UNIT 6: Competition

1 Introduction

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 single-species 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?
  - **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:** $\tilde{N}_1 = K_1$ (carrying capacity): the species has the right amount of competitive pressure to make $\mathcal{R} = 1$
  - **Answer:** $N_1 = 0$ (extinction): the species is not present

Logistic model

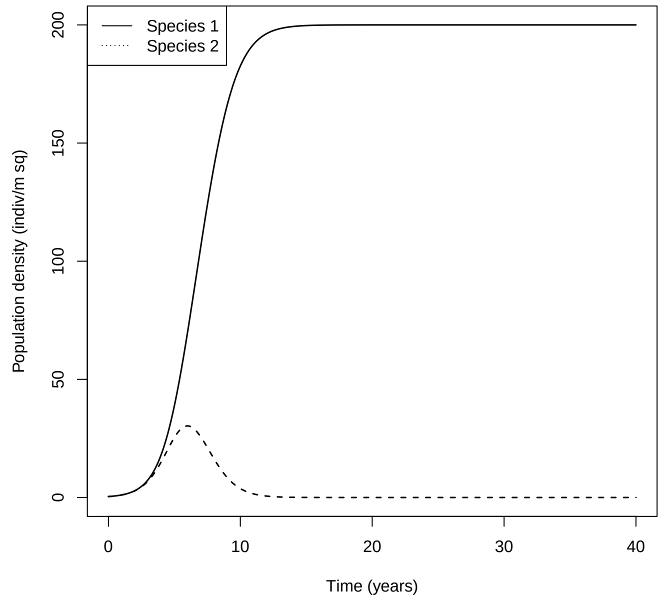
- One popular approach (as we discussed in non-linear models)
- As before, our model is similar to the logistic model, except:
  - Birth and death are tracked separately
  - We don't assume functions are straight lines

2.1 Balanced competition

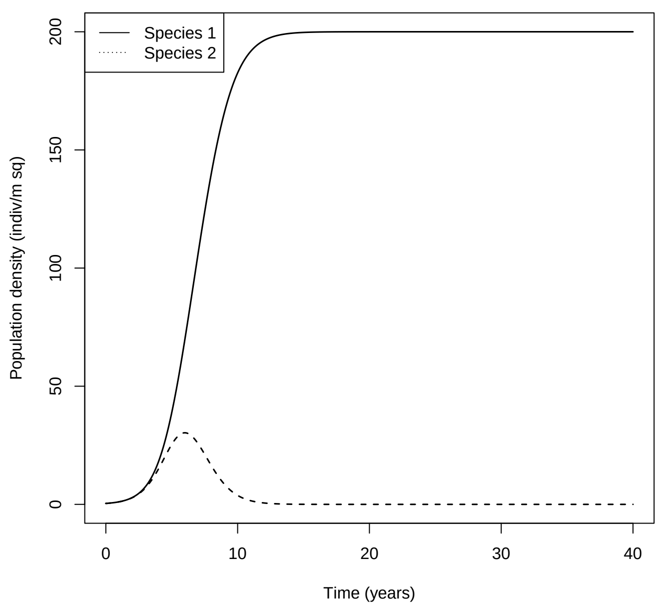
Equal competition

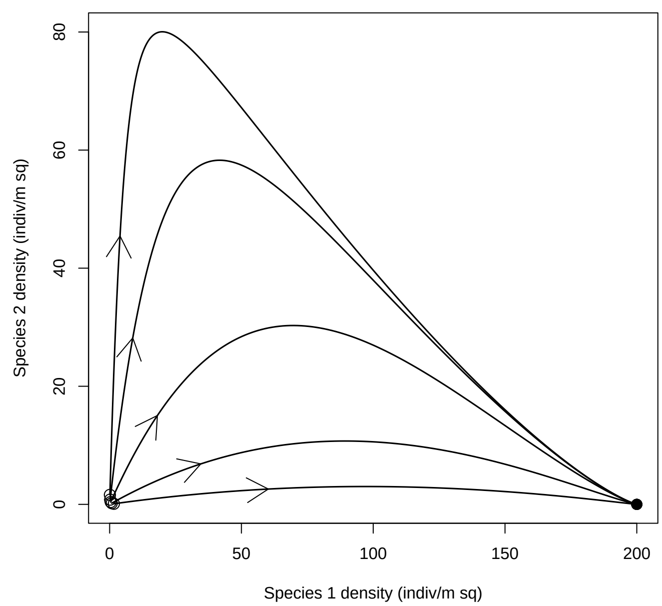
- If the αs are both equal to one, we have equal competition. This means that the competitive effect of an individual from either species is the same.
- If $\bar{N} = N_1 + N_2$, then:
  - $\frac{dN_1}{dt} = (b_1(\bar{N}) - d_1(\bar{N}))N_1$
  - $\frac{dN_2}{dt} = (b_2(\bar{N}) - d_2(\bar{N}))N_2$
- 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*

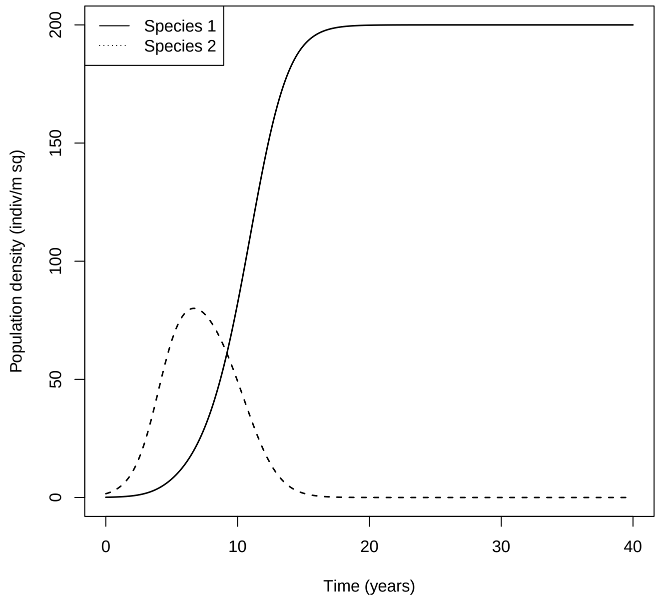


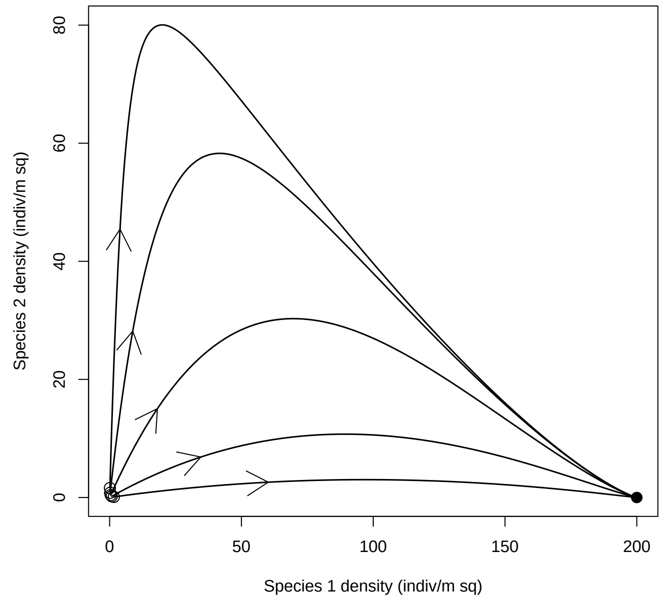
Dominance





Comment slide: *Dominance*





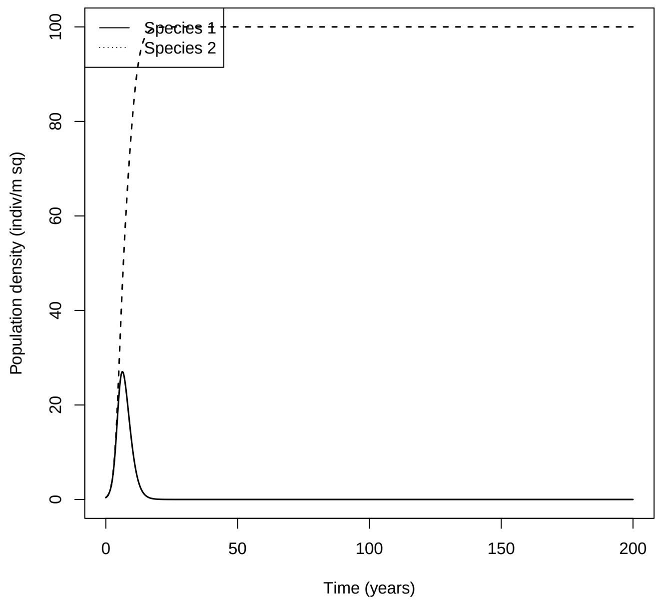
Time plots and phase plots

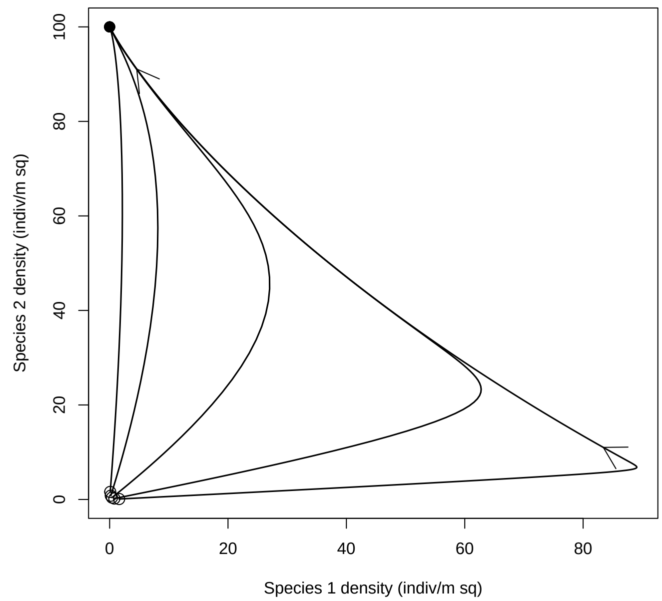
- *Time plots* have time on one axis and show population quantities on another
  - Fixed parameters (usually)
  - Single starting points
- *Phase plots* have population quantities on both axes
  - Fixed parameters (usually)
  - Multiple starting points (usually)
  - Better for seeing overall pattern 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

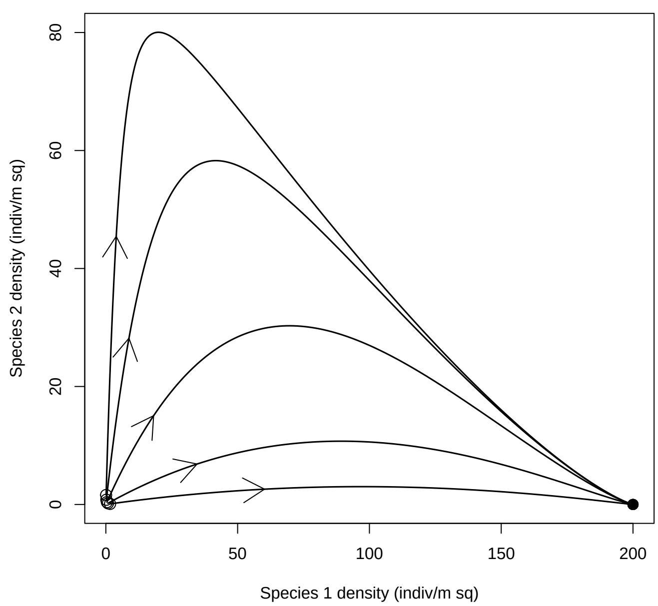


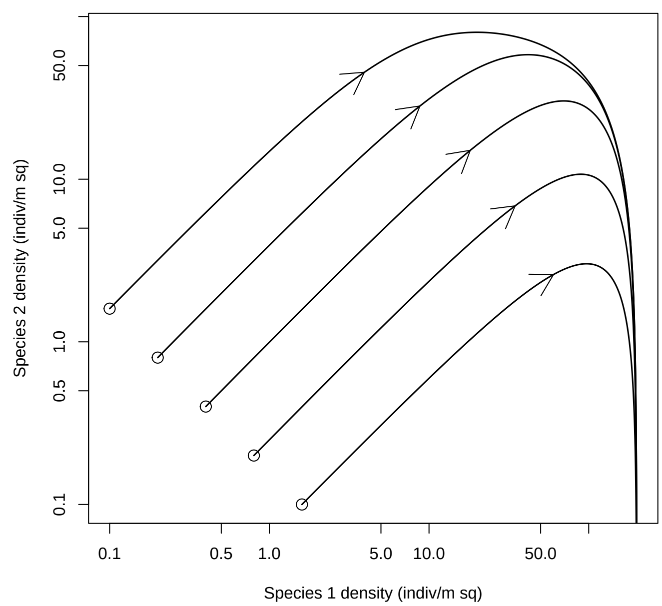


Log plots and linear plots

- 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:** $\mathrm{indiv}_1/\,\mathrm{indiv}_2$ (usually; depending on units of the Ns)
- 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:** $4\,\mathrm{indiv}_1$ have as much impact as $1\,\mathrm{indiv}_2$
  - **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:** $1\,\mathrm{indiv}_2$ has as much impact as $4\,\mathrm{indiv}_1$
  - **Answer:** The two ratios convey the same information in this case

Balanced competition

- Poll: What results do we expect from balanced competition?
  - **Answer:** 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
  - **Answer:** This is not necessarily the bigger species
- If competition is balanced, there is 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)

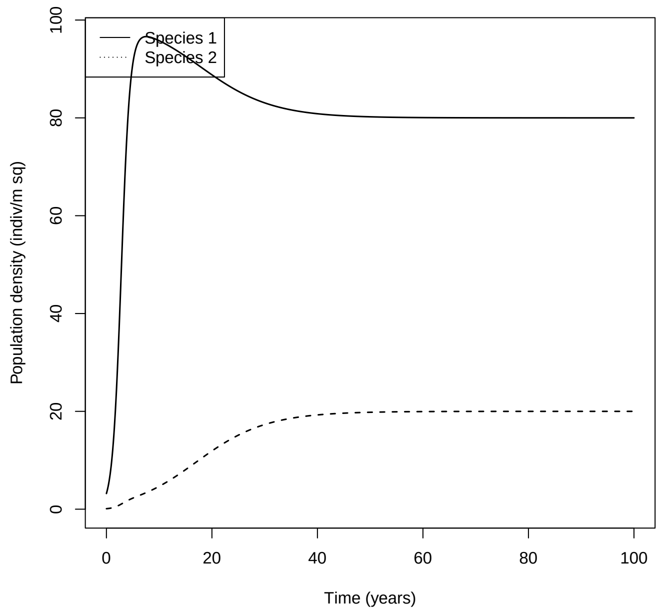
2.2 Unbalanced competition

- 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

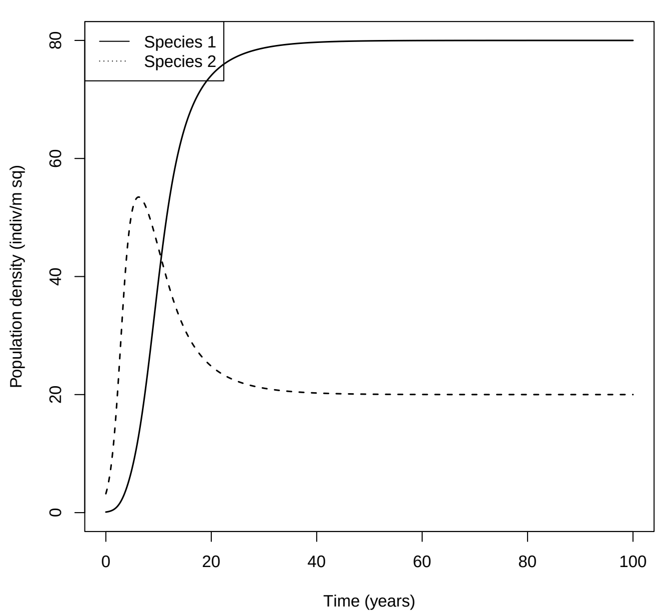
Coexistence

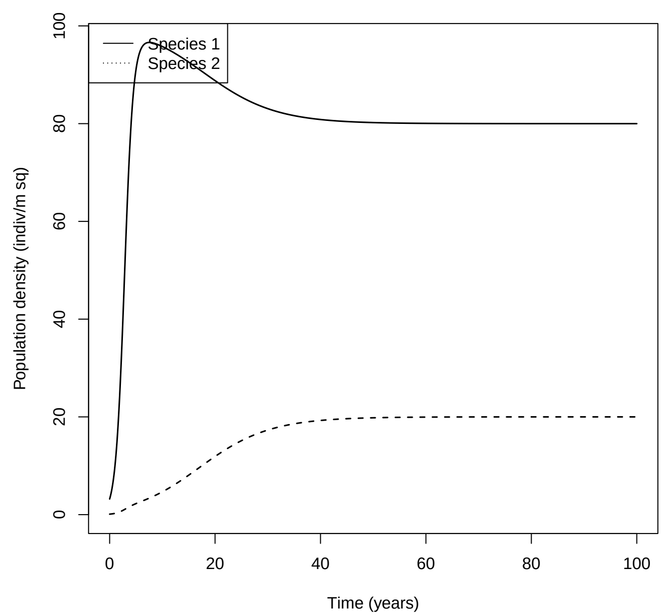
- Coexistence *may* occur when $C < 1$
- Poll: Why might individuals have relatively weaker competitive interactions with members of the other species?
  - **Answer:** They may compete for mates or mating sites
    * **Answer:** Example: birds with different nesting preferences
  - **Answer:** Organisms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

Comment slide: *Coexistence*

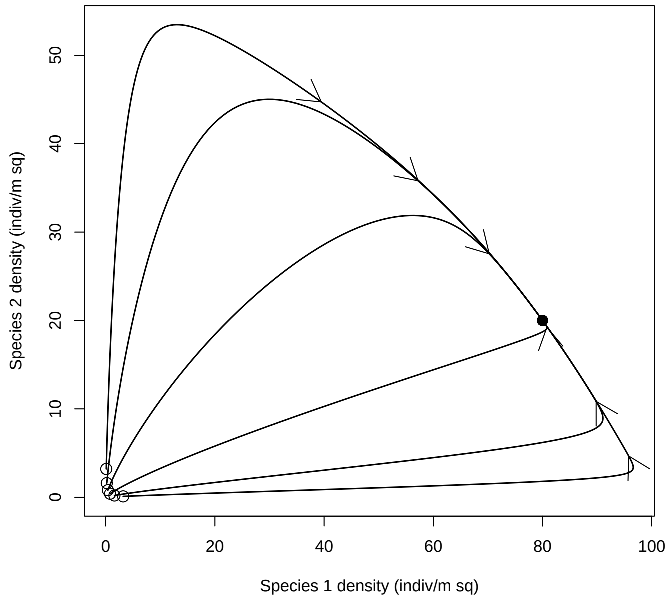


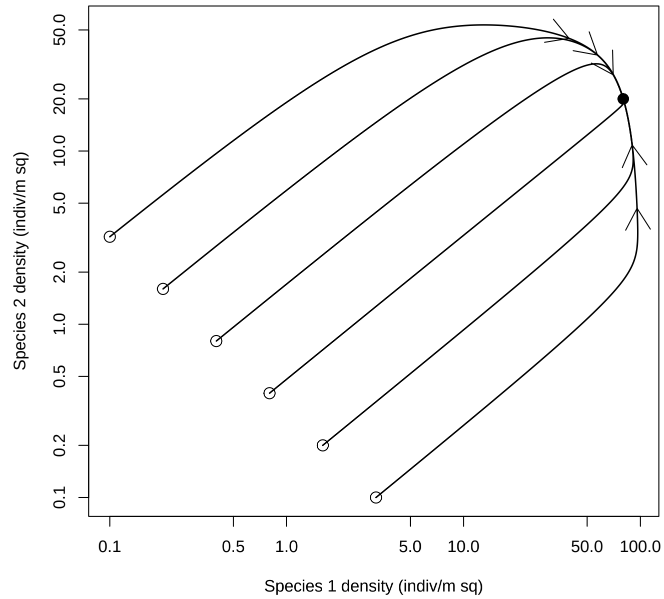
Coexistence





Coexistence phase plots

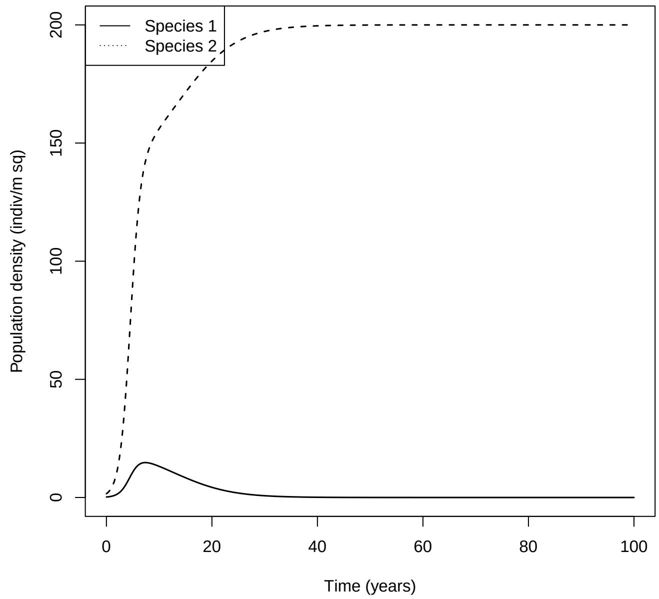




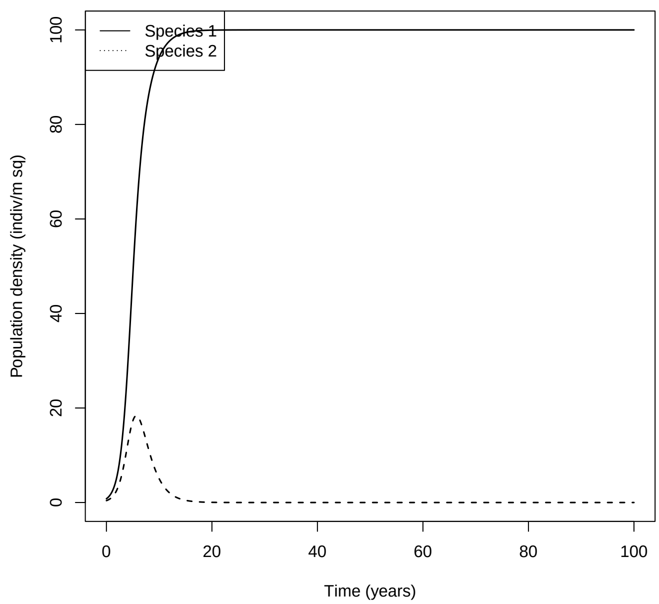
Founder control

- 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

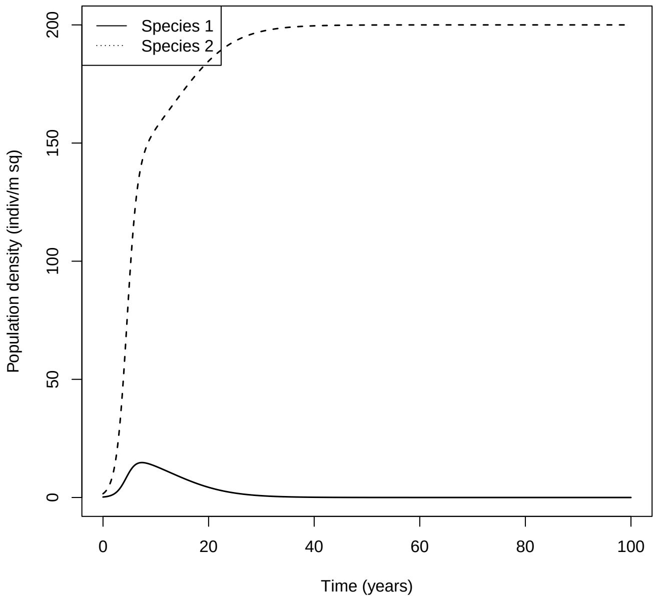
Comment slide: *Founder control*

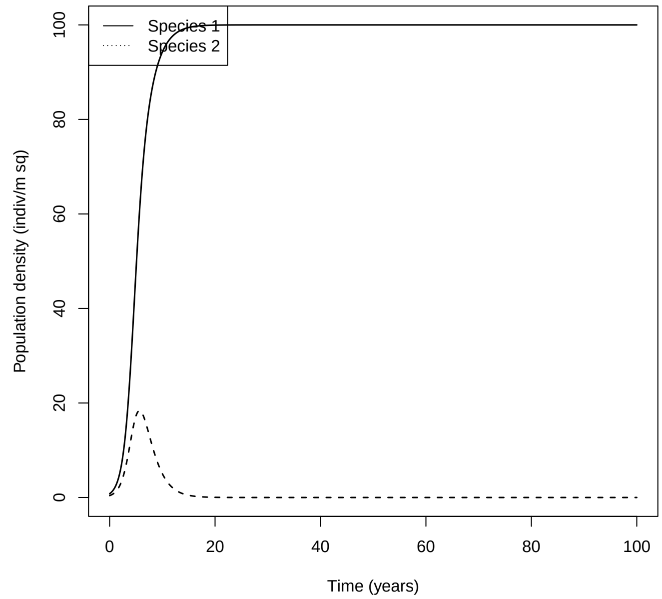


Comment slide: *Founder control*

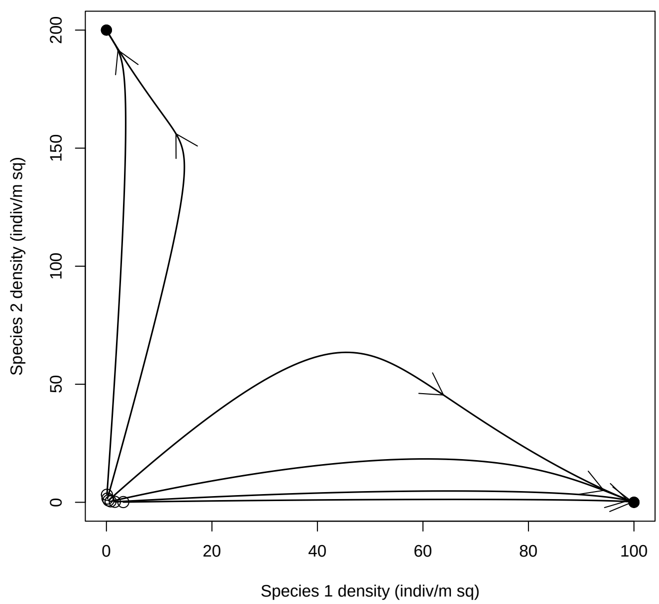


Founder control

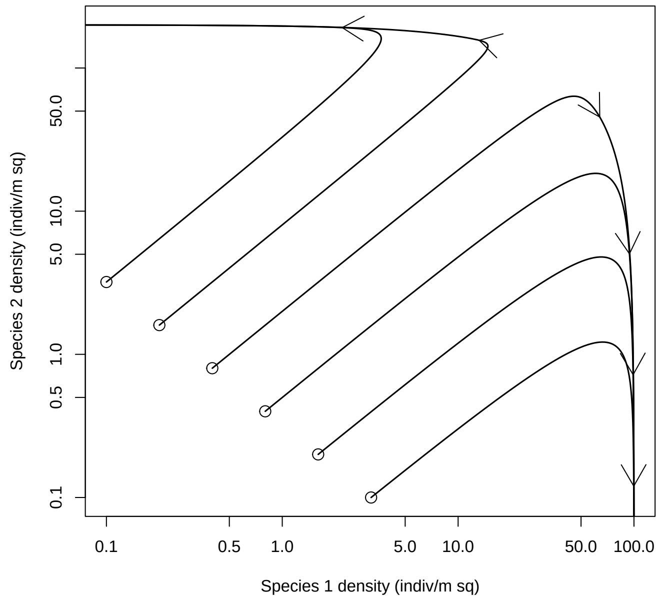




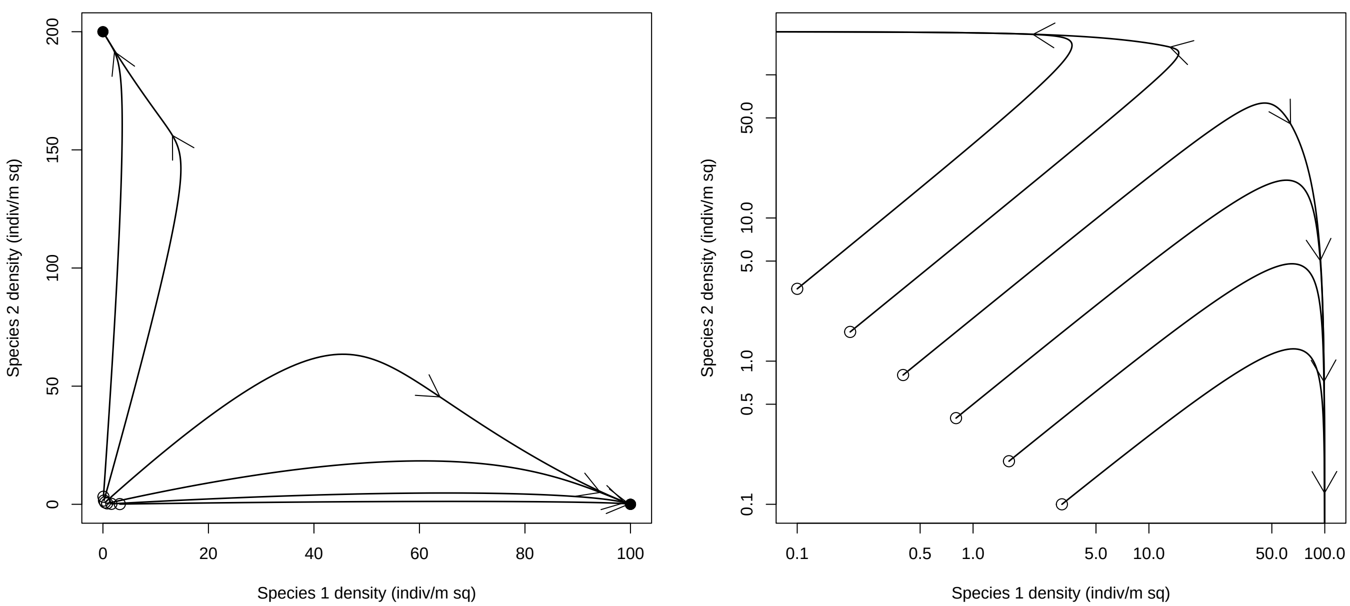
<u>Comment slide</u>: *Founder control phase plot*



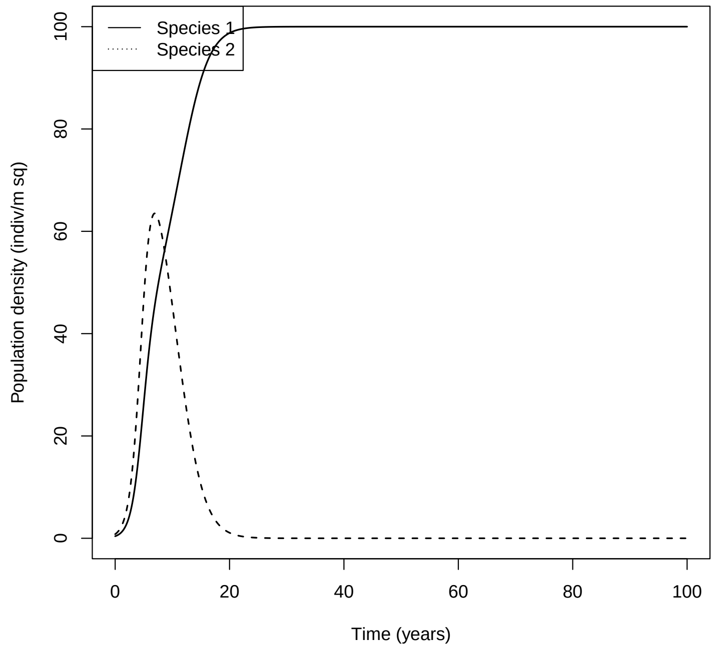
<u>Comment slide</u>: *Founder control phase plot (log scale)*



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
  - **Answer:** Like when we tune the conditions so that neither species of flour beetle wins

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
- **Answer:** In the absence of Allee effects, invasion is all you need to know

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**.

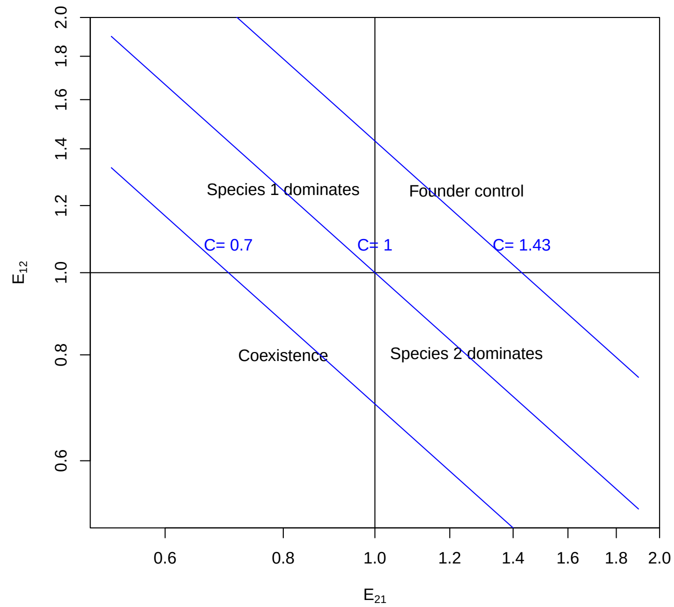
Population-level competitive effects

- 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

3.2 Colonization and co-existence

- Up until now, we've thought about the question of which species controls a particular area in the long term
- But if available habitat is changing, it also matters what happens in the short term
- rK tradeoff

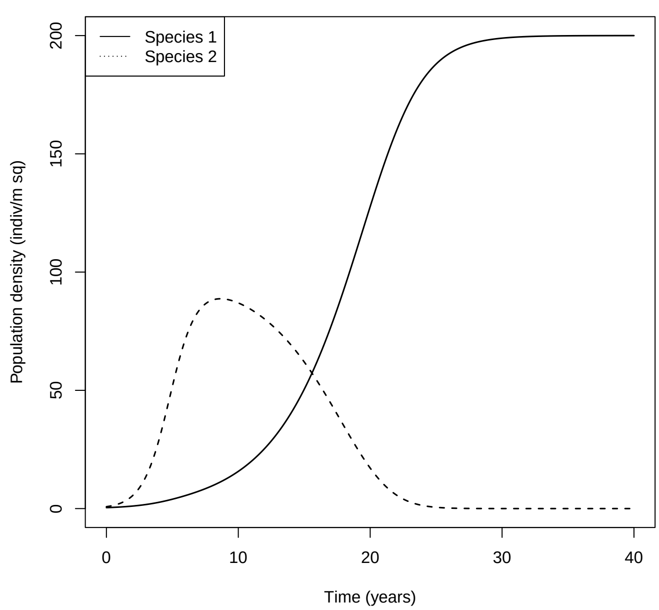
- r strategists do better in the short term; K strategists do better do better in the long term

- Poll: When can you survive by doing better in the short term?
  - **Answer:** When new opportunities (empty habitat) keep coming available
    - **Answer:** When there is a lot of disturbance: fire, flood ...

Growth rates

- The maximum growth rate (for each species) is $r_0 = (b(0) - d(0))$:
  - **Answer:** The net growth rate when crowding pressure is very low
- The species with the better r_0 should do better in the short run
  - Faster exponential growth
- If patches are very stable, then K species wins
- If they are very unstable, then r species wins
- In between, we get coexistence at the level of multiple populations
  - i.e., at the landscape level species may coexist

rK tradeoff



4 Niches and coexistence

Ecological niches

- An ecological niche refers to the way an organism makes a living:
  - What resources does it need?
  - What sort of environmental conditions does it need?

Fundamental niches

- A **fundamental** niche is defined as the conditions under which an organism could make a living (in other words, survive with $\mathcal{R} > 1$) *in the absence of competition.*
- Many plants have very large fundamental niches
  - The reason spruce trees don't grow in Cootes Paradise is not that they can't grow there
  - **Answer:** They can't compete with the other trees that grow there

Realized niche

- The realized niche is defined as the conditions under which an organism can make a living, including the effects of competing species
  - The realized niche of spruce trees does not include Cootes Paradise

Example: chipmunks

- There are several species of chipmunks in the Sierra Nevada mountains
  - The most aggressive can only survive where the rainfall is good, and it out-competes all the other species
  - The least aggressive can survive anywhere in the mountain range, but it cannot co-exist with any of the other species
- What are the fundamental and realized niches of these species?
  - **Answer:** The aggressive species has the same fundamental and realized niches: the places where rainfall is good
  - **Answer:** The mild-mannered species has a large fundamental niche, but its realized niche is the area that's too dry for the other species

4.1 The competitive exclusion principle

- If two species use resources in the same way, we expect that $C = 1$.
  - The effect of an individual of each species can be measured by its impact on resources. If individuals of species one have (e.g.) twice the impact, this should be seen by both species equally.
- If two species use resources in the same way, we do not expect them to co-exist
  - One species will use the resources more efficiently (nothing in biology is exactly equal)

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"!
  - **Answer:** There may be stabilizing factors outside competitive dynamics (e.g., natural enemies)