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CONTINUOUS-TIME MODELS (part II)

Based on J.Engelstädter, U. of Queensland, and Otto and Day 2007

ODE MODEL FOR EXPONENTIAL POPULATION GROWTH

The first discrete-time model for population growth was one where we assumed that for each time step, every individual produces a certain, fixed number of offspring. Let's try to reproduce the model with continuous time, using an ODE

Individuals in the population reproduce continuously throughout the year

$$N'(t) = rN(t)$$

- Linear
- First order

We can also derive this differential equation more formally by starting from the corresponding discrete time model

$$N_{t+1} = aN_t$$

$$\Delta N = N_{t+1} - N_t = (a - 1)N_t$$

= Difference equation

Can also be written as:

$$N(t + \Delta t) - N(t) = (a - 1)\Delta t N(t)$$

ODE MODEL FOR EXPONENTIAL POPULATION GROWTH

$$N(t) - N(t + \Delta t) = (a - 1)\Delta t N(t)$$

$$\lim_{\Delta t \to 0} \frac{N(t) - N(t + \Delta t)}{\Delta t} = \frac{dN(t)}{dt} = N'(t)$$

- In the discrete-time model, $\Delta t = 1$
- In the continuous-time model, Δt is infinitely small

$$N'(t) = (a - 1)N(t)$$

$$\frac{N(t) - N(t + \Delta t)}{\Delta t} = \frac{(a - 1)\Delta t N(t)}{\Delta t} = (a - 1)N(t)$$

We define r as $r \coloneqq \mathrm{a} - 1$

Continuous :
$N'(t) = rN(t)$
Discrete :
$N(t + 1) = aN(t)$

ODE MODEL FOR EXPONENTIAL POPULATION GROWTH

$$N(t) - N(t + \Delta t) = (a - 1)\Delta t N(t)$$

$$N'(t) = rN(t)$$

The solution to the model is:
$N(t) = N_0 e^{rt}$

$$N'(t) = rN_0 e^{rt}$$

$$N'(t) = r(N_0 e^{rt})$$

$$N'(t) = r\mathrm{N(t)}$$

At: $t = 0,\ N(t) = N_0$

When $N_0 = 0$, the population size remains at zero no matter the growth rate

When $N_0 > 0$, the population size increases exponentially when $r > 0$, and shrinks towards 0 for $r < 0$

ODE MODEL FOR EXPONENTIAL POPULATION GROWTH

For discrete-time models, an equilibrium is defined by:

$N_{t+1} = N_t$

For continuous-time models, an equilibrium is defined by:

$N'(t) = 0$

Formally, if the differential equation is of the form:

$x'(t) = f(x(t))$

we can find the equilibria by solving

$f\left(\hat{x}\right) = 0$

for $\hat{x}$

In order to determine the stability of the equilibria in a **Continuous-Time Model**:

1. Obtain the derivative f' of the function f that defines the ODE.

2. Insert the formula for the equilibrium (e.g., $f'(\hat{x})$) and simplify.

3. If the expression is :
< 0, the equilibrium is locally stable,
> 0, the equilibrium is unstable.

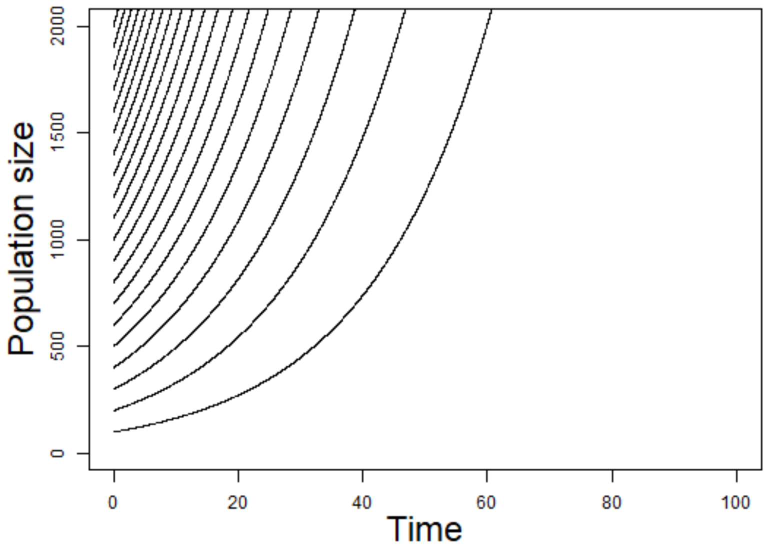
If this expression is negative, there will be oscillations around this equilibrium

EQUILIBRIA AND STABILITY OF ODE MODEL FOR EXPONENTIAL POPULATION GROWTH

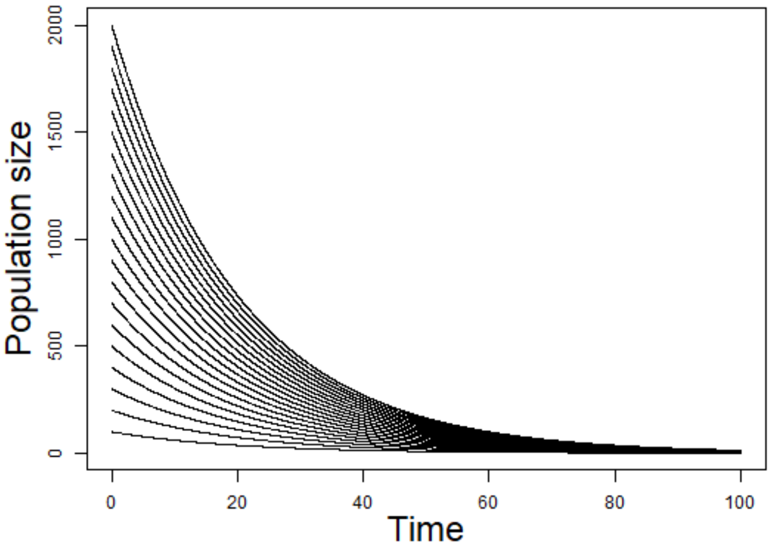
$$rN(t) = 0$$

$N(t) = 0$
is a general equilibrium
$r = 0$
is a particular equilibrium, no matter the size of the population

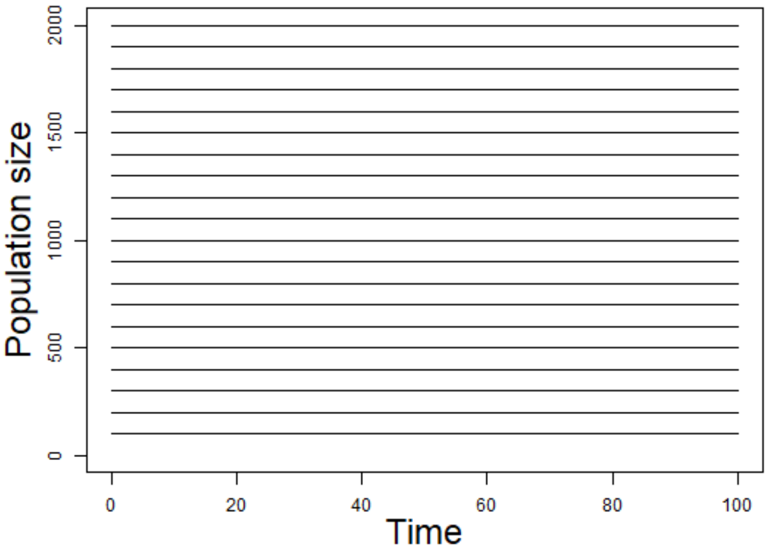
$N = 0$ is an unstable equilibrium for $r > 0$
Ex: $r = 0{,}05$



$N = 0$ is a stable equilibrium for $r < 0$
Ex: $r = -0{,}05$



$r = 0$
Every population size is stable



EQUILIBRIA AND STABILITY OF ODE MODEL FOR LOGISTIC POPULATION GROWTH

Logistic growth model:
Assume that the number of surviving offspring that an individual produces isn't constant but instead decreases with increasing population size

$$N'(t) = rN(t)(1 - \frac{N(t)}{K})$$

- $N(t)$ is the size of the population at time t
- K is the carrying capacity of the environment
- r is the growth rate

In order to identify the equilibria of the ODE, we need to find values of N where the function f defining the ODE is zero, i.e.:

$$f(N) = rN\left(1 - \frac{N}{K}\right) = 0$$

Solve this equation for N, i.e. for which value(s) of N is the equality true ?

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EQUILIBRIA AND STABILITY OF ODE MODEL FOR LOGISTIC POPULATION GROWTH

$$N'(t) = rN(t)(1 - \frac{N(t)}{K})$$

- N(t) is the size of the population at time t
- K is the carrying capacity of the environment
- r is the growth rate

In order to identify the equilibria of the ODE, we need to find values of N where the function f defining the ODE is zero, i.e.:

$$f(N) = rN\left(1 - \frac{N}{K}\right) = 0$$

For

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

To be true, two possibilities:

$$rN = 0$$

Or

$$\left(1 - \frac{N}{K}\right) = 0$$

Given $r \neq 0$, once again, a simple equilibrium:

$$N_1 = 0$$

And for the other part of the equation to be true, the only solution is:

$$N_2 = K$$

EQUILIBRIA AND STABILITY OF ODE MODEL FOR LOGISTIC POPULATION GROWTH

Exercise: give the stability of the model.

1. Obtain the derivative f' of the function f that defines the ODE.

2. Insert the formula for the equilibrium (e.g., $f'(\hat{x})$) and simplify.

3. If the expression is :
< 0, the equilibrium is locally stable,
> 0, the equilibrium is unstable.

If this expression is negative, there will be oscillations around this equilibrium

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

$$N_1 = 0$$

$$N_2 = K$$

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EQUILIBRIA AND STABILITY OF ODE MODEL FOR LOGISTIC POPULATION GROWTH

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

- N(t) is the size of the population at time t
- K is the maximum population size
- r is the growth rate

$$N_1 = 0$$

$$N_2 = K$$

Start with the derivative:

$$f'(N) = r\left(1 - \frac{N}{K}\right) + rN\left(-\frac{1}{K}\right)$$

$$f'(N) = r\left(1 - \frac{2N}{K}\right)$$

Inserting the first equilibrium:

$$f'(0) = r\left(1 - \frac{0}{K}\right) = r$$

And the second equilibrium:

$$f'(K) = r\left(1 - \frac{2K}{K}\right) = -r$$

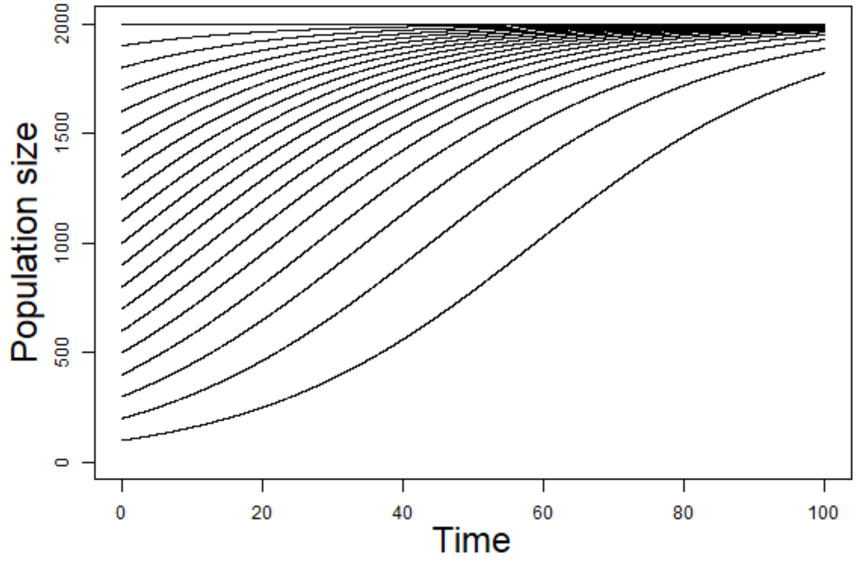
EQUILIBRIA AND STABILITY OF ODE MODEL FOR LOGISTIC POPULATION GROWTH

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

First equilibrium:
$f'(0) = r$

The equilibrium is locally stable for $r < 0$, and locally unstable for $r > 0$

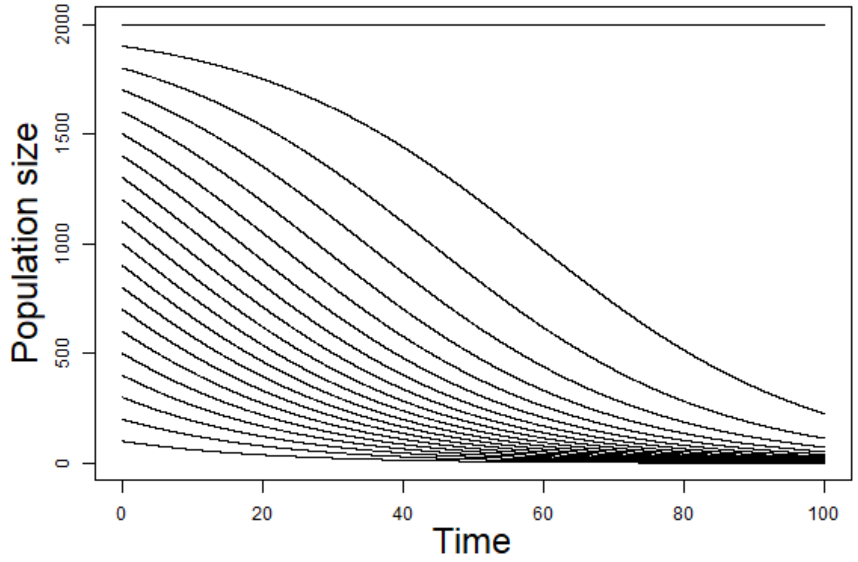
$r > 0$
$K = 2000$
Ex: $r = 0{,}05$



And the second equilibrium:
$f'(K) = -r$

The equilibrium is locally stable for $r > 0$, and locally unstable for $r < 0$

$r < 0$
$K = 2000$
Ex:
$r = -0{,}05$



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CONTINUOUS-TIME MODELS IN MULTIPLE VARIABLES

Based on J.Engelstädter, U. of Queensland, and Otto and Day 2007

THE SI MODEL

We start by considering the simplest of what we call *Compartmental models*, commonly used in epidemiology: the *SI model*

2 types of individuals in the SI model:

- Susceptibles
- Infected

We denote the number of these two types of individuals by S and I

We assume that:

- Infected people never recover
- Susceptibles can become infected by contact with infected individuals

Compartmental models are often run by differential equation, so they are usually continuous and deterministic models, but they can also be used with a stochastic framework. There is no link between discrete/continuous and stochastic/ deterministic.

- Both susceptible and infected individuals die at a rate μ
- Infected individuals can also die from the disease at a rate α, also called the *virulence* of the disease

- Finally, we assume that new susceptible individuals enter the population at a fixed rate ν

THE SI MODEL

- Two types of individuals in the SI model:
  - Susceptibles = S
  - Infected = I
- We assume that:
  - Susceptibles can become infected by contact with infected individuals
  - Infected people never recover
  - Both susceptible and infected individuals die at a rate μ
  - Infected individuals can also die from the disease at a rate α, also called the virulence of the disease
  - New susceptible individuals enter the population at a fixed rate ν

The infection rate can evolve in many different ways, intuitively depending on the number of infected

- We assume that the force of infection increases linearly with the number of susceptible individuals at a rate β
- I.e. the force of infection at any given time t is $\beta I(t)$

The equations defining the model are:

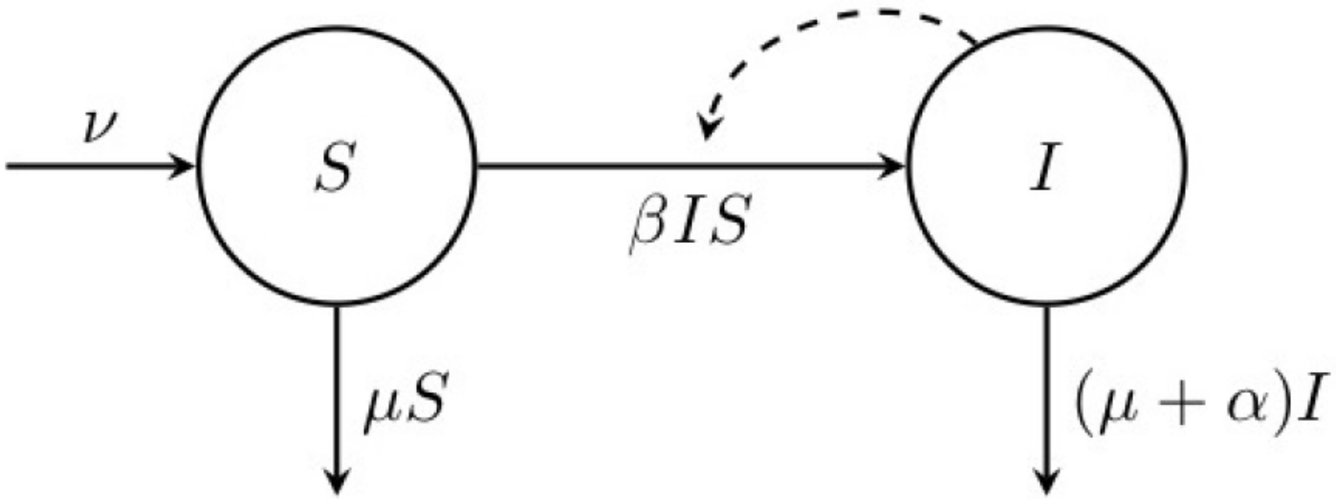
$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$
$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

THE SI MODEL

The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$

$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$



These two equations are said to be **coupled** because the equation for each of the two variables also contains the other variable

Solid arrows indicate flow in and out of compartments, and
the dashed arrow indicates that I has an impact on the rate of transition from S to I.

EQUILIBRIA OF THE SI MODEL

The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$

$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

With more than one variable, a system is said to be in equilibrium if none of its variables exhibit any change in time.

We need solutions to our system that verify **simultaneously**:

$S'(t) = 0$

$I'(t) = 0$

From the second equation of our system, we can see that $I'(t) = 0$ holds for:

$$I(t)\big(\beta S(t) - \mu - \alpha\big) = 0$$

One solution to this equality is:

$I(t) = 0$

Inserting this in the first equation, verifying S'(t)=0, gives us

$$\nu - \beta I(t)S(t) - \mu S(t) = 0$$

$$\nu - \mu S(t) = 0$$

$$S(t) = \frac{\nu}{\mu}$$

EQUILIBRIA OF THE SI MODEL

The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$

$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

We need solutions to our system that verify simultaneously:

$S'(t) = 0$

$I'(t) = 0$

i.e.:

$\nu - \beta I(t)S(t) - \mu S(t) = 0$

$I(t)\left(\beta S(t) - \mu - \alpha\right) = 0$

One solution to this equality is:

$I(t) = 0$

$$S(t) = \frac{\nu}{\mu}$$

So a first solution to our system would be:

$$\left(\hat{S}_1, \hat{I}_1\right) = (\frac{\nu}{\mu}, 0)$$

This equilibrium corresponds to the case when the disease is not present in the population and the number of uninfected individuals has reached a balance between migration and death.

EQUILIBRIA OF THE SI MODEL

We need solutions to our system that verify simultaneously:

$$S'(t) = 0$$
$$I'(t) = 0$$

I.e.:

$$\nu - \beta I(t)S(t) - \mu S(t) = 0$$
$$I(t)\big(\beta S(t) - \mu - \alpha\big) = 0$$

We now assume that:

$$I(t) > 0$$

We need the solution to:

$$\big(\beta S(t) - \mu - \alpha\big) = 0$$

$$\beta S(t) = \mu + \alpha$$

$$\hat{S}_2(t) = \frac{\mu + \alpha}{\beta}$$

We can again insert this solution into our first equation:

$$\nu - \beta I(t)\hat{S}_2(t) - \mu \hat{S}_2(t) = 0$$

EQUILIBRIA OF THE SI MODEL

We need the solution to:

$$\left(\beta S(t) - \mu - \alpha\right) = 0$$

$$\beta S(t) = \mu + \alpha$$

$$\hat{S}_2(t) = \frac{\mu + \alpha}{\beta}$$

We can again insert this solution into our first equation:

$$\nu - \beta I(t)\hat{S}_2(t) - \mu\hat{S}_2(t) = 0$$

$$\beta I(t)\hat{S}_2(t) = \nu - \mu\hat{S}_2(t)$$

$$I(t) = \frac{\nu}{\beta\hat{S}_2(t)} - \frac{\mu}{\beta}$$

$$I(t) = \frac{\nu}{\beta\frac{\mu+\alpha}{\beta}} - \frac{\mu}{\beta}$$

$$I(t) = \frac{\nu}{\mu + \alpha} - \frac{\mu}{\beta}$$

The second solution and equilibrium of our system is:

$$\left(\hat{S}_2, \hat{I}_2\right) = \left(\frac{\mu + \alpha}{\beta}, \frac{\nu}{\mu + \alpha} - \frac{\mu}{\beta}\right)$$

EQUILIBRIA OF THE SI MODEL

The second solution and equilibrium of our system is:

$$\left(\hat{S}_2, \hat{I}_2\right) = \left(\frac{\mu + \alpha}{\beta}, \frac{\nu}{\mu + \alpha} - \frac{\mu}{\beta}\right)$$

In order to be biologically meaningful, both $\hat{S}_2$ and $\hat{I}_2$ must not be negative

μ, α and β are all positive rates, so $\hat{S}_2$ is always positive as well

However, $\hat{I}_2$ is only positive if

$$\frac{\nu}{\mu + \alpha} > \frac{\mu}{\beta}$$

Or when

$$\frac{\beta\nu}{\mu(\mu + \alpha)} > 1$$

Which is equal to

$$\frac{\beta\hat{S}_1}{\mu + \alpha} > 1$$

As $\left(\hat{S}_1, \hat{I}_1\right) = \left(\frac{\nu}{\mu}, 0\right)$

EQUILIBRIA OF THE SI MODEL

So $\hat{I}_2$ is only positive for

$$\frac{\beta\nu}{\mu(\mu+\alpha)} = \frac{\beta\hat{S}_1}{\mu+\alpha} > 1$$

The left-hand side of that inequality is called R_0, the **basic reproductive number**

This number determines whether or not a disease can spread in a population.

It can be interpreted as the number of new infections that an infected individual causes in an otherwise uninfected population.

Per unit of time, an individual will cause $\beta\hat{S}_1$ new infections because at equilibrium 1 there will be $\hat{S}_1$ uninfected individuals.

The individual will be able to infect other individuals for a duration of $1/(\mu+\alpha)$ since it will die at a rate $(\mu + \alpha)$

Multiplying the infection rate per unit of time with the duration of infectivity then gives us R_0

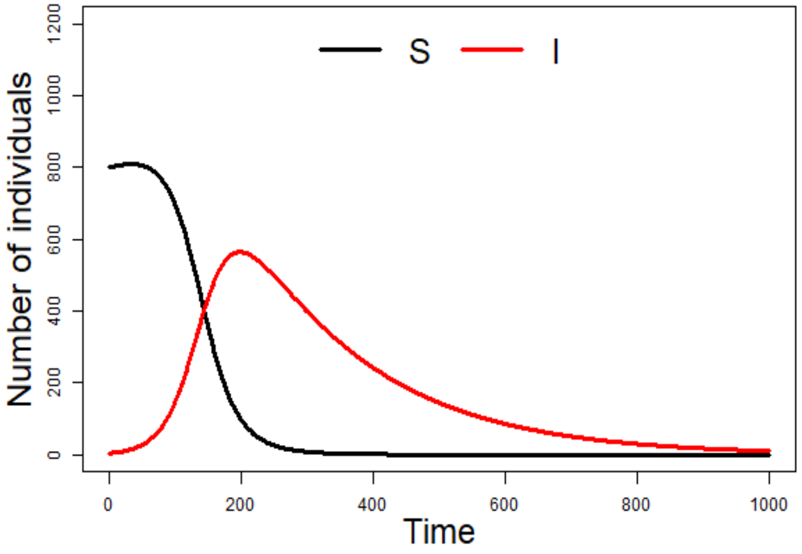
Intuitively, an infected individual must infect more than one new individual over the course of infection for the disease to spread, which is exactly the condition $R_0 > 1$

EQUILIBRIA OF THE SI MODEL

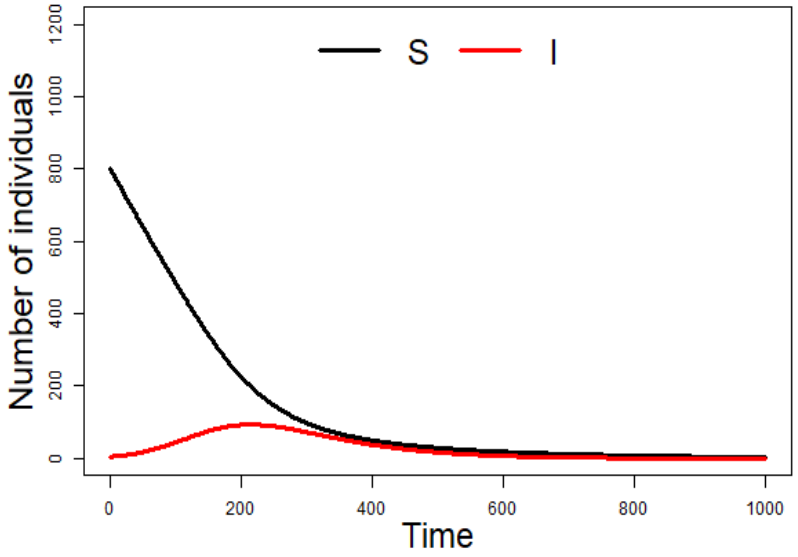
The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$
$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

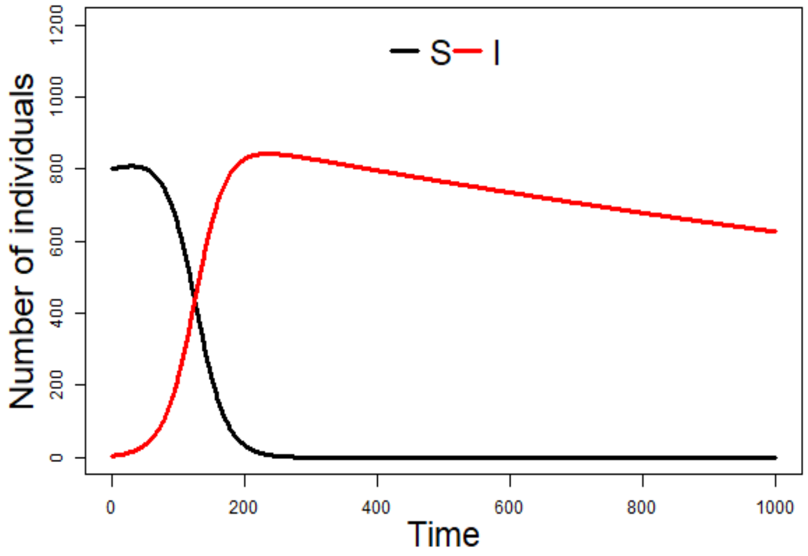
Natural death rate:
$\mu = 0,0002$
Disease death rate:
$\alpha = 0,005$
Susceptible growth:
$\nu = S * 0{,}001$
Transmission rate:
$\beta = 0,00005$
Initial S individuals:
$S_0 = 800$
Initial I individuals:
$I_0 = 5$



Natural death rate: $\mu = 0,005$



Disease death rate: $\alpha = 0,0002$



EQUILIBRIA OF THE SI MODEL

The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$
$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

Natural death rate:
$\mu = 0,0002$

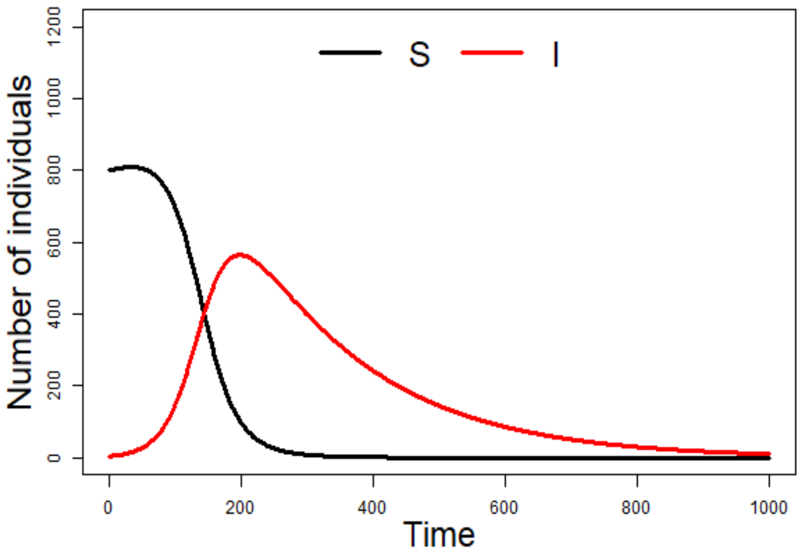
Disease death rate:
$\alpha = 0,005$

Susceptible growth:
$\nu = S * 0{,}001$

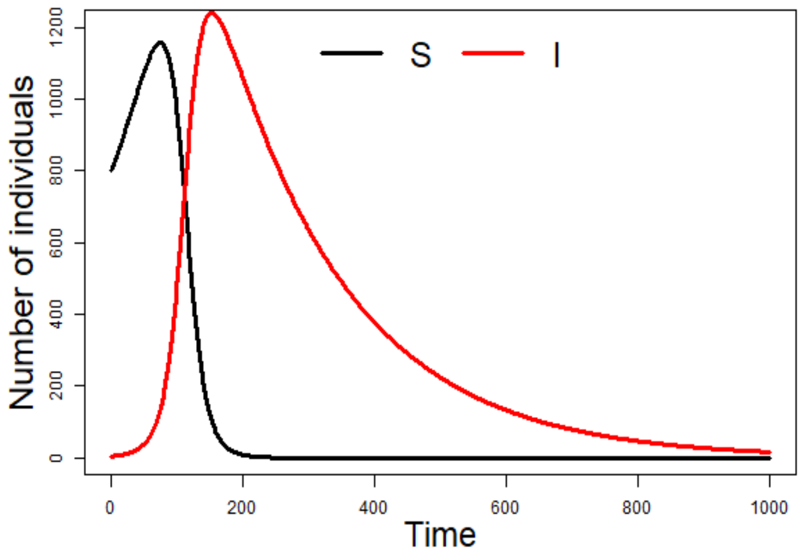
Transmission rate:
$\beta = 0,00005$

Initial S individuals:
$S_0 = 800$

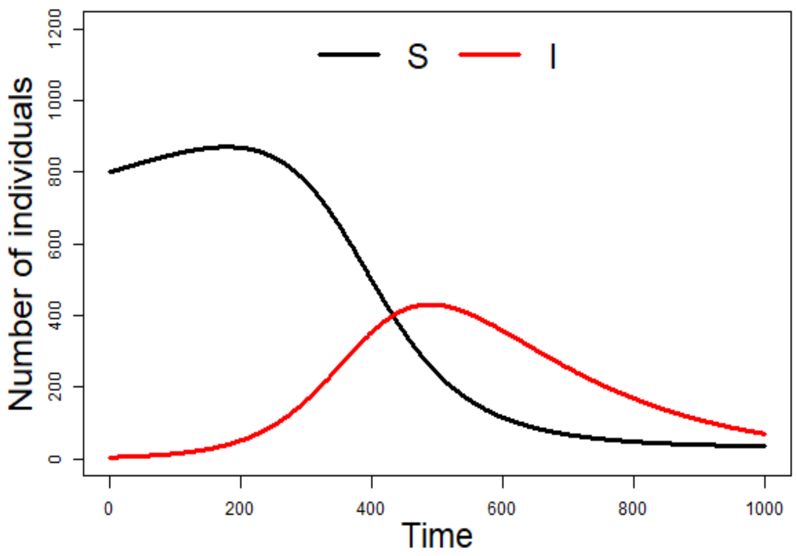
Initial I individuals:
$I_0 = 5$



Susceptible growth:
$\nu = S * 0{,}007$



Transmission rate:
$\beta = 0,0002$



EQUILIBRIA OF THE SI MODEL

The equations defining the model are:

$$S'(t) = \nu - \beta I(t)S(t) - \mu S(t)$$
$$I'(t) = \beta I(t)S(t) - (\mu + \alpha)I(t)$$

Natural death rate:

$\mu = 0,0002$

Disease death rate:

$\alpha = 0,005$

Susceptible growth:

$\nu = S * 0{,}001$

Transmission rate:

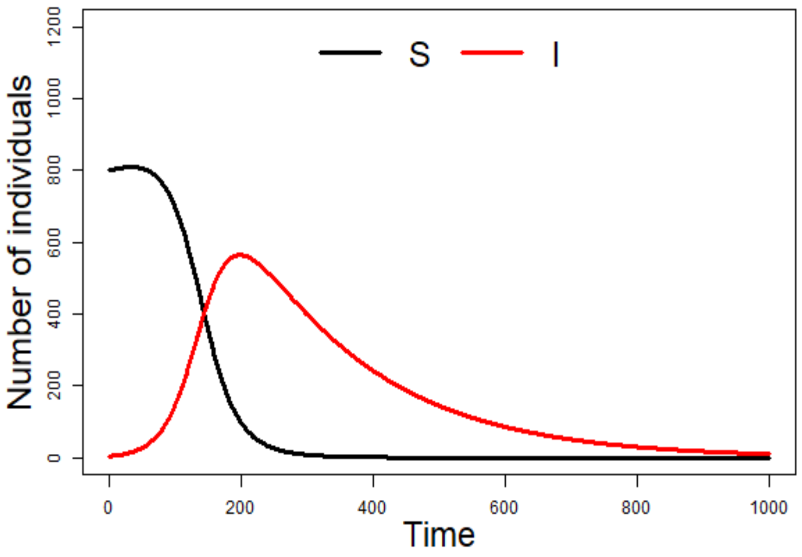
$\beta = 0,00005$

Initial S individuals:

$S_0 = 800$

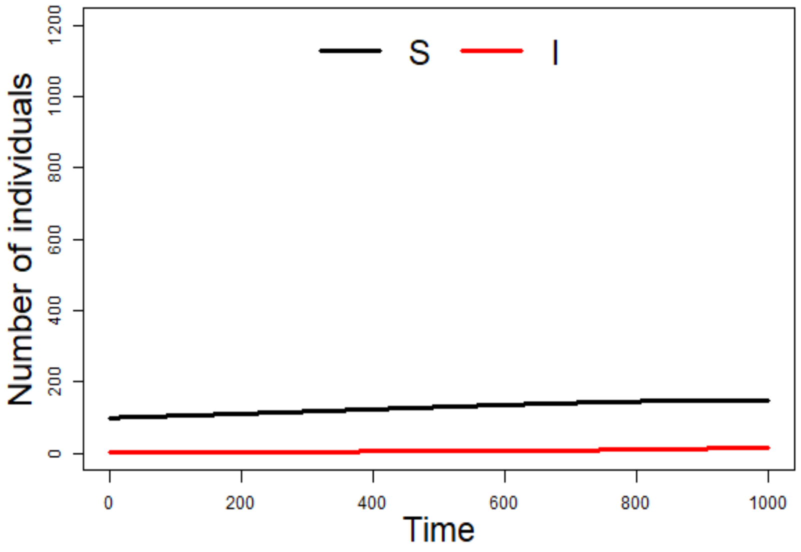
Initial I individuals:

$I_0 = 5$



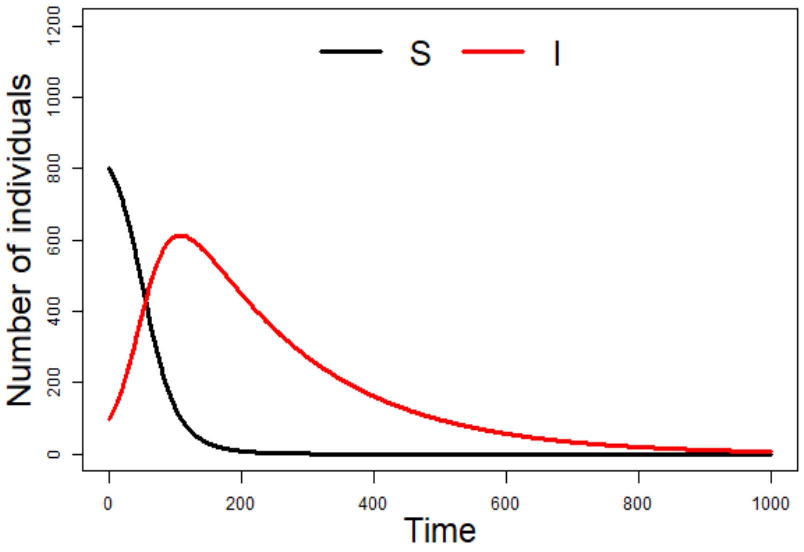
Initial S individuals:

$S_0 = 100$



Initial I individuals:

$I_0 = 100$



THE SIR MODEL

The SI model is only one out of a large number of epidemiological models that differ in the number of compartments as well as the assumptions concerning demography and transmission, amongst others.

The most famous of these models is the SIR model. Here, a third class of individuals R is considered, that have recovered from the disease and are immune to future infections.

In the simplest form, this model can be written down by the following ODE system:

$$S'(t) = \ - \ \beta I(t)S(t)$$
$$I'(t) = \ \beta I(t)S(t) - \gamma I(t)$$
$$R'(t) = \gamma I(t)$$

- β is again the per capita transmission rate
- γ is the recovery rate, which also means that $1/\gamma$ can be interpreted as the average infectious period of the disease.
- For simplicity, we now ignore all demographic processes, i.e. no new individuals enter the population, and there is no death

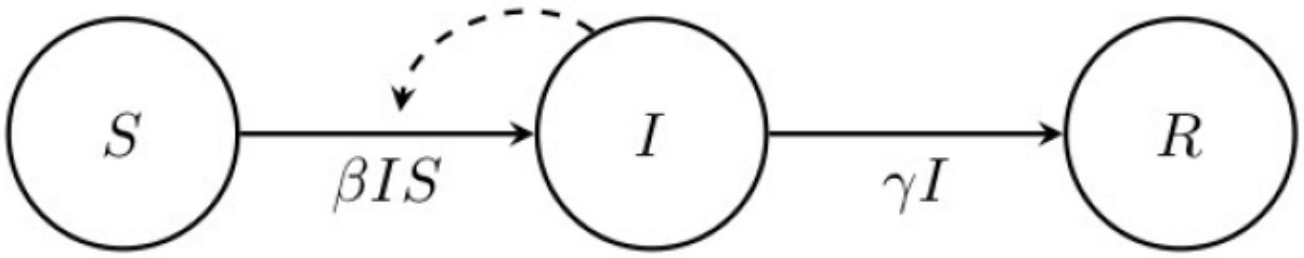
THE SIR MODEL

The model is defined by the following system of equations:

$$
\begin{aligned}
S'(t) &= -\ \beta I(t)S(t) \\
I'(t) &= \beta I(t)S(t) - \gamma I(t) \\
R'(t) &= \gamma I(t)
\end{aligned}
$$

- β is again the per capita transmission rate
- γ is the recovery rate, which also means that $1/\gamma$ can be interpreted as the average infectious period of the disease.
- For simplicity, we now ignore all demographic processes, i.e. no new individuals enter the population, and there is no death

- Three types of individuals in the SIR model:
  - Susceptibles = S
  - Infected = I
  - Recovered = R
- We assume that:
  - Susceptibles can become infected by contact with infected individuals
  - Infected can now recover
  - Recovered individuals are immune



EQUILIBRIA OF THE SIR MODEL

The model is defined by the following system of equations:

$$S'(t) = \; - \; \beta I(t)S(t)$$
$$I'(t) = \; \beta I(t)S(t) - \gamma I(t)$$
$$R'(t) = \gamma I(t)$$

With more than one variable, a system is said to be in equilibrium if none of its variables exhibit any change in time.

We need solutions to our system that verify simultaneously:

$S'(t) = 0$

$I'(t) = 0$

$R'(t) = 0$

We can assume that $I(t) = 0$ will once again reveal an equilibrium

And indeed, if we insert $I(t) = 0$ in the three equation of our model, we get:

$$S'(t) = \; - \; \beta I(t)S(t) = 0$$
$$I'(t) = \; \beta I(t)S(t) - \gamma I(t) = 0$$
$$R'(t) = \gamma I(t) = 0$$

$S'(t)$, $I'(t)$ and $R'(t)$ become zero, no matter the value of $S(t)$ and $R(t)$

There is an infinite number of equilibria given by all possible values of $S(t)$ and $R(t)$, provided that $I(t) = 0$

EQUILIBRIA OF THE SIR MODEL

The model is defined by the following system of equations:

$$S'(t) = -\beta I(t)S(t)$$
$$I'(t) = \beta I(t)S(t) - \gamma I(t)$$
$$R'(t) = \gamma I(t)$$

With more than one variable, a system is said to be in equilibrium if none of its variables exhibit any change in time.

We need solutions to our system that verify simultaneously:

$$S'(t) = 0$$
$$I'(t) = 0$$
$$R'(t) = 0$$

We need to find out under what conditions $I'(t) = \beta I(t)S(t) - \gamma I(t) > 0$

Assuming there are some infected individuals to start an epidemic, this inequality can be solved to yield:

$$\frac{\beta S(t)}{\gamma} > 1$$

The left-hand side of this inequality can again be interpreted as the basic reproductive number R_0.

If we assume $I(t) > 0$ and reconsider our system of equation, we can see that there are no more solutions, so no more equilibrium.

EQUILIBRIA OF THE SIR MODEL

The model is defined by the following system of equations:

$$S'(t) = -\beta I(t)S(t)$$
$$I'(t) = \beta I(t)S(t) - \gamma I(t)$$
$$R'(t) = \gamma I(t)$$

Recovery rate: $\gamma = 0{,}25$

Transmission rate: $\beta = 0{,}0007$

Initial S individuals: $S_0 = 800$

Initial I individuals: $I_0 = 10$

The disease can spread into a population of susceptible individuals when:

$$R_0 = \frac{\beta S(t)}{\gamma} \geq 1$$

$$\frac{\beta}{\gamma} = \frac{0{,}0007}{0{,}25} = 0{,}0028$$

So for R_0 to be superior to 1, you need:

$$S(t) \geq \frac{1}{0{,}0028} = 357{,}14$$