Mathematical Ecology

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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 ($\sim$ 72 Euro)

- Mark Kot: Elements of Mathematical Ecology, Cambridge University Press ($\sim$ 62 Euro)

- Josef Hofbauer and Karl Sigmund: Evolutionary Games and Population Dynamics, Cambridge University Press ($\sim$ 49 Euro)

- Linda Allen: An Introduction to Stochastic Processes with Applications to Biology, Prentice Hall ($\sim$ 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

- 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.

- *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

- 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:

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

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

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

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

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

From the Master equation follows

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

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

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

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:

$$\frac{\partial \overline{N^2}}{\partial t} = \sum_{N=0}^{\infty} N^2 \frac{\partial P_N(t)}{\partial t}$$

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

$$= \sum_{N=0}^{\infty} \left(d(N-1)^2 N P_N(t) + b(N+1)^2 N P_N(t) - N^3(b+d)P_N(t) \right)$$

$$= \sum_{N=0}^{\infty} \left((2N^2(b-d) + N(b+d))P_N(t) \right) = 2(b-d)\overline{N^2}(t) + (b+d)\bar{N}(t). \quad (6)$$

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

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

which is solved by

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

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

$$\text{Var}[N(t)] = \frac{b+d}{b-d} \left(\exp(rt) - 1 \right) \exp(rt)N_0. \quad (8)$$

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,

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

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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

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

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) birth-death 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

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

We see that for $r > 0$ $\mathrm{CV}[N(t)]$ 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

$$N(t) \to N(t) + 1 : \quad b(t, N(t)) \cdot N(t) + m(t, N(t)) \tag{12}$$
$$N(t) \to N(t) - 1 : \quad d(t, N(t)) \cdot N(t) \tag{13}$$

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

$$E[\Delta N | N(t)] = \Big(r(t, N(t)) \cdot N(t) + m(t, N(t)) \Big) \Delta t \,. \tag{14}$$

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

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

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:

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

$N(t) \in \mathbf{R}$ 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

$$\dot{N}(t) = rN(t)$$

  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

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

  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.

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- 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

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

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

$$|N(t_0) - N^*| < \delta \quad \Rightarrow \quad \lim_{t \to \infty} |N(t) - N^*| = 0$$
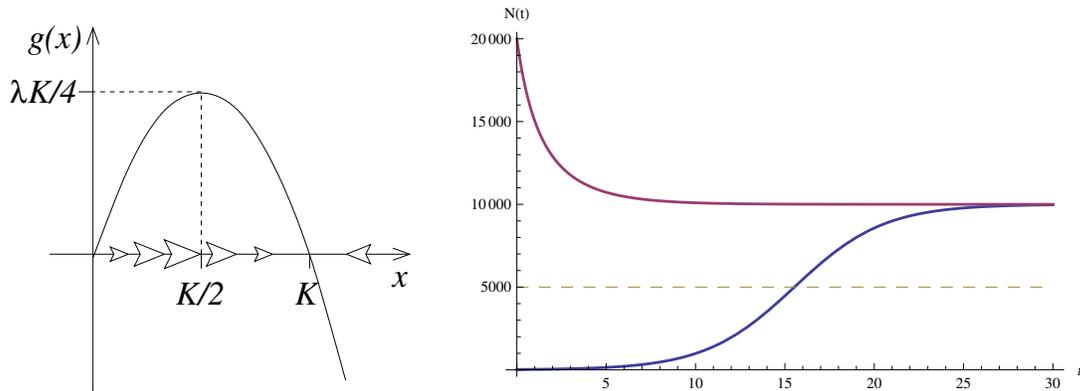
Figure 1: Phase-line diagram and dynamics for logistic growth (with $K = 10000$ and $r = 0.4$). The growth dynamics has an inflection point at $K/2$: maximal absolute increase in population density.

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:
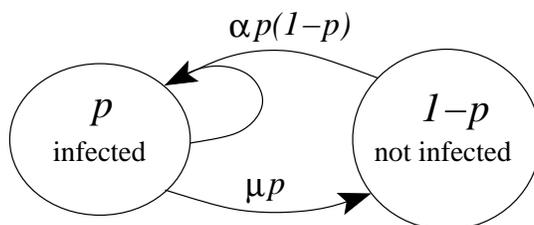
- Construct an ODE model for the dynamical variable $p(t)$ and discuss the equilibria.

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

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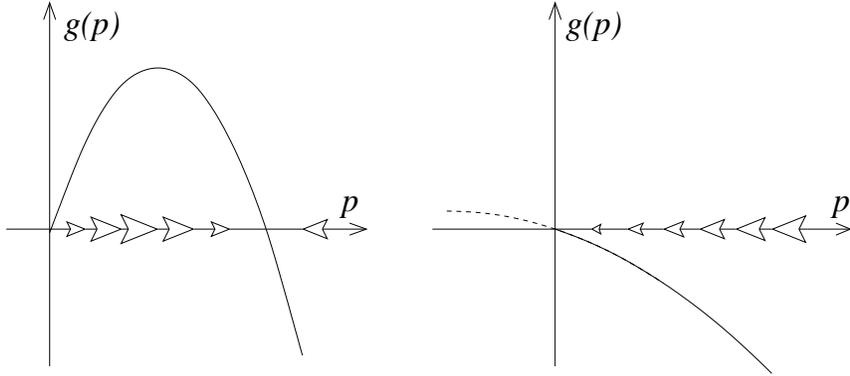
Figure 2: Phase-line diagram for the infection model (20). Left: $\alpha > \mu$, right: $\alpha < \mu$.

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 so-called *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.,

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

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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 $\lim_{N \to \infty} f(N) << 0$, 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

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

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.

1a/2a) 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?

1b/2b) 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

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

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.,

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

We get equilibria at $N = 0$ and at the solutions of $E = r((N/K_0) - 1)(1 - (N/K))$. The maximum of the parabola is at $N = (K_0 + K)/2$, where we have a saddle-node bifurcation at

$$E = E_{\text{crit}} = \frac{r(K - K_0)^2}{4KK_0} \, .$$

We can also calculate the maximum sustainable yield or simply transform the bifurcation diagram to show the yield $E \cdot N$ on the y-axis. We see that the optimal harvesting rate is very close to the bifurcation point!

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

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

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

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

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

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

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:

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

- 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:

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

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

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

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

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

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:

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

We then have

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

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

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

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

Although $\dot{N}(t)$ 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 difference-differential 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

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

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?