UNIT 6: Competition

1 Introduction

Inter-species interactions

- Competition: interaction hurts the growth rate of both species
  - **Answer postponed:**
- Exploitation: interaction is good for one species but bad for the other
  - **Answer postponed:**
- Mutualism: interaction is good for both species
  - **Answer postponed:**
- Commensalism: interaction is good for one species, and close to neutral for the other
  - **Answer postponed:**

Competition

- Competition occurs when two species both depend on the same resource, or resources
- Each species' ability to reproduce successfully is reduced by the presence of the other
- Via effects on any component of successful reproduction:
  - **Answer:** Survival, growth, producing offspring
- Species may be very similar, or very different
  - **Answer:** Oaks and maples competing for light
  - **Answer:** Ants and mammals competing for leaves
  - **Answer:** Mussels and algae competing for space in the intertidal zone

Competition in ecology

- What factors determine which species survive in which habitats?
- What factors determine how many similar species can co-exist?
- Why do similar species coexist at all?

Flour beetles

- There is a series of experiments where researchers allow two species of flour beetles to compete in different laboratory environments
- The larger species survives better in drier conditions, and the smaller species reproduces faster in moister conditions
- Poll: What outcomes do you expect under wet vs dry conditions?
  - **Answer:** Each species wins when conditions are better for it
- Poll: What if I "tune" the conditions to something in between?
  - **Answer:** The species could both survive together
  - **Answer:** Sometimes one survives, and sometimes the other
    * **Answer:** Whichever species got a "head start" would survive

Outcomes of competition

- In a given stable environment, we generally expect the competitive interaction between two species to have one of the following results
  - **Dominance**: one species wins every time
  - **Co-existence**: if both species are present, they will both persist
  - **Founder control**: whichever species gets established first will exclude the other

2 Population model with competition

- We modeled a single species using the equation:
  - $\frac{dN}{dt} = (b(N) - d(N))N$
- We want to modify this for a species which is competing with another species
  - $\frac{dN_1}{dt} = ?$
- The amount of competition seen by species 1 is $\tilde{N}_1 = N_1 + \alpha_{21} N_2$
- How should our equation change?
  - **Answer:** $\frac{dN_1}{dt} = (b_1(\tilde{N}_1) - d_1(\tilde{N}_1))N_1$
  - **Answer:** $\frac{dN_2}{dt} = (b_2(\tilde{N}_2) - d_2(\tilde{N}_2))N_2$

Carrying capacity

- For this unit, we will mostly ignore Allee effects
- Therefore, we expect each species to converge to its *carrying capacity* K (or K_1 and K_2) when it is alone
- How do we define carrying capacity in this system?
  - **Answer:** The birth rate equals the death rate: $b(K) = d(K)$

Carrying capacity with competition

- $\frac{dN_1}{dt} = (b_1(\tilde{N}_1) - d_1(\tilde{N}_1))N_1$
- How can this population be at equilibrium?
  - **Answer:** $\tilde{N}_1 = K_1$: the species has the right amount of competitive pressure to make $\mathcal{R} = 1$
  - **Answer:** $N_1 = 0$: the species is not present

Logistic model

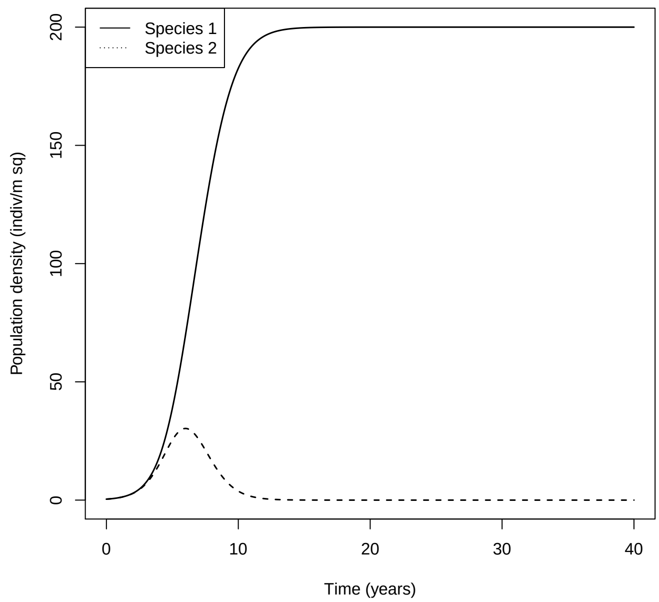
- You've probably learned about the logistic model, if not you may learn about it later
- This model is similar to the logistic model, except:
  - Birth and death are tracked separately
  - We don't assume functions are straight lines
- Everything we say about this model also applies to the logistic model

2.1 Balanced competition

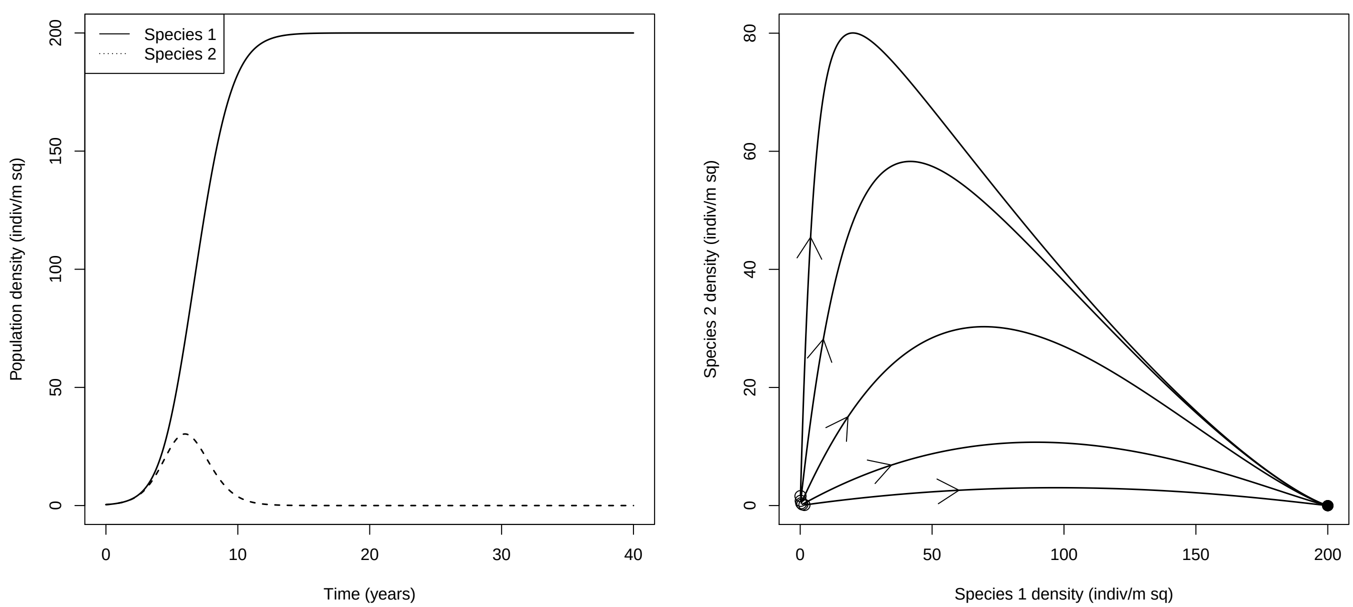
Equal competition

- If the αs are both equal to one, we have equal competition. This means that the competitive effect of an individual from either species is the same.
- If $\bar{N} = N_1 + N_2$, then:
  - $\frac{dN_1}{dt} = (b_1(\bar{N}) - d_1(\bar{N}))N_1$
  - $\frac{dN_2}{dt} = (b_2(\bar{N}) - d_2(\bar{N}))N_2$
- What happens in this case?
  - **Answer:** Competition is mediated by only one quantity, $\bar{N}$.
  - **Answer:** Whichever species has a higher value of K can survive at a density where the other one can't
  - **Answer:** Dominance!

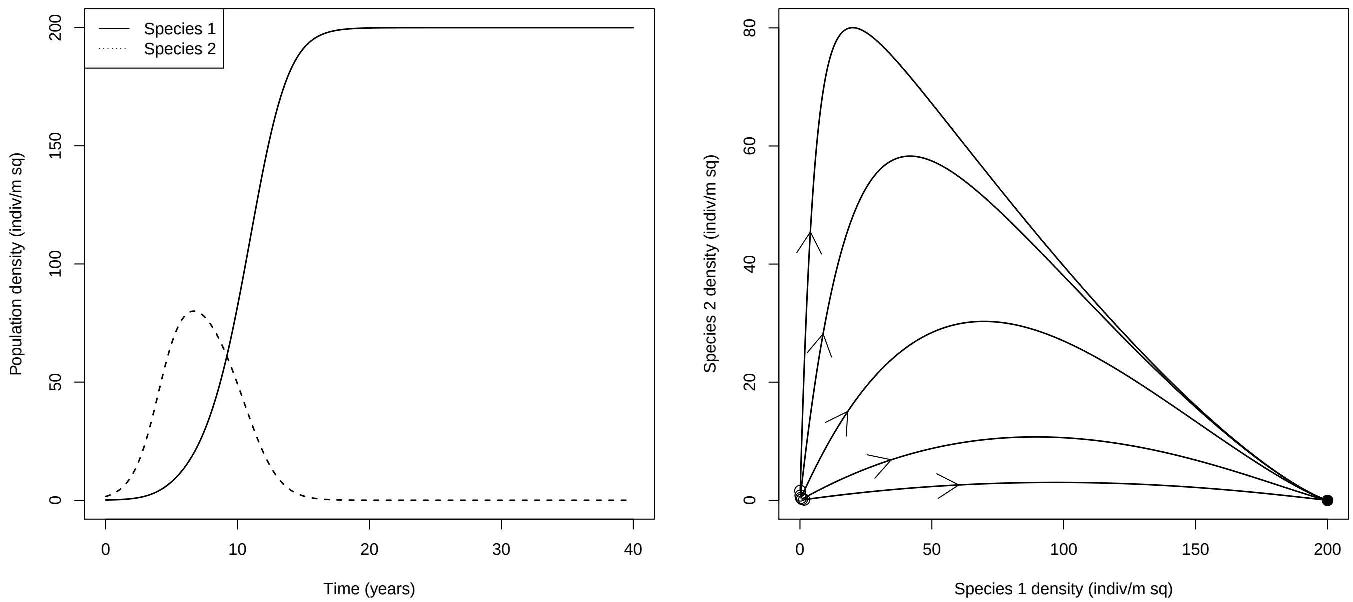
Comment slide: *Dominance time plot*



Dominance



Comment slide: *Dominance*



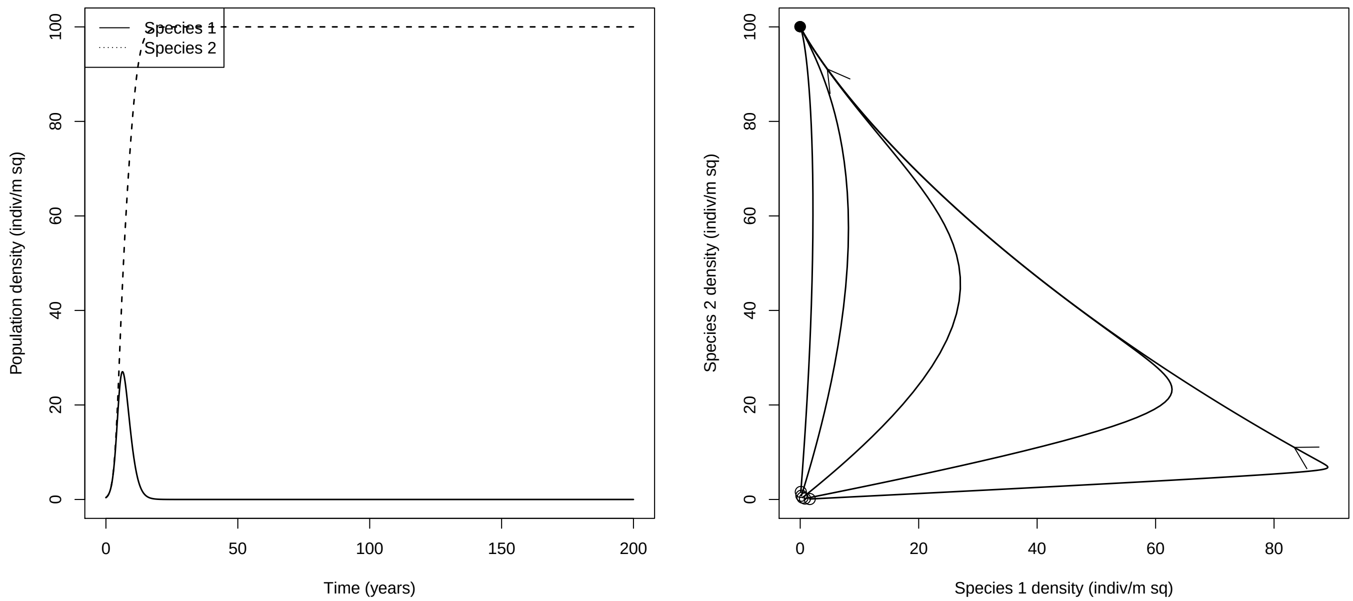
Time plots and phase plots

- *Time plots* have time on one axis and show population quantities on another
  - Fixed parameters (usually)
  - Single starting points
- *Phase plots* have population quantities on both axes
  - Fixed parameters (usually)
  - Multiple starting points (usually)
  - Better for seeing overall pattern of results
  - Worse for seeing rates (how quickly things change)

Reading phase plots

- Log or linear (per capita vs. total perspective)
- Open circles are starting points
- Closed circles are ending points
- Arrows show direction of time

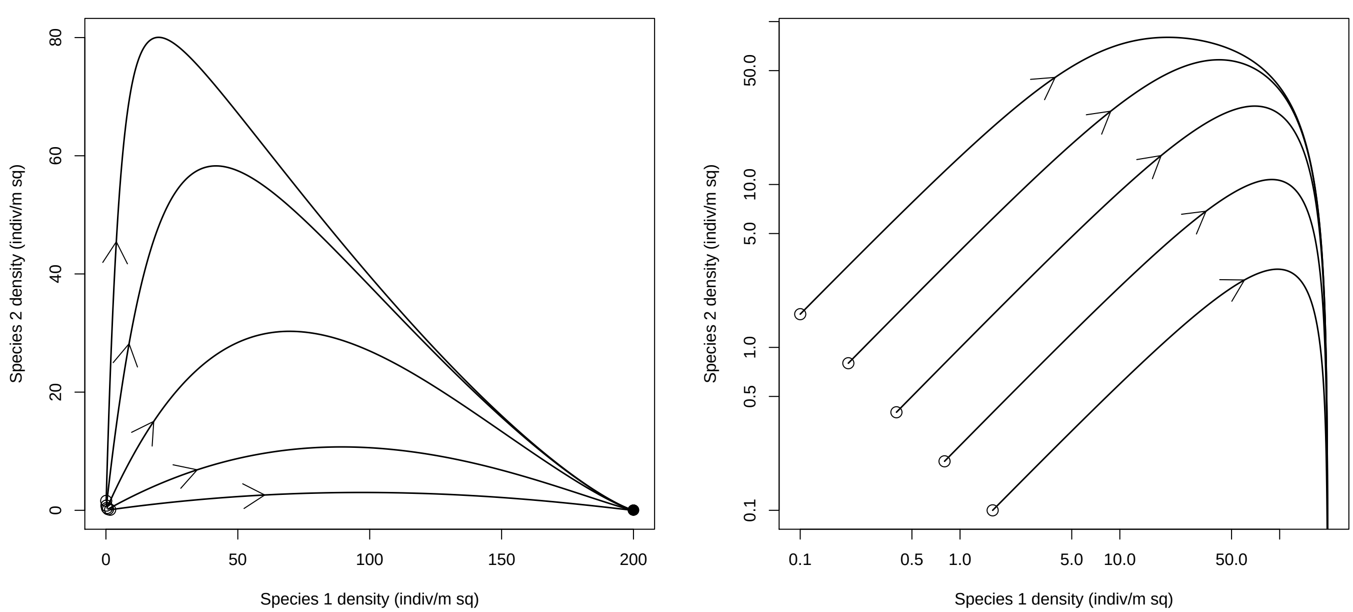
Dominance again



Log plots and linear plots

- We will look at *population* quantities on either a *log* or *linear* scale
- Log plots show *proportional* differences
- Linear plots show *absolute* differences

Different scales



Units of α

- $\tilde{N}_1 = N_1 + \alpha_{21} N_2$; $\tilde{N}_2 = N_2 + \alpha_{12} N_1$
- α_{21} measures the strength of the competitive effect *of* individuals of species 2 *on* the growth rate of species 1.
- What are the units of α_{21}?
  - **Answer:** $\mathrm{indiv}_1/\,\mathrm{indiv}_2$
- Since α has units, we don't expect there to be anything special about $\alpha = 1$
- Equal competition (both species have the same effect on each other) is a special case of balanced competition (both species have the same *relative* effect on each other)

Balanced competition example

- Two plants compete with each other for water. The value of α_{21} is $4\,\mathrm{indiv}_1/\,\mathrm{indiv}_2$
- Poll: Which species is bigger?
  - **Answer:** $4indiv_1$ have as much impact as $indiv_2$
  - **Answer:** Species 2 individuals are bigger
- If they're only competing for water, what's the value of α_{12}?
  - **Answer:** $\alpha_{12} = 1\,\mathrm{indiv}_2/4\,\mathrm{indiv}_1$
  - **Answer:** $1indiv_2$ has as much impact as $4indiv_1$

Balanced competition

- Poll: What results do we expect from balanced competition?
  - **Answer:** It seems like the bigger species should win
  - **Answer:** But that's not always the case
- Balanced competition works just like equal competition
  - **Answer:** Both species experience total density in the same way
  - **Answer:** So the species with the higher carrying capacity (compared using the same units) will dominate
- Balanced competition means (exactly) no tendency for founder control or for coexistence

Measuring competitive effects

- It makes sense that we have a range of parameters that give us balanced competition, because we know qualitative changes in dynamics are explained by unitless parameters
- What's the unitless parameter here?
  - **Answer:** $C = \alpha_{21}\alpha_{12}$
- C measures the relative effect of between-species and within-species competition
  - $C = 1$ means competition is balanced
  - $C < 1$ means there is more competition within species (tendency for coexistence)
  - $C > 1$ means there is more competition between species (tendency for founder control)

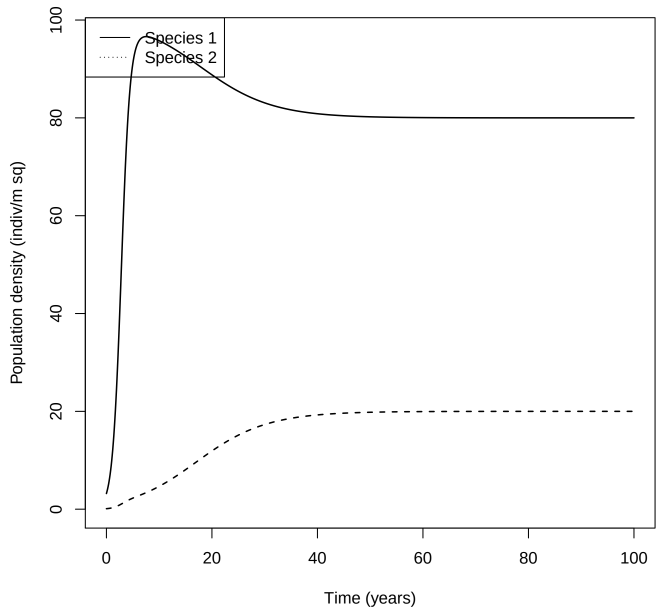
2.2 Unbalanced competition

- If two species are competing by using a simple resource, we expect competition to be balanced
  - Both αs measure the relative effect of the two species on the resource
- In more realistic situations, competition may not be balanced

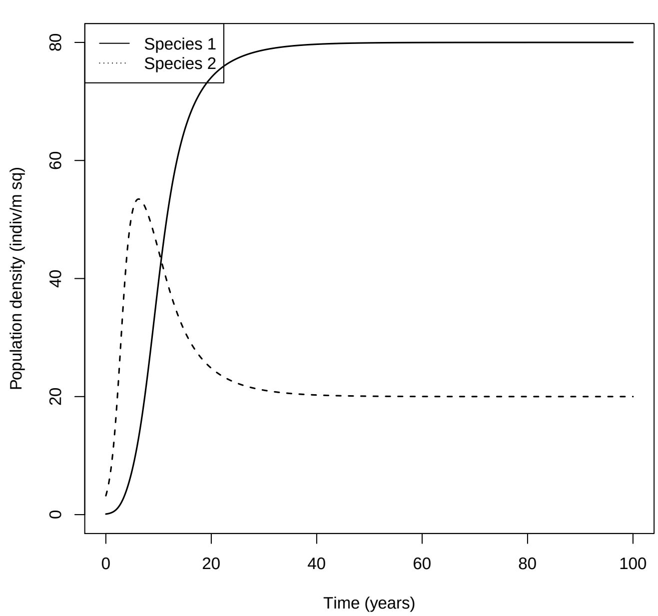
Coexistence

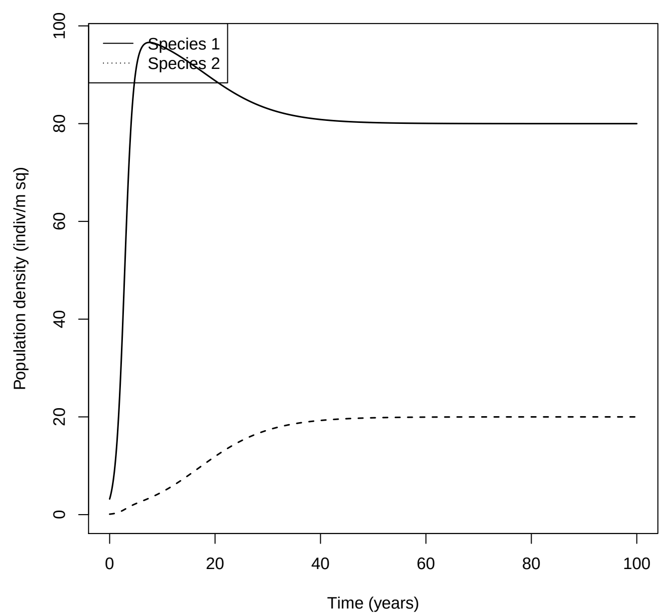
- Coexistence *may* occur when $C < 1$
- Poll: Why might individuals have relatively weaker competitive interactions with members of the other species?
  - **Answer:** They may compete for mates or mating sites
    - **Answer:** Example: birds with different nesting preferences
  - **Answer:** Organisms may use resources in different ways
    - **Answer:** Trees may produce leaves at different times

<u>Comment slide</u>: *Coexistence*

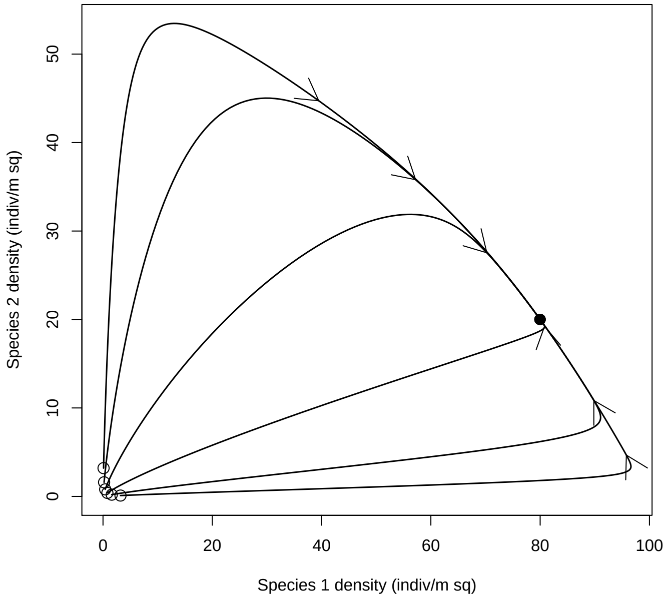


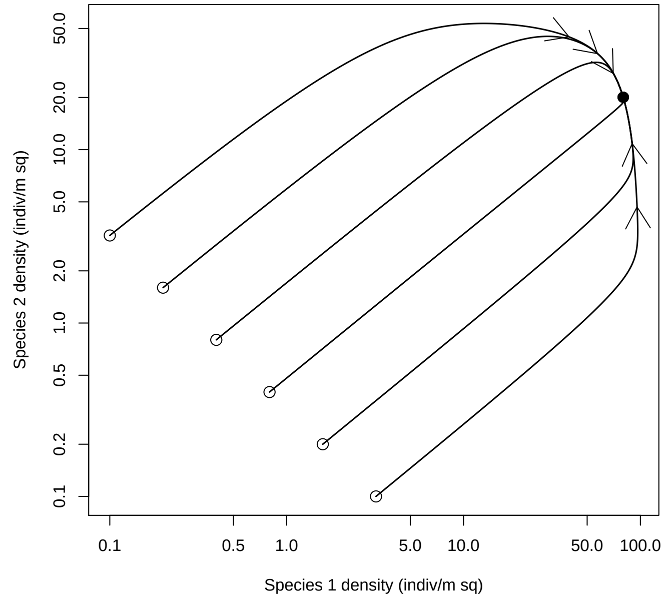
Coexistence





Coexistence phase plots

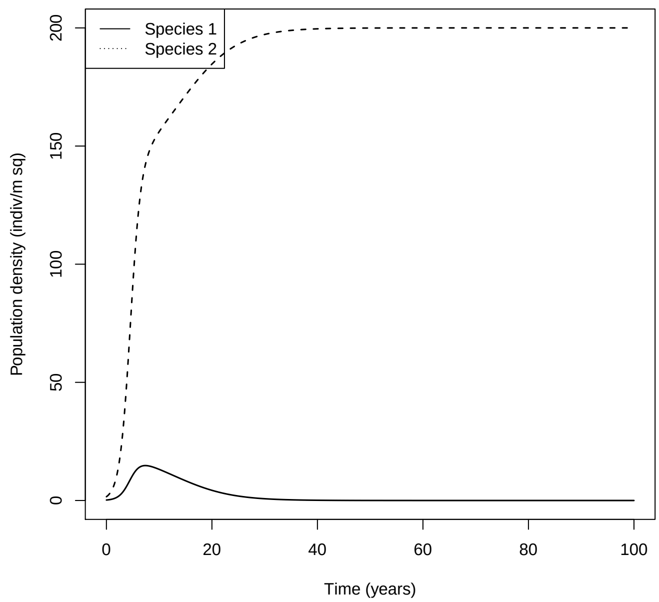




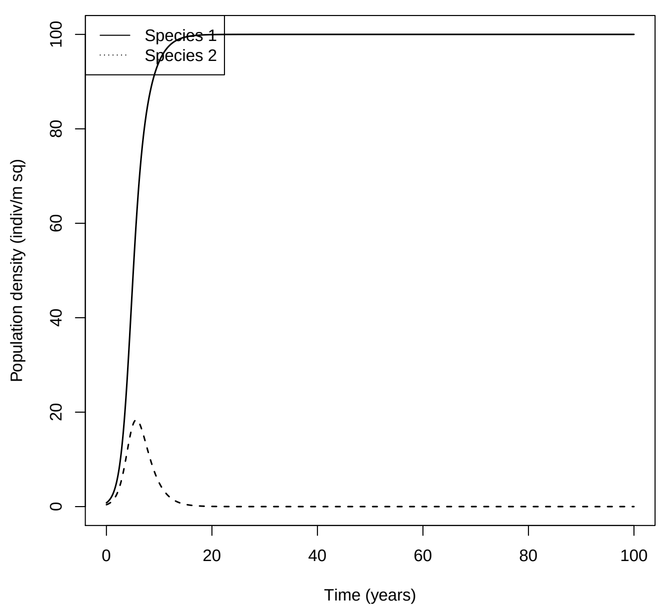
Founder control

- Founder control *may* occur when $C > 1$
- Poll: Why might individuals have relatively stronger competitive interactions with members of the other species?
  - **Answer:** Conspecifics might co-operate to defend resources
    - **Answer:** Example: dogs and leopards
  - **Answer:** Organisms might change the environment in a way that favors their own species
    - **Answer:** Example: trees and grasses

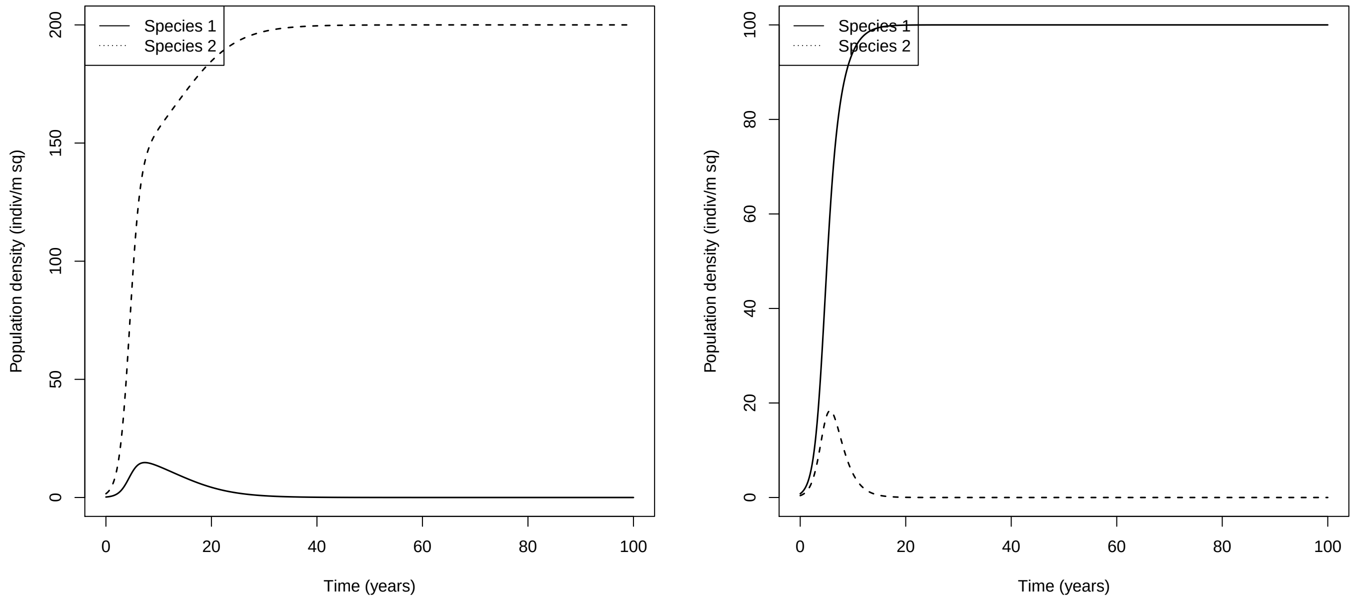
Comment slide: *Founder control*



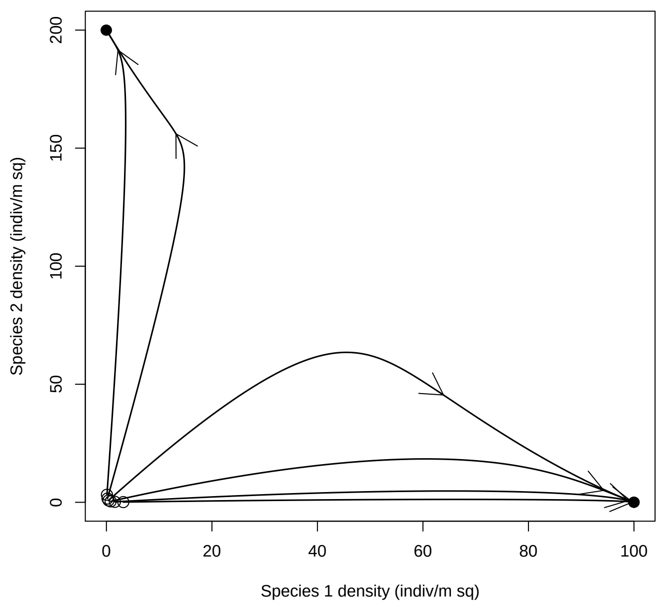
<u>Comment slide</u>: *Founder control*



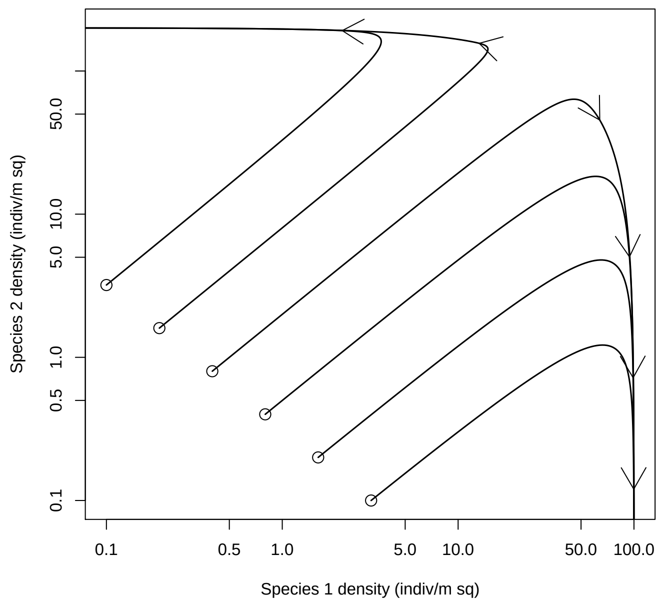
Founder control



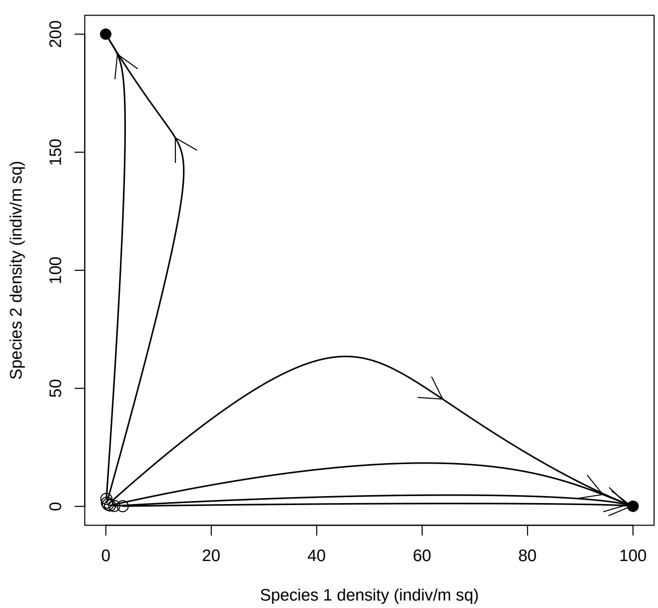
Comment slide: *Founder control phase plot*

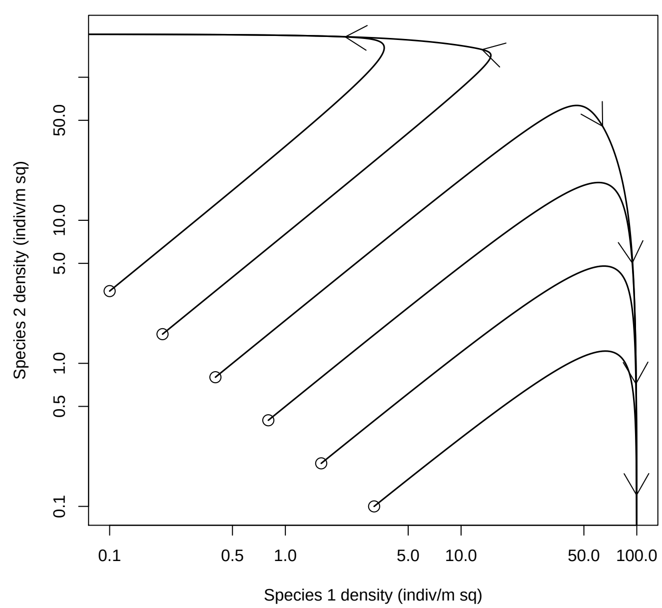


Comment slide: *Founder control phase plot (log scale)*

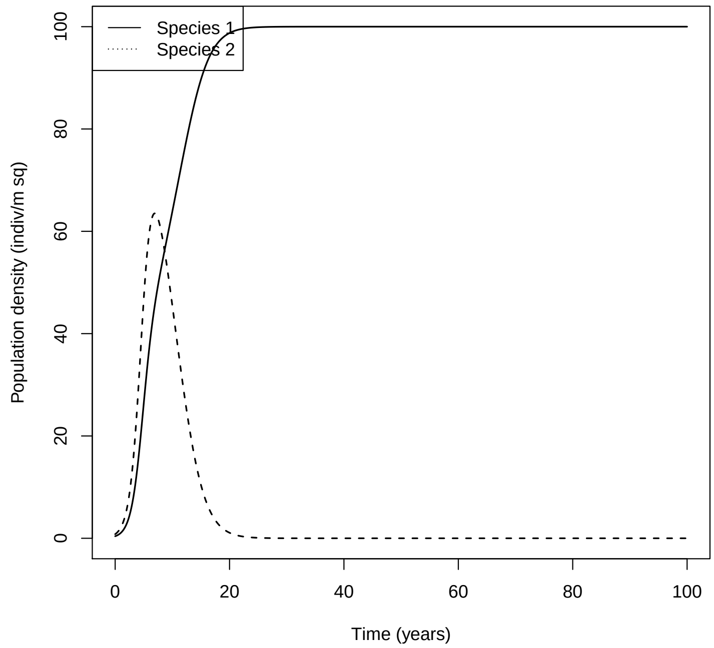


Founder control phase plots





Founder control can be complicated



- Founder control really means each species can win with a *big enough* head start

Results of competition

- C measures the relative effect of each species on each other, but it doesn't reflect growth rates or how strongly each species is affected by competition
- C may stay (about) the same, even as we switch conditions so that one or the other species dominates
- Poll: C tells us what will happen *if* neither species is dominating.
  - **Answer:** Founder effects, neutrality or coexistence

3 Population-level interactions

3.1 Invasion theory

- The competitive relationship between two species can be investigated by studying two **invasion** scenarios:
- What happens if one species is established, and the other one tries to invade (ie., some individuals are introduced)?
  - **Answer:** Dominance occurs when one species can invade the other
  - **Answer:** Coexistence occurs when each species can invade the other
  - **Answer:** Founder control occurs when neither species can invade the other

Allee effects

- This analysis assumes that species that can be successful under a certain competitive environment can also invade that environment
- That is, it neglects Allee effects
- Would this assumption work with Allee effects?
  - **Answer:** No. With Allee effects a species may be able to do well if established, but not be able to "invade" if it's rare

Competitive results

- The competitive effect felt by species 1 is measured by $\tilde{N}_1$
- The *amount* of competition needed for species 1 to be at equilibrium is:
  - **Answer:** $\tilde{N}_1 = K_1$
- The amount of competition species 1 feels when trying to invade a population of species 2 is:
  - **Answer:** $\tilde{N}_1 = \alpha_{21} N_2$
  - **Answer:** $= \alpha_{21} K_2$, if species 2 is at equilibrium
- If species 1 feels more competition from invading species two than it feels at its own equilibrium, it cannot invade. And **conversely**.

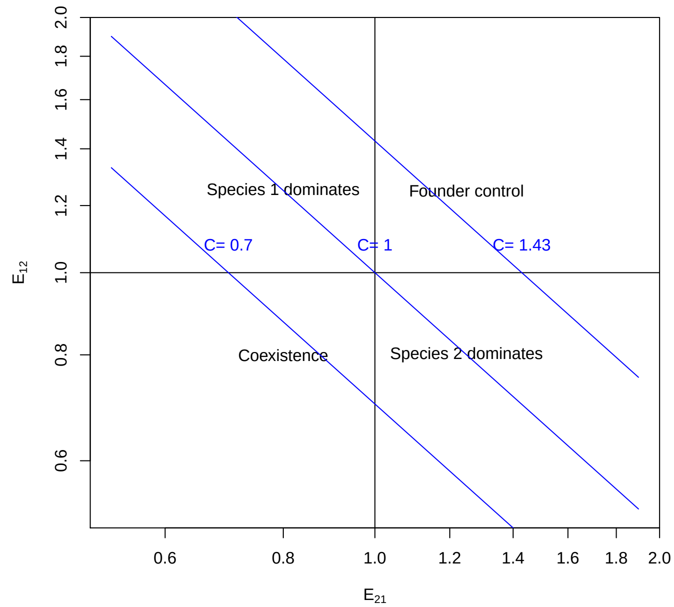
Population-level competitive effects

- The population-level competitive effect of species 2 on species one is $E_{21} \equiv \alpha_{21} K_2 / K_1$
- This is the unitless ratio of the two measures of effect on species 1 from the previous slide.
- The two values of E determine the competitive dynamics between the two species.
- If $E_{21} > 1$ species 2 can exclude species 1 (species 1 cannot invade). And **conversely**.

Results of competition

- If both Es are < 1, neither can exclude the other
  - **Answer:** We expect coexistence
- If both Es are > 1, they both exclude each other
  - **Answer:** which species wins will depend on starting conditions: founder control
- If one E is > 1, the large-E species can exclude the other
  - **Answer:** We expect that species to always win: dominance

Results of competition



Measuring competition

- α measures competitive effects at the individual level
  - has units (ratios of types of individuals)
- E measures competitive effects at the population level, using equilibrium populations
  - unitless
- $C = \alpha_{21}\alpha_{12} = E_{21}E_{12}$
  - C tells us: do the species have a *tendency* for founder control or coexistence?
- For specific conditions, we also need to know values of E
  - Each species may dominate when conditions are good for it
  - We see the tendency for founder control or coexistence in intermediate conditions

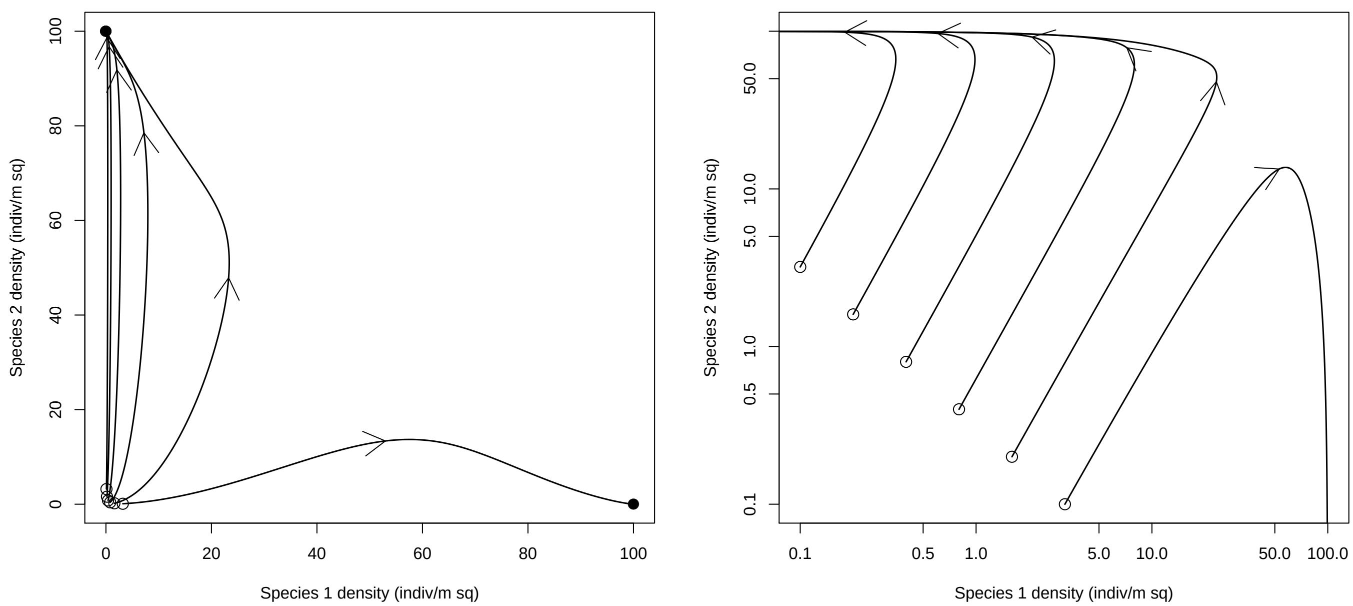
Neutral competition

- If competition is balanced, and neither species dominates, this is called neutral competition
- No tendency for either species to win
- No tendency for founder control or for coexistence
- If there's any small difference between the species, one may dominate
- Even if there's no difference, one should win eventually, by random "drift"

Founder control

- Up until now, we've thought of founder control as a single outcome
- But from the point of view of the competing species, it's pretty important which one of them gets control
- Poll: What factors determine who gets control?
  - **Answer:** Who gets there first
  - **Answer:** Initial maximum growth rate
  - **Answer:** How strongly they affect each other

Growth rate and founder control



Competitive exclusion and biodiversity

- Two species that use resources the same way cannot co-exist in a stable environment in the long term due to their competitive dynamics
- This statement can be justified mathematically, and it has important implications for real populations ...
- ... but it must also break down
- Poll: How?
  - **Answer:** Species may not use resources in the same way
  - **Answer:** The environment may not be stable
  - **Answer:** Co-existence may not be "long term"!

- **<u>Answer</u>:** There may be stabilizing factors outside competitive dynamics (e.g., natural enemies)