Lecture 4

Stochasticity

WILD3810 (Spring 2020)

Readings

> Mills 84-92

Assumptions of the B-D models

Remember from the lecture 3 that our simple models of population growth were based on the following assumptions:

1) Population closed to immigration and emigration

2) Model pertains to only the limiting sex, usually females

3) Birth and death rates are independent of an individual's age or biological stage

4) Birth and death rates are constant [1]

Assumptions of the B-D models

In reality, we know that assumption 4 is almost never true

Birth and death rates are determined by many external forces

These forces often vary across space, time, and individuals:

- body condition
- temperature
- drought
- fire

The B-D population model ignored all of these sources of variation [2]

Stochasticity

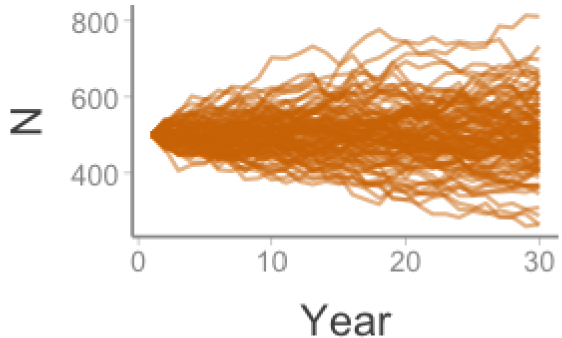
Stochasticity

In many cases, we do not know exactly why populations go up or down from year-to-year

Often don't know what these causes are so from our perspective, the variation appears to be **random**

Processes that are governed by some element of chance (randomness) are referred to as **stochastic** processes

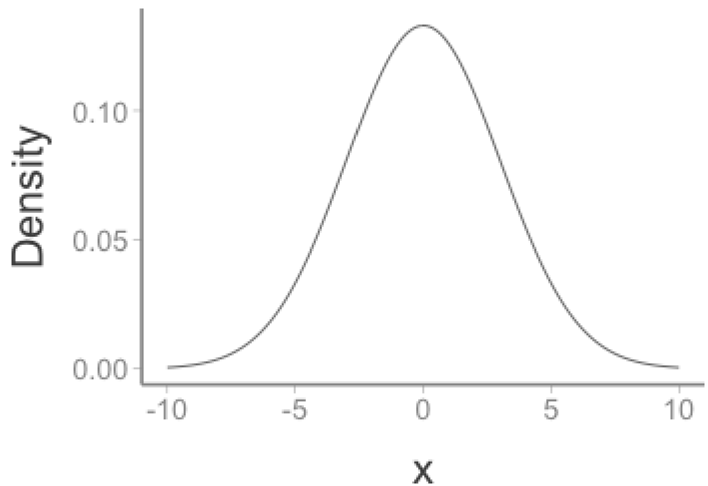
Just because something is stochastic doesn't mean it's completely unpredictable [3]



Stochasticity

We can predict how often we expect different random outcomes using *probability*

Probability distributions characterize the frequency of different outcomes [4]



In population models, we can use probability to characterize and account for stochastic processes that effect population growth

Two types of stochastic processes

With regards to population models, we generally distinguish between two types of stochasticity:

1) **Environmental stochasticity**

> variation in the *mean* demographic parameters and population growth that occurs due to random changes in environmental conditions

2) **Demographic stochasticity**

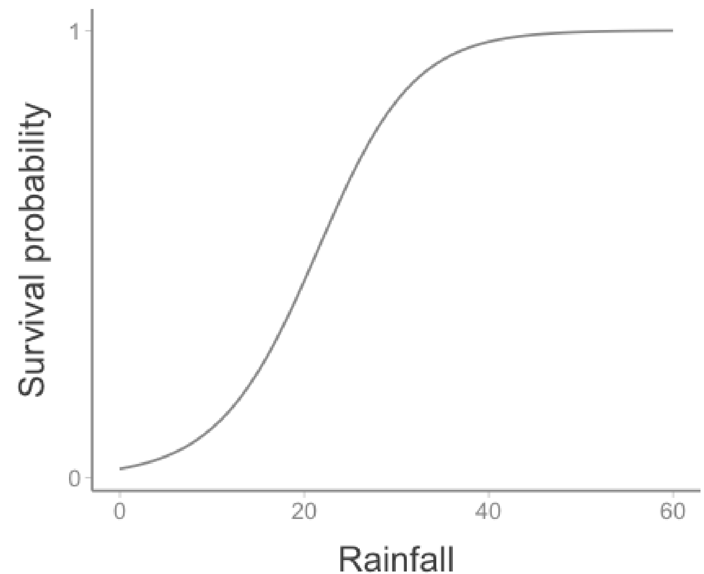
> variability in demographic parameters and population growth that arises from random outcomes among *individual* survival and reproductive fates due to random chance alone

Environmental stochasticity

Environmental stochasticity

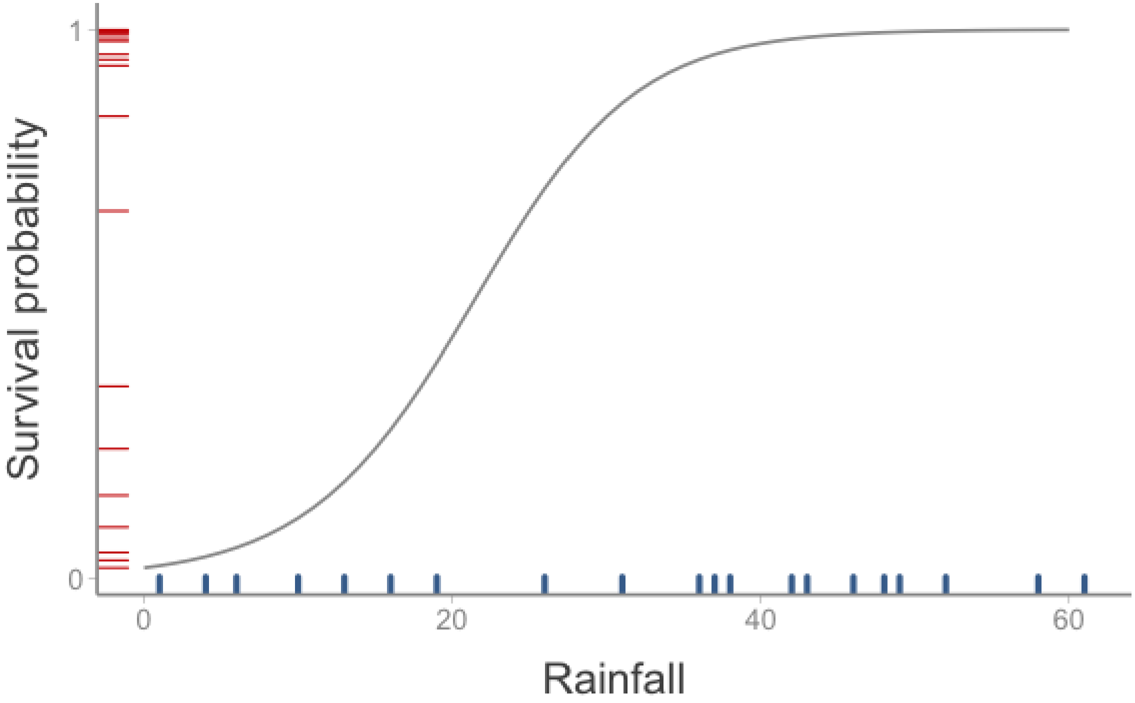
The expected value of demographic parameters can fluctuate over time in response to:

- rainfall
- temperature
- fires and disturbance
- competitors
- predators
- pathogens



Environmental stochasticity

If environmental attributes change stochastically over time, so will demographic vital rates and population growth rate



Modeling environmental stochasticity

If we want to take into account changes in demographic parameters as environmental conditions change, we need time-specific demographic parameters:

$$N_{t+1} = N_t \times (1 + b_t - d_t)$$
$$N_{t+1} = N_t \times \lambda_t$$

Over T years, abundance will be:

$$N_T = N_0 \times \left(\lambda_0 \times \lambda_1 \times \lambda_2 \times \ldots \lambda_{T-1}\right)$$

Modeling environmental stochasticity

For example, if $N_0 = 50$ and:

$$\lambda_0 = 1.1$$

$$\lambda_1 = 0.9$$

$$\lambda_2 = 0.7$$

$$\lambda_3 = 1.2$$

$$\lambda_4 = 1.1$$

then:

$$N_5 = 50 \times 1.1 \times 0.9 \times 0.7 \times 1.2 \times 1.1 = 46$$

Modeling environmental stochasticity

It's clear that this population is declining

- the *average* value of λ must be < 1

What *is* the average λ (which we'll call $\bar{\lambda}$)?

Modeling environmental stochasticity

An obvious way to calculate $\bar{\lambda}$ is the *arithmetic mean* of the annual λ's:

$$\bar{\lambda} = \frac{\lambda_0 + \lambda_1 + \lambda_2 + \ldots \lambda_{T-1}}{T}$$

In our example, this equals:

$$\bar{\lambda} = \frac{1.1 + 0.9 + 0.7 + 1.2 + 1.1}{5} = \frac{5}{5} = 1$$

Modeling environmental stochasticity

But that can't be right!

$\bar{\lambda} = 1$ means the population should have, on average, remained at 50 individuals

The issue that the population growth is a multiplicative process

This means that shrinking by 30% $(\lambda = 0.7)$ and then growing by 30% $(\lambda = 1.3)$ does not get you back to where you started

- For example, $100 \times 0.7 = 70$ but $70 \times 1.3 = 91$.

Modeling environmental stochasticity

To estimate the average of a multiplicative process, we need to take the *geometric* mean rather than the arithmetic mean:

$$\bar{\lambda} = \left(\lambda_0 \times \lambda_1 \times \lambda_2 \times \ldots \lambda_{T-1}\right)^{\frac{1}{T}}$$

For our population, that means:

$$\bar{\lambda} = \left(1.1 \times 0.9 \times 0.7 \times 1.2 \times 1.1\right)^{\frac{1}{5}} = 0.98$$

Modeling environmental stochasticity

As you can see, the geometric mean $<$ arithmetic mean

This is a *critical point* about environmental stochasticity

> Populations with variable growth rates will tend to grow more slowly (or decrease faster) than populations in constant environments even if their mean vital rates are the same.

Modeling environmental stochasticity

Let's see what that looks like:

Initially, assume a large population $(N_0 = 500)$ with:

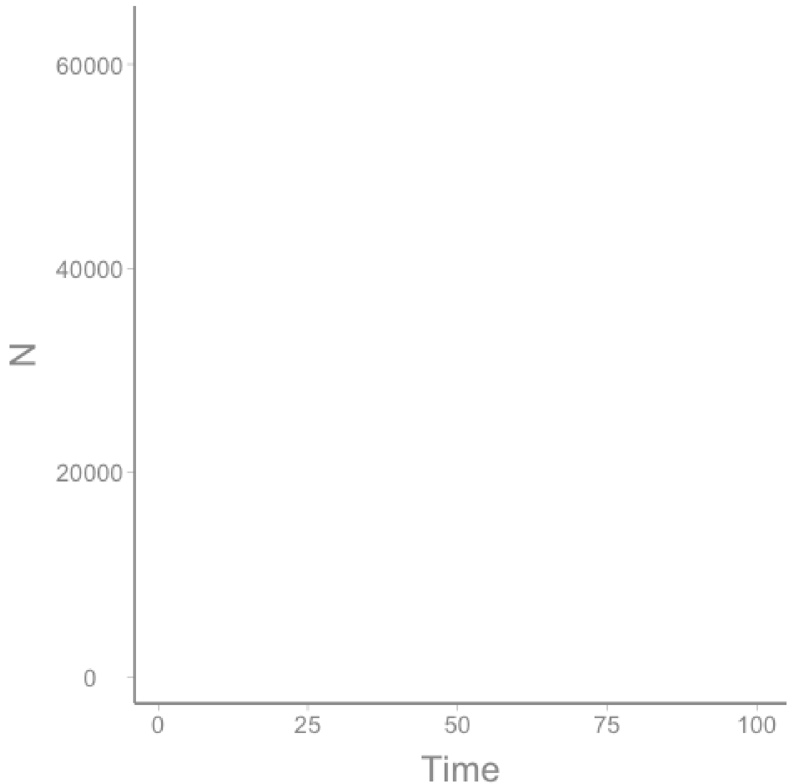
- $\bar{b_t} = 0.55$
- $\bar{d_t} = 0.50$
- and **neither parameter varies over time**

Thus:

$$\bar{\lambda} = (1 + \bar{b_t} - \bar{d_t}) = (1 + 0.55 - 0.5) = 1.05$$

Modeling environmental stochasticity

Over 100 years, the population growth will be:

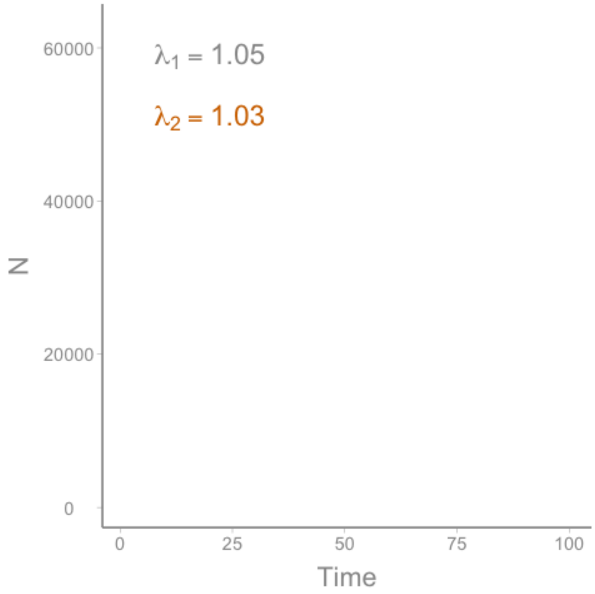


Modeling environmental stochasticity

Now let's look at the dynamics of a second population with the same starting population size, the same mean demographic rates but with annual variation of 20%

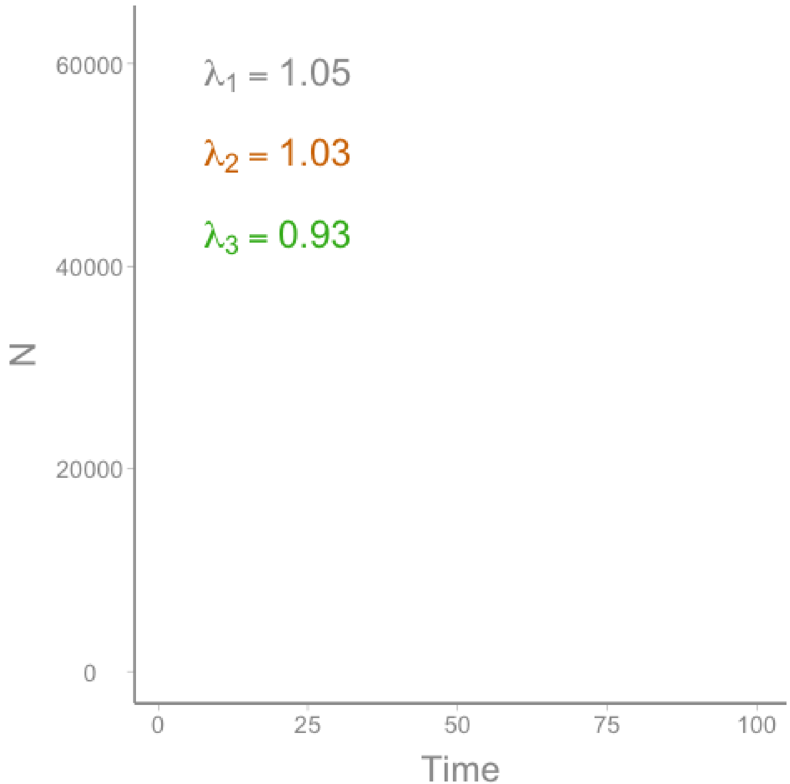
Notice that the mean rates are the same so intuitively,

$$\bar{\lambda} = (1 + \bar{b_t} - \bar{d_t}) = (1 + 0.55 - 0.5) = 1.05$$



Modeling environmental stochasticity

Finally, let's add a third population with the same starting population size, the same mean demographic rates but now with annual variation of 40%.



Modeling environmental stochasticity

Because environmental stochasticity tends to reduce $\bar{\lambda}$ regardless of population size, it has important consequences for the extinction risk of **both small and large populations**

We'll explore this idea more in lab

Demographic stochasticity

Demographic stochasticity

In the preceeding examples, we treated the demographic outomes (individual survival and reproductive success) at each time step as non-random variables

- If the mean survival probability in a given year is 80%, then exactly 80% of the population survived and 20% died

This is not a realistic assumption

Imagine flipping a coin 10 times:

- we know that the probability of getting a heads is 50%
- but we would not be suprised to get 4 heads. Or 7
- we wouldn't even be that surprised to get 2 or 9

This is because the outcome of the coin flip is a *random variable* - the outcome is governed by chance

Demographic stochasticity

The same is true to demographic outcomes

Even if the *expected* survival rate is 80%, the *realized* survival rate could be higher or lower

Likewise, we might expect individuals to produce 3 offspring on average, but some individuals will have more and some fewer based on chance [5]

Demographic stochasticity is essentially the difference between the **expected** survival/reproductive rate and the **realized** rates in our population.

Demographic stochasticity

Demographic stochasticity occurs because our population is a *finite sample*

Going back to the coin flip, if we flip the coin 1000 times, we would expect to get pretty close to 50% heads

But as the number of flips gets smaller, the realized success rate could differ more from the expected value

Effects of demographic stochasticity

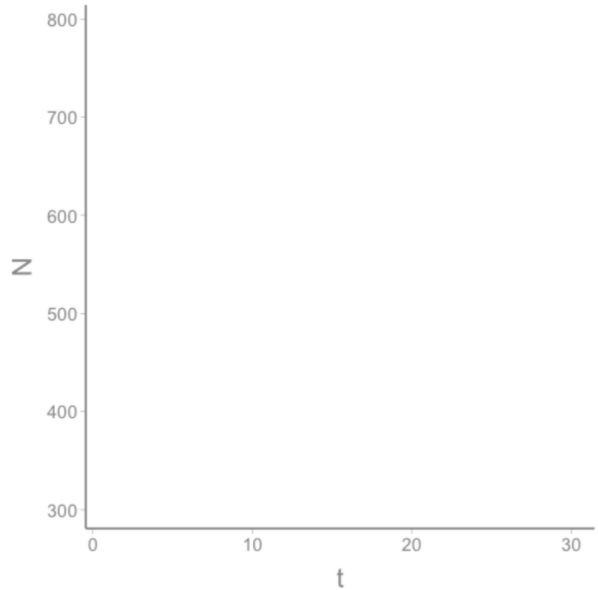
Demographic stochasticity is mainly an issue at **small population sizes** because each individual is a larger proportion of the total sample size

To see this in action, we can use R to simulate the abundance of populations that experience demographic stochasticity

Effects of demographic stochasticity

Start with 100 populations with a relatively large population size $(N = 500)$ [6]

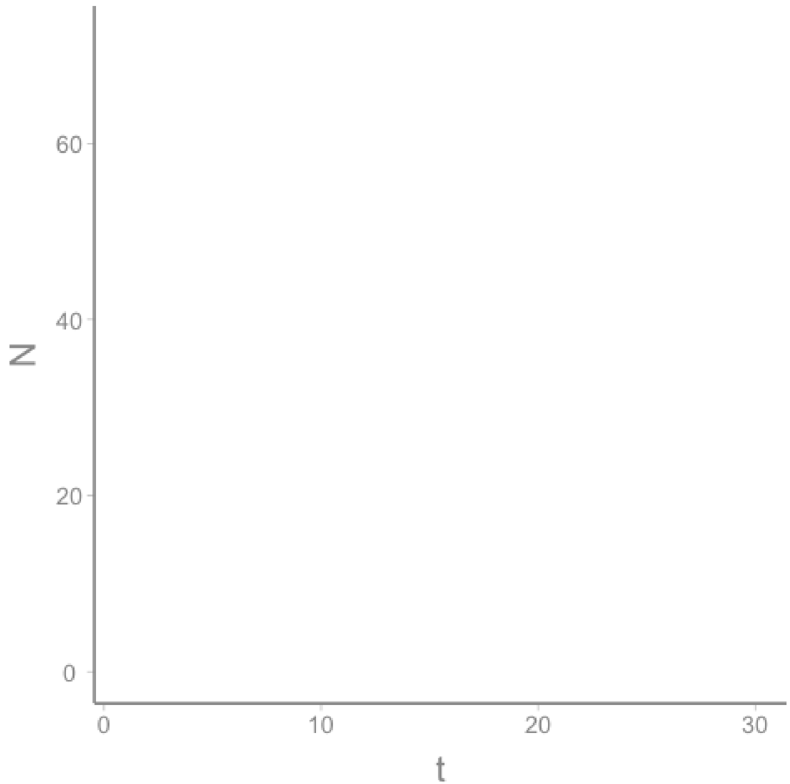
- Further assume that the mean survival and reproductive rates remain constant so all stochastisticity is demographic



With $N_0 = 500$ no populations went extinct

Effects of demographic stochasticity

What happens if we start with 10 individuals instead?



Now 41% went extinct [7]

Effects of demographic stochasticity

Demographic stochasticity increase extinction risk of small populations because there's an increased chance that, purely due to randomness, more individuals die than are born

At large abundances, this is much less likely

Stochasticity and extinction risk over time

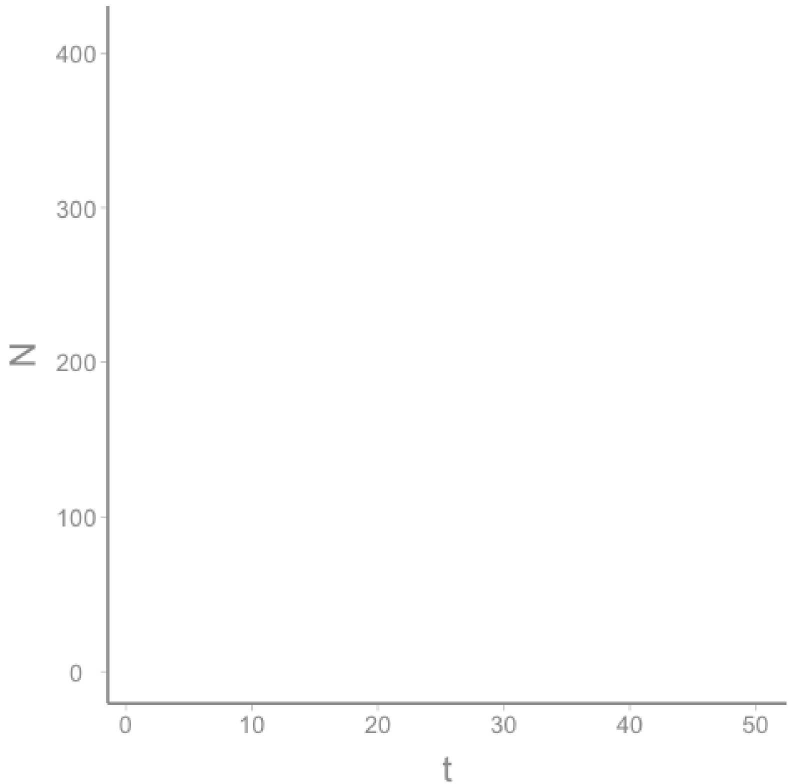
Another important consequences of stochasticity is that, over long-enough time periods, populations that exeperience stochasticity (both demographic and environmental) will eventually go extinct

Given long enough, each population will eventually experience a string of years with high mortality and low reproductive success

The time it takes for this to occur will be longer for large populations but even still, it will eventually happen

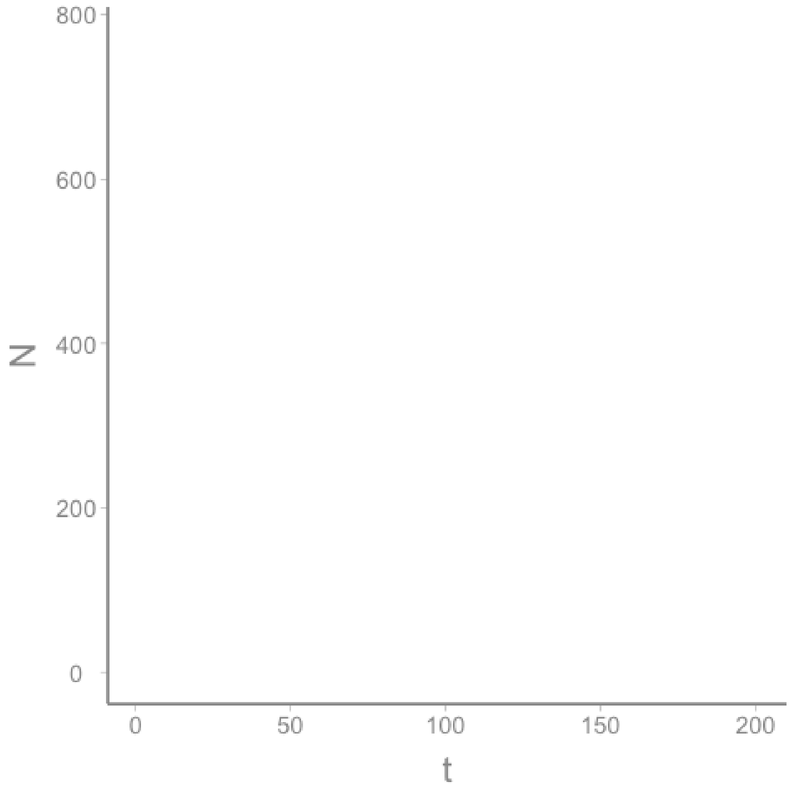
Stochasticity and extinction risk over time

Again, we can use data simulations to show this: If we start with populations of 100 individuals and simulate 50 years of population change, 1% of populations go extinct



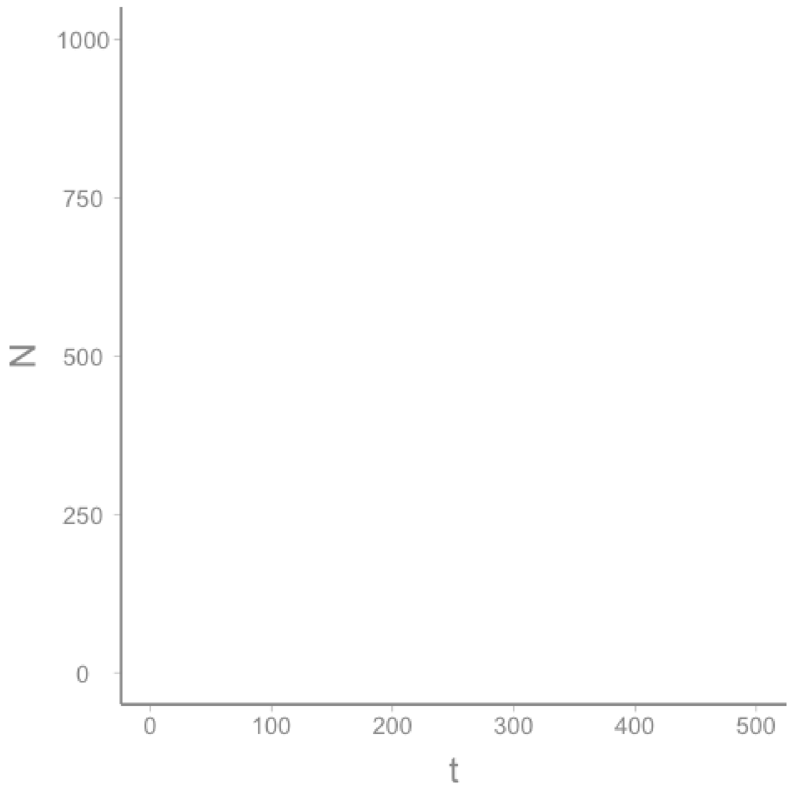
Stochasticity and extinction risk over time

If we extend our simulation out to 200 years, 23% of populations go extinct



Stochasticity and extinction risk over time

500 years? 57% of populations go extinct



Stochasticity and extinction risk over time

10,000 years? 99% of populations go extinct [8]