

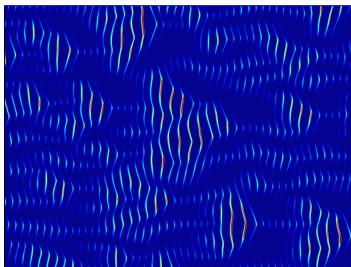
# Ecological Dynamics

## Disease ecology

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# Diseases as determinants of population dynamics

- We have seen that competition and predation can play an important role in controlling the structure and dynamics of natural ecosystems
- Diseases can play a similar role by regulating the size of populations
- Much of the work on disease ecology was pioneered by two teams of researchers: Kermack and McKendrick (1927, 1932, 1933) and Anderson and May (1979); May and Anderson (1979).

## A minimal *SI* model

A minimal *SI* model may be written as follows:

$$\begin{aligned}\frac{ds}{dt} &= -\beta is \\ \frac{di}{dt} &= \beta is\end{aligned}$$

Where  $s = S/N$ ,  $i = I/N$  represent respectively the proportion of the total population  $N$  that is susceptible or infected and  $\beta$  is the contact rate between susceptible and infected individuals.

At equilibrium, the model will clearly consist of  $N$  infected individuals and zero susceptible individuals.

## A minimal *SI* model

Since this simple model only has two compartments, the proportion of susceptible individuals is simply  $1 - i$ , so we can rewrite the second differential equation as:

$$\frac{di}{dt} = \beta i (1 - i)$$

Solving this equation will allow us to quantify the **prevalence** (proportion of individuals infected) and **incidence** (number of new cases) of the disease in the population.

# Deriving the epidemic curve for the *SI* model

To solve the *SI* model, begin by separating the variables:

$$\frac{di}{i(1-i)} = \beta dt$$

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

$$\frac{1}{i(1-i)} = \frac{A}{i} + \frac{B}{(1-i)}$$

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

$$\frac{1}{i(1-i)} = \frac{A(1-i) + Bi}{i(1-i)}$$

# Deriving the epidemic curve for the $SI$ model

Focus on the numerators and factor by  $i$ :

$$1 = i(A + B) + A$$

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

$$\frac{di}{i(1-i)} = \frac{di}{i} - \frac{di}{1-i} = \beta dt$$

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

$$\int \frac{di}{i} + \int \frac{di}{1-i} = \int \beta dt$$

## Deriving the epidemic curve for the $SI$ model

The second term is going to be a bit tricky to integrate as-is, so we introduce the following substitution  $u = 1 - i$  so that  $du = -di$ . We can now replace the problematic term in the original equation:

$$\int \frac{di}{i} - \int \frac{du}{u} = \int \beta dt$$

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

$$\ln\left(\frac{i}{1-i}\right) = \beta t + P$$

Exponentiate both sides:

$$\frac{i}{1-i} = e^{\beta t + P} = e^{\beta t} e^P$$

## Deriving the epidemic curve for the $SI$ model

Rewrite the equation by setting  $C = e^P$  at  $t = 0$ ,  $C = e^P = \frac{i_0}{1-i_0}$ :

$$\frac{i}{1-i} = Ce^{\beta t}$$

Replace all instances of  $C$  and isolate  $i$  to obtain the solution:

$$i(t) = \frac{i_0 e^{\beta t}}{1 + i_0 (e^{\beta t} - 1)}$$

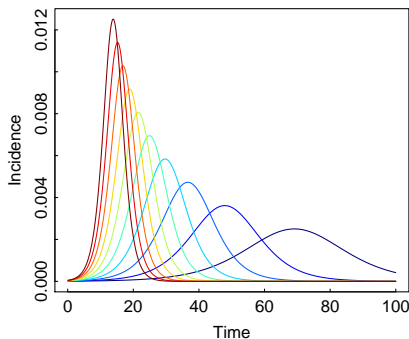
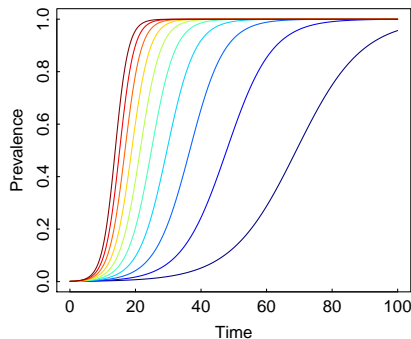
We can make sure that the solution makes sense by dividing all terms by  $e^{\beta t}$  and taking the limit as  $t \rightarrow \infty$ :

$$\lim_{t \rightarrow \infty} \frac{i_0}{\frac{1}{e^{\beta t}} + i_0 - \frac{i_0}{e^{\beta t}}} = \frac{i_0}{i_0} = 1$$

As  $t \rightarrow \infty$ , the proportion of infected individuals or **prevalence**  $i(t)$  will be 1.



# Disease prevalence and incidence over time



Increasing the transmission rate  $\beta$  increases the spread of the disease, leading to earlier peaks in disease incidence.

Note that the incidence curves are hump-shaped but almost never symmetrical.

## A minimal *SIR* model

Kermack and McKendrick (1927) developed the following minimal *SIR* model:

$$\frac{ds}{dt} = -\beta si$$

$$\frac{di}{dt} = \beta si - \gamma i$$

$$\frac{dr}{dt} = \gamma i$$

Where  $s = S/N$ ,  $i = I/N$  and  $r = R/N$  represent respectively the proportion of the total population  $N$  that is susceptible, infected or recovered.

$\beta$  and  $\gamma$  represent respectively the contact rate and removal rate.

# A minimal *SIR* model

The disease will spread if  $\frac{di}{dt} > 0$ :

$$\frac{di}{dt} = \beta si - \gamma i > 0$$

Simplifying this equation yields:

$$\frac{\beta s}{\gamma} > 1$$

At the onset, we have  $s \approx 1$ , so this yields:

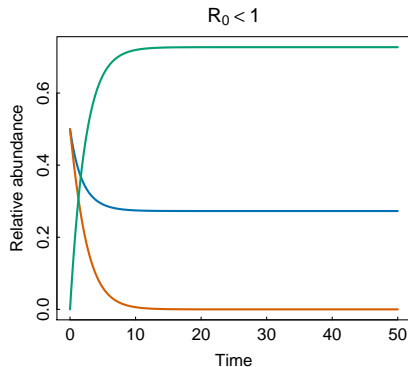
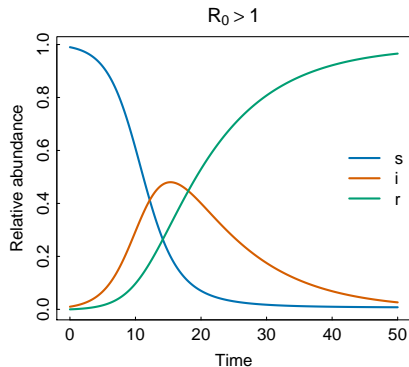
$$R_0 = \frac{\beta}{\gamma} > 1$$

# Interpreting $R_0$

The quantity  $R_0$  is called the **basic reproduction number** and it represents the expected number of secondary infections generated by a single infection in a completely susceptible population.

Condition	Outcome	Description
$R_0 > 1$	Epidemic	The disease will spread
$R_0 = 1$	Endemic	The disease will persist without spreading
$R_0 < 1$	Die-out	The disease will not spread

# SIR model dynamics



When  $R_0 > 1$ , the disease will persist as long as susceptible individuals remain in the population whereas when  $R_0 < 1$ , the disease will not spread.

## The relationship between $\beta$ and $R_0$

$\beta$  technically represents the *per capita* rate of infection given contact between a susceptible and infected individual.

It combines the transmissibility of the pathogen  $\tau$  and the frequency of contact  $\bar{c}$  into a single parameter.

Since we assumed that removal rate  $\gamma$  was constant, the expected time to removal is  $\delta = \frac{1}{\gamma}$ .

$\delta$  thus represents the average duration of an infection in an individual prior to his/her removal.

# The relationship between $\beta$ and $R_0$

We can now rewrite  $\beta = \tau\bar{r}$  and  $R_0$  as:

$$R_0 = \frac{\beta}{\gamma} = \frac{\tau\bar{c}}{\gamma} = \tau\bar{c}\delta$$

Note that since  $\tau$  has units of  $\frac{\text{infection}}{\text{contact}}$ ,  $\bar{c}$  has units of  $\frac{\text{contact}}{\text{time}}$  and  $\delta$  has units of  $\frac{\text{time}}{\text{infection}}$ ,  $R_0$  is dimensionless.

# Controlling diseases via $R_0$

$R_0$  suggests three possible ways to limit the spread of diseases:

- 1 **Reduce transmissability**  $\tau$ : this can be achieved via vaccination, contraceptives or antiviral medication
- 2 **Reduce contact rate**  $\bar{c}$ : this can be achieved by imposing quarantines, implementing health education programs
- 3 **Reduce duration of infectious period**  $\delta$ : this can be achieved by using antibiotic treatments for bacterial infections, antivirals for virus infections and other therapies to boost immune response



## Example: designing vaccination strategies

To determine the proportion of the population  $0 < p_C \leq 1$  that needs to be vaccinated in order to avoid an epidemic, one can define  $R_0^*$  as the reproduction number of the immunized population and  $R_0$  as that of the susceptible population:

$$R_0^* = R_0 (1 - p_C)$$

Since the criterion for an epidemic is  $R_0^* > 1$ , we can solve the equality above to find the critical proportion of the population  $p_C$  that needs to be immunized in order to avoid an epidemic:

$$R_0 (1 - p_C) = 1$$

$$p_C = 1 - \frac{1}{R_0}$$

## Example: the *SIRV* model

We can extend the *SIR* model by adding a vaccinated compartment *V*:

$$\frac{ds}{dt} = -\beta si - ps$$

$$\frac{di}{dt} = \beta si - \gamma i$$

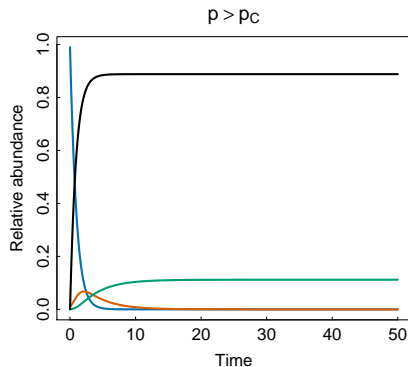
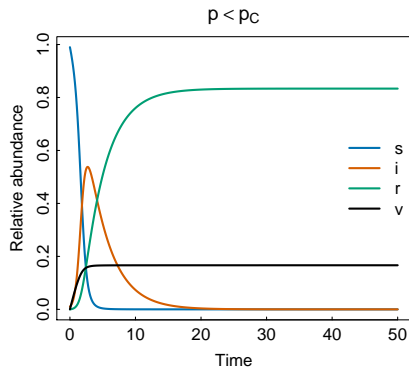
$$\frac{dr}{dt} = \gamma i$$

$$\frac{dv}{dt} = ps$$

Where  $s = S/N$ ,  $i = I/N$ ,  $r = R/N$ , and  $v = V/N$  represent respectively the proportion of the total population  $N$  that is susceptible, infected, recovered or vaccinated.

Setting  $p > p_C$  will prevent an epidemic.

## Example: the *SIRV* model



Setting  $p > p_c$  prevents the disease from spreading through the population.

## $R_0$ and $p_C$ of human diseases

Disease	Mode of transmission	$R_0$	$p_C$
Measles	Airborne	12–18	0.92–0.94
Pertussis	Airborne droplet	12–17	0.92–0.94
Diphtheria	Saliva	6–7	0.83–0.86
Smallpox	Airborne droplet	5–7	0.8–0.86
HIV/AIDS	Sexual contact	2–5	0.5–0.8
SARS	Airborne droplet	2–5	0.5–0.8
Influenza	Airborne droplet	2–3	0.5–0.67
Ebola	Bodily fluids	1.5–2.5	0.33–0.6

# *SIR* model with immigration

Anderson and May (1979) described an *SIR* model with constant immigration as:

$$\begin{aligned}\frac{dS}{dt} &= A - \delta S - \beta SI \\ \frac{dI}{dt} &= \beta SI - (\delta + \alpha + \omega) I \\ \frac{dR}{dt} &= \omega I - \delta R\end{aligned}$$

Where  $A$  is the number of susceptibles immigrating into the population,  $\delta$  is the natural mortality rate,  $\beta$  the contact rate,  $\alpha$  the disease induced mortality rate (sometimes called **virulence**), and  $\omega$  the recovery rate.

## SIR model with immigration

The dynamics of the total population size  $N = S + I + R$  can be determined by summing the terms from the differential equation system above:

$$\frac{dN}{dt} = A - bN - \alpha \frac{I}{N}$$

We can now solve the model at equilibrium:

$$\begin{aligned}\hat{R} &= \frac{\omega}{\delta} \left[ \frac{A}{\delta + \alpha + \omega} - \frac{\delta}{\beta} \right] \\ \hat{I} &= \frac{A}{\delta + \alpha + \omega} - \frac{\delta}{\beta} \\ \hat{S} &= \frac{\delta + \alpha + \omega}{\beta}\end{aligned}$$

## SIR model with immigration

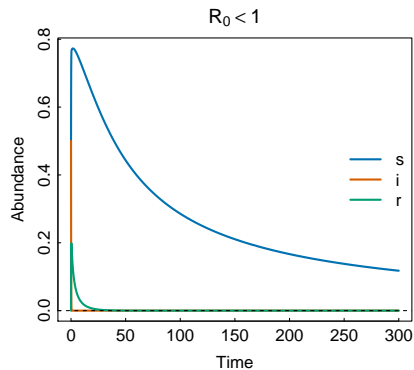
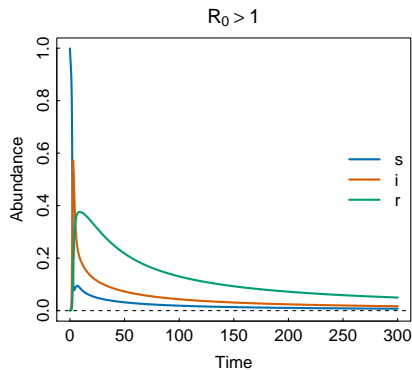
The disease will spread if  $\frac{dI}{dt} > 0$  or:

$$\frac{A}{\delta} > \frac{\delta + \alpha + \omega}{\beta}$$

This means that increasing the natural mortality rate  $\delta$ , the disease induced mortality rate  $\alpha$  or the recovery rate  $\omega$  will reduce the likelihood that the disease will persist in the population.

Under such conditions, the disease will **die-out** by initially spreading very rapidly through the population and then going extinct due to the lack of susceptible individuals left to infect.

# SIR with immigration dynamics





## Building-in delays: *SEIR* models

Most diseases have a gestation or incubation period during which exposed individuals are not yet infected and thus cannot infect others.

To model these diseases, we must turn to *SEIR* models:

$$\frac{dS}{dt} = A - \beta SI - \delta S$$

$$\frac{dE}{dt} = \beta SI - (\gamma + \delta) E$$

$$\frac{dI}{dt} = \gamma E - (\alpha + \delta + \omega) I$$

$$\frac{dR}{dt} = \omega I - \delta R$$

Where  $E$  is the number of individuals who have been exposed to the disease but are not yet infected and  $N = S + E + I + R$ .

## Seasonal forcing in *SIR* models

One of the hallmarks of disease models is that they tend to exhibit fluctuations over time due to temporally varying parameters.

This type of seasonal forcing can be implemented in simple *SIR* models by having  $\beta$  vary according to a sinusoidal wave with a specific amplitude  $a$  and frequency  $f$ :

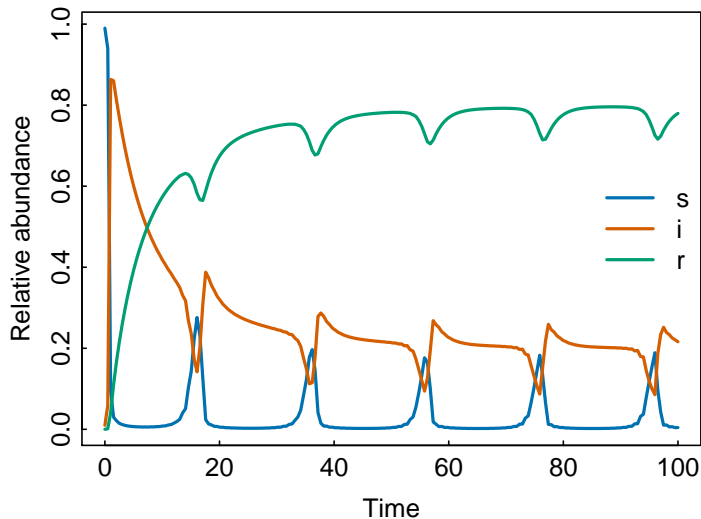
$$\frac{dS}{dt} = A - \beta(t)SI - \delta S$$

$$\frac{dI}{dt} = \beta(t)SI - (\alpha + \delta + \omega)I$$

$$\frac{dR}{dt} = \omega I - \delta R$$

Where the population size  $N = S + I + R$ .

# Dynamics of *SIR* model with seasonality



# Seasonal forcing in *SIR* models

```
library(deSolve)
solve.sir3 <- function(t, y, parms) {
  y[y < 0] <- 0
  # Set the current time step for beta
  ct <- floor(t + 1)
  with(c(parms, y), {
    dS <- A - beta[ct] * S * I - delta * S
    dI <- beta[ct] * S * I - (delta + omega + alpha) *
      I
    dR <- omega * I - delta * R
    return(list(c(dS, dI, dR)))
  })
}
times <- seq(from = 0, to = 100, len = 200)
beta <- 3 * (sin(seq(from = 0, to = 10 * 2 * pi, len = 200)) +
  1)
parms <- list(A = 5, alpha = 0.3, gamma = 0.1, beta = beta,
  delta = 0.05, omega = 0.2)
sol <- ode(y = c(S = 0.99, I = 0.01, R = 0), parms = parms,
  time = times, func = solve.sir3, method = "ode45")
```

# References

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