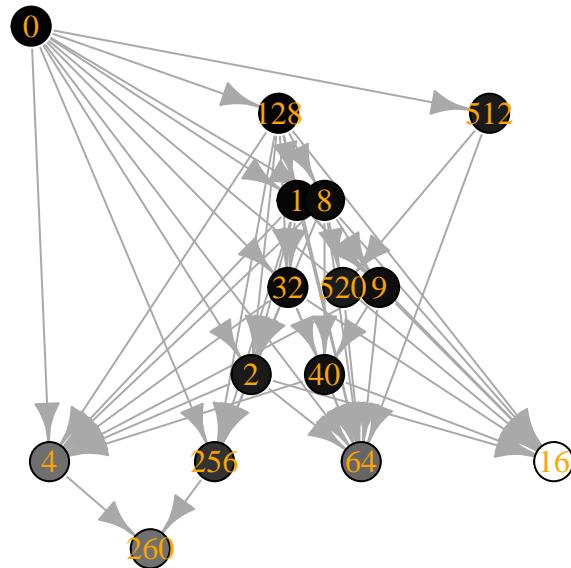
```
[1] "Community 30: 0.855081379845787"
```

This result would have pleased Cowles, Gleason, Odum, and many of the pioneers of succession! For these (restrictive) conditions, assembly is indeed an orderly, predictable process, culminating in a “climax” with a clear ecological interpretation. (For a similar result in a completely different context, see Suweis et al. (2013)).

7.4.8 How many assembly endpoints?

What happens when the matrix A is still nonpositive and symmetric, but not stable? In this case, it is Gleason who can laugh—for unstable matrices we can have several assembly endpoints, thereby reinstating the role of chance in determining the ultimate fate of the community.

```
source("dat/general_code_assembly.R")
source("dat/build_assembly_graph_unstable.R")
set.seed(5)
n <- 10
A <- build_competitive_unstable(n)
r <- runif(n)
tmp <- build_assembly_graph_unstable(r, A)
plot_assembly_graph(tmp$graph, tmp$info, TRUE)
```



Note that the Lyapunov function still holds (locally): when moving on the graph, the “energy” is always increased.

The number of “assembly endpoints” (i.e., saturated equilibria) depends on the stability of the matrix—what if we reduce the stability even further?

```
# these are the diagonal elements
diag(A)
```

```
[1] -1.1244467 -1.7740170 -0.9204892 -1.4486570 -0.1384223 -2.9264971 -0.3754522
-2.0440457 [9] -1.1836697 -0.2244013
```

```
# and these the eigenvalues
eigen(A, symmetric = TRUE, only.values = TRUE)$values
```

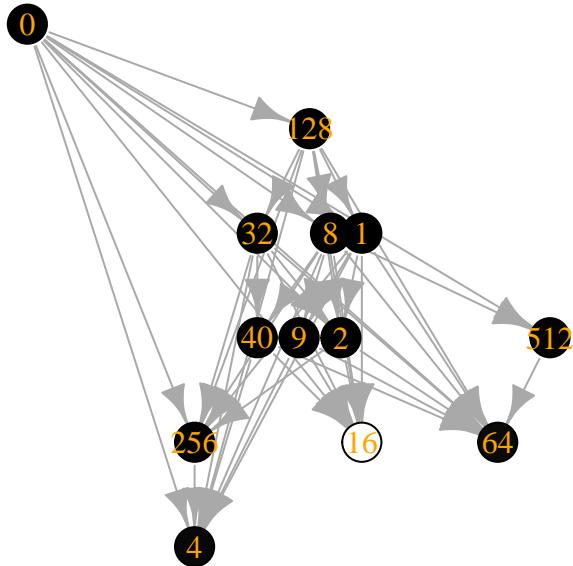
```
[1] 6.6159328 5.3603879 3.1108237 1.1950182 -0.1931400 -0.5697615 -2.2641869
-3.2814435 [9] -3.5994749 -18.5342540
```

Let’s add 0.13 to the diagonal (such that the fifth species has almost no self-regulation)—this shifts all of the eigenvalues to the right:

```
A2 <- A
diag(A2) <- diag(A2) + 0.13
eigen(A2, symmetric = TRUE, only.values = TRUE)$values
```

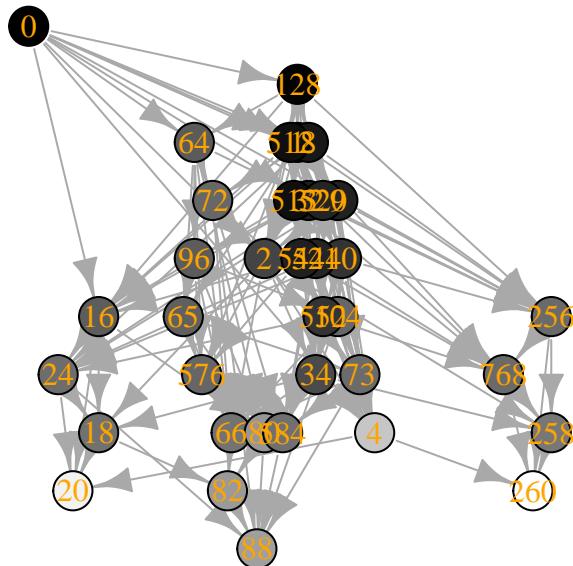
```
[1] 6.74593280 5.49038786 3.24082373 1.32501822 -0.06313999 -0.43976150 -
2.13418688 [8] -3.15144351 -3.46947493 -18.40425400
```

```
tmp <- build_assembly_graph_unstable(r, A2)
plot_assembly_graph(tmp$graph, tmp$info, TRUE)
```



Similarly, by shifting the eigenvalues to the left, we can get access larger communities:

```
A3 <- A
diag(A3) <- diag(A3) - 2
tmp <- build_assembly_graph_unstable(r, A3)
plot_assembly_graph(tmp$graph, tmp$info, TRUE)
```



Interestingly, how the number of assembly endpoints changes when we change the parameters of the model is an open problem—in fact we haven't even

characterized the worse-case scenario. See Biroli et al. (2018) for a derivation showing that they should be growing exponentially with size.

7.4.9 Build your own assembly graph!

Building the assembly graph is computationally very expensive, even with all these results at hand. Fortunately, we do not need to integrate the dynamics (a point that was greatly debated in the literature, see Morton et al. (1996) for one of the rare cases in which a debate ends up with consensus between opposing factions).

Currently, the algorithm can be sketched as:

- for each of the 2^n possible sub-communities (ranging from bare ground to all species present), determine whether the sub-community is feasible and stable (this is the most computationally expensive step);
- now go through all the feasible, stable communities; for each determine the “neighbor” communities that can be reached with (say, one) invasion(s).
- call S the feasible, stable community we are considering, and add species j (or multiple species), and check that j can invade when rare. If it cannot, move to the next neighbor; If it can, there are two cases:
 - if the community $\{S, j\} = S'$ is feasible and stable, draw an edge $S \rightarrow S'$
 - if the community $\{S, j\} = S'$ is not feasible and stable, the system will collapse to a smaller sub-community; to determine which sub-community it will collapse to, **check all the possible sub-communities** of S' , and take the one with the greatest $V(x^*)$, S'' . Draw an an edge $S \rightarrow S''$

Can a better (faster, more efficient) algorithm be devised?

Homework 5

Build the assembly graph for a GLV model in which the growth rates of all species are the same, and interactions are given by phylogenetic relatedness.

In particular, consider an ultrametric phylogenetic tree T , and the “variance-covariance” matrix induced by the tree, Σ . Because the tree is ultrametric, then $\Sigma_{ii} = 1$ for all i . The off-diagonal elements Σ_{ij} express the proportion of shared ancestry (and as such $1 \geq \Sigma_{ij} \geq 0$).

Take the GLV model:

$$\frac{dx}{dt} = D(x)(1 - \Sigma x)$$

Notice that Σ is positive (semi-)definite by construction. Now build the assembly graph: does it have any interesting property?

7.4.10 Conclusions

We have explored the problem of ecological assembly by working with the Generalized Lotka-Volterra model and three main assumptions: 1) invasions are rare, such that invaders always find the local community at the attractor; 2) invasion sizes are small; and 3) dynamics always lead to equilibria—thereby allowing us to determine the unique outcome of any invasion event.

These three assumptions made the study of assembly **tractable, and yet not trivial**, allowing us to map the complex dynamics of the system into an **assembly graph**: the properties of this graph translate directly into ecological properties of the assembly process.

For competitive Lotka-Volterra with symmetric interactions, when the interaction matrix is stable, all assembly paths will eventually lead to the same state (the “saturated equilibrium” we’ve seen in Lectures 1 and 2). In this case, the history that led to the community cannot be reconstructed from the final state. When the matrix of interactions is unstable, on the other hand, the system can end up in different places depending on the history of assembly.

We have also found that for these cases, **top-down** (all in one go) and **bottom-up** (sequential) assembly can reach exactly the same states. Top-down assembly experiments (e.g., with bacterial communities) are much easier to perform than bottom-up ones, and I believe that this approach has been underexploited (both theoretically, and experimentally).

Much more work remains to be done to reach a general theory of ecological assembly (even for GLV), but the results shown here provide a good springboard, and an expectation, for the study of more complex cases.

Chapter 8

Metapopulation dynamics on networks

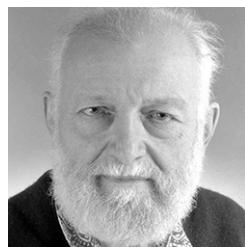
Lesson plan:

1. We analyze Levins' metapopulation model, which we've encountered before.
2. We introduce the idea of a network of dispersal, and see how metapopulation persistence depends on network structure.
3. We draw a parallel with Susceptible-Infected-Susceptible models, in which individuals play the role of habitable patches and parasites disperse on a network of contacts.

8.1 Metapopulations

In 1969, Richard Levins—then a professor at U. Chicago—proposed a simple model for a “metapopulation”, i.e., a “population of populations in which local extinctions are balanced by remigration from other populations” (Levins (1969)).

History: Richard Levins (1930-2016)



Born in Brooklyn, New York, he studied agriculture and mathematics at Cornell. Early on, influenced by geneticist and polymath Haldane, he became a Marxist

activist. Upon graduation, having been blacklisted as a communist (and with the Korean War raging), he moved to Puerto Rico with his wife, and set up a farm. In his spare time, he conducted experiments on fruit flies, organized anti-colonialist rallies and anti-war protests, and taught at the University of Puerto Rico. In 1964, he was invited to Cuba to help organize the biology department of the University of Havana. He received his doctorate from Columbia University in 1965. In 1967 he moved to the University of Chicago, where he joined Richard Lewontin—whith whom he established a lifelong collaboration. They both moved to Harvard in the late 1970s.

It is impossible to summarize his numerous contributions to ecology, mathematics, political science, and the philosophy of science. He has inspired countless ecologists, and his approach and style are still visible in many of the research programs being carried out today. Of particular interest for this class, his theory of evolution in a changing environment (Levins (1968)), the development of the idea of limiting similarity (MacArthur and Levins (1967)), his work on metapopulation dynamics (Levins (1969)), and the development of Loop Analysis (i.e., a qualitative theory for dynamical systems, Puccia and Levins (2013)).

Key paper: Levins (1966)

A must read for anyone interested in modeling (in biology and elsewhere). Just two quotes that resonate with the approach taken in these lectures:

- *there are too many parameters to measure; some are still only vaguely defined; many would require a lifetime each for their measurement.*
- *The equations are insoluble analytically and exceed the capacity of even good computers,*
- *Even if soluble, the result expressed in the form of quotients of sums of products of parameters would have no meaning for us.*

...

Therefore, we attempt to treat the same problem with several alternative models each with different simplifications but with a common biological assumption. Then, if these models, despite their different assumptions, lead to similar results we have what we can call a robust theorem which is relatively free of the details of the model. Hence our truth is the intersection of independent lies.

The model is very simple. Suppose that there are very many patches of suitable habitat, and that we track the proportion of patches occupied by a certain species, $x(t)$. Two processes affect the proportion of occupied patches: **extinction**, turning an occupied patch into a vacant patch, and **colonization**, turning a vacant patch into an occupied patch. For the simplest case, suppose that occupied patches can send “propagules” to empty patches at a fixed rate γ , and that the rate at which local populations go extinct is the same for all patches, δ .

Call $y(t) = 1 - x(t)$ the proportion of vacant patches. Then, the dynamics for the occupied patches are described by the equation:

$$\frac{dx(t)}{dt} = -\delta x(t) + \gamma x(t)y(t)$$

in which we assume mass-action (like in GLV). Similarly, the equation for the proportion of vacant patches is:

$$\frac{dy(t)}{dt} = \delta x(t) - \gamma y(t)x(t)$$

Note that the two equations sum to zero (i.e., we're in a zero-sum setting), as $x(t) + y(t) = 1$. Then, we can turn the model into a single equation, by substituting $y(t) = 1 - x(t)$ in the first equation:

$$\frac{dx(t)}{dt} = -\delta x(t) + \gamma x(t)(1 - x(t)) = x(t)(\gamma - \delta - \gamma x(t))$$

which is the usual equation for the logistic growth. As such, the equilibrium $x^* = (\gamma - \delta)/\gamma = 1 - \delta/\gamma$ is globally stable.

Calling $S(t) = y(t)$ and $I(t) = x(t)$ we obtain an SIS model in which a pathogen infect (“occupies”) individuals (“patches”). The equilibrium $I^* = (\gamma - \delta)/\gamma$ is reached whenever $\gamma > \delta$ (i.e., $\gamma/\delta = \mathcal{R}_0 > 1$). We carry this parallel through the lecture.

8.2 Hanski Ovaskainen 2000

In Levins' model, all patches are connected with all other patches, such that the rate of colonization does not depend on the identity of the patch serving as the source of propagules.

History: Ilkka A. Hanski (1953-2016)



Photo by Otso Ovaskainen.

Born in Lempaala, Finland, he studied at the University of Helsinki, and received his doctorate from the University of Oxford in 1979. From 1981 to his premature death in 2016, he worked at various Finnish institutions, lastly at the Academy of Finland.

His work on metapopulation theory is extremely well-known, thanks also to the amazing work on the Glanville fritillary butterfly *Melitaea cinxia*. This butterfly inhabits the dry meadows in Åland Islands archipelago—with about 4000 meadows, sampled yearly by an army of students since 1991, the fragmented landscape is an ideal testing ground for metapopulation theory.

Hanski won numerous awards, and served as a strong advocate for ecological conservation.

Hanski and Ovaskainen (2000) (mathematical details in Ovaskainen and Hanski (2001)) consider a model in which patches are spread geographically, and colonization from patch i to patch j depends on the distance (actually, an “effective distance”) between patches. In particular, they start from Levins’ model, written for a focal patch. We take x_i to be the probability that patch i is occupied at time t (and therefore $1 \geq x_i \geq 0$) as:

$$\frac{dx_i}{dt} = [\text{Colonization rate } i](1 - x_i) - [\text{Extinction rate } i]x_i$$

They also consider the patches a_1, \dots, a_n to have different “values” (i.e., support populations of different sizes). In this context, it makes sense to assume that the extinction rate in patch i is $\delta_i = \delta/a_i$. Similarly, the probability of colonization should decrease with distance, and be directly proportional to patch values; for example, one could choose $\gamma_{ij} = \gamma e^{-\alpha D_{ij}} a_j$, where D is a matrix of Euclidean distances between patches, α models the typical mobility of the species (i.e., the typical “dispersal bout” is of length $1/\alpha$), and γ is a constant. With these assumptions, the dynamics are described by:

$$\frac{dx_i}{dt} = \gamma(1 - x_i) \sum_{j \neq i} e^{-\alpha D_{ij}} a_j x_j - \frac{\delta}{a_i} x_i$$

Now we want to derive a condition for the existence of a positive equilibrium (i.e., at equilibrium the species is expected with probability nonzero in all patches). At equilibrium, we have:

$$\gamma(1 - x_i^*) \sum_{j \neq i} e^{-\alpha D_{ij}} a_j x_j^* = \frac{\delta}{a_i} x_i^*$$

It is convenient to multiply both sides by a_i , and to define the **dispersal matrix** M , with zero on the diagonal, and $M_{ij} = M_{ji} = a_i a_j \gamma e^{-\alpha D_{ij}}$. Then, the equilibrium condition reads:

$$(1 - x_i^*) \sum_j M_{ij} x_j^* - \delta x_i^* = 0$$

The matrix M has zero on the diagonal. Then, $\sum_{j \neq i} M_{ij}x_j^* = \sum_j M_{ij}x_j^*$. Note that then if $\sum_j M_{ij}x_j^* = 0$ for any i , we have $x_i^* = 0$. This means that patches that are disconnected ($\sum_j M_{ij} = 0$), or that are connected to patches where the species is absent ($\sum_j M_{ij}x_j^* = 0$ with $\sum_j M_{ij} > 0$). If, on the other hand, we assume that not all x_j are zero, we can write:

$$1 - x_i^* = \delta \frac{x_i^*}{\sum_j M_{ij}x_j^*}$$

Which can be written compactly as:

$$x_i^* = 1 - \delta \frac{x_i^*}{(Mx^*)_i}$$

Now we need a result from the theory of nonnegative matrices (such as M).

Collatz-Wielandt formula

A matrix A is called nonnegative $A \geq 0$ if $A_{ij} \geq 0$ for all i, j . There exists a positive eigenvalue ρ with associated eigenvector v such that $Av = \rho v$ and v has positive components (Perron-Frobenius). Moreover, $|\rho| \geq |\lambda_i|$ for all other eigenvalues, and every other eigenvector has at least a negative component. Finally, we have that for a nonnegative vector x

$$\rho = \max_{x \in \mathbb{R}_{0+}^n, x \neq 0} \min_{x_i \neq 0} \frac{(Ax)_i}{x_i}$$

As such, $\rho \geq \min_{x_i \neq 0} \frac{(Ax)_i}{x_i}$.

Because of the Collatz-Wielandt formula, we have that, whenever $1 - \delta \frac{x_i^*}{(Mx^*)_i} \geq 1 - \frac{\delta}{\rho} \geq 0$ we have all $x_i > 0$. As such, in this model, the spectral radius ρ plays the same role as the colonization rate in Levins' model. The spectral radius is therefore called the *metapopulation capacity*.

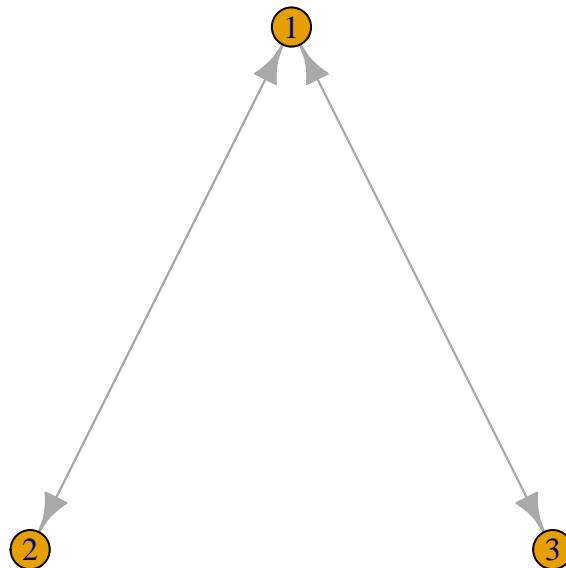
Note also that the same result is found for any $M \geq 0$ (not necessarily based on distances etc.).

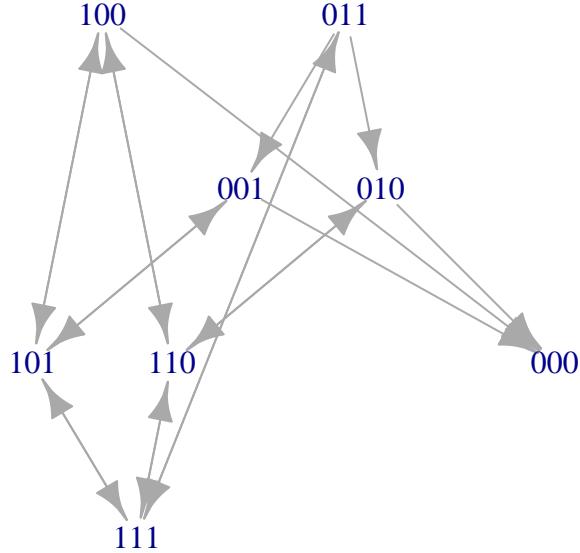
8.3 SIS on a contact network

Interestingly, the same results above have been derived in the context of virus spread on networks by Van Mieghem et al. (2008). We follow their derivation as it shows what type of approximations we're making when writing the equations above.

8.3.1 The full model

We can imagine the process of the spread of a pathogen on a network of n individuals as a graph, in which each node is a label detailing who is infected. There are 2^n nodes, ranging from $V_0 = (0, 0, \dots, 0)$ (the state in which the pathogen is extinct) to $V_{2^n-1} = (1, 1, \dots, 1)$ (the state in which all individuals are infected). Recovery flips a one into a zero, and infection a zero into a one (without loss of generality, we can assume only one event happens at each “time step”). We connect any two nodes in the network $V_i \rightarrow V_j$ if an event (i.e., infection, recovery) can send the system from state i to state j . The system therefore describes a Markov Chain with 2^n states. Note also that the state 0 is the “coffin state” for the system (once the pathogen is extinct, there is no way to go back).





8.3.2 The mean-field approximation

For simplicity, make the following assumptions: a) all individuals have the same recovery rate, δ ; b) the (symmetric/undirected) contact network A defines who can infect whom; c) when a node/individual is infected, it attempts infecting the neighbors at a rate β .

We track the probability that individual i is infected at time t (mathematically, this is an expectation). In particular, take x_i to be an indicator variable taking value 1 when i is infected, and 0 when i is susceptible. Then

$$\frac{dE[x_i(t)]}{dt} = E \left[-\delta x_i(t) + \beta(1 - x_i(t)) \sum_j A_{ij} x_j(t) \right]$$

The $-\delta x_i(t)$ models the recovery, and when an individual is susceptible (i.e., when $(1 - x_i(t)) = 1$) the neighbors (i.e., j such that $A_{ij} = 1$) attempt to infect node i . Expanding (and dropping the dependency on time to keep the equation compact), we obtain:

$$\frac{dE[x_i]}{dt} = -\delta E[x_i] + \beta \sum_j A_{ij} E[x_j] - \beta \sum_j A_{ij} E[x_i x_j]$$

which looks very much like Levins' model, with the difference that we need to choose how to deal with $E[x_i x_j]$ (a covariance/correlation). If we assume $E[x_i x_j] \approx E[x_i] E[x_j]$ (e.g., independence), we can simplify the model to:

$$\frac{dE[x_i]}{dt} = -\delta E[x_i] + \beta(1 - E[x_i]) \sum_j A_{ij} E[x_j]$$

which is the same as the model of Hanski and Ovaskainen above. Interestingly, this is but an approximation of the full model described by the Markov Chain above—for example Cator and Van Mieghem (2012) derive the model when tracking all the $E[x_i x_j]$, resulting in a better approximation of the full model (at the cost of having an additional $\binom{n}{2}$) equations.

Homework 8 [Long]

Implement an event-driven simulation of the spread of a disease on a network. The simulation approach is taken from Li et al. (2012):

“we take a nodal-central, event-driven approach. An event can either be the curing of a node or the spreading of the infection from one node to another. Events are stored in a timeline as tickets. [...] Tickets are continuously taken from the timeline and passed on to the owner. If the ticket owner is a node, the ticket indicates either a curing or a spreading event. In the case of a curing event, the node simply changes its state from infected to healthy; in the case of a spreading event, it will spread the infection to the neighbor mentioned in the ticket. If the neighbor was not already infected, it will now become infected and create one or more tickets. A newly infected node will always create a ticket for its own curing event. According to continuous-time Markov theory, the time between infection and curing is exponentially distributed with rate δ and is stored by the node for future reference. An infected node also generates spreading times at which it will spread the infection to its neighbors. The spreading times are again exponentially distributed but now with rate β . If the spreading time does not exceed the node’s curing time, a ticket is created for the spreading event. All newly created tickets are stored in the timeline. Finally, the owner of the original ticket generates a new spreading time, which, if not exceeding its own curing time, creates a new spreading ticket for the same neighbor. If the ticket is not owned by a node, it is a system ticket.”

Simulate the spread of a disease on an adjacency matrix (with at least 10 nodes and 30 connections) of your choice. Initialize the simulation by generating an infection for one of the nodes. Repeat the simulation 100 times, tracking and averaging the amount of time each node is infected.

Optional

Then write the system of differential equations above, and follow dynamics until an equilibrium is reached. Compare the results of the simulation with those from the dynamical model.

8.4 Metapopulations on randomly distributed patches

Grilli et al. (2015) considered the case in which a) N patches are uniformly, randomly arranged in a d -dimensional landscape (e.g., 1-dimensional for the dunes ecosystems on the shore of Lake Michigan, 2-dimensional for an agricultural landscape; for 3 dimensions consider mountains, for 4 dimensions add time [e.g., temporary ponds in the Alps], for 5 or more dimensions, invoke string theory!)—we indicate the position of patch i as x_i ; b) one can choose a “dispersal kernel” $f(\|x_i - x_j\|\xi)$, c) patch values are randomly sampled from a distribution with mean 1 (which we can do w.l.o.g.) and variance σ^2 .

For example, when dispersal decreases exponentially with distance (as above), we have an exponential kernel:

$$f\left(\frac{|x_i - x_j|}{\xi}\right) = \exp\left(-\frac{|x_i - x_j|^2}{2\xi^2}\right)$$

Because the matrices M formed by a given kernel belong to the ensemble of *Euclidean Random Matrices*, one can compute an approximation for ρ quite easily. In particular, for a given number of dimensions d , the size of the landscape, etc., we define an “effective number of neighbors” n_e and we have $\rho \geq n_e(1 + \sigma^2)$. Take the landscape to be a hypercube with length L . Then whenever the “dispersal range” $\xi \ll L$, we can approximate

$$n_e \approx \frac{N}{L^d} G_f(d) \xi^d$$

Where $G_f(d)$ is a constant that depends on the kernel shape. Call $\mu = N/L^d$ to be the density of patches in the landscape. We can simplify the calculation by considering the density to be fixed, but both N and L tending to infinity (see SI of Grilli et al. (2015)). Then, for the exponential kernel, we have:

$$\begin{aligned} n_e &= \mu \int \exp\left(-\frac{\sqrt{\sum_{k=1}^d x_{(k)}^2}}{\xi}\right) dx_{(1)} \cdots dx_{(d)} \\ &= \frac{2\pi^{d/2}\Gamma(d)}{\Gamma(d/2)} \mu \xi^d, \end{aligned}$$

where $\Gamma(d)$ is the Gamma function. Similarly, for the Gaussian kernel:

$$f\left(\frac{|x_i - x_j|}{\xi}\right) = \exp\left(-\frac{|x_i - x_j|^2}{2\xi^2}\right)$$

we obtain:

$$\begin{aligned} n_e &= \mu \int \exp \left(-\frac{\sum_{k=1}^d x_{(k)}^2}{2\xi^2} \right) dx_{(1)} \cdots dx_{(d)} \\ &= (2\pi)^{d/2} \mu \xi^d \end{aligned}$$

and finally, for a Rectangular kernel:

$$f \left(\frac{|x_i - x_j|}{\xi} \right) = \begin{cases} 1, & |x_i - x_j| \leq \xi \\ 0, & |x_i - x_j| > \xi \end{cases}$$

we have

$$n_e = \frac{\pi^{d/2}}{\Gamma(d/2 + 1)} \mu \xi^d$$

This means for example that, when $d = 1$ the exponential and the rectangular kernel have the same value of n_e , while in two dimensions the Gaussian and exponential kernel have the same value of n_e . This means that two large matrices built with different kernels can have approximately the same ρ .

Using similar techniques, one can determine that “disordered” patch arrangements always lead to higher capacity than “ordered” arrangements.

Chapter 9

Quasi-polynomial systems

Lesson plan:

1. We discuss a fairly general class of dynamical systems, called “Quasi-Polynomial” (QP-)systems.
2. We show how any QP-system can be written as a larger-dimensional Generalized Lotka-Volterra model.
3. This means that the machinery we built for analyzing GLV models can be used to tackle a variety of models that at face value do not seem to fall in this class. We show how to determine global stability in several ecological and epidemiological models using this method.
4. This also shows that the GLV model is in a way a “universal” model.

9.1 Global stability

Many dynamical models describing ecological, epidemiological and evolutionary systems have equilibria that are globally stable (e.g., SIR, SIS, logistic growth, Levins’ metapopulation model, MacArthur’s consumer-resource model).

By far, the most powerful method to prove the global stability of an equilibrium is the so-called “Lyapunov direct method”, which we’ve encountered several times already. The main drawback of this method is that devising an appropriate Lyapunov function requires ingenuity and—as Strogatz (2018) put it—a good deal of “divine inspiration”. Here we take a different approach: we embed our model of interest into a (possibly larger) GLV model, and then attempt applying the typical Lyapunov function for GLV to our transformed system (an embedding originally proposed by Brenig (1988)). In practice, this will require us to think carefully about how perturbations in the original system translate into the perturbations of the (larger) GLV model.

We first show how systems that are in “Quasi-Polynomial” (QP) form can be

embedded into a larger GLV by means of simple matrix operations. Then, we discuss strategies to determine global stability for the embedding. Finally, we show that other models can be turned into QP, and from there into GLV.

9.2 From QP to GLV

We call a Quasi-Polynomial system a system of n ODEs that can be written as:

$$\frac{dx_i(t)}{dt} = x_i(t) \left(s_i + \sum_{j=i}^m A_{ij} \prod_{k=1}^n x_k(t)^{B_{jk}} \right)$$

where s is a vector of “growth rates” (not necessarily positive), A is a matrix of interactions, and B a $m \times n$ matrix of exponents. Note that if we take $m = n$ and $B = I_n$ (the identity matrix), we recover the GLV model. If B contains only integers, then we have a polynomial system. Extending this model to real (but not necessarily integer) numbers B_{jk} , we have a “Quasi-Polynomial” (QP) system (Hernández-Bermejo et al. (1998)).

In general, we assume that A is of size $n \times m$, B is $m \times n$, and that the $x_i(t)$ are real and positive (if that’s not the case, one needs to perform a change of variables that ensures positivity). The system has n variables (the $x_i(t)$), and we can identify m “quasi-monomials”:

$$z_j = \prod_{k=1}^n x_k^{B_{jk}}$$

Several models in ecology and evolution belong to this class. For example, a model that departs from the GLV family is the so-called Leslie-Gower predator-prey model (Leslie (1948)):

$$\begin{cases} \frac{dH}{dt} = H(\rho_h - \alpha_h P - \beta_h H) \\ \frac{dP}{dt} = P \left(\rho_p - \alpha_p \frac{P}{H} \right) \end{cases}$$

The equation for the prey (H) is in GLV form. However, the rate of increase (decrease) of the predator depends on the ratio between predators and prey: when prey are abundant, predators grow with rate close to ρ_p ; if prey are scarce, on the other hand, predators decline.

History: Patrick H. Leslie (1900-1972)



Born in Scotland, he studied physiology at Oxford University (Christ Church College). He worked for a few years in the department of pathology, and in 1935 he joined the Bureau of Animal Population, a new center led by Charles Elton. There, he worked on population dynamics merging theoretical work and applications.

In 1945 he published in Biometrika his masterpiece, *On the use of matrices in certain population mathematics* (Leslie (1945)). In this paper, he developed models for structured populations, which were then extended in several ways, and are still in use today. The so-called Leslie-Gower predator-prey model is developed in a follow-up paper in the same journal (Leslie (1948)).

Solving for the coexistence equilibrium, we find:

$$\begin{cases} H^* = \frac{\alpha_p \rho_h}{\alpha_p \beta_h + \alpha_h \rho_p} \\ P^* = \frac{\rho_p \rho_h}{\alpha_p \beta_h + \alpha_h \rho_p} \end{cases}$$

Note that the model is in QP-form. We recognize three monomials:

$$\begin{pmatrix} H \\ P \\ P \\ H \end{pmatrix} = \begin{pmatrix} H^1 P^0 \\ H^0 P^1 \\ H^{-1} P^1 \end{pmatrix}$$

And the associated parameters:

$$s = (\rho_h, \rho_p) \quad A = \begin{pmatrix} -\beta_h & -\alpha_h & 0 \\ 0 & 0 & -\alpha_p \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 \\ 0 & 1 \\ -1 & 1 \end{pmatrix}$$

Now we want to turn this models into a Generalized Lotka-Volterra model. We take the new variables to be our monomials:

$$z = \begin{pmatrix} z_1 \\ z_2 \\ z_3 \end{pmatrix} = \begin{pmatrix} H^1 P^0 \\ H^0 P^1 \\ H^{-1} P^1 \end{pmatrix}$$

and transform the growth rates:

$$r = \begin{pmatrix} r_1 \\ r_2 \\ r_3 \end{pmatrix} = Bs = \begin{pmatrix} \rho_h \\ \rho_p \\ \rho_p - \rho_h \end{pmatrix}$$

and the matrix of interactions:

$$M = BA = \begin{pmatrix} -\beta_h & -\alpha_h & 0 \\ 0 & 0 & -\alpha_p \\ \beta_h & \alpha_h & -\alpha_p \end{pmatrix}$$

The GLV system is clearly equivalent (topologically) to the original system, but has now three equations instead of two. Using the transformation $r = Bs$, $M = BA$, we can embed any QP system into a (typically, larger) GLV.

9.3 Stability of GLV

Before proceeding to prove the stability of the coexistence equilibrium for the Leslie-Gower model, we need to revisit the Lyapunov function for the GLV introduced by Goh (1977), which we have encountered before. Take a GLV:

$$\frac{dz}{dt} = D(z)(r + Mz) = D(z)(M(z - z^*)) = D(z)M\Delta z$$

where Δz is a vector of deviations from the equilibrium. Suppose that all species densities remain positive through the dynamics; then, we can write the dynamics of the logarithm of the species densities (where $\log z$ is a vector containing the logarithms of the densities):

$$\frac{d \log z}{dt} = r + Mz = M\Delta z$$

We can take the “candidate Lyapunov function”:

$$V = 1^T D(c)(z - z^* - D(z^*) \log(z/z^*))$$

where $D(c)$ is a diagonal matrix with positive diagonal coefficients. Deriving w.r.t. time, we find:

$$\frac{dV}{dt} = 1^T D(c) \left(\frac{dz}{dt} - D(z^*) \frac{d \log z}{dt} \right)$$

substituting:

$$\frac{dV}{dt} = \mathbf{1}^T D(c) (D(z)M\Delta z - D(z^*)M\Delta z) = \mathbf{1}^T D(c)D(\Delta z)M\Delta z$$

Because diagonal matrices commute (i.e., $D_1D_2 = D_2D_1$), we can write:

$$\frac{dV}{dt} = \mathbf{1}^T D(\Delta z)D(c)M\Delta z$$

Finally, we absorb the $D(\Delta z)$:

$$\frac{dV}{dt} = \Delta z^T D(c)M\Delta z$$

If a matrix K is negative definite (semi-definite), then $x^T K x < 0$ (≤ 0) for any $x \neq 0$. As such, if we were to find a positive definite, diagonal matrix $D(c)$ such that $D(c)M$ is negative semi-definite, we would have proved the global stability of the equilibrium (V is positive whenever $z > 0$ and $z \neq z^*$, and if $D(c)M$ is negative definite V decreases in time). Because it is typically easier to work with symmetric matrices, w.l.o.g. we can take $K = \frac{1}{2}(D(c)M + M^T D(c))$, which yields exactly the same result: $\Delta z^T D(c)M\Delta z = \Delta z^T K\Delta z$.

The expression above has been used countless times to prove the stability of GLV models. Note that when our model is indeed a GLV, the Δz_i are radially unbounded: $\Delta z_i \in [-z_i^*, \infty)$ (where the left bound is given by the fact that z_i must be positive). In this case, it therefore makes much sense to try to make K negative definite.

9.4 Stability for GLV embeddings

This is however not the case when our equations have obtained by embedding a lower-dimensional system into a larger GLV. Because we have created new “species” by combining the original species, the perturbations of the “new species” are set by the perturbations of the original species. For example, in the Leslie-Gower embedding we have that $z_3 = P/H = z_2/z_1$, and therefore:

$$\Delta z = \begin{pmatrix} \Delta z_1 \\ \Delta z_2 \\ \Delta z_3 \end{pmatrix} = \begin{pmatrix} \Delta z_1 \\ \Delta z_2 \\ \frac{\Delta z_2 + z_2^*}{\Delta z_1 + z_1^*} - \frac{z_2^*}{z_1^*} \end{pmatrix} = \begin{pmatrix} \Delta z_1 \\ \Delta z_2 \\ \frac{\Delta z_2 - \frac{z_2^*}{z_1^*} \Delta z_1}{z_1} \end{pmatrix}$$

showing that the third perturbation is a function of the first two.

Computing the matrix K for this system, we obtain:

$$K = \frac{1}{2}(D(c)M + M^T D(c)) = \frac{1}{2} \begin{pmatrix} -2c_1\beta_h & -c_1\alpha_h & c_3\beta_h \\ -c_1\alpha_h & 0 & -c_2\alpha_p + c_3\alpha_h \\ c_3\beta_h & -c_2\alpha_p + c_3\alpha_h & -2c_3\alpha_p \end{pmatrix}$$

and taking $\Delta z^T K \Delta z$, we obtain:

$$\frac{dV}{dt} = \Delta z^T K \Delta z = -c_1 \Delta z_1 (\beta_h \Delta z_1 + \alpha_h \Delta z_2) + (c_3 \beta_h \Delta z_1 + (c_3 \alpha_h - c_2 \alpha_p) \Delta z_2) \Delta z_3 - c_3 \alpha_p \Delta z_3^2$$

Note that the last term is negative for any choice of $c_3 > 0$, which is a good start. We can also make $c_1 = 0$, thereby killing the first term. What remains to be determined is how to handle $(c_3 \beta_h \Delta z_1 + (c_3 \alpha_h - c_2 \alpha_p) \Delta z_2) \Delta z_3$. Because we know that Δz_3 is a function of Δz_1 and Δz_2 , we can try to choose appropriate constants to make $(c_3 \beta_h \Delta z_1 + (c_3 \alpha_h - c_2 \alpha_p) \Delta z_2)$ proportional to $-\Delta z_3$, thereby obtaining a function that decreases in time, with form $-\theta \Delta z_3^2$ and θ positive.

We have shown above that $-\Delta z_3 \propto \frac{z_2^*}{z_1^*} \Delta z_1 - \Delta z_2 = \frac{\rho_p}{\alpha_p} \Delta z_1 - \Delta z_2$. Take:

$$(c_3 \beta_h \Delta z_1 + (c_3 \alpha_h - c_2 \alpha_p) \Delta z_2)$$

extract the term $(c_2 \alpha_p - c_3 \alpha_h)$:

$$(c_2 \alpha_p - c_3 \alpha_h) \left(\frac{c_3 \beta_h}{c_2 \alpha_p - c_3 \alpha_h} \Delta z_1 - \Delta z_2 \right)$$

To recover the right form, we need to make $\frac{c_3 \beta_h}{c_2 \alpha_p - c_3 \alpha_h} = \frac{\rho_p}{\alpha_p}$. Clearly, there are infinitely many choices.

A convenient choice is $c_1 = 0$, $c_2 = \alpha_p \beta_h + \alpha_h \rho_p$, and $c_3 = \alpha_p \rho_p$. In this case, we have:

$$\frac{dV}{dt} = -\alpha_p \Delta z_3 (\alpha_p \beta_h \Delta z_2 - \beta_h \rho_p \Delta z_1 + \alpha_p \Delta z_3)$$

Which can be rewritten as:

$$\frac{dV}{dt} = -\alpha_p^2 (z_1 \beta_h + \rho_p) \Delta z_3^2$$

which is clearly always negative whenever $\Delta z_3 \neq 0$, given that $z_1 > 0$ and all parameters are positive. We can write the Lyapunov function directly for the original system:

$$W = c_2(P - P^* - P^* \log(P/P^*)) + c_3(P/H - P^*/H^* - (P^*/H^*) \log(PH^*/HP^*))$$

yielding:

$$\frac{dW}{dt} = -\frac{\rho_p + \beta_h H}{H^2}(\rho_p H - \alpha_p P)^2$$

which again is negative when we are not at equilibrium, proving global stability.

9.5 Numerical analysis

The derivation above is quite complex, and as always it is easier to find an answer when we know that an answer exists. One of the great advantages of the GLV embedding is that one can quite easily search for the constants numerically. The algorithm is as follows:

- Randomly generate Δz_i by choosing random values between 0 and a sufficiently large number (say 10 times their respective equilibria) for each of the original species; from these random numbers, compute the corresponding Δz for the new “species”;
- Build the matrix M ;
- For each choice of $D(c)$, compute $K = (1/2)(D(c)M + M^T D(c))$, and then the value of dV/dt for each of the randomly determined Δz : $dV/dt = \Delta z^T K \Delta z$.
- If the value is negative for every choice of Δz , then the constants in $D(c)$ are appropriate; if not, modify $D(c)$, trying to minimize the number of Δz leading to a positive result.

For example, this code finds a set of constants for the Leslie-Gower model:

```
set.seed(1)
# choose random parameters
# (of course the same can be done for specific parameters)
rh <- runif(1)
ah <- runif(1)
bh <- runif(1)
rp <- runif(1)
ap <- runif(1)
# compute equilibria
z1s <- ap * rh / (ap * bh + ah * rp)
z2s <- rp * rh / (ap * bh + ah * rp)
# this is the equilibrium for "z3"
z3s <- z2s / z1s
# now choose random values
npoints <- 1000
```

```

# for each zi
z1 <- runif(npoints, 0, 10 * z1s)
z2 <- runif(npoints, 0, 10 * z2s)
z3 <- z2 / z1
# now compute delta z
deltaZ <- cbind(z1 - z1s,
                  z2 - z2s,
                  z3 - z3s)
# compute M
A <- matrix(c(
  -bh, -ah, 0,
  0, 0, -ap), 2, 3, byrow = TRUE)
B <- matrix(c(
  1, 0,
  0, 1,
  -1, 1), 3, 2, byrow = TRUE)
M <- B %*% A

# this is the function we want to minimize
LG_to_minimize <- function(const){
  # keep constants positive, and
  # with mean of 1 (for numerics)
  const <- abs(const) / mean(abs(const))
  Dc <- diag(const)
  K <- (Dc %*% M)
  K <- 0.5 * (K + t(K))
  # now compute dVdt for each deltaZ
  target <- apply(deltaZ, 1,
                  function(dz) dz %*% K %*% dz)
  # solution found
  if (all(target < 0)) return(-1)
  # otherwise, try to minimize
  return(sum(target[target > 0]))
}

# use optim to find a solution
tmp <- optim(par = runif(3), fn = LG_to_minimize)
if(tmp$value == -1) {
  print("Found a set of constants")
  solution <- tmp$par
  print(round(abs(solution) / mean(abs(solution)),3))
}

```

[1] “Found a set of constants” [1] 0.573 1.902 0.525

Which shows that a solution indeed exists. Note that, provided that the choice

of Δz is extensive enough, the constants found in this way indeed determine the global stability of the equilibrium. Typically, infinitely many choices are possible—but certain choices of constants are better than others, for example allowing for a clean analytical derivation.

Naturally, the constants we have derived analytically are also appropriate:

```
c1 <- 0
c2 <- ap * bh + ah * rp
c3 <- ap * rp
LG_to_minimize(c(c1, c2, c3))

[1] -1
```

9.6 Systems with many equations

The same type of embedding can help derive Lyapunov functions for systems with many equations. For example, let's examine a MacArthur consumer resource model in which resources are supplied externally. There are n resources, with dynamics:

$$\frac{dx_i}{dt} = k_i - d_i x_i - x_i \sum_j C_{ij} y_j$$

where $k_i > 0$ is the external input to resource i , $d_i \geq 0$ models the degradation of the resource, and C is a matrix containing the consumption rates for the consumers y_j .

The dynamics of the consumers are governed by:

$$\frac{dy_i}{dt} = -m_i y_i + y_i \epsilon_i \sum_j C_{ji} x_j$$

where $m_i > 0$ is the mortality, and for simplicity the transformation efficiency $\epsilon_i > 0$ is set to be predator-specific, but equal for all resources. Our goal is to show that if a feasible coexistence equilibrium exists, it is globally stable.

We rewrite the system in matrix form as:

$$\begin{cases} \frac{dx}{dt} = D(x)(-d - Cy - D(k)x^{-1}) = D(x)(-d - Cy - D(k)v) \\ \frac{dy}{dt} = D(y)(-m + D(\epsilon)C^T x) \end{cases}$$

which is a QP system. To highlight the monomials that will give rise to new equations, we have defined $v_i = 1/x_i$. Using the GLV embedding, we recover a system of $3n$ equations:

$$s = (-d, -m)^T \quad A = \begin{pmatrix} 0_n & -C & D(k) \\ D(\epsilon)C^T & 0_n & 0_n \\ 0_n & C & -D(k) \end{pmatrix} \quad B = \begin{pmatrix} I_n & 0_n \\ 0_n & I_n \\ -I_n & 0_n \end{pmatrix}$$

Where I_n is the $n \times n$ identity matrix, and 0_n is an $n \times n$ matrix of zeros.

The GLV is therefore defined by the vector of growth rates:

$$r = Bs = (-m, -d, m)^T$$

and the matrix of interactions:

$$M = BA = \begin{pmatrix} 0_n & -C & D(k) \\ D(\epsilon)C^T & 0_n & 0_n \\ 0_n & C & -D(k) \end{pmatrix}$$

Now compute K ; taking as constants $c = (1_n, \epsilon^{-1}, 0_n)$ makes K very sparse:

$$K = \frac{1}{2}(D(c)M + M^T D(c)) = \frac{1}{2} \begin{pmatrix} 0_n & 0_n & D(k) \\ 0_n & 0_n & 0_n \\ D(k) & 0_n & 0_n \end{pmatrix}$$

Now define $z = (x, y, v)^T$, and compute dV/dt :

$$\frac{dV}{dt} = \Delta x^T D(k) \Delta v$$

Finally, notice that $v = 1/x$, and therefore:

$$\Delta v_i = \frac{1}{x_i} - \frac{1}{x_i^*} = \frac{1}{\Delta x_i + x_i^*} - \frac{1}{x_i^*} = -\frac{\Delta x_i}{x_i^* x_i}$$

This proves the stability of the equilibrium, given that

$$\frac{dV}{dt} = \Delta x^T D(k) \Delta v = -k^T \frac{\Delta x^2}{x^* x}$$

9.7 GLV embedding for non-QP systems

Finally, we consider a simple case in which the original system is not already in QP form. Consider a very simple model for facultative mutualism:

$$\begin{cases} \frac{dx_1}{dt} = x_1(1 - x_1 + \alpha \frac{x_2}{1+x_2}) \\ \frac{dx_2}{dt} = x_2(1 - x_2 + \alpha \frac{x_1}{1+x_1}) \end{cases}$$

In the absence of the mutualist, each species grows logistically. However, they can coexist at higher abundance—though the beneficial effect eventually saturates. Again, our task is to prove the global stability of the coexistence equilibrium.

This model is not in QP form. To turn it into QP form, we need to define $v_1 = x_1/(1+x_1)$ and $v_2 = x_2/(1+x_2)$. We write two new equations for v_1 and v_2 , resulting in a system of four equations:

$$\begin{cases} \frac{dx_1}{dt} = x_1(1 - x_1 + \alpha v_2) \\ \frac{dx_2}{dt} = x_2(1 - x_2 + \alpha v_1) \\ \frac{dv_1}{dt} = v_1(1 - 2v_1 + \alpha v_2 - \alpha v_1 v_2) \\ \frac{dv_2}{dt} = v_2(1 - 2v_2 + \alpha v_1 - \alpha v_1 v_2) \end{cases}$$

which is in QP form. Now we can perform the GLV embedding, resulting in a new equation for $p = v_1 v_2$:

$$z = (x_1, x_2, v_1, v_2, p)^T$$

$$s = (1, 1, 1, 1)^T \quad A = \begin{pmatrix} -1 & 0 & 0 & \alpha & 0 \\ 0 & -1 & \alpha & 0 & 0 \\ 0 & 0 & -2 & \alpha & -\alpha \\ 0 & 0 & \alpha & -2 & -\alpha \end{pmatrix} \quad B = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ 0 & 0 & 1 & 1 \end{pmatrix}$$

We have:

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

and

$$r = (1, 1, 1, 1, 2)^T$$

Setting $c = (1, 1, 0, 0, 0)$, we obtain

$$\frac{dV}{dt} = -\Delta z_1^2 - \Delta z_2^2 + \alpha(\Delta z_1 \Delta z_4 + \Delta z_2 \Delta z_3)$$

Note however that Δz_3 and Δz_4 are defined by Δz_1 and Δz_2 :

$$\Delta z_3 = \frac{x_1}{1+x_1} - \frac{x_1^*}{1+x_1^*} = \frac{1}{1+x_1^*} - \frac{1}{1+x_1^* + \Delta z_1}$$

and

$$\Delta z_4 = \frac{x_2}{1+x_2} - \frac{x_2^*}{1+x_2^*} = \frac{1}{1+x_2^*} - \frac{1}{1+x_2^* + \Delta z_2}$$

Plugging in the values for the equilibrium, and simplifying, we finally obtain:

$$\frac{dV}{dt} = -\Delta z_1^2 - \Delta z_2^2 + \frac{8\alpha\Delta z_1\Delta z_2(\sqrt{\alpha^2+4}+\alpha+\Delta z_1+\Delta z_2+2)}{(\sqrt{\alpha^2+4}+\alpha+2)(\sqrt{\alpha^2+4}+\alpha+2\Delta z_1+2)(\sqrt{\alpha^2+4}+\alpha+2\Delta z_2+2)}$$

which is never positive if $\Delta z_1 > -x_1^*$, $\Delta z_2 > -x_2^*$ and $\alpha > 0$. This proves the stability of the coexistence equilibrium.

- Allesina, S., and J. Grilli. 2020. Models for large ecological communities—a random matrix approach. Pages 74–92 in K. S. McCann and G. Gellner, editors. *Theoretical ecology: Concepts and applications*. Oxford University Press.
- Allesina, S., and J. M. Levine. 2011. A competitive network theory of species diversity. *Proceedings of the National Academy of Sciences* 108:5638–5642.
- Allesina, S., and S. Tang. 2012. Stability criteria for complex ecosystems. *Nature* 483:205.
- Allesina, S., and S. Tang. 2015. The stability–complexity relationship at age 40: A random matrix perspective. *Population Ecology* 57:63–75.
- Amor, D. R., C. Ratzke, and J. Gore. 2020. Transient invaders can induce shifts between alternative stable states of microbial communities. *Science advances* 6:eaay8676.
- Anderson, R. M., and R. M. May. 1992. *Infectious diseases of humans: Dynamics and control*. Oxford university press.
- Axelrod, R., and W. D. Hamilton. 1981. The evolution of cooperation. *science* 211:1390–1396.
- Baez, J. C. 2021. The fundamental theorem of natural selection. *Entropy* 23:1436.
- Baigent, S. A. 2016. *Lotka-volterra dynamics: An introduction*. World Scientific.
- Biroli, G., G. Bunin, and C. Cammarota. 2018. Marginally stable equilibria in critical ecosystems. *New Journal of Physics* 20:083051.

- Bittleston, L. S., M. Gralka, G. E. Leventhal, I. Mizrahi, and O. X. Cordero. 2020. Context-dependent dynamics lead to the assembly of functionally distinct microbial communities. *Nature communications* 11:1–10.
- Brandl, F. 2017. The distribution of optimal strategies in symmetric zero-sum games. *Games and Economic Behavior* 104:674–680.
- Brenig, L. 1988. Complete factorisation and analytic solutions of generalized lotka-volterra equations. *Physics Letters A* 133:378–382.
- Cadotte, M. W. 2013. Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences* 110:8996–9000.
- Cadotte, M. W., and T. J. Davies. 2016. *Phylogenies in ecology: A guide to concepts and methods*. Princeton University Press.
- Capitán, J. A., J. A. Cuesta, and J. Bascompte. 2009. Statistical mechanics of ecosystem assembly. *Physical Review Letters* 103:168101.
- Case, T. J., and R. G. Casten. 1979. Global stability and multiple domains of attraction in ecological systems. *The American Naturalist* 113:705–714.
- Cator, E., and P. Van Mieghem. 2012. Second-order mean-field susceptible-infected-susceptible epidemic threshold. *Physical review E* 85:056111.
- Clutton-Brock, T. 2009. Cooperation between non-kin in animal societies. *Nature* 462:51–57.
- Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336:1175–1177.
- Dambacher, J. M., H.-K. Luh, H. W. Li, and P. A. Rossignol. 2003. Qualitative stability and ambiguity in model ecosystems. *The American Naturalist* 161:876–888.
- Diamond, J. M. 1975. Assembly of species communities. *Ecology and evolution of communities*:342–444.
- Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist* 137:1–26.
- Ellner, S. P., and J. Guckenheimer. 2011. *Dynamic models in biology*. Princeton University Press.
- Fisher, D. C., and R. B. Reeves. 1995. Optimal strategies for random tournament games. *Linear Algebra and its Applications* 217:83–85.
- Fukami, T. 2015. Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23.
- Goh, B. S. 1977. Global stability in many-species systems. *The American Naturalist* 111:135–143.
- Gotelli, N. J. 1999. How do communities come together? *Science* 286:1684–1685.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of san marco and the pan-glossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B. Biological Sciences* 205:581–598.
- Grilli, J., G. Barabás, and S. Allesina. 2015. Metapopulation persistence in random fragmented landscapes. *PLoS Comput Biol* 11:e1004251.

- Grilli, J., G. Barabás, M. J. Michalska-Smith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. *Nature* 548:210.
- Hadeler, K. P., M. C. Mackey, and A. Stevens. 2017. Topics in mathematical biology. Springer.
- Haldane, A. G., and R. M. May. 2011. Systemic risk in banking ecosystems. *Nature* 469:351–355.
- Hang-Kwang, L., and S. L. Pimm. 1993. The assembly of ecological communities: A minimalist approach. *Journal of Animal Ecology*:749–765.
- Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758.
- Hector, A., B. Schmid, C. Beierkuhnlein, M. Caldeira, M. Diemer, P. Dimitrakopoulos, J. Finn, H. Freitas, P. Giller, J. Good, and others. 1999. Plant diversity and productivity experiments in european grasslands. *science* 286:1123–1127.
- Hernández-Bermejo, B., V. Fairén, and L. Brenig. 1998. Algebraic recasting of nonlinear systems of ODEs into universal formats. *Journal of Physics A: Mathematical and General* 31:2415.
- Hirsch, M. W., S. Smale, and R. L. Devaney. 2012. Differential equations, dynamical systems, and an introduction to chaos. Academic press.
- Hofbauer, J., and K. Sigmund. 1998. Evolutionary games and population dynamics. Cambridge University Press.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press.
- Law, R., and R. D. Morton. 1993. Alternative permanent states of ecological communities. *Ecology* 74:1347–1361.
- Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762–775.
- Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33:183–212.
- Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. *Biometrika* 35:213–245.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *The American Naturalist* 104:413–423.
- Levins, R. 1966. The strategy of model building in population biology. *American scientist* 54:421–431.
- Levins, R. 1968. Evolution in changing environments: Some theoretical explorations. Princeton University Press.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *American Entomologist* 15:237–240.
- Li, C., R. van de Bovenkamp, and P. Van Mieghem. 2012. Susceptible-infected-susceptible model: A comparison of n-intertwined and heterogeneous mean-field approximations. *Physical Review E* 86:026116.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences* 95:5632–5636.
- Loreau, M., and A. Hector. 2001. Partitioning selection and complementarity in

- biodiversity experiments. *Nature* 412:72–76.
- Loreau, M., and A. Hector. 2019. Not even wrong: Comment by loreau and hector. *Ecology* 100:e02794.
- Lotka, A. J. 1920. Analytical note on certain rhythmic relations in organic systems. *Proceedings of the National Academy of Sciences* 6:410–415.
- Lotka, A. J. 1926. The frequency distribution of scientific productivity. *Journal of the Washington academy of sciences* 16:317–323.
- Lotka, A. J. 2002. Contribution to the theory of periodic reactions. *The Journal of Physical Chemistry* 14:271–274.
- Ludwig, D., D. D. Jones, C. S. Holling, and others. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and forest. *Journal of animal ecology* 47:315–332.
- MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533–536.
- MacArthur, R. 1970. Species packing and competitive equilibrium for many species. *Theoretical population biology* 1:1–11.
- MacArthur, R. H., and E. O. Wilson. 2001. *The theory of island biogeography*. Princeton university press.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The american naturalist* 101:377–385.
- Marsland III, R., W. Cui, and P. Mehta. 2019. The minimum environmental perturbation principle: A new perspective on niche theory. arXiv preprint arXiv:1901.09673.
- May, R. M. 1972. Will a large complex system be stable? *Nature* 238:413–414.
- May, R. M. 1973. Qualitative stability in model ecosystems. *Ecology* 54:638–641.
- May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature* 261:459–467.
- May, R. M. 1988. How many species are there on earth? *Science* 241:1441–1449.
- May, R. M. 1997. The scientific wealth of nations. *Science* 275:793–796.
- Maynard, D. S., C. A. Serván, and S. Allesina. 2018. Network spandrels reflect ecological assembly. *Ecology letters* 21:324–334.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge university press.
- McCann, K. S. 2000. The diversity–stability debate. *Nature* 405:228–233.
- Morton, R. D., R. Law, S. L. Pimm, and J. A. Drake. 1996. On models for assembling ecological communities. *Oikos*:493–499.
- Nash, J. F. 1950. Equilibrium points in n-person games. *Proceedings of the National Academy of Sciences* 36:48–49.
- Neubert, M. G., and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology* 78:653–665.
- Nowak, M. A., and R. M. May. 1992. Evolutionary games and spatial chaos. *Nature* 359:826–829.
- Nowak, M. A., and K. Sigmund. 2005. Evolution of indirect reciprocity. *Nature* 437:1291–1298.
- O'Rourke, S., and D. Renfrew. 2014. Low rank perturbations of large elliptic random matrices. *Electronic Journal of Probability* 19.

- Ovaskainen, O., and I. Hanski. 2001. Spatially structured metapopulation models: Global and local assessment of metapopulation capacity. *Theoretical population biology* 60:281–302.
- Page, K. M., and M. A. Nowak. 2002. Unifying evolutionary dynamics. *Journal of theoretical biology* 219:93–98.
- Pielou, E. C. 1977. Mathematical ecology. Wiley,.
- Pillai, P., and T. C. Gouhier. 2019b. Not even wrong: Reply to loreau and hector. arXiv preprint arXiv:1910.13563.
- Pillai, P., and T. C. Gouhier. 2019c. Not even wrong: Reply to wagg et al. arXiv preprint arXiv:1910.13670.
- Pillai, P., and T. C. Gouhier. 2019a. Not even wrong: The spurious measurement of biodiversity’s effects on ecosystem functioning. *Ecology* 100:e02645.
- Puccia, C. J., and R. Levins. 2013. Qualitative modeling of complex systems: An introduction to loop analysis and time averaging. Harvard University Press.
- Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. Van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. *Nature* 461:53–59.
- Schreiber, S. J., and S. Rittenhouse. 2004. From simple rules to cycling in community assembly. *Oikos* 105:349–358.
- Serván, C. A., and S. Allesina. 2020. Tractable models of ecological assembly. bioRxiv.
- Serván, C. A., J. A. Capitán, J. Grilli, K. E. Morrison, and S. Allesina. 2018. Coexistence of many species in random ecosystems. *Nature ecology & evolution* 2:1237.
- Seydel, R. 2009. Practical bifurcation and stability analysis. Springer Science & Business Media.
- Sigmund, K. 1995. Darwin’s “circles of complexity”: Assembling ecological communities. *Complexity* 1:40–44.
- Solé, R. V., and S. Valverde. 2006. Are network motifs the spandrels of cellular complexity? *Trends in ecology & evolution* 21:419–422.
- Strogatz, S. H. 2018. Nonlinear dynamics and chaos: With applications to physics, biology, chemistry, and engineering. CRC Press.
- Suweis, S., F. Simini, J. R. Banavar, and A. Maritan. 2013. Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature* 500:449–452.
- Szederkenyi, G., A. Magyar, and K. M. Hangos. 2018. Analysis and control of polynomial dynamic models with biological applications. Academic Press.
- Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. *Proceedings of the national academy of sciences* 94:1857–1861.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845.
- Van Mieghem, P., J. Omic, and R. Kooij. 2008. Virus spread in networks. *IEEE/ACM Transactions On Networking* 17:1–14.

- Volterra, V. 1926b. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. *Memor. Accad. Lincei.* 6:31–113.
- Volterra, V. 1926a. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:558–560.
- Wagg, C., K. E. Barry, M. J. O'Brien, A. McKenzie-Gopsill, C. Roscher, N. Eisenhauer, and B. Schmid. 2019. Not even wrong: Comment by wagg et al. *Ecology* 100:e02805.
- Weiher, E., and P. Keddy. 2001. Ecological assembly rules: Perspectives, advances, retreats. Cambridge University Press.