UNIT 8: Infectious disease

Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

► Extremely common

- Extremely common
- ► Huge impacts on ecological interactions

- Extremely common
- Huge impacts on ecological interactions
- ► A form of exploitation, but doesn't fit well into our previous modeling framework

- Extremely common
- Huge impacts on ecological interactions
- A form of exploitation, but doesn't fit well into our previous modeling framework
 - ► How many people are there?

- Extremely common
- Huge impacts on ecological interactions
- A form of exploitation, but doesn't fit well into our previous modeling framework
 - ► How many people are there?
 - ► How many influenza viruses are there?

- Extremely common
- Huge impacts on ecological interactions
- ► A form of exploitation, but doesn't fit well into our previous modeling framework
 - ► How many people are there?
 - How many influenza viruses are there?
 - ► How do they find each other?

- Extremely common
- Huge impacts on ecological interactions
- A form of exploitation, but doesn't fit well into our previous modeling framework
 - ► How many people are there?
 - How many influenza viruses are there?
 - ► How do they find each other?

▶ Name an infectious agent that causes disease in humans.

- ▶ Name an infectious agent that causes disease in humans.
- ► Disease agents vary tremendously:

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - ► Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - * SARS-CoV-2, influenza virus, HIV, measles
 - ► Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways

- Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - *

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - * Tuberculosis, anthrax, pertussis

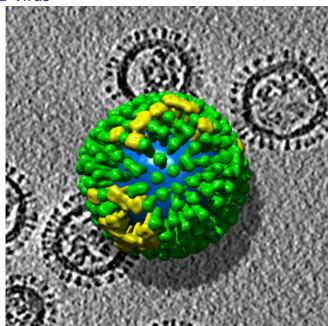
- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - * Tuberculosis, anthrax, pertussis
 - ► Eukaryotic pathogens are nucleated cells who are more closely related to you than they are to bacteria

- Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles
 - Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - * Tuberculosis, anthrax, pertussis
 - Eukaryotic pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - > *

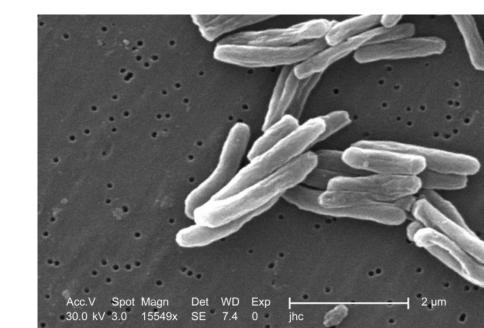
- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - * Tuberculosis, anthrax, pertussis
 - Eukaryotic pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - * Malaria, intestinal worms, trichomoniasis

- ▶ Name an infectious agent that causes disease in humans.
- Disease agents vary tremendously:
 - Most viruses have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ► * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ Bacteria are independent, free-living cells with hundreds or thousands of chemical pathways
 - * Tuberculosis, anthrax, pertussis
 - Eukaryotic pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - * Malaria, intestinal worms, trichomoniasis

Influenza virus



Tuberculosis bacilli



Malaria sporozoite



► For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages

- ► For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ► Latently infected

- ► For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - Latently infected
 - ► Productively infected

- ► For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ► Latently infected
 - Productively infected
 - Recovered

- ► For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ► Latently infected
 - Productively infected
 - Recovered

► We model microparasites by counting the number of hosts in various **states**:

- We model microparasites by counting the number of hosts in various states:
 - ► Susceptible individuals can become infected

- We model microparasites by counting the number of hosts in various states:
 - ▶ Susceptible individuals can become infected
 - ► Infectious individuals are infected and can infect others

- We model microparasites by counting the number of hosts in various states:
 - Susceptible individuals can become infected
 - ▶ Infectious individuals are infected and can infect others
 - Resistant individuals are not infected and cannot become infected

- We model microparasites by counting the number of hosts in various states:
 - Susceptible individuals can become infected
 - ▶ Infectious individuals are infected and can infect others
 - Resistant individuals are not infected and cannot become infected
- More complicated models might include other states, such as latently infected hosts who are infected with the pathogen but cannot yet infect others

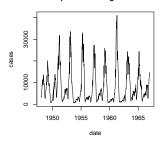
- We model microparasites by counting the number of hosts in various states:
 - Susceptible individuals can become infected
 - ▶ Infectious individuals are infected and can infect others
 - Resistant individuals are not infected and cannot become infected
- More complicated models might include other states, such as latently infected hosts who are infected with the pathogen but cannot yet infect others

Models as tools

► Models are the tools that we use to connect scales:



Measles reports from England and Wales

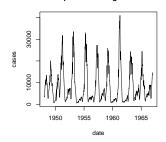


Models as tools

- Models are the tools that we use to connect scales:
 - ► individuals to populations



Measles reports from England and Wales

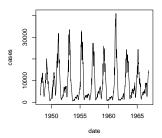


Models as tools

- Models are the tools that we use to connect scales:
 - individuals to populations
 - single actions to trends through time



Measles reports from England and Wales

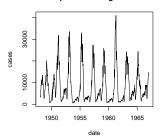


Models as tools

- Models are the tools that we use to connect scales:
 - individuals to populations
 - single actions to trends through time



Measles reports from England and Wales



Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

► For many diseases, especially new diseases, we can *observe* and *estimate r*.

► For many diseases, especially new diseases, we can *observe* and *estimate r*.

> 3

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)

4□ > 4□ > 4 亘 > 4 亘 > □ 9 Q (P)

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ► * Units of 1/t

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - **▶** ३

- For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- ightharpoonup Want to know what factors contribute to that, and how it relates to \mathcal{R} .

- For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- Nant to know what factors contribute to that, and how it relates to \mathcal{R} .
 - *

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- Want to know what factors contribute to that, and how it relates to R.
 - * number of new cases per case

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- Nant to know what factors contribute to that, and how it relates to \mathcal{R} .
 - * number of new cases per case
 - *

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- Nant to know what factors contribute to that, and how it relates to \mathcal{R} .
 - * number of new cases per case
 - * Unitless

- ► For many diseases, especially new diseases, we can *observe* and *estimate r*.
 - * Instantaneous rate of increase (per capita)
 - ▶ * Units of 1/t
 - * Gives the exponential rate of spread
- Nant to know what factors contribute to that, and how it relates to \mathcal{R} .
 - * number of new cases per case
 - * Unitless

 \blacktriangleright People in the disease field love to talk specifically about \mathcal{R}_0

- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :

- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ightharpoonup Actual value of $\mathcal R$ before an epidemic

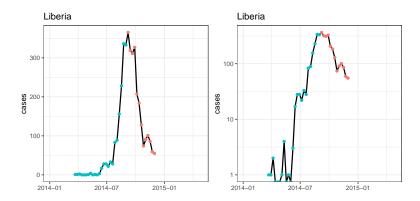
- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - Actual value of R before an epidemic
 - Hypothetical value assuming no immunity

- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ightharpoonup Actual value of $\mathcal R$ before an epidemic
 - Hypothetical value assuming no immunity
 - Hypothetical value assuming no immunity and no control efforts whatsoever

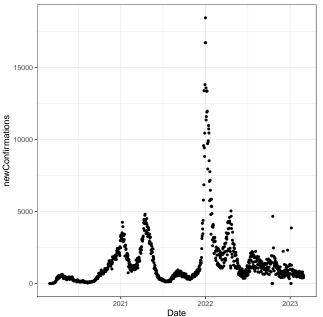
- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - Actual value of R before an epidemic
 - Hypothetical value assuming no immunity
 - Hypothetical value assuming no immunity and no control efforts whatsoever
- ▶ Often easier to talk simply about \mathcal{R} .

- lacktriangle People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - Actual value of R before an epidemic
 - Hypothetical value assuming no immunity
 - Hypothetical value assuming no immunity and no control efforts whatsoever
- lacktriangle Often easier to talk simply about ${\cal R}.$

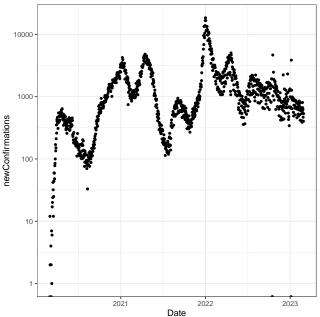
Example: the West African Ebola epidemic



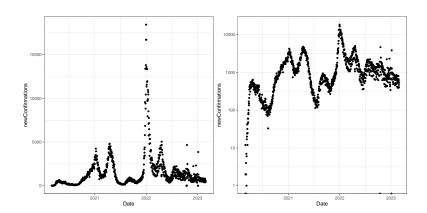
COVID in Ontario (preview)



COVID in Ontario (preview)



COVID in Ontario



► Which scale should we look at?

▶ Which scale should we look at?



- ▶ Which scale should we look at?
 - * Log scale is better for looking at trends

- ▶ Which scale should we look at?
 - * Log scale is better for looking at trends
 - *

- ► Which scale should we look at?
 - * Log scale is better for looking at trends
 - ▶ * Linear scale is better for looking at impacts

- ► Which scale should we look at?
 - * Log scale is better for looking at trends
 - ▶ * Linear scale is better for looking at impacts

Population biology

► What quantities do we want to look at?

Population biology

▶ What quantities do we want to look at?

*

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*
 - *

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*
 - \blacktriangleright * Finite rate of increase λ

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*
 - \blacktriangleright * Finite rate of increase λ
 - *

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*
 - \blacktriangleright * Finite rate of increase λ
 - ▶ * Lifetime reproduction, *R*

- ▶ What quantities do we want to look at?
 - ► * Speed of exponential growth *r*
 - \blacktriangleright * Finite rate of increase λ
 - ▶ * Lifetime reproduction, *R*

► What are the components?

▶ What are the components?

*

- ▶ What are the components?
 - ► * Birth rate

- ▶ What are the components?
 - ► * Birth rate
 - *

- ▶ What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - **▶** ≯

- ▶ What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - *

- What are the components?
 - * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate

- What are the components?
 - * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - **▶** *

- What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!

- What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - *

- What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - ► * Rate of death, recovery, or effective quarantine

- What are the components?
 - * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?

- What are the components?
 - * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - *

- What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - ► * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease

- What are the components?
 - ▶ * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - **▶** ≯

- What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - ► * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - ▶ * Then we use that to estimate b = d + r

- What are the components?
 - * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - ▶ * Then we use that to estimate b = d + r
 - *

- What are the components?
 - * Birth rate
 - * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - ▶ * Then we use that to estimate b = d + r
 - * Models go both directions!

- What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - ▶ * Then we use that to estimate b = d + r
 - * Models go both directions!
 - ► Individuals ↔ Populations

- What are the components?
 - * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - * [case/(case · time]
 - ▶ * Death rate
 - * Virus-centered!
 - * Rate of death, recovery, or effective quarantine
- How do you think we estimate?
 - ▶ * We estimate *r* from the population-level increase in disease
 - ▶ * Then we use that to estimate b = d + r
 - * Models go both directions!
 - ► Individuals ↔ Populations

► Why do we want this?

▶ Why do we want this?



- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public

- ► Why do we want this?
 - * to communicate with policy-makers or the public
 - **▶** *

- ▶ Why do we want this?
 - * to communicate with policy-makers or the public
 - \triangleright * maybe to make concrete predictions, though we could use r

- ► Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - \triangleright * maybe to make concrete predictions, though we could use r
- ► How do we calculate it?

- ► Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - \triangleright * maybe to make concrete predictions, though we could use r
- ► How do we calculate it?
 - *

- ▶ Why do we want this?
 - * to communicate with policy-makers or the public
 - ightharpoonup * maybe to make concrete predictions, though we could use r
- ► How do we calculate it?
 - * Pick a time step (week? year?)

Finite rate of growth λ

- ► Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ightharpoonup * maybe to make concrete predictions, though we could use r
- How do we calculate it?
 - ► * Pick a time step (week? year?)
 - *

Finite rate of growth λ

- ▶ Why do we want this?
 - * to communicate with policy-makers or the public
 - ightharpoonup * maybe to make concrete predictions, though we could use r
- How do we calculate it?
 - * Pick a time step (week? year?)
 - ▶ * Use a formula $\lambda = \exp(r\Delta t)$

Finite rate of growth λ

- ▶ Why do we want this?
 - * to communicate with policy-makers or the public
 - ightharpoonup * maybe to make concrete predictions, though we could use r
- How do we calculate it?
 - * Pick a time step (week? year?)
 - ▶ * Use a formula $\lambda = \exp(r\Delta t)$

 $ightharpoonup r pprox 0.14/\,{
m day}$ for early COVID spread

- $ightharpoonup r pprox 0.14/\,{
 m day}$ for early COVID spread
- ▶ What is λ ?

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$ for early COVID spread
- ▶ What is λ ?
 - ► At a time scale of a day?

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$ for early COVID spread
- \blacktriangleright What is λ ?
 - At a time scale of a day?
 - ► At a time scale of a week?

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$ for early COVID spread
- \blacktriangleright What is λ ?
 - At a time scale of a day?
 - ► At a time scale of a week?

► What is it?

Reproductive number ${\cal R}$

- ► What is it?
 - 7

- ► What is it?
 - ► * Expected number of new cases per case over the lifetime of a case

- ► What is it?
 - * Expected number of new cases per case over the lifetime of a case
- ► Why do we want this?

- ► What is it?
 - * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - >

- ▶ What is it?
 - * Expected number of new cases per case over the lifetime of a case
- Why do we want this?
 - ► * An important measure of how hard the epidemic will be to stop

- ▶ What is it?
 - * Expected number of new cases per case over the lifetime of a case
- ► Why do we want this?
 - ► * An important measure of how hard the epidemic will be to stop
- ► How do we calculate it?

- ▶ What is it?
 - * Expected number of new cases per case over the lifetime of a case
- ► Why do we want this?
 - ► * An important measure of how hard the epidemic will be to stop
- ► How do we calculate it?
 - *

- ▶ What is it?
 - * Expected number of new cases per case over the lifetime of a case
- Why do we want this?
 - * An important measure of how hard the epidemic will be to stop
- ► How do we calculate it?
 - * $\mathcal{R} = b/d$; if we can estimate those

- ▶ What is it?
 - * Expected number of new cases per case over the lifetime of a case
- Why do we want this?
 - * An important measure of how hard the epidemic will be to stop
- ► How do we calculate it?
 - * $\mathcal{R} = b/d$; if we can estimate those

 $ightharpoonup r \approx 0.14/\,\mathrm{day}$

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?
 - *

- $r \approx 0.14/\text{ day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?
 - * $d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$

- $r \approx 0.14/\text{ day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

*

- $r \approx 0.14/\text{ day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

•
$$* b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$$

- $r \approx 0.14/\text{ day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

*
$$b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$$

*

- $r \approx 0.14/\text{ day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

*
$$b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

- $ightharpoonup r \approx 0.14/\,\mathrm{day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \text{ day}) = 0.2/ \text{ day}$$

• *
$$b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

- $ightharpoonup r \approx 0.14/\,\mathrm{day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \text{ day}) = 0.2/ \text{ day}$$

$$ightharpoonup$$
 * $b = 0.14 \, day + 0.2 \, day = 0.34 / \, day$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

▶ When average length of infection $L = 10 \,\mathrm{day}$?

•

- $r \approx 0.14/\text{ day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

$$ightharpoonup$$
 * $b = 0.14 \, day + 0.2 \, day = 0.34 / \, day$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

- ▶ When average length of infection $L = 10 \,\text{day}$?
 - * $d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$

- $r \approx 0.14/\text{ day}$
- What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

• *
$$b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

▶ When average length of infection $L = 10 \,\text{day}$?

• *
$$d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$$

*

- $ightharpoonup r pprox 0.14/\,\mathrm{day}$
- \blacktriangleright What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

$$ightharpoonup$$
 * $b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

• *
$$d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$$

*
$$b = 0.14 \, \text{day} + 0.1 \, \text{day} = 0.24 / \, \text{day}$$

- $r \approx 0.14/\text{ day}$
- ▶ What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

$$ightharpoonup$$
 * $b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

• *
$$d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$$

•
$$*b = 0.14 \, \text{day} + 0.1 \, \text{day} = 0.24 / \, \text{day}$$

- $r \approx 0.14/\text{ day}$
- What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

$$ightharpoonup$$
 * $b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

• *
$$d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$$

•
$$b = 0.14 \, \text{day} + 0.1 \, \text{day} = 0.24 / \, \text{day}$$

$$ightharpoonup * \mathcal{R} = 0.24/0.1 = 2.4$$

- $r \approx 0.14/\text{ day}$
- What is our estimate of R?
 - ▶ When average length of infection $L = 5 \,\text{day}$?

• *
$$d = 1/(5 \, \text{day}) = 0.2/ \, \text{day}$$

$$ightharpoonup$$
 * $b = 0.14 \, \text{day} + 0.2 \, \text{day} = 0.34 / \, \text{day}$

$$ightharpoonup * \mathcal{R} = 0.34/0.2 = 1.7$$

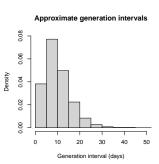
• *
$$d = 1/(10 \,\mathrm{day}) = 0.1/\,\mathrm{day}$$

•
$$b = 0.14 \, \text{day} + 0.1 \, \text{day} = 0.24 / \, \text{day}$$

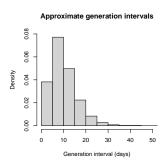
$$ightharpoonup * \mathcal{R} = 0.24/0.1 = 2.4$$

Generation intervals

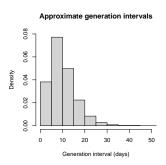
 Researchers try to estimate the proportion of transmission that happens for different ages of infection



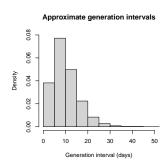
- Researchers try to estimate the proportion of transmission that happens for different ages of infection
- ► How long from the time you are infected to the time you infect someone else?



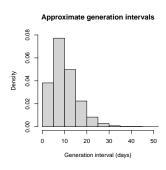
- Researchers try to estimate the proportion of transmission that happens for different ages of infection
- How long from the time you are infected to the time you infect someone else?
- ► Analogous to a life table



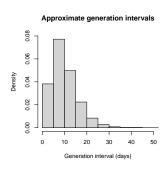
- Researchers try to estimate the proportion of transmission that happens for different ages of infection
- How long from the time you are infected to the time you infect someone else?
- Analogous to a life table
- ► The effective generation time \hat{G} has units of time

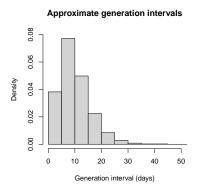


- Researchers try to estimate the proportion of transmission that happens for different ages of infection
- How long from the time you are infected to the time you infect someone else?
- Analogous to a life table
- The effective generation time \hat{G} has units of time
 - \[
 \hat{G}\] is fairly deep; we'll skip
 the details
 \]

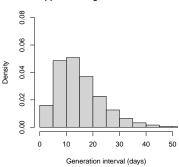


- Researchers try to estimate the proportion of transmission that happens for different ages of infection
- How long from the time you are infected to the time you infect someone else?
- Analogous to a life table
- ► The effective generation time \hat{G} has units of time
 - \hat{G} is fairly deep; we'll skip
 the details
 \]





Approximate generation intervals



► Which is more dangerous, a fast disease, or a slow disease?

Approximate generation intervals

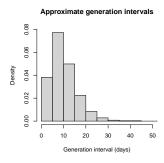
- ► Which is more dangerous, a fast disease, or a slow disease?
 - ► How are we measuring speed?

Approximate generation intervals

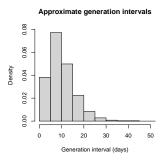
- ► Which is more dangerous, a fast disease, or a slow disease?
 - How are we measuring speed?
 - How are we measuring danger?

Approximate generation intervals 80 0 90 0 10 20 30 40 50 Generation interval (days)

- Which is more dangerous, a fast disease, or a slow disease?
 - How are we measuring speed?
 - How are we measuring danger?
 - ► What do we already know?



- ► Which is more dangerous, a fast disease, or a slow disease?
 - How are we measuring speed?
 - How are we measuring danger?
 - What do we already know?



Fighting Ebola



▶ If we know \mathcal{R} , what does the generation time tell us about r?

▶ If we know \mathcal{R} , what does the generation time tell us about r?

- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)

- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r, what does the generation time tell us about \mathbb{R} ?

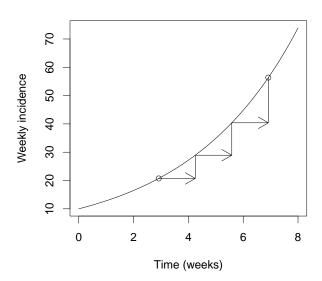
- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r, what does the generation time tell us about \mathcal{R} ?

- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r, what does the generation time tell us about R?
 - ▶ * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})

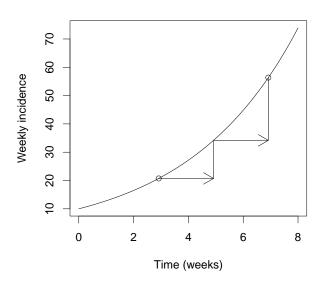
- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r, what does the generation time tell us about R?
 - ▶ * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})
- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$

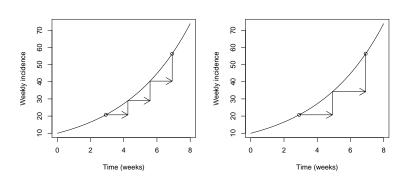
- ▶ If we know \mathcal{R} , what does the generation time tell us about r?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r, what does the generation time tell us about R?
 - * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})
- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$

Generation time and risk (repeat)



Generation time and risk (repeat)





$$ightharpoonup \mathcal{R} = \exp(r\hat{G})$$

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- ► An intuitive view:

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ► If we know generation speed, then a faster epidemic speed means:

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - *

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ► If we know generation speed, then a faster epidemic speed means:
 - ► * More strength required (greater R)

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ► If we know generation speed, then a faster epidemic speed means:
 - ► * More strength required (greater R)
- ▶ If we know epidemic speed, a faster generation speed means

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ► If we know generation speed, then a faster epidemic speed means:
 - ► * More strength required (greater R)
- If we know epidemic speed, a faster generation speed means
 - *

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater R)
- If we know epidemic speed, a faster generation speed means
 - ► * Less strength required (smaller R)

- $ightharpoonup \mathcal{R} = \exp(r\hat{G})$
- An intuitive view:
 - ightharpoonup Epidemic speed = Generation strength imes Generation speed
 - Mathematically: $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater R)
- If we know epidemic speed, a faster generation speed means
 - ► * Less strength required (smaller R)

Outline

Introduction

Rate of spread

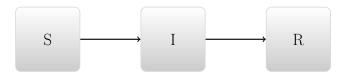
Single-epidemic model Epidemic size

Recurrent epidemic models Dynamics

Reproductive numbers and risk

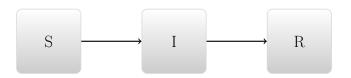
Pathogen aggressiveness

Single-epidemic model



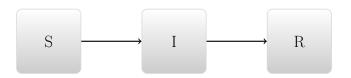
ightharpoonup Susceptible ightarrow Infectious ightarrow Recovered

Single-epidemic model

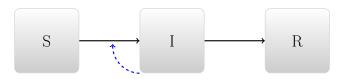


- ightharpoonup Susceptible ightarrow Infectious ightarrow Recovered
- ▶ We also use *N* to mean the total population

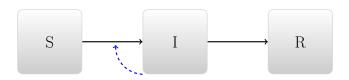
Single-epidemic model



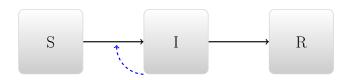
- ightharpoonup Susceptible ightarrow Infectious ightarrow Recovered
- ▶ We also use *N* to mean the total population



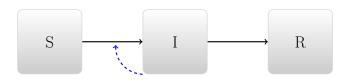
▶ What factors govern movement through the boxes?



- ▶ What factors govern movement through the boxes?
 - ► People get better independently



- ▶ What factors govern movement through the boxes?
 - People get better independently
 - ► People get infected by infectious people



- ▶ What factors govern movement through the boxes?
 - People get better independently
 - People get infected by infectious people

What happens in the long term if we introduce an infectious individual?



What happens in the long term if we introduce an infectious individual?





- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - *



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - *



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered
 - *



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered
 - ▶ * ... or susceptible

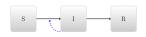


- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered
 - ▶ * ... or susceptible

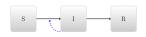
> ×



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered
 - ▶ * ... or susceptible
 - * Or, there may not be an outbreak



- What happens in the long term if we introduce an infectious individual?
 - ► * There *may be* an **epidemic**
 - an outbreak of disease
 - * Disease burns out
 - * Everyone winds up recovered
 - ▶ * ... or susceptible
 - * Or, there may not be an outbreak



► Why might there not be an epidemic?

▶ Why might there not be an epidemic?



- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - * Could depend on season, or immunity . . .

- ▶ Why might there not be an epidemic?
 - * If the disease can't spread well enough in the population
 - * Could depend on season, or immunity . . .
 - **▶** *

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - * Could depend on season, or immunity . . .
 - * Demographic stochasticity: if we only start with one individual, we expect an element of chance

- ▶ Why might there not be an epidemic?
 - * If the disease can't spread well enough in the population
 * Could depend on season, or immunity . . .
 - ► * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ► Why doesn't everyone get infected?

- ▶ Why might there not be an epidemic?
 - * If the disease can't spread well enough in the population
 * Could depend on season, or immunity . . .
 - * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - *

- Why might there not be an epidemic?
 - * If the disease can't spread well enough in the population
 * Could depend on season, or immunity . . .
 - * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - *

- Why might there not be an epidemic?
 - * If the disease can't spread well enough in the population
 * Could depend on season, or immunity . . .
 - * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - *

► The simplest way to implement this conceptual model is with differential equations:



The simplest way to implement this conceptual model is with differential equations:

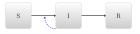
$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$



The simplest way to implement this conceptual model is with differential equations:

$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$

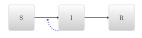


The simplest way to implement this conceptual model is with differential equations:

$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

 $\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$

$$\frac{dR}{dt} = \gamma I$$



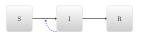
The simplest way to implement this conceptual model is with differential equations:

$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$

$$rac{dR}{dt} = \gamma I$$

$$N = S + I + R$$



The simplest way to implement this conceptual model is with differential equations:

$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

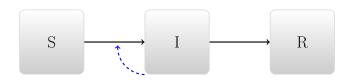
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$

$$rac{dR}{dt} = \gamma I$$

$$N = S + I + R$$

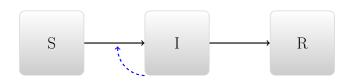


Quantities



State variables

ightharpoonup S, I, R, N: [people] or [people/ha]



State variables

 \triangleright S, I, R, N: [people] or [people/ha]

Parameters

▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])

- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ► These are contacts that would lead to infection if the person contacted is infectious

- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - These are contacts that would lead to infection if the person contacted is infectious
 - ► Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious

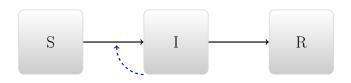
- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - These are contacts that would lead to infection if the person contacted is infectious
 - ► Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])

- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ► These are contacts that would lead to infection if the person contacted is infectious
 - ► Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ► Total recovery rate is γI

- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - These are contacts that would lead to infection if the person contacted is infectious
 - ► Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ightharpoonup Total recovery rate is γI
 - ▶ Mean time infectious is $D = 1/\gamma$ (units [time])

- Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - These are contacts that would lead to infection if the person contacted is infectious
 - ► Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ▶ Total recovery rate is γI
 - Mean time infectious is $D=1/\gamma$ (units [time])

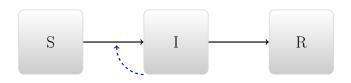
Quantities (repeat)



State variables

ightharpoonup S, I, R, N: [people] or [people/ha]

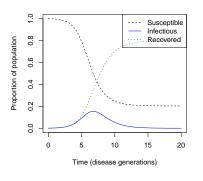
Quantities (repeat)

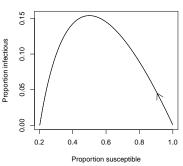


State variables

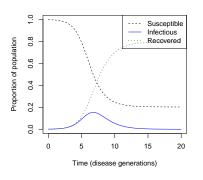
 \triangleright S, I, R, N: [people] or [people/ha]

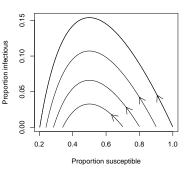
Simulating the model (repeat)





Simulating the model





▶ What *unitless* parameter can you make from the model above?

▶ What *unitless* parameter can you make from the model above?

>

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - >

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual
 - **▶** ≯

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual
 - ► * That is: the number they would cause on average if everyone else were susceptible

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual
 - * That is: the number they would cause on average if everyone else were susceptible
 - *

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual
 - * That is: the number they would cause on average if everyone else were susceptible
 - ▶ * The product of the rate β (units [1/t]) and the duration D ([t])

- ▶ What *unitless* parameter can you make from the model above?
 - * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the basic reproductive number
 - * The potential number of infections caused by an average infectious individual
 - * That is: the number they would cause on average if everyone else were susceptible
 - ▶ * The product of the rate β (units [1/t]) and the duration D ([t])

▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?

▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?

×

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - * Number of infected individuals grows exponentially

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - **>** *

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - * Number of infected individuals does not grow (disease cannot invade)

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - * Number of infected individuals does not grow (disease cannot invade)



$$ightharpoonup$$
 * $\mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$

The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:

$$ightharpoonup * \mathcal{R}_{ ext{eff}} = \mathcal{R}_0 S/N$$

Is the disease increasing or decreasing?

$$ightharpoonup * \mathcal{R}_{ ext{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - **>** *

$$ightharpoonup * \mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$$

- ▶ Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)

• *
$$\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$$

- ▶ Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - *

$$ightharpoonup$$
 * $\mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$

• *
$$\mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ► Why doesn't everyone get infected?

• *
$$\mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - *

$$ightharpoonup * \mathcal{R}_{ ext{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - lacktriangle * When susceptibles are low enough $\mathcal{R}_{\mathrm{eff}} < 1$

• *
$$\mathcal{R}_{\mathrm{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- Why doesn't everyone get infected?
 - lacktriangle * When susceptibles are low enough $\mathcal{R}_{\mathrm{eff}} < 1$
 - *

$$ightharpoonup * \mathcal{R}_{ ext{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - lacktriangle * When susceptibles are low enough $\mathcal{R}_{\mathrm{eff}} < 1$
 - ▶ * When $\mathcal{R}_{\rm eff}$ < 1, the disease dies out on its own (less than one case per case)

$$ightharpoonup * \mathcal{R}_{ ext{eff}} = \mathcal{R}_0 S/N$$

- Is the disease increasing or decreasing?
 - lacktriangleright * It will increase when $\mathcal{R}_{\mathrm{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - lacktriangle * When susceptibles are low enough $\mathcal{R}_{\mathrm{eff}} < 1$
 - ▶ * When $\mathcal{R}_{\rm eff}$ < 1, the disease dies out on its own (less than one case per case)

Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

► In this model, the epidemic always burns out

- In this model, the epidemic always burns out
 - ► No source of new susceptibles

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- ► Epidemic size is determined by:

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- ► Epidemic size is determined by:
 - >

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- ► Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - *

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - •

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - **>** 4

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end
 - >

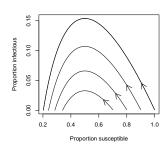
- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end
 - * The number of infected individuals at the beginning of the epidemic

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end
 - * The number of infected individuals at the beginning of the epidemic
 - *

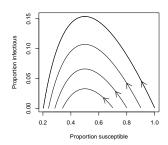
- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end
 - * The number of infected individuals at the beginning of the epidemic
 - * Usually relatively small (and a relatively small effect)

- In this model, the epidemic always burns out
 - ► No source of new susceptibles
- Epidemic size is determined by:
 - * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - * ... and fewer susceptibles at the end
 - * The number of infected individuals at the beginning of the epidemic
 - * Usually relatively small (and a relatively small effect)

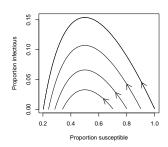
► Why does more susceptibles at the beginning mean fewer susceptibles at the end?



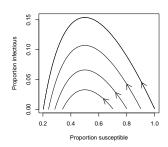
► Why does more susceptibles at the beginning mean fewer susceptibles at the end?



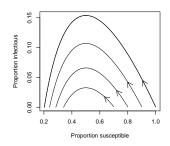
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒



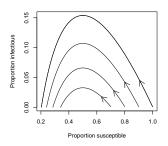
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - **▶** ≯



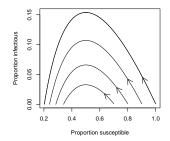
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ightharpoonup * Faster initial growth \implies



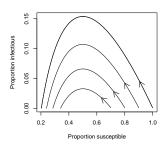
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ▶ * Faster initial growth ⇒⇒
 - **>** *



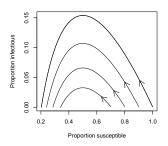
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ▶ * Faster initial growth ⇒⇒
 - ► * Bigger epidemic ⇒



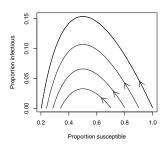
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic ⇒
 - > 1



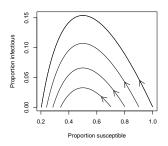
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ▶ * Faster initial growth ⇒
 - ▶ * Bigger epidemic ⇒
 - ► * More infections at peak (same number of susceptibles) ⇒



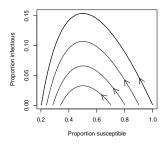
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ▶ * Faster initial growth ⇒⇒
 - ▶ * Bigger epidemic ⇒
 - ► * More infections at peak (same number of susceptibles) ⇒
 - *



- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - ▶ * Faster initial growth ⇒
 - ▶ * Bigger epidemic ⇒
 - ➤ * More infections at peak (same number of susceptibles) ⇒
 - ► * More generations needed for disease to fade out ⇒

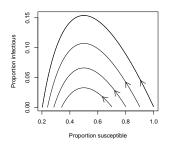


- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ► * More susceptibles ⇒
 - * Faster initial growth \Rightarrow
 - ► * Bigger epidemic ⇒
 - * More infections at peak (same number of susceptibles) =>
 - ➤ * More generations needed for disease to fade out ⇒
 - *



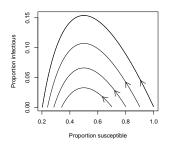
Overshoot

- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles ⇒
 - * Faster initial growth \Longrightarrow
 - * Bigger epidemic ⇒
 - * More infections at peak (same number of susceptibles) \Longrightarrow
 - * More generations needed for disease to fade out \implies
 - * More infections after peak

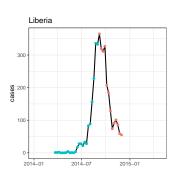


Overshoot

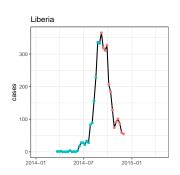
- Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles ⇒
 - * Faster initial growth \Longrightarrow
 - * Bigger epidemic ⇒
 - * More infections at peak (same number of susceptibles) \Longrightarrow
 - * More generations needed for disease to fade out \implies
 - * More infections after peak



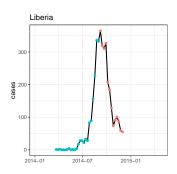
► In September, the US CDC predicted "as many as" 1.5 million Ebola cases in Liberia by January



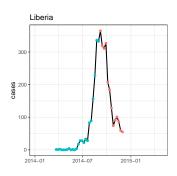
- ► In September, the US CDC predicted "as many as" 1.5 million Ebola cases in Liberia by January
- ► In fact, their model predicted many *more* cases than that by April



- ► In September, the US CDC predicted "as many as" 1.5 million Ebola cases in Liberia by January
- In fact, their model predicted many more cases than that by April
- ► What happened?



- ► In September, the US CDC predicted "as many as" 1.5 million Ebola cases in Liberia by January
- ► In fact, their model predicted many more cases than that by April
- ► What happened?



► What limits epidemics in our simple models?

▶ What limits epidemics in our simple models?



- What limits epidemics in our simple models?
 - ► * Depletion of susceptibles

- What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- ► What else limits epidemics in real life?

- What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - *

- ▶ What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines

- ▶ What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines
 - **×**

- ▶ What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines
 - ► * Behaviour change; people stay home, wear masks, avoid sick people

- ▶ What limits epidemics in our simple models?
 - ► * Depletion of susceptibles
- What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines
 - * Behaviour change; people stay home, wear masks, avoid sick people
 - *

- ▶ What limits epidemics in our simple models?
 - * Depletion of susceptibles
- What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines
 - * Behaviour change; people stay home, wear masks, avoid sick people
 - ▶ * Heterogeneity (differences between hosts, locations, etc.)

- What limits epidemics in our simple models?
 - * Depletion of susceptibles
- What else limits epidemics in real life?
 - * Interventions; changes in government policy, medicine, vaccines
 - ► * Behaviour change; people stay home, wear masks, avoid sick people
 - ▶ * Heterogeneity (differences between hosts, locations, etc.)

Outline

Introduction

Rate of spread

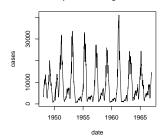
Single-epidemic model Epidemic size

Recurrent epidemic models
Dynamics

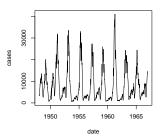
Reproductive numbers and risk

Pathogen aggressiveness

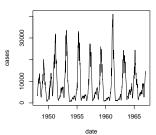
► If epidemics tend to burn out, why do we often see repeated epidemics?



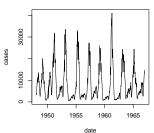
- ► If epidemics tend to burn out, why do we often see repeated epidemics?
 - *



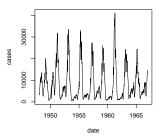
- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - * People might lose immunity



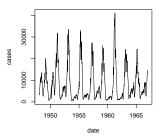
- ► If epidemics tend to burn out, why do we often see repeated epidemics?
 - * People might lose immunity
 - , ×



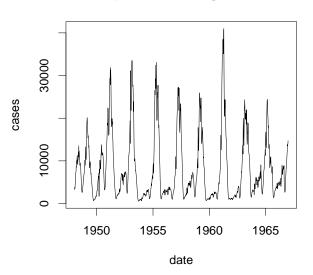
- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - * People might lose immunity
 - * Births and deaths; newborns are susceptible

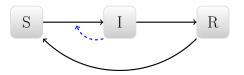


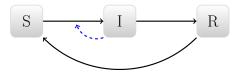
- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - * People might lose immunity
 - * Births and deaths; newborns are susceptible



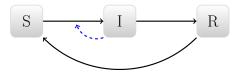
Recurrent epidemics



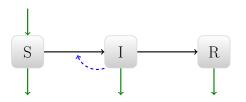




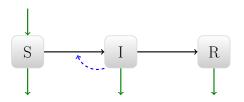
* Loss of immunity



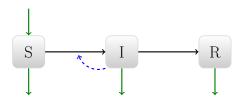
▶ * Loss of immunity





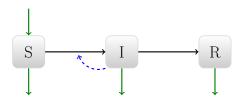


▶ * Births and deaths

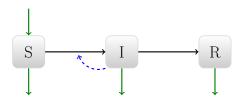


* Births and deaths





- ▶ * Births and deaths
 - * Effect on dynamics is similar to loss of immunity



- ▶ * Births and deaths
 - * Effect on dynamics is similar to loss of immunity

Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$

$$\frac{dR}{dt} = \gamma I - dR$$



Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$

$$\frac{dR}{dt} = \gamma I - dR$$

ightharpoonup We often assume b = d



Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$

$$\begin{array}{c|c} \downarrow & & \\ \hline S & & I & \\ \hline \end{array}$$

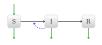
$$\frac{dR}{dt} = \gamma I - dR$$

- \blacktriangleright We often assume b=d
 - ▶ ⇒ population is constant

Births and deaths

$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$

$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



$$\frac{dR}{dt} = \gamma I - dR$$

- ightharpoonup We often assume b = d
 - ▶ ⇒ population is constant

Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

 \blacktriangleright At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$

- lacktriangle At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$
 - ► One case per case

- lacktriangle At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance

- lacktriangle At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance

$$\blacktriangleright \ S/N = 1/\mathcal{R}_0$$

- lacktriangle At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - \triangleright $S/N = 1/\mathcal{R}_0$
- ► What does this remind you of?

- lacktriangle At equilibrium, we know that $\mathcal{R}_{\mathrm{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance

$$ightharpoonup S/N = 1/\mathcal{R}_0$$

- ▶ What does this remind you of?
 - *****

- lacktriangle At equilibrium, we know that $\mathcal{R}_{ ext{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance

$$\triangleright$$
 $S/N = 1/\mathcal{R}_0$

- ▶ What does this remind you of?
 - ► * Reciprocal control!

- lacktriangle At equilibrium, we know that $\mathcal{R}_{ ext{eff}}=1$
 - One case per case
 - Number of susceptibles at equilibrium determined by the number required to keep infection in balance

$$\triangleright$$
 $S/N = 1/\mathcal{R}_0$

- ▶ What does this remind you of?
 - ► * Reciprocal control!

► Number of infectious individuals determined by number required to keep susceptibles in balance.

- Number of infectious individuals determined by number required to keep susceptibles in balance.
- ► As susceptibles go up, what happens?

- Number of infectious individuals determined by number required to keep susceptibles in balance.
- ► As susceptibles go up, what happens?
 - ► Per capita replenishment goes down

- Number of infectious individuals determined by number required to keep susceptibles in balance.
- ► As susceptibles go up, what happens?
 - ▶ Per capita replenishment goes down
 - ► Infections required goes down

- Number of infectious individuals determined by number required to keep susceptibles in balance.
- As susceptibles go up, what happens?
 - Per capita replenishment goes down
 - Infections required goes down

► What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?

▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?

▶ ≯

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ightharpoonup * Equation for dI/dt does not change

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - *****

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change
 - **▶** *

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - *

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ▶ What else could happen?

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - ► * Less disease
- ► What else could happen?
 - *

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct
 - *

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate . . .

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - \blacktriangleright * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate . . .
 - *

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate . . .
 - ▶ * Number of susceptibles goes down

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dI/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - * Fewer susceptibles removed by infection (some are removed by us)
 - * Less disease
- ► What else could happen?
 - ► * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate . . .
 - ▶ * Number of susceptibles goes down

► What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?

► What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?



- ► What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt

- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - *

- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - ► * If we have more susceptibles, then per capita replenishment goes down

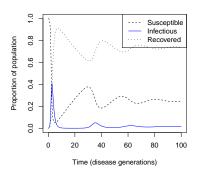
- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - ► * If we have more susceptibles, then per capita replenishment goes down
 - *

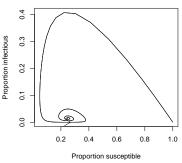
- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - * If we have more susceptibles, then per capita replenishment goes down
 - * So the number of infectious individuals required for balance goes down

- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - * If we have more susceptibles, then per capita replenishment goes down
 - ► * So the number of infectious individuals required for balance goes down
 - **×**

- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - ► * If we have more susceptibles, then per capita replenishment goes down
 - ► * So the number of infectious individuals required for balance goes down
 - ► * If we remove infectious individuals fast enough, the infection could go extinct

- What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - \blacktriangleright * We need more susceptibles to balance dI/dt
 - ► * If we have more susceptibles, then per capita replenishment goes down
 - ► * So the number of infectious individuals required for balance goes down
 - ► * If we remove infectious individuals fast enough, the infection could go extinct





"Closed-loop" SIR models (ie., with births or loss of immunity):

- "Closed-loop" SIR models (ie., with births or loss of immunity):
 - ► Tend to oscillate

- "Closed-loop" SIR models (ie., with births or loss of immunity):
 - ► Tend to oscillate
 - Oscillations tend to be damped

- "Closed-loop" SIR models (ie., with births or loss of immunity):
 - ► Tend to oscillate
 - Oscillations tend to be damped
 - ► System reaches an **endemic** equilibrium disease persists

- "Closed-loop" SIR models (ie., with births or loss of immunity):
 - ► Tend to oscillate
 - Oscillations tend to be damped
 - ► System reaches an **endemic** equilibrium disease persists

► Similar to predator-prey systems

- Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?

- Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - **▶** ×

- Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic

- Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - *

- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - * ... then a very low number of susceptibles

- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - * ...then a very low number of susceptibles
 - *

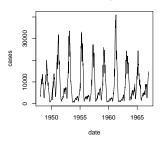
- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles
 - ▶ * ... then a very low level of disease

- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - * ...then a very low number of susceptibles
 - ▶ * ... then a very low level of disease
 - *

- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - * ... then a very low number of susceptibles
 - ▶ * ... then a very low level of disease
 - * ... then an increase in the number of susceptibles

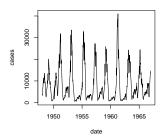
- Similar to predator-prey systems
- What happens if we start with a lot of susceptibles?
 - ► * There will be a big epidemic
 - * ... then a very low number of susceptibles
 - ▶ * ... then a very low level of disease
 - * ... then an increase in the number of susceptibles

If oscillations tend to be damped in simple models, why do they persist in real life?

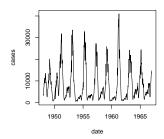


If oscillations tend to be damped in simple models, why do they persist in real life?

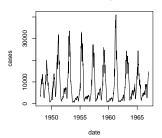
> *



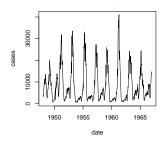
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather



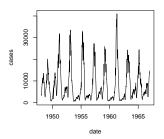
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather



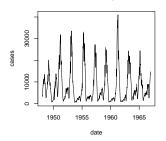
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality



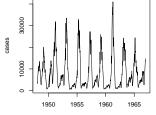
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - **>** ×



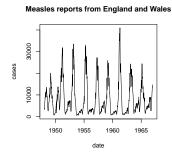
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity



- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity



- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms



- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - *

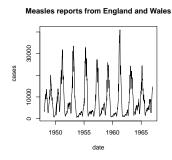
Measles reports from England and Wales

date

- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity

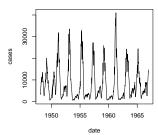
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - . .

- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour

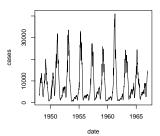


- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour
 - *

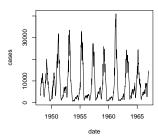
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour
 - * People are more careful when disease levels are high



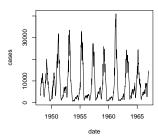
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour
 - * People are more careful when disease levels are high
 - *



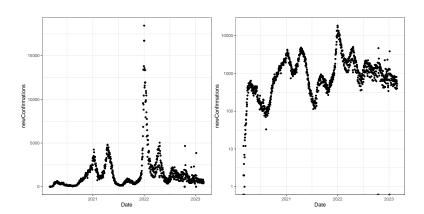
- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour
 - * People are more careful when disease levels are high
 - ► * Pathogen mutations



- If oscillations tend to be damped in simple models, why do they persist in real life?
 - * Weather
 - * Seasonality
 - * Environmental stochasticity
 - * School terms
 - * Demographic stochasticity
 - * Changes in Behaviour
 - * People are more careful when disease levels are high
 - ► * Pathogen mutations



COVID in Ontario



► Why did SARS-CoV-2 not follow this pattern?

▶ Why did SARS-CoV-2 not follow this pattern?

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ► * People and governments changed behaviour
 - *

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general

- Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - **>** *

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity
 - *

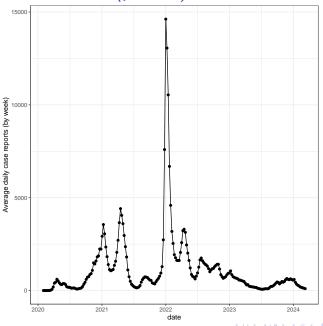
- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - *

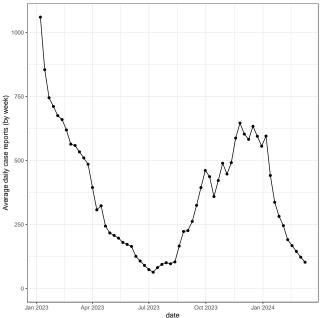
- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - ▶ * Is SARS-CoV-2 following a similar pattern now?

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ► * Fear of overflowing hospitals and chaos in general
 - * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - ▶ * Is SARS-CoV-2 following a similar pattern now?

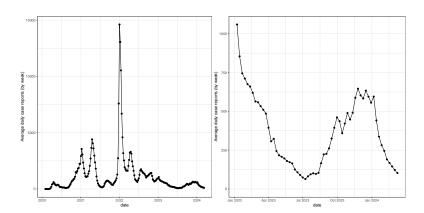
Post-pandemic COVID (preview)



Post-pandemic COVID (preview)



Post-pandemic COVID



Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

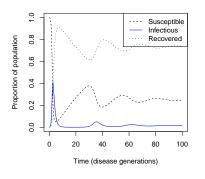
At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N=1/\mathcal{R}_0$

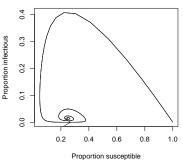
- At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$
- ightharpoonup Proportion "affected" (infectious or immune) should be approximately $V/N=1-1/\mathcal{R}_0$

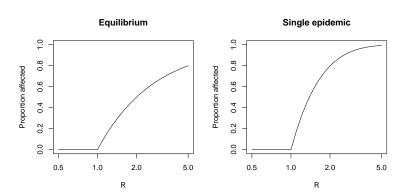
- At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N=1/\mathcal{R}_0$
- Proportion "affected" (infectious or immune) should be approximately $V/N=1-1/\mathcal{R}_0$
- ▶ If you have a single, fast epidemic, the size is also predicted by \mathcal{R}_0 .

- At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$
- Proportion "affected" (infectious or immune) should be approximately $V/N=1-1/\mathcal{R}_0$
- If you have a single, fast epidemic, the size is also predicted by \mathcal{R}_0 .

Reproductive numbers and risk (repeat)







► Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would *eliminate* malaria

- Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would eliminate malaria
- Gradual disappearance of polio, typhoid, etc., without risk factors going to zero

- Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would eliminate malaria
- Gradual disappearance of polio, typhoid, etc., without risk factors going to zero
- Eradication of smallpox!

- Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would eliminate malaria
- Gradual disappearance of polio, typhoid, etc., without risk factors going to zero
- Eradication of smallpox!

Threshold for elimination

► What proportion of the population should be vaccinated to eliminate a disease?

Threshold for elimination

► What proportion of the population should be vaccinated to eliminate a disease?



- What proportion of the population should be vaccinated to eliminate a disease?
 - * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1-1/\mathcal{R}$ should be vaccinated (effectively)

- What proportion of the population should be vaccinated to eliminate a disease?
 - * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1-1/\mathcal{R}$ should be vaccinated (effectively)
 - *

- What proportion of the population should be vaccinated to eliminate a disease?
 - * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 1/\mathcal{R}$ should be vaccinated (effectively)
 - * You may need to give vaccines to a larger fraction, since they don't always work

- What proportion of the population should be vaccinated to eliminate a disease?
 - * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 1/\mathcal{R}$ should be vaccinated (effectively)
 - * You may need to give vaccines to a larger fraction, since they don't always work

▶ Polio has an \mathcal{R}_0 of about 5.

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ► What proportion of the population should be vaccinated to eliminate polio?

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ► What proportion of the population should be vaccinated to eliminate polio?
 - *

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ► What proportion of the population should be vaccinated to eliminate polio?
 - * At least 1-1/5 = 80%

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ► What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least 1-1/5 = 80%
 - *

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - * At least 1-1/5 = 80%
 - * Kind of worked in much of the world

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - *

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ► * At least 1-1/20 = 95%

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ► * At least 1-1/20 = 95%
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - * At least 1-1/20 = 95%
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - *

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ► * At least 1-1/20 = 95%
- ▶ If gonorrhea has an R₀ of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ► * At least 1-1/2 = 50%

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - * At least 1-1/20 = 95%
- ▶ If gonorrhea has an R₀ of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ► * At least 1-1/2 = 50%
 - *

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - * At least 1-1/20 = 95%
- ▶ If gonorrhea has an R₀ of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - * At least 1-1/2 = 50%
 - * Does not actually work . . .

- ▶ Polio has an \mathcal{R}_0 of about 5.
- What proportion of the population should be vaccinated to eliminate polio?
 - ► * At least 1-1/5 = 80%
 - * Kind of worked in much of the world
- Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - * At least 1-1/20 = 95%
- ▶ If gonorrhea has an R₀ of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - * At least 1-1/2 = 50%
 - * Does not actually work . . .

► Why have infectious diseases persisted?

- ▶ Why have infectious diseases persisted?
 - ► The pathogens *evolve*

- ▶ Why have infectious diseases persisted?
 - ► The pathogens *evolve*
 - ► Human populations are **heterogeneous**

- Why have infectious diseases persisted?
 - ► The pathogens *evolve*
 - Human populations are heterogeneous
 - ▶ People differ in: nutrition, exposure, access to care

- Why have infectious diseases persisted?
 - ► The pathogens *evolve*
 - Human populations are heterogeneous
 - ▶ People differ in: nutrition, exposure, access to care
 - ► Information and misinformation

- Why have infectious diseases persisted?
 - ► The pathogens *evolve*
 - Human populations are heterogeneous
 - ▶ People differ in: nutrition, exposure, access to care
 - Information and misinformation
 - ► Vaccine scares, trust in health care in general

- Why have infectious diseases persisted?
 - ► The pathogens *evolve*
 - ► Human populations are **heterogeneous**
 - ▶ People differ in: nutrition, exposure, access to care
 - Information and misinformation
 - Vaccine scares, trust in health care in general

▶ Heterogeneity *increases* \mathcal{R}_0

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high
 - ► Elimination is harder

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high
 - Elimination is harder
- ► Marginal populations

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high
 - Elimination is harder
- Marginal populations
 - ► Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high
 - Elimination is harder
- Marginal populations
 - Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease
 - ► Humans rarely do this, however: the populations that need the most support typically have the least access

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - When disease is rare, it is concentrated in the most vulnerable populations
 - Cases per case is high
 - ► Elimination is harder
- Marginal populations
 - Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease
 - Humans rarely do this, however: the populations that need the most support typically have the least access

Outline

Introduction

Rate of spread

Single-epidemic model Epidemic size

Recurrent epidemic models Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Pathogen aggressiveness

► Should viruses evolve to become more or less dangerous?

▶ Should viruses evolve to become more or less dangerous?

*

- ▶ Should viruses evolve to become more or less dangerous?
 - ► * It depends

- ▶ Should viruses evolve to become more or less dangerous?
 - ► * It depends

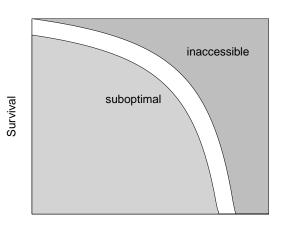
- ▶ Should viruses evolve to become more or less dangerous?
 - * It depends
 - ▶ * The virus evolves in the way that's best for the virus

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ * The virus evolves in the way that's best for the virus
 - *

- Should viruses evolve to become more or less dangerous?
 - * It depends
 - ► * The virus evolves in the way that's best for the virus
 - * Host death and host recovery are equally bad!

- Should viruses evolve to become more or less dangerous?
 - * It depends
 - ► * The virus evolves in the way that's best for the virus
 - * Host death and host recovery are equally bad!

Tradeoffs (repeat)



Reproduction

► If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:

▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:

▶ *

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - *

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - * Removes the largest number from susceptible pool

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - ▶ * Removes the largest number from susceptible pool
 - *

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - ▶ * Removes the largest number from susceptible pool
 - * Highest \mathcal{R}_0

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - * Removes the largest number from susceptible pool
 - * Highest \mathcal{R}_0
 - *

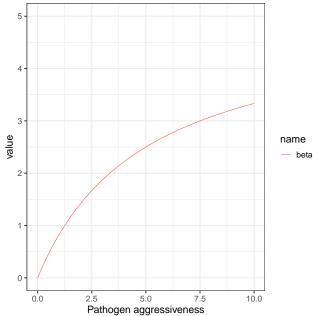
- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - * This could be more or less deadly

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ * This could be more or less deadly
 - *

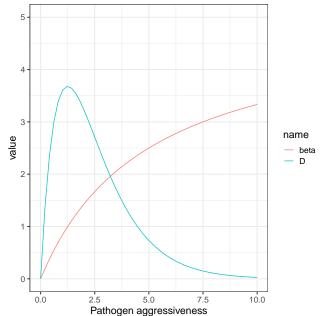
- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - * This could be more or less deadly
 - * Removal by killing and removal by recovery have similar effects on the virus

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - * Susceptible humans
- ► The winner will be the strain that has the highest "carrying capacity":
 - * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - * This could be more or less deadly
 - * Removal by killing and removal by recovery have similar effects on the virus

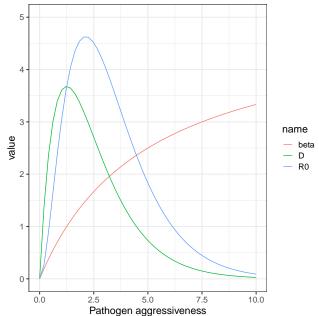
Pathogen aggressiveness (repeat)

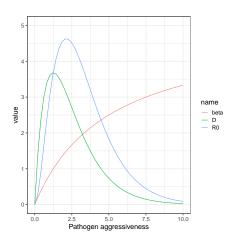


Pathogen aggressiveness (repeat)

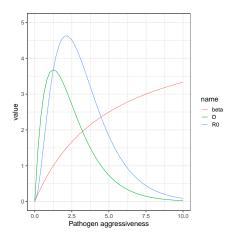


Pathogen aggressiveness (repeat)

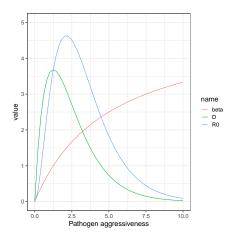




Pathogen will evolve to maximize \mathcal{R}_0 .



- Pathogen will evolve to maximize \mathcal{R}_0 .
- ► Pattern does not depend on whether duration *D* is ended by host death, or by immune system clearing the pathogen



- Pathogen will evolve to maximize \mathcal{R}_0 .
- ▶ Pattern does not depend on whether duration *D* is ended by host death, or by immune system clearing the pathogen

► We have evolved very good immune systems, but we can't always stay ahead of the viruses

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - *****

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - *

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better
 - *

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better
 - * Viruses that do well in the lower respiratory tract are more dangerous

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better
 - * Viruses that do well in the lower respiratory tract are more dangerous
 - *

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better
 - * Viruses that do well in the lower respiratory tract are more dangerous
 - ▶ * Have we evolved to make this a tradeoff for viruses?

- We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ► Should people evolve to favor the spread of more or less dangerous viruses?
 - * Less dangerous!
 - * Viruses that do well in the upper respiratory tract may spread better
 - * Viruses that do well in the lower respiratory tract are more dangerous
 - ▶ * Have we evolved to make this a tradeoff for viruses?

▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ► SARS-CoV-2 apparently evolved to be less dangerous

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ► SARS-CoV-2 apparently evolved to be less dangerous
 - ► This is a pattern, but not a guarantee

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ► SARS-CoV-2 apparently evolved to be less dangerous
 - This is a pattern, but not a guarantee