UNIT 3: Structured populations

1 Introduction

- Up until now we've tracked populations with a single state variable (population size or population density)
- What assumption are we making?
  - **Answer:** All individuals can be counted the same. At least at census time
  - **Answer:** Never exactly true
- What are some organisms for which this seems like a good approximation?
  - **Answer:** Dandelions, bacteria, insects
- What are some organisms that don't work so well?
  - **Answer:** Trees, people, codfish

Structured populations

- If we think age or size is important to understanding a population, we might model it as an **structured** population
- Instead of just keeping track of the total number of individuals in our population . . .
  - Keeping track of how many individuals of each age
    - or size
    - or developmental stage

1.1 Example: biennial dandelions

- Imagine a population of dandelions
  - Adults produce 80 seeds each year
  - 1% of seeds survive to become adults
  - 50% of first-year adults survive to reproduce again
  - Second-year adults never survive
- Will this population increase or decrease through time?

How to study this population

- Choose a census time
  - Before reproduction or after
  - Since we have complete cycle information, either one should work
- Figure out how to predict the population at the next census

Census choices

- Before reproduction
  - All individuals are adults
  - We want to know how many adults we will see next year
- After reproduction
  - Seeds, one-year-olds and two-year-olds
  - Two-year-olds have already produced their seeds; once these seeds are counted, the two-year-olds can be ignored, since they will not reproduce or survive again

What determines λ?

- If we have 20 adults before reproduction, how many do we expect to see next time?
- $\lambda = p + f$ is the total number of individuals per individual after one time step
- What is f in this example?
  - **Answer:** 0.8
- What is p in this example?
  - **Answer:** 0.5 for 1-year-olds and 0 for 2-year-olds.
  - **Answer:** We can't take an average, because we don't know the population structure

What determines $\mathcal{R}$?

- $\mathcal{R}$ is the average total number of offspring produced by an individual over their lifespan
- Can start at any stage, but need to close the loop
- What is the reproductive number?
- **Answer:** If you become an adult you produce (on average)
  - **Answer:** 0.8 adults your first year
  - **Answer:** 0.4 adults your second year
- **Answer:** $\mathcal{R} = 1.2$

What does $\mathcal{R}$ tell us about λ?

- **Answer:** Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- If $\mathcal{R} = 1.2$, then λ
  - **Answer:** > 1 – the population is increasing
  - **Answer:** < 1.2 – the life cycle takes more than 1 year, so it should take more than one year for the population to increase 1.2 times

1.2 Modeling approach

- In this unit, we will construct *simple* models of structured populations
  - To explore how structure might affect population dynamics
  - To investigate how to interpret structured data

Regulation

- *Simple* population models with regulation can have extremely complicated dynamics
- *Structured* population models with regulation can have insanely complicated dynamics
- Here we will focus on understanding structured population models *without regulation*:
  - **Answer:** Individuals behave independently, or (equivalently)
  - **Answer:** Average per capita rates do not depend on population size

Age-structured models

- The most common approach is to structure by age
- In age-structured models we model how many individuals there are in each "age class"
  - Typically, we use age classes of one year
  - Example: salmon live in the ocean for roughly a fixed number of years; if we know how old a salmon is, that strongly affects how likely it is to reproduce

Stage-structured models

- In stage-structured models, we model how many individuals there are in different stages
  - Ie., newborns, juveniles, adults
  - More flexible than an age-structured model

  - Example: forest trees may survive on very little light for a long time before they have the opportunity to recruit to the sapling stage

Discrete vs. continuous time

- Structured models can be done in either discrete or continuous time
- Continuous-time models are structurally simpler (and smoother)
- How do population characteristics affect the choice?
  - **Answer:** Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
  - **Answer:** Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- Adding age structure is conceptually simpler with discrete time
  - **Answer:** So we'll do that.

2 Constructing a model

- This section will focus on **linear, discrete-time, age-structured** models
- State variables: how many individuals of each age at any given time
- Parameters: p and f *for each age that we are modeling*

When to count

- We will choose a census time that is appropriate for our study
  - Before reproduction, to have the fewest number of individuals
  - After reproduction, to have the most information about the population processes
  - Some other time, for convenience in counting
    * **Answer:** A time when individuals gather together
    * **Answer:** A time when they are easy to find (insect pupae)

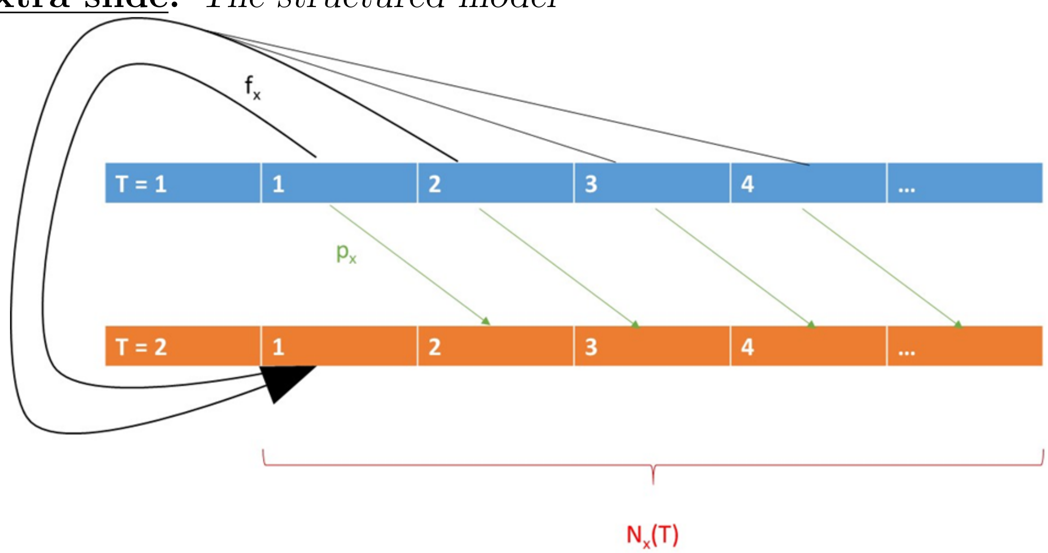
The conceptual model

- Once we choose a census time, we imagine we know the population for each age x after time step T.
  - We call these values $N_x(T)$
- Now we want to calculate the expected number of individuals in each age class at the next time step
  - We call these values $N_x(T+1)$
- What do we need to know?
  - **Answer:** The survival probability of each age group: p_x
  - **Answer:** The average fecundity of each age group: f_x

Closing the loop

- f_x and p_x must close the loop back to the census time, so we can use them to simulate our model:
  - f_x has units [new indiv (at census time)]/[age x indiv (at census time)]
  - p_x has units [age $x+1$ indiv (at census time)]/[age x indiv (at census time)]

Extra slide: *The structured model*



2.1 Model dynamics

Short-term dynamics

- This model's short-term dynamics will depend on parameters ...
  - It is more likely to go up if fecundities and survival probabilities are high
- ... and starting conditions
  - If we start with mostly very old or very young individuals, it might go down; with lots of reproductive adults it might go up

Long-term dynamics

- If a population follows a model like this, it will tend to reach
  - a **stable age distribution**:
    * the *proportion* of individuals in each age class is constant
  - a stable value of λ
    * if the proportions are constant, then we can average over f_x and p_x, and the system will behave like our simple model
- What are the long-term dynamics of such a system?
  - **Answer:** Exponential growth or exponential decline

Exception

- Populations with **independent cohorts** do not tend to reach a stable age distribution
  - A **cohort** is a group that enters the population at the same time
  - We say my cohort and your cohort interact if my children might be in the same cohort as your children
  - or my grandchildren might be in the same cohort as your great-grandchlidren
  - ...
- As long as all cohorts interact (none are independent), then the unregulated model leads to a stable age distribution (SAD)

Independent cohorts

- Some populations might have independent cohorts:
  - If salmon reproduce *exactly* every four years, then:
    * the 2015 cohort would have offspring in 2019, 2023, 2027, 2031, ...
    * the 2016 cohort would have offspring in 2020, 2024, 2028, 2032, ...
    * in theory, they could remain independent – distribution would not converge
- Examples could include 17-year locusts, century plants, ...