Ecological Dynamics

Demographic models

Dr. Tarik C. Gouhier

⟨tarik.gouhier@gmail.com⟩

Northeastern University
`http://blackboard.neu.edu`

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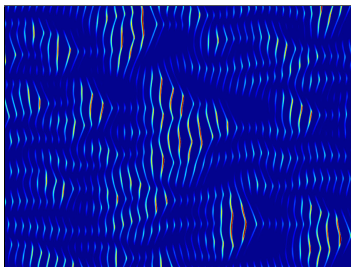
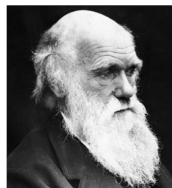# The behavior of biological populations

Population growth

Biological populations tend to increase exponentially in size in the absence of any constraints

Thomas Malthus
"The power of population is so superior to the power of the earth to produce subsistence for man, that premature death must in some shape or other visit the human race." – Malthus (1798)

Charles Darwin
"As more individuals of each species are born than can possibly survive, there is a recurring struggle for existence such that any being that varies in a profitable manner will be naturally selected." – Darwin (1859)

Malthusian catastrophes

Malthus (1798) went on to suggest that human societies would outgrow their resources and generate what is called a **Malthusian catastrophe**:
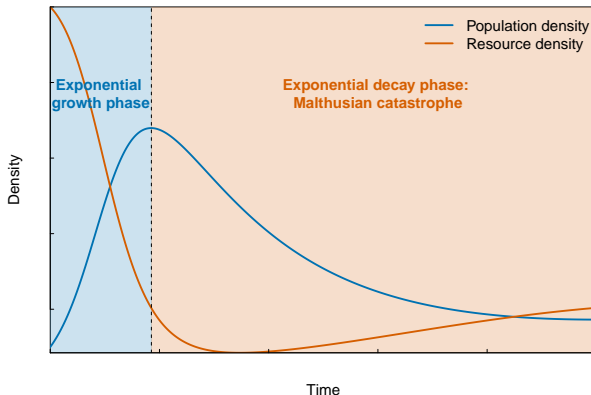
This continues to be a point of contention today but it is important to note that Malthusian catastrophes have never happened; care to guess why?
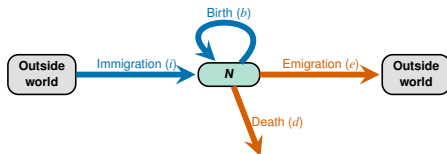
A minimal model of population growth in discrete time

Let's build and depict a minimal model of population size N to understand these basic principles:
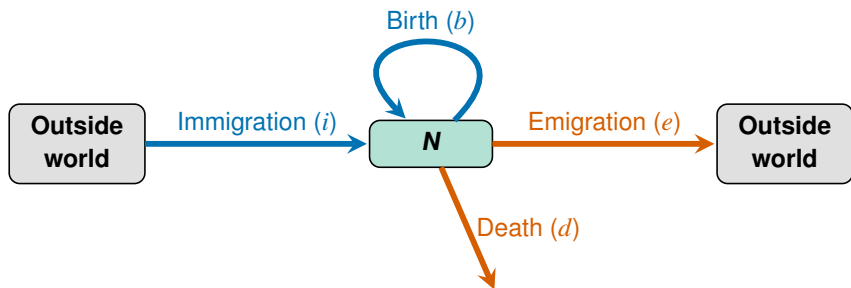
N depends on the balance between the number of individuals entering and leaving the population via local and regional processes.

A minimal model of population growth in discrete time

A minimal model of population size N at time $t + 1$ can be written as:

$$N(t + 1) = N(t) + N(t) \cdot \underbrace{(b - d)}_{\text{Local processes}} + \underbrace{(i - e)}_{\text{Regional processes}}$$

This can be simplified by assuming a closed population (i.e., $i - e = 0$):

$$N(t + 1) = N(t) + N(t) \cdot (b - d)$$

Setting $R = b - d$ and defining the dimensionless **finite rate of increase** $\lambda = 1 + R$:

$$\boxed{N(t + 1) = N(t) \cdot (1 + R) = N(t)\lambda}$$

A minimal model of population growth in discrete time

The following equation is called the **geometric growth model**:

$$N(t+1) = N(t) \cdot (1+R) = N(t)\lambda$$

It describes a **recursive process** that can be solved by induction. We begin by solving for $t = 1$:

$$N(1) = N(0)\lambda$$

Now, let's solve the equation for $t = 2$:

$$N(2) = N(1)\lambda = (N(0)\lambda)\,\lambda = (N(0))\,\lambda^2$$

By induction, $N(t)$ will be

$$\boxed{N(t) = N(0)\lambda^t}$$

This means that if $\lambda = 0$, the population will neither grow nor decrease. If $\lambda > 0$, the population will increase exponentially. If $\lambda < 0$, the population will decay exponentially.

We can compute the time it takes for a population experiencing geometric growth to double in size by solving for $N(t) = 2 \cdot N(0)$:

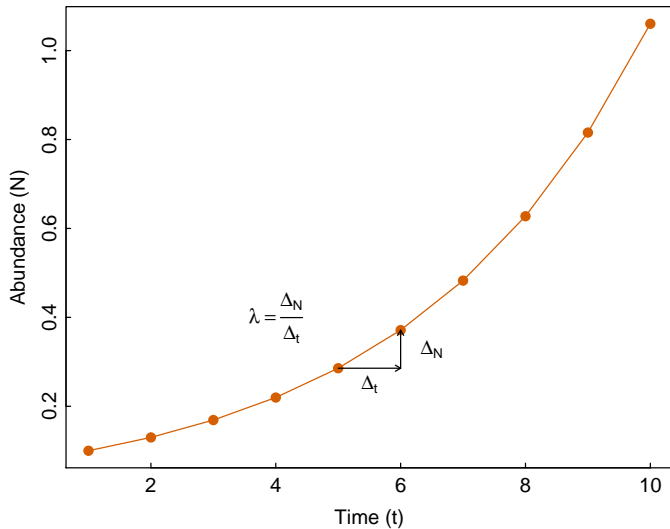$$2 \cdot N(0) = N(0)\lambda^t$$

The $N(0)$ cancel out:

$$2 = \lambda^t$$

Taking the logarithm on both sides and rearranging yields:

$$\boxed{t = \frac{\ln(2)}{\lambda}}$$

This result makes sense since it shows that the time it takes for a population to double in size decreases with its finite rate of increase λ.

John Graunt, one of the first demographers, found that London was doubling in size every 64 years ($\lambda \approx 0.0108$).

Example of geometric growth

$$\lambda = \frac{\Delta_N}{\Delta_t}$$

Taking he natural logarithm of both sides of the equation can help us understand the behavior of the model and estimate its parameters using simple regression:
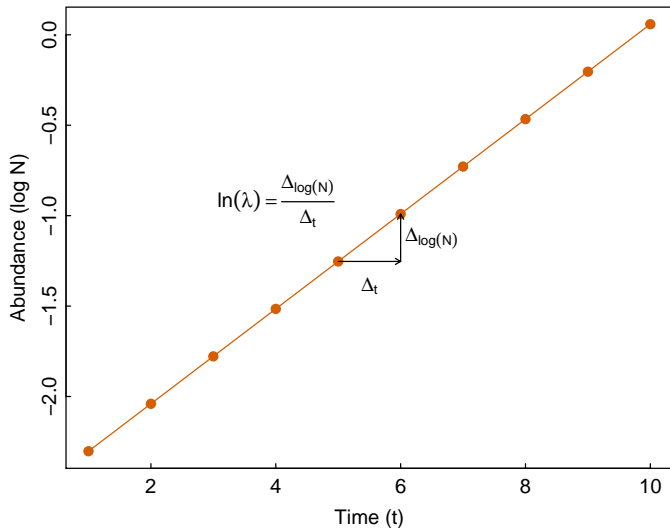
$$\ln(N(t)) = \ln\left(N(0)\lambda^t\right)$$

Using the laws of logarithms, we have:

$$\boxed{\ln(N(t)) = \ln(N(0)) + \ln\left(\lambda^t\right) = \ln(N(0)) + t \cdot \ln(\lambda)}$$

This means that we can estimate $N(0)$ and λ by regressing $\ln(N(t))$ against time. The intercept will be $\ln(N(0))$ and the slope will be $\ln(\lambda)$.

Estimating the finite rate of increase statistically

$$\ln(\lambda) = \frac{\Delta_{\log(N)}}{\Delta_t}$$

Abundance (log N) vs Time (t)

Assumptions of the geometric growth model

- **Constant growth**: λ is constant over time and does not change due to environmental or demographic stochasticity
- **Non-overlapping generations**: individuals reproduce once and then die (e.g., annual plants or insects)
- **No interactions:** individuals in the population are not affected by other species

But what about populations with overlapping generations like humans?

A minimal model of population growth in continuous time

We can use the geometric growth model as a starting point to a develop a continuous time model. To do so, we rewrite the difference equation as follows:

$$N(t + \Delta t) = N(t) + r \cdot \Delta t \cdot N(t)$$

This means that the population size at time $t + \Delta t$ is equal to population size at time t plus the growth that occurred during the Δt time period. Note that setting $\Delta t = 1$ allows us to recover the original model.

Now, we group the terms and take the limit as $\Delta t \to 0$:

$$\lim_{\Delta t \to 0} \frac{N(t + \Delta t) - N(t)}{\Delta t} = rN = \frac{dN}{dt}$$

This **exponential growth model** can thus be derived from the geometric growth model when $\Delta t \to 0$, with r representing the **intrinsic growth rate** with units of time^{-1}

Solving the exponential growth model

We have to integrate the equation by first separating the variables:

$$\frac{\mathrm{d}N}{N} = r\mathrm{d}t$$

We now prepare to integrate from $t = 0$ to t:

$$\int_{N_0}^{N_t} \frac{\mathrm{d}N}{N} = \int_0^t r\mathrm{d}t$$

Integrating and using the properties of logarithms yields:

$$\ln(N_t) - \ln(N_0) = \ln\left(\frac{N_t}{N_0}\right) = rt$$

Exponentiating both sides and multiplying by N_0 yields the solution:

$$\boxed{N_t = N_0 \cdot e^{rt}}$$

Assumptions of the exponential growth model

- **Constant growth**: r is constant over time and does not change due to environmental or demographic stochasticity
- **Overlapping generations**: individuals reproduce continuously over time (e.g., perennial plants or humans)
- **No interactions:** individuals in the population are not affected by other species

Relationship between discrete R vs. continuous r

To understand the relationship between r (continuous-time) and R (discrete-time), recall that the solution for the discrete time model is:

$$N_t = N_0 \lambda^t = N_0 (1 + R)^t$$

and that the solution for the continuous time model is:

$$N_t = N_0 e^{rt}$$

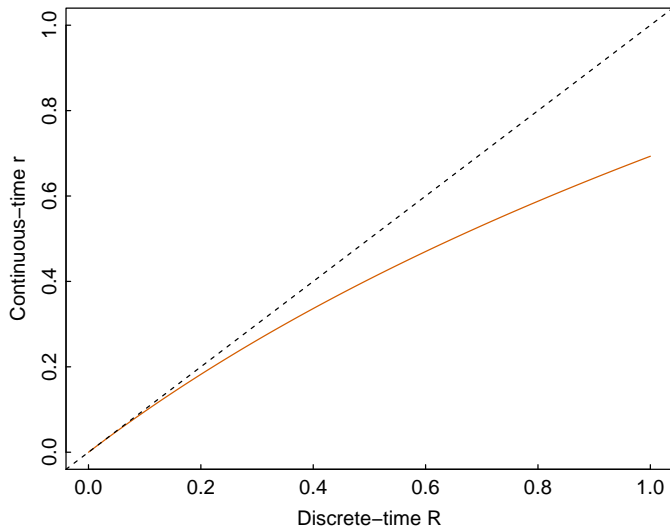Combining these equations and simplifying, we get:

$$\boxed{R = e^r - 1}$$

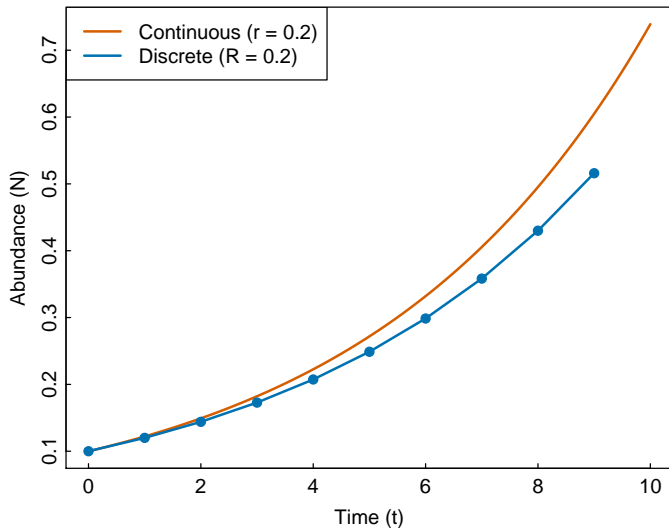Or we can express it in terms of r:

$$\boxed{r = \ln(R + 1)}$$

These terms are also very important in the world of finance. For instance, r is typically referred to as the **annual rate** for a loan whereas R is typically called **annual percentage yield (APY)**.
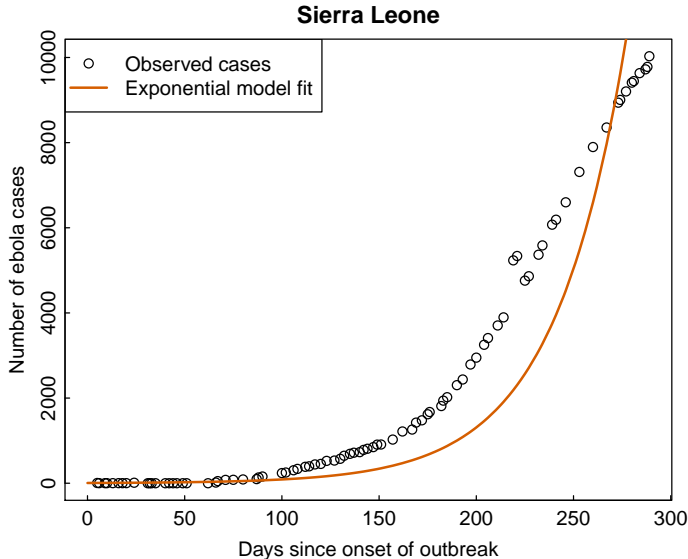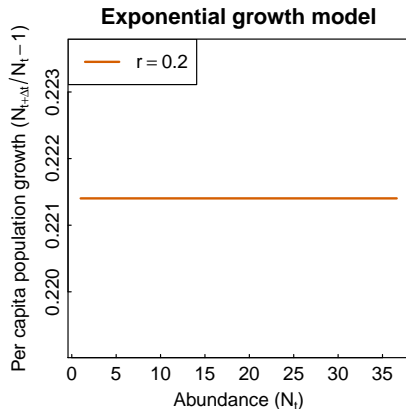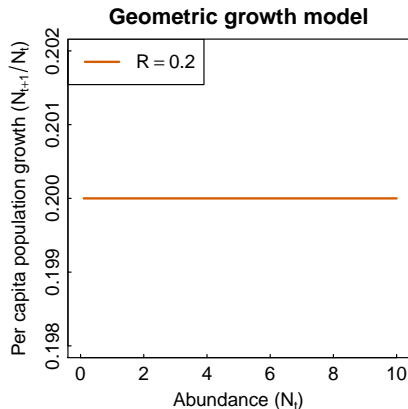
Relationship between discrete R vs. continuous r

Relationship between discrete R vs. continuous r

Example of exponential growth: Ebola from 2014-2015

Sierra Leone

Observed cases
Exponential model fit

Number of ebola cases

Days since onset of outbreak

Density-independent growth

Geometric growth model — Per capita population growth (N_{t+1}/N_t) vs Abundance (N_t), $R = 0.2$

Exponential growth model — Per capita population growth ($N_{t+\Delta t}/N_t - 1$) vs Abundance (N_t), $r = 0.2$

Both the exponential and geometric models are used to describe **density-independent** growth. This means that population growth is independent of population size.

Density-dependence and limitations on growth

P. F. Verhulst

- Verhulst (1845) introduced the **logistic growth model** to account for resource limitation
- Resource limitation was purely **phenomenological** as opposed to **mechanistic** in that it was not modeled explicitly
- Instead, it was modeled by adding a parameter K representing the **carrying capacity** or maximum population size reached as $t \to \infty$

The model simulates **density-dependent** growth: $\boxed{\dfrac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \dfrac{N}{K}\right)}$

Solving the logistic growth model I

To solve the logistic growth model, begin by separating the variables

$$\frac{\mathrm{d}N}{N\left(1 - \frac{N}{K}\right)} = r\mathrm{d}t$$

Use partial fractions to rewrite the left-hand side of the equation:

$$\frac{1}{N\left(1 - \frac{N}{K}\right)} = \frac{A}{N} + \frac{B}{\left(1 - \frac{N}{K}\right)}$$

Combine the fractions on the right hand side by multiplying by their respective denominator:

$$\frac{1}{N\left(1 - \frac{N}{K}\right)} = \frac{A - \frac{AN}{K} + BN}{N\left(1 - \frac{N}{K}\right)}$$

Solving the logistic growth model II

Focus on the numerators and factor by N:

$$1 = N\left(B - \frac{A}{K}\right) + A$$

Since there is no N on the left-hand side we must have $B = \frac{A}{K}$ and $A = 1$. We can rewrite our original equation as follows:

$$\frac{\mathrm{d}N}{N\left(1 - \frac{N}{K}\right)} = \frac{\mathrm{d}N}{N} + \frac{\mathrm{d}N}{K - N} = r\mathrm{d}t$$

We can now prepare both sides of the equation for integration:

$$\int \frac{\mathrm{d}N}{N} + \int \frac{\mathrm{d}N}{K - N} = \int r\mathrm{d}t$$

Solving the logistic growth model III

The second term is going to be a bit tricky to integrate as-is, so we introduce the following substitution $u = K - N$ so that $du = -dN$. We can now replace the problematic term in the original equation:

$$\int \frac{dN}{N} - \int \frac{du}{u} = \int r dt$$

We can finally integrate all three parts and use the properties of logarithms to gather terms:

$$\ln\left(\frac{N}{K - N}\right) = rt + P$$

Exponentiate both sides:

$$\frac{N}{K - N} = e^{rt+P} = e^{rt} e^P$$

Solving the logistic growth model IV

Rewrite the equation by setting $C = e^P$ at $t = 0$, $C = e^P = \frac{N_0}{K - N_0}$:

$$\frac{N}{K - N} = Ce^{rt}$$

Replace all instances of C and isolate N to obtain the solution:
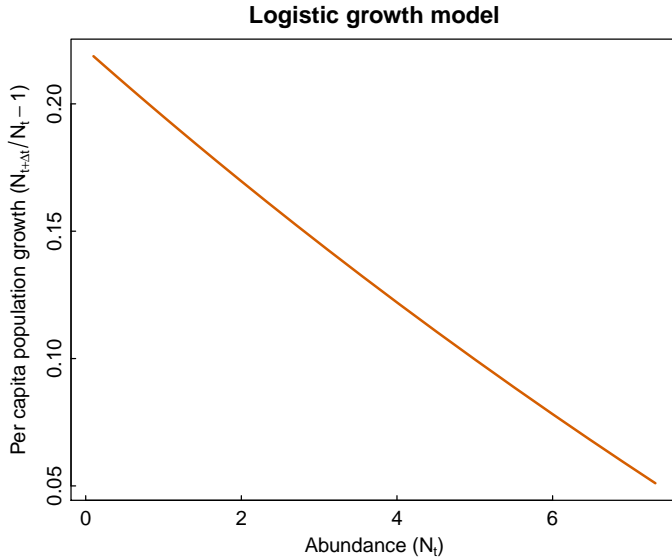
$$N(t) = \frac{KN_0 e^{rt}}{K + N_0 \left(e^{rt} - 1\right)}$$

We can make sure that the solution makes sense by dividing all terms by e^{rt} and taking the limit as $t \to \infty$:

$$\lim_{t \to \infty} \frac{KN_0}{\frac{K}{e^{rt}} + N_0 - \frac{N_0}{e^{rt}}} = \frac{KN_0}{N_0} = K$$

Hence, at equilibrium (i.e., $t \to \infty$), the population size $N(t)$ will be K.

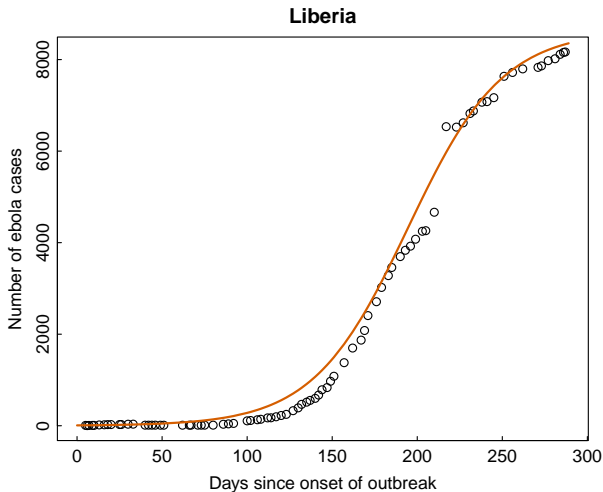# Density-dependent growth in the logistic model

Logistic growth model

Example of density-dependence in microbes
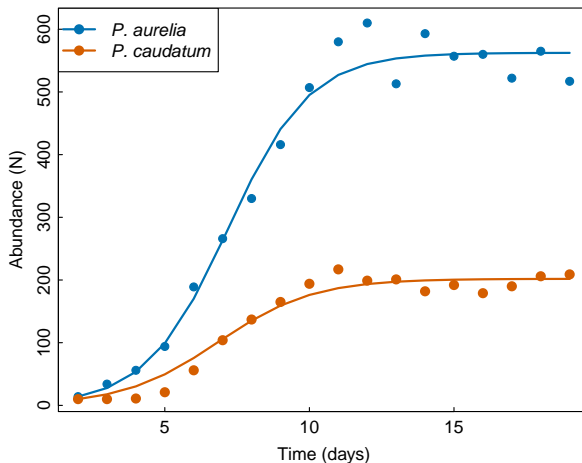
Gause (1934) showed that Paramecium species grown in isolation underwent logistic growth.

# Example of density-dependence in disease outbreaks


Liberia

The 2014-2015 Ebola outbreak shows signs of density-dependent growth in Liberia indicating resource (host) limitation.

Density-dependence in discrete time

Naturally, a discrete-time version of the logistic growth model exists and it is called the **logistic map**: $N_{t+1} = N_t \left(1 + R \left(1 - \frac{N}{K} \right) \right)$

May (1974) was the first to show that increasing R leads populations over/undershooting their carrying capacity K and complex 'equilibrium' behavior such as **limit cycles** or **chaos**.

Limit cycles describe regular oscillations in population size whereas **chaos** represents irregular oscillations that persist over time.
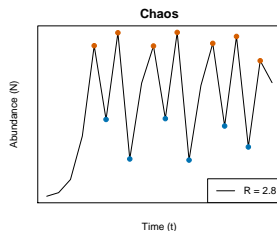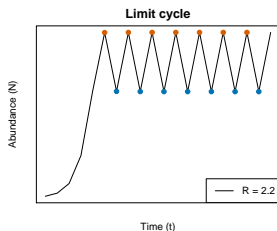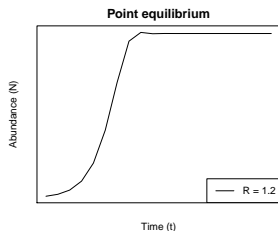
Understanding discrete-time models via cobwebbing

Cobwebbing is a technique used to describe the behavior of discrete-time models of the type $N_{t+1} = f(N_t)$ and it consists of the following steps:

1. Simulate the model for t time steps with initial abundance N_0, carrying capacity K and growth R

2. Create a vector of N_t values between 0 and K and compute $N_{t+1} = f(N_t)$

3. Plot N_{t+1} against N_t, which is called the function curve $f(N_t)$,

4. Plot the 1:1 line (slope of 1, intercept of 0)

5. Plot an arrow from the initial abundance N_0 with coordinates $(N_0, f(N_0))$ to the 1:1 line with coordinates $(f(N_0), f(N_0))$

6. Plot an arrow from the 1:1 line with coordinates $(f(N_0), f(N_0))$ to the next point on the function curve with coordinates $(f(N_0), f(f(N_0))$

7. Repeat for subsequent points in the time series generated in step 1

The arrows describe the trajectory of the abundance over time and the behavior of the model.

Example of cobwebbing for logistic map
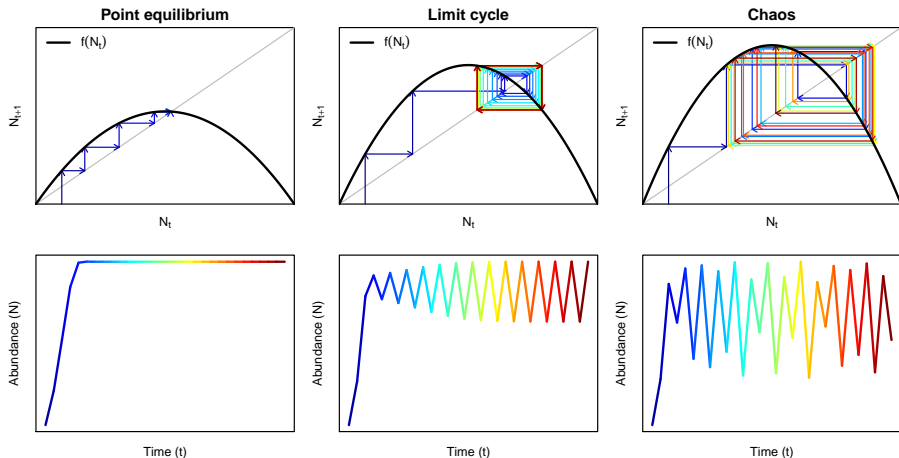
A **point equilibrium** occurs when the trajectory converges and remains on the function curve. A **limit cycle** occurs when the trajectory arrows increasingly overlap and circle the function curve. **Chaos** occurs when the trajectory arrows do not overlap and circle the function curve.

Bifurcation analysis

The complex equilibrium behavior of discrete-time models is often analyzed by producing **bifurcation diagrams**. These describe how the equilibrium behavior of the model behaves in response to changes in a forcing parameter.

One easy way to identify shifts in the equilibrium behavior of a model is to plot the local minimum and maximum values of population size (i.e., the peaks and troughs in the time series) as a function of R.

A model that reaches a **point equilibrium** will have no local minimum/maximum. A model that exhibits a **limit cycle** will fluctuate between the same set of local minima/maxima. Finally, a model that experiences **chaotic dynamics** will fluctuate between many different local minima/maxima.

Example of bifurcation diagram for logistic map
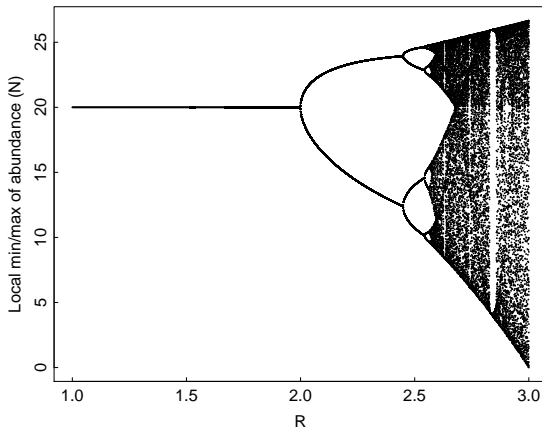
The model is characterized by a point equilibrium for $0 < R < 2$, a two-point limit cycle for $2 < R < 2.449$ followed by a series of period-doubling limit cycles and then chaos for $R > 2.570$ (May, 1974).

Taylor expansion and stability analysis

Most functions $f(x)$ can be approximated at location $x = a$ via Taylor expansion such that: $f(x) = \sum_{k=0}^{\infty} \frac{f^k(a)}{k!}(x-a)^k$, where $f^k(a)$ is the kth derivative of f at location $x = a$.

This means that we can use Taylor expansion to determine how a system with initial conditions x near equilibrium a will behave over time (i.e., will it converge on or diverge from a?).

If x is very close to a, then the term $(x-a)^k$ will be very small for $k > 1$, so we can safely approximate the behavior of f by performing a Taylor expansion with $k \in \{0, 1\}$ such that: $\boxed{f(x) \approx f(a) + f'(a)(x-a)}$

Note that this approximation becomes increasingly poor as the distance between initial conditions x and equilibrium a increases.

Example of Taylor expansion
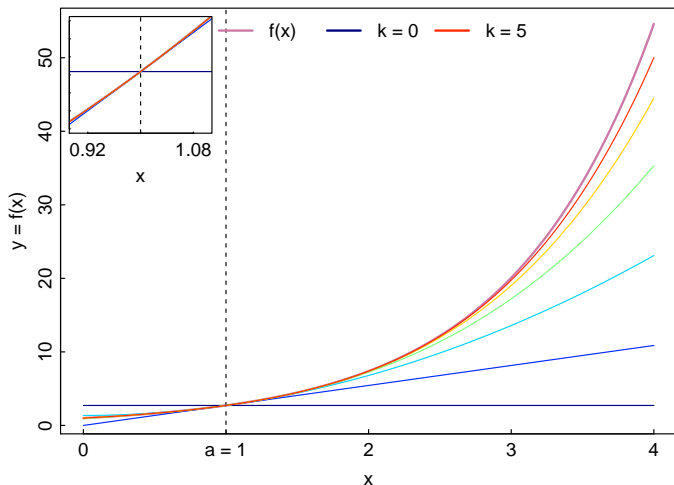
The approximation becomes progressively more accurate as k increases.

Stability of a (discrete) equilibrium

Consider a discrete model $x_{t+1} = f(x_t)$ perturbed from its equilibrium $\hat{x}$ by ϵ_t at time t:

$$x_{t+1} + \epsilon_{t+1} = f(\hat{x} + \epsilon_t)$$

The stability of the equilibrium depends on whether the perturbation ϵ_t will grow or decay over time. To determine its stability, we Taylor expand around equilibrium $\hat{x}$ to approximate $f(x)$ at initial condition $x = \hat{x} + \epsilon_t$:

$$x_{t+1} + \epsilon_{t+1} = f(\hat{x}) + f'(\hat{x})(\hat{x} + \epsilon_t - \hat{x}) = f(\hat{x}) + f'(\hat{x})\epsilon_t$$

Since we are at equilibrium, $x_{t+1} = f(\hat{x}) = \hat{x}$, so the expression simplifies to:

$$\epsilon_{t+1} = f'(\hat{x})\epsilon_t$$

Dividing through by ϵ_t yields the solution:

$$\boxed{\frac{\epsilon_{t+1}}{\epsilon_t} = f'(\hat{x})}$$

Stability of a (discrete) equilibrium

There are four possible outcomes for the stability of a discrete equilibrium $\hat{x}$:

$f'(\hat{x}) > 0$; ϵ_t and ϵ_{t+1} have the same sign (i.e., on same side of equilibrium)

1. $f'(\hat{x}) > 1$: **unstable equilibrium**; perturbation will grow over time
2. $0 < f'(\hat{x}) < 1$: **stable equilibrium**; perturbation will decay over time

$f'(\hat{x}) < 0$; ϵ_t and ϵ_{t+1} have opposite signs (i.e., on opposite sides of equilibrium)

1. $f'(\hat{x}) < -1$: **unstable equilibrium**; perturbation will grow over time
2. $-1 \leq f'(\hat{x}) < 0$: **stable equilibrium**; perturbation will decay over time

Note that an equilibrium $\hat{x}$ is said to be locally stable if all initial conditions that are (infinitesimally) close to $\hat{x}$ converge to $\hat{x}$ as time goes to infinity.

Can you guess why that is?

Stability of a (continuous) equilibrium

Consider a continuous model $\frac{dx}{dt} = f(x)$ perturbed from its equilibrium $\hat{x}$ by ϵ_t at time t:

$$\frac{d(\hat{x} + \epsilon_t)}{dt} = f(\hat{x} + \epsilon_t)$$

The stability of the equilibrium depends on whether the perturbation ϵ_t will grow or decay over time. To determine its stability, we Taylor expand around equilibrium $\hat{x}$ to approximate $f(x)$ at initial condition $x = \hat{x} + \epsilon_t$:

$$\frac{d(\hat{x} + \epsilon_t)}{dt} = f(\hat{x}) + f'(\hat{x})(\hat{x} + \epsilon_t - \hat{x}) = f(\hat{x}) + f'(\hat{x})\epsilon_t$$

Since we are at equilibrium, $f(\hat{x}) = 0$ and $\frac{d\hat{x}}{dt} = 0$, so the expression simplifies to:

$$\boxed{\frac{d(\hat{x} + \epsilon_t)}{dt} = \frac{d\epsilon_t}{dt} = f'(\hat{x})\epsilon_t}$$
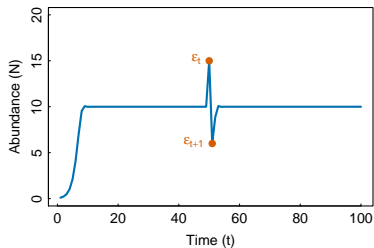
Stability of a (continuous) equilibrium

There are two possible outcomes for the stability of a continuous equilibrium $\hat{x}$:

1. $f'(\hat{x}) > 0$: **unstable equilibrium**; perturbation will grow over time
2. $f'(\hat{x}) < 0$: **stable equilibrium**; perturbation will decay over time
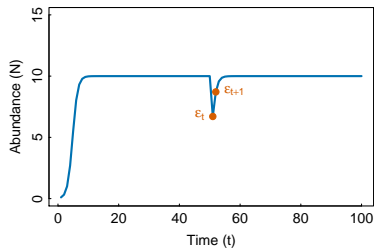
Stability outcomes for discrete vs. continuous models

Discrete logistic map
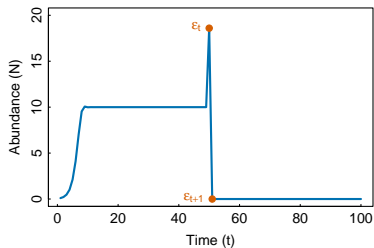Stable equilibrium $(-1 \leq f'(x) < 0)$

Continuous logistic growth
Stable equilibrium $(f'(x) < 0)$

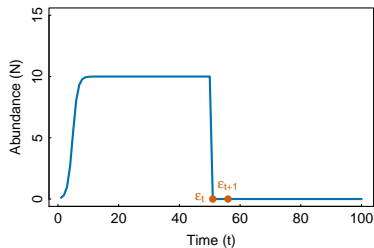**Discrete logistic map**
Unstable equilibrium $(f'(x) < -1)$

Continuous logistic growth
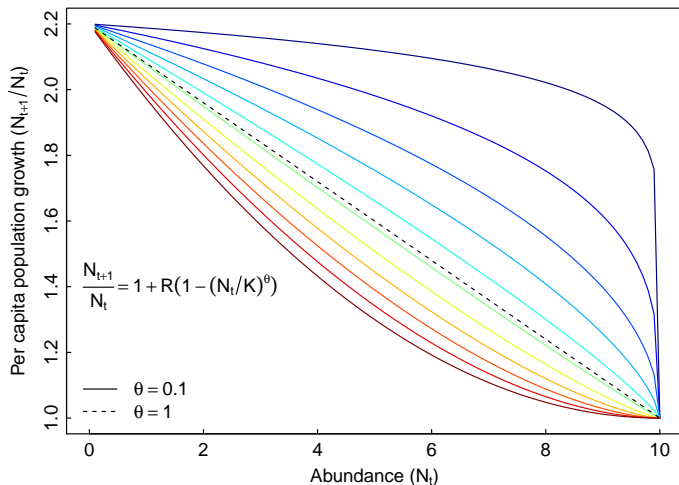Unstable equilibrium $(f'(x) > 0)$

Extensions of the logistic model

The θ-logistic model is a simple extension of the logistic map and logistic growth models introduced by Gilpin and Ayala (1973) that has gained a lot of attention because of its flexible nature (Sibly et al., 2005).

The discrete-time θ-logistic model is $N_{t+1} = N_t \left(1 + R \left(1 - \left(\frac{N}{K} \right)^{\theta} \right) \right)$ and the continuous-time version is $\frac{dN}{dt} = rN \left(1 - \left(\frac{N}{K} \right)^{\theta} \right)$.

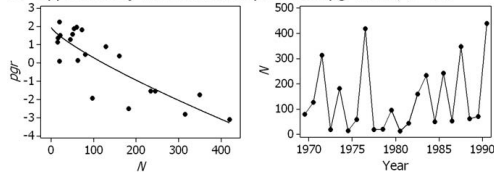The θ-logistic model can be used simulate different types of **density-dependence** by varying θ.

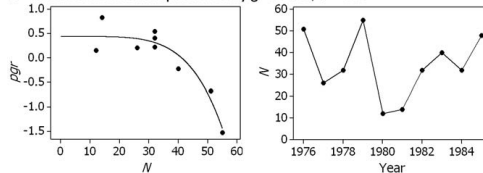# Example of density-dependence with the θ-logistic model

Per capita population growth (N_{t+1}/N_t)

$$\frac{N_{t+1}}{N_t} = 1 + R(1 - (N_t/K)^{\theta})$$

— $\theta = 0.1$
- - - $\theta = 1$

Abundance (N_t)

Increasing θ increases the strength of density-dependence.

Examples of θ-logistic growth in nature (Sibly et al., 2005)

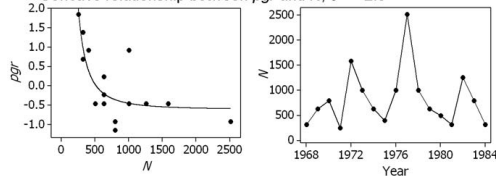# Discrete-time models and stock-recruitment

Determining the relationship between stock (number of reproducing adults at time t) and recruitment (number of offspring produced at time $t + 1$) is critical to properly manage fisheries.

Beverton and Holt (1957) and Ricker (1954) developed discrete-time models of density-dependence to estimate stock-recruitment relationships.

The Ricker model describes population size at time $t + 1$ as $N_{t+1} = N_t e^{R\left(1 - \frac{N_t}{K}\right)}$, where K represents the carrying capacity and R the maximum growth from time t to $t + 1$

The Beverton-Holt model describes population size at time $t + 1$ as $N_{t+1} = \frac{vKN}{K+(v-1)N}$, where K represents the carrying capacity and v the maximum growth from time t to $t + 1$

Density-dependence in Beverton-Holt and Ricker models
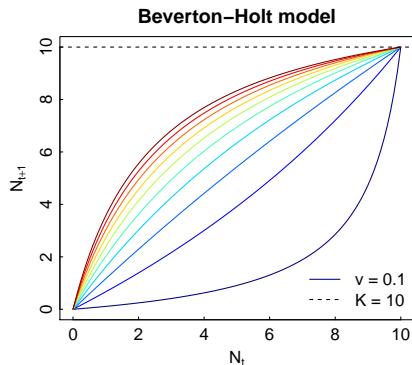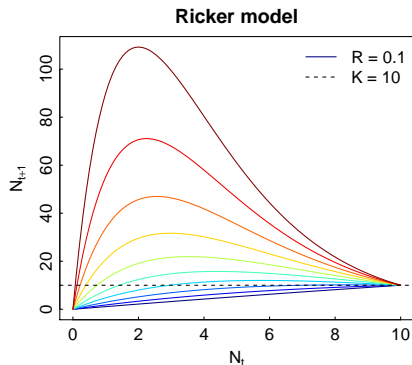
Geritz and Kisdi (2004) provides a great overview of discrete models and their mechanistic underpinnings.

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