EVOLUTION AND ECOLOGY – BIOS 20197

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René Magritte, La condition humaine, 1933.

Ecology Part, Winter 2014-2015

PREAMBLE

HOW TO USE THIS DOCUMENT

In this document, some areas are left intentionally blank. During the lectures, you will fill in the blanks with equations, graphs, etc. In this way, there is no need to take notes.

LIST OF TOPICS

In the 5 weeks dedicated to ecology, we will explore the following topics:

1. Age-structured and stage-structured populations.
2. Simple models for population growth.
3. Metapopulations and conservation.
4. Interspecific Competition.
5. Predator-Prey Interactions.
6. Dynamics of large ecological communities.

TEXTBOOKS

There are no textbooks. However, each Chapter contains a list of suggested readings.

MISCELLANEA

- Homework: the text contains several exercises. You should do them at home. At the beginning of each class, I will ask a volounteer to do them on the board.
- No laptops, no messaging, no iPads, no, no, no!
- Feel free to ask any question either in the classroom or at *sallesina@uchicago.edu*.
- Office hours: I receive by appointment.

1

THEORY IN ECOLOGY

1.1 WHY IS ECOLOGY SO THEORETICAL?

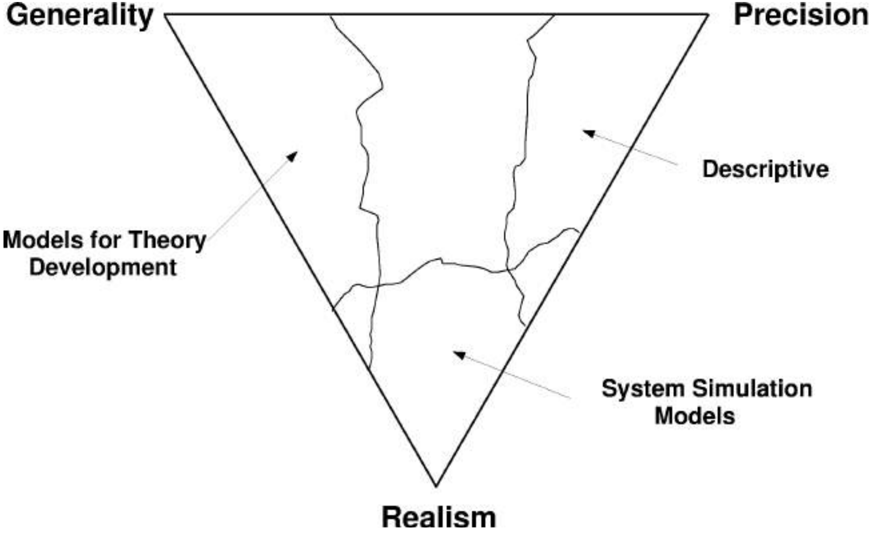
Since the beginning of the discipline, ecology has always been very theoretical. This is due to a number of reasons:

Complexity	Ecological systems are very large and complex. Many ecosystems contain thousands of species, all interacting with other species and with the surrounding environment. Idealized mathematical models are tools conceived to make sense of this staggering complexity.
Difference	All ecological systems are somewhat unique. Take two lakes that are only a few miles apart. Despite important similarities in the geology, climate, etc., the two lakes harbor different species, and have different dynamics. Theory let us find generalities among different systems.
Data	Gathering large ecological dataset requires much time, money and effort. Theory helps us finding general patterns from a limited number of data points.
Change	Many ecological problems (e.g., global climate change) require predicting the development of ecological systems under conditions that have never been experienced before. Out-of-fit forecasting requires a mechanistic understanding of ecological dynamics.
Experiments	Large-scale experiments in ecology are impractical, immoral, or extremely expensive. Mathematical models let us run "virtual" experiments using pen-and-paper or computer simulations.

1.2 MATHEMATICAL MODELS IN ECOLOGY

In this course, we are going to explore many different mathematical models found in ecology. Eugene Wigner (physicist and Nobel laureate), once wrote an article titled "The Unreasonable Effectiveness of Mathematics in the Natural Sciences", and ecology is no exception. We will see that mathematical models can help us understand the mechanisms responsible for the dynamics of populations, the effect of disturbances, and the spatial and temporal distribution of species. Given the short amount of time available to cover the material, the choice of models is naturally idiosyncratic. The goal is to provide a broad introduction to ecological concepts through the use of simple mathematical models.

A useful way to think about mathematical models in ecology is through the trade-off triangle introduced by Richard Levins:



This graph stresses the idea that there are three qualities (Generality, Precision, Realism) that a model cannot maximize at the same time. Ecological theory produces simple models that sit at the corner closer to Generality; for accurate predictions, one needs descriptive, specific models which might not embed much biology (e.g., purely statistical models, close to the Precision corner); in many cases (e.g., individual based models) one can build much Realism into models and see whether this produces the overall patterns observed in the data.

In this course, we will mostly work with models that are quite general, but we will see specific applications to conservation biology.

READING LIST

- E. P. Wigner (1960). *The Unreasonable Effectiveness of Mathematics in the Natural Sciences* Communications in Pure and Applied Mathematics, 13:1–14.

Part I

MODELS FOR A SINGLE POPULATION

In this part we explore the growth of a single population.

We start by analyzing models in which the population is divided into age/size classes, and introduce matrix population models. We develop an application of these models to conservation ecology.

We then move to models based on differential equations and briefly review models you should be familiar with: the exponential and logistic growth models. We emphasize the notion of stability, as we will use it throughout the rest of the course.

We conclude discussing “meta-populations”, in which local populations are connected by dispersal.

2

MATRIX POPULATION MODELS

In this Chapter, we explore the effects of having age-structured or stage-structured populations. In natural populations, in fact, mortality and fecundity are not constant, but rather depend strongly on the age/size/stage of the individuals. For example, older individuals typically display higher mortality and lower fecundity.

2.1 RATE OF INCREASE

In most of the models we are going to explore, we write down equations for the rate of increase (or growth) of a population. For example, the US population in 2013 grew of about 0.7 percent. January 1st, 2013, there were about 315 millions Americans. A growth of 0.7 percent puts the population on Jan 1st 2014 at about $315 \cdot (1 + 0.007) = 317.2$ millions. In this case, when we write the rate of increase as $x = 0.007$, we mean:

$$n(t+1) = (1+x)n(t) \tag{1}$$

where $n(t)$ is the population size at the beginning of year t, and $n(t+1)$ is the size at the beginning of the next year. Hence, the growth rate can be computed as:

$$x = \frac{n(t+1) - n(t)}{n(t)} \tag{2}$$

Using this formula, we can find the growth rate at for any year knowing the size of the population at the beginning and end of the year.

2.1.1 *Doubling Time*

What is the population size at time $t+2$ is we keep x fixed?

$$n(t+2) = (1+x)n(t+1) = (1+x)(1+x)n(t) = (1+x)^2 n(t) \tag{3}$$

in general,

$$n(t+T) = (1+x)^T n(t) \tag{4}$$

We want to find how long does it take to the population to double in size. Thus, we want to solve:

$$\begin{aligned} n(t+T) &= 2n(t) \\ 2n(t) &= (1+x)^T n(t) \\ 2 &= (1+x)^T \end{aligned} \tag{5}$$

Taking the log of both sides:

$$T = \frac{\log 2}{\log(1+x)} \approx \frac{0.693}{x - \frac{x^2}{2} + \frac{x^2}{3} + \cdots} \tag{6}$$

where the denominator can be written knowing that $\log(1+x) = x - x^2/2 + x^3/3 - x^4/4 + \cdots$ (MacLaurin series expansion). Disregarding the higher order terms, we say that a population with growing at $z\%$ a year, will double approximately every $69.3/z$ years.

Homework

In 1980, the US Census reported a population of 226,545,805; in 2010 of 308,745,538. Calculate the rate of increase x for the model $n(t+1) = (1+x)n(t)$.

Homework

The database Scopus (`www.scopus.com`) indexes scientific publications. In 2011, it indexed 2,352,087 scientific articles. Considering that the number of publications grew of about 6% every year since 2001, find approximately how many articles were published in 2001. How long does it take for the number of articles published to double?

2.2 MATRIX POPULATION MODELS

2.2.1 *Leslie Matrices*

Divide a population in s classes, one for each age class (e.g., newborns, 1-year old, 2-year old, etc.): each year, individuals in class k survive and move to the class $k+1$ with probability $0 < p_k \leq 1, \quad k < s$. Individuals in the last class cannot grow any further and die at the end of the year.

To reiterate, class 1 contains the individuals of age 0-1, class 2 the individuals of age 1-2, etc. At the end of the year, individuals move to the next class with probability p_k or die with probability $1 - p_k$. For starters, individuals in the first class can move to the second class. Mathematically,

$$n_2(t+1) = p_1 n_1(t) \tag{7}$$

where n_1 is the number of individuals in class 1. The same equation can be written for each other class. Because individuals of class 1 cannot be survivors of any other class, they must have originated from reproduction. We can write:

$$n_1(t+1) = f_1 n_1(t) + f_2 n_2(t) + f_3 n_3(t) + \ldots \tag{8}$$

where f_i is the fecundity of individuals in class i: each individual in class i will produce on average f_i offspring (individuals of class 1) in a time step.

We can express the system in matrix form:

$$n(t+1) = A \times n(t) \tag{9}$$

$$A = \begin{bmatrix} f_1 & f_2 & f_3 & \ldots & f_{s-1} & f_s \\ p_1 & 0 & 0 & \ldots & 0 & 0 \\ 0 & p_2 & 0 & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & 0 & 0 \\ \ldots & \ldots & \ldots & \ldots & 0 & 0 \\ 0 & 0 & 0 & \ldots & p_{s-1} & 0 \end{bmatrix} \tag{10}$$

$n(t)$ is a population vector, describing how many individuals are in class i in a given year (t), and A is called a Leslie matrix or projection matrix. The matrix is non-negative (i.e., all the elements are positive or zero). In a Leslie matrix, the non-zero terms are either on the first row (fertility) or on the sub-diagonal (transition probabilities). The values on the sub-diagonal are probabilities, and are therefore between 0 and 1. The top row coefficient f_x represents the number of offspring an individual of age x will produce in a year (and thus are positive numbers or 0, in case the corresponding class is not fertile). In all the cases we will examine, the matrix A is considered to be constant within an experiment. We next study how perturbing the coefficients affects the growth of the population.

2.2.2 *Projections*

Take the Leslie matrix A:

$$A = \begin{bmatrix} 0 & 1 & 5 \\ 0.3 & 0 & 0 \\ 0 & 0.5 & 0 \end{bmatrix} \tag{11}$$

which can be translated into English as follows: the population is divided into three classes. Newborns have probability 0.3 of reaching the first year of age. 1-year old transition in the third class with probability 0.5. Individuals start reproducing in year 1, and have on average one offspring per year. 2-year old have higher fertility, producing five offspring per year.

At the beginning of our experiment, we have 1 individual in class 1 and 0 individuals in the other classes (note that typically we deal with asexually reproducing populations, or track only the number of females). The number of individuals is to be considered for some unit of time/space, so it is actually a density. In this way, it makes sense to have fractionary numbers.

$$n(0) = \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} \tag{12}$$

We want to find the number of individuals at time $t = 1$. To do so, we have to multiply the matrix × the vector. Remember the multiplication rule:

$$A \times n = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix} = \begin{bmatrix} a_{11}n_1 + a_{12}n_2 + a_{13}n_3 \\ a_{21}n_1 + a_{22}n_2 + a_{23}n_3 \\ a_{31}n_1 + a_{32}n_2 + a_{33} \end{bmatrix} \tag{13}$$

Therefore the population at time $t = 1$ becomes:

$$n(1) = A \times n(0) = \begin{bmatrix} 0 \cdot 1 + 1 \cdot 0 + 5 \cdot 0 \\ 0.3 \cdot 1 + 0 \cdot 0 + 0 \cdot 0 \\ 0 \cdot 1 + 0.5 \cdot 0 + 0 \cdot 0 \end{bmatrix} = \begin{bmatrix} 0 \\ 0.3 \\ 0 \end{bmatrix} \tag{14}$$

Similarly, at time $t = 2$ we have:

$$n(2) = A \times n(1) = \begin{bmatrix} 0 \cdot 0 + 1 \cdot 0.3 + 5 \cdot 0 \\ 0.3 \cdot 0 + 0 \cdot 0.3 + 0 \cdot 0 \\ 0 \cdot 0 + 0.5 \cdot 0.3 + 0 \cdot 0 \end{bmatrix} = \begin{bmatrix} 0.3 \\ 0 \\ 0.15 \end{bmatrix} \tag{15}$$

We can compactly write the densities at any point in time using matrix algebra:

$$
\begin{aligned}
&n(3) = A \times n(2) = A \times (A \times n(1)) = \\
&A \times (A \times (A \times n(0))) = A^3 n(0)
\end{aligned}
\tag{16}
$$

In general,

$$
n(t) = A \times n(t-1) = A^2 \times n(t-2) = \ldots = A^t \times n(0) \tag{17}
$$

Because computing the densities at a given time is quite boring, let's plug the values in a computer. In Figure 1 I plotted the densities in the three classes for $t = 0, 2, \ldots, 100$. As you can see, the number of individuals in the three classes increases exponentially after some ups and downs at the beginning. In Figure 2 I plot the proportion of individuals in each class. As you can see, the proportion of individuals in each class stabilizes quite rapidly, so that about 70% of the individuals are in the first class, 20% in the second and 10% in the third.

What happens if we change the initial conditions (i.e., the number of individuals in each class at time 0)? In Figure 3 and 4 I show that starting with $n(0) = (1, 2, 3)$ does change the actual number of individuals in each class at time t, but not the qualitative behavior of the system: the population is still growing exponentially, and the fraction of individuals in each of the classes, after some ups and downs, stabilizes to the same proportions.

2.2.3 *Matrix Models*

Leslie matrices are of limited applicability, as typically individuals can live for a variable number of years, and it is difficult to determine the exact age of plants and animals. It would be better to classify the individuals as belonging to "stages" (e.g., juveniles, young adults, fully-grown adults, etc.) or classes of sizes/weights (esp. for fish). To do so, we can extend Leslie matrices to Lefkovitch matrices.

In a Lefkovich matrix, there are fecundities (top row), transition probabilities (sub-diagonal) as in Leslie matrices, but we include the diagonal elements, standing for the probability of remaining in a given class/stage/size.

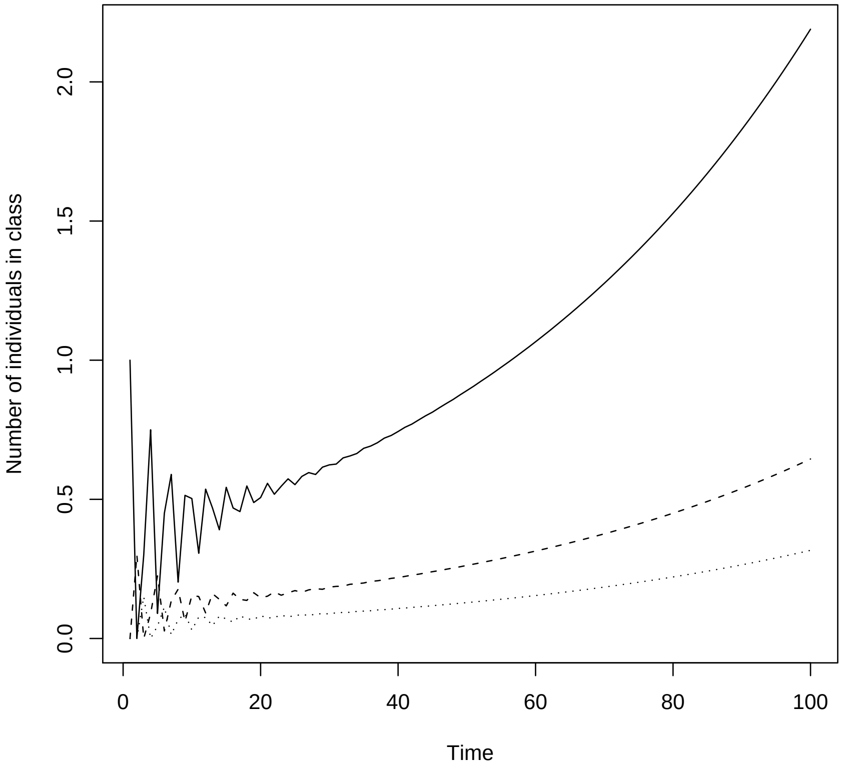


Figure 1: Projection of the 3-stage population in time starting with $(1, 0, 0)$. After some initial jiggling, the population grows exponentially.

The matrix therefore becomes:

$$A = \begin{bmatrix} q_1 & f_2 & f_3 & \dots & f_{s-1} & f_s \\ p_1 & q_2 & 0 & \dots & 0 & 0 \\ 0 & p_2 & q_3 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & 0 & 0 \\ 0 & 0 & 0 & \dots & p_{s-1} & q_s \end{bmatrix} \tag{18}$$

where q_x is the probability that an individual remains in class x (for simplicity, assume that the first class cannot reproduce). These matrix models are used in fisheries, conservation ecology and many other fields.

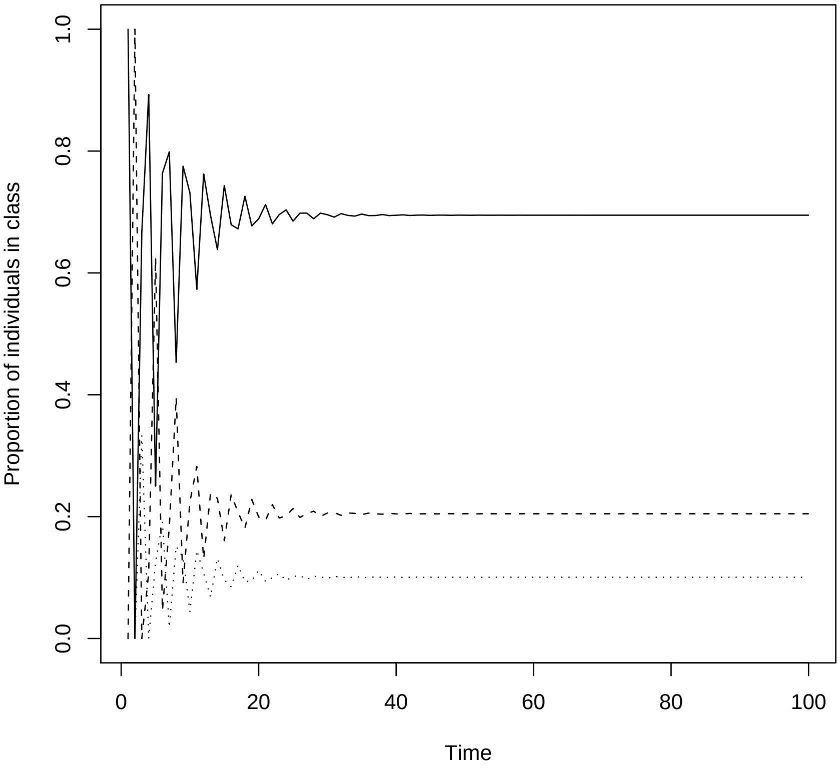


Figure 2: Projection of the proportion of the individuals in each class in time starting with $(1,0,0)$. After some years, about 70% of the individuals are in the first class, 20% in the second and 10% in the third.

2.2.4 *Life Cycle Graphs*

A simpler representation of a matrix, given the quantity of zeros, is in terms of directed graphs (i.e., mathematical constructs composed of nodes – the stages, and arrows – the probabilities and fecundities).

In Figure 5 I show a directed graph representation of a Leslie and a Lefkovich matrix model.

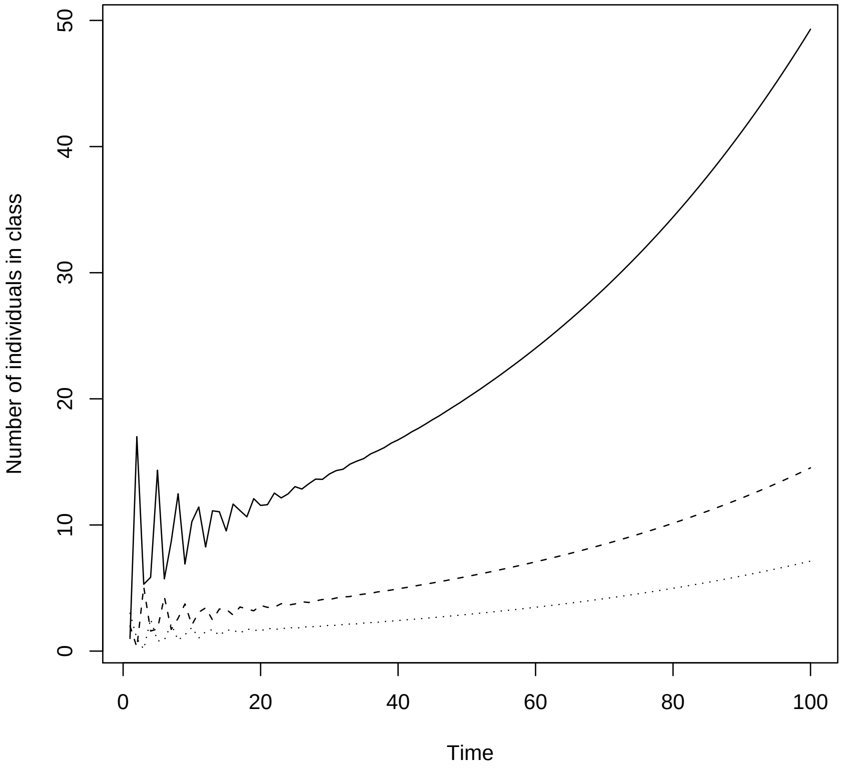
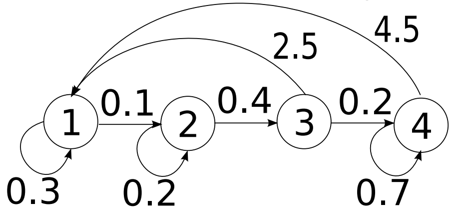


Figure 3: Projection of the 3-stage population in time starting with $(1, 2, 3)$.

HOMEWORK

Write the transition matrix corresponding to the graph



Is this is a Leslie or Lefkovich matrix?

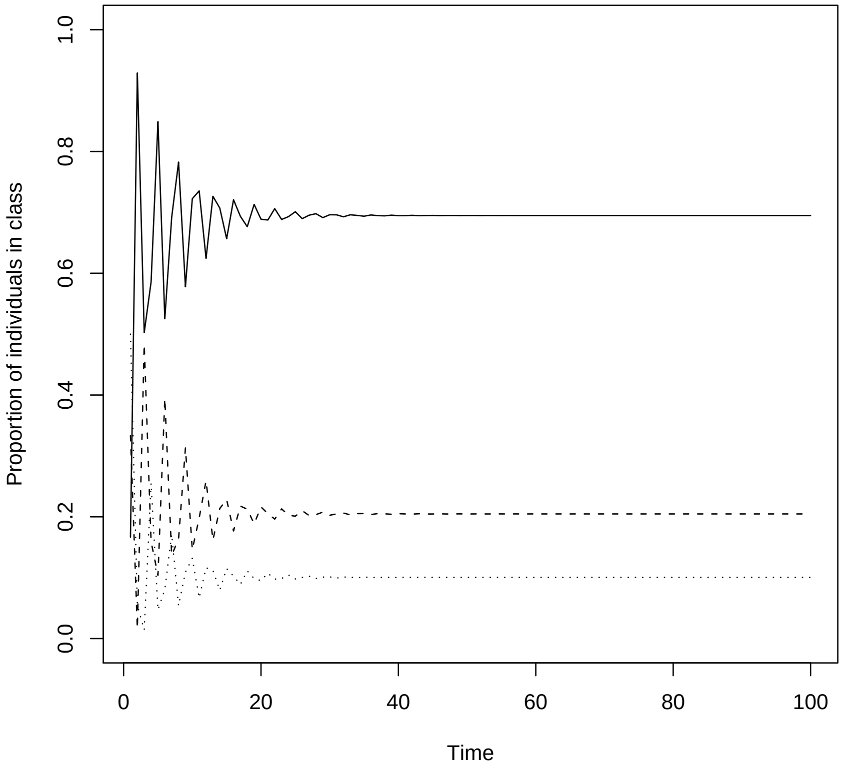


Figure 4: Projection of the proportion in each class in time starting with $(1, 2, 3)$.

2.3 MATH REFRESHER: EIGENVALUES AND EIGENVECTORS

We have seen that after some time, the fraction of individuals in each class stabilizes to some constant proportion. Mathematically, this means that:

$$n(t+1) = A \times n(t) = \lambda n(t) \tag{19}$$

i.e., the matrix multiplication has the simple effect of multiplying the number of individuals in each class for a constant, λ. In this way, if $\lambda > 1$, the number of individuals in each class will grow, if $0 < \lambda < 1$ the number of individuals in each class will shrink and if $\lambda = 1$ the numbers will remain unchanged. Because we are multiplying each element of the vector $n(t)$ by a constant, the proportion in each class does not change.

If you remember from the classes you took before, this resembles closely the definition of eigenvalues and eigenvectors. Take a matrix A, a vector v and a constant λ. If:

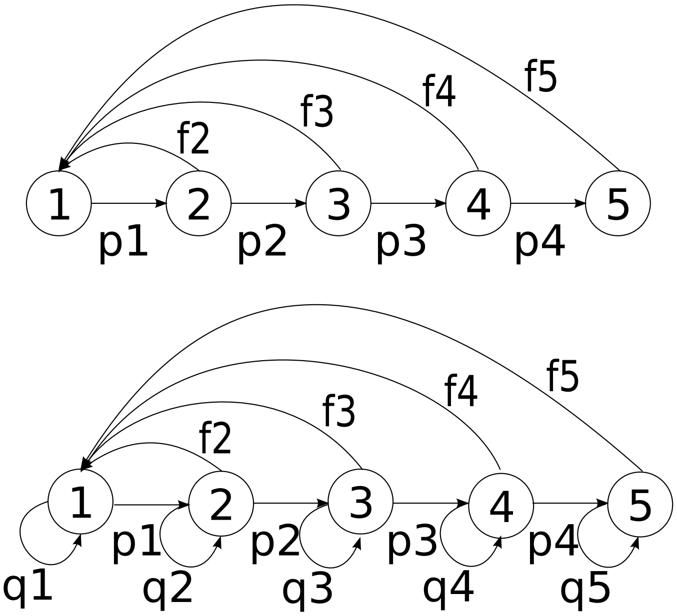


Figure 5: Directed Graph representation of Leslie (top) and Lefkovich (bottom). The arrows stand for fecundities and probabilities. The nodes represent ages in the Leslie model, and stages in the Lefkovich model.

$$A \times v = \lambda v \tag{20}$$

then λ is an eigenvalue of A and v its corresponding (right) eigenvector. Note that λ is a scalar (a number) and v is a vector. The easiest way to think about this problem is the following: we know that the matrix A projects our population at time t into the population at time $t+1$. The transformation entails growing or shrinking of the number of individuals in the various classes. What we are asking is if there is any distribution into classes at time t (call it v) for which the distribution at time $t+1$ is simply obtained by multiplying the distribution at time t for some constant λ. If this is true, then v is an eigenvector and λ an eigenvalue of A.

What follows is a short refresher of eigenvalues and eigenvectors, with a focus on their actual computation for small matrices. In case you are not familiar with these topics, read the tutorials you find in the "Reading List" at the end of the Chapter.

2.3.1 *Matrices*

A matrix is simply a $n \times m$ table of numbers. In our case, the numbers in the matrix are all real (i.e., no imaginary part). We deal with squared matrices (i.e., the number of rows equals the number of columns). In particular, we study $S \times S$ matrices where S is the number of stages in the population.

We have seen that:

$$n(t+T) = A^T n(t) \tag{21}$$

If our projections matrices have two special properties (they are irreducible and primitive, both typically satisfied), then the growth of A^k for $k \to \infty$ is controlled by the eigenvalue of A with the largest modulus. We call this eigenvalue the "dominant" eigenvalue. Moreover, if the two properties are met, the dominant eigenvalue is unique, and the eigenvector associated with the eigenvalue is positive (which is quite comforting, given that we would not know how to deal with "-6 juveniles").

The population will grow when the dominant eigenvalue > 1, or shrink when the dominant eigenvalue < 1. The eigenvalues of a squared matrix can be found solving an equation that involves the coefficients of the matrix.

2.3.2 *Trace and Determinant*

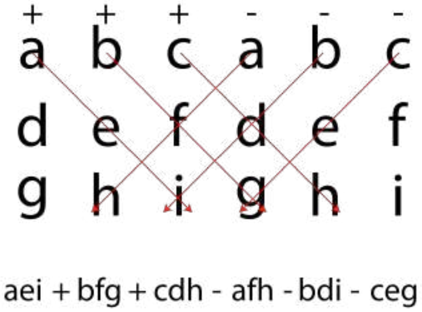
The determinant of a squared matrix, $\det(A)$, is a quantity of great importance in linear algebra. For a 2×2 matrix, it is computed as:

$$\det(A) = \begin{vmatrix} a & b \\ c & d \end{vmatrix} = ad - bc \tag{22}$$

For a 3×3 matrix, we can compute it by writing the determinant of three smaller matrices (minors):

$$\begin{aligned} \det(A) &= \\ \begin{vmatrix} a & b & c \\ d & e & f \\ g & h & i \end{vmatrix} &= \\ a\begin{vmatrix} e & f \\ h & i \end{vmatrix} - b\begin{vmatrix} d & f \\ g & i \end{vmatrix} + c\begin{vmatrix} d & e \\ g & h \end{vmatrix} &= \\ aei + bfg + cdh - ceg - bdi - afh \end{aligned} \tag{23}$$

or by using a trick involving diagonals:



The trace of a matrix $\mathrm{tr}(A)$ is the sum of its diagonal elements.

$$\mathrm{tr}(A) = \mathrm{tr}\begin{pmatrix} a & b \\ c & d \end{pmatrix} = a + d \tag{24}$$

$$\mathrm{tr}(A) = \mathrm{tr}\begin{pmatrix} a & b & c \\ d & e & f \\ g & h & i \end{pmatrix} = a + e + i \tag{25}$$

2.3.3 *Finding Eigenvalues*

The identity matrix I is a matrix with ones on the diagonal and zeros elsewhere. It is the equivalent of the number 1 for matrix multiplication.

The eigenvalues of a matrix can be found solving the polynomial:

$$\det(A - \lambda I) = 0 \tag{26}$$

For a 2×2 matrix, we have:

$$\begin{aligned} \det(A - \lambda I) = \begin{vmatrix} a-\lambda & b \\ c & d-\lambda \end{vmatrix} &= 0 \\ \lambda^2 - \lambda(a+d) + (ad - bc) &= 0 \\ \lambda^2 - \lambda \mathrm{tr}(A) + \det(A) &= 0 \end{aligned} \tag{27}$$

which we can solve:

$$\begin{aligned} \lambda &= \frac{\mathrm{tr}(A) \pm \sqrt{\mathrm{tr}(A)^2 - 4\det(A)}}{2} \\ \lambda &= \frac{a + d \pm \sqrt{a^2 + 4bc - 2ad + d^2}}{2} \end{aligned} \tag{28}$$

Because for matrix population models, the coefficients are always non-negative, the dominant eigenvalue is always:

$$\begin{aligned} \lambda_d &= \frac{\mathrm{tr}(A) + \sqrt{\mathrm{tr}(A)^2 - 4\det(A)}}{2} \\ \lambda_d &= \frac{a + d + \sqrt{a^2 + 4bc - 2ad + d^2}}{2} \end{aligned} \tag{29}$$

For a 3×3 matrix, we have:

$$\begin{aligned} \det(A - \lambda I) &= 0 \\ \begin{vmatrix} a-\lambda & b & c \\ d & e-\lambda & f \\ g & h & i-\lambda \end{vmatrix} &= 0 \\ -\lambda^3 + \mathrm{tr}(A)\lambda^2 - ((ae - bd) + (ei - hf) + (ai - cg))\lambda + \det(A) \end{aligned} \tag{30}$$

Note that $((ae - bd) + (ei - hf) + (ai - cg))$ is the sum of the determinants of the three 2×2 matrices obtained removing row and column three, one and two respectively.

Because we're only interested in matrices containing real numbers, the eigenvalues can either be real numbers, $\lambda_i = x$, or paired eigenvalues with the same real part, and imaginary parts with opposite signs: $\lambda = x \pm yi$, where $i = \sqrt{-1}$. In this case we call the eigenvalues complex conjugates.

The trace and the determinant of the matrix appear in the characteristic polynomial. In fact, the trace is the sum of the eigenvalues of the matrix:

$$\mathrm{tr}(A) = \sum_i \lambda_i \tag{31}$$

and the determinant is the product of all the eigenvalues:

$$\det(A) = \prod_i \lambda_i \tag{32}$$

For the matrix models we are studying in this Chapter, the dominant (i.e., largest) eigenvalue determines whether the population grows or shrink: if $\lambda_d > 1$ we have growth, if $0 < \lambda_d < 1$ the population shrinks and for $\lambda_d = 1$ the population size is constant.

HOMEWORK

Compute the determinant and the eigenvalues of the following matrices:

$$A_1 = \begin{bmatrix} 0.3 & 0.8 \\ 0.7 & 0.2 \end{bmatrix} \tag{33}$$

$$A_2 = \begin{bmatrix} 0.3 & 0.7 \\ 0.8 & 0.2 \end{bmatrix} \tag{34}$$

$$A_3 = \begin{bmatrix} 0.7 & 0.45 \\ 0.3 & 0.55 \end{bmatrix} \tag{35}$$

Compute the determinant (and, if you can, the eigenvalues) of:

$$A_4 = \begin{bmatrix} 0.0 & 0.3 & 0.7 \\ 0.1 & 0.8 & 0.1 \\ 0.0 & 0.5 & 0.5 \end{bmatrix} \tag{36}$$

2.3.4 *Eigenvectors*

The eigenvector associated with the dominant eigenvalue determines the stationary distribution into stages/classes. Eigenvectors can be recovered with the following method. We want to find a vector v for which:

$$A \times v = \lambda v \tag{37}$$

Take the simplest Lefkovich matrix:

$$A \times v = \begin{bmatrix} 0 & F \\ p & q \end{bmatrix} \times \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = \lambda \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} \tag{38}$$

The right-hand side is simply:

$$\begin{bmatrix} 0 & F \\ p & q \end{bmatrix} \times \begin{bmatrix} v_1 \\ v_2 \end{bmatrix} = \begin{bmatrix} \lambda v_1 \\ \lambda v_2 \end{bmatrix} \tag{39}$$

For the left-hand side, we want to multiply the matrix and the vector:

$$\begin{bmatrix} 0 \cdot v_1 + F \cdot v_2 \\ p \cdot v_1 + q \cdot v_2 \end{bmatrix} = \begin{bmatrix} \lambda v_1 \\ \lambda v_2 \end{bmatrix} \tag{40}$$

$$\begin{bmatrix} F \cdot v_2 \\ p \cdot v_1 + q \cdot v_2 \end{bmatrix} = \begin{bmatrix} \lambda v_1 \\ \lambda v_2 \end{bmatrix} \tag{41}$$

We can see this result as a set of equations:

$$\begin{cases} Fv_2 & = \lambda v_1 \\ pv_1 + qv_2 & = \lambda v_2 \end{cases} \tag{42}$$

From the first equation we find:

$$v_2 = \frac{\lambda v_1}{F} \tag{43}$$

Substituting in the second equation, we find that v_1 vanishes:

$$pv_1 + \frac{\lambda q}{F} v_1 = \lambda \frac{\lambda}{F} v_1 \tag{44}$$

Thus, we can choose any value for v_1 and compute the value of v_2. For any choice of v_1, we will obtain a different eigenvector. For example, take the matrix above and set $v_1 = 1$. Then, v_2 becomes:

$$v_2 = \frac{\lambda v_1}{F} = \frac{\lambda}{F} \tag{45}$$

2.3.5 *Eigenvalues and Eigenvectors for* 2×2 *Matrix Models*

As we saw above, the dominant eigenvalue of the matrix:

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \tag{46}$$

in which all the coefficients are non-negative, has dominant eigenvalue:

$$\lambda_d = \frac{a + d + \sqrt{a^2 + 4bc - 2ad + d^2}}{2} \tag{47}$$

A similar expression holds for the dominant eigenvector. If $c > 0$, the eigenvector v is an eigenvector associated with λ_d:

$$v = \begin{bmatrix} \lambda_d - d \\ c \end{bmatrix} \tag{48}$$

while, if $b > 0$:

$$v = \begin{bmatrix} b \\ \lambda_d - a \end{bmatrix} \tag{49}$$

If both b and c are non-zero, you can choose either. If both are zero, then the eigenvector is:

$$v = \begin{bmatrix} 1 \\ 0 \end{bmatrix} \tag{50}$$

HOMEWORK

Using these expressions, compute the dominant eigenvalue and eigenvector for the 2×2 matrices of the previous homework.

2.4 INTERPRETING EIGENVALUES AND EIGENVECTORS

Suppose that the population at time t is equal to $c \cdot v$ where c is a constant.

$$n(t) = c \cdot v \tag{51}$$

Then we can plug this in and find:

$$n(t+1) = A \times n(t) = A \times cv = c \cdot \lambda_d \cdot v \tag{52}$$

That is, the although the number of individuals in each class may change, the proportion in each class does not. If $\lambda_d > 1$ then each class will grow in number, if $\lambda_d < 1$ each class will shrink and finally if $\lambda_d = 1$ the population is constant.

For each eigenvalue, there are infinite eigenvectors. In fact, eigenvectors are defined up to a constant. If a and b are constants:

$$\begin{aligned} A \times v &= \lambda \cdot v \\ A \times a \cdot v &= a \cdot \lambda \cdot v \\ A \times b \cdot v &= b \cdot \lambda \cdot v \\ &\dots \end{aligned} \tag{53}$$

That is, v, av, bv are all eigenvectors of the matrix A corresponding to the eigenvalue λ.

Because we like to think about proportions, we take as the eigenvector that for which the elements sum to one hundred, and call it w.

$$\sum_i w_i = 100 \tag{54}$$

For the matrix A that generated the Figures, the dominant eigenvalue is 1.01815 and the corresponding eigenvector is:

$$w \approx \begin{bmatrix} 69.5 \\ 20.5 \\ 10 \end{bmatrix} \tag{55}$$

Because the matrix has dominant eigenvalue > 1, the population will grow exponentially, in this case with a rate close to 2%. In fact, suppose that at time t the total number of individuals is T:

$$T(t) = \sum_i n_i(t) \tag{56}$$

If we initialize the population at time 0 with 100 individuals partitioned into classes as w, then $T(0) = 100$, $T(1) = 101.815$, $T(2) = 103.663$, $T(3) = 105.5445$ and so on:

$$T(t) = \lambda T(t-1) = \lambda^2 T(t-2) = \ldots = \lambda^t T(0) \tag{57}$$

READING LIST

The paper that started it all:

- Leslie, P. H. 1945. *On the use of matrices in certain population mathematics.* Biometrika 33: 183-212.

The definitive book on matrix models:

- Caswell, H. 2001. Matrix Population models, Second Edition. Sinauer Associates, Inc. Sunderland, MA.

A very good paper on the algebra behind Google:

- Bryan, K., and Leise, T., *The $25,000,000,000 Eigenvector: The Linear Algebra Behind Google*, SIAM Review, August 2006, Volume 48, Issue 3, p. 569-581.

Tutorials on Eigenvalues and Eigenvectors:

- math.mit.edu/linearalgebra/ila0601.pdf
- www.math.hmc.edu/calculus/tutorials/eigenstuff/eigenstuff.pdf

3

MODELING LOGGERHEAD SEA TURTLES

3.1 BUILDING THE MODEL

Loggerhead sea turtles (*Caretta caretta*) are among the most common sea turtles observed in the southeastern US. However, they are not as common as they used to be, and in fact are protected under the Endangered Species Act ("threatened" species).

Turtles lay eggs on soft beaches (Figure 6). A female starts laying eggs around the age of 20 years, and will lay eggs four times a year in the same season. Turtles can live for more than 50 years and weight more than 400 pounds (Figure 6).

Figure 6: Left: nest on a beach. Right: adult Loggerhead.

The causes of the decline observed in the last decades are many, but the main include habitat loss (loss of nesting habitat), increase in predation by natural enemies, entanglement in fishing nets and failure of hatchlings to reach the sea due to light pollution. In fact, newly hatched individuals rely on the reflection of the moon on the sea to guide them.

A panel from the National Academy of Science found that drowning in shrimp trawls accounted for more turtle deaths than all other human activities combined, resulting in more than 40,000 sea turtle deaths annually.

A possible solution to this problem is the use of Turtle Excluder Devices (TEDs) that would allow turtles to escape from the nets. Prior to the implementation of TEDs, most sea turtle conservation efforts aimed at improving egg and hatchling survival through protection of nests on beaches or removal of eggs to protected hatcheries. In this example we will model both conservation strategies using real data to measure which one is most effective.

The main vital statistics are reported in Table 1 (from Crowder *et al.*, 1994).

Stage	Description	Stage Duration (yr)	Survivorship	Fecundity
1	Eggs/hatchlings	1	0.6747	0
2	Small Juveniles	7	0.75	0
3	Large Juveniles	8	0.6758	0
4	Subadults	6	0.7425	0
5	Adults	> 32	0.8091	76.5

Table 1: Vital statistics for the loggerhead population.

Using this data one can derive (but it is not straightforward, see Crowder *et al.*) a matrix model:

$$A = \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix} \tag{58}$$

To refresh what we saw in the first Chapter: this is a stage-structured model. Each number on the diagonal represents the probability of surviving while remaining in the same class. Numbers below the diagonal stand for the probability of moving from the row-stage to the column-stage. Finally, the numbers in the first row are the fertility values (i.e., average number of offspring for each individual in the column-stage).

First, we want to find the dominant eigenvalue. It is 0.951. This means that the population is declining with a rate of 4.9% per year. Then, we want to examine the corresponding dominant eigenvector. However, there are infinite of them. For convenience, choose the eigenvector w whose sum of all the coefficients is 100:

$$w = \begin{bmatrix} 23.9 \\ 64.8 \\ 10.3 \\ 0.7 \\ 0.3 \end{bmatrix} \tag{59}$$

meaning that the largest fraction of the population is represented by small juveniles, constituting almost two thirds of the total. If at a given year we start with 100 individuals, we expect the total to drop to:

$$T(10) = \lambda^t T(0) = 0.951^{10} \cdot 100 \approx 60.51 \tag{60}$$

individuals in 10 years. We now examine two possible strategies to rescue the population, and show which one is most effective.

3.2 CONSERVATION STRATEGIES

3.2.1 *Patrolling Beaches*

One possible strategy is to patrol the beaches and move the eggs that are in non-protected areas into nurseries. Assume that in this way we can reduce the mortality of the hatchlings by 90%. The mortality right now is $1 - 0.675 = 0.325$ per year. Reducing it by 90% would mean bringing it to $0.325 \cdot 0.1 = 0.0325$. Therefore the element in the matrix would change from 0.675 to 0.9675:

$$A' = \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.9675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix} \tag{61}$$

What is the effect on the population? First, we inspect the dominant eigenvalue, which changed to 0.9724. That is, the population is still declining, with a rate of approximately 2.76% a year. That would mean that in 10 year, starting with 100 turtles at the stationary age distribution we would end up with 75.6 — a decisive improvement, but not sufficient to rescue the species. The stationary age distribution w becomes:

$$w' = \begin{bmatrix} 19.3 \\ 69.4 \\ 10.4 \\ 0.7 \\ 0.2 \end{bmatrix} \tag{62}$$

meaning that the small juveniles become even more predominant, while the fertile classes still represent around 1% of the population.

3.2.2 *TEDs*

Another possibility is to use Turtle Excluder Devices (TEDs). These are special nets (especially for shrimps) that allow turtles to escape (see Figure 2). In fact, as all amphibians, turtles have to breathe air from the sea surface. The typical dive lasts between 15 and 30 minutes, but in case of necessity, individuals can spend up to 4 hours submerged (!). However, if caught in nets for an extended period of time, turtles will drown.

In our original matrix, 65.7% of the large juveniles remain in the same class in the next year, while 1.9% of them grow to the next class. The mortality rate is therefore $1 - (0.657 + 0.019) = 0.324$. If we assume that TEDs can reduce the mortality rate by 90%, we have to redistribute a mortality rate of 0.0324 (and therefore a survival probability of 0.9676) between the two components. This can be done by computing $0.9676 \cdot 0.657/(0.657 + 0.019) = 0.9404$ and $0.9676 \cdot 0.019/(0.657 + 0.019) = 0.0272$. The new matrix becomes:

$$A'' = \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.9404 & 0 & 0 \\ 0 & 0 & 0.0272 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix} \tag{63}$$

The dominant eigenvalue is 1.06, and the stable class distribution becomes:

$$w'' = \begin{bmatrix} 27 \\ 51 \\ 20.1 \\ 1.5 \\ 0.4 \end{bmatrix} \tag{64}$$

Therefore, TEDs alone can rescue the population from extinction. An analysis similar to that we performed today is at the base of American policy on TEDs. Since the introduction of TEDs the loggerhead population has been growing at a rate of approximately 3%. Currently, larger TEDs are being examined, as they could potentially reduce the mortality of adults that are too big to escape from the nets.

HOMEWORK

A population is described by the following matrix:

$$A = \begin{bmatrix} 0 & 1.3 \\ x & 0.2 \end{bmatrix} \tag{65}$$

Compute the dominant eigenvalue and eigenvector. For which values of x does the population grow? When the population is growing, do juveniles or adults dominate the population?

READING LIST

The study on Loggerhead:

- L.B. Crowder, D.T. Crouse, S.S. Heppell and T.H. Martin (1994). *Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Populations*. Ecological Applications 4:437–445.

More on the interpretation and sensitivity of eigenvalues and eigenvectors:

- H. Caswell (2010). *Reproductive value, the stable stage distribution, and the sensitivity of the population growth rate to changes in vital rates.* Demographic Research 19:531-548.

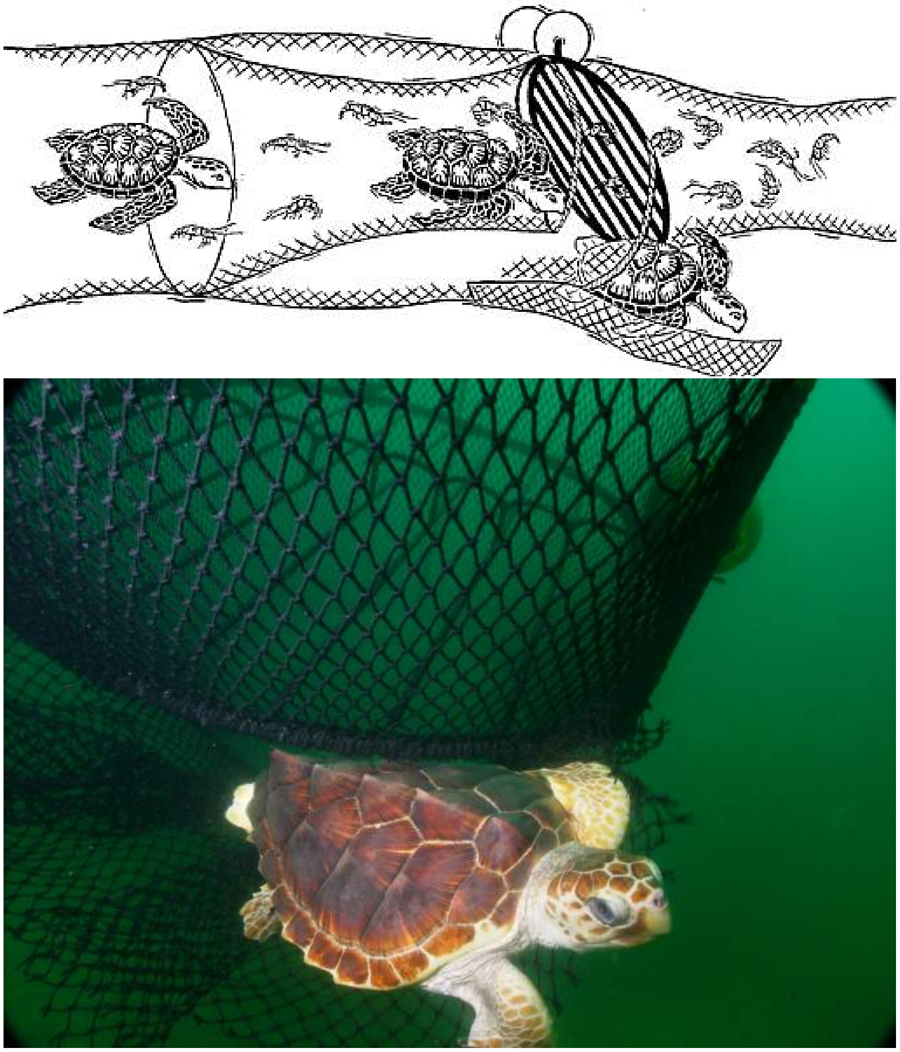


Figure 7: Top: Example of Turtle Excluder Device. Bottom: turtle escaping from a TED.

4

EXPONENTIAL AND LOGISTIC GROWTH

4.1 EXPONENTIAL GROWTH

We now switch gears from discrete to continuous growth. Continuous growth models are especially suited for populations where reproduction can happen at any point in time.

For discrete time models, we wrote:

$$r = \frac{N(t + \Delta t) - N(t)}{N(t)} \tag{66}$$

meaning that the rate of increase is equal to the increase in the number of individuals $N(t + \Delta t) - N(t)$ divided by the initial number of individuals. What happens if we make the interval Δt shorter and shorter? For Δt going to zero, we obtain:

$$r = \frac{1}{N(t)} \frac{dN(t)}{dt} \tag{67}$$

rearranging:

$$\frac{dN(t)}{dt} = rN(t) \tag{68}$$

which is the differential equation for the exponential (Malthusian) growth you should be familiar with.

4.1.1 *Analysis*

Given the initial condition:

$$N(0) = N_0 \geq 0 \tag{69}$$

we can solve the equation. The equation is separable:

$$\frac{dN(t)}{dtN(t)} = r \tag{70}$$

Integrating both sides:

$$\int_0^T \frac{dN(t)}{N(t)} = \int_0^T r dt \tag{71}$$

$$[\ln(N)]_{N(0)}^{N(T)} = [rt]_0^T \tag{72}$$

$$\ln(N(T)) - \ln(N(0)) = rT \tag{73}$$

$$\ln\left(\frac{N(T)}{N(0)}\right) = rT \tag{74}$$

$$\frac{N(T)}{N(0)} = e^{rT} \tag{75}$$

$$N(T) = N(0)e^{rT} \tag{76}$$

The interpretation of the solution is the following: for $r > 0$ the population grows exponentially. For $r < 0$ the decay is exponential. For $r = 0$ the population is constant.

4.2 THE LOGISTIC GROWTH MODEL

4.2.1 *Intraspecific Competition*

We have considered a model in which populations grow without constraint. However, due to the finiteness of resources, an environment cannot sustain an infinite population. When resources start being scarce, a fierce competition among individuals of the same species begins. We call this effect intraspecific competition (i.e., within the same species).

To set the stage, let's examine some data from Gause (1932). To test the effects of intraspecific competition, Gause used brewer's yeast (*Saccharomyces cerevisiae*). His experiments were based on the growth of yeast in an environment with a limited nutrients. He started the population at some low level and then he measured the volume of the cells in time. The data is represented in Figure 8.

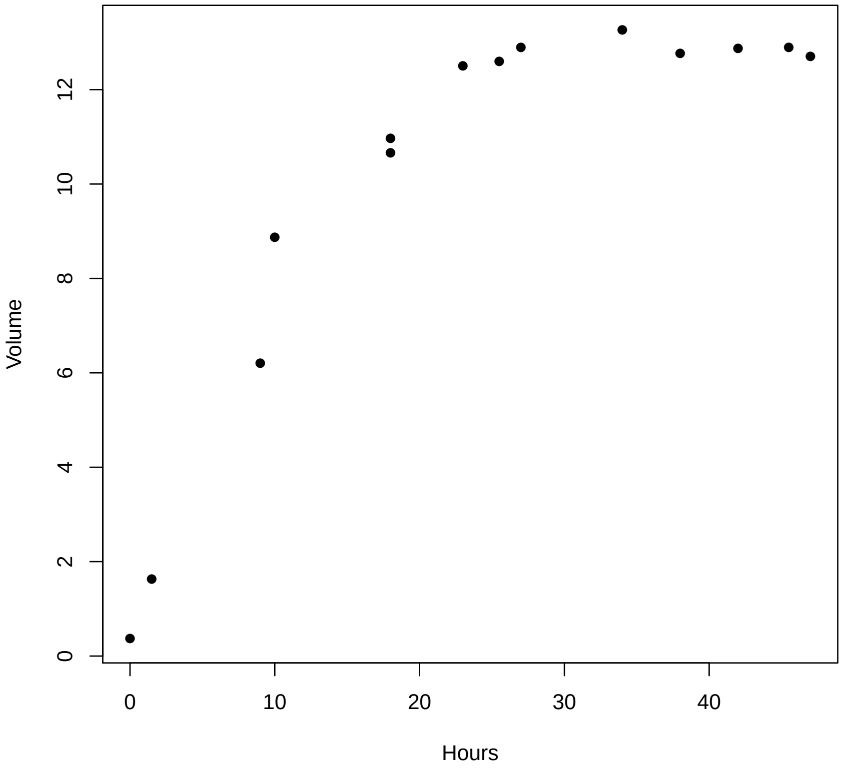


Figure 8: Data measured by Gause. Growth of brewer's yeast in an environment with limited nutrients.

Clearly, yeast does not grow to infinity. Rather, after 1 day or so the population stops growing and remains around a given volume. Suppose that a population can grow up to a certain threshold K, usually known as carrying capacity. This model can be represented by the differential equation:

$$\frac{dN(t)}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right) \tag{77}$$

where r can be measured as the growth rate at very low density and K is the carrying capacity for the system, i.e., the density of individuals the habitat can support. Note that $r > 0$ and $K > 0$, otherwise it does make biological sense (Why if $r < 0$ the equation does not make sense?)

4.2.2 *Analysis*

Plot $\frac{dN(t)}{dt}$ vs. $N(t)$ (see Figure 9). Using this graphical method we can count the number of equilibria and investigate their stability.

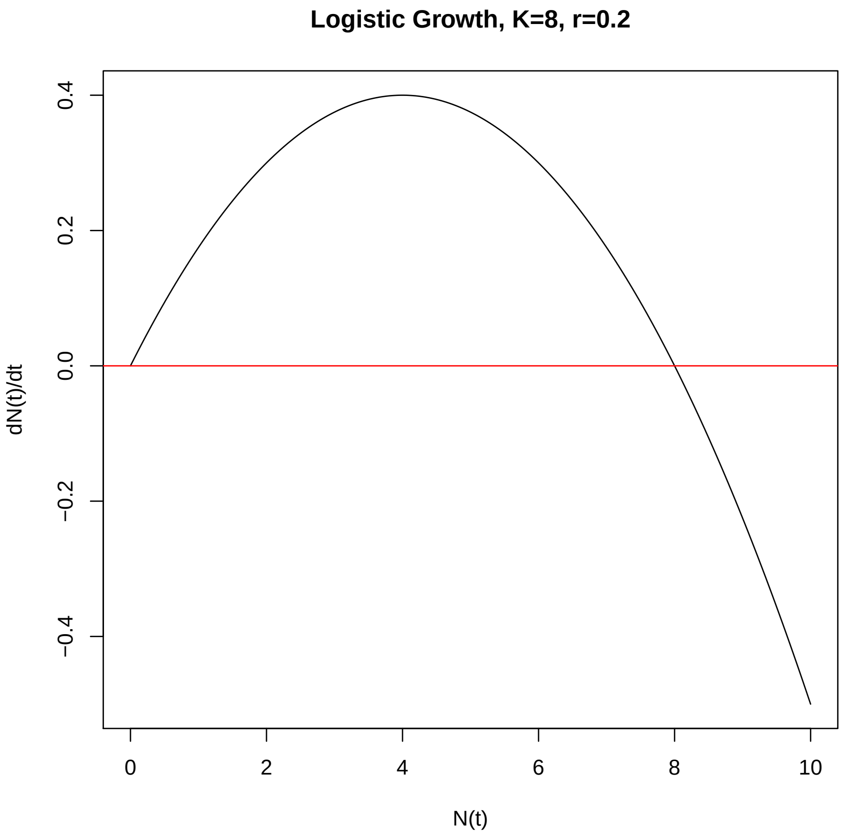


Figure 9: Graphical methods for logistic growth.

We define an equilibrium point (or steady state, or fixed point or critical point) a point in which $\frac{dN}{dt} = 0$. In this point, the growth rate is zero: left alone, the population will not grow nor decay. In the logistic growth equation we have two fixed points: $N^* = 0$, $N^* = K$. This can be seen in the graph whenever $\frac{dN}{dt}$ crosses the zero line.

An equilibrium point N^* is stable if when we slightly perturb the system that is resting at N^*, $\lim_{t\to\infty} N(t) = N^*$. We can think about stability using the cartoon in Figure 10.

The red ball is at an unstable equilibrium point: slightly perturbing its position will set it in motion ending up at another point. The blue balls, on the other hand, will return to the same

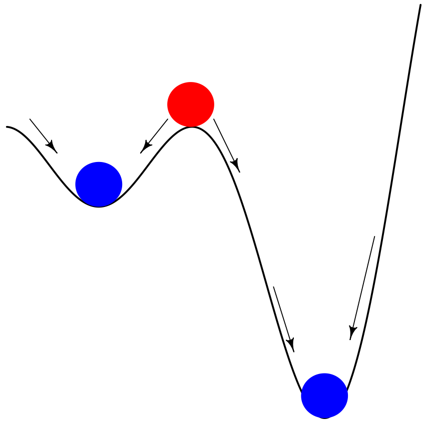


Figure 10: Stability as a metaphor.

point once slightly perturbed: they are at stable equilibrium points.

For the logistic growth, we have that $N_1^* = 0$ is unstable, while $N_2^* = K$ is stable. For single species dynamics, whenever growth rate is > 0 on the left of the fixed point and < 0 on the right of the fixed point we have stability. Therefore, if a species has density 0 and we slightly increase its density (decreasing it would be a biological nonsense) it will start growing until it reaches density K, when it will stop growing.

We will now use some mathematics to get a qualitative understanding of equilibria. First, we want to find the equilibria. By definition, we want to solve the equation:

$$rN^* \left(1 - \frac{N^*}{K}\right) = 0 \tag{78}$$

There is a trivial solution:

$$N^* = 0 \tag{79}$$

while the other solution can be found using:

$$1 - N^*/K = 0 \tag{80}$$

$$N^*/K = 1 \tag{81}$$

$$N^* = K \tag{82}$$

We now want to measure the growth rate in the vicinity of an equilibrium. First, let us assume that $N(0) \ll K$ (i.e., the population at time 0 is at a much lower level than the carrying capacity). Then, $(1 - N(0)/K) \approx 1$. This means that the growth rate equation is approximately:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \approx rN \tag{83}$$

the population, when close to 0, will grow almost exponentially. In the same way, we can evaluate what happens when $N(0) \approx K$. In this case $(1 - N(0)/K) \approx 0$ and therefore:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \approx 0 \tag{84}$$

the population will remain constant.

Finally, when $N(0) \gg K$ the term $(1 - N(0)/K)$ becomes negative (say the value is some unspecified $-y$). Then the approximate growth becomes:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \approx -rNy \tag{85}$$

the population decreases exponentially.

We want to know where the population grows at the fastest rate. To do so, we first take the derivative:

$$\frac{\partial \frac{dN}{dt}}{\partial N} = r - \frac{2rN}{K} \tag{86}$$

and equate it to zero:

$$r - \frac{2rN}{K} = 0 \tag{87}$$

$$N = \frac{K}{2} \tag{88}$$

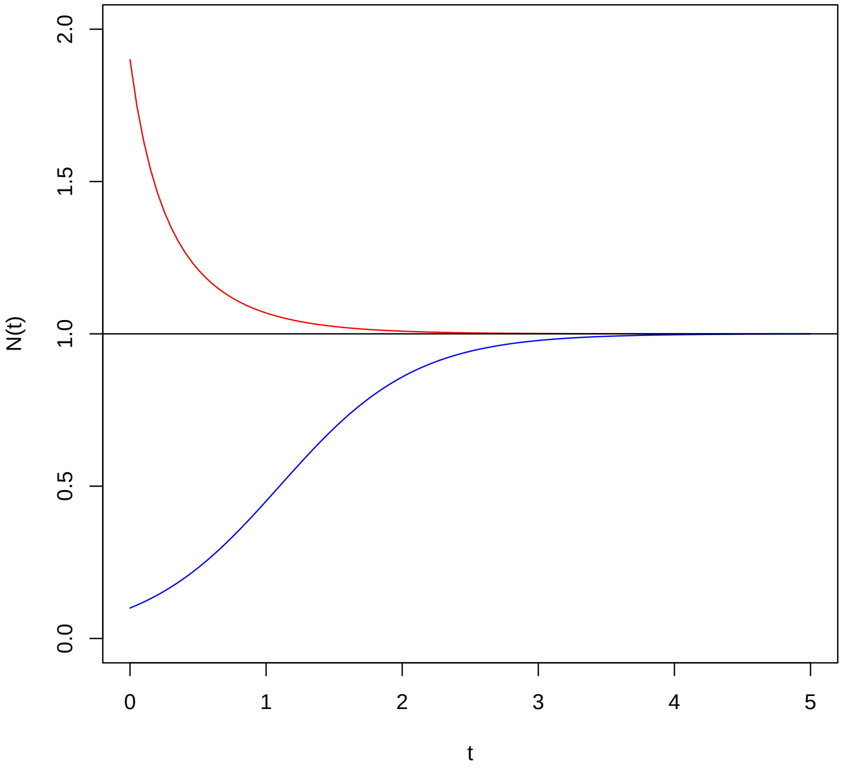


Figure 11: Logistic Growth: $K = 1$, $r = 2$. Blue: $N(0) = 0.1$, Red: $N(0) = 1.9$

we find that when the population is half-saturated, it grows at the fastest rate. Piecing these facts together, we can draw a qualitative solution for the differential equation (Figure 11).

This qualitative drawing captures the essential features of the solution:

$$N(t) = \frac{K}{1 + (K/N_0 - 1)e^{-rt}} \tag{89}$$

The solution can be obtained using partial fractions, and is reported below.

4.2.3 *Optional - Solving the Logistic Equation*

Non-Dimensionalization

Numerical solutions for a model depend on the actual values of all the parameters and initial conditions. However, the possible behavior of the model is controlled by the relation among the parameters (e.g., if you express the mass in grams or Kg, the numbers will change, but the stability of equilibria will not). A useful technique to investigate which combination of parameters is critical for the dynamics of the system is the rescaling of models so that they become dimensionless. Dimensionless models typically contain less parameters than their counterpart.

For example, take the logistic growth model above and set $x = N/K$. Because both N and K are of the same unit (e.g., biomass, or density), then x has no dimension.

$$\frac{dx}{dt} = \frac{1}{K} \tag{90}$$

$$\frac{dN}{dt} = \frac{1}{K} rN\left(1 - \frac{N}{K}\right) = rx(1-x) \tag{91}$$

now let's set $rt = \tau$. Note that r is in units of $1/time$, so that τ is dimensionless. This makes the system dimensionless (use chain rule with $dt = d\tau/r$):

$$\frac{dx}{d\tau} = \frac{dx}{dt}\frac{dt}{d\tau} = \frac{1}{r}\frac{dx}{dt} = \frac{1}{r} rx(1-x) = x(1-x) \tag{92}$$

Solving the logistic dimensionless model

This is a separable differential equation:

$$\int \frac{1}{x(1-x)} dx = \int d\tau \tag{93}$$

For the left part we use partial fractions:

$$\frac{1}{x(1-x)} = \frac{A}{x} + \frac{B}{x-1} \tag{94}$$

multiply by $x(x-1)$ both sides.

$$-1 = A(x-1) + Bx \tag{95}$$

when $x = 0$ we find $A = 1$, when $x = 1$ we have $B = -1$. Therefore:

$$\int \frac{1}{x(1-x)} dx = \int \left(\frac{1}{x} - \frac{1}{x-1} \right) dx \tag{96}$$

Integrating by substitution:

$$\int \left(\frac{1}{x} - \frac{1}{x-1} \right) dx = \int \frac{1}{x} dx - \int \frac{1}{x-1} dx = \int \frac{1}{x} dx - \int \frac{1}{u} du \tag{97}$$

with $u = x - 1$. The integrals are simply solved:

$$log(x)|_{x(0)}^{x(\tau)} - log(x-1)|_{x(0)}^{x(\tau)} = \tau \tag{98}$$

From this, setting $x(0) = x_0$ we can write:

$$log(x(\tau)) - log(x_0) - log(x(\tau) - 1) + log(x_0 - 1) = \tau \tag{99}$$

$$log \frac{x(\tau)(x_0 - 1)}{(x(\tau) - 1)x_0} = \tau \tag{100}$$

$$\frac{x(\tau)(x_0 - 1)}{(x(\tau) - 1)x_0} = e^{\tau} \tag{101}$$

$$x(\tau)(x_0 - 1) = e^{\tau}((x(\tau) - 1)x_0) \tag{102}$$

$$x(\tau)(x_0 - 1 - x_0 e^{\tau}) = -x_0 e^{\tau} \tag{103}$$

$$x(\tau) = \frac{x_0 e^{\tau}}{(1 + x_0 e^{\tau} - x_0)} = \frac{x_0 e^{\tau}}{(1 + x_0(e^{\tau} - 1))} \tag{104}$$

Now we can substitute back $\tau = rt$ and $x(t) = N(t)/K)$ to recover the solution of the logistic growth:

$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)} \tag{105}$$

4.3 DOUBLING TIMES

For the case of exponential growth, calculating doubling times is especially easy. We simply need to plug the value in the solution:

$$N(T) = N(0)e^{rT} \tag{106}$$

Setting the left-hand side to $2N(0)$, we get

$$2N(0) = N(0)e^{rT} \tag{107}$$

If $N(0) > 0$, we can cancel on both sides:

$$2 = e^{rT} \tag{108}$$

$$\log 2 = rT \tag{109}$$

$$\frac{\log 2}{r} = T \approx \frac{0.3}{r} \tag{110}$$

meaning that the double time is independent of the initial conditions. From the approximation, we see that a growth rate of about 0.03 leads to doubling the population every ≈ 10 years.

For the logistic growth, the solution is more complex. First, the population cannot double if its above $K/2$. Second, the time it takes to double in size depends on the initial conditions.

Plugging $N(t) = 2N_0$ in the solution, we have:

$$2N_0 = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}} \tag{111}$$

multiplying both sides by $1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}$,

$$2N_0 + 2Ke^{-rt} - 2N_0e^{-rt} = K \tag{112}$$

$$2Ke^{-rt} - 2N_0e^{-rt} = K - 2N_0 \tag{113}$$

$$e^{-rt} = \frac{K - 2N_0}{2K - 2N_0} \tag{114}$$

$$e^{rt} = \frac{2K - 2N_0}{K - 2N_0} \tag{115}$$

$$t = \frac{\log\left(\frac{2K-2N_0}{K-2N_0}\right)}{r} \tag{116}$$

Note that this expression makes sense only when $N_0 < K/2$. For N_0, we recover the doubling time for the exponential growth.

Homework

A population is at density $N(0) = 0.2$, and has a growth rate $r = 0.1$. When will it grow to 0.9 assuming exponential growth?
What if the population is regulated, with carrying capacity $K = 1$?

4.4 THE ALLEE EFFECT

Warder Clyde Allee was a professor at the University of Chicago. In 1932 he showed that goldfish grow faster in a tank laced with colloidal silver suspension when their density is higher. The so-called Allee effect now more generally denotes the fact that under certain conditions, an increase in density leads to an increase in growth rate (i.e., the contrary of what seen in the logistic equation).

The causes of an Allee effect could be several. For example, increasing the density of a small population could improve its growth rate because it could make it simpler to find a mate, improve cooperative hunting or defense, and would alleviate genetic problems due to small population size.

A simple model describing a population with Allee effect:

$$\frac{dN}{dt} = rN\left(\frac{N}{A} - 1\right)\left(1 - \frac{N}{K}\right) \tag{117}$$

where $0 < A < K$.

HOMEWORK

Find the three equilibria for the Allee model and study their stability using the graphical model introduced above.

READING LIST

I am a big fan of the work of Richard Levins, and I think that anybody interested in modeling should read:

- Levins, R. (1966) *The Strategy of Model Building in Population Biology.* American Scientist, 54:421-431.

You are going to read this article in the laboratory section of the class.

5

SPATIALLY-STRUCTURED POPULATIONS

Populations may be structured in space. For example, a species might thrive in presence of suitable habitat, but not be found in unsuitable habitat. Spatial models take two main forms: patch-occupancy (metapopulation) models, and reaction-diffusion models (modeling directly the movement of individuals). Here we concentrate on the former.

We can think of a landscape from the point of view of our species of interest: individuals sees patches of suitable habitat (islands) arranged in a background of unsuitable habitat (sea). They move through the landscape, but only "live" (breed, nest, forage, etc.) in the patches of suitable habitat. Hence we might model the landscape of a network of patches: the nodes of the networks are the patches themselves (possibly characterized by a patch "value"), and the connections between the nodes stand for dispersal (typically with dispersal decreasing with distance — Euclidean, or "perceived").

5.1 levins's metapopulation model

The first usage of the word "metapopulation" (i.e., a population of local populations connected by dispersal) is due to Richard "Dick" Levins (formerly at U. of Chicago), who in 1969/70 proposed the simplest model for a metapopulation.

Levins's main idea is quite simple: local populations live in patches, and the dynamics are dominated by local extinction and colonization of patches.

Local populations can go extinct for a variety of reasons, such as low population numbers (demographic stochasticity), fluctuating environmental conditions (environmental stochasticity), disease, over-exploitation of resources, introduction of predators, etc. Thus, there is a process of extinction, turning occupied patches into empty patches.

This process of extinction might be counter-balanced (rescue effect) by colonization from neighboring occupied patches. Clearly, colonization is a function that in general depends on the ability of the population to disperse, and we can expect dispersal to decrease with distance and with the difficulty of crossing inhospitable habitat.

Levins's model makes many simplifying assumptions. It considers infinitely many patches of suitable habitat, all reachable from each other at the same dispersal rate. Take $p(t)$ to be the proportion of patches occupied by the species of interest at time t. The extinction rate is the same in all patches, δ (i.e., the time a patch stays occupied is Poisson with rate δ, such that the probability of remaining occupied from time 0 to time t is $e^{-\delta t}$). When a patch is not occupied, it can be colonized by the other occupied patches at rate c. Then, we can write a differential equation tracking the proportion of occupied patches:

$$\frac{dp(t)}{dt} = -\delta p(t) + (1 - p(t))cp(t) \tag{118}$$

This equation is in fact identical to that of the logistic growth:

$$\frac{dp(t)}{dt} = -\delta p(t) + cp(t) - cp^2(t) \tag{119}$$

$$\frac{dp(t)}{dt} = p(t)(c - \delta) - cp^2(t) \tag{120}$$

$$\frac{dp(t)}{dt} = (c - \delta)p(t)\left(1 - \frac{c}{(c-\delta)}p(t)\right) \tag{121}$$

setting $r = (c - \delta)$ and $K = (c - \delta)/c$, we can say that there are two equilibria, $p^* = 0$ and $p^* = K = (c - \delta)/c = 1 - \delta/c$, of which the positive is stable. Hence, the metapopulation will persist at a positive proportion of occupied patches whenever $c > \delta$.

HOMEWORK

Suppose that not all patches are habitable: due to habitat destruction, only the fraction h of patches is actually suitable for the species.
This modifies the model to:

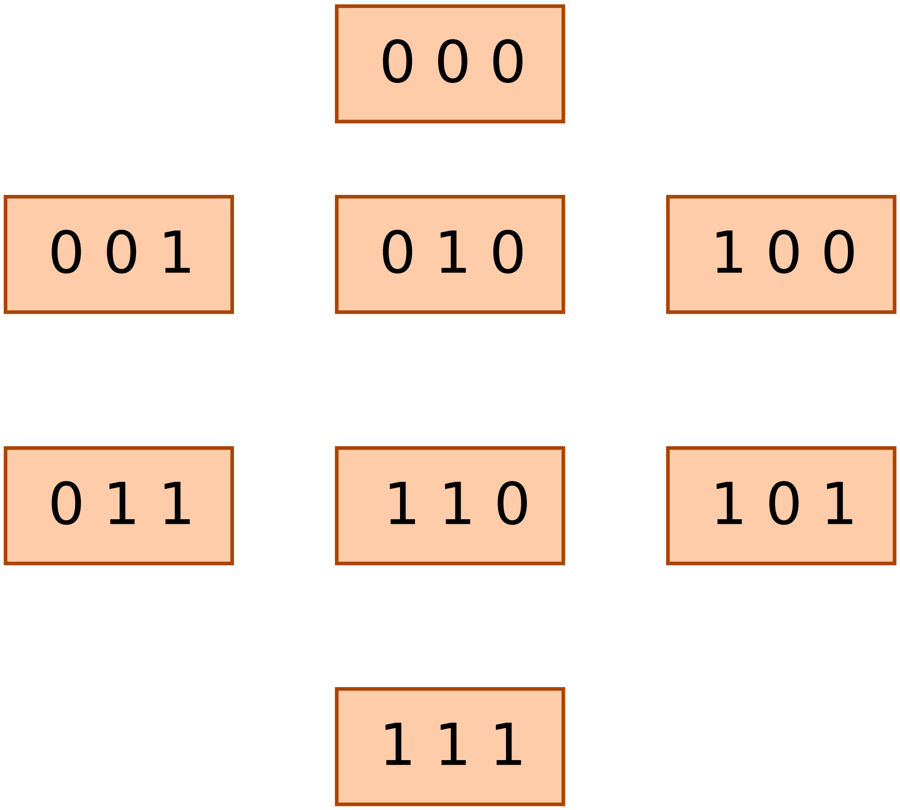
$$\frac{dp(t)}{dt} = -\delta p(t) + (h - p(t))cp(t) \tag{122}$$

Compute the new equilibrium. For which value of h will the metapopulation go extinct?

5.2 REALISTIC LANDSCAPES

We now want to model spatially-explicit, realistic landscapes. We will write species-occupancy models (i.e., models where each patch of suitable habitat is either occupied — $X_i = 1$, or empty — $X_i = 0$). We allow for two types of event: local extinction (patch i going from $X_i = 1$ to $X_i = 0$) and colonization from other occupied patches (leading to patch i changing from $X_i = 0$ to $X_i = 1$).

If we assume that in a small time interval only one event can occur, we can model the dynamics exactly using a Markov chain.



One interesting aspect is that there is a single absorbing state, that in which all patches are empty. Thus, in case there is no external immigration, for $t \to \infty$ the metapopulation will go extinct.

Even though this is the ultimate fate of the metapopulation, a meta-stable (quasi-stable) regime dominates the dynamics for a long time: until we have especially bad luck and all patches go extinct, a typical proportion of patches is occupied. This is the regime we are most interested in.

Another problem is that the size of the Markov chain grows rapidly with the number of patches. If we have hundreds of patches (which is quite common in real applications), the number of states of the Markov chain (2^N, where N is the number of patches) exceeds the number of atoms in the visible universe, rendering the approach completely useless.

We therefore turn to approximate models. In particular, we will examine the approximation by Hanski and Ovaskainen, which models the approximate dynamics of the system as a set of N differential equations. This approach, besides being more tractable mathematically, has the added advantage that the meta-stable state of the Markov chain is the equilibrium state of the system.

5.2.1 *Tracking expectations*

We model $\mathbb{E}[X_i(t)]$, which can be interpreted as the probability of finding patch i occupied at time t.

$$\frac{d\mathbb{E}[X_i(t)]}{dt} = \mathbb{E}\left[-\delta_i X_i(t) + (1 - X_i(t)) \sum_{j \neq i} D_{ij} X_j(t)\right] \tag{123}$$

where the dynamics of the patch i are influenced by a patch-specific extinction rate δ_i, and the colonization from other occupied patches, modeled as D_{ij} (the rate at which individuals from patch j —when occupied— colonize patch i —when empty). Because the expectation of a sum is the sum of the expectations, we can write

$$\frac{d\mathbb{E}[X_i(t)]}{dt} = -\delta_i \mathbb{E}[X_i(t)] + \sum_{j \neq i} D_{ij} \mathbb{E}[X_j(t)] - \sum_{j \neq i} D_{ij} \mathbb{E}[X_i(t) X_j(t)] \tag{124}$$

Here's where the approximation kicks in: we assume that $\mathbb{E}[X_i(t)X_j(t)] = \mathbb{E}[X_i(t)]\mathbb{E}[X_j(t)]$, i.e., that the probabilities of having patch i and patch j occupied are independent. Turns out, this is not a terrible approximation, as in general we expect the two probabilities to be positively correlated, so that we are being conservative in our approximation.

With this approximation at hand, and writing $p_i(t) = \mathbb{E}[X_i(t)]$ for brevity, we obtain the model

$$\frac{dp_i(t)}{dt} = (1 - p_i(t)) \sum_{j \neq i} D_{ij} p_j(t) - \delta_i p_i(t) \tag{125}$$

5.2.2 *Modeling extinction*

In the Hanski-Ovaskainen model, each patch i is associated with a value, A_i (think of it as its "area", or "carrying capacity"). The extinction rate of patch i depends on a background extinction rate, δ, whose effect is mitigated in patches of high value:

$$\delta_i = \frac{\delta}{A_i} \tag{126}$$

5.2.3 *Modeling dispersal*

The dispersal rate from patch j to patch i depends on the distance between the patches (in general, we believe dispersal to eventually decrease with distance). In the simplest case, we can model it as a function of the Euclidean distance between patches. Suppose that d_{ij} is the distance between patches i and j. Then, we write the "dispersal kernel" as a function of the distance, measured in ξ, the typical dispersal length of the species in question (so that 1 Km would be much for a snail, but not for a wolf).

Example of kernel functions:

1. Exponential: $f(d_{ij}, \xi) = e^{\frac{-d_{ij}}{\xi}}$.
2. Gaussian: $f(d_{ij}, \xi) = e^{\frac{-d_{ij}^2}{2\xi^2}}$.
3. Rectangular: $f(d_{ij}, \xi) = 1$ if $d_{ij} < \xi$, 0 otherwise.

The three kernel functions are represented in Figure 12. In the Hanski-Ovaskainen model, dispersal rate increases with patch value:

$$D_{ij} = f(d_{ij}, \xi) A_j \tag{127}$$

5.2.4 *Metapopulation capacity*

Hanski and Ovaskainen were able to prove that the metapopulation is persistent only if the dominant eigenvalue of the dispersal matrix, M, dubbed the "metapopulation capacity" λ, exceeds the baseline extinction rate δ.

The dispersal matrix is defined as:

$$\begin{cases} M_{ij} = f(d_{ij}, \xi) A_i A_j \\ M_{ii} = 0 \end{cases} \tag{128}$$

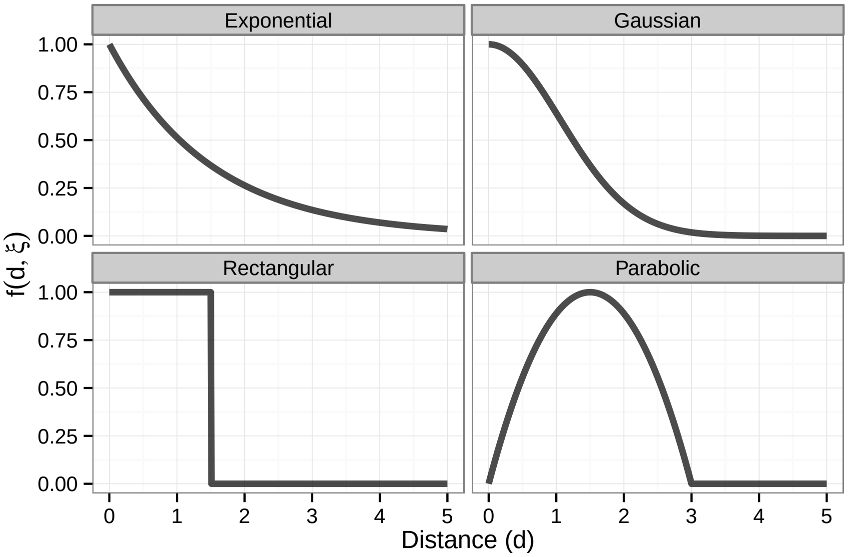


Figure 12: Different kernels of dispersal, for $\xi = 3/2$.

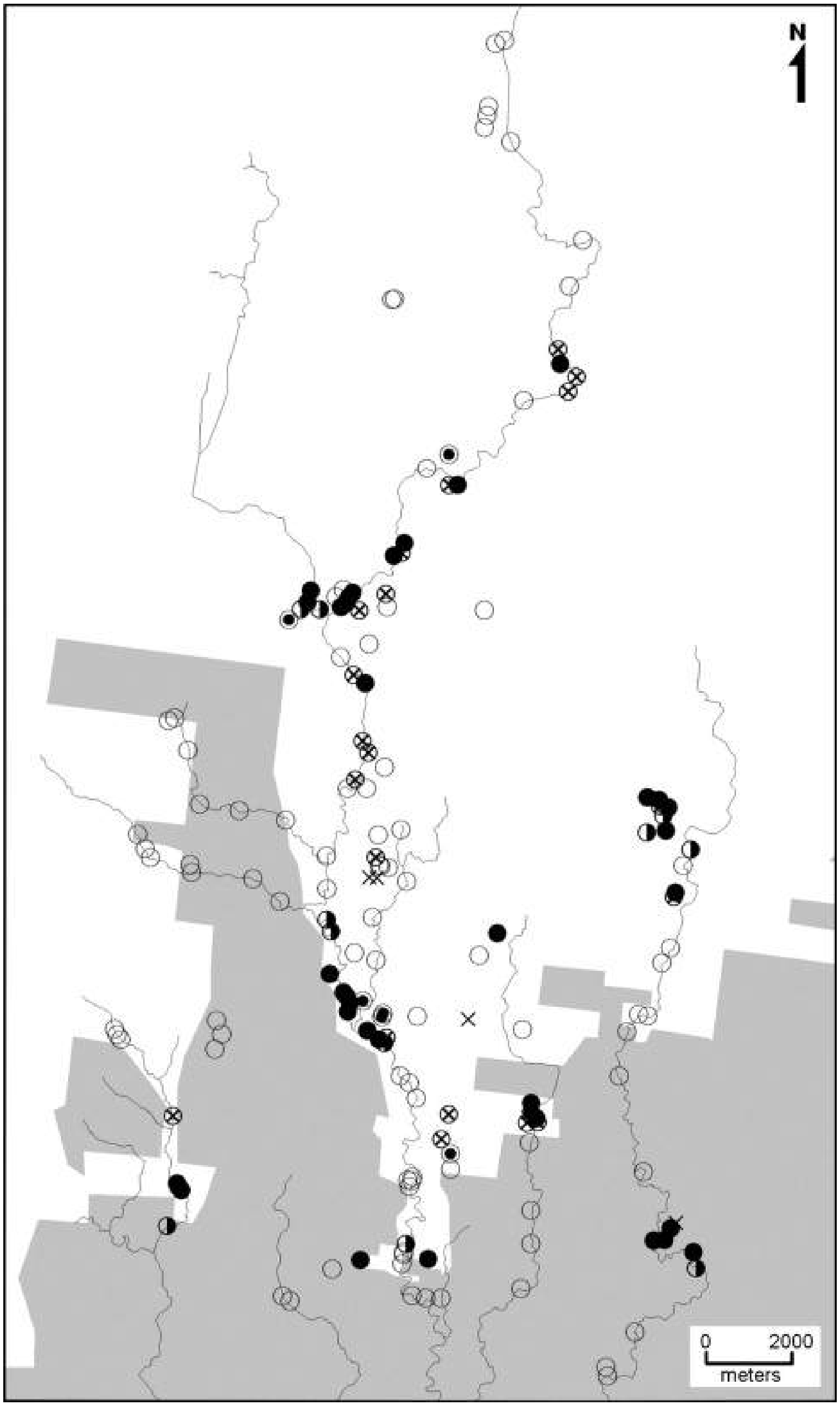
The metapopulation can persist only if the dominant eigenvalue of M, $\lambda > \delta$, which can be interpreted exactly as Levins's model results: the colonization rate has to exceed the extinction rate.

5.2.5 *Growling grass frog*

Just to have an idea of how metapopulation models are used in conservation biology, we can look at some graphs from the recent Heard *et al.* 2012 paper in the journal *Biological Conservation*. Heard and colleagues sampled patches of habitat suitable for the growth of the growling grass frog (*Litoria raniformis*), an endangered species of frog living in south-east Australia and Tasmania.

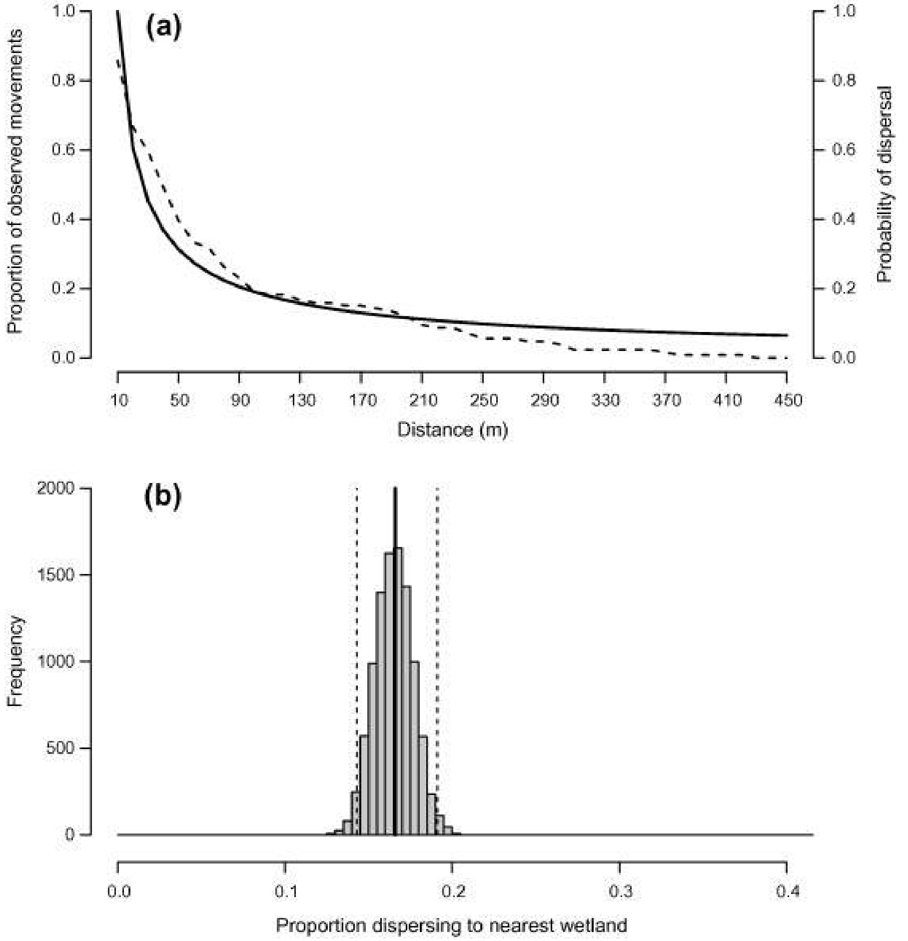
The authors studied the landscape around Melbourne, and recorded all the wetlands where the frog could potentially live. They surveyed 167 locations (patches) over six seasons (from 2001 to 2007).

This is what they found:



Note that the occupied patches (filled dots) are clustered spatially; that the colonized patches (half-filled dots) are close to occupied patches; that the extinct patches (dots with a cross) typically belong to small isolated clusters or are associated to habitat destruction (crosses).

By means of capture-recapture, the authors were also able to estimate the dispersal kernel, which is similar to the cases studied above.



In the top graph, the dashed-line is the empirical data (proportion of observed movements at each distance, left-scale), and the solid line is the fitted dispersal kernel using a power function ($p \propto d_{ij}^{\alpha}$). The bottom panel shows that less than 20% of the frogs disperse over their lifetime, while the majority spends the whole life in the same wetland.

5.2.6 *Effect of habitat destruction*

Suppose that we were to solve the model by Hanski and Ovaskainen, and to compute the probability that a patch is occupied at equilibrium (i.e., in the meta-stable state). Then, the probability that a randomly drawn patch is occupied can be approximated by:

$$p^* \approx 1 - \delta/\lambda \tag{129}$$

This means that the dominant eigenvalue λ plays about the same role as the colonization rate of the unstructured model by Levins.

If the dominant eigenvalue determines the long-term behavior of the system, the dominant eigenvector (i.e., the eigenvector associated with the dominant eigenvalue) determines the contribution of each patch to the overall persistence of the metapopulation. In fact, for metapopulations that are close to extinction, we can measure the importance of patch i as $v_i^2 \lambda$, where v_i is the i^{th} component of the eigenvector. In this way, we can "rank" patches for their importance in maintaining the landscape connected and the metapopulation viable. Clearly, for conservation, we need to focus on the patches with high v_i, which—fortunately—tend to cluster together spatially.

5.3 METAPOPULATION AND SUSCEPTIBLE-INFECTED-SUSCEPTIBLE MODELS

We can think of patches being "infected" by the population of interest. Then, migration would correspond to infection, and extinction to recovery. Hence, the metapopulation models we examined have much in common with Susceptible-Infected-Susceptible (SIS) models for the spread of infectious diseases (also known as "contact processes"). These models are widely used to determine the fate of epidemics for diseases that do not confer immunity (e.g., computer viruses, many bacterial infections).

5.3.1 *Mean-field SIS*

In the simplest case, we consider a population composed of either Susceptibles (S) or Infected (I) individuals, such that $S(t) + I(t) = N$, i.e., the population does not grow or shrink in the interval of time considered by the model. We can write a system of differential equations modeling the spread of the disease:

$$\begin{cases} \dfrac{dS(t)}{dt} = -\beta S(t) I(t) + \gamma I(t) \\ \dfrac{dI(t)}{dt} = \beta S(t) I(t) - \gamma I(t) \end{cases} \tag{130}$$

The interpretation of the model is as follows: individuals get in contact with each other at random ("mass-action"), so that the rate at which susceptible individuals are transformed into infected individuals is given by $\beta S(t)I(t)$. The disease has typical duration $1/\gamma$, such that the rate of recovery of infective individuals are cured becomes $\gamma I(t)$.

Because the population is fixed, $S(t) + I(t) = N$, we can substitute $S(t) = N - I(t)$, finding:

$$\frac{dI(t)}{dt} = \beta S(t)I(t) - \gamma I(t) = \beta(N - I(t))I(t) - \gamma I(t) \tag{131}$$

a model we've seen many times before:

$$\frac{dI(t)}{dt} = (\beta N - \gamma)I(t)\left(1 - \frac{\beta}{\beta N - \gamma} I(t)\right) \tag{132}$$

i.e., a logistic growth model with $r = \beta N - \gamma$ and $K = N - \gamma/\beta$. Hence, there are two equilibria: $I^* = 0$ and $I^* = K = N - \gamma/\beta$. The disease-free equilibrium is stable whenever the population of infective individuals cannot grow when rare. This happens when $r = \beta N - \gamma < 0$. Usually, this inequality is written as

$$\mathcal{R}_0 = \frac{\beta N}{\gamma} < 1 \tag{133}$$

The quantity $\mathcal{R}_0$ (R-naught, or basic reproductive number) tells us how many individuals can "the first" infected individual can infect before recovering from the disease. The calculation of $\mathcal{R}_0$ plays a central role in more complex models (for example, Susceptible-Infected-Recovered — SIR, or Susceptible-Exposed-Infected-Recovered — SEIR).

5.3.2 *SIS on a network*

In the simple model above, contacts between individuals happen "at random". This is clearly not the case in reality, where the probability of transmission is mediated by a social network of interactions. Interestingly, the same exact model of Hanski and Ovaskainen has appeared in the literature on infectious diseases (the "NIMFA" approximation by Van Meighem and colleaguess—see the Reading List). In this case, the social network determines who is close to whom, but other than that the models are identical, allowing for the cross-pollination between the fields of research. The interplay between geographic and social interactions are of great interest for current research on the modeling of epidemics.

READING LIST

The Hanski-Ovaskainen model:

- Hanski, I., and Ovaskainen, O., 2000. *The metapopulation capacity of a fragmented landscape.* Nature 404:755–758.

Metapopulations and the conservation of *Litoria raniformis*:

- Heard, G.W. *et al.*, 2012. *Classical metapopulation theory as a useful paradigm for the conservation of an endangered amphibian* Biological Conservation 148:156–166.

SIS models on a network:

- Van Mieghem, P. *et al.*, 2009. *Virus Spread in Networks* IEEE/ACM Transactions on Netorking, 17:1–14.

Part II

MODELS FOR TWO INTERACTING POPULATIONS

In this part we analyze the behavior of a small ecological community composed of two species.

We start by analyzing a system composed of two competitors, and we derive the principle of competitive exclusion, one of the few laws of ecology.

We then turn our attention to consumer-resource dynamics, studying predator-prey systems, the building blocks of food webs.

6

INTERSPECIFIC COMPETITION

We already saw the effect of intraspecific (i.e., within the same species) competition, and we used this fact to justify the logistic growth model. Now we want to add to the picture interspecific (i.e., between different species) competition. In particular, we want to find whether and how two similar species can coexist. We will experience the effects of interspecific competition in the laboratory, when we will fit very similar models using experimental data.

6.1 THE LOTKA-VOLTERRA COMPETITION MODEL

We have two species, N_1 and N_2. In isolation, each species grows logistically. When the two species come into contact, however, they compete reducing their respective growth rates:

$$\begin{cases} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{1,2}\frac{N_2}{K_1}\right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{2,1}\frac{N_1}{K_2}\right) \end{cases} \tag{134}$$

where $K_1, K_2, r_1, r_2, b_{1,2}, b_{2,1} > 0$. The coefficient $b_{1,2}$ represents the competitive effect of N_2 on N_1. Typically, $b_{1,2} \neq b_{2,1}$. What is the interpretation of $b_{1,2}$ and $b_{2,1}$? Let's take $b_{1,2}$, describing the effect of N_2 on N_1. If $b_{1,2} = 1$ then adding one individual of species 2 has the same effect on the growth of species 1 found adding an individual of species 1. If, on the other hand, $b_{1,2} > 1$, adding one individual of species 2 will depress the growth of 1 more than found adding an individual of species 1. Finally, if $b_{1,2} < 1$ adding individuals of species 2 depresses the growth of 1 less than expected adding an equivalent number of conspecifics.

6.1.1 *Analysis*

First, we want to find the equilibria of the system. A point (N_1^*, N_2^*) is an equilibrium if at that point both species do not grow nor shrink. We can start by listing some "trivial" solutions. Both species can be extinct:

$$\begin{cases} N_1^* & = 0 \\ N_2^* & = 0 \end{cases} \tag{135}$$

Or one of the two species may be absent:

$$\begin{cases} N_1^* & = 0 \\ N_2^* & = K_2 \end{cases} \tag{136}$$

$$\begin{cases} N_1^* & = K_1 \\ N_2^* & = 0 \end{cases} \tag{137}$$

Finally, the more interesting case:

$$\begin{cases} N_1^* & = K_1 - b_{1,2} N_2^* \\ N_2^* & = K_2 - b_{2,1} N_1^* \end{cases} \tag{138}$$

In the previous equations, we are expressing the equilibrium of species 1 in terms of individuals of species 2 and vice versa. It is therefore convenient to plug the second equation into the first:

$$\begin{cases} N_1^* & = K_1 - b_{1,2}(K_2 - b_{2,1} N_1^*) = K_1 - b_{1,2} K_2 + b_{1,2} b_{2,1} N_1^* \\ N_2^* & = K_2 - b_{2,1} N_1^* \end{cases} \tag{139}$$

which becomes:

$$\begin{aligned} & N_1^* = K_1 - b_{1,2} K_2 + b_{1,2} b_{2,1} N_1^* \\ & N_1^* - b_{1,2} b_{2,1} N_1^* = K_1 - b_{1,2} K_2 \\ & N_1^* (1 - b_{1,2} b_{2,1}) = K_1 - b_{1,2} K_2 \\ & N_1^* = \frac{K_1 - b_{1,2} K_2}{1 - b_{1,2} b_{2,1}} \end{aligned} \tag{140}$$

Similarly,

$$N_2^* = \frac{K_2 - b_{2,1} K_1}{1 - b_{1,2} b_{2,1}} \tag{141}$$

This equilibrium point is more interesting, as for particular values of the parameters both species can coexist.

6.1.2 *Nullclines*

If we have only two species, we can draw their growth in the so-called "phase plane", in which we track what happens to dN_1/d_t and dN_2/dt for different values of N_1 and N_2. We are interested in points at which the first equation is 0:

$$\frac{dN_1}{dt} = 0 = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{1,2}\frac{N_2}{K_1}\right) \tag{142}$$

There are two cases:

$$\begin{aligned} N_1 &= 0 \\ \left(1 - \tfrac{N_1}{K_1} - b_{1,2}\tfrac{N_2}{K_1}\right) &= 0 \end{aligned} \tag{143}$$

The second case becomes:

$$\begin{aligned} \left(1 - \tfrac{N_1}{K_1} - b_{1,2}\tfrac{N_2}{K_1}\right) &= 0 \\ 1 = \tfrac{N_1}{K_1} + b_{1,2}\tfrac{N_2}{K_1} \\ N_2 = \tfrac{K_1 - N_1}{b_{1,2}} \end{aligned} \tag{144}$$

Similarly, the growth of the second species is 0 when:

$$N_1 = \tfrac{K_2 - N_2}{b_{2,1}} \tag{145}$$

These equations are of the form $y = ax + b$: they are lines in the phase plane. In Figure 13 I show how we can find the areas in which each species grows or shrinks.

We can now put the two lines together. There are four cases, represented in Figure 14. For each case, we can describe qualitatively the behavior of the system.

6.1.3 *Competitive Exclusion*

We want to assess the ability of a species to invade an environment dominated by the other species. We start by defining the growth rate per individual of species 1.

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1 \left(\frac{K_1 - N_1 - b_{1,2}N_2}{K_1}\right) \tag{146}$$

When species 1 is very rare, we can approximate:

$$\frac{1}{N_1}\frac{dN_1}{dt} = r_1 \left(\frac{K_1 - 0 - b_{1,2}K_2}{K_1}\right) \tag{147}$$

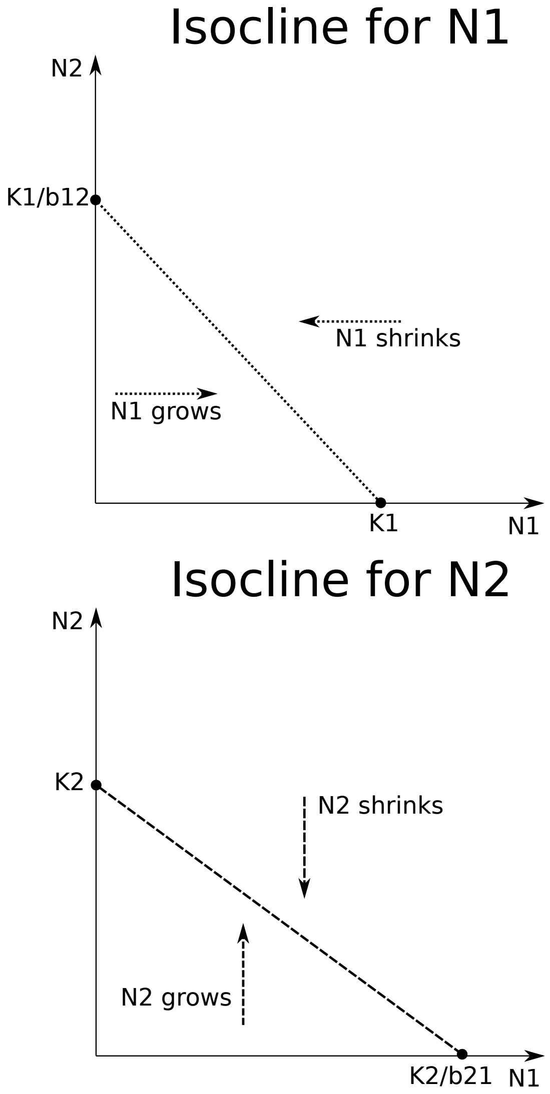


Figure 13: Nullclines for N_1 and N_2 in the phase plane.

This equation tells us that species 1 will grow when rare (be able to invade) if

$$\left(\frac{K_1 - b_{1,2} K_2}{K_1} \right) > 0 \tag{148}$$

Which implies:

$$\frac{K_1}{K_2} > b_{1,2} \tag{149}$$

Similarly, species 2 can invade when rare if:

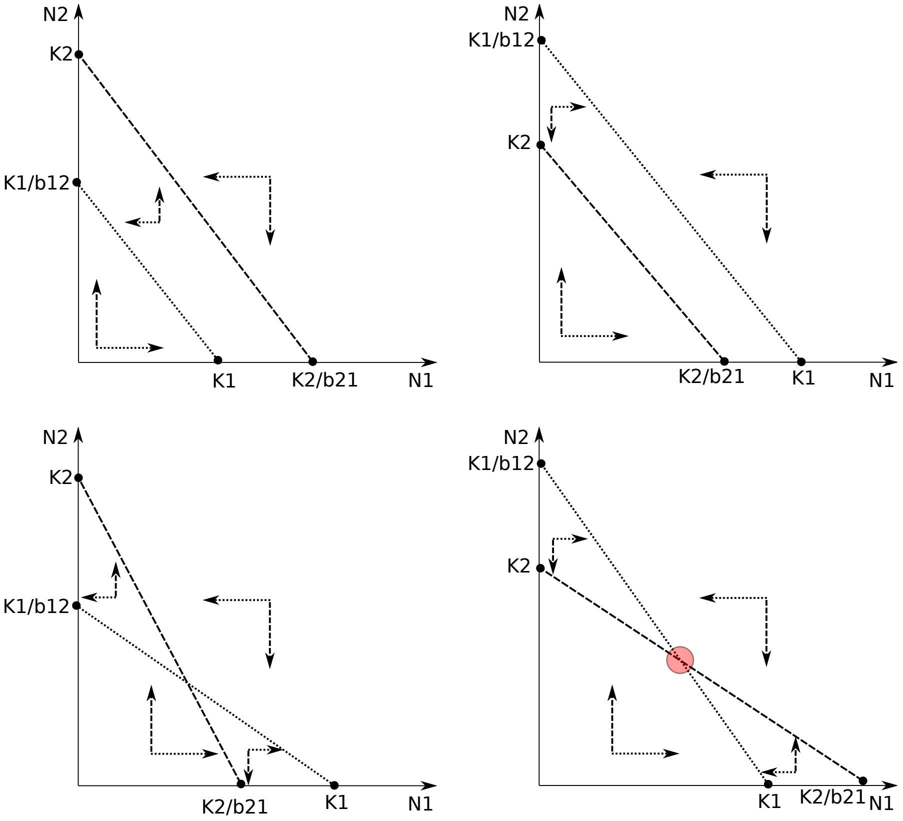


Figure 14: Nullclines for N_1 and N_2 in the phase plane.

$$\frac{K_1}{K_2} < \frac{1}{b_{2,1}} \tag{150}$$

These inequalities map back into the four cases examined before. The first case is when:

$$\frac{1}{b_{2,1}} < \frac{K_1}{K_2} > b_{1,2} \tag{151}$$

In this case, only species 1 persists (top right graph). Similarly, when:

$$\frac{1}{b_{2,1}} > \frac{K_1}{K_2} < b_{1,2} \tag{152}$$

Only species 2 persists (top left graph). When:

$$\frac{1}{b_{2,1}} > \frac{K_1}{K_2} > b_{1,2} \tag{153}$$

Both species coexist stably (bottom right graph). Finally, when:

$$\frac{1}{b_{2,1}} < \frac{K_1}{K_2} < b_{1,2} \tag{154}$$

The equilibrium is unstable. Depending on the initial conditions, either species 1 or species 2 will win (precedence effect).

The principle of competitive exclusion states that two species that have similar resource use can not coexist. To show this suppose that $K_2 = 10$ and that $b_{1,2} = b_{2,1} = 0.95$ (this is a way to model a great overlap in the use of resources). Then stable coexistence can happen only when:

$$\frac{1}{0.95} > \frac{K_1}{10} > 0.95 \tag{155}$$

which becomes:

$$1.053 > \frac{K_1}{10} > 0.95 \tag{156}$$

$$10.53 > K_1 > 9.5 \tag{157}$$

That is, there is a very narrow range of K_1 for which coexistence is possible. On the contrary, when the two species do not have a great overlap in resource use ($b_{1,2} = b_{2,1} = 0.1$), we find:

$$\frac{1}{0.1} > \frac{K_1}{10} > 0.1 \tag{158}$$

$$10 > K_1 > 0.1 \tag{159}$$

That is, the range of coexistence is greatly expanded.

6.2 LOCAL ASYMPTOTIC STABILITY ANALYSIS

We have seen a powerful graphical method to determine the stability of an equilibrium when we're dealing with one equation (Figure 15).

The equilibrium is stable if the slope of the curve dN/dt is negative at N^*. Mathematically, we can write the slope of dN/dt at any point as:

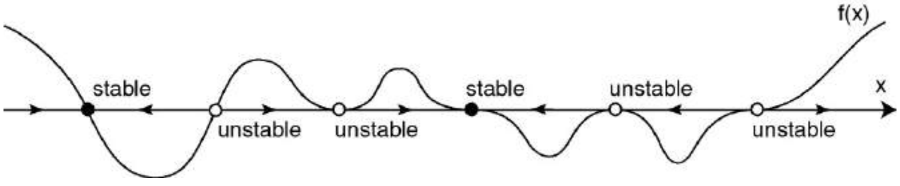


Figure 15: Stability for a single population (from dx.doi.org/10.4249/scholarpedia.2014).

$$\text{slope} = \frac{\partial \frac{dN}{dt}}{\partial N} \tag{160}$$

We can then plug in the value N^* and check whether the slope is negative. For example, in the logistic growth:

$$\frac{\partial \frac{dN}{dt}}{\partial N} = \frac{\partial \left(rN - r\frac{N^2}{K} \right)}{\partial N} = r - 2r\frac{N}{K} \tag{161}$$

We can see that if $N^* = 0$, the slope is positive (r), and thus the equilibrium is unstable, while if $N^* = K$, the slope is negative ($-r$) and thus the equilibrium stable. Note also that the analysis is "local": it only holds for small perturbations of N^* (remember the graph for the Allee model, in which we could take a population and make it go extinct through a sufficiently large perturbation). Moreover, the stability is "asymptotic": small perturbations will eventually die out and the system will return to the equilibrium, but the speed at which this happen can be very low (we're only checking whether the slope is negative).

Can this analysis be extended to multiple species? Yes, but when we take the "slopes" now we have to compute S^2 of them (where S is the number of species), giving raise to the so-called Jacobian matrix of the system:

$$J = \begin{bmatrix} \frac{\partial \frac{dN_1}{dt}}{\partial N_1} & \frac{\partial \frac{dN_1}{dt}}{\partial N_2} & \cdots & \frac{\partial \frac{dN_1}{dt}}{\partial N_S} \\ \frac{\partial \frac{dN_2}{dt}}{\partial N_1} & \frac{\partial \frac{dN_2}{dt}}{\partial N_2} & \cdots & \frac{\partial \frac{dN_2}{dt}}{\partial N_S} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial \frac{dN_S}{dt}}{\partial N_1} & \frac{\partial \frac{dN_S}{dt}}{\partial N_2} & \cdots & \frac{\partial \frac{dN_S}{dt}}{\partial N_S} \end{bmatrix} \tag{162}$$

This matrix is a "function". When we evaluate this function at a given equilibrium, we obtain a matrix of numbers, which in ecology is called the "Community Matrix" (M). Its study was pioneered by Richard Levins (whom we encountered before) and by Robert May (whom we will encounter later).

Now that we have a matrix, what do we mean by "negative slope"? It turns out that an equilibrium is locally asymptotically stable if the eigenvalues of the corresponding community matrix have all negative real part.

6.2.1 *Checking Local Asymptotic Stability*

Here's an "algorithm" detailing the steps needed to assess the stability of the equilibria of a system. We will next apply the algorithm to the Lotka-Volterra competition model studied above.

1. The starting point is a system of differential equations: $dN_i/dt = f_i$.
2. Compute the equilibria, solving the system of equations $f_i = 0$. Each equilibrium is a set of N_i^*.
3. Compute the Jacobian matrix J: for each function f_i and each species N_j, compute $\partial f_i/\partial N_j$.
4. For each equilibrium, substitute $N_i = N_i^*$ in J, obtaining the community matrix M.
5. For each M, compute the eigenvalues. If they're all with negative real part, then the equilibrium is stable.

6.2.2 *Asymptotic Stability for Two Populations*

We have seen in Chapter 1 that the eigenvalues of a 2×2 matrix can be written as:

$$\lambda = \frac{\operatorname{tr}(A) \pm \sqrt{\operatorname{tr}(A)^2 - 4\det(A)}}{2} \tag{163}$$

For stability, we need therefore to have negative trace and positive determinant. Moreover, the eigenvalues are complex whenever $\operatorname{tr}(A)^2 - 4\det(A) < 0$. This divides the plane defined by the trace and determinant in five areas (Figure 16):

- $\det < 0$: unstable equilibrium (saddles).
- $\det > 0$, $\operatorname{tr} > 0$, $\operatorname{tr}^2 > 4\det$: unstable equilibrium (node).

- det > 0, tr > 0, $\text{tr}^2 < 4\,\text{det}$: unstable equilibrium (focus).
- det > 0, tr < 0, $\text{tr}^2 > 4\,\text{det}$: stable equilibrium (node: species return to equilibrium without oscillations).
- det > 0, tr < 0, $\text{tr}^2 < 4\,\text{det}$: stable equilibrium (focus: species return to equilibrium oscillating).

The cases in which either tr or det are 0 are degenerate, and of little ecological relevance. However, we're going to see one of these cases in the next Chapter.

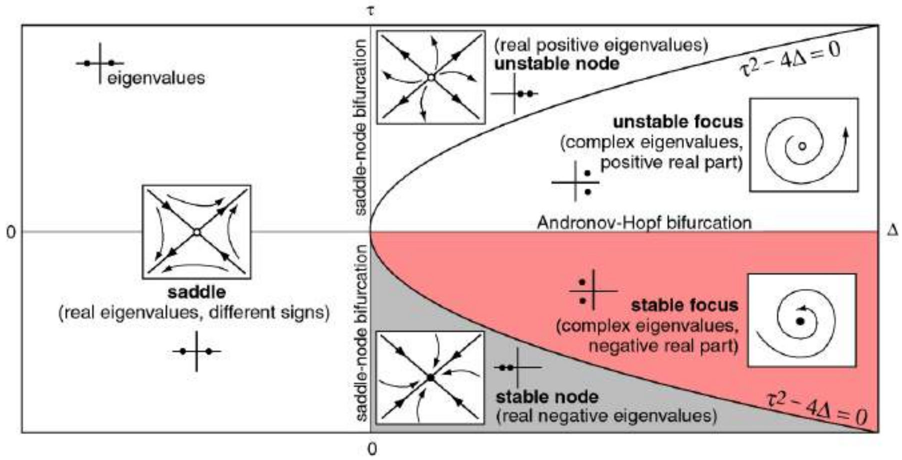


Figure 16: Stability portrait for two populations. τ is the trace of the community matrix, and Δ its determinant (from dx.doi.org/10.4249/scholarpedia.2014).

6.3 STABILITY OF THE COMPETITION MODEL

The system of equations is:

$$\begin{cases} \frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{1,2}\frac{N_2}{K_1}\right) = f_1 \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} - b_{2,1}\frac{N_1}{K_2}\right) = f_2 \end{cases} \tag{164}$$

And the equilibria:

$$N_1 = 0,\ N_2 = 0 \tag{165}$$

$$N_1 = K_1,\ N_2 = 0 \tag{166}$$

$$N_1 = 0, \; N_2 = K_2 \tag{167}$$

$$N_1 = \frac{K_1 - b_{1,2}K_2}{1 - b_{1,2}b_{2,1}}, \; N_2 = \frac{K_2 - b_{2,1}K_1}{1 - b_{1,2}b_{2,1}} \tag{168}$$

Take the partial derivatives

$$\frac{\partial f_1}{\partial N_1} = \frac{r_1}{K_1}(K_1 - 2N_1 - b_{1,2}N_2) \tag{169}$$

$$\frac{\partial f_1}{\partial N_2} = \frac{-r_1}{K_1}b_{1,2}N_1 \tag{170}$$

$$\frac{\partial f_2}{\partial N_1} = \frac{-r_2}{K_2}b_{2,1}N_2 \tag{171}$$

$$\frac{\partial f_2}{\partial N_2} = \frac{r_2}{K_2}(K_2 - 2N_2 - b_{2,1}N_1) \tag{172}$$

An thus the Jacobian becomes:

$$J = \begin{bmatrix} \frac{r_1}{K_1}(K_1 - 2N_1 - b_{1,2}N_2) & \frac{-r_1}{K_1}b_{1,2}N_1 \\ \frac{-r_2}{K_2}b_{2,1}N_2 & \frac{r_2}{K_2}(K_2 - 2N_2 - b_{2,1}N_1) \end{bmatrix} \tag{173}$$

Let's substitute the first equilibrium ($N_1 = 0, N_2 = 0$). After some simplifications, we obtain:

$$M = \begin{bmatrix} r_1 & 0 \\ 0 & r_2 \end{bmatrix} \tag{174}$$

Is this equilibrium stable or unstable? The trace is positive, and therefore the equilibrium is necessarily unstable.

When we substitute the second equilibrium ($N_1 = K_1, N_2 = 0$), we obtain:

$$M = \begin{bmatrix} -r_1 & -b_{1,2}r_1 \\ 0 & r_2\left(1 - \frac{b_{2,1}K_1}{K_2}\right) \end{bmatrix} \tag{175}$$

the trace $-r_1 - r_2(b_{2,1}K_1/K_2 - 1)$ is and the determinant is $(b_{2,1}K_1/K_2 - 1)r_1r_2$. Therefore, the trace is negative and the determinant positive whenever $b_{2,1}K_1/K_2 > 1$. In this case the equilibrium is stable (exactly what found before). The case $(N_1 = 0, N_2 = K_2)$ is very similar (stable whenever $b_{1,2}K_2/K_1 > 1$).

Substituting the most interesting equilibrium $(N_1 = \frac{K_1 - b_{1,2}K_2}{1 - b_{1,2}b_{2,1}}, N_2 = \frac{K_2 - b_{2,1}K_1}{1 - b_{1,2}b_{2,1}})$, we find:

$$M = \frac{1}{1 - b_{1,2}b_{2,1}} \begin{bmatrix} \frac{r_1}{K_1}(b_{1,2}K_2 - K_1) & \frac{r_1}{K_1}b_{1,2}(b_{1,2}K_2 - K_1) \\ \frac{r_2}{K_2}b_{2,1}(b_{2,1}K_1 - K_2) & \frac{r_2}{K_2}(b_{2,1}K_1 - K_2) \end{bmatrix} \tag{176}$$

which, assuming that $N_1^* > 0$ and $N_2^* > 0$ is stable whenever:

$$b_{2,1} < \frac{K_2}{K_1}, \; b_{1,2} < \frac{K_1}{K_2} \tag{177}$$

Therefore, the analysis of the Jacobian matrix matches the analysis we performed "graphically": two competitors can coexist only whenever their amount of overlap in resource utilization (measured as $b_{1,2}$ and $b_{2,1}$) is low enough.

HOMEWORK

For which values of α and β are these matrices stable?

$$M = \begin{bmatrix} -1 & -2 \\ \alpha & -2 \end{bmatrix} \tag{178}$$

$$M = \begin{bmatrix} \beta & -3 \\ -4 & 0 \end{bmatrix} \tag{179}$$

HOMEWORK

For which value of $b_{2,1}$ can two competitors stably coexist when $r_1 = 1$, $r_2 = 2$, $K_1 = 10$, $K_2 = 15$ and $b_{1,2} = 1/2$?

READING LIST

An introduction to simple models for population dynamics:

- P.J. Wangersky (1978). *Lotka-Volterra population models.* Annual Review of Ecology and Systematics 9:189–218.

Fitting Lotka-Volterra competition models using empirical data:

- M.A. Pascual & P. Kareiva (1996). *Predicting the Outcome of Competition Using Experimental Data: Maximum Likelihood and Bayesian Approaches.* Ecology 77:337–349.

7

CONSUMER-RESOURCE INTERACTIONS

In the previous Chapter we saw the effect of competitive $(-,-)$ interactions among species. In this Chapter we study two cases of consumer-resource interactions $(+,-)$. Other possible interactions among species include mutualism (mutually reinforcing interactions) $(+,+)$, amensalism $(0,-)$, and commensalism $(0,+)$. Also, we have examined only models where two species interact, while in nature we can find hundreds and even thousands of species connected by very complex networks of interactions (food webs and other ecological networks).

7.1 THE LOTKA-VOLTERRA PREDATOR-PREY MODEL

This model was proposed independently in 1925 by Alfred Lotka, an American demographer, statistician and chemist and in 1926 by Vito Volterra, an Italian mathematician. Volterra was introduced to the problem of the fish in the Adriatic sea by his son-in-law Umberto D'Ancona, a zoologist and naturalist. In fact, during WWI the fishing in the Adriatic was completely halted. This led to a "large-scale" experiment on the dynamics of fish population that had at the time no mathematical explanation. The Lotka-Volterra model is by far the simplest (and quite unrealistic) representation of the interaction between a prey and its predator. Although not currently used to model real populations, it has inspired a century of developments in population ecology.

We have a prey that would grow exponentially in isolation, and a predator that in isolation would decay exponentially:

$$\begin{aligned} \tfrac{dN}{dt} &= \alpha N \\ \tfrac{dP}{dt} &= -\delta P \end{aligned} \tag{180}$$

However, when the predator and the prey meet, with some probability the predator catches the prey and consumes it (βPN). This type of interaction is referred to as "mass-action" (borrowed from chemistry). The idea is that the probability of an encounter between a predator and a prey depends on the product of their densities (as if predators and prey were atoms of gas in a jar). In fact, the probability increases whenever we increase either the density of the prey or that of the predator. The equations become:

$$\begin{aligned} \frac{dN}{dt} &= N(\alpha - \beta P) \\ \frac{dP}{dt} &= P(\gamma N - \delta) \end{aligned} \tag{181}$$

Where $\alpha, \beta, \gamma, \delta > 0$. We see from the equations that although the prey is decreased of βPN, the predator is increased of γPN. This is to model the fact that consuming one prey could generate less than one predator ($\gamma < \beta$, typical of macro-predators, e.g., fish) or that one prey actually can be converted into many predators ($\gamma > \beta$, typical of micro-predators and parasites).

7.1.1 *Analysis*

As we did for the competition case, we start by determining the equilibria and the isoclines of null growth. First, we want to find the nullcline for the prey:

$$\begin{aligned} 0 &= N(\alpha - \beta P) \\ P &= \frac{\alpha}{\beta} \end{aligned} \tag{182}$$

And that for the predator:

$$\begin{aligned} 0 &= P(\gamma N - \delta) \\ N &= \frac{\delta}{\gamma} \end{aligned} \tag{183}$$

Thus, the predators grow when the prey are above δ/γ, while the prey when the predators are below α/β (Fig. 17). This is also the only equilibrium where the species coexist. In the competition model, we could combine the lines in four ways, while here we find only one case (Fig. 18). Given the direction of the arrows, we expect the predator and prey to draw counterclockwise closed orbits in the phase plane.

If we start from the top right quadrant, both predator and prey are abundant. However, because of predator pressure, the number of prey declines (moves to the left) and the system enters the top left quadrant. In this quadrant, both populations decline, until the number of predators is reduced enough to enter the bottom left quadrant. Here the number of prey increases,

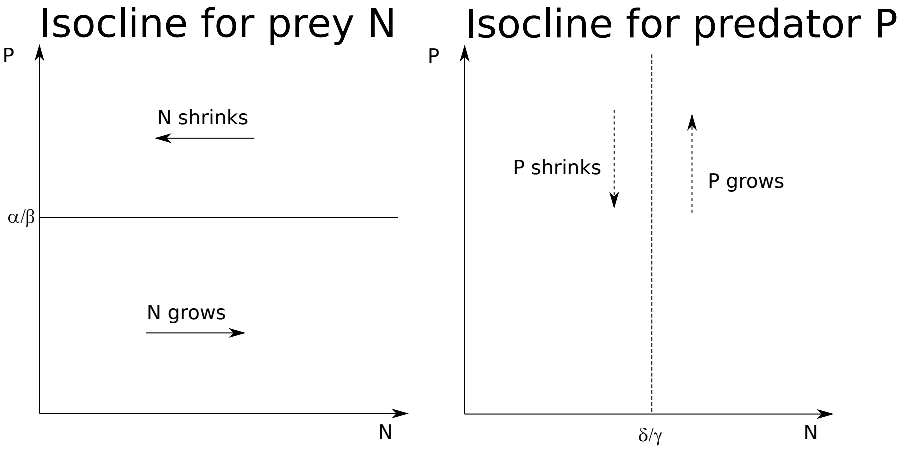


Figure 17: Nullclines for N and P in the phase plane.

until the system enters the bottom right quadrant. In the bottom right quadrant both species increase in density until they enter the top right quadrant, where the "cycle" starts again. The system has only one equilibrium, which is "neutrally stable": depending on initial conditions, they system will cycle with a given amplitude and perturbations will increase or decrease the amplitude.

Depending on the initial conditions, in fact, the orbits can be wider or smaller. The closer the system is to the equilibrium point (intersection of the nullclines), the smaller the amplitude of the cycle. For any possible initial point, the system will move on an orbit, unless the curve crosses the zero density for predator or prey, in which case the system crashes.

If we plot the density of the predator and the prey in time, we can see the boom and bust dynamics unfolding (Fig. 19). It can be noted that the prey peaks before the predator. When the predator depresses the prey to low values, it declines almost exponentially until the prey has grown enough to support the predator again.

7.1.2 *Stability Analysis*

We first write down the Jacobian matrix:

$$J_{11} = \frac{\partial N(\alpha - \beta P)}{\partial N} = \alpha - \beta P \tag{184}$$

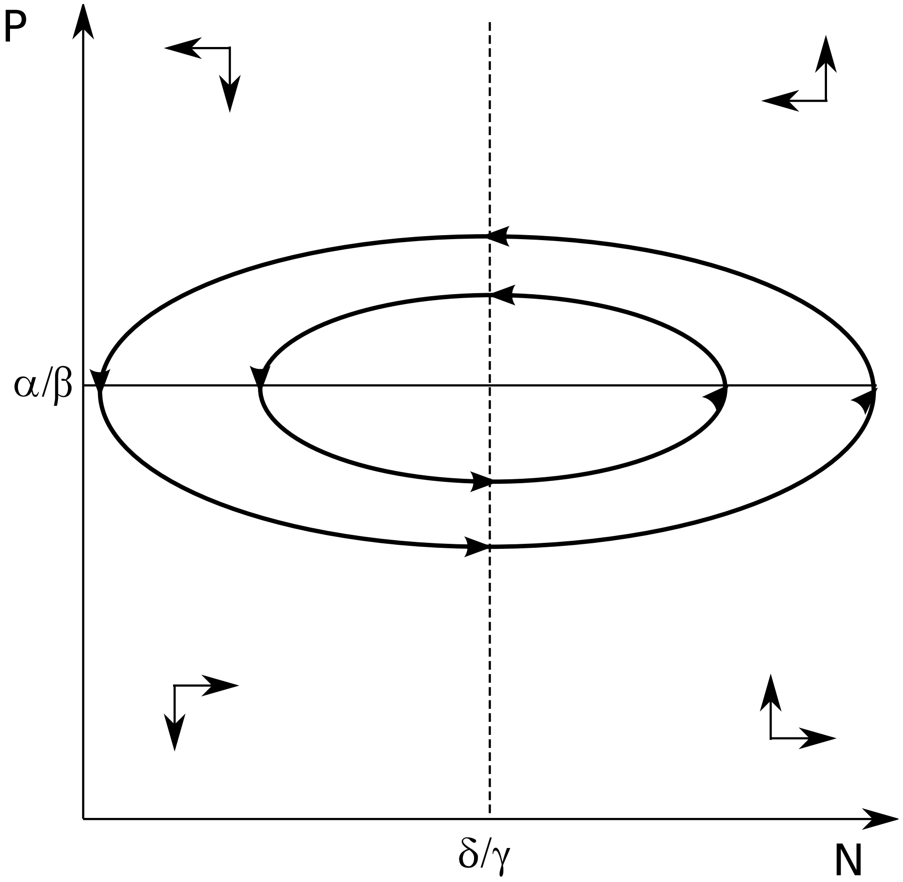


Figure 18: Cycling predators and prey. To express the qualitative behavior, I drew ellipses. However, the actual shapes are slightly more complex, as we'll see below.

$$J_{12} = \frac{\partial N(\alpha - \beta P)}{\partial P} = -\beta N \tag{185}$$

$$J_{21} = \frac{\partial P(\gamma N - \delta)}{\partial N} = \gamma P \tag{186}$$

$$J_{22} = \frac{\partial P(\gamma N - \delta)}{\partial P} = \gamma N - \delta \tag{187}$$

$$J = \begin{bmatrix} \alpha - \beta P & -\beta N \\ \gamma P & \gamma N - \delta \end{bmatrix} \tag{188}$$

We now substitute the equilibrium $P^* = \alpha/\beta$ and $N^* = \delta/\gamma$ to find the community matrix M:

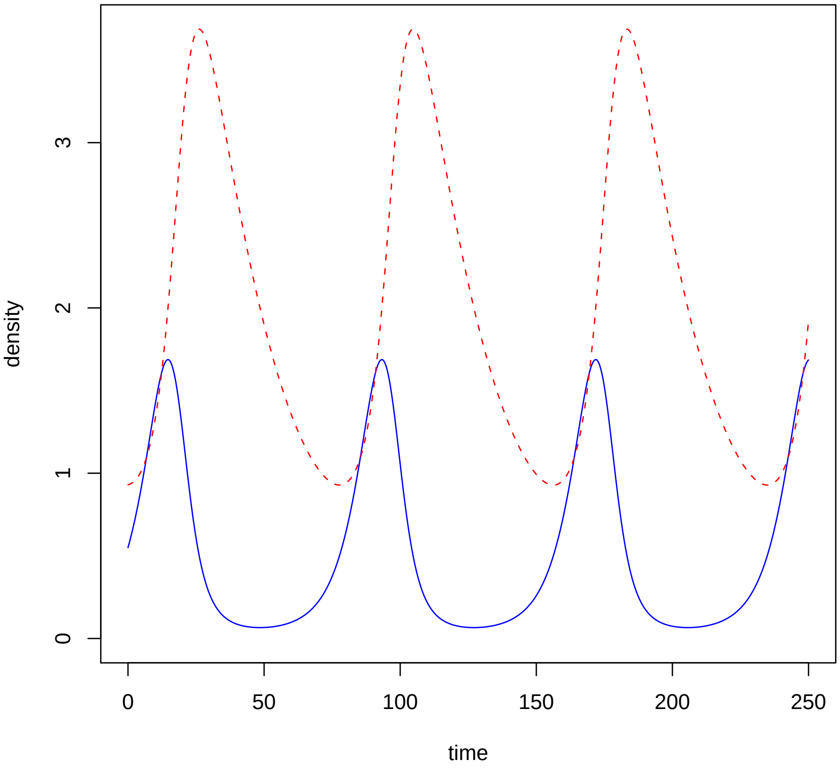


Figure 19: Cycling predators (red, dashed) and prey.

$$M = \begin{bmatrix} \alpha - \beta\frac{\alpha}{\beta} & -\beta\frac{\delta}{\gamma} \\ \gamma\frac{\alpha}{\beta} & \gamma\frac{\delta}{\gamma} - \delta \end{bmatrix} = \begin{bmatrix} 0 & -\beta\frac{\delta}{\gamma} \\ \gamma\frac{\alpha}{\beta} & 0 \end{bmatrix} \tag{189}$$

Because the matrix has trace 0, then the equilibrium cannot be stable, but it is not unstable either: it turns out to be neutrally stable.

7.1.3 *Ecological Orbits*

When populations follow closed orbits, such as in this case, typically one can find a conserved quantity, called the "constant of motion", which describes the orbits and does not depend on the time t. For example Kepler's second law of planetary motion tells us that the areal velocity (i.e., the area swept by the line connecting the sun and a planet) is constant for each planet: this is due to the conservation of the angular momentum.

How can we find a constant of motion for the Lotka-Volterra equations? We take the equations and multiply both sides by $1/NP$:

$$\frac{1}{NP}\frac{dN}{dt} = N(\alpha - \beta P)\frac{1}{NP} = \frac{\alpha}{P} - \beta \tag{190}$$

$$\frac{1}{NP}\frac{dP}{dt} = P(\gamma N - \delta)\frac{1}{NP} = -\frac{\delta}{N} + \gamma \tag{191}$$

Then we multiply each equation for the "other" derivative:

$$\frac{dP}{dt}\frac{1}{NP}\frac{dN}{dt} = \frac{dP}{dt}\left(\frac{\alpha}{P} - \beta\right) \tag{192}$$

$$\frac{dN}{dt}\frac{1}{NP}\frac{dP}{dt} = \frac{dN}{dt}\left(-\frac{\delta}{N} + \gamma\right) \tag{193}$$

Note that now the left sides are identical. Thus:

$$\frac{dP}{dt}\left(\frac{\alpha}{P} - \beta\right) - \frac{dN}{dt}\left(-\frac{\delta}{N} + \gamma\right) = 0 \tag{194}$$

We are looking for a function that is conserved (call it $E(N, P)$). This expression must be invariant in time: $dE(N, P)/dt = 0$ (given that is must be a constant). By chain-rule:

$$\frac{dE(N,P)}{dt} = \frac{dP}{dt}\frac{\partial E(N,P)}{\partial P} + \frac{dN}{dt}\frac{\partial E(N,P)}{\partial N} \tag{195}$$

Because we want $\frac{dE(N,P)}{dt}$ to be 0, we need:

$$\frac{\partial E(N,P)}{\partial P} = \left(\frac{\alpha}{P} - \beta\right) \tag{196}$$

and:

$$\frac{\partial E(N,P)}{\partial N} = \left(-\frac{\delta}{N} + \gamma\right) \tag{197}$$

Because by definition $E(N, P) = \int \frac{\partial E(N,P)}{\partial N} dN = \int \frac{\partial E(N,P)}{\partial P} dP$, we can write:

$$E(N,P) = \int \left(-\frac{\delta}{N} + \gamma\right) dN = \int 0 \left(\frac{\alpha}{P} - \beta\right) dP \qquad (198)$$

And solving the integrals:

$$E(N,P) = \gamma N - \delta \log(N) + K_1(N,P) = \alpha \log(P) - \beta P + K_2(N,P) \qquad (199)$$

where K_1 and K_2 are constants depending on the value of each species. Therefore (subtracting):

$$\delta \log(N) + \alpha \log(P) - \gamma N - \beta P = K \qquad (200)$$

where, finally, K is a constant of motion for the system, depending only on the initial conditions. The actual trajectories can be seen in Fig. 20.

HOMEWORK

After WWI, there was an increase in the number of predatory fish in the Adriatic sea. However, non-predatory fish did not increase as much. To solve this apparent contradiction, Vito Volterra set up the famous set of differential equations.

- You can model the absence of fishing during wartime as a decrease in δ and an increase in α. Why?

- N^* and P^* are the equilibrium values for the population. What happens to the equilibrium when fishing is halted? Can this explain the pattern observed in the Adriatic sea?

7.2 THE LYNX AND THE HARE

The Hudson's Bay Company has kept meticulous records of the pelts collected in a given year for more than 300 years. It has been found a striking cycle of about 10 years in the number of snowshoe hare and lynx pelts collected by trappers (Fig. 21). For many years, this data has been used as evidence for Lotka-Volterra cycles, but we will see this is not the case.

The cycles are so impressive because of their regularity, but also because the species fluctuate as predicted by the model, with cycles moving counterclockwise (Fig. 22) and predators peaking after the prey.

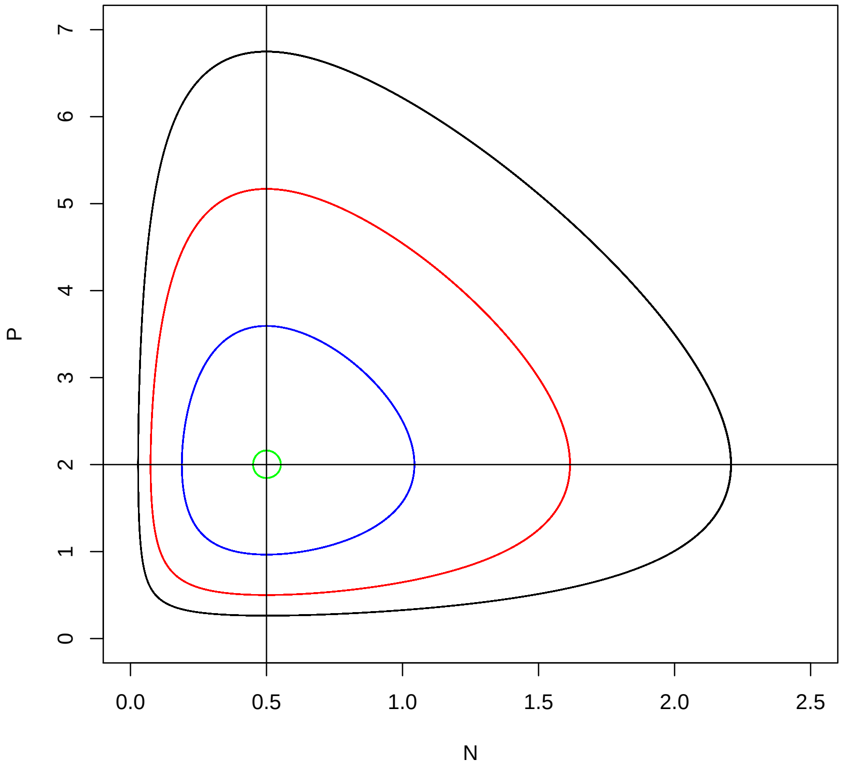


Figure 20: Trajectory of the Lotka-Volterra predator-prey system. The parameters are $\alpha = 1/2$, $\beta = 1/4$, $\gamma = 3/5$ and $\delta = 3/10$. The equilibrium is $(2, 1/2)$. Starting the system closer to the equilibrium yields trajectories that are closer to the equilibrium.

However, a closer scrutiny reveals that these cycles cannot be of the Lotka-Volterra type. First, the cycles show very little geographical variations. That is, we can assume that in different areas the parameters and local conditions would be changing, leading to different periods in the cycles. Second, and even more convincing, the hares cycle with the same period also in places where the lynx is absent. Therefore, the cycles have to do with the hare, with the lynx tracking (but not causing) the cycles. More detailed information can be found in the Reading List.

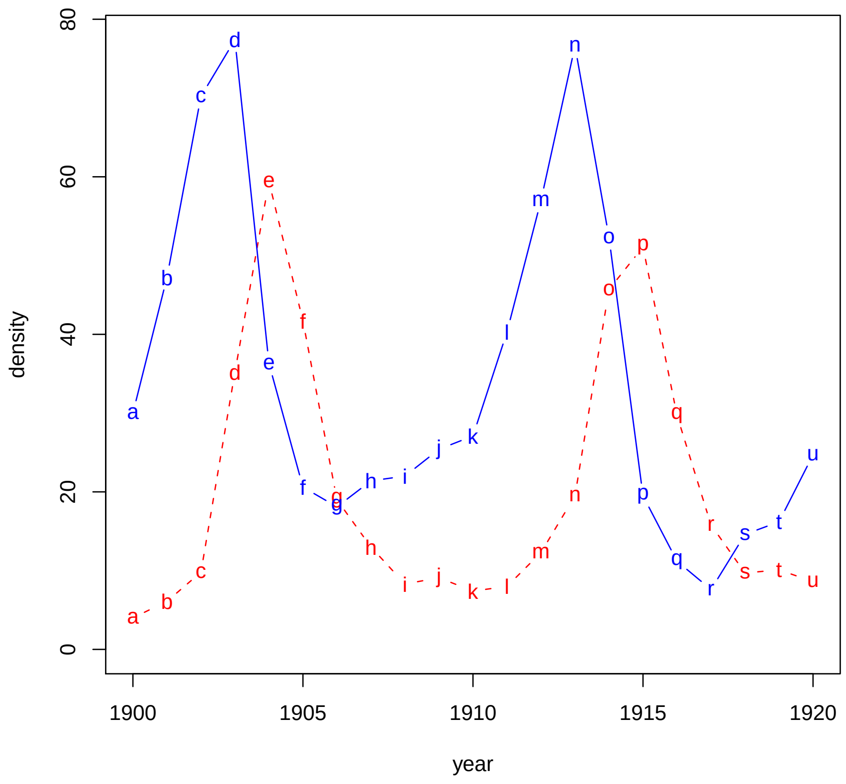


Figure 21: Fluctuations of lynx and hare populations - Hudson's Bay Company.

7.3 A MORE REALISTIC MODEL

We will now incorporate a carrying capacity for the first population. In fact, when the density is high, the population is going to be self-regulated, rather than limited by the number of predators.

$$\begin{aligned} \frac{dN}{dt} &= N\left(\alpha - \alpha\frac{N}{K} - \beta P\right) \\ \frac{dP}{dt} &= P\left(\gamma N - \delta\right) \end{aligned} \tag{201}$$

How does this addition modify the isoclines? The isocline for the prey becomes:

$$\begin{aligned} 0 &= (\alpha - \alpha N/K - \beta P) \\ P &= \frac{\alpha}{\beta}\left(1 - \frac{N}{K}\right) \end{aligned} \tag{202}$$

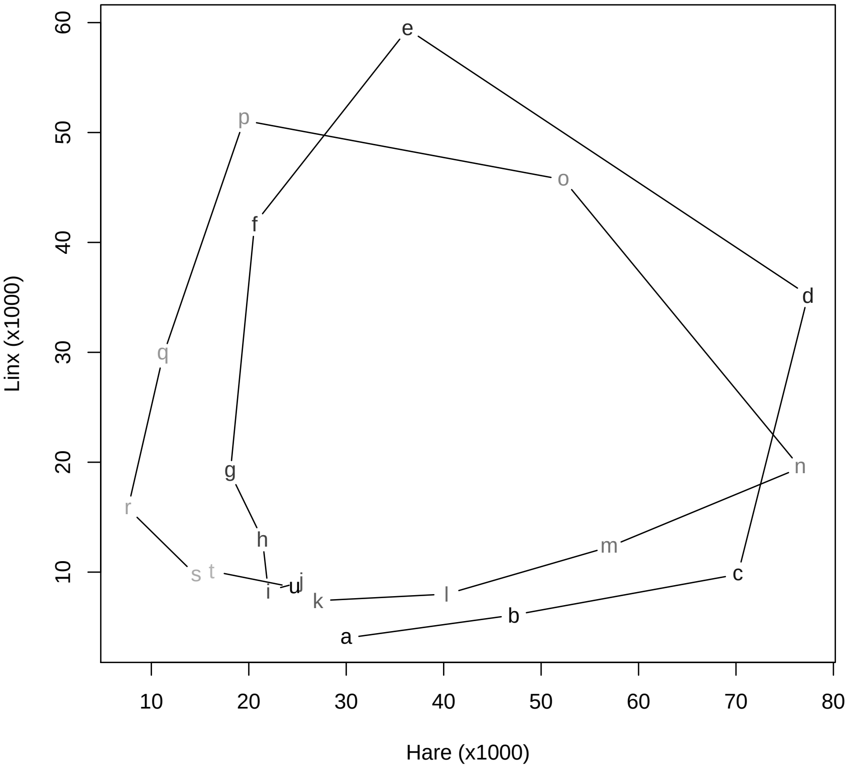


Figure 22: Lynx and Hare - phase plane. The cycles move counterclockwise.

The isocline meets the horizontal axis at $N = K$ (in absence of the predator, the prey population grows logistically). The isocline meets the vertical axis at $P = \alpha/\beta$ (when the population is low, it is mainly controlled by predators. The isocline for the predator is unchanged.

The two isoclines meet at:

$$\begin{aligned} 0 &= (\alpha - \alpha N/K - \beta P) \\ 0 &= P(\gamma N - \delta) \end{aligned} \tag{203}$$

which becomes:

$$\begin{aligned} N &= \frac{\delta}{\gamma} \\ P &= \frac{\alpha}{\beta\gamma}\left(\gamma - \frac{\delta}{K}\right) \end{aligned} \tag{204}$$

This simple change modified the nature of the equilibrium. Instead of having cycles, we now have a stable equilibrium. Any trajectory starting in the positive quadrant will end up in the equilibrium point (Fig. 23,. 24).

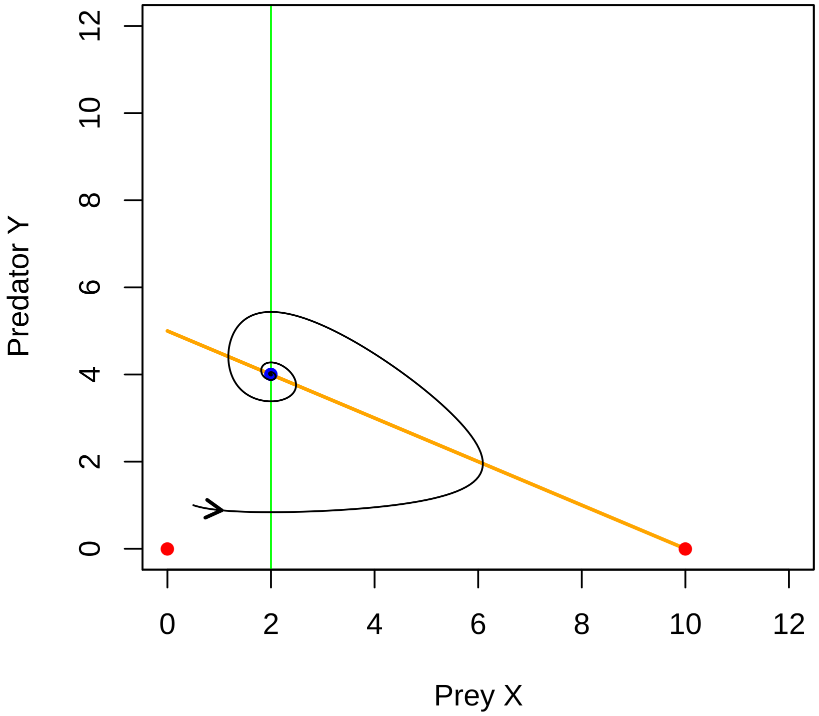


Figure 23: Stable equilibrium for predator-prey system with carrying capacity.

7.3.1 *Stability Analysis*

We have the equilibria $(N^* = 0, P^* = 0)$, $(N^* = K, P^* = 0)$, and $(N^* = \frac{\delta}{\gamma}, P^* = \frac{\alpha}{\beta\gamma}\left(\gamma - \frac{\delta}{K}\right)$.

The derivatives for the Jacobian:

$$J_{NN} = \frac{\partial N\left(\alpha - \alpha\frac{N}{K} - \beta P\right)}{\partial N} = \alpha - 2\alpha\frac{N}{K} - \beta P \qquad (205)$$

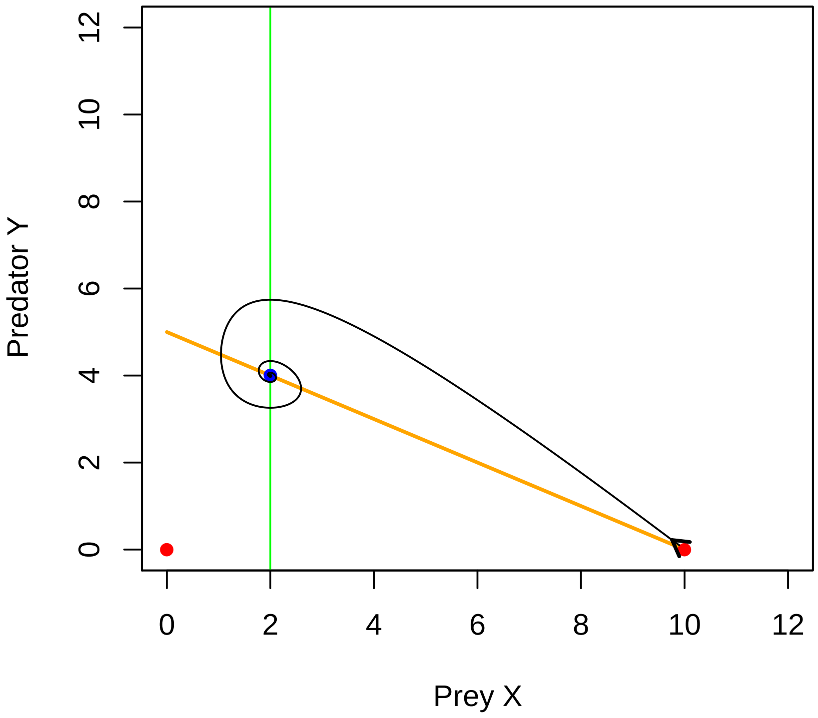


Figure 24: Stable equilibrium for predator-prey system with carrying capacity.

$$J_{NP} = \frac{\partial N\left(\alpha - \alpha\frac{N}{K} - \beta P\right)}{\partial P} = -\beta N \tag{206}$$

$$J_{PN} = \frac{P\left(\gamma N - \delta\right)}{\partial N} = \gamma P \tag{207}$$

$$J_{PP} = \frac{P\left(\gamma N - \delta\right)}{\partial P} = \gamma N - \delta \tag{208}$$

$$J = \begin{bmatrix} \alpha - 2\alpha\frac{N}{K} - \beta P & -\beta N \\ \gamma P & \gamma N - \delta \end{bmatrix} \tag{209}$$

Substituting the equilibrium where both species coexist we obtain the Community Matrix:

$$M = \begin{bmatrix} -\frac{\alpha\delta}{\gamma K} & -\beta N^* \\ \gamma P^* & 0 \end{bmatrix} \tag{210}$$

Therefore, the trace is always negative and the determinant is always positive. As such, any predator-prey system with negative trace is stable.

Homework

The Lotka-Volterra predator-prey model is by no means the only model for predators and prey dynamics. For example, the Leslie-Gower model can be written as:

$$\begin{cases} \frac{dX}{dt} = X(\alpha - \beta Y) \\ \frac{dY}{dt} = Y\left(\gamma - \epsilon \frac{Y}{X}\right) \end{cases} \tag{211}$$

where X is the predator and Y is the prey.

1. Write the isoclines of null growth for the two species.
2. Draw the two isoclines of the space of phases (i.e., the X, Y plane). Also, draw the "arrows" as we did in class. Is there an equilibrium in which the species coexist?
3. Perform the stability analysis of this system.

READING LIST

- M. E. Gilpin (1973). *Do Hares Eat Linx?* The American Naturalist 107:727–730.
- C. J. Krebs, R. Boonstra, S. Boutin, and A.R.E. Sinclair (2001). *What Drives the 10-year Cycle of Snowshoe Hares?* Bioscience 51:25-35.

Part III

MODELS FOR MANY INTERACTING POPULATIONS

Typically population ecology books for undergraduate courses start with one species and end with two species. However, there are very many species on Earth! As such, in this Part we're going to explore the dynamics of very large, complex ecological systems.

8

STABILITY IN MULTISPECIES COMMUNITIES

8.1 HOW MANY SPECIES, HOW MANY INTERACTIONS?

I report here a brief passage from a recent commentary[1] by Robert May (very appropriate, given that we're going to talk about his work later in the Chapter) on the number of species on Earth:

> *It is a remarkable testament to humanity's narcissism that we know the number of books in the US Library of Congress on 1 February 2011 was 22,194,656, but cannot tell you —to within an order-of-magnitude—how many distinct species of plants and animals we share our world with. Something like 1.5 million distinct eukaryotes have been named and recorded, but, lacking synoptic databases, even this number is uncertain owing to synonyms (the same species separately named in two or more different collections).*
>
> *Part of the problem is that taxonomic effort is approximately divided 1:1:1 among vertebrates, plants, and invertebrates, whereas plant species are roughly 10 times, and invertebrates 100 times, more numerous than vertebrates. Mammals[2] and birds[3] are the best known, again reflecting our narcissism: their features are akin to our own.*
>
> *In this issue of PLoS Biology, Mora et al.[4] offer an interesting new approach to estimating the total number of distinct eukaryotic species alive on earth today. They begin with an excellent survey of the wide variety of previous estimates, which give a range of different numbers in the broad interval 3 to 100 million species. I have favoured a number between 2 and 10 million, and if I had to buy a ticket in a sweepstakes, I'd have chosen 5 million.*
>
> *Mora et al.'s imaginative new approach begins by looking at the hierarchy of taxonomic categories, from the details of species and genera, through orders and classes, to phyla and kingdoms. They documented the fact that for eukaryotes, the higher taxonomic categories are "much more completely described than lower levels", which in retrospect is perhaps not surprising. They also show that, within well-known tax-*

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[1] May R.M. 2011, Why Worry about How Many Species and Their Loss? PLoS Biol 9:e1001130

[2] That we know of, there are about 5,500 mammal species.

[3] Birds are more speciose: about 10,000 recorded species.

[4] Mora et al., 2011 How many species are there on Earth and in the ocean? PLoS Biol 9:e1001127

onomic groups, the relative numbers of species assigned to phylum, class, order, family, genus, and species follow consistent patterns. If one assumes these predictable patterns also hold for less well-studied groups, the more secure information about phyla and class can be used to estimate the total number of distinct species within a given group.

In this way, Mora et al. arrive at a global total of 8.7 million eukaryotic species, with a standard error of ±1.3 million. Most are terrestrial, with 2.2 (±0.2) million being marine.

This is higher than my earlier "best guess", but I like the simplicity of this new method.

Hence, there are about 10 million species on Earth, and surely less than 100 millions. But how many species are in the same ecosystem? Figure 25 shows the estimated number of species (and families) per biome. As you can see, tropical biomes can house more than 10,000 species of vertebrates! This is especially remarkable, given that only about 30,000 terrestrial/amphibian species have been recorded. Imagine the incredible diversity that is concentrated in some of the most amazing ecosystems on Earth.

Species-rich ecosystems, such as tropical rainforests and coral reefs, contain thousands of species. These species feed on each other species giving rise to complex networks of feeding interactions, called food webs. The largest published food web based on empirical data (Weddell Sea ecosystem) contains about 500 species and more than 16,000 feeding interactions (Figure 26).

8.2 THE DIVERSITY-STABILITY DEBATE

For forty years, ecologists debated whether complex and diverse systems would be more or less vulnerable to disturbances than simpler ones. The history of the problem is well summarized by Kevin McCann[5]:

The relationship between diversity and stability has fascinated ecologists. Before the 1970s, ecologists believed that more diverse communities enhanced ecosystem stability. A strong proponent of this view was Charles Elton, who argued that "simple communities were more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, and more vulnerable to invasions". In fact, both Odum and Elton arrived at similar conclusions based on the repeated observation that greatly simplified terrestrial communities are characterized by more violent fluctuations in population

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[5] McCann, K. S. 2000. The diversity-stability debate. Nature, 6783:228–233.

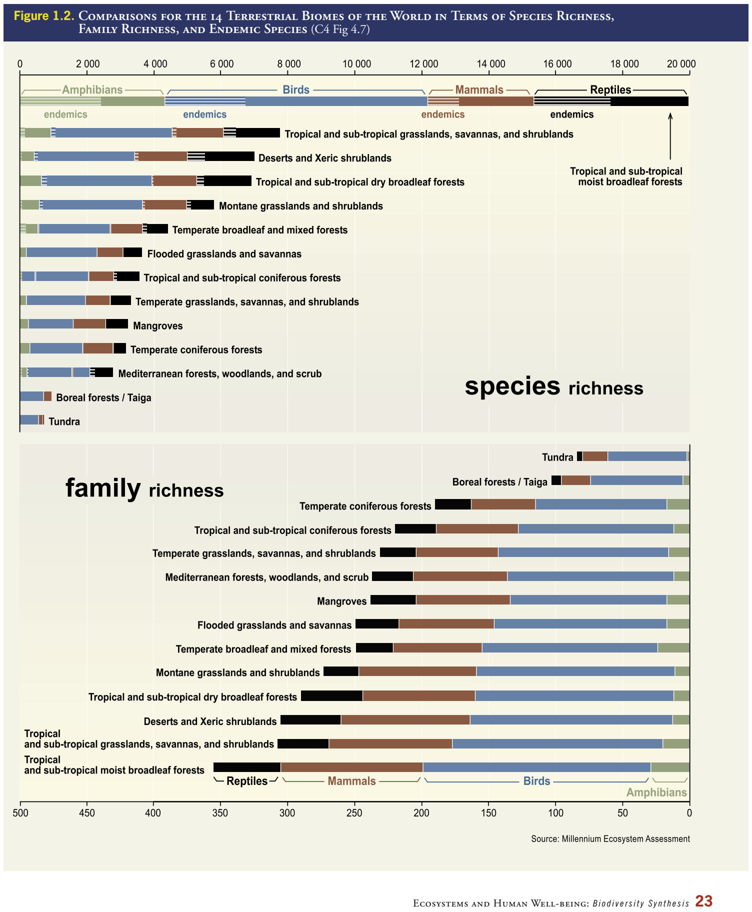

Figure 25: Biodiversity in different biomes. Figure from Millennium Ecosystem Assessment.

density than diverse terrestrial communities. For example, invasions most frequently occur on cultivated land where human influence had produced greatly simplified ecological communities, and outbreaks of phytophagous insects occur readily in boreal forests but are unheard of in diverse tropical forests. These observations led Elton to believe that complex communities, constructed from many predators and parasites, prevented populations from undergoing explosive growth. His ideas were closely akin to MacArthur, who reasoned that multiplicity in the number of prey and predator species associated with a population freed that population from dramatic changes in abundance when one of the prey or predator species declined in density. These early intuitive ideas were challenged by the work of Robert May in 1973. May turned to mathematics to rigorously explore the diversity-stability re-

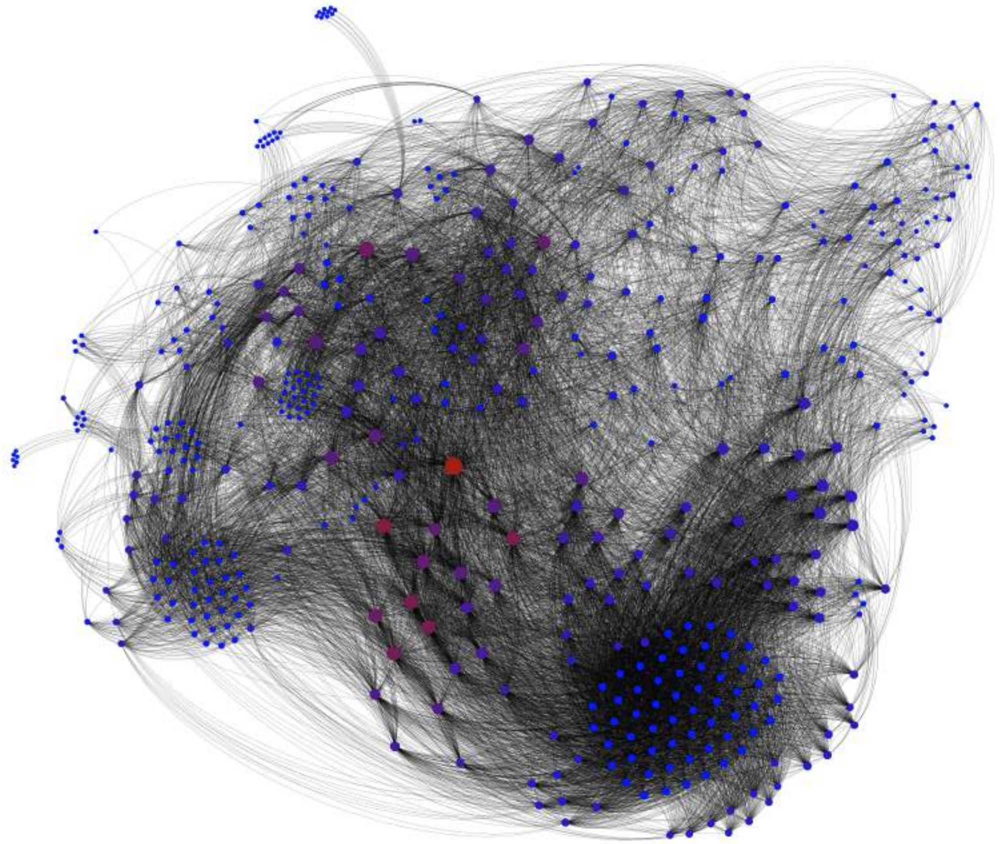

Figure 26: The food web of Weddell Sea. Dots are species and arrows connect prey to their predators.

lationship. By using linear stability analysis on models constructed from a statistical universe (that is, randomly constructed communities with randomly assigned interaction strengths), May found that diversity tends to destabilize community dynamics.

8.3 THE MATHEMATICS OF THE COMPLEXITY-STABILITY DEBATE

My former student Si Tang and I just finished writing a review of this long-standing problem in ecology. Here below I report an adapted version of the forthcoming paper.

8.3.1 *Local asymptotic stability*

We start with some preliminaries on local asymptotic stability. We model an ecological community composed of S populations as a continuous-time dynamical system, described by a set of S autonomous (i.e., which do not explicitly contain the time variable) ordinary differential equations, where each equation describes the growth rate of a population:

$$\frac{dX_i(t)}{dt} = f_i(\mathbf{X}(t)) \qquad (i = 1, \ldots, S) \tag{212}$$

Here, $X_i(t)$ represents the density of population i at time t, the vector $\mathbf{X}(t)$ is the vector of all population densities, and f_i is a function relating the growth rate of population i to the density of the S populations. We say that the system is at an equilibrium point $\mathbf{X}^*$ whenever

$$\left.\frac{dX_i(t)}{dt}\right|_{\mathbf{X}^*} = f_i(\mathbf{X}^*) = 0 \tag{213}$$

for all i. Hence, if it is not perturbed, the system will remain at the equilibrium point indefinitely. In ecology, we are interested in feasible equilibria, for which $\mathbf{X}^* > \mathbf{0}$.

Stability analysis assesses whether infinitesimal perturbations of the equilibrium can be buffered by the system. The equilibrium is said to be locally stable if all infinitesimal perturbations die out eventually, and locally unstable if there exists an infinitesimal perturbation after which the system never goes back to the equilibrium. The analysis is carried out by linearization of the system at the equilibrium point. First, one builds the Jacobian matrix $\mathbf{J}$, whose elements J_{ij} are defined as:

$$J_{ij}(\mathbf{X}) = \frac{\partial f_i(\mathbf{X}(t))}{\partial X_j} \tag{214}$$

Therefore, the coefficients of the Jacobian matrix are functions of the densities of the populations ($\mathbf{X}$). Then, one can substitute into the Jacobian (which is uniquely defined for each system), the equilibrium point whose stability one wants to evaluate (there could be many feasible equilibria). This produces the so-called "community-matrix" $\mathbf{M}$, defined as:

$$M_{ij} = J_{ij}\big|_{\mathbf{X}^*} = \left.\frac{\partial f_i(\mathbf{X}(t))}{\partial X_j}\right|_{\mathbf{X}^*} \tag{215}$$

Each equilibrium corresponds to a community matrix (note that infinitely many systems at equilibrium can yield exactly the same community matrix). The coefficient M_{ij} measures the effect of a slight increase in the population j on the growth rate of population i. The eigenvalues of $\mathbf{M}$, which have units of $time^{-1}$ and therefore measure rates, determine the stability of the underlying equilibrium point: if all eigenvalues have negative real parts, then the equilibrium is stable, while if any eigenvalue has positive real part, the equilibrium is unstable, as there is at least one direction in which infinitesimal perturbations would drive the system away from the equilibrium.

Local asymptotic stability is limited in scope because it is based on linearization. First, the results hold only locally, and in the simple case outlined here, can be applied only to equilibria. Thus, local stability analysis has limited bearing for populations operating out-of-equilibrium. Second, instability does not necessarily imply lack of persistence: populations could coexist thanks to limit cycles or chaotic attractors, which typically originate from unstable equilibrium points. Third, the basin of attraction of a stable equilibrium point is difficult to measure analytically, so that local stability holds with certainty only for infinitesimal perturbations.

Given that the community matrix of an ecological system is composed of real numbers, its eigenvalues are either real (of the form $\lambda = a$), or complex forming conjugate pairs (of the form $\lambda = a \pm ib$, where a and b are real numbers, and i is $\sqrt{-1}$). Thus, if we plot the eigenvalues on a complex plane where the horizontal axis is to the real axis, and the vertical the imaginary axis, the eigenvalues are always symmetric about the real axis. The stability of the equilibrium is exclusively determined by the real part of the "rightmost" eigenvalue(s). We order the eigenvalues according to their real part, and we denote the rightmost eigenvalue by λ_1 and its corresponding real part by $\Re(\lambda_1)$, so that the equilibrium is stable whenever $\Re(\lambda_1) < 0$. Note that the rightmost eigenvalue could in fact be several eigenvalues with the same real part.

8.3.2 *Will a large complex system be stable?*

To evaluate the stability of an equilibrium, we need to calculate $\Re(\lambda_1)$, which in turn requires knowledge of the community matrix. Then, we would need to know the exact form of the functions $f_i(\mathbf{X}(t))$ as well as to calculate precisely the equilibrium $\mathbf{X}^*$, both of which are required to construct $\mathbf{M}$. This means that any different set of equations, and each equilibrium of the same set of equations, would lead to a different community matrix.

May's insight was to skip the Jacobian matrix altogether, to consider directly the community matrix, modeled as a large random matrix, and to attempt estimating $\Re(\lambda_1)$ based on the characteristics of the random matrix. Here we briefly review the construction of such random matrices, and state May's stability criterion. In the next section, we will show how May's result can be derived using Random Matrix Theory.

For a species to be self-regulating, we need $M_{ii} < 0$. This self-regulation is equivalent to setting a carrying capacity (or other similar density-dependent mechanism) for the population. May set all the diagonal elements $M_{ii} = -1$. He then set the off-diagonal elements to 0 with probability $1 - C$, and with probability C, he drew them independently from a distribution with mean 0 and variance σ^2. Note that, although in the subsequent literature this distribution is often assumed to be Normal, May did not specify a shape for the distribution. In the next section, we will see that this was an excellent idea, as the actual details of the distribution do not matter in the limit of S large. The only important quantities in this case are the mean and the variance of the distribution.

For such matrices, May claimed that the eigenvalues all have negative real parts with very high probability whenever:

$$\sigma\sqrt{SC} < 1 \tag{216}$$

and therefore, the equilibrium is very likely to be stable whenever the inequality is met. On the other hand, when the inequality is not met, then the equilibrium is unstable with high probability (Fig. 27). The 1 on the right-hand side of the inequality descends from having -1 on the diagonal. For matrices with $-d < 0$ on the diagonal, the inequality has d on the righ-hand side.

This inequality set into motion the so-called "stability-complexity" debate (also known as "May's paradox"), given that in order

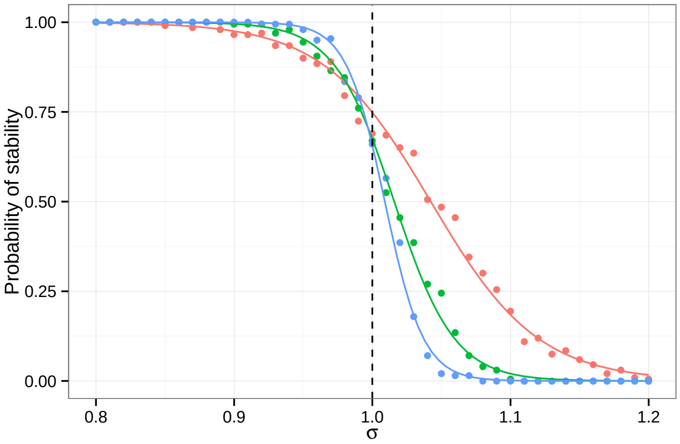

Figure 27: Probability of stability (y-axis) as a function of σ (x-axis) for random $S \times S$ matrices whose off-diagonal coefficients are sampled independently from the uniform distribution $\mathcal{U}[-\sqrt{3}\sigma, \sqrt{3}\sigma]$ with probability $C = 0.5$ and are set to 0 otherwise. The diagonal elements are set to $-\sqrt{SC}$, so that in this case the stability criterion reduces to $\sigma < 1$, i.e., the transition from stability to instability should happen at $\sigma \approx 1$. We varied σ from 0.8 to 1.2 in steps of 0.01 (points). The color indicates the size of the random matrices, with $S = 100$ for red, 250 for green, and 500 for blue. The solid lines are the best-fitting logistic curves. The probability of stability is estimated using 200 randomizations for each combination of σ and S. When S increases, the transition becomes sharper, and for S very large it would approach a step function.

to satisfy the inequality (216) a system cannot be too large (S large), too connected (large C), or with a large variance of the interactions (large σ).

8.3.3 *Circular law and stability*

May was inspired by Wigner's work on symmetric matrices (for which all eigenvalues are real), even though the matrices he studied are not symmetric. In his article, May signaled that he was aware of the contemporary work on the non-Hermitian (non-symmetric) case: he stated in a footnote that the work of Metha and Ginibre were "indirectly relevant".

The analog of Wigner's "semicircle law" in the case of non-symmetric matrices is known as the "circular law". The circular law has a long and complicated history. It was possibly first put forward by Ginibre in 1965, studied extensively by Girko, proved by Metha for the normal case, extended considerably by Bai, and finally proved in the most general case by Tao *et al.* in 2010. In its latest and more general incarnation, the circular law can be stated as follows. Take an $S \times S$ matrix $\mathbf{M}$, whose entries are independent and identically distributed (i.i.d.) random variables with mean zero and variance one. Then, the empirical spectral distribution (i.e., the distribution putting $1/S$ probability mass on each eigenvalue) of $\mathbf{M}/\sqrt{S}$ converges to the uniform distribution on the unit disk as $S \to \infty$.

Note that the statement does not contain any specifics on the distribution of the coefficients: as long as the mean is zero and the variance is one, the empirical spectral distribution of the rescaled matrix $\mathbf{M}/\sqrt{S}$ is expected to converge to the uniform distribution on the unit disk as S gets sufficiently large. This property is known as "universality". To demonstrate this point numerically, in Fig. 28 we show the eigenvalue distribution of a 1000×1000 matrix whose entries are sampled from a normal distribution $\mathcal{N}(0, 1)$ (Fig. 28(a)) and from a uniform distribution $\mathcal{U}[-\sqrt{3}, \sqrt{3}]$ (Fig. 28(b)), so that both distributions have mean zero and variance 1. We plot the eigenvalues of $\mathbf{M}/\sqrt{S}$, and show that in both cases the eigenvalues are about uniformly distributed on the unit disk of the complex plane.

One subtle point to consider is that the circular law only describes the behavior of the "bulk" of the eigenvalues of the rescaled matrix $\mathbf{M}/\sqrt{S}$ in the limit $S \to \infty$. As such, given that in the empirical spectral distribution each eigenvalue only contributes $1/S$ to the density—which becomes negligible as

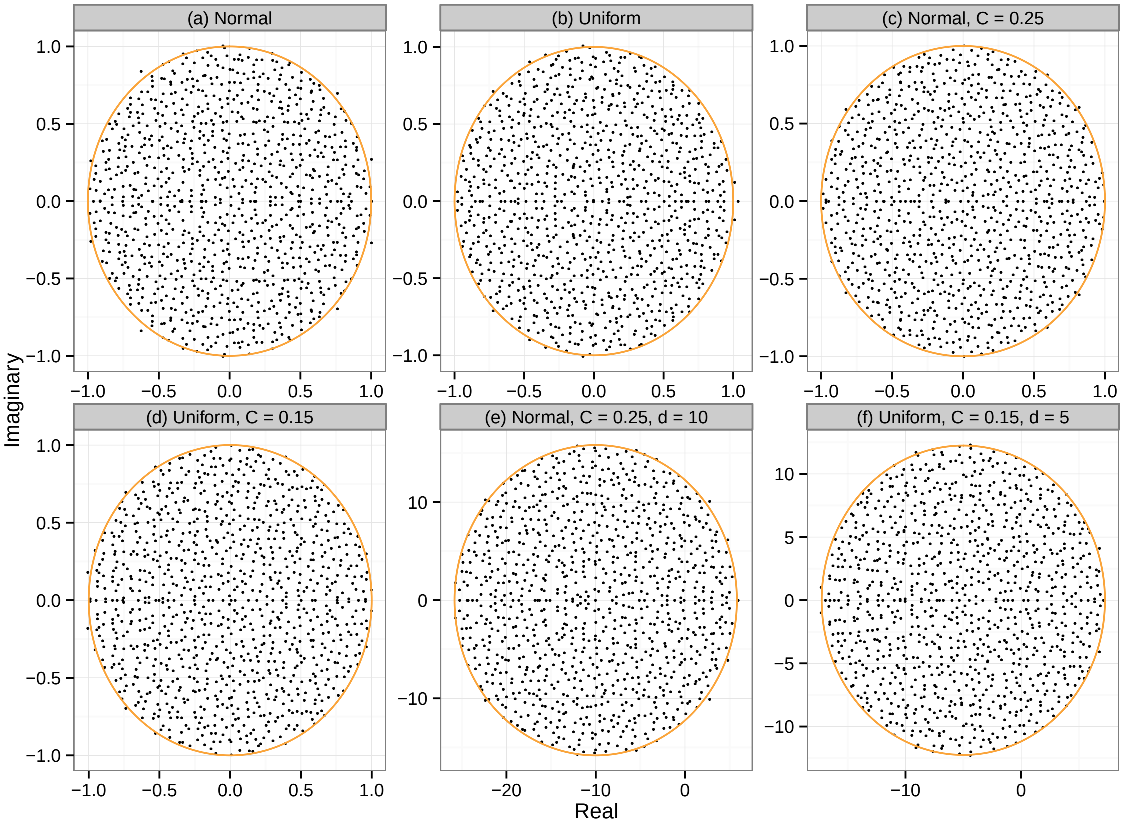

Figure 28: Circular law. (a) Eigenvalues of the matrix $\mathbf{M}/\sqrt{S}$, with $S = 1000$. The x-axis represents the real part, and the y-axis the imaginary part of the eigenvalues (points). The coefficients of $\mathbf{M}$ are sampled independently from a normal distribution $\mathcal{N}(0, 1)$. The eigenvalues are approximately uniformly distributed in a disk of radius 1 (orange). (b) As (a), but with entries sampled from the uniform distribution $\mathcal{U}[-\sqrt{3}, \sqrt{3}]$ (which has variance 1). (c) Eigenvalues of the matrix $\mathbf{M}/\sqrt{SC}$, where the entries are sampled as in (a) with probability $C = 0.25$, and are set to 0 otherwise. Normalizing the matrix using $\sqrt{SC}$ yields eigenvalues falling in the unit disk. (d) As (c), but with non-zero coefficients sampled from the uniform distribution $\mathcal{U}[-\sqrt{3}, \sqrt{3}]$. (e) Eigenvalues of $\mathbf{M}$, where the matrix is constructed as in (c), but all the diagonal elements are set to $-d = -10$. When the matrix is not normalized and has a non-zero diagonal, the eigenvalues are approximately uniform in a disk centered at $-d$, and with radius $\sigma\sqrt{SC}$. (f) As (e), but with non-zero coefficients sampled from the uniform distribution $\mathcal{U}[-\sqrt{3}, \sqrt{3}]$, and diagonal entries set to -5.

$S \to \infty$—, the fact that the bulk converges to the unit disk does not necessarily mean that all eigenvalues are contained in the disk. This could greatly limit our ability to predict the position of any single eigenvalue, including λ_1. Fortunately, it has been shown that if the distribution of the coefficients of $\mathbf{M}$ has mean zero, variance one, and bounded (i.e., not infinite) fourth moment, then all the eigenvalues, as $S \to \infty$, are contained in the disk. Because in biology we are always confronted with distributions with finite moments, then we can confidently assume that all the eigenvalues, for S sufficiently large, are contained in the disk.

Hence, for sufficiently large S, all the eigenvalues of $\mathbf{M}$ are approximately uniformly distributed in the disk in the complex plane centered at $(0, 0)$ and with radius $r_x = \sqrt{S}$, so that $\Re(\lambda_1) \approx \sqrt{S}$. Next, we relax the assumptions of the circular law to derive May's result. We start by analyzing the case in which the variance of the entries of $\mathbf{M}$ is not one.

When the variance of the i.i.d. entries is $\sigma^2 > 0$, not necessarily one, we can rescale the matrix to achieve a unit variance by simply dividing each entry by σ. Combining this fact with the circular law, we estimate $\Re(\lambda_1) \approx \sigma\sqrt{S}$ when S is sufficiently large. Generally speaking, the variance of the entries, denoted by $V = \mathrm{Var}(M_{ij})$, acts as a scaling factor for the radius of the disk formed by the eigenvalues of $\mathbf{M}$: the radius is multiplied by an additional factor of $\sqrt{V}$, compared to the unit variance case.

Ecological systems are typically only sparsely connected: most of the coefficients in the community matrix are zero, and only few are non-zero. In this case, the universality of the circular law turns out to be key: we can think of sampling the coefficients from a "zero-inflated" distribution, such that the coefficients are zero with probability $1 - C$, and with probability C are taken from a given distribution with mean zero and variance σ^2. While the mean of M_{ij} sampled from such "zero-inflated" distribution is still zero, the variance is reduced to $C\sigma^2$. Consequently, the entries of $\mathbf{M}/\sqrt{C\sigma^2}$ have unit variance, and thus $\Re(\lambda_1) \approx \sigma\sqrt{SC}$, as shown in Fig. 2(c-f). This intuitive argument based on universality is confirmed by the rigorous study of sparse matrices.

We next want to consider the effect of the diagonal entries of $\mathbf{M}$ on its eigenvalue distribution. As we stated above, the diagonal elements of the community matrix $\mathbf{M}$ model self-effects, and in the case of negative diagonal coefficients, we typically refer to “self-regulation”. Most models for consumer-resource interactions would predict the diagonal elements of the community matrix to be non-positive. The diagonal of a matrix determines the mean of the eigenvalues, due to the relation $\mathrm{Tr}(\mathbf{M}) = \sum_{i=1}^{S} M_{ii} = \sum_{i=1}^{S} \lambda_i$. Hence, the eigenvalues have the same mean as that of the diagonal elements, which we denote by $-d$. In May’s case, we have $d = 1$, whereas for the circular law, since the diagonal entries of $\mathbf{M}$ are also assumed to be drawn from the same distribution as the off-diagonal entries, the mean of the diagonal is zero.

The fact that subtracting a constant from the diagonal elements shifts the distribution of the eigenvalue can be easily proved by the following argument. Take a matrix $\mathbf{A}$: its eigenvalues can be obtained setting $\det(\lambda \mathbf{I} - \mathbf{A}) = 0$, where $\mathbf{I}$ is the identity matrix, and $\det(\cdot)$ is the determinant. Denote the eigenvalues of $\mathbf{A}$ as $\lambda_i^{(\mathbf{A})}$. Now take $\mathbf{B} = \mathbf{A} - d\mathbf{I}$, i.e., a matrix that is identical to $\mathbf{A}$, but with diagonal elements $B_{ii} = A_{ii} - d$. The eigenvalues of $\mathbf{B}$ can be found setting to zero $\det(\lambda \mathbf{I} - \mathbf{B}) = \det(\lambda \mathbf{I} - \mathbf{A} + d\mathbf{I}) = \det((\lambda + d)\mathbf{I} - \mathbf{A})$. As such $\lambda_i^{(\mathbf{A})} = \lambda_i^{(\mathbf{B})} + d$, and thus $\lambda_i^{(\mathbf{B})} = \lambda_i^{(\mathbf{A})} - d$: all the eigenvalues of $\mathbf{B}$ are equal to those of $\mathbf{A}$ shifted by $-d$. The shape of the eigenvalue distribution is completely unaffected, but its position is shifted horizontally.

The circular law has been studied for the case in which all the entries (including the diagonal ones) are sampled from the same distribution. However, numerical simulations show that sampling all the off-diagonal elements from one distribution, and all the diagonal entries from some other distribution with mean zero and variance $\sigma_d^2 < \infty$ does not qualitatively alter the results: the circular law still holds in the $S \to \infty$ limit. For finite S, we recover the same result as long as the variance of the diagonal coefficients σ_d is relatively small. When diagonal coefficients have very large variance, we have to assess the matrices numerically, as the result depends on the exact arrangement of the coefficients along the diagonal. For simplicity, we may set the diagonal entries of $\mathbf{M}$ to be identically zero (in which case $\sigma_d = 0$), and the eigenvalue distribution does not deviate appreciably from the circular law, when S is sufficiently large.

These considerations are sufficient to recover May’s result. The off-diagonal coefficients are zero with probability $1 - C$, and are sampled independently from a distribution with mean 0 and variance σ^2 with probability C. The diagonal coefficients are all set to $-d$. Then, for S large, the eigenvalues are about uniformly distributed in a disk centered at $-d$, and with radius $\sigma\sqrt{SC}$. For stability, we need the rightmost eigenvalue to have negative real part, $\Re(\lambda_1) < 0$. Substituting the approximation from the circular law, we obtain $\Re(\lambda_1) \approx \sqrt{SC\sigma^2} - d < 0$, which becomes $\sigma\sqrt{SC} < d$.

Having considered the effects stemming from the variance of the off-diagonal entries, and from the distribution of the diagonal entries, we want to assess the effect of having a nonzero mean for the off-diagonal entries on the eigenvalue distribution of **M**. This case is especially important, since in natural systems we do not expect the positive effects of resources on consumers to exactly offset the negatives of consumers on resources. The setting is as follows: with probability C, the off-diagonal coefficients are sampled independently from a distribution of mean μ and variance σ^2, and they are set to zero otherwise. Therefore, we have $E = \mathbb{E}[M_{ij}] = C\mu$. The diagonal entries are all $-d$.

Note that any matrix with constant row sum has **1** as its eigenvector and the row sum as the corresponding eigenvalue. When **M** is randomly constructed with i.i.d. off-diagonal entries and identical diagonal entries, although the row sum is not a constant, they have the same expectation, i.e.,

$$\mathbb{E}\left[\sum_j M_{ij}\right] = -d + (S-1)\mathbb{E}[M_{ij}] = -d + (S-1)E \quad (217)$$

for any row i. When **M** is large, its row averages are approximately the same due to the law of large numbers. Thus, for sufficiently large S, one of the eigenvalues of **M** will be close to the expectation of the row sum given in Eqn. (217), as confirmed by numerical simulations. Regarding the other $(S-1)$ eigenvalues, numerical simulations also show that they are still closely approximated by a uniform distribution on a disk. However, the disk has slightly shifted to account for the fact that the mean of all eigenvalues must still be $-d$. The center of the shifted disk is given by the mean of the $S-1$ values, and it can be computed subtracting $-d + (S-1)E$ from the sum of all the eigenvalues $-dS$ and dividing by $S-1$. We also need to recompute the variance of the off-diagonal elements of **M**, which becomes $V = \mathrm{Var}[M_{ij}] = \mathbb{E}[M_{ij}^2] - E^2 = C(\sigma^2 + (1-C)\mu^2)$. This means that the rightmost eigenvalue on the disk is located approximately at $-(d+E) + \sqrt{SV}$, where $-(d+E)$ is the center of the disk and $\sqrt{SV}$ estimates its radius.

We then estimate $\Re(\lambda_1)$ for the nonzero mean case, when S is sufficiently large. If μ is negative (thus $E < 0$), then $-d + (S-1)E < 0$. The rightmost eigenvalue of $\mathbf{M}$ corresponds to the rightmost point of the disk (Fig. 29(a)), and in this case, we estimate $\Re(\lambda_1) \approx -d - E + \sqrt{SV}$. If μ is positive, on the other hand, we can have two situations: either the row sum is large enough to send an eigenvalue to the right of the disk (Fig. 29(b)), or it is weak enough such that the corresponding eigenvalue falls inside the disk (Fig. 29(c)). In the first case, $\Re(\lambda_1) \approx -d + (S-1)E$, whereas in the second case $\Re(\lambda_1) \approx -d - E + \sqrt{SV}$. To consider all three scenarios, one can write a criterion for stability that takes into account both the eigenvalue corresponding to the row sum and the rightmost eigenvalue on the disk.

$$\max\{\sqrt{SV} - E, (S-1)E\} < d \tag{218}$$

which, when writing the mean E and the variance V in terms of C, μ, and σ becomes

$$\max\{\sqrt{SC(\sigma^2 + (1-C)\mu^2)} - C\mu, (S-1)C\mu\} < d \tag{219}$$

8.3.4 *Elliptic law and stability*

In the matrices above, the coefficients M_{ij} and M_{ji}—expressing the effects of species i on j, and that of j on i—are independent and identically distributed. In ecological networks, we often want to model pairwise interactions such as consumer-resource, mutualism, and competition, in which cases M_{ij} is not independent from M_{ji}. Take consumer-resource interactions: then, for any $M_{ij} < 0$, representing the negative effect of the consumer j on the resource i, we would expect a $M_{ji} > 0$, measuring the positive effect of the resource on the consumer. For this reason, we would like to sample directly the coefficients in pairs, rather than each coefficient separately. Doing so leads to the "elliptic law".

The elliptic law is a generalization of the circular law to the case in which the pairs of coefficients (M_{ij}, M_{ji}) are sampled from a bivariate distribution. A simplified statement of this law is as follows. Take an $S \times S$ matrix $\mathbf{M}$, whose off-diagonal coefficients are independently sampled in pairs from a bivariate

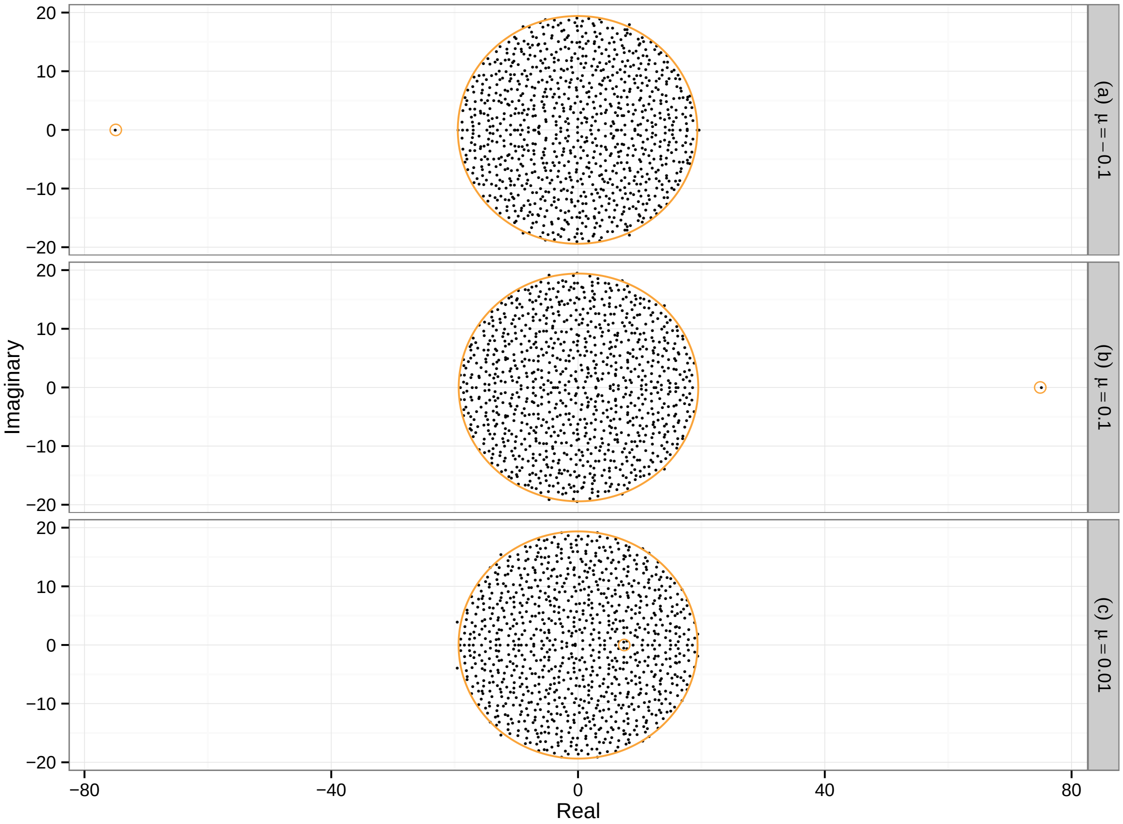

Figure 29: (a) The eigenvalue distribution of a 1000×1000 matrix $\mathbf{M}$ whose off-diagonal coefficients are 0 with probability $1 - C$, and with probability C are sampled from a normal distribution of mean μ and variance σ^2. The diagonal elements are all set to $-d$. In this case, $C = 0.75$, $d = 0$, $\sigma^2 = \frac{1}{2}$, and $\mu = -0.1$. The negative mean results in a slight shift of the disk towards the right, and the appearance of an eigenvalue on the left of the disk, in correspondence of the expected row sum (orange, small circle). The disk centered at $-d + C\mu$ and with radius $\sqrt{SC(\sigma^2 + (1 - C)\mu^2)}$, containing all other eigenvalues, is also drawn in orange. (b) As (a), but with $\mu = 0.1$. In this plot, the eigenvalue determining stability is the one on the right of the disk. (c) As (a), but with $\mu = 0.01$. In this case, the eigenvalue corresponding to the expected row sum is contained in the disk.

distribution with zero marginal means, unit marginal variances, and correlation ρ (i.e., $\rho = \mathbb{E}[M_{ij}M_{ji}]$). Then, as $S \to \infty$, the eigenvalue distribution of $\mathbf{M}/\sqrt{S}$ converges to the uniform distribution on an ellipse centered at $(0, 0)$ with horizontal semi-axis of length $1 + \rho$ and vertical semi-axis of length $1 - \rho$.

Similar to the circular law, the elliptic law has a long history. Again, this law was conjectured early on and was investigated by Girko. This phenomenon was also independently discovered in the physics literature. Recently, proofs of the universality of the elliptic law started appearing in the mathematical literature. The elliptic law is illustrated in Fig. 30(a).

Just as for the circular law, the elliptic law can be extended to more general cases accounting for i) partially connected matrices, ii) diagonal elements different from zero, iii) off-diagonal coefficients sampled from a bivariate distribution with non-zero marginal means, and iv) matrices with diagonal $-d$. Suppose we are setting the off-diagonal pair (M_{ij}, M_{ji}) to $(0, 0)$ with probability $1 - C$, and with probability C we are sampling the pair from a bivariate distribution of mean ¯ and covariance matrix $\mathbf{\Sigma}$:

$$\bar{} = \begin{bmatrix} \mu \\ \mu \end{bmatrix}, \ \mathbf{\Sigma} = \begin{bmatrix} \sigma^2 & \tilde{\rho}\sigma^2 \\ \tilde{\rho}\sigma^2 & \sigma^2 \end{bmatrix} \tag{220}$$

The diagonal elements are set to $-d$. As before, we need to track two eigenvalues: the one corresponding to the row sum, and the rightmost eigenvalue on the ellipse.

To this end, we compute the relevant statistics for the off-diagonal coefficients. The mean of the off-diagonal coefficients is $E = \mathbb{E}[M_{ij}] = C\mu$, their variance is $V = \text{Var}[M_{ij}] = C(\sigma^2 + (1 - C)\mu^2)$, and, finally, the correlation between the pairs of coefficients is

$$\rho = \frac{\mathbb{E}[M_{ij}M_{ji}] - \mathbb{E}^2[M_{ij}]}{\text{Var}[M_{ij}]} = \frac{\tilde{\rho}\sigma^2 + (1 - C)\mu^2}{\sigma^2 + (1 - C)\mu^2} \tag{221}$$

Since each off-diagonal coefficient is equally likely to come from either component of the bivariate distribution, the expected row sum is $-d + (S - 1)E$ (as for the circular case). Again, using the same strategy illustrated above, we find that the ellipse is centered at $-d - E$, and has horizontal semi-axis $\sqrt{SV}(1 + \rho)$. Using this notation, the criterion for stability becomes:

$$\max\{\sqrt{SV}(1 + \rho) - E, (S - 1)E\} < d \tag{222}$$

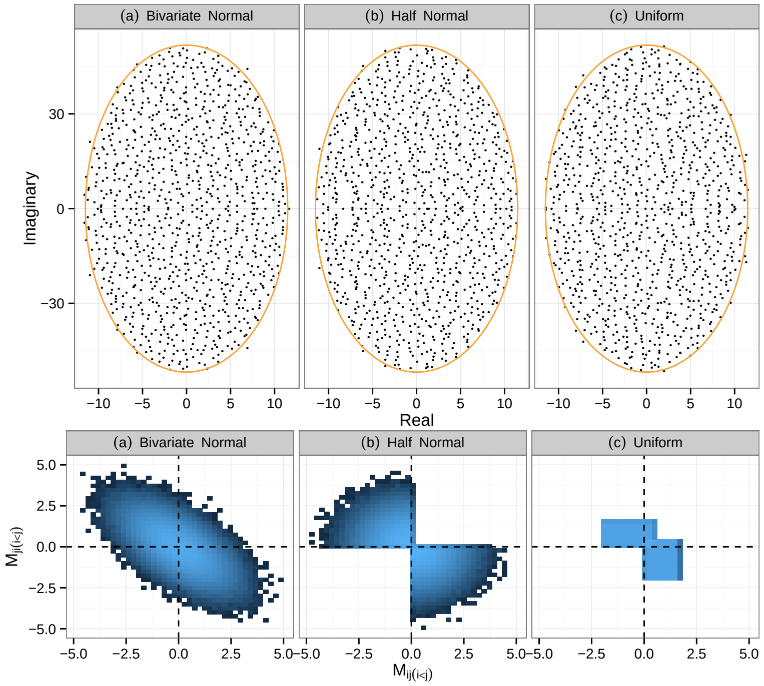

Figure 30: Elliptic law. (a) Top: Eigenvalues of $\mathbf{M}$, a 1000×1000 matrix with zero on the diagonal and off-diagonal coefficients (M_{ij}, M_{ji}) are sampled in pairs from the bivariate normal distribution illustrated below, so that the marginals have mean zero, variance one and correlation $\rho = -2/\pi$. (b) As (a), but, for each pair, sampling one of the coefficients from the half-normal distribution $|\mathcal{N}(0,1)|$, and the other from a negative half-normal. Because this leads to the same covariance matrix found in case (a), the eigenvalues have approximately the same distribution (top), even though the coefficients have very different distributions (bottom). (c) As (a-b), where, however for each pair (M_{ij}, M_{ji}), we sample one coefficient from the uniform distribution $\mathcal{U}[0, 2x]$, and the other from $\mathcal{U}[-y-x, y-x]$. Setting $x = \sqrt{2/\pi}$ and $y = \sqrt{6 - 14/\pi}$, we obtain a covariance matrix identical to cases (a-b), and thus the same ellipse.

In the first application of the elliptic law to the stability of ecological networks (Allesina & Tang, 2012), we showed that when we model a food web in which the elements of the non-zero pairs have opposite signs ($(+,-)$), then this necessarily yields a negative correlation ρ, which in turn is highly stabilizing. For example, in Fig. 30(b) we show the spectrum of a matrix in which, for each non-zero pair, one coefficient is taken from the half-normal distribution $|\mathcal{N}(0,1)|$, and the other is taken from the negative half-normal $-|\mathcal{N}(0,1)|$. As such, $E = 0$, $V = 1$ and $\rho = -2/\pi$: the sign-pairing produces a negative correlation, which in turn is stabilizing. Moreover, thanks to the universality property, any bivariate distribution with the same covariance matrix would lead to identical results, as shown in Fig. 30.

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CONTENTS