Mathematical Ecology

Joachim Hermisson, Claus Rueffler & Meike Wittmann*

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Literature and Software

- Sarah P. Otto, Troy Day: A Biologist's Guide to Mathematical Modeling in Ecology and Evolution, Princeton University Press (~ 72 Euro)
- Mark Kot: Elements of Mathematical Ecology, Cambridge University Press (~ 62 Euro)
- Josef Hofbauer and Karl Sigmund: Evolutionary Games and Population Dynamics, Cambridge University Press (~ 49 Euro)
- \bullet Linda Allen: An Introduction to Stochastic Processes with Applications to Biology, Prentice Hall (~ 70 Euro)
- Peter Yodzis: Introduction to Theoretical Ecology (1989), Harper & Row. This book is out of print. A pdf can be downloaded from www.rug.nl/research/institute-evolutionary-life-sciences/tres/_downloads/bookyodzis.pdf
- Gerald Teschl: Ordinary Differential Equations and Dynamical Systems, American Mathematical Society, pdf online at www.mat.univie.ac.at/ gerald/ftp/book-ode/
- Populus simulation and visualization software: http://cbs.umn.edu/populus/overview

Ecology

Oikos = house, dwelling place. Logos = word, study of. Ecology refers to the scientific study of living organisms in their natural environment. It is a diverse scientific discipline and covers various levels of biological organization.

• On the individual level, *physiological ecology* discusses the influence of food, light, humidity, pesticide concentrations, etc, on the life histories of individuals.

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- *Population ecology* studies the interactions of populations with their environment, with consequences on population structure and demography. On the same level, *behavioral ecology* discusses the consequences of different behavioral strategies.
- Finally, *community ecology* and *ecosystems ecology* treat the fate of complex ecosystems with anything from two to tens of thousands of interacting species and groups of species.

Ecology is closely related to evolution and the interactions of population dynamics and evolution are the subject of *evolutionary ecology*. Many branches of ecological research use mathematical models. For example, behavioral ecology makes use of game theoretical methods to explore the impact of behavioral strategies. Evolutionary ecology draws heavily on the mathematical models of evolutionary genetics. The focus of this lecture must be much more narrow. It will mainly be on population ecology, where we study the dynamics of population sizes, equilibria, growth and extinction, under various ecological boundary conditions. We will make a few side-steps into evolutionary ecology, but we won't treat aspects of behavior and we won't cover inheritance and the dynamics of genotypes. These topics are devoted to the specialized lectures on game theory and on population genetics.

Ecological Modeling

Any biological model is a map of some part of Nature to a mathematical formalism. Models are always abstractions, i.e. simplifying representations of reality. Modeling thus starts with a series of model assumptions: some aspects of Nature are integrated into the model, because we assume that they are essential for the problem at hand. Many other aspects are ignored (or abstracted from), either because they are much less important or because we want to take a reductionist perspective. In the latter case, we hope that we can understand a complex system by studying of several (sets of) factors one by one. As an example, if we want to model future population size in Austria, the current size and age structure are certainly essential. Other factors like progress in medical treatment might also have some impact on death rates, but can be ignored in a simple model. Still other factors, such as immigration, are likely important, but a treatment without immigration may already provide us with some valuable information and we may want to study the impact of immigration in a separate step.

With an increasing number of factors included, a model gets more precise and specific. This is needed, in particular, for reliable quantitative predictions (weather forecast, demographic models). However, added complexity always means reduced manageability and often also reduced generality. From a model that is as complex as the system that it represents we cannot obtain any new insights. Complex quantitative models that are used for predictions can usually only be treated by computer simulations. In contrast, many questions we might ask are of qualitative nature (e.g., whether population size approaches an equilibrium or whether there will be cycles). In these cases, one often aims for a minimal set of factors to explain a phenomenon. The art of modeling thus consists of selecting the essential factors to include in a model. On the one hand, this requires experience and some knowledge of the biological system of interest. On the other hand, this also requires an understanding of the mathematical mechanism, in order to see which factors can have crucial consequences, even if they may look like small effects initially. As such, ecological modeling relies on a broad mathematical tool-box, including elements from the theory of stochastic processes, dynamical systems, differential equations, and statistics.

1 Dynamics of single, unstructured populations

The dynamical process of population growth and decline is a function of factors that are intrinsic to a population (e.g., its potential to reproduce, its life-cycle, or its density) and the environmental conditions. The environment comprises all resources that are essential for a population to thrive, like food and space, and factors that may reduce its size, such as predation and disease. In nature, many of these factors are indeed reproducing populations themselves, which can act as predators, competitors, or as food resource. As such, these populations should follow their own population dynamics. Since the dynamical processes of (e.g.) predators and prey interact, we quickly obtain a complex multi-dimensional problem. We deal with these complexities further on. As our first step, we make the simplifying assumption that we can ignore all interactions with other dynamical aspects of the environment and just model the dynamics of a single population. This can sometimes be justified if the dynamics of all interacting populations happens on different time scales: either much faster, such that we can always assume that the interacting population is at a dynamical equilibrium, or much slower, such that the size of an interacting population does not change much over time-spans of interest. We also assume that the population is unstructured. This means, all individuals of the population are treated as equal. In particular, there are no age classes, no phenotypic differences (of relevance to the dynamics), and we can ignore the distribution of the population across physical space.

1.1 Birth and death processes

We describe the development of a population through time as a dynamical process. For a single, unstructured population, we have a single dynamic variable N(t), measuring the population size or population density (individuals per square meter) at time t. The variable N(t) may be affected by various demographic events, such as:

- birth
- \bullet death
- immigration and emigration

Demographic events in nature are stochastic. In the most explicit "individual based" demographic models, the population dynamics is therefore described as a stochastic process. Define $P_N(t)$ as the probability to observe N individuals at time t. We assume that each individual can give birth at a constant rate b and may die at rate d. Birth and death occurs for all individuals independently of all other individuals and independently of age. Formally, the process then follows a continuous-time Markov chain with states $N \in \mathbf{N}$ and time-homogeneous transition probabilities. We have:

$$P_N(t + \Delta t) = (N - 1)b\Delta t P_{N-1}(t) + (N + 1)d\Delta t P_{N+1}(t) + (1 - Nb\Delta t - Nd\Delta t)P_N(t)$$
(1)

and thus in the limit $\Delta t \to 0$ (Kolmogorov forward equation or Master equation):

$$\dot{P}_N(t) = \frac{\partial P_N(t)}{\partial t} = d(N+1)P_{N+1}(t) + b(N-1)P_{N-1}(t) - N(b+d)P_N(t)$$
(2)

with some initial condition $P_N(0) = 1$ for $N = N_0$ and $P_N(0) = 0$ else. (In particular, we have $P_N(t) = 0$ for all N < 0 and all t.) The Master equations are a system of infinitely many ordinary differential equations. We consider the expected population size

$$\bar{N}(t) = \sum_{N=0}^{\infty} N P_N(t).$$
(3)

From the Master equation follows

$$\frac{\partial \bar{N}}{\partial t} = \sum_{N=0}^{\infty} N \frac{\partial P_N(t)}{\partial t}
= \sum_{N=0}^{\infty} \left(dN(N+1)P_{N+1}(t) + bN(N-1)P_{N-1}(t) - N^2(b+d)P_N(t) \right)
= \sum_{N=0}^{\infty} \left(d(N-1)NP_N(t) + b(N+1)NP_N(t) - N^2(b+d)P_N(t) \right)
= \sum_{N=0}^{\infty} \left(N(b-d)P_N(t) \right) = (b-d)\bar{N}(t)$$
(4)

Defining the net growth rate r = b - d, we obtain the solution

$$\bar{N}(t) = N_0 \cdot \exp[rt]. \tag{5}$$

We thus see that the expected value of the stochastic process follows simple exponential growth. The long-term behavior follows a simple dichotomy: the expected population size declines to zero as the population dies out for d > b, while it grows without bounds for b > d. However, the behavior of the stochastic process is richer than predicted just by the expected value. Similar to the derivation above, we can derive the variance. We start with

the dynamics of the second moment:

$$\frac{\partial N^2}{\partial t} = \sum_{N=0}^{\infty} N^2 \frac{\partial P_N(t)}{\partial t}
= \sum_{N=0}^{\infty} \left(dN^2(N+1)P_{N+1}(t) + bN^2(N-1)P_{N-1}(t) - N^3(b+d)P_N(t) \right)
= \sum_{N=0}^{\infty} \left(d(N-1)^2 N P_N(t) + b(N+1)^2 N P_N(t) - N^3(b+d)P_N(t) \right)
= \sum_{N=0}^{\infty} \left((2N^2(b-d) + N(b+d))P_N(t) \right) = 2(b-d)\overline{N^2}(t) + (b+d)\overline{N}(t). \quad (6)$$

Defining $\overline{N^2}(t) := Q(t)N_0 \exp(rt)$ and with the solution for $\overline{N}(t)$ from above, we obtain:

$$\dot{Q}(t) = (b-d)Q(t) + (b+d)$$
(7)

which is solved by

$$Q(t) = C \exp(rt) - \frac{b+d}{b-d}.$$

With $\operatorname{Var}[N(t)] = \overline{N^2}(t) - (\overline{N}(t))^2$ and the boundary condition $\operatorname{Var}[N(0)] = 0$ we now obtain $C = N_0 + (b+d)/(b-d)$ and thus

$$\operatorname{Var}[N(t)] = \frac{b+d}{b-d} \big(\exp(rt) - 1 \big) \exp(rt) N_0.$$
(8)

Just like the expected value, the variance increases exponentially with time if b > d. What kind of biological consequences does this stochastic scattering around the expected value have? Most significantly, since extinction (N = 0) is a stationary point of the process, we may ask for the probability that this point is reached from a starting population $N = N_0$. Define u_N as the probability that a population of current size N will go extinct at some time in the future. How can we derive u_N ? We know the following:

- 1. Birth and death is independent for all individuals in our model. The population will go extinct if and only if none of the individuals in the starting population will leave offspring in the distant future. Let $u = u_1$ be the probability that a single individual does not leave any offspring. Because of independence, we have $u_N = u^N$.
- 2. Consider a population currently in state N. We may ask for the state of our population right after the next demographic event, i.e., after a single birth or death. From our current state N, we can only reach one of the neighboring states. For given birth and death rates b and d, we will be in state N + 1 with probability b/(b + d) and in state N - 1 with probability d/(b + d). We thus obtain the following recursion for our extinction probabilities,

$$u_N = \frac{b}{b+d} u_{N+1} + \frac{d}{b+d} u_{N-1} \quad \text{for} \quad N \ge 1,$$
(9)

with boundary condition $u_0 = 1$. Formally, this corresponds to the transition matrix of a one-dimensional random walk with absorbing state at 0.

We thus obtain the condition

$$(b+d)u = bu^2 + d \tag{10}$$

The two solutions of this quadratic equation are

$$u_{(1)} = \frac{d}{b}$$
; $u_{(2)} = 1$.

For d > b, u = 1 is the only valid solution and we see that extinction is certain. For b > d, the population can escape extinction. However, there is still a probability given by $u_{N_0} = u^{N_0} = (d/b)^{N_0}$ that the population dies out – even if the expected value grows without bounds. Note that this probability becomes $u_{N_0} = 1$ for r = 0, although the expected population size stays constant in this case. However, for b > d and sufficiently large N_0 the extinction probability becomes very small. [A formal proof that u = d/b is the correct solution for d < b requires some further arguments, see lecture on stochastic processes or the book by Kot.]

Stochastic and deterministic models We can interpret a deterministic population model as an approximation to a more detailed stochastic process. For a (linear) birthdeath model we have seen that the dynamics of the expected population size reproduces deterministic exponential growth. However, there are important aspects of the stochastic dynamics that are not covered by a deterministic model. These differences are most important in small populations, where random fluctuations can easily drive a population to extinction. Once the population size is sufficiently large, the deterministic system is a valid approximation of the stochastic model. This can be justified from the coefficient of variation, which derives as

$$CV[N(t)] = \frac{\sqrt{Var[N(t)]}}{\bar{N}(t)} = \sqrt{\frac{1}{N_0} \frac{b+d}{b-d} (1 - \exp(-rt))}.$$
 (11)

We see that for r > 0 CV[N(t)] is limited for all t and gets small for large initial population size N_0 . It is straightforward to define more complex stochastic models for population dynamics – even with multiple interacting populations. [Some theory that exists along these lines is summarized in the book by Allen]. However, most of these models cannot be solved and our potential to obtain explicit analytical results is very limited. For this reason, the bulk of population dynamical research uses a deterministic approach. For a general stochastic model of a single, unstructured population with birth, death, and immigration, we obtain

$$N(t) \to N(t) + 1: \quad b(t, N(t)) \cdot N(t) + m(t, N(t))$$
 (12)

$$N(t) \to N(t) - 1: \quad d(t, N(t)) \cdot N(t) \tag{13}$$

where b(t, N(t)), d(t, N(t)) and m(t, N(t)) are birth-, death-, and immigration rates, respectively, which can depend on the population density and on time. (Note that emigration can be subsumed in the death rates). We then have the expected change

$$E[\Delta N|N(t)] = \left(r(t, N(t)) \cdot N(t) + m(t, N(t))\right) \Delta t.$$
(14)

This can be transformed into a deterministic process using the following correspondence:

$$\dot{N}(t) = r(t, N(t)) \cdot N(t) + m(t, N(t)).$$
 (15)

We thus obtain an ODE, which in general can be non-linear and time-dependent. This ODE approximates the dynamics of the stochastic system for large population sizes. (We note that it is generally not true that it represents the - exact - dynamics of the expected population size, like in the linear birth-death model). A general strategy in ecological modeling is to use a deterministic model for derivations and to use stochastic computer simulations as back-up, in order to test the robustness of the results.

1.2 Deterministic models in continuous time

The general deterministic model for the dynamics of a single, unstructured population reads:

$$\dot{N}(t) = f(N,t) = f(N(t),t)$$
 (16)

 $N(t) \in \mathbf{R}$ is usually interpreted as population density rather than the total size. There are (only) a few models with explicit solutions:

• The most basic model is exponential growth with

$$N(t) = rN(t)$$

and explicit solution $N(t) = N_0 \exp(rt)$. The net growth rate r is also called the Malthusian parameter (Thomas Malthus, 1798: Essay on the Principle of Population). Exponential growth with r > 0 leads to population explosion and is unsustainable in Nature. With r < 0, there is a trivial stable equilibrium at N = 0.

• The simplest model with a stable equilibrium population derives from a dynamics with immigration and death (negative growth),

$$\dot{N}(t) = c - dN(t)$$

with c, d > 0 and explicit solution

$$N(t) = \frac{c}{d} + \left(N_0 - \frac{c}{d}\right) \exp\left[-dt\right].$$
(17)

The model describes the dynamics in a population sink. It also describes pure migration if immigration is constant and emigration occurs with a constant per-capita rate. • The simplest model with population regulation of a population that can sustain itself is the logistic growth model with

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t)}{K}\right)$$

It is characterized by linear density dependence with per-capita growth rate r(1 - N/K). The parameter r is also called the intrinsic growth rate. K is the carrying capacity. The explicit solution for the logistic growth model follows (e.g. by separation of variables) as

$$N(t) = \frac{K}{1 - (1 - K/N_0) \exp[-rt]}.$$
(18)

The logistic growth model can even be solved with time-dependent per-capita growth rate r(t), simply by replacing the exponent rt by $\int_0^t r(t)dt$.

Very few other models of relevance in the ecological literature have explicit solutions. Luckily, we are usually not so much interested in the explicit dynamics, but rather in key qualitative properties. The most fundamental property of a dynamical model is its equilibrium structure, which governs the long-term behavior and defines the landmarks of the dynamics.

1.3 Equilibria and stability of single-species models in constant environments

Consider a general (unstructured) population model in one dimension with autonomous dynamics, i.e.,

$$\dot{N}(t) = f(N) \tag{19}$$

The long-term behavior of a general population model in one dimension with an autonomous dynamics can be read off from the phase-line diagram, where $\dot{N} = f(N)$ is plotted as a function of N. See Figure 1 for the case of logistic growth.

Definition In general, we define $N = N^*$ is an equilibrium point (fixed point) of the dynamics if

$$f(N^*) = 0$$

• The equilibrium is Lyapunov stable if for any $\epsilon > 0$ there is a $\delta > 0$, such that

$$|N(t_0) - N^*| < \delta \quad \Rightarrow \quad |N(t) - N^*| < \epsilon \quad \forall t > t_0.$$

This means: if we start close, we stay close.

• A (Lyapunov) stable equilibrium is called *asymptotically stable* if an $\delta > 0$ exists, such that

 $|N(t_0) - N^*| < \delta \quad \Rightarrow \quad \lim_{t \to \infty} |N(t) - N^*| = 0$



Figure 1: Phase-line diagram and dynamics for logistic growth (with K = 10000 and r = 0.4). The growth dynamics has an inflection point at K/2: maximal absolute increase in population density.

This means that sufficiently small deviations will only produce (small) excursions that eventually return to the equilibrium. In the biological literature, this is often also called "locally stable".

Elementary facts

- If f(N) is continuously differentiable at $N = N^*$ then an equilibrium point N^* is asymptotically stable if $f'(N^*) < 0$. It is unstable if $f'(N^*) > 0$. For $f'(N^*) = 0$, stability depends on higher derivatives (e.g., an internal equilibrium is unstable in this case if $f''(N^*) \neq 0$, etc). In general: An equilibrium N^* is asymptotically stable if and only if $f(N^* + \epsilon) < 0$ and $f(N^* - \epsilon) > 0$ for some $\delta > 0$ and all $0 < \epsilon < \delta$. – **Proof**: obvious from the phase-line diagram, or see Kot.
- Let f(N) be continuously differentiable. We call an unstable equilibrium a *breakpoint* if and only if $f(N^*+\epsilon) > 0$ and $f(N^*-\epsilon) < 0$ for some $\delta > 0$ and all $0 < \epsilon < \delta$. If f(N) has a finite number of equilibria, asymptotically stable equilibria and breakpoints are always interlaced (i.e., there is exactly one stable fixed point between any two breakpoints and vice-versa).
- Assume that all fixed points are either asymptotically stable equilibria or breakpoints (this is the generic case). Then the domain (or basin) of attraction of any stable equilibrium extends to the neighboring breakpoints, or to the boundaries of the parameter space.
- Asymptotically stable equilibria and breakpoints are *structurally stable* in the sense that small perturbations to f(N) may lead to small changes in the positions of the equilibria, but they persist otherwise. All other equilibria are structurally unstable.

1.4 Example: Malaria infection model

In 1897, Sir Ronald Ross (1857 – 1932, Nobel prize 1902) discovered that malaria is transmitted by *Anopheles* mosquitoes. He suggested to fight the mosquitoes to get rid of the disease. However, it is clear that a total extinction of all mosquitoes is not realistic. People argued that *Plasmodium*, the malaria parasite, would survive in some mosquitoes and return together with the mosquitoes after a (costly) program to fight the mosquitoes has ended. Sir Ronald designed a mathematical model to convince his contemporaries that this is not necessarily true.

In a simplified version (e.g., ignoring immunity), the model works like this:

- The model assumes a human population with two parts: infected and uninfected people. Let p be the proportion of infected people.
- Uninfected people can get malaria from infected people via Anopheles mosquitoes. Let the density of (human active) mosquitoes be α . Then the infection rate (per uninfected) is αp .
- Infected people can also recover at rate μ

We can summarize the model in the following figure:



- Construct an ODE model for the dynamical variable p(t) and discuss the equilibria.
- How does the phase diagram look like?
- How does the dynamics depend on the mosquito density α ? Draw a figure for the equilibria p^* as a function of α .
- What are the prospects for getting rid of the disease without getting rid of Anopheles?

We have

$$\dot{p} = \alpha p(1-p) - \mu p = (\alpha - \mu) p \left(1 - \frac{p}{(\alpha - \mu)/\alpha} \right).$$
(20)

For $\alpha > \mu$, this is the dynamics of logistic growth with $r = \alpha - \mu$ and $K = (\alpha - \mu)/\alpha$. We then get a stable equilibrium of infected people at the carrying capacity K. This is the so-called *endemic equilibrium*. In contrast, for $\alpha < \mu$, we have a stable equilibrium at p = 0. The disease is extinct although the mosquitoes are still there at some density. Sir Ronald Ross always considered his mathematical models his most important contribution



Figure 2: Phase-line diagram for the infection model (20). Left: $\alpha > \mu$, right: $\alpha < \mu$.

to science! Only very few of his contemporaries understood and appreciated these models. Only two decades after his death, people started to construct mathematical models for infection and disease in his tradition. For malaria, the qualitative finding that the disease cannot persist with a low mosquito density is confirmed (e.g., parts of USA and Italy). Of course, modern models used in the fight against malaria in Africa and Asia are many levels more complex.

1.5 Bifurcations

For qualitative analysis, it is often of central interest how the equilibrium structure of a model changes if we change some of the model parameters. As a consequence, new equilibria may be created or old ones destroyed, or equilibria may collide and exchange their stability. The resulting qualitative changes in the behavior of the dynamical systems are called bifurcations. We can visualize this "dynamics of the equilibria" in a so-called bifurcation diagram. In the malaria example above, we have α as a model parameter and the following equilibria: $p_1^*(\alpha) = 0$ and $p_2^*(\alpha) = K = 1 - \mu/\alpha$. This corresponds to a socalled *transcritical bifurcation*. We consider a "sufficiently smooth" (at least continuously differentiable) function f(N). The basic types of bifurcations in one dimension are the following:

1. Transcritical bifurcation: two equilibria cross and exchange stability properties. The *normal form* of a transcritical bifurcation at x = 0 (think of $x = N - N^*$) and perturbation parameter α reads

$$\dot{x} = \alpha x - x^2 \,. \tag{21}$$

2. Saddle-node bifurcation: two equilibria (with opposite stability) collide and vanish (or vice-versa), e.g.,

$$\dot{x} = \alpha - x^2 \,. \tag{22}$$

3. Pitchfork bifurcation: three equilibria collide. There are two possibilities. For the supercritical case, the three equilibria are stable – unstable – stable and turn into a stable equilibrium, e.g.,

$$\dot{x} = \alpha x - x^3 \,. \tag{23}$$

For the subcritical case, the three equilibria are unstable – stable – unstable and turn into a single unstable equilibrium,

$$\dot{x} = \alpha x + x^3 \,. \tag{24}$$

- 4. Higher-order bifurcations with four or more equilibria colliding are in principle possible, but non-generic.
- 5. In addition to bifurcations, equilibria can also enter or leave the biological state space. For a population density N the critical boundary is usually at N = 0. Equilibria can also emerge (or vanish) from infinity. However, most biologically relevant models have $\lim_{N\to\infty} f(N) \ll 0$, in which case this is not possible.

1.6 Exercise 1: Harvest models

Consider a population of fish with dynamics according to logistic growth. We want to use this population as a resource and we are looking for a harvesting strategy that guarantees large and stable yield. We consider the following two strategies:

1. With constant-rate harvesting (e.g., because of fishing quota), we have

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - H.$$
(25)

2. With relative-rate harvesting, we will catch fish proportional to the stock size,

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - EN,\tag{26}$$

where E measures the fishing effort (this could be a quota on fishing boats).

We define the *maximum sustainable yield* (MSY) as the largest yield that can be taken from the species' stock over an infinite period.

- Make a bifurcation analysis for both harvesting strategies with H and E as parameters (diagrams and formulas for bifurcation points). What kinds of bifurcations occur?
- What is the MSY and for which parameter values of H and E do we get this yield? Which implications for harvesting strategies do you see?

From the solution we see that constant rate harvesting at MSY is dangerous, since any higher rate can lead to a collapsing fish population. With relative rate harvesting, the risk of a sudden crash is avoided. Here, we get the maximal *cumulative* yield for an intermediate *cumulative* effort E. It is interesting to consider a situation where multiple fisheries (or countries) compete and try to maximize their share of the harvest. In many cases, we will find that the *individual* yield increases monotonically with the *individual* effort – although the cumulative yield decreases. This is an example of the so-called "tragedy of the commons" (see lecture on game theory).

Allee effect In the models we have considered so far, the per-capita growth rate $g(N) = \dot{N}/N$ was either independent of N (as in exponential growth) or decreased with increasing N (as in logistic growth). In some species, however, the per-capita growth rate is reduced at small population densities, for example because individuals have difficulty finding mates, because group defense (like swarming) or hunting do not work properly, or because of increased predation pressure. Formally, a population experiences a *demographic Allee effect* if $\lim_{N\to 0} dg/dN > 0$. If the reduction in per-capita growth rate at small densities is so strong that populations below a certain critical density have a negative per-capita growth rate, we say that there is a *strong* demographic Allee effect. Otherwise the Allee effect is called weak and small populations can still grow. A typical model with strong Allee effect reads

$$\dot{N} = rN\left(\frac{N}{K_0} - 1\right)\left(1 - \frac{N}{K}\right),\tag{27}$$

where $K_0 < K$ defines the critical density for which growth becomes positive.

• We can consider relative-rate harvesting on such a population, i.e.,

$$\dot{N} = rN\left(\frac{N}{K_0} - 1\right)\left(1 - \frac{N}{K}\right) - EN.$$
(28)

We get equilibria at N = 0 and at the solutions of $E = r((N/K_0) - 1)(1 - (N/K))$. A bifurcation analysis reveals that an allee effect can lead to qualitative changes in the dynamics (see exercises).

1.7 Nondimensionalization

Understanding the qualitative behavior of a model with several parameters can be difficult. If we vary one parameter at a time while fixing the other parameters at certain values, we cannot be sure that we get the full picture of the model's behavior. Fortunately, often the only quantity that matters is the relative magnitude of parameters. This is exploited by a model simplification technique called *nondimensionalization*. The idea is to rescale variables and time such that the rescaled model has fewer parameters but maintains all other model features. As an example, we will nondimensionalize the Allee effect model (27) above. First, we rescale population size by expressing it relative to the carrying capacity K (scaling by K_0 would work as well). Now our new variable is x = N/K. Second, we define a new time scale $\tilde{t} = r \cdot t$, i.e. rate r on the original time scale corresponds to rate 1 on the new time scale.

With this, we get the new differential equation

$$\frac{dx}{d\tilde{t}} = \frac{dx}{dt} \cdot \frac{dt}{d\tilde{t}} = \frac{1}{Kr} \frac{dN}{dt} = x(1-x) \left(\frac{Kx}{K_0} - 1\right).$$
(29)

We set $k_0 = K_0/K$ and drop the tilde (keeping in mind the difference in time scale):

$$\dot{x} = x(1-x)\left(\frac{x}{k_0} - 1\right).$$
 (30)

Our new model has just one parameter, which makes the computation of equilibria, bifurcation analyses etc. more transparent. After we have completed our analyses, we can translate the results back to the original scale. This is especially important if we want to relate them to biological data.

1.8 Bifurcations and structural stability

We have seen that for relative-rate harvesting the inclusion of the Allee effect transforms a transcritical bifurcation into a saddle-node bifurcation. This is indeed typical: Consider a small constant perturbation to a transcritical bifurcation, i.e.,

$$\dot{x} = \alpha x - x^2 + \epsilon \,. \tag{31}$$

There are equilibria for $1/2(\alpha \pm \sqrt{\alpha^2 + 4\epsilon})$. We see that there is no bifurcation for $\epsilon > 0$, because the equilibria never cross. And there are two saddle-node bifurcations for $\epsilon < 0$, where there is no equilibrium at all for $|\alpha| < 2\sqrt{-\epsilon}$. In an extended parameter space with two perturbation parameters α and ϵ , the transcritical bifurcation will only be seen on a low-dimensional manifold (for $\epsilon = 0$). [In dynamical systems theory, this kind of analysis is called an "unfolding" of a bifurcation.] We say, the transcritical bifurcation is structurally unstable with respect to constant perturbations. There is a similar effect for the pitchfork bifurcation, but not for the saddle-node bifurcation. In this sense, saddle-node bifurcations represent the most "generic" bifurcation type in one dimension.

1.9 Functional response

Define the functional response F(N): the per capita resource consumption as a function of resource density N per unit time. We set

$$F(N) = \frac{T_s \cdot eN}{T_s + T_h} \tag{32}$$

where T_s is the time spent searching for food, e the search efficiency, and T_h the handling time, i.e., the time needed to process all the attacked prey items. With $T_h = eNT_s \cdot t_h$, where t_h is the time needed to process a single prey item, we get

$$F(N) = \frac{eN}{1 + eNt_h}.$$
(33)

After Holling, we can distinguish three types of feeders

- 1. $t_h = 0$: Type 1 functional response, e.g. for filter feeders.
- 2. $t_h > 0$: Type 2 functional response, with asymptote at $1/t_h$.
- 3. $t_h > 0$ and e = e(N) = e'N: Type 3 functional response. Here, the search efficiency increases with the prey density, for example because a search image is created as the predator get "practice". This type of functional response is often assumed for higher organisms like vertebrates.

Based on these functional responses, we can now consider the resource dynamics as a function of the consumer density. For the type 1 functional response, this coincides with the relative-rate harvesting model. For type 2 or type 3, we obtain a different behavior.

Resource dynamics for type 2 functional response Consider a model for a resource population with logistic growth, a constant consumer density C, and type 2 functional response:

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - \frac{CeN}{1 + et_hN}.$$
(34)

- Explore the model by plotting Eq. (34) for different parameter combinations.
- Set $r = 0.1, K = 1000, t_h = 0.25, e = 0.05$. Make a graphical bifurcation analysis for C. If you want, you can use mathematica, R, maple or some other software package.
- For which consumer densities C does the resource experience an Allee effect? Is the Allee effect weak or strong?

Resource dynamics for type 3 functional response For a type 3 response, the model looks as follows:

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - \frac{CgN^2}{N_0^2 + N^2}$$
(35)

where C is the number of consumers, g the asymptote of the response curve, and N_0 the half saturation point. We may, for example, think of C as the number of sheep on a meadow and N as the grass biomass. We can analyze this case qualitatively purely graphically.

Take-home message from bifurcation theory Small changes can have a large effect. This is typical for ecosystems, where these abrupt shifts are frequently seen. The fact that continuous change may lead to discontinuous consequences is counterintuitive for most people. This can have dangerous consequences. Providing insight into the bifurcation structure of natural systems is one of the most important tasks of theoretical ecology. Examples:

• Fisheries: extinction risk because of overfishing.

• Grasslands turning into deserts because of overgrazing. Very difficult to revert after erosion of top soil.

Of course, it will often be difficult to obtain quantitative estimates of the positions of bifurcation points. Note also that natural systems exhibit environmental and demographic stochasticity. For this reason, it will be wise to stay at a safety distance from any catastrophic bifurcation point.

1.10 Stability revisited

We have seen that for asymptotically stable equilibria the population will return to the equilibrium after a single and "sufficiently small" disturbance. However, disturbances in biology are frequent and not necessarily small. How can we deal with this problem? We will treat the case that perturbations are still small, but can be frequent. The relevant question for a second (and each further) perturbation is whether the system has already returned to the equilibrium after the previous perturbation. With a small perturbation $N(0) = N^* + \delta$, we can linearize the dynamics around N^* ,

$$\dot{N}(t) \approx \Lambda (N^* - N(t)) \tag{36}$$

with

$$\Lambda = -\frac{\partial f(N)}{\partial N}\Big|_{N=N^*}.$$
(37)

For an asymptotically stable equilibrium, we have $\Lambda > 0$. Now, Eq. (36) is precisely the dynamics of an immigration-death model (see above) and can be solved exactly. We get

$$N(t) = N^* + \delta \exp[-\Lambda t].$$
(38)

We thus obtain an exponential return to the equilibrium with rate given by Λ . We can define a characteristic return time to the equilibrium as

$$T_R = \frac{1}{\Lambda} \,. \tag{39}$$

For $t \gg T_R$ we will be close to N^* , for $t \ll T_R$, we are still about a distance δ away. We can now compare T_R with the average time T_D between disturbances. For $T_R < T_D$, the system is stable and will remain in the neighborhood of N^* . In contrast, for $T_D < T_R$, we get larger excursions away from N^* . In this case, the exact behavior cannot be predicted anymore from a local analysis alone.

1.11 Systems with time delay

One-dimensional autonomous ODE models have a simple equilibrium structure: only stable or unstable equilibrium points can occur. Stable equilibria have simple intervals as domains of attraction. In particular, there are no oscillations or chaotic behavior. All this quickly changes if the dynamics of a focal population can depend on other factors than just its current size. As already mentioned, \dot{N} could depend explicitly on time (non-autonomous systems), or on the dynamics of a different population (multidimensional ODEs). As yet another possibility, we consider the following dynamics of a population with damped oscillations:

$$N(t) = N^* + (N_0 - N^*) \cos[\gamma t] \cdot \exp[-dt].$$
(40)

We then have

$$\dot{N}(t) = (N_0 - N^*) \exp[-dt] \left(-\gamma \sin(\gamma t) - d\cos(\gamma t)\right)$$
(41)

$$= (N_0 - N^*) \exp[-dt] \left(\gamma \cos[\gamma (t - 3\pi/2\gamma)] - d\cos(\gamma t)\right).$$
(42)

With $\tau = 3\pi/2\gamma$ and using Eq. (40) to solve for and substitute $\cos[\gamma(t - 3\pi/2\gamma)]$ and $\cos(\gamma t)$, we obtain

$$\dot{N}(t) = \gamma \exp[-d\tau] N(t-\tau) - dN(t) + (d-\gamma \exp[-d\tau]) N^* \,.$$
(43)

Although N(t) only depends on the size of the focal population, it is not only its current size, but also the size at some earlier time $t - \tau$. Defining $b := \gamma \exp[-d\tau]$, we recognize this as a time delay in the effect of birth events. Biologically, this can easily be understood if N measures adult individuals, and if it takes some time for juveniles to grow up to reproductive age. There is a lot of theory on ODE's with time delay (also called differencedifferential equations), but analytical results are sparse. Formally, these equations are equivalent to infinite-order ODE's, which depend on initial conditions on a whole time interval. The math gets quite complex. Nevertheless, delay effects can obviously be relevant in biological systems. If this is the case, they need to be included into a model. As it turns out, however, this is most easily done in a discrete time model using difference equations.

Further example: Lagged logistic growth We can also introduce a time-lag into the logistic growth model, e.g., if the negative feedback of the population density on population growth is not immediate, but only sets in once individuals have grown up. For a lag time τ we get

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t-\tau)}{K}\right).$$
(44)

There is no analytical solution of this ODE, but we can study its behavior numerically.

• Use the "Populus" software to plot numerical solutions for the lagged logistic model (single species/density-dependent growth). Which types of behaviors do you get when you vary the model parameters?

2 One-dimensional models in discrete time

So far, we have assumed that demographic events happen continuously over time and can thus be written as rates. For many biological species with overlapping generations and continuous reproduction this is a valid approximation. However, many other populations, like annual plants, have discrete generations and many species have clearly defined breeding seasons. These are better modeled in a discrete time framework. More fundamentally, we have already discussed that the effect of biological events (like birth) on the population dynamics is often not immediate as it is assumed in an ODE system, but only becomes apparent after some time delay. While in continuous time this leads to complex difference-differential equations, effects of time delay (by one time unit or generation) are automatically included in discrete time models. In this section, we will consider a population with dynamics given by the following first-order, autonomous (= constant coefficient) difference equation,

$$N_{t+1} = F(N_t), \quad t \in \mathbf{N}.$$

$$\tag{45}$$

An initial value N_0 is specified and the reproduction function F can take any shape. The simplest example is the linear difference equation

$$N_{t+1} = FN_t \tag{46}$$

of geometric growth (for F > 1) or decline (for 0 < F < 1). Geometric growth has the explicit solution

$$N_t = F^t N_0 \,. \tag{47}$$

Very few other discrete time systems have explicit solutions. Next, we need to include density-dependent population regulation. Rather than "dropping down" a model, we want to construct a model from biological principles.

2.1 Non-linear discrete population growth

Consider a fish population of adult stock size N_t . From one breading season to the next (t to t+1), the survival probability for any adult is given by s. (For s = 0, we have the special case of no generation overlap). During breeding season, the adults produce a number of $L_t = bN_t$ larvae. We assume that larvae grow up to reproductive age during one season. Surviving larvae are recruited to the adult population. We thus need a model for larval survival.

1. Assume that the larvae L develop according to (continuous time) logistic decline, i.e.,

$$\frac{\partial L_t(\tau)}{\partial \tau} = -m_1 L_t(\tau) - m_2 L_t^2(\tau) , \qquad (48)$$

where m_1 measures mortality due to extrinsic (e.g. abiotic) factors and m_2 the density dependent component (e.g., due to competition for resources). With $L_t(0) = bN_t$ and a time Δ between seasons we get

$$L_t(\Delta) = \frac{bN_t m_1}{(bN_t m_2 + m_1) \exp[m_1 \Delta] - bN_t m_2}.$$
(49)

We thus get

$$N_{t+1} = sN_t + L_t(\Delta) = sN_t + \frac{c_1N_t}{1 + c_2N_t}$$
(50)

with positive constants

$$c_1 = b \exp[-m_1 \Delta]$$
, $c_2 = b \frac{m_2}{m_1} (1 - \exp[-m_1 \Delta])$

This is the *Beverton-Holt model* for stock recruitment. For s = 0, the model is also called the *Verhulst model*.

2. An alternative approach assumes that larvae (or juveniles) do not compete primarily among themselves, but with their adult conspecifics. This will be true, in particular, if adult fish eat eggs and larvae of their own species (which is indeed true for many species, where predation is purely size-dependent). We then get

$$\frac{\partial L_t(\tau)}{\partial \tau} = -m_1 L_t(\tau) - m_2 N_t L_t(\tau) \,, \tag{51}$$

which simply results in

$$L_t(\Delta) = bN_t \exp[-(m_1 + m_2 N_t)\Delta].$$
(52)

We then get a so-called *Ricker model* for stock recruitment

$$N_{t+1} = sN_t + N_t \exp[r(1 - N_t/K)]$$
(53)

with constants

$$r = \log[b] - m_1 \Delta$$
 , $K = \frac{\log[b] - m_1 \Delta}{m_2 \Delta}$

3. Finally, we can assume that density-dependent competition is entirely among adults (e.g. for breeding places). Then we get a discretized version of logistic growth

$$N_{t+1} = rN_t \left(1 - \frac{N_t}{K}\right),\tag{54}$$

where r = s + b accounts for the surviving adult and juvenile individuals from the previous generation.

Recruitment in the Beverton-Holt model is called normal compensation. It increases monotonically with stock size and reaches an asymptote for $N_t \to \infty$ at $L_{\max}(\Delta) = c_1/c_2$. In contrast, recruitment for the Ricker model is over-compensating. Here, $L_{\max}(\Delta)$ runs through an intermediate maximum and approaches zero for $N_t \to \infty$. As a consequence, the reproduction function of the Ricker model is usually non-monotonic. The same holds true for the discrete logistic growth model. All three models can be derived in many different ways and for various underlying mechanisms. They are archetypical models of theoretical ecology.

2.2 Discrete versions of continuous models

One special application of discrete models consists simply of an observation in discrete time intervals of a population with continuous birth and death. Thus, we simply set $N_t = N(t \cdot \Delta)$. An explicit reproduction function can be derived if and only if the ODE can be solved. For logistic growth, in particular, we obtain

$$N_{t+1} = \frac{K}{1 - (1 - K/N_t) \exp[-r]} = \frac{\lambda N_t}{1 + (\lambda - 1)N_t/K}$$
(55)

with $\lambda = \exp[r]$. We recognize this as a special case of the Beverton-Holt model with s = 0, $c_1 = \lambda$, and $c_2 = (\lambda - 1)/K$. Note that we do not get the discrete logistic growth as the corresponding model. This correspondence also implies that the Beverton-Holt model (with s = 0) is explicitly solvable. In more general, we can define a corresponding discrete model for every autonomous ODE model. The converse is not true, however. In this sense, there are "more" discrete models than continuous models. As we will see, they also show a larger variety of phenomena.

2.3 Equilibria and Stability of Discrete Dynamics

Consider a general discrete dynamical system (1-dim., etc) with continuously differentiable reproduction function,

$$N_{t+1} = F(N_t) \quad ; \quad F'(N) := \frac{\partial F(N)}{\partial N}$$
 continuous (56)

We can then characterize equilibria as follows

1. Equilibria (or fixed points) of the dynamics are all intersections of the reproduction function with Id(N) (the identity line with slope 1),

$$F(N^*) = N^* \tag{57}$$

2. Let

$$\Lambda := \frac{\partial F(N)}{\partial N}\Big|_{N^*}$$

Then N^* is locally (asymptotically) stable for $|\Lambda| < 1$ and locally unstable for $|\Lambda| > 1$.

Proof: Consider some starting value N_0 close to an equilibrium point N^* . Due to the mean value theorem, there is a $c \in (N_0, N^*)$ such that

$$\frac{\partial F(N)}{\partial N}\Big|_{N=c} = \frac{F(N_0) - F(N^*)}{N_0 - N^*} = \frac{F(N_0) - N^*}{N_0 - N^*}$$

Since the derivative of F(N) is continuous, we have

$$\left|\frac{\partial F(N)}{\partial N}\right|_c \left| < 1\right|$$

if $|\Lambda| < 1$, and thus $|F(N_0) - N^*| < |N_0 - N^*|$. We thus get a sequence N_i that converges to the equilibrium point N^* . Similarly, we are (locally) driven away from the optimum for $|\Lambda| > 1$.



Figure 3: Cobwebbing method to determine the stability of equilibria.

Cobwebbing We can represent the discrete dynamics easily using the cobwebbing method:

- Start at N_0 , go (vertically) to $F(N_0)$.
- Project (horizontally) to the identity line Id(N) to get $N_1 = F(N_0)$.
- Go vertically to $F(N_1)$ and iterate.

Depending on the slope Λ near an equilibrium point, we get four types of characteristic behavior.

- 1. $0 < \Lambda < 1$: monotone convergence.
- 2. $-1 < \Lambda < 0$: oscillating convergence (damped oscillations)
- 3. $\Lambda > 1$: monotone divergence
- 4. $\Lambda < -1$: oscillating divergence (driven oscillations)

2.4 Analysis of the Beverton-Holt and the Ricker model

Beverton Holt model Consider the dynamics of the Beverton-Holt model defined by

$$N_{t+1} = F(N_t) = sN_t + \frac{c_1 N_t}{1 + c_2 N_t}.$$
(58)

• We have

$$N(1-s)(1+c_2N) = c_1N$$

and thus $N_1^* = 0$ and

$$N_2^* = \frac{c_1 - 1 + s}{c_2(1 - s)}$$

• With

$$F'(N) = \frac{\partial F(N)}{\partial N} = s + \frac{c_1}{(1 + c_2 N)^2} \le s + c_1 = F'(0)$$

and $F'(N_2^*) = s + \frac{c_1}{(1+(c_1-1+s)/(1-s))^2} = 1 + \frac{(1-s)(1-s-c_1)}{c_1} < 1$ for $s + c_1 > 1$ and thus $N_2^* > 0$. We get monotonic approach of N_2^* for $s + c_1 > 1$ and monotonic approach of $N_1^* = 0$ otherwise.

Lemma In general, if F(N) is continuous and monotonic on a closed interval $I \subseteq \mathbf{R}_+$ (e.g., $I = [0, \infty)$) with $F(I) \subseteq I$, then every sequence $N_i = F^i(N_0)$ with $N_0 \in I$ converges monotonically to a fixed point of F or to ∞ .

Proof For $F(N_0) > N_0$, we have $F(F(N_0)) \ge F(N_0)$ because of monotony, and thus $N_0 < F(N_0) \le F(F(N_0)) \le \dots$ The sequence will either converge to some N^* or diverge to infinity. In the former case, we have $F(N^*) = N^*$ since F is continuous. The case $F(N_0) < N_0$ works analogously, $F(N_0) = N_0$ is trivial.

Ricker model Consider now the Ricker model (we use s = 0, without restriction under rescaling),

$$N_{t+1} = F(N_t) = N_t \exp[r(1 - N_t/K)].$$
(59)

- We obtain equilibria at $N_1^* = 0$ and $N_2^* = K$.
- We have

$$F'(N) = \left(1 - \frac{Nr}{K}\right) \exp[r(1 - N/K)].$$

and thus

$$\Lambda_1 = F'(0) = \exp[r] > 1, \tag{60}$$

$$\Lambda_2 = F'(K) = 1 - r.$$
(61)

• We have a unique maximum of F(N) at $N_{\text{max}} = K/r$ (and, of course a minimum $N_{\text{min}} = 0$).

We thus can distinguish three dynamical regimes (see, for example, Populus, densitydependent population growth, "discrete logistic" = Ricker)

- 1. For r < 1, the interval $I = [0, N_{\max}]$ contains both equilibrium points. Since we have F(N) monotonically increasing in I, with $F(I) \subseteq I$, we obtain monotonic convergence to the stable equilibrium $N_2^* = K$ for every start value $N_0 \in I$. For start values $N_0 \notin I$, we have $F(N_0) \in I$ and the same applies after the first step.
- 2. For 1 < r < 2, we have no longer monotonic convergence, but still $|\Lambda_2| < 1$. Hence, $N_2^* = K$ is still asymptotically stable and approached by damped oscillations.
- 3. For r > 2, we have $|\Lambda_2| > 1$ and therefore do no longer have a stable equilibrium. In particular, we get oscillating divergence for the equilibrium at $N_2^* = K$. Since the Ricker model has a finite maximum population size, we can ask what happens.

2.5 Limit cycles

The basic idea to gain further insights of the long-term dynamics of the Ricker model and similar systems is to consider the iterated map

$$F^{(2)}(N) = F(F(N))$$
 resp. $F^{(k)}(N) = F(\dots F(F(N)))$ $k - \text{fold}$ (62)

across k seasons. Obviously, this is again a discrete dynamical system and can be studied in the same way as the original one. Concerning its long-term behavior, we observe the following elementary facts:

- 1. Equilibria of F are also equilibria of $F^{(2)}$ and of every higher iteration $F^{(k)}$.
- 2. For the derivative of $F^{(2)}$ at the fixed points, we have, using the chain rule,

$$\frac{\partial F^{(2)}(N)}{\partial N} = \frac{\partial F(Z)}{\partial Z}\Big|_{Z=F(N)} \cdot \frac{\partial F(N)}{\partial N} \,. \tag{63}$$

and accordingly iterated for $F^{(k)}$. For equilibria N^* of F(N), in particular, this means

$$\frac{\partial F^{(k)}(N)}{\partial N}\Big|_{N=N^*} = \left(\frac{\partial F(N)}{\partial N}\Big|_{N=N^*}\right)^k.$$
(64)

Thus, stable equilibria of F remain stable for all higher iterations, and unstable equilibria remain unstable.

3. Additional (stable or unstable) equilibria of iterated maps $F^{(k)}$ can occur if the original dynamics F leads to cycling.

Definition and basic properties: Limit Cycles

1. A point N_0 is called a *point of period* k or a k-cycle point if it is a fixed point (equilibrium) of the k-fold iterated map $F^{(k)}(N)$, but not a fixed point of any map $F^{(k')}$ with $1 \leq k' < k$. Its orbit

$$\{N_0, F(N_0), \dots, F^{(k-1)}(N_0)\} =: \{N_0, N_1, \dots, N_{k-1}\}\$$

is called the corresponding k-cycle. Note that all points N_i in the cycle are fixed points of $F^{(k)}$.

2. A limit cycle is asymptotically stable, if and only if the corresponding cycle points are asymptotically stable equilibria of the k-fold mapping. In particular, we obtain via the chain rule

$$\Lambda^{(k)} = \frac{\partial F^{(k)}}{\partial N} = \prod_{i=0}^{k-1} \frac{\partial F(N)}{\partial N} \Big|_{N=N_i}$$
(65)

for the derivative of $F^{(k)}$ at all points of the cycle. The cycle and the corresponding fixed points of $F^{(k)}$ are asymptotically stable if $|\Lambda^{(k)}| < 1$ and unstable if $|\Lambda^{(k)}| > 1$.

3. We define the characteristic exponent (or Floquet exponent)

$$\lambda = \frac{1}{k} \log \left| \Lambda^{(k)} \right| = \frac{1}{k} \sum_{i=0}^{k-1} \log \left| \frac{\partial F(N)}{\partial N} \right|_{N=N_i} \right|.$$
(66)

Obviously, the cycle is stable for $\lambda < 0$ and unstable for $\lambda > 0$.

2.6 Example: Discrete logistic growth

As an example, we consider logistic growth

$$N_{t+1} = F(N_t) = rN_t \left(1 - \frac{N_t}{K}\right),$$
(67)

which behaves similar as the Ricker equation, but is easier to analyze. We have a maximum of F(N) at N = K/2, where F(K/2) = rK/4. There are two equilibria at $N_1^* = 0$ and at $N_2^* = K(r-1)/r$. With F'(N) = r(1-2N/K), we obtain F'(0) = r and $F'(N_2^*) = 2 - r$.

- 1. For 0 < r < 1, we have a single stable equilibrium at $N_1^* = 0$ and the population dies out.
- 2. For 1 < r < 3, a second equilibrium N_2^* appears and is stable, while N_1^* is unstable. Approach to the stable equilibrium is monotonic for r < 2 and oscillating for r > 2.
- 3. For r > 3, both equilibria N_1^* and N_2^* are unstable and we can expect limit cycles or other types of limit behavior.

Finally, for a reasonable biological model, r should not be larger than 4 since otherwise F(N) can get larger than K and then negative in the next iteration. To study the dynamics via iterated maps, assume K = 1 for simplicity. We then obtain:

$$F(N) = rN(1-N) \tag{68}$$

$$F^{(2)}(N) = r(rN(1-N))(1-rN(1-N)) = r^2N(1-N)(1-rN+rN^2)$$
(69)

$$\frac{\partial F^{(2)}(N)}{\partial N} = r \big(1 - 2rN(1 - N) \big) r (1 - 2N) \tag{70}$$

(Note that, in general, we have the symmetry $F^{(k)}(1-N) = F^{(k)}(N)$.) We find equilibria $F^{(2)}(N) = N$ for

$$N_1^* = 0$$
 , $N_2^* = \frac{r-1}{r}$, $N_{3,4}^* = \frac{1+r \pm \sqrt{(r-1)^2 - 4}}{2r}$ (71)

Obviously, $N_{3,4}^*$ exist for $r \ge 3$. We also find that $F(N_3^*) = N_4^*$ and vice-versa $F(N_4^*) = N_3^*$. The corresponding derivatives are

$$\Lambda_1^{(2)} = r^2 \qquad \Lambda_2^{(2)} = (2-r)^2 \quad , \quad \Lambda_{3,4}^{(2)} = 4 + 2r - r^2 \tag{72}$$

- At r = 3, we have $N_2^* = N_3^* = N_4^*$. We see that, by increasing r beyond this threshold, the previously stable equilibrium N_2^* turns unstable. At the same time two new equilibria of $F^{(2)}(N)$, N_3^* and N_4^* , appear and are stable: $|\Lambda_{3,4}^{(2)}| < 1$ for $3 < r < 1 + \sqrt{6} \approx 3.45$. This is the typical signature of a pitchfork bifurcation. For the original map F(N), the number of equilibria does not change. The new equilibria for $F^{(2)}$ correspond to a stable limit cycle with period 2.
- For $r > 1 + \sqrt{6}$, we have $\Lambda_{3,4}^{(2)} < -1$ and the equilibria N_3^* and N_4^* of $F^{(2)}$ turn unstable. For the iterated map $F^{(4)}$ this means that the slope at both equilibria increases to $(\Lambda_{3,4}^{(2)})^2 > 1$, thereby generating, once again, two new equilibria in a pitchfork bifurcation. We thus obtain a 2-cycle for $F^{(2)}$, corresponding to a 4-cycle for F(N), in each case. In general, every time when a stable equilibrium of $F^{(k)}$ becomes unstable, we get two new stable equilibria of $F^{(2k)}$, and thus a limit cycle with the period 2k. This is the so-called *period doubling cascade* of the logistic map and many similar discrete maps (such as the Ricker model).

2.7 Bifurcations for discrete time dynamics

We have encountered several cases of bifurcations in the examples, where fixed points originate or disappear or change their stability. They can be summarized as follows. First, the same three types of bifurcations that exist for the continuous time dynamics, $\dot{N} = f(N)$, also exist in discrete time with iteration function $N_{t+1} = F(N_t)$. Instead of the zeros of f(N), we now need to consider the zeros of F(N) - N. We obtain a

- transcritical bifurcation if two zeros of F(N) N cross and the corresponding fixed points exchange stability (e.g. Beverton Holt model for $s + c_1 = 1$);
- saddle node bifurcation if two fixed points (one stable, one unstable) are either newly generated or annihilated. This happens if Id(N) is tangent to F(N) and F(N) then either crosses or moves away from this line;
- *pitchfork bifurcation* if a single fixed point splits into three fixed points or, vice-versa, if three fixed points merge and a single one remains (e.g. bifurcation at r = 3 for the iterated logistic map F(2)).

All these bifurcation readily occur also for monotonically increasing iteration functions F(N). With decreasing F(N), another type of bifurcation is possible when a fixed point becomes unstable as F'(N) drops below -1. As described for the logistic map, this typically leads to a pitchfork bifurcation for $F^{(2)}$. For F(N), it leads to a (stable) limit cycle instead of a single fixed point. This type of bifurcation that cannot occur in the continuous time dynamics. More generally, we call it a

• *period doubling bifurcation* if a stable fixed point or an existing stable limit cycle becomes unstable and a new stable limit cycle (with a period of double length) emerges.

2.8 Chaos

For the logistic map, we get a series of critical values r_{2^k} (with $r_2 = 3$ and $r_4 = 1 + \sqrt{6} \approx 3.45$), above which stable cycles of period 2^k exist. As it turns out, this sequence of *period doubling* bifurcation points quickly converges to a finite value $r_c = r_{\infty} \approx 3.57$. We can ask what happens beyond this point. As an example, we can consider the logistic map with r = 4 and dissect the interval [0, 1] as follows

- 1. Two intervals $I_0 = [0, 1/2]$ and $I_1 = [1/2, 1]$. Both intervals are mapped by F(N) to the full domain [0, 1].
- 2. Dissect I_0 such that $I_{00} = [0,q]$ is mapped by F to I_0 and $I_{01} = [q, 1/2]$ is mapped to I_1 . Similarly, dissect I_1 into I_{10} and I_{11} .
- 3. Iterate this: $I_{000} \subset I_{00}$ is mapped by F to I_{00} and by $F^{(2)}$ to I_0 ; $I_{001} \subset I_{00}$ is mapped to I_{01} and then to I_1 , etc. In general, $I_{i_0i_1i_2...i_k} \subset I_{i_0}$ with $i_j \in \{0, 1\}$ is mapped by Fto $I_{i_1i_2...i_k} \subset I_{i_1}$ and by $F^{(k)}$ to I_{i_k} .
- 4. In general, if (e.g.) $N \in I_{0100}$, then $N \in I_0$, $F(N) \in I_1$, $F^{(2)}(N) \in I_0$, $F^{(3)}(N) \in I_0$. We can identify each point with an infinite interval nesting (dyadic transformation).
- 5. Points with periodic nesting correspond to periodic orbits. There are points with every period, starting with $I_{0000...}$ and $I_{1111...}$, which encode the (unstable) fixed points.

- 6. All points on interval boundaries are attracted by 0 (dense set: population on the verge of extinction; this is special for r = 4).
- 7. Almost all points (with no period in the nesting) must have orbits of infinite length. We also see that orbits of very close points can differ widely after even a few generations. This is the signature of *chaos*.
- 8. For the special case r = 4, there is an explicit solution for the dynamics

$$N_k = \sin^2[2^{k-1}\pi\theta] \text{ where } \theta = \frac{1}{\pi}\sin^{-1}[N_0^{1/2}].$$
 (73)

We see that we get aperiodic orbits for all irrational θ .

These observed phenomena are not specific to r = 4, but occur for most values $r > r_c$. We can summarize them as follows:

- There are infinitely many periodic points, with all kinds of periods, even and odd.
- For most r values, we obtain chaos, indicated by orbits of infinite length that never come back to a starting point. Another characteristic of chaotic solutions is that very small initial differences are magnified due to the mapping. This means that the long-term predictability of the system gets lost (butterfly effect).
- As analog to the Floquet exponent for finite cycles, one defines the Lyapunov exponent

$$\lambda = \lim_{k \to \infty} \frac{1}{k} \sum_{i=0}^{k-1} \log \left| \frac{\partial F(N)}{\partial N} \right|_{N=N_i} \right|$$
(74)

for any point N_0 with infinite orbit. A positive Lyapunov exponent indicates that small initial differences are magnified and the resulting orbit is chaotic.

• The chaotic regimes are interlaced by intervals with stable limit cycles with low period (e.g. 3-cycles).

Periodicity and Chaos in Biology Our examples show that even very simple models (in one dimension!) can give rise to very complex phenomena. Periodic dynamics are a frequent observation in biology, also in population dynamics. There can be multiple causes for such cycles. With discrete dynamics, cycling is created by an overshooting of the equilibrium, which is typical of many systems where regulation is not immediately effective, but acts with a certain delay. Essentially the same behavior is seen in continuous delay ODE's. Chaotic behavior in biology has been speculated a lot. From a theoretical point of view, we should expect chaos in particular for systems with higher dimension (multiple interacting species). Even with continuous dynamics, chaos exists in dimension ≥ 3 . However, convincing empirical evidence is hard to obtain. In particular, it is often difficult (or impossible) to distinguish long cycles and/or stochastic noise from "real" deterministic chaos. Finally, true chaos is never strictly possible in populations with a discrete number of individuals. Nevertheless, chaos is a field where biology has inspired mathematics and has helped to found chaos theory as a research field (Robert May 1974, 1976).

3 Structured populations

In all dynamical models considered so far, we have assumed that all individuals behave equally with respect to the population dynamics. All have the same birth and death rates, and all contribute to competition in the same way. Although for the discrete dynamics, we did consider individuals at different life stages (juveniles and adults), this only had an indirect effect on the recurrence equation F(N). Indeed, there was at least one time point during the life cycle when all individuals were equivalent (adults just before giving birth). We could thus use this life stage for the dynamics, while other stages (juveniles) were "integrated out". However, this is no longer possible if individuals at different life stages coexist at all times.

Age structure and Leslie matrices The typical example is a population with an age-structured demography. Let x_i the number (or density) of individuals in age-class i, $i \in \{1, ..., n\}$. Let p_i be the survival probability from age class i to i + 1 and let f_i be the fertility (expected number of offspring) of each member of age-class i. Then

$$x_{i+1}(t+1) = p_i x_i(t) \quad i = 1, \dots, n-1$$
(75)

$$x_1(t+1) = \sum_{i} f_i x_i(t)$$
(76)

which can be summarized as

$$\mathbf{x}(t+1) = \mathbf{L}\mathbf{x}(t) \tag{77}$$

with the Leslie matrix (Leslie 1945)

$$\mathbf{L} = \begin{pmatrix} f_1 & f_2 & \cdots & f_{n-1} & f_n \\ p_1 & 0 & \cdots & 0 & 0 \\ 0 & p_2 & \cdots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \cdots & p_{n-1} & 0 \end{pmatrix}$$
(78)

Other examples of structure

- 1. Spatial structure: A population lives in a structured habitat. Birth and death rates depend on the local characteristics and there is migration among the demes.
- 2. Different genotypes: Birth and death rates depend on the heritable genotype. Transition between genotype classes can occur due to mutation during reproduction.
- 3. Size structure: instead of age as such, for many species (like trees) the size is the more decisive factor.

- In general, the art of modeling is to decide which structure best describes a population. It is not necessary that individuals in one class have all the same demographic parameters: we can consider average quantities. However: these average quantities should only depend on the state the individuals are in and *not* on the history (i.e., where they came from): We thus want to make sure that the population dynamics can be described by a generalized *Markov model* (but note that the transition matrix is not normalized).
- We can illustrate all these models as graphs. Arrows between states represent nonzero transition probabilities. The transition matrix is also called the population projection matrix.

General formalism: linear model Let $x_i(t)$ the number of individuals in class i at time $t, i \in \{1, ..., n\}$. Let $m_{ij} := m_{i \leftarrow j}$ be the transition rate from state j to state i and **M** the corresponding population projection matrix. We assume that the transition rate (= demographic parameters) are constant. We thus consider a (time)-homogeneous process. In particular, we also assume ignore any density- or frequency-dependence. We then have a linear model with explicit solution

$$\mathbf{x}(t) = \mathbf{M}^t \mathbf{x}(0) \,. \tag{79}$$

We ask the following questions:

- What is the long-term growth rate of the population? Do we get growth or extinction?
- What kind of distribution over the states x_i does result in the long run? \longrightarrow Analog to stationary distribution of a Markov process.

Definitions: Irreducible, primitive, spectral radius

• A non-negative matrix **M** is called *irreducible* if for each pair [i, j] there is some $k(i, j) \in \mathbf{N}$, such that $[\mathbf{M}^{k(i,j)}]_{i,j}$ is positive.

Biologically, a population projection matrix is irreducible if and only if a path exists from every state to any other state in the corresponding (life-cycle) graph. Most population models are irreducible. Exceptions are life-cycles with post-reproductive states and spatially structured models with sources and sinks.

• A non-negative matrix **M** is called *primitive* if there is some $k \in \mathbf{N}$, such that \mathbf{M}^k is positive.

Obviously, primitive implies irreducible. Irreducible, but non-primitive projection matrices are characterized by loops in their corresponding graphs. An irreducible matrix \mathbf{M} is primitive if and only if the greatest common divisor of the loop lengths is 1. Sufficient conditions for an irreducible matrix to be primitive are (1) any self-loop (2) positive fertility of adjacent age-classes in a Leslie matrix.

• The spectral radius of a matrix \mathbf{M} is $r(\mathbf{M}) := \max_i |\lambda_i|$, where $\lambda_1, \ldots, \lambda_n$ are the eigenvalues of \mathbf{M} .

Theorem: Perron-Frobenius (Perron 1907, Frobenius 1912) Let $\mathbf{M} := (m_{ij})_{1 \le i,j \le n}$ a matrix with real, non-negative entries $m_{ij} \ge 0$. Then

- 1. M has a real leading eigenvalue $\lambda_1 = r(\mathbf{M})$ (called dominant EV). Right and left eigenvectors \mathbf{v} and \mathbf{u} corresponding to λ_1 with non-negative entries exist.
- 2. If further **M** is *irreducible*, it has a dominant EV $\lambda_1 > 0$, which is simple (has geometric and algebraic dimension one). All entries of the corresponding eigenvectors **v** and **u** are strictly positive.
- 3. Assume further that **M** is primitive. Then λ_1 is strictly dominant, i.e., larger than all other eigenvalues, $\lambda_1 > |\lambda_i|, i \neq 1$.

Proof

(a) Convergent matrices

For any (square) matrix \mathbf{M} ,

$$r(\mathbf{M}) < 1 \quad \Leftrightarrow \quad \mathbf{M}^k \to \mathbf{0} \quad \text{for } k \to \infty$$

$$\tag{80}$$

Proof: Obvious for any matrix **D** in Jordan from and $\mathbf{M}^k = \mathbf{S}\mathbf{D}^k\mathbf{S}^{-1}$ (a matrix **M** with this property is called *convergent*).

(b) Lower bound for the spectral radius

Let $\mathbf{M} \ge 0$ and $\mathbf{0} \ne \mathbf{v} \ge 0$ and $\lambda \ge 0$. Then

$$\forall i: \ [\mathbf{M}\mathbf{v}]_i = \sum_{j=1}^n m_{ij} v_j > \lambda v_i \ \Rightarrow \ r(\mathbf{M}) > \lambda \,. \tag{81}$$

Proof: $\exists \epsilon > 0$: $\mathbf{Mv} > (\lambda + \epsilon)\mathbf{v}$ (for every component). Thus

$$\mathbf{v} < \frac{\mathbf{M}}{\lambda + \epsilon} \mathbf{v} < \left(\frac{\mathbf{M}}{\lambda + \epsilon}\right)^2 \mathbf{v} < \left(\frac{\mathbf{M}}{\lambda + \epsilon}\right)^k \mathbf{v} \quad \forall k > 2$$

because \mathbf{Mv} with $m_{ij} \geq 0$ is monotonic in every component v_i . For $k \to \infty$ we see that $\mathbf{M}/(\lambda + \epsilon)$ has a lower bound and is thus not convergent. With (a) we conclude that $r(\mathbf{M}) \geq \lambda + \epsilon > \lambda$.

(c) Positivity of the leading eigenvalue and -vector

Let $\mathbf{M} > 0$ and λ_1 eigenvalue with $|\lambda_1| = r(\mathbf{M})$. Then $\lambda_1 = r(\mathbf{M})$ and any corresponding right eigenvector is strictly positive, $\mathbf{v} > 0$ (up to a common scalar factor for all entries of \mathbf{v}). The same holds for any dominant left eigenvector.

Proof: Let $\lambda_1 \mathbf{v} = \mathbf{M} \mathbf{v}$ and assume that the entries of \mathbf{v} are not collinear in the complex plane (where collinear means positive real or zero up to a common scalar factor). Then

$$|\lambda_1||v_i| = \left|\sum_{j=1}^n m_{ij}v_j\right| < \sum_{j=1}^n m_{ij}|v_j| \quad \forall i = 1, \dots, n.$$

Thus $|\lambda_1||\mathbf{v}| < \mathbf{M}|\mathbf{v}|$ (in each row) and thus $|\lambda_1| < r(\mathbf{M})$ due to (b), contradicting the assumption. Thus all entries of \mathbf{v} are collinear and can be chosen as ≥ 0 . Since

$$\sum_{j=1}^{n} m_{ij} v_j = \lambda_1 v_i$$

also λ_1 must be real and positive. Since $m_{ij} > 0$, we also have $v_i > 0 \forall i$. Proof for the left eigenvector follows by switching to \mathbf{M}^T .

(d) Geometric and algebraic dimension of the dominant eigenvalue

Let $\mathbf{M} > 0$. Then the geometric and algebraic dimension of the dominant eigenvalue $\lambda_1 = r(\mathbf{M})$ is one.

Proof: Geometric: Assume that there are two eigenvectors \mathbf{v} and \mathbf{w} corresponding to λ_1 . Then a linear combination $\mathbf{v} + \kappa \mathbf{w}$ exists with at least one component zero, contradicting (c). The proof for the left eigenvector follows again by switching to \mathbf{M}^T . Algebraic: Assume that \mathbf{w} exists, such that $(\mathbf{M} - \lambda_1 \mathbf{I})^2 \mathbf{w} = 0$, but $(\mathbf{M} - \lambda_1 \mathbf{I}) \mathbf{w} \neq 0$ (generalized eigenvector). Then $\mathbf{x} = (\mathbf{M} - \lambda_1 \mathbf{I}) \mathbf{w}$ is an eigenvector of \mathbf{M} with eigenvalue $\lambda_1 = r(\mathbf{M})$. Due to (c) we can choose $\mathbf{x} > 0$. Let $\mathbf{u} > 0$ be the dominant left eigenvector. Then we obtain a contradiction with

$$0 = \mathbf{u}^T \cdot (\mathbf{M} - \lambda_1 \mathbf{I}) \mathbf{w} = \langle \mathbf{u}; \mathbf{x} \rangle > 0.$$

Remark: c) and d) imply strict dominance of λ_1 . This completes the proof of the Perron-Frobenius Theorem for strictly positive matrices.

(e) **Primitive matrices**

Let \mathbf{M} be primitive and $\mathbf{M}^k > 0$. Let λ_1 be some eigenvalue of \mathbf{M} with $|\lambda_1| = r(\mathbf{M})$ and corresponding eigenvector \mathbf{v} . Then \mathbf{v} is also eigenvector of \mathbf{M}^k with eigenvalue $\lambda_1^k = r(\mathbf{M}^k)$. From the theorem for positive matrices we know $\mathbf{v} > 0$, thus also λ_1 is strictly dominant, real and positive and has dimension one. This proves part 3 of the Theorem.

(f) Irreducible matrices

Let \mathbf{M} be irreducible. Then $\mathbf{M} + \epsilon \mathbf{I}$ is primitive. Let $\lambda_{\epsilon} = \lambda + \epsilon$ be the strictly dominant eigenvalue of $\mathbf{M} + \epsilon \mathbf{I}$ with corresponding eigenvector \mathbf{v} . Note that \mathbf{v} does not depend on ϵ and is, in particular, also eigenvector of \mathbf{M} with eigenvalue λ . Since $\mathbf{v} > 0$, we must have $\lambda > 0$. Since $\epsilon \mathbf{I}$ just shifts the spectrum, λ has dimension one and we have $\lambda = r(\mathbf{M})$ due to continuity, but other eigenvalues $|\tilde{\lambda}| = r(\mathbf{M})$ may exist.

(g) Non-negative matrices

Let $\mathbf{M} \geq 0$ and $\epsilon > 0$. The theorem for positive matrices holds for any matrix $\mathbf{M}_{\epsilon} = (m_{ij} + \epsilon)_{1 \leq i,j \leq n}$. Let $\lambda_{\epsilon} = r(\mathbf{M}_{\epsilon})$ be the strictly dominant eigenvalue and $\mathbf{v}_{\epsilon} > 0$ the corresponding eigenvector. For $\epsilon \to 0$ we get $\mathbf{v}_{\epsilon} \to \mathbf{v} \geq 0$, where \mathbf{v} is eigenvector of \mathbf{M} with eigenvalue $\lambda = r(\mathbf{M})$. Note that λ need not be strictly dominant and its dimension need not be one.

3.1 Long term behavior

Consider the linear population dynamics

$$\mathbf{x}(t) = \mathbf{M}^t \mathbf{x}(0) \,. \tag{82}$$

Assume first that **M** is primitive. (This is the case for most models.) Then there is a strictly dominant eigenvalue $\lambda_1 = r(\mathbf{M})$ with positive left and right eigenvectors \mathbf{u}_1 and \mathbf{v}_1 . We can normalize these according to $\|\mathbf{v}_1\| = 1$ and $\langle \mathbf{u}_1; \mathbf{v}_1 \rangle = 1$. We then have

$$\left(\frac{\mathbf{M}}{\lambda_1}\right)^t \longrightarrow \mathbf{v}_1 \otimes \mathbf{u}_1^T \quad \text{for } t \to \infty.$$
 (83)

If **M** can be diagonalized with eigenvalues $\{\lambda_i\}_i$, and corresponding sets of left and right eigenvectors, $\{\mathbf{u}_i\}_i$ and $\{\mathbf{v}_i\}_i$, respectively, with $\langle \mathbf{u}_i; \mathbf{v}_j \rangle = \delta_{ij}$. Then

$$\mathbf{M}^{t} = \sum_{i=1}^{n} \lambda_{i}^{t} \mathbf{v}_{i} \otimes \mathbf{u}_{i}^{T} \,.$$
(84)

Proof. Let **U** be the orthogonal complement of the vector \mathbf{u}_1^T . Note that **M** maps **U** onto itself. Let \mathbf{M}' be the restriction of \mathbf{M} to \mathbf{U} . Then the spectral radius of \mathbf{M}'/λ_1 is smaller than one, and the matrix hence convergent. Since \mathbf{v}_1 is not orthogonal to \mathbf{u}_1 we can chose \mathbf{v}_1 and any basis of **U** as basis of the full vector space. The proof follows from the action of $(\mathbf{M}/\lambda_1)^t$ on this basis in the limit $t \to \infty$. The proof of (84) is analog, using the pairwise orthogonality of sets of left and right eigenvectors. It also holds if **M** is not primitive.

Consequences.

• For any population vector $\mathbf{x}(0)$ and any irreducible matrix \mathbf{M} observe that $\langle \mathbf{u}_1; \mathbf{x}(0) \rangle > 0$. For any primitive matrix \mathbf{M} we then obtain the long-term growth rate

$$r_{\infty} = \lim_{t \to \infty} \frac{\|\mathbf{x}(t+1)\|_{1}}{\|\mathbf{x}(t)\|_{1}} = \lambda_{1} \lim_{t \to \infty} \frac{\|(\mathbf{M}/\lambda_{1})^{(t+1)}\mathbf{x}(0)\|_{1}}{\|(\mathbf{M}/\lambda_{1})^{t}\mathbf{x}(0)\|_{1}} = \lambda_{1}.$$
 (85)

• The limit distribution reads

$$\lim_{t \to \infty} \frac{\mathbf{x}(t)}{\|\mathbf{x}(t)\|_1} = \mathbf{v}_1 \,. \tag{86}$$

For age structured models, this is also called a stable age structure.

• We can estimate the rate at which the limit distribution is approached by considering the second largest eigenvalue $|\lambda_2|$, as follows

$$r_t = r_\infty + C(\mathbf{x}(0)) \left| \frac{\lambda_2}{\lambda_1} \right|^t \tag{87}$$

with a constant C that depends on the initial conditions. An analog results holds for the limit distribution.

- For any irreducible, but periodic matrix, Eq. (85) still holds, but there is no unique limit distribution (86). We can still characterize the long-term behavior by considering all eigenvectors to eigenvalues $|\lambda_i| = r(\mathbf{M})$ and their linear combinations.
- For reducible matrices, we first try to identify absorbing states or subspaces and then consider the dynamics on irreducible subsystems defined by this absorbing states and their complements.

3.2 Eigenvalues of Leslie matrices

In general, it is difficult (or impossible) to derive the eigenvalues and eigenvectors of highdimensional matrices. For the special form of the Leslie matrix, however, this is simplified. Here, we have from $\mathbf{L}\mathbf{x} = \lambda \mathbf{x}$,

$$p_1 x_1 = \lambda x_2 \quad \Rightarrow \quad x_2 = \frac{p_1}{\lambda} x_1$$
 (88)

$$p_2 x_2 = \lambda x_3 \quad \Rightarrow \quad x_3 = \frac{p_2}{\lambda} x_2 = \frac{p_1 p_2}{\lambda^2} x_1$$
(89)

$$p_{n-1}x_{n-1} = \lambda x_n \quad \Rightarrow \quad x_n = \frac{p_{n-1}}{\lambda} x_{n-1} = \frac{p_1 \cdots p_{n-1}}{\lambda^{n-1}} x_1 \tag{90}$$

We thus have

$$\lambda x_1 = f_1 x_1 + \ldots + f_n x_n \tag{91}$$

$$= x_1 \left(f_1 + f_2 \frac{p_1}{\lambda} + f_3 \frac{p_1 p_2}{\lambda^2} + \ldots + f_n \frac{p_{n-1} \cdots p_1}{\lambda^{n-1}} \right).$$
(92)

If we define the probability for a newborn to survive until age i as $l_1 = 1$ and $l_i = p_1 \cdots p_{i-1}, i > 1$, we obtain the so-called Euler-Lotka equation

$$1 = \sum_{i=1}^{n} f_i l_i \lambda^{-i} =: \phi(\lambda) .$$
(93)

The Euler-Lotka equation relates the asymptotic growth rate (also called the fitness of an individual) to the life-history parameters f_i and p_i (or l_i). It is easy to see that the expression on the right-hand-side is strictly monotonically decreasing. We thus obtain exactly one solution for a real eigenvalue $\lambda = r(\mathbf{L})$. One can further show that Leslie matrices are always diagonalizable; all other eigenvalues are complex. There is still no general explicit solution for λ_1 , but we can at least determine whether $\lambda_1 > 1$ (the population is growing) or $\lambda_1 < 1$ (shrinking) population. For this, define the life-time reproductive success $R_0 = \sum_i f_i l_i$. We see that R_0 is the value of the Euler-Lotka equation at $\lambda = 1$. From the shape of the graph, we immediately see that $\lambda_1 > 1 \Leftrightarrow R_0 > 1$ (which makes intuitive sense). Once we know λ , it is easy to obtain the corresponding eigenvector

$$\mathbf{v}_1 = \left(\frac{l_1}{\lambda_1}, \frac{l_2}{\lambda_1^2}, \dots, \frac{l_n}{\lambda_1^n}\right)^T \tag{94}$$

3.3 Application: Life history evolution

Typical problems of life history theory are as follows:

- Why do we age? Why are there widely different life spans among species?
- At a given age class: is it better to invest into survival or into reproduction?
- Is it better to have many offspring once or fewer offspring more often during life?

All these problems ask why certain life-history parameters in a Leslie matrix take their given values. We can try and approach this problem from an evolutionary point of view: Consider a resident population that is characterized by a certain set of life-history parameters. Assume now that a mutant appears in this population with a different set of parameters. We can always ask: Will the mutant replace the resident? To answer this question, we first need to know how individuals of different types compete and how population regulation is included into our framework of structured models. Since this leads to non-linear models, this can be very complicated, indeed! So simplify things, we will assume here that population regulation occurs in an independent step and affects all individuals in the same way, i.e.,

$$\mathbf{x}(t) \rightarrow \mathbf{x}(t+1/2) = \mathbf{L}\mathbf{x} \rightarrow \mathbf{x}(t+1) = f(N)\mathbf{x}(t+1/2)$$
(95)

where $N = \sum_{i} x_{i}$ is the total population size and f(N) takes care of density regulation. For example we could have

$$f(N) = \frac{1}{1+cN} \,. \tag{96}$$

This scheme has two important properties

- 1. First, since density regulation acts only as a factor on the population vector, it does not alter the distribution. In the long term, we will thus reach the same stable age distribution as with the linear model.
- 2. Assume now that this stable age distribution has been reached. We then have

$$N(t+1) = \lambda N(t) \cdot f(N(t)) \tag{97}$$

where λ is the long-term growth rate of the linear model.

We thus can separate our problem and treat both parts (age distribution and density regulation) independently. Indeed, this is also the reason why models without age structure make some sense at all. We simply assume (implicitly) that a stable age distribution has been reached. Now, what will happen with a rare mutant in such a case? (We assume no recurrent mutation)

• A mutant will start its own clone and both clones will reach a stable age distribution. Since they are subject to joint density regulation, the clone with the higher limiting growth rate (higher fitness) will win and displace the other type.

Example: Iteroparous versus semelparous reproduction Why do many plants and some animals reproduce only once in their lifetime and then die (semelparous reproduction), while others reproduce multiple times (iteroparous reproduction)? – In principle, being able to reproduce multiple times is of course be an advantage and should be selected. However, there may be a cost: concentration on a single reproduction event could increase the expected litter size. In a much simplified version, compare two strategies:

- 1. On the one hand, consider an immortal iteroparous clone with fertility f_{it} every season.
- 2. On the other hand, consider a semel parous clone, where individuals reproduce after the first season with fertility f_{sem} and then die.

How large must f_{sem} be that the semelparous clone matches the growth rate of the iteroparous clone? (Assume that all our results can be extended to infinite dimensional matrices in this case.)

• Iteroparous: Euler-Lotka equation

$$1 = f_{\rm it} \sum_{i=1}^{\infty} \lambda^{-i} = f_{\rm it} \frac{\lambda^{-1}}{1 - \lambda^{-1}}$$

and hence $\lambda = f_{\rm it} + 1$

• Semelparous:

$$1 = f_{\rm sem} \lambda^{-1}$$

and thus $\lambda = f_{\text{sem}}$.

We thus see that only a single individual more in the first year is worth as much as eternal life and offspring every year. The question arises why there are so many iteroparous species! More generally, we can derive the predictions for an adult survival probability p_a and a juvenile survival probability p_j . Here, we assume that p_j is the probability that juveniles survive even until the first census. then p_j acts like a factor to the fertility. We obtain:

• Iteroparous:

$$1 = f_{\mathrm{it}} p_j \sum_{i=1}^{\infty} (p_a^{(i-1)} \lambda^{-i})$$

and thus $\lambda = p_a + p_j f_{it}$.

• Semelparous:

$$1 = f_{\rm sem} p_j \lambda^{-1}$$

thus $\lambda = f_{\text{sem}} p_j$.

We get equal long-term growth rates for

$$f_{\rm sem} = f_{\rm it} + \frac{p_a}{p_j} \,.$$

This leads to the prediction that species with a higher ratio of adult / juvenile survival probability should more likely be iteroparous (or have more breeding seasons, on average). This is, indeed, confirmed by data.

3.4 Reproductive values and sensitivity analysis

How important are the different (age-)classes for the population growth? Or: How much does an individual in the initial population contribute to future population growth? We have

$$\mathbf{x}(t) \approx \lambda^t \mathbf{v} \sum_i u_i x_i(0) \tag{98}$$

where \mathbf{v} is the leading right eigenvector and u_i are the entries of the leading left eigenvector. We thus see that the u_i are weighting factors that determine the importance of age-class i for future population growth. They are called *reproductive values*. For the Leslie matrix, we can derive the reproductive values as follows. Let u_1 be the reproductive value of newborns. In the distant future, the clones started from any individual at time zero will grow with factor λ per time step. But initially, the relative growth rates are different. We can relate the size of a clone started from an individual in age class i to the size of a clone started from a newborn as follows:

$$u_{i} = \left(\frac{f_{i}}{\lambda} + \frac{l_{i+1}}{l_{i}}\frac{f_{i+1}}{\lambda^{2}} + \frac{l_{i+2}}{l_{i}}\frac{f_{i+2}}{\lambda^{3}} + \dots + \frac{l_{n}}{l_{i}}\frac{f_{n}}{\lambda^{n-i+1}}\right)u_{1}$$
(99)

$$= \frac{\lambda^{i-1}}{l_i} \sum_{j=i}^n l_j f_j \lambda^{-j} u_1 \,. \tag{100}$$

The factors λ^j in the denominator accounts for the delay of j time steps for the newborn offspring individuals produced by our focal individual in age class i. Note that the equation for u_1 , in particular, reproduces the Euler-Lotka equation. With the choice $u_0 = \lambda$, we have

$$u_i = \frac{\lambda^i}{l_i} \sum_{j=1}^n l_j f_j \lambda^{-j} \tag{101}$$

Typically, the reproductive value increases until an individual reaches maturity and then decreases. For post-fertility age-classes it is zero. Reproductive values also tell us how severe perturbations in the number of individuals in a given age class are for future population dynamics (relevant for population management). Another use of the reproductive value is in sensitivity analysis.
Sensitivity analysis In general, we can ask, which demographic parameter "matters most" for the long-term growth rate. In an evolutionary perspective, this corresponds to the parameters that experience the strongest selection pressure. For a general projection matrix $\mathbf{M} = (m_{ij})_{1 \le i,j \le n}$, the answer is given by the so-called sensitivities

$$s_{ij} := \frac{\partial \lambda}{\partial m_{ij}} \,. \tag{102}$$

Frequently, sensitivities are measured on a scale of relative change rather then absolute change. We then obtain the so-called elasticities

$$e_{ij} := \frac{\partial \log \lambda}{\partial \log m_{ij}} = \frac{m_{ij}}{\lambda} s_{ij} \,. \tag{103}$$

With

$$\lambda = \frac{\mathbf{u}^T \cdot \mathbf{M} \mathbf{v}}{\mathbf{u}^T \cdot \mathbf{v}} \tag{104}$$

we simply get

$$s_{ij} = \frac{u_i v_j}{\mathbf{u}^T \cdot \mathbf{v}} \,. \tag{105}$$

In general, if several entries of the projection matrix depend on some model parameter x, $m_{i,j} = m_{i,j}(x)$, we obtain the sensitivity with respect to any such x as a linear combination of the s_{ij} ,

$$s_x = \frac{\partial \lambda}{\partial x} = \sum_{i,j} s_{ij} \cdot \frac{\partial m_{i,j}}{\partial x} \,. \tag{106}$$

For Leslie matrices $\mathbf{M} = \mathbf{L}$, we have

$$\mathbf{u}^T \cdot \mathbf{v} = \sum_{k=1}^n \sum_{j=k}^n l_j f_j \lambda^{-j} = \sum_{k=1}^n k f_k l_k \lambda^{-k}$$
(107)

and hence

$$s_{ij} = \frac{(l_j/l_i)\lambda^{i-j}\sum_{k=i} l_k f_k \lambda^{-k}}{\sum_{k=1}^n k \, l_k f_k \lambda^{-k}} \,.$$
(108)

In particular, this gives

$$\frac{\partial \lambda}{\partial f_j} = s_{1j} = \frac{l_j \lambda^{1-j}}{\sum_{k=1}^n k \, l_k f_k \lambda^{-k}} \tag{109}$$

and

$$\frac{\partial \lambda}{\partial p_j} = s_{j+1,j} = \frac{(l_j/l_{j+1})\lambda \sum_{k=j+1}^n l_k f_k \lambda^{-k}}{\sum_{k=1}^n k \, l_k f_k \lambda^{-k}}.$$
(110)

We can make the following observations

• Early-in-life fecundities are under stronger selection than late-in-life fecundities (for $\lambda \geq 1$).

- Also selection on viabilities monotonically decreasing and only > 0 as long as the fertility later in life is still positive. As a consequence, we have weak sekection against deleterious mutations with an effect late in life: evolutionary explanation for senescence and death.
- Assume that there is a trade-off between viability and fecundity at age i. We have

$$\left(\frac{\partial\lambda}{\partial p_j}\right) / \left(\frac{\partial\lambda}{\partial f_j}\right) = u_j / \lambda \tag{111}$$

Thus, age classes with high reproductive value should invest more into survival than age classes with low reproductive value. In particular, survival at maturity is more strongly selected than survival of newborns.

3.5 Other formalisms to model population structure

We have discussed in some detail the projection matrix approach to population structure. This formalism works in discrete time and it assumes that the population can be structured into discrete classes. Both of these assumptions are convenient, but analogous approaches, which do not make these assumptions also exist. This leads either to so-called *Lotka integral equation* or to the *McKendrick-von Foerster partial differential equation*. Similar to the matrix approach, both formalisms allow for (partial) solutions as long as the dynamics is linear. In general, also similar conclusions can be drawn.

4 Dynamics of interacting populations

So far, we have considered the dynamics of a single species. However, the major part of ecology is really about interactions of species that live in the same ecosystem. And even if we are only interested in a single species, we need to take into account that its dynamics in nature will crucially be influenced by the presence (or absence) of other species. Whenever these other species dynamics on a similar time scale, we need to include them into the model. For a pair of species, there are three basic types of interactions:

- 1. **Competition** (e.g. for food or for nesting sites). Presence of individuals from the other species reduces population growth.
- 2. Mutualism. Both species profit from the presence of the respective other species. Typical examples are plant-pollinator interactions, or seed-dispersal systems, where plants produce fruit to reward animal-aided dispersal. Another class are the interactions of endosymbionts (bacteria, fungi) and their hosts (most animals).
- 3. Host-parasite or predator-prey. Asymmetric consequences of the interactions. Presence of the host/prey is good for the predator but not vice-versa.

In these scenarios, the density regulation for a given species will typically not only depend on the total density of individuals across all species, but on the individual densities of all species: for a predator it will matter a lot whether other individuals around are prey or rather competing predators. We therefore cannot use the simplistic modeling scheme of the previous section, where we have assumed that density regulation depends only on the total number of all individuals (in various age classes) and affects all these individuals in the same way. We will therefore introduce a new class of models for the population dynamics of interacting species. We will use the formalism in continuous time, which leads to coupled ordinary differential equations. Let $x_i(t)$ be the density of species *i* at time *t* and $1 \leq i \leq n$. Then

$$\dot{x}_i(t) := f_i(x_1(t), x_2(t), \dots, x_n(t))$$
(112)

with f_i continuously differentiable on some subset of \mathbb{R}^n . Collectively, we can write

$$\dot{\mathbf{x}}(t) = \mathbf{f}(\mathbf{x}(t)) \tag{113}$$

defining a time-homogeneous, coupled, first-order ODE system. There is a unique solution for each initial condition \mathbf{x} , which can be represented as a line $\mathbf{x}(t)$ in the phase space, where $\mathbf{f}(\mathbf{x})$ are tangent vectors to $\mathbf{x}(t)$ defining the velocity of the dynamics. In this notation, $\mathbf{x}(t), \mathbf{y}(t)$ etc. are solutions of a system of differential equations $\dot{\mathbf{x}} = f(\mathbf{x})$ with the same f, but with different initial conditions \mathbf{x} and \mathbf{y} . In general, solutions need not exist for all times t (but only for an open time interval). However, if the dynamics keep $\mathbf{x}(t)$ in a compact set, the solution exists for all times $-\infty < t < \infty$. Since population densities are non-negative and also won't increase without bounds, this is always the case for a meaningful biological model.



Figure 4: Phase space with vector field for the Lotka-Volterra predator-prey model ($r_x = 1$, $c_x = -10^{-4}$, $c_{xy} = -10^{-4}$, $r_y = -0.05$, $c_y = -10^{-5}$, $c_{yx} = 10^{-5}$) with solutions for various starting conditions.

4.1 Lotka-Volterra model

As our main example, we will consider interactions between two species, x(t) and y(t), following the Lotka-Volterra dynamics,

$$\dot{x} = f_x(x, y) = r_x x + c_x x^2 + c_{xy} x y$$
, (114a)

$$\dot{y} = f_y(x, y) = r_y y + c_y y^2 + c_{yx} y x$$
. (114b)

The model has the following properties:

- r_x and r_y describe the intrinsic growth rates of both species while rare and in the absence of the other species. These growth rates can be positive or negative, for example for a predator in the absence of prey or for two mutualists that crucially depend on each other.
- The constants c_x and c_y describe the consequences of within-population interactions. These are usually (but not always) dominated by competition, such that c_x and c_y are negative.
- If the interaction parameter c_{xy} (or c_{yx}) is zero, the x (or y) population follows a single-species dynamics. With $c_x = -r_x/K_x$ (resp. $c_y = -r_y/K_y$), we obtain 1-dim. logistic growth.

- In general, the sign of the interaction parameters determines the type of the biological interaction:
 - 1. For $c_{xy}, c_{yx} < 0$ we obtain a competition model;
 - 2. $c_{xy} < 0$ and $c_{yx} > 0$ corresponds to an x-host-y-parasite (or x-prey-y-predator) model;
 - 3. finally, $c_{xy}, c_{yx} > 0$ indicates mutualism.
- The classical Lotka-Volterra model has $r_x > 0$, $r_y < 0$, $c_x = c_y = 0$, $c_{xy} < 0$, and $c_{yx} > 0$. It was designed in the 1920's by Vito Volterra to describe the increased percentage of sharks and rays among all caught fish in the Adriatic Sea after fishing had been interrupted for multiple years due to WW1. The equations were independently derived and analyzed by Alfred Lotka (from Lemberg, Austria-Hungary).

4.2 Equilibria

All points \mathbf{x}^* with $\dot{\mathbf{x}}^* = \mathbf{0}$ are called equilibrium points (or fixed points, rest points, stationary states) of the dynamics. For example, the Lotka-Volterra model has a trivial equilibrium at $\mathbf{x} = 0$. In general, we consider the so-called *isoclines*. The x_i -isocline is the set of all points where $\dot{x}_i = 0$, i.e. where the vector field is vertical to the x_i axis. For the Lotka-Volterra model, we obtain:

• *x*-isocline for $f_x(x, y) = 0$:

$$x = 0$$
 and $y = -\frac{r_x + c_x x}{c_{xy}}$ (115)

• y-isocline for $f_y(x, y) = 0$:

$$y = 0$$
 and $y = -\frac{r_y + c_{yx}x}{c_y}$ (116)

The equilibria are given by the intersections of the x- and y-isoclines (in general: of all x_i -isoclines). We obtain:

$$(x_1^*, y_1^*) = (0, 0)$$
; $(x_2^*, y_2^*) = (0, -r_y/c_y)$; $(x_3^*, y_3^*) = (-r_x/c_x, 0)$ (117)

$$(x_4^*, y_4^*) = \left(\frac{c_{xy}r_y - c_yr_x}{c_xc_y - c_{xy}c_{yx}}, \frac{c_{yx}r_x - c_xr_y}{c_xc_y - c_{xy}c_{yx}}\right).$$
(118)

Only equilibrium points with $x_i^*, y_i^* \ge 0$ are attainable and make biological sense. With this information about equilibria and isoclines, we already obtain a qualitative graphical representation of the dynamics in the phase plane. For concreteness, we consider the predator-prey case with $r_x > 0$, $r_y < 0$, $c_x, c_y < 0$, $c_{xy} < 0$, and $c_{yx} > 0$. We see that the (second part of the) x-isocline is monotonically decreasing, starting from $(0, |r_x/c_{xy}|)$ on the y-axis. The second part of the y-isocline is monotonically increasing, starting from the unbiological equilibrium $(0, -|r_y/c_y|)$ on the negative y-axis. It intersects with the x-axis at $\hat{x} = -r_y/c_{yx} > 0$. There are two fundamentally different dynamical regimes.

- For $\hat{x} > x_3^* = -r_x/c_x > 0$, the x and y isoclines intersect in the negative-y half plane and the forth equilibrium point (x_4^*, y_4^*) is unbiological (and cannot be reached from positive starting values). Adding schematic velocity arrows to the various regions of the phase plane, we quickly see that $(x_3^*, y_3^*) = (-r_x/c_x, 0)$ is the only stable equilibrium of the dynamics: predators cannot be maintained and die out.
- For $\hat{x} < x_3^*$, the x and y isoclines intersect for positive y and the forth equilibrium point (x_4^*, y_4^*) is biologically meaningful. Adding velocity arrows to the phase plane, we see that (x(t), y(t)) trajectories will oscillate around this point, but it remains unclear whether the equilibrium is stable or unstable. A more detailed analysis is needed.

4.3 Stability

Extending the one-dimensional case, we define:

• A fixed point \mathbf{x}^* of an ODE $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ is (Lyapunov) stable iff, for any $\epsilon > 0$ there is a $\delta > 0$, such that

 $\mathbf{x}(0) \in \mathcal{B}(\mathbf{x}^*, \delta) \quad \Rightarrow \quad \mathbf{x}(t) \in \mathcal{B}(\mathbf{x}^*, \epsilon)$

for all $t \ge 0$.

• A fixed point is asymptotically stable iff it is stable and

$$\lim_{t \to \infty} |\mathbf{x}(t) - \mathbf{x}^*| = 0$$

for all $\mathbf{x}(0) \in \mathcal{B}(\mathbf{x}^*, \epsilon)$ and some $\epsilon > 0$.

- The set of points $\{\mathbf{x}\}$ with $\mathbf{x}(t) \to \mathbf{x}^*$ is called the domain (or basin) of attraction of \mathbf{x}^* . The fixed point is said to be globally attracting iff its domain of attraction is the entire state space.
- As generalization of a fixed point, we define the ω -limit of any point \mathbf{x} as the set of all accumulation points of $\mathbf{x}(t)$ for $t \to \infty$ with $\mathbf{x}(0) = \mathbf{x}$. Obviously, the ω -limit of any point in the domain of attraction of a fixed point \mathbf{x}^* is just \mathbf{x}^* . In general, ω -limits can also be empty, but this is not possible if the dynamics is confined to a compact set.
- Analogous to ω -limits, we define α -limits as accumulation points for $t \to -\infty$.

As in the one-dimensional case, we can relate stability to local properties of the dynamics in the neighborhood of a fixed point. To this end, we consider the linearized dynamics for some point $\mathbf{x} \in \mathcal{B}(\mathbf{x}^*, \epsilon)$ according to a Taylor expansion

$$f_i(\mathbf{x}) = f_i(\mathbf{x}^*) + \left(\frac{\partial f_i}{\partial x_1}\Big|_{\mathbf{x}=\mathbf{x}^*}, \dots, \frac{\partial f_i}{\partial x_n}\Big|_{\mathbf{x}=\mathbf{x}^*}\right) \cdot (\mathbf{x} - \mathbf{x}^*) + \mathcal{O}[\epsilon^2]$$
(119)

and

$$\mathbf{f}(\mathbf{x}) = \mathbf{f}(\mathbf{x}^*) + \mathbf{J} \cdot (\mathbf{x} - \mathbf{x}^*) + \mathcal{O}[\epsilon^2]$$
(120)

with the Jacobian matrix

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \cdots & \frac{\partial f_1}{\partial x_n} \\ \vdots & & \vdots \\ \frac{\partial f_n}{\partial x_1} & \cdots & \frac{\partial f_n}{\partial x_n} \end{pmatrix} \Big|_{\mathbf{x} = \mathbf{x}^*}$$
(121)

For a fixed point, we have $\mathbf{f}(\mathbf{x}^*) = \mathbf{0}$ and defining $\mathbf{y} := \mathbf{x} - \mathbf{x}^*$ we obtain the local linear map

$$\dot{\mathbf{y}} = \mathbf{J}\mathbf{y} \,. \tag{122}$$

Linear ODE's Linear differential equations are not capable of describing meaningful interactions among species. However, as we have seen, any ODE system can be approximated by a linear system locally around a fixed point. It is therefore worthwhile to consider the linear dynamics. Let

$$\dot{\mathbf{x}} = \mathbf{J}\mathbf{x} \,. \tag{123}$$

with real-valued $n \times n$ matrix **J**. Then the solution can be written as

$$\mathbf{x}(t) = \exp\left[\mathbf{J}t\right]\mathbf{x}(0) \tag{124}$$

with the matrix exponential

$$\exp\left[\mathbf{J}t\right] = \mathbf{I} + \mathbf{J}\frac{t}{1!} + \mathbf{J}^2\frac{t^2}{2!} + \cdots$$
(125)

Eigenvalues of \mathbf{J} can either be real or occur in complex conjugate pairs. Note that if λ is an eigenvalue of \mathbf{J} with corresponding eigenvector \mathbf{v} , then \mathbf{v} is also an eigenvector of $\exp[\mathbf{J}t]$ with eigenvalue $\exp[\lambda t]$. Representing $\mathbf{x}(0)$ as linear combination of (generalized) eigenvectors of \mathbf{J} , we see that the components $x_i(t)$ of the solution $\mathbf{x}(t)$ can be written as linear combinations of the following functions:

- (i) $\exp[\lambda t]$ whenever λ is a real eigenvalue of **J**.
- (ii) $\exp[at]\cos[bt]$ and $\exp[at]\sin[bt]$ whenever $a \pm ib$ are eigenvalues of **J**.
- (iii) $t^j \exp[\lambda t]$, or $t^j \exp[at] \cos[bt]$ and $t^j \exp[at] \sin[bt]$, with $0 \le j < m$, whenever the eigenvalue λ or the eigenvalue $a \pm ib$ occurs with (algebraic) multiplicity m.

Obviously, $\mathbf{x}^* = \mathbf{0}$ is a fixed point of the linear ODE (the only one if det $\mathbf{A} \neq 0$). We can note that positive real parts in the eigenvalues ($\lambda > 0$ or a > 0) of \mathbf{J} lead to components in $\mathbf{x}(t)$ that diverge away from $\mathbf{0}$, while negative real parts lead to components that vanish in the limit $t \to \infty$. Any imaginary part $b \neq 0$ leads to oscillations, which are damped if and only if a < 0. We can define the following types of fixed points:

• A fixed point is called *hyperbolic* if none of the eigenvalues has zero real part. A hyperbolic fixed point is...

1. A sink if the real parts of all eigenvalues are negative. In this case,

$$\lim_{t \to \infty} \mathbf{x}(t) = \mathbf{0} \tag{126}$$

for any starting vector $\mathbf{x}(0)$. Hence, $\mathbf{0}$ is globally stable (the ω -limit of every point). A sink can be either a *stable node* (all eigenvalues real) or a *stable spiral/sink focus* (some eigenvalues complex).

- 2. A source if the real parts of all eigenvalues are positive. In this case any orbit $\mathbf{x}(t)$ grows exponentially and $\mathbf{0}$ is the α -limit of every point. A source can be either an *unstable node* (all eigenvalues real) or an *unstable spiral/source-focus* (some eigenvalues complex).
- 3. A saddle point if some eigenvalues have positive real parts and some have negative real parts, but none are on the imaginary axis. The points with ω -limit **0** and the points with α -limit **0** each form a linear submanifold of \mathbb{R}^n , called the stable and unstable manifold, respectively, which together span \mathbb{R}^n . Sometimes, saddle points are also further characterized, for example by attaching the word "focus" when there are complex eigenvalues. However, this is only possible in more than two dimensions.
- Eigenvalues on the imaginary axis correspond to degenerate solutions. In particular, an eigenvalue $\lambda = 0$ leads to a manifold of fixed points and a purely imaginary eigenvalue to a manifold of periodic orbits.
- Hyperbolic eigenvalues are structurally stable in the sense that small changes of the parameters lead to (only) small changes of the equilibrium structure. In contrast, non-hyperbolic equilibria are structurally unstable with respect to any perturbation that introduces a small component on the real axis.

Two-dimensional systems. A classification of fixed points depends on the roots of the characteristic polynomial. For a real-valued two-dimensional matrix

$$\mathbf{A} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \tag{127}$$

this can be written in terms of the trace and the determinant as

$$\lambda^2 - \lambda \operatorname{tr}[\mathbf{A}] + \det[\mathbf{A}] \tag{128}$$

and hence

$$\lambda_{1,2} = \frac{\operatorname{tr}[\mathbf{A}] \pm \sqrt{\operatorname{tr}[\mathbf{A}]^2 - 4 \operatorname{det}[\mathbf{A}]}}{2} \,. \tag{129}$$

According to the so-called *Routh-Hurwitz criterion*, we have

 $\operatorname{Re}(\lambda_{1,2}) < 0 \quad \Leftrightarrow \quad \operatorname{tr}[\mathbf{A}] < 0 \quad \text{and} \quad \det[\mathbf{A}] > 0$ (130)



Figure 5: Classification of the asymptotic equilibrium behavior of 2-dim linear ODE systems. For each part of the trace-determinant space, the figure displays the location of eigenvalues in the complex plane (real part on the x-axis and imaginary part on the y-axis) and a representative phase portrait. Modified from http://www.augustana.ualberta.ca/ hackw/mat332/exhibit/fxdpt2d.html.

(proof immediate). Further, both roots will be real if and only if $tr[\mathbf{A}]^2 \ge 4 \det[\mathbf{A}]$. We obtain a full classification of possible equilibria of the linear system (Fig. 5).

So far, we have derived a classification framework for equilibria in linear systems of ODEs. The *Hartman-Grobman theorem* guarantees that this classification can also be used to characterize the fixed points of nonlinear ODE system. In particular,

- A fixed point is a sink if all eigenvalues of the corresponding Jacobian have negative real parts. In this case, the fixed point is asymptotically stable.
- Any eigenvalue of the Jacobian with strictly positive real part leads to an unstable fixed point.
- For fixed points, where some (or all) eigenvalues of the Jacobian have real part zero, and all others negative real parts, the Hartman-Grobman theorem does not apply and stability depends on higher order terms.

With this, we can now apply this classification framework to equilibria in the Lotka-Volterra model.



Figure 6: The three isocline configurations for the Lotka-Volterra predator-prey model. (a) Isoclines do not intersect. The point $(-r_y/c_{yx})$ equilibrium is globally stable. (b) Isoclines intersect but prey grows exponentially in the absence of the predator. The interior equilibrium is neither a sink nor a source but a center. The whole interior of the phase plane is filled with periodic orbits (hatched lines). (c) Isoclines intersect. The interior equilibrium (x^*, y^*) is globally stable.

4.4 Stability for the Lotka-Volterra model

We consider the general Lotka-Volterra model. We have the Jacobian

$$\mathbf{J} = \begin{pmatrix} \frac{\partial f_x}{\partial x} = r_x + 2c_x x + c_{xy} y & \frac{\partial f_x}{\partial y} = c_{xy} x \\ \frac{\partial f_y}{\partial x} = c_{yx} y & \frac{\partial f_y}{\partial y} = r_y + 2c_y y + c_{yx} x \end{pmatrix}$$
(131)

which can be analyzed for arbitrary parameters. We will discuss the three models for the basic biological interactions in turn.

Predator-prey We start with the predator-prey model, defined by $c_{xy} < 0$ and $c_{yx} > 0$. We assume logistic growth of the prey with $r_x > 0$ and $c_x = -r_x/K_x < 0$. The predator cannot grow on its own. Thus $r_y < 0$. For computational simplicity, we chose $c_y = 0$. For the trivial fixed point (0, 0), we obtain

$$\mathbf{J}(\mathbf{x}_1^*) = \begin{pmatrix} r_x & 0\\ 0 & r_y \end{pmatrix}.$$
 (132)

It is thus a saddle point and unstable. The second fixed point is unbiological. For the third one,

$$\mathbf{J}(\mathbf{x}_3^*) = \begin{pmatrix} -r_x & -r_x c_{xy}/c_x \\ 0 & r_y - r_x c_{yx}/c_x \end{pmatrix},\tag{133}$$

with eigenvalues $-r_x < 0$ and $r_y - r_x c_{yx}/c_x$. This fixed point is stable if and only if

$$K_x = \left| \frac{r_x}{c_x} \right| < \left| \frac{r_y}{c_{yx}} \right| \,. \tag{134}$$



Figure 7: Bifurcation diagram for the prey x^* and predator y^* equilibrium density with bifurcation parameter $K = -r_x/c_x$. Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria. At $K_x = -r_y/c_y$ a transcritical bifurcation occurs.

This means that the prey carrying capacity is too small to satisfy the needs of the predator, which will then die out. For the fourth equilibrium

$$\mathbf{x}_{4}^{*} = \left(-\frac{r_{y}}{c_{yx}}, -\frac{c_{yx}r_{x} - c_{x}r_{y}}{c_{xy}c_{yx}}\right)$$
(135)

we have

$$\mathbf{J}(\mathbf{x}_{4}^{*}) = \begin{pmatrix} -c_{x}r_{y}/c_{yx} & -c_{xy}r_{y}/c_{yx} \\ -(c_{yx}r_{x} - c_{x}r_{y})/c_{xy} & 0 \end{pmatrix}.$$
 (136)

We have $\operatorname{tr}[\mathbf{J}] = -c_x r_y / c_{yx} < 0$ and

$$\det[\mathbf{J}] = -\frac{r_y(c_{yx}r_x - c_xr_y)}{c_{yx}} > 0 \quad \Leftrightarrow \quad K_x = \left|\frac{r_x}{c_x}\right| > \left|\frac{r_y}{c_{yx}}\right|.$$
(137)

Using the Routh-Hurwitz criterion, we see it is stable if and only if the fixed point \mathbf{x}_3^* is unstable. This is the case if and only if there is a positive predator frequency $y_4^* > 0$. The fixed point can be either a node (for $4 \text{ det} < \text{tr}^2$) or a spiral. We get spirals for

$$\frac{|c_x|}{c_{yx}} < 2\left(\sqrt{1 + r_x/|r_y|} - 1\right),\tag{138}$$

this is, if intraspecific competition for the prey is weak (little self-regulation) relative to the predator's benefit from the prey. In the limit $c_x \to 0$, we get center-type behavior (Fig. 6b). This is the original model by Volterra. Since it is "on the boundary" between stable and unstable spirals, it is structurally unstable. Note that the prey equilibrium density depends only on growth parameters of the predator. [This holds strictly only for $c_y = 0$.] In particular, only the predator profits from increased growth (large r_x) and carrying capacity (low c_x) of the prey. This served as the explanation of the Adriatic fish-and-shark data after WW1.



Figure 8: Four possible isocline configurations in the Lotka-Volterra two-species competition model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a) Species x dominates species y. (b) Species y dominates species x. (c) Each species dominates when frequent. The interior equilibrium is a saddle point. (d) Each species increases in frequency when rare. The interior equilibrium point is asymptotically stable.

Competition With the Lotka-Volterra competition model, we have the parameters $r_x, r_y > 0$, $c_x, c_y < 0$, and $c_{xy}, c_{yx} < 0$. It is easy the determine the whole dynamics purely graphically.

- First, we have simple logistic growth for both species in the absence of the other one. This determines the dynamics on the axes with the carrying capacities $K_x = |r_x/c_x|$ and $K_y = |r_y/c_y|$ as stable equilibria.
- Second, presence of some individuals of the other species contributes to a reduction in the population size that can be maintained. We can conclude that both the xand y-isoclines have a negative slope. For the Lotka-Volterra model, both isoclines are linear.
- The x-isocline intersects the x axis at K_x . The intersection point $|r_x/c_{xy}|$ with the y axis can either be larger or smaller than K_y . Similarly, the y-isocline extends from K_y to some intersection point $|r_y/c_{yx}|$ with the x axis that may be larger or smaller than

 K_x . The direction of the flow in the various domains follows easily from extrapolation of the flow on the axes.

We obtain four different possibilities (see Fig. 8), corresponding to three different patterns:

- 1. **Dominance** If both isoclines do not cross, one species (with the higher isocline) always dominates the other. (For example: $K_x = |r_x/c_x| > |r_y/c_{yx}|$ and $|r_x/c_{xy}| > |r_y/c_y| = K_y$ for a dominating species x.)
- 2. Mutual exclusion If both isoclines intersect below the carrying capacity of the other species, both species dominate when frequent. Biologically, this is the case if competition against the other species is stronger than competition against conspecifics (weighted by intrinsic growth): $|c_{yx}/r_y| > |c_x/r_x|$ and $|c_{xy}/r_x| > |c_y/r_y|$. As a result, the intersection of both isoclines corresponds to an unstable saddle point.
- 3. Coexistence If both isoclines intersect above the carrying capacity of the other species, both species dominate when rare. We then obtain a stable equilibrium where both species coexist. Biologically, this means that competition among conspecifics is stronger than competition with the other species, $|c_{yx}/r_y| < |c_x/r_x|$ and $|c_{xy}/r_x| < |c_y/r_y|$. This is possible if both species also have their own "private" resource and only compete for some (shared) resources. We then say that each species has its own ecological niche. To this end, both species must not be "too similar" in an ecological sense. This is known as the *principle of limiting similarity* as condition for coexistence.

Mutualism See Exercise 5.

4.5 Global stability

So far, we have analyzed only the local stability of equilibria. For a full understanding of the long-term dynamics of an ODE system, we need to know the ω -limit for each point in the interior of the state space. In particular, a locally stable equilibrium point is globally stable iff it is the ω -limit of all points in (the interior of) the state space. From our graphical analysis of the LV competition scenario, it seems to be clear that asymptotic stability implies global stability whenever only a single locally stable equilibrium exists. For mutual exclusion, where two stable equilibria exist, the attraction basins of these equilibria divide the state space (a more formal proof in provided in the next chaper). In general, however, the global dynamics cannot easily be inferred from local stability properties alone, even if there is only a single stable equilibrium. For example, given our current knowledge, we cannot exclude periodic orbits (running around the stable \mathbf{x}_4^* equilibrium) for the coexistence case of the LV predator-prey model. We therefore need methods that go beyond a local analysis. In the following, we use the short-hand notation that $\mathbf{x}(t), \mathbf{y}(t)$ etc. are solutions of a system of differential equations $\dot{\mathbf{x}} = f(\mathbf{x})$ with the same f, but with different initial conditions $\mathbf{x} \equiv \mathbf{x}(0)$ and $\mathbf{y} \equiv \mathbf{y}(0)$.

Elements of ω -limits In addition to fixed points, x^* with $\dot{x}^* = 0$, ω -limits can contain various further points.

- Periodic points \boldsymbol{x} such that $\boldsymbol{x}(kT) = \boldsymbol{x}$ for some T > 0 and $k \in \mathbb{N}$, but $\boldsymbol{x}(t) \neq \boldsymbol{x}$ for 0 < t < T. Then all other points on the orbit $\boldsymbol{x}(t)$ are also periodic points and together they form a periodic orbit γ . A periodic orbit γ is called
 - *limit cycle* if $\exists x \notin \gamma$ such that $\omega(x) = \gamma$ and
 - attractor if $\omega(\mathbf{x}) = \gamma \,\forall \mathbf{x}$ in some neighborhood of γ .
- It is also possible for ω -limits to contain points that are neither fixed points nor periodic points (e.g., with chaotic behavior).

For the Lotka-Volterra model and most other biological models of interest, we do not know the full solution $\boldsymbol{x}(t)$ of the nonlinear system of ODEs. Therefore, we cannot simply obtain ω -limits as accumulation points of the solution. Fortunately, there are two results that allow us to determine (or at least to narrow down) ω -limits even without knowing the full solution. Importantly, these results also apply in cases where the Jacobian matrix has eigenvalues with zero real part such that the Hartman-Grobman theorem does not apply.

Theorem: Every ω -limit is invariant: $y \in \omega(x) \Rightarrow y(t) \in \omega(x)$.

Proof Let \boldsymbol{y} be in $\omega(\boldsymbol{x})$. Then $\boldsymbol{x}(t_k) \to \boldsymbol{y}$ for some sequence t_k . Since solutions are continuous functions of their initial condition, we have $\boldsymbol{x}(t_k + t) \to \boldsymbol{y}(t)$ for arbitrary t's and for $k \to \infty$. Therefore, $\boldsymbol{y}(t)$ belongs to $\omega(\boldsymbol{x})$.

The second result is based on the concept of Lyapunov functions. The idea is as follows. We construct a function V of \boldsymbol{x} that has a maximum at \boldsymbol{x}_4^* . Thus, the "peak of a mountain" in the plane spanned by \boldsymbol{x} is located at \boldsymbol{x}_4^* . The aim is to construct this function V such that a solution of the dynamical system under consideration can only travel in an uphill direction on this landscape. Alternatively, we can construct V in such a way that we travel always downhill and the focal equilibrium is a minimum.

Theorem: Lyapunov Let $\dot{\boldsymbol{x}} = f(\boldsymbol{x})$ be a time-independent ODE defined on some subset G of \mathbb{R}^n . Let $V: G \to \mathbb{R}$ be continuously differentiable. If the derivative \dot{V} of the map $t \to V(\boldsymbol{x}(t))$ satisfies the inequality $\dot{V} \ge 0$ (or $\dot{V} \le 0$) for all solutions $\boldsymbol{x}(t)$, then $\omega(\boldsymbol{x}) \cap G$ is contained in the set { $\boldsymbol{x} \in G : \dot{V}(\boldsymbol{x}) = 0$ } (and so is $\alpha(\boldsymbol{x}) \cap G$). In particular, if this set only contains a single point, this point is a globally stable equilibrium.

Proof Let $\boldsymbol{y} \in \omega(\boldsymbol{x}) \cap G$. Then there exists a sequence $t_k \to +\infty$ with $\boldsymbol{x}(t_k) \to \boldsymbol{y}$. Since $\dot{V} \geq 0$ along the orbit of \boldsymbol{x} , we have $\dot{V}(\boldsymbol{y}) \geq 0$ by continuity. Also by continuity, $V(\boldsymbol{x}(t_k))$ converges to $V(\boldsymbol{y})$, and hence

$$V(\boldsymbol{x}(t)) \le V(\boldsymbol{y}) \tag{139}$$

for every $t \in \mathbb{R}$. To prove the statement by contradiction, assume $\dot{V}(\boldsymbol{y}) > 0$. Since the value of V can never decrease along the orbit, this implies

$$V(\boldsymbol{y}(t)) > V(\boldsymbol{y}) \tag{140}$$

for t > 0. From $\boldsymbol{x}(t_k) \to \boldsymbol{y}$ it follows by continuity that $\boldsymbol{x}(t_k + t) \to \boldsymbol{y}(t)$ and hence

$$V(\boldsymbol{x}(t_k+t)) \to V(\boldsymbol{y}(t)).$$
 (141)

With Eq. (140) it follows that

$$V(\boldsymbol{x}(t_k+t)) > V(\boldsymbol{y}) \tag{142}$$

for k sufficiently large. This is in contradiction to Eq. (139).

Lyapunov function for the Lotka-Volterra predator-prey model Lyapunov's theorem does not tell us how to find a Lyapunov function V and unfortunately no general recipe exists. In mechanical or electrical systems, energy is often a Lyapunov function. We will now attempt to construct a Lyapunov function to determine whether or not the interior equilibrium of the LV model given by Eq. (114) is globally stable. For this, we look for a function V that has a maximum at

$$\boldsymbol{x}_{4}^{*} = (x_{4}^{*}, y_{4}^{*}) = \left(\frac{c_{xy}r_{y} - c_{y}r_{x}}{c_{x}c_{y} - c_{xy}c_{yx}}, \frac{c_{yx}r_{x} - c_{x}r_{y}}{c_{x}c_{y} - c_{xy}c_{yx}}\right).$$

We do some reverse engineering. A simple function would have the form

$$V(x,y) = aH(x) + bG(y)$$
(143)

for some a, b > 0. To get a maximum at \boldsymbol{x}_4^* , we need

$$0 = \frac{\mathrm{d}V}{\mathrm{d}x}\Big|_{\boldsymbol{x}=\boldsymbol{x}^*} = a \frac{\mathrm{d}H}{\mathrm{d}x}\Big|_{\boldsymbol{x}=\boldsymbol{x}^*} \quad , \quad 0 = \frac{\mathrm{d}V}{\mathrm{d}y}\Big|_{\boldsymbol{x}=\boldsymbol{x}^*} = b \frac{\mathrm{d}G}{\mathrm{d}y}\Big|_{\boldsymbol{y}=\boldsymbol{y}^*}.$$

Simple derivatives fulfilling these requirements are

$$\frac{\mathrm{d}H}{\mathrm{d}x} = \frac{x^*}{x} - 1$$
 and $\frac{\mathrm{d}G}{\mathrm{d}y} = \frac{y^*}{y} - 1$

resulting in

$$V(x,y) = a(x^* \ln x - x) + b(y^* \ln y - y), \qquad (144)$$

which is defined on \mathbb{R}^2_+ . Checking the second derivates shows that this choice produces indeed a maximum. Does this V do the job? The derivative of the function $t \to V(x(t), y(t))$ is

$$\dot{V}(x,y) = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y}$$
$$= a\left(\frac{x^*}{x} - 1\right)x(r_x + c_xx + c_{xy}y) + b\left(\frac{y^*}{y} - 1\right)y(r_y + c_yy + c_{yx}x)$$
(145)

Recall that the nontrivial isoclines of Eq. (114) are given by

$$r_x = -c_x x - c_{xy} y \tag{146a}$$

$$r_y = -c_y y - c_{yx} x \tag{146b}$$

and that x_4^* is the solution of Eq. (146). Thus, we can replace r_x and r_y with $-c_x x^* - c_{xy} y^*$ and $-c_y y^* - c_{yx} x^*$, respectively. This yields

$$\dot{V}(x,y) = a(x^* - x)(-c_xx^* - c_{xy}y^* + c_xx + c_{xy}y) + b(y^* - y)(-c_yy^* - c_{yx}x^* + c_yy + c_{yx}x)$$

= $-ac_x(x - x^*)^2 - bc_y(y - y^*)^2 + (ac_{xy} + bc_{yx})(x - x^*)(y - y^*).$ (147)

The sign of (147) is not obvious. However, if we choose $a = c_{yx}$ and $b = -c_{xy}$, then the last term in (147) becomes zero and we have

$$\dot{V}(x,y) = -c_x c_{yx} (x - x^*)^2 + c_y c_{xy} (y - y^*)^2 \ge 0.$$
(148)

We may therefore apply Lyapunov's theorem. The ω -limit of every orbit in \mathbb{R}^2_+ is contained in the set $K = \{(x, y) : \dot{V}(x, y) = 0\}$. We can distinguish three cases:

- 1. For $c_x, c_y < 0$, K consists only of the point \boldsymbol{x}_4^* . All trajectories in \mathbb{R}^2_+ converge to \boldsymbol{x}_4^* . This point is globally stable.
- 2. For $c_y = 0$, but $c_x < 0$ (no self limitation in the predator, the case studied above), $K = \{(x, y) \in \mathbb{R}^2_+ : x = x_4^*\}$. However, the ω -limit must be an invariant subset of K, and therefore reduces to \mathbf{x}_4^* . This point is again globally stable. The same holds for the case $c_y < 0$ and $c_x = 0$.
- 3. If both $c_y = 0$ and $c_x = 0$ (Lotka's original model in which both species are not self-regulated), we have $K = \mathbb{R}^2_+$ and thus

$$V(x(t), y(t)) = \text{const.}$$

along any orbit $\boldsymbol{x}(t)$. In this case, V is called a *constant of motion*. V has a unique maximum at \boldsymbol{x}_4^* and approaches $-\infty$ along every half-line starting at \boldsymbol{x}_4^* . The constant level sets $\{(x, y) \in \mathbb{R}^2_{>0} : V(x, y) = \text{const.}\}$ are closed curves around \boldsymbol{x}_4^* . Hence, the orbits are periodic and \boldsymbol{x}_4^* is a center (Fig. 6 b). It is neither locally nor globally stable.

In particular, we see that stable limit cycles are impossible in the LV predator-prey system. We have previously seen that this also holds for the competition model. In general, one can show also for versions of the LV model that do not have a biological interpretation:

Theorem The two-dimensional Lotka-Volterra Eq. (114) has either no periodic orbits or a continuum of periodic orbits. [For a proof see Hofbauer & Sigmund, 1998, p. 33].

5 The Dynamics of Two Interacting Populations: Beyond the Lotka-Volterra model

Many insights into the dynamics of interacting species rely on the Lotka-Volterra framework. This raises the question how reliable and general these results can be. Indeed, the model makes several rather restrictive assumptions, such as a linear dependence of per capita birth rates on the densities (e.g. no Allee effect) and no density dependence of the pair interaction parameters $(c_x, c_y, c_{xy}, c_{yx}$ do not depend on x or y). This can have unbiological consequences, e.g. for mutualism, where populations can grow without bounds for some parameter choices. In more general, we should ask for any model whether changes in the modeling assumptions can lead to qualitatively new effects.

5.1 A general two-species competition model

A general model of interacting populations (without immigration) is of the form

$$\dot{x} = x F(x, y) \tag{149a}$$

$$\dot{y} = y G(x, y), \tag{149b}$$

with continuously differentiable functions G(x, y) and F(x, y). For most natural systems it will be impossible to determine the exact functional form of F and G. It is therefore desirable to obtain results without specifying F and G but only constraining them by certain boundary conditions. Here, we follow this approach for the case of competition between two populations. We make the following assumptions:

1. Competing populations affect each others growth rates negatively. Therefore,

$$\frac{\partial F(x,y)}{\partial y} < 0$$
 and $\frac{\partial G(x,y)}{\partial x} < 0.$ (150)

2. Competition occurs due to shared resources (e.g., food, nesting sites). Here, we assume that the two competing types both require the same essential resource. Thus, if one competitor is very common both species have a negative growth rate: there exists a K > 0 so that F(x, y) < 0 and G(x, y) < 0 if x > K or y > K.

In the following we derive the qualitative dynamics of a competition model based on assumptions (1) and (2). The following statements can be made about the isoclines.

• The non-trivial *x*-isocline is given by

$$\bar{F} = \{ (x, y) \in \mathbb{R}^2_{>0} : F(x, y) = 0 \}.$$
(151)

Above \overline{F} we have $\dot{x} < 0$ and below \overline{F} we have $\dot{x} > 0$. Indeed, for x fixed, F(x, y) decreases as a function of y (cf. Eq. 150). Therefore, a vertical line through a point (x, y) intersects with \overline{F} at most once.



Figure 9: Four examples for possible isocline configurations in the general two-species competition model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a&b) Isoclines do not intersect. (b&c) Both species show an Allee effect. (d) Example with a stable interior equilibrium point P. The gray area Bis positively invariant: all orbits that cross its ordinary boundary points go into B. The isocline for the x-species is labelled \overline{F} . It passes through the equilibria that lie on the x-axis. The isocline for the y-species is labelled \overline{G} . It passes through the equilibria that lie on the y-axis.

• The non-trivial *y*-isocline is given by

$$\bar{G} = \{ (x, y) \in \mathbb{R}^2_{>0} : G(x, y) = 0 \}.$$
(152)

To the right of \overline{G} we have $\dot{y} < 0$ and to the left of \overline{G} we have $\dot{y} > 0$. For y fixed, G(x, y) decreases as a function of x (cf. Eq. 150). Therefore, a horizontal line through a point (x, y) intersects with \overline{G} at most once.

Both \bar{F} and \bar{G} are continuous. Due to our second assumption above, they both lie within the square

$$\{(x, y) : 0 \le x \le K, 0 \le y \le K\}.$$

Every orbit in $\mathbb{R}^2_{>0}$ flows into this square.

• The situation is simple if \overline{F} and \overline{G} do not intersect. Then either one or both species go extinct (Fig. 9a,b).

• Next, consider the case that \overline{F} and \overline{G} intersect finitely many times (this is the generic case). The points of intersection are equilibria of Eq. (149). The isoclines \overline{F} and \overline{G} divide $\mathbb{R}^2_{>0}$ into regions B in which the signs of \dot{x} and \dot{y} do not change. The boundary of these regions consists of equilibrium points, of segments of the coordinate axes, and of points that belong to \overline{F} or \overline{G} , but not to both. Let us call the latter ordinary boundary points.

Lemma For each region B, either all orbits passing through its ordinary boundary points enter B, or all orbits passing through its ordinary boundary points leave B.

Proof Four cases have to be distinguished: (i) $\dot{x} > 0$, $\dot{y} > 0$; (ii) $\dot{x} > 0$, $\dot{y} < 0$; (iii) $\dot{x} < 0$, $\dot{y} < 0$; (iv) $\dot{x} < 0$, $\dot{y} < 0$. Consider (ii), a region B with $\dot{x} > 0$ and $\dot{y} < 0$ (gray region in Fig. 9d). This means that B lies below \bar{F} (this is where we have $\dot{x} > 0$) and to the right of \bar{G} (this is where we have $\dot{y} < 0$). Next we consider an ordinary boundary point P. If $P \in \bar{F}$, then P is to the right of \bar{G} : the orbit through P goes vertically downwards into B. If $P \in \bar{G}$, then P is below \bar{F} : the orbit through P goes horizontally to the right into B. In this case, all orbits passing ordinary boundary points P of B go into B. The argument is analogous for the other three cases. We find that regions of type (ii) and (iii) can never be left again: they are *positive invariant*. Conversely, regions of type (i) and (iv) can never be entered from outside (*negative invariant*).

For the asymptotic behavior, we can conclude the following:

- Because the signs of x and y are constant in the interior of a region B, the ω-limit of any orbit x(t) can never be contained in the interior of a single region. In the positive invariant regions all orbits converge toward an equilibrium. In regions of type (i) and (iv), orbits either also converge to an equilibrium or they enter a positive invariant region through an ordinary boundary point. In conclusion, in the general competition model the dynamics always converges towards an equilibrium.
- Which equilibria are asymptotically stable? It is easy to see that equilibria at which both \overline{F} and \overline{G} have a negative slope with \overline{F} steeper than \overline{G} are asymptotically stable (Fig. 9d). An investigation of all other cases in which \overline{F} and \overline{G} can intersect each other shows that the only other asymptotically stable fixed point is $(K_x, 0)$ when K_x is to the right of \overline{G} and $(0, K_y)$ when K_y is above \overline{F} .
- How do ω -limits depend on initial conditions? In Fig. 9(d) point Q is a saddle point. Then exactly two trajectories, α and β , exist that approach Q. These are known as *stable manifolds* of Q or *separatrices* of Q. The separatrix α divides the unbounded region into a part with points \boldsymbol{x} with $\omega(\boldsymbol{x}) = (0, K_y)$ and a part with points \boldsymbol{x} with $\omega(\boldsymbol{x}) = P$. Thus, two points \boldsymbol{x} and \boldsymbol{x}' that are very close to each other but separated by α have different ω -lime sets.

Summarizing, we see that the qualitative dynamics of the Lotka-Volterra competition model matches the general competition model in that there are no limit cycles or chaotic orbits. However, in the general case multiple stable equilibria in the interior and on the boundary can exist. Biologically, whether species can coexist or one species goes extinct can depend on the starting conditions.

5.2 Equilibria in 2-dimensional ODEs

In the last section, we have determined which kind of equilibrium behavior can result from a general competition model. Before we try to obtain similar results for other biological scenarios, we should first get a better idea about which types of equilibria are possible at all for a 2-dimensional dynamical system. We thus assume a general ODE

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$$

on an open subset $M \subset \mathbb{R}^2$ and $f \in C^1(M, \mathbb{R}^2)$. Which kind of ω -limits can we get for such a system? In one dimension, all ω -limits are fixed points. In two dimensions, the following theorem shows that the situation is still relatively simple.

Poincaré-Bendixson Theorem Let $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$ be a time-independent 2-dimensional ODE as defined above with at most finitely many fixed points. Let $\boldsymbol{x} \in M$ and $\omega(\boldsymbol{x})$ be a non-empty, connected, and compact ω -limit set. Then one of the following applies:

- 1. $\omega(\boldsymbol{x})$ is a fixed point.
- 2. $\omega(\boldsymbol{x})$ is a periodic (or closed) orbit.
- 3. $\omega(\mathbf{x})$ consist of finitely many fixed points and orbits connecting these fixed points (with these fixed points as ω and α -limits).

We note the following

- One can easily show that for any orbit that is bounded forward in time the corresponding ω -limit is non-empty, connected, and compact. Since this should be the case for any realistic population dynamical model, the Poincaré-Bendixson Theorem will apply. For orbits that are bounded backward in time, the analogous result holds for the α -limit.
- A direct consequence of the theorem is that chaotic attractors cannot occur in two dimensions.
- The theorem can be used to demonstrate the existence of periodic orbits: if we can identify a compact *trapping region*, which can only be entered, but never left by any orbit, and if this region does not contain a fixed point, then it must contain at least one periodic orbit.

- Since a periodic orbit and its interior is a compact region that cannot be entered or left (forward and backward invariant), a fixed point must exist in the interior of each closed orbit. (Intuitively: An orbit starting from an internal point must have an ω-limit or α-limit in the interior of the region. This limit is either a fixed point or a closed orbit. If it is a closed orbit, iterate the argument.) This implies that periodic orbits can only occur around fixed points. A compact trapping region to demonstrate the existence of a periodic orbit must therefore always contain a hole (with the fixed point in it).
- One can further show that in 2d dynamical systems all isolated closed orbits are indeed limit cycles. Vice versa, closed orbits that are not isolated (center-type behavior like in the Lotka-Volterra predator-prey model) are not limit cycles.
- For two dynamical variables x_1 and x_2 with derivatives \dot{x}_1 and \dot{x}_2 given as polynomials of x_1 and x_2 with finite degree n, the question how many (isolated) limit cycles can exist is known as *Hilbert's 16th problem* and no answer is known for n > 1 (where no limit cycle can exist). For n = 2, systems with up to four limit cycles are known. For general n, it is at least known that the maximal number is always finite.
- A formal proof of the Pointcaré-Bendixson Theorem can be found, for example, in the book by Gerald Teschl *Ordinary Differential Equations and Dynamical Systems*, available form his webpage. The proof relies on the Jordan Curve Theorem, which states that any closed curve divides the plane into two disjoint sets: the interior and the exterior. Any two points in the interior can be connected by a path which never intersects the curve, but every path between interior and exterior has to cross the curve. This seems a trivial observation which, however, is very difficult to prove.
- The theorem uses that solutions of ODEs in the plain are subject to strong geometric constraints. Since the orbits can never cross (uniqueness of the solution) they can easily be trapped in the interior of some region where they can no longer escape. Since this constraint does not exist in higher dimensions, the equilibrium structure of dynamical systems in 3 or more dimensions can be much more complex (including chaotic behavior).

The first step in the analysis of a dynamical system is usually to characterize the fixed points and their stability. In simple cases, we can still do this analytically. For a full characterization of the stationary behavior, we need to account for limit cycles, which is generally a more difficult task. To exclude cycling, we can try to find a Lyapunov function, as explained above. An alternative criterion is provided by the following theorem.

Bendixson-Dulac Theorem Let $\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x})$ be an ODE defined on a simply connected set (i.e., a set without holes) $G \subset \mathbb{R}^2$. Let B be a positive scalar function defined on G. If the divergence of the vector field $B\boldsymbol{f}$,

$$\operatorname{div}[B\boldsymbol{f}](\boldsymbol{x}) = \frac{\partial Bf_1}{\partial x_1}(\boldsymbol{x}) + \frac{\partial Bf_2}{\partial x_2}(\boldsymbol{x})$$
(153)

has the same sign (strictly positive or strictly negative) on G almost everywhere, then $\dot{x} = f(x)$ admits not periodic orbits in G.

- A function B with the above property is known as *Dulac function*. For B = 1, expression (153) equals the divergence of f and is given by the trace of the Jacobian matrix. Indeed, div $f(x) \neq 0$ means that the flow defined by the ODE is *area expanding* or *contracting*, i.e., averaging over the boundary, leaves or enters every compact and simply connected set. This is not possible with a closed orbit, which defines a region that can neither be entered nor left by the flow.
- The proof of the theorem follows from *Green's theorem*, see *Hofbauer & Sigmund* for details. Note that a positive Dulac function $B(\mathbf{x})$ can always be chosen since the transformed ODE

$$\dot{\boldsymbol{x}} = B(\boldsymbol{x})\boldsymbol{f}(\boldsymbol{x})$$

has the same orbits as the original ODE, with a change in the velocity defined by B. In particular, the stationary behavior of both ODE systems is the same.

5.3 General predator-prey models and Hopf-bifurcations

In this section, we revisit predator-prey models. In the Lotka-Volterra predator-prey model isolated (and stable) limit cycles do not exist. However, predator-prey cycles seem to be common in nature. Famous examples: lynx and snowshoe hare in Canada, many populations of voles and their predators. Is the Lotka-Volterra predator-prey model missing something?

A (somewhat) general predator prey model: the Gause model

Georgy Gause was a Russian biologist who experimentally tested the Lotka-Volterra predator-prey model with protists and yeast. After he was not able to reproduce the predictions of Lotka and Volterra, he proposed modifications to original Lotka-Volterra model. (This is an interaction between theory and empiricism at its best!) As in the case of competition, it is desirable to study a predator-prey model in which not all functional forms are specified. For the Gause model, we study

$$\dot{x} = xg(x) - yf(x) \tag{154a}$$

$$\dot{y} = y(c(x) - d), \tag{154b}$$

where

- 1. g(x) is the growth rate of the prey population in the absence of predation. Selfregulation in the prey implies that there exists a $K_x > 0$ so that g(x) > 0 for $x < K_x$, $g(K_x) = 0$, and g(x) < 0 for $x > K_x$.
- 2. f(x) is the functional response of the predator, describing the effect of predation on the prey. We require that f(0) = 0 and f(x) > 0 for x > 0.



Figure 10: The three generic isocline configurations in the Gause predator-prey model. Open and filled circles indicate unstable and asymptotically stable equilibria, respectively. (a) Isoclines do not intersect. (b) Prey isocline has a negative slope at the interior equilibrium. The equilibrium is then asymptotically stable. (c) Prey isocline has a positive slope at the interior equilibrium. The equilibrium is then unstable. For the special case of the Rosenzweig-MacArthur model we prove that it is then surrounded by a stable limit cycle (dotted line). The hatched line in (b) and (c) represents the unstable manifold of the saddle point $(K_x, 0)$.

- 3. c(x) describes consumption of prey and conversion into predator individuals. c(x) may be independent of f(x). We require that c(0) = 0 and dc(x)/dx > 0 for x > 0.
- 4. *d* is the constant consumer mortality rate. There is thus no self-regulation in the predator. Indeed, the basic assumption of the Gause model is that the predator density remains low, such that its effect on the dynamics is only linear.

We can determine the isoclines for this model.

- Assume x^* exists with $c(x^*) = d$. This simply means that predators can eat enough to exist. The predator-isocline equals to the vertical line $x = x^*$ and the line y = 0 (absence of predators).
- The non-trivial part of the prey isocline $\{(x, y) \in \mathbb{R}^2_{>0} : \dot{x} = 0\}$ is determined by the equation

$$y_{\rm iso} = \frac{xg(x)}{f(x)}.$$

We have $y_{iso} \ge 0$ (in the biological parameter range) for $x \in]0, K_x]$. This function intersects the predator-isocline at $(K_x, 0)$ (the prey equilibrium in the absence of predators). Furthermore, it may have at most one intersection with the line $x = x^*$. Two scenarios are relevant:

1. $x^* > K_x$: Isoclines do not intersect (Fig. 10). Then the predator goes extinct.

2. $x^* < K_x$: Isoclines have a unique point of intersection $(x^*, y^*) \in \mathbb{R}^2_{\geq 0}$ (Fig. 10b&c). We focus on this case in the following.

The Jacobian matrix at (x^*, y^*) equals

$$\mathsf{J} = \begin{pmatrix} H(x^*) & -f(x^*) \\ y^* \frac{\mathrm{d}c(x^*)}{\mathrm{d}x} & 0 \end{pmatrix}$$

where

$$H(x) = g(x) + x \frac{\mathrm{d}g(x)}{\mathrm{d}x} - \frac{xg(x)}{f(x)} \frac{\mathrm{d}f(x)}{\mathrm{d}x}.$$
(155)

We apply the Routh-Hurwitz criterion (Eq. 130). We have det J > 0 and trace $= H(x^*)$. The point (x^*, y^*) is asymptotically stable if and only if $H(x^*) < 0$. Note that

$$\frac{\mathrm{d}}{\mathrm{d}x}\frac{xg(x)}{f(x)} = \frac{H(x)}{f(x)}.$$
(156)

Thus, $H(x^*) < 0$ if and only if

$$\left. \frac{\mathrm{d}}{\mathrm{d}x} \frac{xg(x)}{f(x)} \right|_{x=x^*} < 0.$$
(157)

- In conclusion, the interior equilibrium is a sink when the prey-isocline has a negative slope at the equilibrium and a source when the prey-isocline has a positive slope (Fig. 10b&c).
- We see from the graph (and can easily derive) that the two other equilibria, (0,0) and $(K_x, 0)$, are both are saddle points. Their stable manifolds are given by the x and y axes.
- What can we conclude for the global behavior? Consider, in particular, a point on the unstable manifold that departs from $(K_x, 0)$ (i.e., a point for which $(K_x, 0)$ is the α -limit). The orbit starting from such a point is bounded. Indeed, for a point on the manifold near $(K_x, 0)$, the prey density x is initially declining and must reach x^* at some finite value $\tilde{y} \ge y^*$. At this point, the predator density cannot increase any further and the orbit enters a region that is bounded by the axes, the unstable manifold from $(K_x, 0)$ to (x^*, \tilde{y}) and the line $y = \tilde{y}$, that cannot be left anymore. From the Pointcaré-Bendixson theorem, we conclude that there are two possibilities:
 - 1. If $\omega(\boldsymbol{x})$ contains an equilibrium point it must be (x^*, y^*) (the other two equilibrium points are out of question). In fact, then (x^*, y^*) is even globally stable because all orbits have to circle around (x^*, y^*) , but cannot intersect the unstable manifold of $(K_x, 0)$ (Fig. 10b).
 - 2. If $\omega(\boldsymbol{x})$ contains no equilibrium point, then $\omega(\boldsymbol{x})$ is a periodic orbit γ . This orbit surrounds (x^*, y^*) and is a limit cycle: since other orbit cannot cross the unstable manifold, every point in the exterior converges to γ (Fig. 10c).

• One might think that the first scenario applies when (x^*, y^*) is a sink and that the second scenario applies when (x^*, y^*) is a source. However, this need not to be the case. For example, the limit cycle can be an attractor from the outside but not from the inside (*half-stable*) or more than one limit cycle can exist. For the general model the analysis cannot be completed. Below, we therefore specify the functions g(x), f(x), and c(x).

The Rosenzweig-MacArthur model

The easiest choice for competition among prey is the logistic model with linear density dependence in g(x). A natural choice for the interaction between predator and prey is type two functional response, which, in contrast to the Lotka-Volterra model (with type one functional response), assumes a saturation effect for large prey densities x. We then arrive at the following model first studied by Rosenzweig and MacArthur.

$$\dot{x} = f_1(x, y) = xr_x \left(1 - \frac{x}{K_x}\right) - \frac{xyc_{xy}}{a+x}$$
(158a)

$$\dot{y} = f_2(x, y) = \frac{xyc_{yx}}{a+x} - dy,$$
 (158b)

where all parameters are positive.

- From the general model we know that the non-trivial prey isocline is determined by the equation $y_{iso} = r_x(1 x/K_x)(a + x)/c_{xy}$.
- The non-trivial predator isocline is given by the vertical line $x^* = ad/(c_{yx} d)$.

If $K_x \leq ad/(c_{yx}-d)$, the predator goes extinct and $(K_x, 0)$ is globally stable. From now on we focus on the case where an internal equilibrium (x^*, y^*) exists. From Eq. (157) already know that it is a sink if $K_x < a + 2x^*$ and a source if $K_x > a + 2x^*$. A more detailed answer concerning global stability is provided by the following proposition, which makes use of the Bendixson-Dulac theorem.

Proposition The internal fixed point (x^*, y^*) of Eq. (158) is globally stable if and only if $K \le a + 2x^*$.

Proof We consider the Dulac function

$$B(x,y) = \frac{a+x}{x}y^{\gamma-1}$$

with γ chosen appropriately. We derive

$$\operatorname{div}[B\boldsymbol{f}] = \frac{\partial Bf_1}{\partial x} + \frac{\partial Bf_2}{\partial y} = \frac{y^{\gamma-1}}{x} \left(r_x x \left(1 - \frac{a+2x}{K_x} \right) - \gamma (c_{yx} - d)(x^* - x) \right).$$
(159)

We argue as follows:

- The term $r_x x(1 (a + 2x)/K_x)$ defines a parabola in x that opens downwards and intersects the x-axis at x = 0 and $x = (K_x a)/2$. The term $\gamma(c_{yx} d)(x^* x)$ describes a line with slope $-\gamma(c_{yx} d)$ that intersects the x-axis at $x = x^*$.
- If $K_x < a + 2x^*$ then $x^* > (K_x a)/2$ and the line intersects the x-axis outside the parabola. It is therefore possible to choose an γ so that the parabola lies below the line (Fig. 11).
- Hence, the parabola and the line never cross and $\operatorname{div}[Bf]$ always has the same sign (< 0). Due to the Bendixson-Dulac theorem, this excludes cycles and with Pointcaré-Bendixson we conclude that the internal fixed point must be globally attracting in the interior of the parameter range.
- For $K_x = a + 2x^*$, we still find an γ for which the line is tangent to the parabola and thus div[Bf] < 0 almost everywhere, but for the point $x = x^*$ where it equals zero. Hence, periodic orbits can still be excluded and the interior fixed point is the global attractor.
- If, $K_x > a + 2x^*$ then we have seen that the internal fixed point is unstable. With the Poincaré-Bendixson theorem and our results for the general Gause model it is clear that in this case a limit cycle around (x^*, y^*) must exist.



Figure 11: Sketch illustrating the proof that an γ can be chosen so that Expression (159) is negative. The parabola is given by $r_x x(1 - (a + 2x)/K_x)$ and the straight line by $\gamma(c_{yx} - d)(x^* - x)$ for an appropriately chosen value of γ . The right parabola applies for K > a and the left one for K < a.

Let us summarize the stationary behavior. The Jacobian matrix J has a pair of complex conjugate eigenvalues $\lambda_{1,2} = \alpha \pm \beta i$ with $\alpha, \beta \in \mathbb{R}$.

- For $K_x < a + 2x^*$ we have $\alpha < 0$. (x^*, y^*) is a sink and is globally stable (Fig. 10b).
- For $K_x = a + 2x^*$ we have $\alpha = 0$. The linearized dynamics has a center at (x^*, y^*) . For the nonlinear dynamics, the point (x^*, y^*) is asymptotically stable.

• For $K_x > a + 2x^*$ we have $\alpha > 0$. (x^*, y^*) is a source that is surrounded by a limit cycle (Fig. 10c). [In fact, one can prove that in this model only a single limit cycle can exist but such a proof is beyond the scope of this lecture.]



Figure 12: Bifurcation diagram for the prey (x^*) and predator (y^*) equilibrium density with bifurcation parameter K_x . Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria. At $K_x = ad/(c_{yx}-d)$ a transcritical bifurcation occurs and at $K_x = a - 2ad/(c_{yx} - d)$ as supercritical Hopf bifurcation occurs.

Some remarks on the equilibrium behavior of the Rosenzweig-MacArthur model:

- 1. It is clear that at $K_x = a + 2x^*$ a bifurcation point of the dynamics has to exist. This type of bifurcation is known as *Hopf bifurcation* and is shown in Fig. 12.
- 2. Increasing the prey carrying capacity beyond the point $ad/(c_{yx} d)$ (the minimal density for predators to exist) benefits only the predator, but not the prey. This "extreme" result is due to the vertical predator isocline at $x = x^*$. However, very steep isoclines readily occur in natural systems if the predator is primarily limited by the availability of prey rather than by direct negative density dependence.
- 3. Increasing the prey carrying capacity even further (beyond the critical point of the Hopf bifurcation) increases the chance for the prey to go extinct due to stochasticity (paradox of enrichment).
- 4. Form an empirical point of view, it is still still not clear whether these models capture the essence of predator-prey cycles in nature. In particular, it is an active research area to determine whether predator-prey cycles are endogenously driven, i.e., by the interactions of predators and their prey, or by exogenous factors.

Hopf bifurcations

The bifurcation that we have seen in the Rosenzweig-MacArthur model is an example of a general type of bifurcations, where stable or unstable fixed points can split a fixed point plus a (stable or unstable) limit cycle. For ODE systems in arbitrary (finite) dimensions, they are characterized by the following theorem. **Hopf's theorem** Let G be an open subset of \mathbb{R}^n and

$$\dot{\boldsymbol{x}} = \boldsymbol{f}_{\mu}(\boldsymbol{x})$$

a family of *n*-dimensional ODEs on *G* depending on some parameter $\mu \in (-\epsilon, \epsilon)$ and f_{μ} analytic (i.e. given by a power series). Let P_{μ} be an equilibrium point at which all eigenvalues of the Jacobian matrix J have negative real parts but for one pair of complex conjugate eigenvalues

$$\lambda_1 = \alpha(\mu) + \beta(\mu)i$$
$$\lambda_2 = \alpha(\mu) - \beta(\mu)i$$

with $\alpha(\mu), \beta(\mu) \in \mathbb{R}$ and $\operatorname{sign}[\alpha] = \operatorname{sign}[\mu]$ and $\beta(0) \neq 0$. Thus, P_{μ} is a sink for $\mu < 0$ (and hence asymptotically stable) and a source for $\mu > 0$ (and hence unstable). We also require that $\partial \alpha / \partial \mu > 0$, i.e. the eigenvalues cross the imaginary axis with non-zero speed. We then have:

- supercritical Hopf bifurcation If P_0 is asymptotically stable, then, for sufficiently small positive values of μ , the unstable equilibrium point P_{μ} is surrounded by a periodic attractor (Fig. 13a).
- subcritical Hopf bifurcation If P_0 is unstable, then, for sufficiently small negative values of μ , the asymptotically stable equilibrium point P_{μ} is surrounded by a periodic repellor (Fig. 13b).



Figure 13: (a) supercritical Hopf bifurcation, (b) subcritical Hopf bifurcation. Solid lines correspond to asymptotically stable equilibria, hatched lines to unstable equilibria.

• At a supercritical Hopf bifurcation, a stable fixed point becomes locally unstable but the flow sufficiently far away does not feel this local change and is still contracting. As a result, a periodic orbit becomes the new attractor. (Analogous for subcritical.)

- The direction of the "far flow" is indicated by the stability or instability of the equilibrium point P_0 for $\mu = 0$. With vanishing real parts of $\lambda_{1,2}$, this equilibrium is non-hyperbolic (neither a sink, a source, nor a saddle). Its stability therefore cannot be deduced from linearization but depends on higher-order terms. These terms are weaker than the linear ones in the direct vicinity of the fixed point, but stronger at some distance. A small perturbation by moving μ away from zero will introduce small, but non-zero linear terms, which dominate in a neighborhood, but not at some greater distance.
- In practice, the dependence on higher order terms makes it difficult to determine the stability of P_0 . Often only a Lyapunov function or a Dulac function can provide definite answers.
- The diameter of the limit cycle generated at the bifurcation points increases continuously from zero and grows initially proportional to the square root of the bifurcation parameter, õ.

6 Dynamics of more than two populations

In dynamical systems of dimension three or higher the Jordan curve theorem does not apply and ω -limit sets of ODEs need not to be equilibrium points or periodic orbits anymore. Instead, also *strange attractors* can exist and the dynamics can show *chaos*.

6.1 The General Lotka-Volterra Equations

The general Lotka-Volterra equation for n populations reads

$$\dot{x}_i = x_i \left(r_i + \sum_{j=1}^n a_{ij} x_j \right), \tag{160}$$

where x_i and r_i denote the density and the intrinsic growth rate of the *i*th species, respectively. The a_{ij} describe the effect of the *j*th species on the growth rate of the *i*th species. In matrix notation this becomes

$$\dot{\boldsymbol{x}} = \boldsymbol{r} \circ \boldsymbol{x} + \boldsymbol{x} \cdot \mathsf{A}\boldsymbol{x},\tag{161}$$

where \circ denotes the element-wise multiplication of two vectors (Hadamard product). The matrix A is known as *interaction matrix*. While the two-dimensional Lotka-Volterra equations are completely classified, this has not been achieved for the general system due to the potential for more complicated attractors. Indeed, chaotic motion is possible already in the system with three species. Nevertheless, we can state some general results and also obtain explicit solutions for some special cases of biological interest.

Equilibria

Note first that all faces of the state space $x_i = 0$, which correspond to states where species i is absent, are invariant under the flow (no individual can immigrate). Consequently, also the flow in the interior of the state space (i.e., for $x_i > 0$, $\forall i$) is invariant. The density $x_i(t)$ may approach zero, however, which means extinction. Internal fixed points are solutions of the linear equation system

$$y_i = r_i + \sum_{j=1}^n a_{ij} x_j = 0$$
 $i = 1, \dots, n$ (162)

with all components $x_j = x_j^* > 0$. Since the restriction of the dynamics to a boundary face $x_i = 0$ again leads to a Lotka-Volterra system (with one fewer dimension), fixed points on the boundaries can be found in an analogous way.

- In general (i.e., if the linear system is not degenerate), there will be at most a single internal fixed point for the Lotka-Volterra system. In the degenerate case, there is a continuum of fixed points.
- A useful theorem states that if there is no internal fixed point, then there is no α-or ω-limit in the interior of the state space at all. I.e., all orbits either flow to the boundary (extinction of one species) or to infinity. For a proof, note that the convex set K defined by the linear system (162) with x_j > 0 is disjoint from 0 if there is no internal fixed point. We then can can define a hyperplane H through 0 that is disjoint from K and a vector c = (c₁,..., c_n) ≠ 0 that is orthogonal to H such that c · y > 0 for all y ∈ K. Then

$$V(\boldsymbol{x}) = \sum_{i} c_i \log x_i$$

is a Lyapunov function (indeed, $\dot{\boldsymbol{V}} = \sum_i c_i \dot{x}_i / x_i = \sum_i c_i y_i > 0$). Since $V(\boldsymbol{x})$ has no internal maximum this proves the theorem.

• If there is a unique internal fixed point x^* , one can further prove that all orbits that neither converge to the boundary nor to infinity must have x^* as their long time average (see Hofbauer & Sigmund, chapter 5 for a proof). Hence, if closed or chaotic attractors exist for an *n*-dimensional Lotka-Volterra model, they must always surround a fixed point.

6.2 Lotka-Volterra Models for Food Chains

A simplified picture of an ecosystem is that of a *food chain*. Basal species in such a chain are *primary producers*, e.g., plants and algae, that convert solar energy and CO_2 into biomass. Primary producers are eaten by *grazers*. Grazers are eaten by predators which themselves are eaten by larger predators. At top of the chain sits the top-predator. Most ecosystems

are more complicated and form food-webs rather than food chains. Nevertheless, food chains are a good starting point to investigate multi-species interactions. The Lotka-Volterra version of a food chain of length n with self-regulation looks as follows:

$$\dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2) \tag{163a}$$

$$\dot{x}_i = x_i(-r_i + a_{i,i-1}x_{i-1} - a_{ii}x_i - a_{i,i+1}x_{i+1}) \quad \text{for} \quad i \in \{2, \dots, n-1\}$$
(163b)

$$\dot{x}_n = x_n(-r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n), \tag{163c}$$

with $r_i, a_{ij} > 0$. For this system we recover the dynamics of the two-dimensional Lotka-Volterra predator-prey model.

Theorem If Eq. (163) has an internal equilibrium point $\boldsymbol{x}^* > 0$, then all orbits in $\mathbb{R}^n_{>0}$ converge to \boldsymbol{x}^* . Thus, \boldsymbol{x}^* is globally stable and (with the results above) periodic or chaotic attractors cannot exist.

Proof We will show that the following function is a Lyapunov function:

$$V(\boldsymbol{x}) = \sum_{i=1}^{n} c_i (x_i^* \log x_i - x_i)$$
(164)

with $c_i > 0$ to be specified later. Note first that $V(\boldsymbol{x})$ has a unique maximum at $\boldsymbol{x} = \boldsymbol{x}^*$. Then derive

$$\dot{V}(\boldsymbol{x}(t)) = \sum_{i=1}^{n} c_i \frac{\dot{x}_i}{x_i} (x_i^* - x_i).$$
(165)

Replacing \dot{x}_i with corresponding equation from Eq. (163) and using that

$$r_{1} = a_{11}x_{1}^{*} + a_{12}x_{2}^{*}$$

$$r_{i} = a_{i,i-1}x_{i-1}^{*} - a_{ii}x_{i}^{*} - a_{i,i+1}x_{i+1}^{*} \text{ for } i \in \{2, \dots, n-1\}$$

$$r_{n} = a_{n,n-1}x_{n-1}^{*} - a_{nn}x_{n}^{*},$$

we get

$$\frac{\dot{x}_{1}}{x_{1}} = a_{11}(x_{1} - x_{1}^{*}) + a_{12}(x_{2} - x_{2}^{*})$$

$$\frac{\dot{x}_{i}}{x_{i}} = a_{i,i-1}(x_{i-1} - x_{i-1}^{*}) - a_{ii}(x_{i} - x_{i}^{*}) - a_{i,i+1}(x_{i+1} - x_{i+1}^{*})$$

$$\frac{\dot{x}_{n}}{x_{n}} = a_{n,n-1}(x_{n-1} - x_{n-1}^{*}) - a_{nn}(x_{n} - x_{n}^{*}).$$

Eq. (165) then becomes

$$\dot{V}(\boldsymbol{x}(t)) = \sum_{i=1}^{n} c_i a_{ii} (x_i - x_i^*)^2 - \sum_{i=1}^{n-1} (x_i - x_i^*) (x_{i+1} - x_{i+1}^*) (c_{i+1} a_{i+1,i} - c_i a_{i,i+1}).$$

If we choose $c_i > 0$ such that $c_{i+1}/c_i = a_{i,i+1}/a_{i+1,i}$, then this equation simplifies to

$$\dot{V}(\boldsymbol{x}(t)) = \sum_{i=1}^{n} c_i a_{ii} (x_i - x_i^*)^2 \ge 0.$$
(166)

With the Lyapunov theorem follows that for all points $\boldsymbol{x} \in \mathbb{R}^n_{>0}$ we have $\omega(\boldsymbol{x}) = \boldsymbol{x}^*$. Note that for the proof it is sufficient if only one species has intraspecific density regulation, i.e., $a_{ii} \geq 0 \forall i$ and $a_{ii} > 0$ for at least one species.

Three-level food chain

Let us have a look at a specific example. A minimal food chain consists of three trophic levels: a primary producer x_1 (plants), a herbivore x_2 and a carnivore x_3 . Here, each level of the food chain need not to consist of only a single species. Instead, each level can represent the whole *functional group*. For simplicity, we assume that intraspecific density regulation on the level of the consumers can be ignored, $a_{22} = a_{33} = 0$ and obtain

$$\dot{x}_1 = x_1(r_1 - a_{11}x_1 - a_{12}x_2) \tag{167a}$$

$$\dot{x}_2 = x_2(-r_2 + a_{21}x_1 - a_{23}x_3) \tag{167b}$$

$$\dot{x}_3 = x_3(-r_3 + a_{32}x_2).$$
 (167c)

Equilibria and stability The trivial equilibrium at **0** is unstable for any $r_1 > 0$. A non-zero single-species equilibrium only exists for the producer, at $x^{*1} = (r_1/a_{11}, 0, 0)$. It is stable for $r_1/a_{11} < r_2/a_{21}$, which is the producer minimal density at which a herbivore can persist. In the absence of the carnivore, this result follows from the 2-species LV model (see Eq. 134). The coordinates of the equilibrium with plants and herbivores coexisting can also be taken from there (135),

$$\boldsymbol{x^{*2}} = \left(\frac{r_2}{a_{21}}, \frac{a_{21}r_1 - a_{11}r_2}{a_{12}a_{21}}, 0\right)$$

Obviously, there cannot be any other 2-species equilibria. x^{*2} is stable until the herbivore density reaches the minimal level for carnivores to invade, at $x_2 = r_3/a_{32}$. Finally, the equilibrium x^{*3} with all three trophic levels present equals

$$x_1^{*3} = \frac{r_1 a_{32} - r_3 a_{12}}{a_{11} a_{32}} \tag{168a}$$

$$x_2^{*3} = \frac{r_3}{a_{32}} \tag{168b}$$

$$x_3^{*3} = \frac{r_1 a_{21} a_{32} - r_2 a_{11} a_{32} - r_3 a_{12} a_{21}}{a_{11} a_{23} a_{32}}.$$
 (168c)

Figure 14 shows the bifurcation diagram for the equilibrium densities as a function of system productivity as given by r_1 . A long standing question in population ecology is whether population densities are regulated *top down* or *bottom up*. Based on this simple model the following conclusions can be drawn.



Figure 14: Bifurcation diagram for the equilibrium densities of Eq. (167) with bifurcation parameter r_1 .

- 1. System productivity controls total biomass and the number of trophic levels.
- 2. In a tritrophic food chain, herbivore density is controlled top down. Plants and carnivores benefit from increased system productivity.
- 3. Increased death rate in the carnivore increases herbivore abundance and thereby suppresses plant abundance (trophic cascade).
- 4. Adding more trophic levels has the following effect: systems with an odd number of trophic levels release plant growth while systems with an even number of trophic levels control plant growth.

Empirical support for this model comes mainly from aquatic system.

• At the east coast of North America different kelp species, invertebrate grazers such as sea urchins, and sea-otters form a tritrophic food chain. Data from Alaska show that as sea otters became rare, sea urchins became more common and many kelp forests disappeared (and with them a very rich ecosystem of organisms living in the kelp forests). Sea otters apparently became rarer when orca whales increased their hunting pressure on them, possibly due to decreased fish stocks.

• The food web in many fresh water lakes essentially consists of phytoplankton as primary producers, zooplankton, planktivorous fish, and possibly piscivorous fish. Whole-lake manipulation experiments show that lakes that lack piscivorous fish tend to be "green" (tritrophic food chain resulting in abundant phytoplankton), whereas "blue" lakes result where piscivorous fish are added as fourth trophic level. This mechanism forms the basis for many lake restoration projects.

6.3 Coexistence and Competitive Exclusion

In many natural systems a set of consumer species shares the same resources. Look at the different species of birds at your feeder. But how many consumer species can coexist on a given set of resources? In the Lotka-Volterra competition model we did not model the cause of competition explicitly but only indirectly via the interaction terms a_{ij} . Two causes of competition can be distinguished. First, competition can be due to direct interactions such as fighting. This is know as *interference competition*. Second, competition can be due to the depletion of shared resources or *exploitation competition*. In the latter case one might want to model the dynamics of the resources explicitly. A minimum model consist of three species: one resource (or prey) and two competing consumers (or predators) and can be modeled as follows,

$$\dot{x} = r_x x - a_{xx} x^2 - a_{xy_1} x y_1 - a_{xy_2} x y_2 \tag{169a}$$

$$\dot{y}_1 = -r_{y_1}y_1 + a_{y_1x}xy_1 \tag{169b}$$

$$\dot{y}_2 = -r_{y_2}y_2 + a_{y_2x}xy_2,\tag{169c}$$

where all parameters are positive. There is no direct interaction among the two types of predators and no direct intraspecific competition in the predators, either. For only a single predator, the system reduces to the Lotka-Volterra predator-prey model that we have discussed above (with intraspecific exploitation competition among predators). For the two predator species to coexist at equilibrium we require

$$\dot{y}_1 = 0 \iff r_{y_1} = a_{y_1x} x^*$$
$$\dot{y}_2 = 0 \iff r_{y_2} = a_{y_2x} x^*$$

This is a system of two linear equations in one unknown and thus overdetermined. In our case, coexistence is only possible if $r_{y_1}/r_{y_2} = a_{y_1x}/a_{y_2x}$. Thus, coexistence is not robust with respect to perturbations in the parameter values: two consumer species cannot robustly coexist on one resource. This results can be stated much more generally, also beyond the Lotka-Volterra framework.

Theorem: Competitive Exclusion In a system of exploitation competition with n consumer species and m < n resources, robust coexistence at an equilibrium point is not possible.

Proof Let the dynamics of m resource and n consumer species be given by

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(\boldsymbol{x}, \boldsymbol{y})$$

and

$$\dot{\boldsymbol{y}} = \boldsymbol{y} \circ \boldsymbol{g}(\boldsymbol{x}),$$

respectively, where \circ denotes the Hadamard product. At a point equilibrium $y^* \in \mathbb{R}^n_{>0}$ it is required that

$$\mathbf{0} = \boldsymbol{g}(\boldsymbol{x}^*).$$

This is a system of n equations in m unknowns. It can only have a robust solution when $m \leq n$.

- Note that the theorem only excludes fixed points. For a general model, there could be closed orbits we have previously seen that predator-prey systems have a tendency to cycle or chaotic attractors. Orbits could also diverge to infinity, although this should not occur for a realistic population dynamical model.
- For Lotka-Volterra systems, absence of an internal fixed point implies that other bounded ω-limits are also impossible (see our general results above). If the dynamics is bounded, we thus can conclude that all orbits converge to the boundary and at least one species will go extinct.
- A crucial assumption of the theorem is that there is no direct intraspecific competition for the consumer species. It is quite obvious that sufficiently strong intraspecific competition will enable coexistence on even just a single (abundant) resource. However, intraspecific competition usually indicates that there is some other limiting resource (space, nesting places, some other prey species), even if this resource is not explicitly included in the dynamics.
- The exclusion principle is an influential concept in ecology: coexistence requires exclusive resources, which can not (or less easily) be exploited by competing species. However, it is not necessarily easy to apply it in practice. What should be counted as different resource types? E.g., if birds feed on the seeds of a certain plant species this may be counted as a single resource or as infinitely many different resources if the size distribution of the seeds is continuous.

Cyclic competition

Consider the Lotka-Volterra competition model with two species, following

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2) \tag{170}$$

$$\dot{x}_2 = x_2(1 - \beta x_1 - x_2), \qquad (171)$$

with $\alpha, \beta > 0$. For simplicity, we have set $r_1 = r_2 = a_{11} = a_{22} = 1$. The single species thus have carrying capacities $K_1 = K_2 = 1$. For $\alpha, \beta < 1$ both species can coexist, but for $\alpha, \beta > 1$ they are mutually exclusive, and for $\alpha < 1$ and $\beta > 1$ ($\alpha > 1, \beta < 1$) species 1 (species 2) dominates and drives the other one to extinction. Consider a case of dominance, e.g., species 2 dominating over species 1. One can ask whether it is possible to introduce a third competing species such that the system of all three species allows for stable coexistence. Intuitively, if such a species 3 exists, it should "beat" (dominate) species 2, but should be dominated by species 1. An easy symmetric example is provided by the system

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3) \tag{172}$$

$$\dot{x}_2 = x_2(1 - \beta x_1 - x_2 - \alpha x_3) \tag{173}$$

$$\dot{x}_3 = x_3(1 - \alpha x_1 - \beta x_2 - x_3) \tag{174}$$

with $0 < \beta < 1 < \alpha$. Clearly, we find circular dominance on the boundary of the state space: in the $x_1 - x_2$ plane x_2 dominates and $e_2 = (0, 1, 0)$ is globally attracting. Similarly, $e_3 = (0, 0, 1)$ and $e_1 = (1, 0, 0)$ are the global attractor on the $x_2 - x_3$ plane and the $x_3 - x_1$ plane, respectively. In the full three species system, however, the unit vectors e_i , i = 1, 2, 3are no longer stable, but are saddle points. The only other fixed point on the boundary is the trivial one (0, 0, 0), which is always a source. Finally, there is a unique internal fixed point at

$$m = {1 \over 1 + \alpha + \beta} (1, 1, 1).$$
 (175)

The Jacobian at \boldsymbol{m} reads

$$\frac{1}{1+\alpha+\beta} \begin{pmatrix} -1 & -\alpha & -\beta \\ -\beta & -1 & -\alpha \\ -\alpha & -\beta & -1 \end{pmatrix} \,.$$

This is a so-called *circulant* matrix with equal entries in each row (and column), with a circular shift by one from one row to the next. The eigenvalues and eigenvectors of circulants are easy to derive.

Lemma The eigenvalues λ_k and eigenvectors \boldsymbol{v}_k , k = 0, ..., n-1 of an *n*-dimensional circulant matrix

$$\boldsymbol{J} = \begin{pmatrix} c_0 & c_1 & \dots & c_{n-1} \\ c_{n-1} & c_0 & \dots & c_{n-2} \\ \vdots & & & \vdots \\ c_1 & c_2 & \dots & c_0 \end{pmatrix}$$

are given by

$$\lambda_k = \sum_{j=0}^{n-1} c_j \mu^{j \cdot k} \quad , \quad \boldsymbol{v}_k = (1, \mu^k, \mu^{2k}, \dots, \mu^{(n-1)k})$$
(176)
where

$$\mu = \exp\left(\frac{2\pi i}{n}\right)$$

is the *n*th root of unity. (The proof follows immediately by inserting λ_k and \boldsymbol{v}_k into the eigenvalue equation.)

We thus obtain for the Jacobian J,

$$\Lambda_0 = -1$$
 , $\boldsymbol{v}_1 = (1, 1, 1),$ (177)

$$\lambda_1 = \bar{\lambda}_2 = \frac{1}{1 + \alpha + \beta} \Big(-1 - \alpha \exp[2\pi i/3] - \beta \exp[4\pi i/3] \Big).$$
(178)

We observe the following

• Since

$$\operatorname{Re}[\lambda_1] = \operatorname{Re}[\lambda_2] = \frac{1}{1+\alpha+\beta} \left(-1 + \frac{\alpha+\beta}{2} \right)$$

 \boldsymbol{m} is a sink (stable) if $\alpha + \beta < 2$ and that \boldsymbol{m} is a saddle (unstable) if $\alpha + \beta > 2$.

- The diagonal $x_1 = x_2 = x_3$ is invariant under the ODE flow. If \boldsymbol{m} is a saddle, it is the stable manifold of the equilibrium.
- All orbits in the interior of a boundary plane have one of the edges e_i as ω -limit. Each of these points has an unstable manifold on the "next" boundary (e.g., e_2 is the ω -limit for all orbits in the interior of the x_1/x_2 plane, but has an unstable manifold on the x_2/x_3 plane). The three unstable manifolds connect the three edges. Together with these they form a closed so-called *heteroclinic cycle*.

To analyze the dynamics in the interior of the state space, we consider two functions

$$S = x_1 + x_2 + x_3 \quad ; \quad P = x_1 \cdot x_2 \cdot x_3 \,. \tag{179}$$

Since we have

$$\dot{S} = x_1 + x_2 + x_3 - \left(x_1^2 + x_2^2 + x_3^2 + (\alpha + \beta)(x_1 x_2 + x_2 x_3 + x_3 x_1)\right) \le \begin{cases} S(1 - S) & \alpha + \beta > 2\\ S(1 - \frac{\alpha + \beta}{2}S) & \alpha + \beta \le 2 \end{cases}$$

the ω -limits of all orbits are confined to a bounded region $S \leq \max[1, 2/(\alpha + \beta)]$ and no population can explode. We further derive

$$\dot{P} = \dot{x}_1 x_2 x_3 + x_1 \dot{x}_2 x_3 + x_1 x_2 \dot{x}_3 = P \left(3 - (1 + \alpha + \beta)S \right).$$

We will now show that P/S^3 is a Lyapunov function in the interior of the state space. Indeed, we have

$$\frac{d}{dx_i} \frac{P}{S^3} = \frac{P(S - 3x_i)}{x_i S^4} = 0 \quad \text{for} \quad x_1 = x_2 = x_3 \,,$$

where it assumes a maximum. We also have $P/S^3 \ge 0$ and $P/S^3 = 0$ (minimum) at the boundary where P = 0. For the time derivative, we derive

$$\frac{d}{dt}\frac{P}{S^3} = \frac{P}{S^4} \left(1 - \frac{\alpha + \beta}{2}\right) \left((x_1 - x_2)^2 + (x_2 - x_3)^2 + (x_3 - x_1)^2\right)$$

and conclude the following

- For $\alpha + \beta < 2$, the Lyapunov function is monotonically increasing and we converges to the diagonal $x_1 = x_2 = x_3$. We have already seen that on this diagonal convergence to \boldsymbol{m} follows, which is thus the global attractor for every orbit in the interior.
- For $\alpha + \beta < 2$, the Lyapunov function is monotonically decreasing. Every orbit not on the diagonal $x_1 = x_2 = x_3$ thus converges to the boundary. at the boundary it must follow the heteroclinic cycle, which is the (almost) globally attracting ω -limit in this case.
- Our symmetric example of cyclic competition does not have a real biological motivation. It mainly demonstrates what kind of phenomena can occur in higher dimensional systems. Indeed in Lotka-Volterra models with two consumers and two resources heteroclinic cycles appear quite naturally (see Hofbauer & Sigmund, chapter 16).
- Heteroclinic cycles can also occur in two-dimensional dynamical systems (but not in 2d Lotka-Volterra systems or other typical population dynamical models). This is why we needed to account for a third category for ω -limits in the Pointcaré-Bendixson Theorem. See the book by Teschl (chapter 7) for an example.

6.4 Coexistence concepts

At this point we should make precise what we mean by *coexistence*. In systems with (potentially) closed orbits, heteroclinic cycles, or chaotic motion this can be a subtle issue. We can rarely expect to obtain a full description of all ω -limits together with their attraction domains. For many purposes, however, the precise asymptotics is less important than the question of *extinction*, i.e., whether all species in the system will survive in the long term or not. We are particularly interested in global concepts, in the sense that survival does not depend on initial conditions (given that all species are initially present). Various mathematical concepts exist, with different biological implications. Consider a dynamical system

$$\dot{x}_i = x_i f_i(\boldsymbol{x}) \quad i = 1, \dots, n$$

that is defined on $\mathbb{R}^n_{>0}$.

Definiton

1. The system is *persistent* if for every orbit with starting value $\boldsymbol{x}(0)$ in the interior of the state space

$$\limsup_{t \to \infty} \boldsymbol{x}_i(t) > 0 \quad \forall i \,. \tag{180}$$

2. We say that a system is *invasible* if every attracting ω -limit on the boundary of the reduced system (with one or several species removed) can be invaded by a missing species when added in very low density. Formally, we require that averaged per captita growth rate for some missing species *i* is positive,

$$\lim_{T\to\infty}\frac{1}{T}\int_0^T f_i(\boldsymbol{x}(t))\,\mathrm{d}t > 0\,.$$

(For chaotic attractors we need to specify whether we require this for every orbit or almost every orbit $\boldsymbol{x}(t)$.)

3. The dynamical system is said to be *permanent* if there exists $\delta, D > 0$ such that $x_i(0) > 0$ for $i \in \{1, \ldots, n\}$ implies

$$\liminf_{t \to +\infty} x_i(t) > \delta \quad \text{for } i \in \{1, \dots, n\}.$$
(181)

and

$$\limsup_{t \to +\infty} x_i(t) \le D \quad \text{for } i \in \{1, \dots, n\}.$$
(182)

Note that δ and D do not depend on the initial condition $x_i(0)$. Condition (182) (uniform boundedness) holds whenever populations cannot grow to infinity, thus, for any well-formulated population dynamical model.

- It is clear that permanence implies persistence, but the opposite is not true, even if we consider only uniformly bounded systems. A system with $\dot{x}_i = 0$ for $x_i < D$ is persistent, but not invasible or permanent. The same holds for the degenerate Lotka-Volterra predator-prey model with center-type behavior.
- For purposes of biological application, *persistence* is usually too weak. There is no force inherent to the system that would protect a species from going extinct. Coexistence is thus not stable. This is different for permanent systems, where the boundary is a repeller. Indeed, a system is permanent if a compact set K in the interior of the state space exists such that all orbits in the interior end up in K.
- *Invasibility* guarantees that species can grow from low densities. The concept thus implies better stability than persistence. However, invasibility does not imply persistence, an example is given in the model below. It can also be "tricked" by heteroclinic cycles, where invasion of one species means that another one will eventually die out. The only concept to exclude an attracting heteroclinic cycle like in the 3-species Lotka-Volterra system discussed above is permanence.

• An advantage of invasibility over permanence as defined here is that it is robust with respect to small perturbations of the system. Indeed, a system can be permanent, but not invasible, if orbits close to the boundary are repelled with zero speed. However, we can extend the definition of permanence to require robustness. A more relevant advantage of invasibility is that the conditions are often easier to check.

6.5 Dynamic coexistence of two predators on a single resource

As an instructive application of coexistence concepts, we study the potential for coexistence of two predator species y_1 and y_2 on one resource species x. Consider the following model due to Armstrong and McGehee:

$$\dot{x} = xr\left(1 - \frac{x}{K}\right) - \frac{y_1 x e_1}{a + x} - y_2 x e_2$$
 (183a)

$$\dot{y}_1 = y_1 f_1(x) = y_1 \left(\frac{xc_1}{a+x} - d_1\right)$$
 (183b)

$$\dot{y}_2 = y_2 f_2(x) = y_2 \left(x c_2 - d_2 \right)$$
 (183c)

We have previously studied the two-species systems (183a) & (183b) and (183a) & (183c) in isolation. For the first system (Rosenzweig-MacArthur, RMA), we have seen that the equilibrium point is either globally stable or, when it is unstable, prey and predator coexist on a limit cycle. For the second system (Lotka-Volterra, LV), the internal equilibrium point is globally stable whenever it exists. We denote the internal equilibrium points of RMA system (183a & 183b) and the LV system (183a & 183c) by (x^*, y_1^*) and (x^{**}, y_2^{**}) , respectively. To study coexistence in the three-species system, we first focus on invasibility. It is easy to see that no predator can survive in the presence of the other one if it cannot even survive without its competitor. We then need to distinguish two cases.

1. Assume first that both the RMA and the LV two-species systems have a stable equilibrium point. It is easy to see that the system is not mutually invasible in this case. Indeed, the second predator can invade the stable equilibrium (x^*, y_1^*) of the RMA system if and only if

$$x^*c_2 - d_2 > 0. (184)$$

Since $x^{**}c_2 - d_2 = 0$, this is possible if and only if $x^* > x^{**}$, in other words, if predator 2 can survive on fewer resources than predator 1. Vice versa, the first predator can invade the equilibrium (x^{**}, y_2^{**}) of the LV system if and only if

$$\frac{x^{**}c_1}{a+x^{**}} - d_1 > 0. ag{185}$$

Since $x^*c_1/(a+x^*)-d_1 = 0$ and the per-capita growth rate $f_1(x)$ is strictly monotonic in x, this is possible if and only if $x^{**} > x^*$. These two conditions cannot be satisfied simultaneously: there is no mutual invasibility. Since we have no interior fixed points in the (y_1, y_2) -plane (we have two equations in one unknown) coexistence is indeed impossible and invasion implies fixation. 2. Since the per-capita growth rates $f_i(x)$ of both predators are monotonic, there are unique minimal prey densities $f_1(x^*) = 0$ and $f_2(x^{**}) = 0$ at which the *i*th predator can maintain itself in a constant environment (with constant x). Let us now drop the assumption of a stable fixed point in the two-species systems. In particular, we allow that the predator and prey density, $y_i(t)$ and x(t), vary in time but return to their initial value after some time τ . The mean prey density over one cycle of period τ is given by

$$\bar{x} := \frac{1}{\tau} \int_0^\tau x(t) \mathrm{d}t.$$
(186)

The mean per-capita predator growth rate over one cycle is

$$\overline{f_i(x)} := \frac{1}{\tau} \int_0^\tau f_i(x(t)) \,\mathrm{d}t.$$
(187)

After one period the population size is unchanged: $y_i(t) = y_i(t + \tau)$. Therefore,

$$\int_{0}^{\tau} f_{i}(x(t)) dt = \int_{0}^{\tau} \frac{1}{y_{i}} \frac{dy_{i}}{dt} dt = \ln y_{i}(\tau) - \ln y_{i}(0) = 0$$
(188)

and thus

$$\overline{f_i(x)} = 0 \tag{189}$$

has to hold.

A species with a linear functional response (LV system) requires the same average resource density to maintain itself in an environment with cycling x as it does in a constant environment, $\bar{x} = x^{**}$. Indeed, for $f_2(x) = c_2 x - d_2$ we have

$$f_2(\bar{x}) = \frac{c_2}{\tau} \int_0^\tau x(t) dt - d_2 = \frac{1}{\tau} \int_0^\tau (c_2 x(t) - d_2) dt = \frac{1}{\tau} \int_0^\tau f_2(x(t)) dt = \overline{f_2(x)} = 0,$$
(190)

where the last equality follows from Eq. (189). It follows that $\bar{x} = x^{**}$.

Next, consider a species with a saturating functional response (RMA system), $f_1 = xc_1/(a+x) - d_1$. In this case, the average resource density required for maintenance in a time-varying environment is higher than in a constant environment. This makes intuitive sense: the predator profits only little from times with abundant prey, but suffers a lot from times with rare prey. To verify this, denote with l(x) the tangent line to $f_1(x)$ at x^* (see Fig. 15). Then $l(x^*) = f_1(x^*) = 0$, but $l(x) > f_1(x)$ for $x \neq x^*$ and therefore $l(\bar{x}) = \overline{l(x)} > \overline{f_1(x)} = 0$. Thus, $l(\bar{x}) > l(x^*)$, which implies $\bar{x} > x^*$.

Consider now mutual invasibility for parameter values with unstable fixed point (x^*, y_1^*) for the RMA system, where predator and the prev coexist along a periodic orbit γ with period τ . Predator 2 can invade the periodic attractor of predator 1 and the resource if and only if its average per capita growth rate over one cycle (while rare) is positive:

$$\frac{1}{\tau} \int_0^\tau f_2(x(t)) dt = \frac{1}{\tau} \int_0^\tau (c_2 x(t) - d_2) dt = c_2 \bar{x} - d_2 > 0.$$
(191)



Figure 15: Graphs of the functions $f_1(x)$ and l(x). l(x) is the tangent line to $f_1(x)$ at x^* . (From Armstrong and McGehee 1980.)

Hence, invasion is possible if and only if $\bar{x} > x^{**}$. We can conclude that the condition for mutual invadability equals

$$x^* < x^{**} < \bar{x}, \tag{192}$$

which can be satisfied for appropriately chosen parameter values. One can show that the three-species community is stable and cycles along a periodic orbit (McGehee & Armstrong, 1977, J.Diff.Eq. 23:30-52; Armstrong & McGehee, 1980, AmNat 115:151-170).

- Why is coexistence in this model possible, seemingly violating the principal of competitive exclusion? Figure 16(a) shows the per capita growth rates for the two predators for the different prey densities that occur during one cycle. We can see that predator 1 is superior at low resource densities while predator 2 is superior at high resource densities. Thus, which predator is superior regularly changes along the periodic orbit, preventing that one predator excludes the other (Figure 16b).
- One can argue that different densities of the same resource species have to be interpreted as different resources. In this sense, the present model contains infinitely many resources. Accordingly, in principle any number of consumer species can coexist on a single cycling resource. The principle of competitive exclusion can be generalized in a way that it still holds. Of course, more consumers can only coexist if the parameters of their functional response are suitably fine-tuned, making their coexistence less robust to perturbations.



Figure 16: (a) Growth rates of predators of Eq. (183) as a function of prey density x. The region C represents the approximate range of variation over x over one cycle in the three species system (from Armstrong and McGehee 1980). (b) Predator 1 has a higher per capita growth rate at low resource densities whereas Predator 2 has a higher per capita growth rate at high resource densities (from Yodzis 1989).

• For stable coexistence in the sense of mutual invasibility we need $x^* < x^{**}$. Note that the unstable fixed point (x^*, y_1^*) of the RMA 2-species system can not be invaded by the second predator under this condition. Indeed, (x^*, y_1^*) is a saddle with stable manifold pointing into the interior of the state space. As a consequence, there is a single orbit (along the stable manifold) that converges to the boundary and the system is neither permanent nor persistent!