UNIT 6: Competition

1 Introduction

Inter-species interactions

- Competition: interaction hurts the growth rate of both species
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- Exploitation: interaction is good for one species but bad for the other
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- Mutualism: interaction is good for both species
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- Commensalism: interaction is good for one species, and close to neutral for the other
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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:
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- Species may be very similar, or very different
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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?
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- Poll: What if I "tune" the conditions to something in between?
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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:
  - $\dfrac{dN}{dt} = (b(N) - d(N))N$
- We want to modify this for a species which is competing with another species
  - $\dfrac{dN_1}{dt} = ?$
- The amount of competition seen by species 1 is $\tilde{N}_1 = N_1 + \alpha_{21} N_2$
- How should our equation change?
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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?
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Carrying capacity with competition

- $\dfrac{dN_1}{dt} = (b_1(\tilde{N}_1) - d_1(\tilde{N}_1))N_1$
- How can this population be at equilibrium?
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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:
  - $\dfrac{dN_1}{dt} = (b_1(\bar{N}) - d_1(\bar{N}))N_1$
  - $\dfrac{dN_2}{dt} = (b_2(\bar{N}) - d_2(\bar{N}))N_2$
- What happens in this case?
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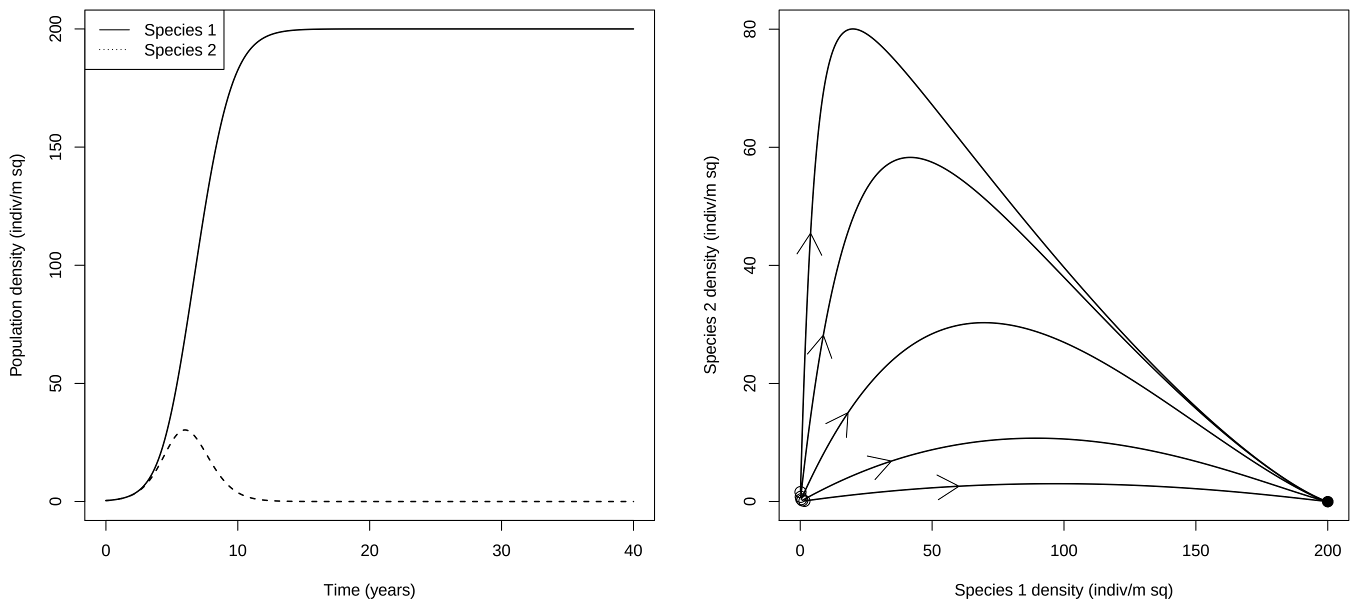
Dominance



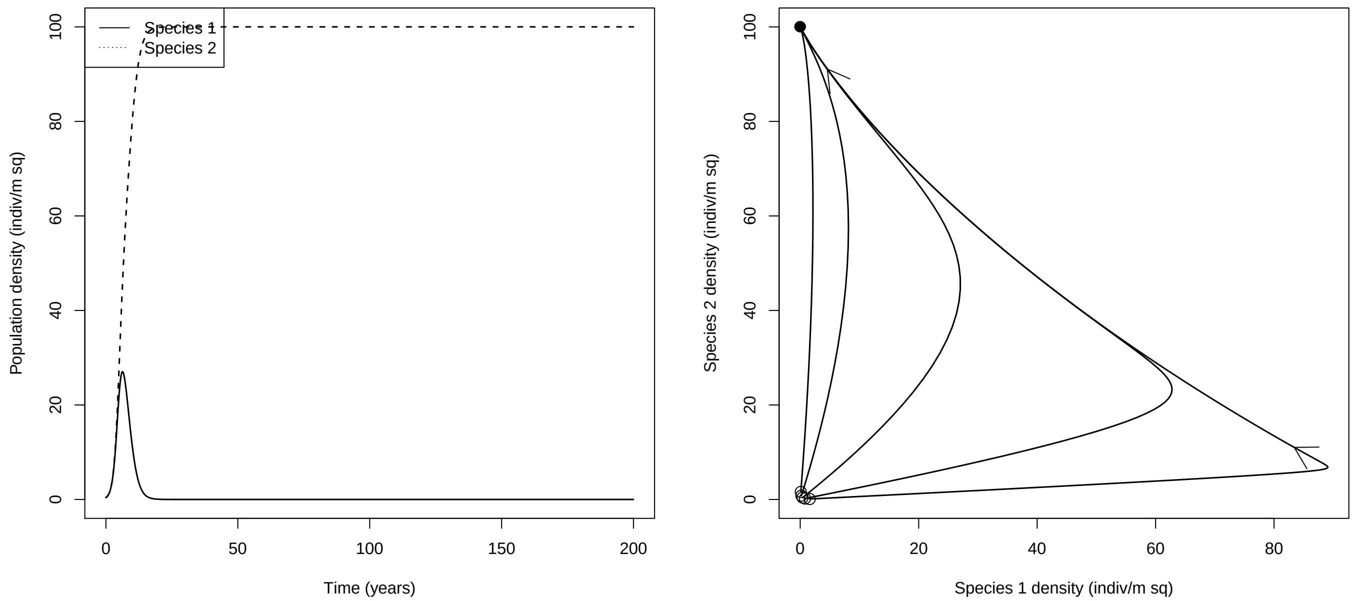
Time plots and phase plots

- *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

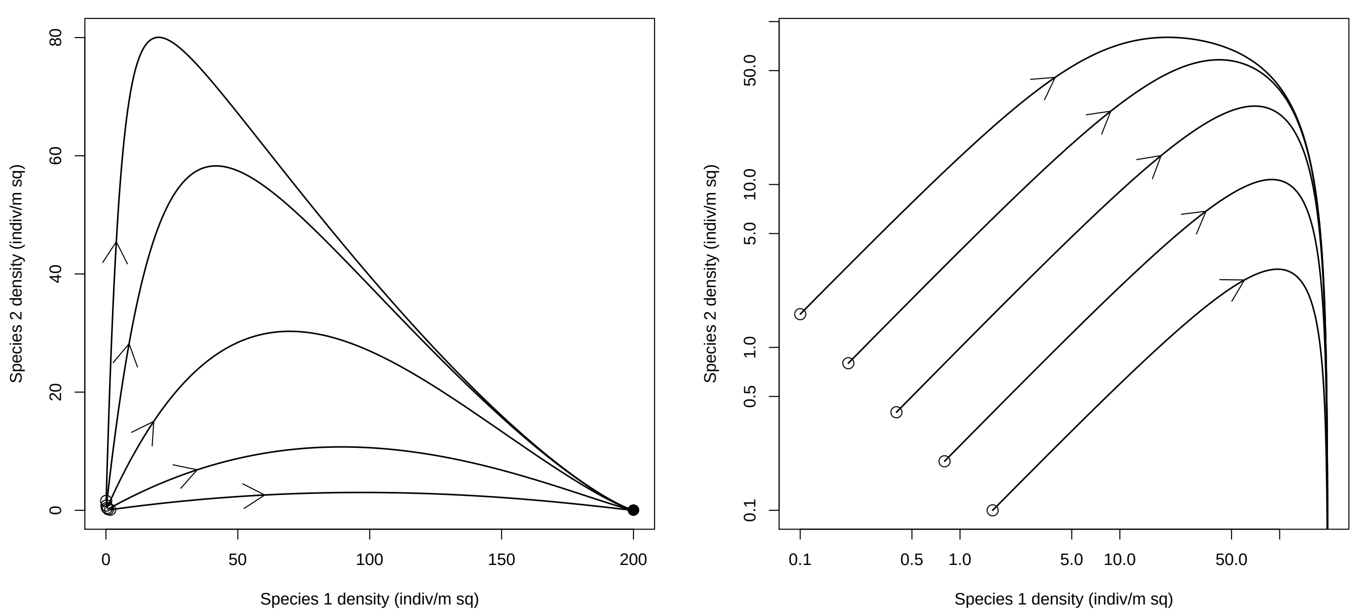
Dominance again



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}?
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- 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?
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- If they're only competing for water, what's the value of α_{12}?
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Balanced competition

- Poll: What results do we expect from balanced competition?
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- Balanced competition works just like equal competition
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- 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?
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- 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?
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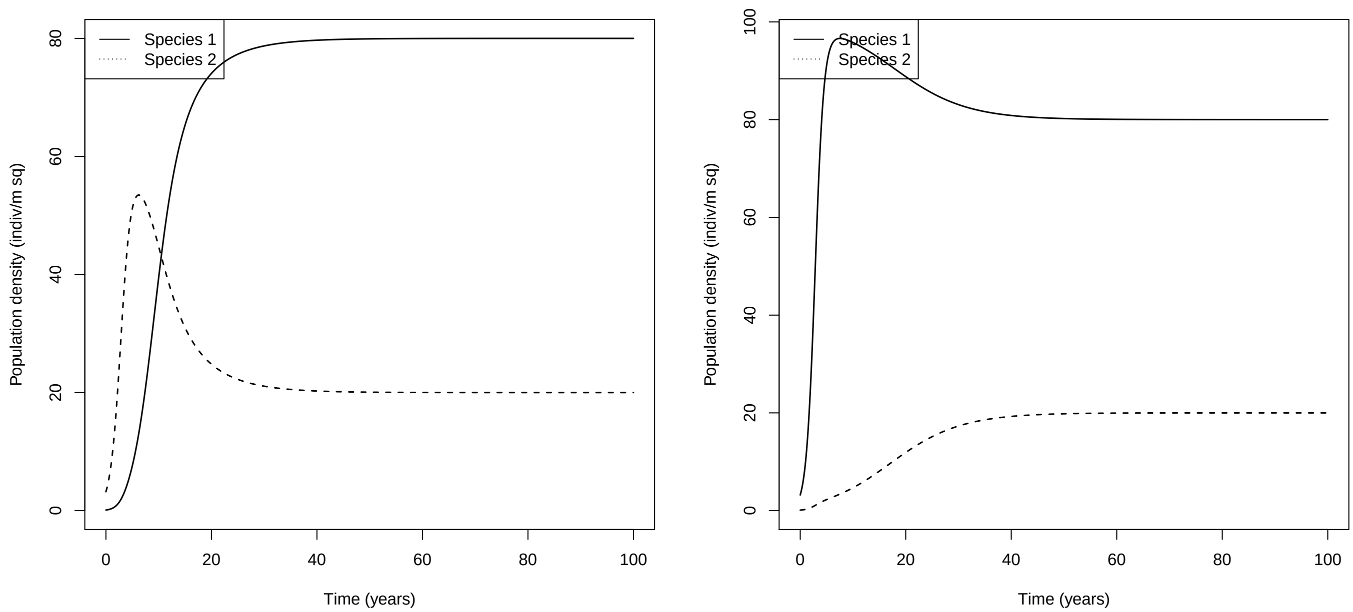
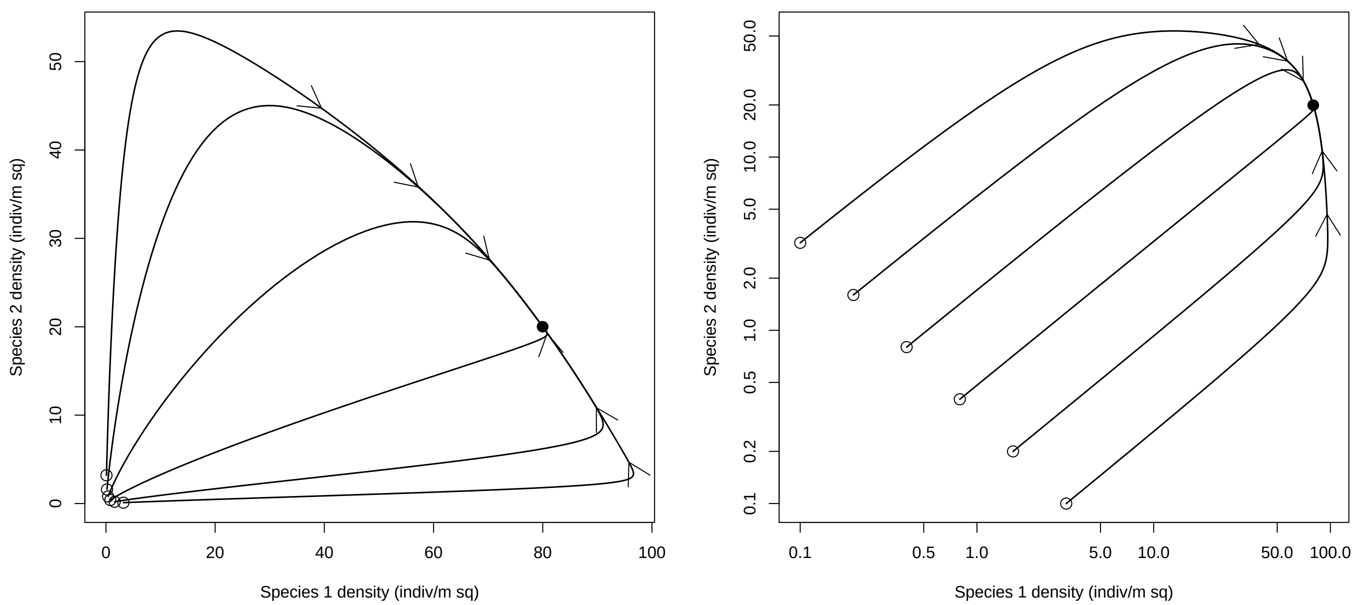
Coexistence



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?
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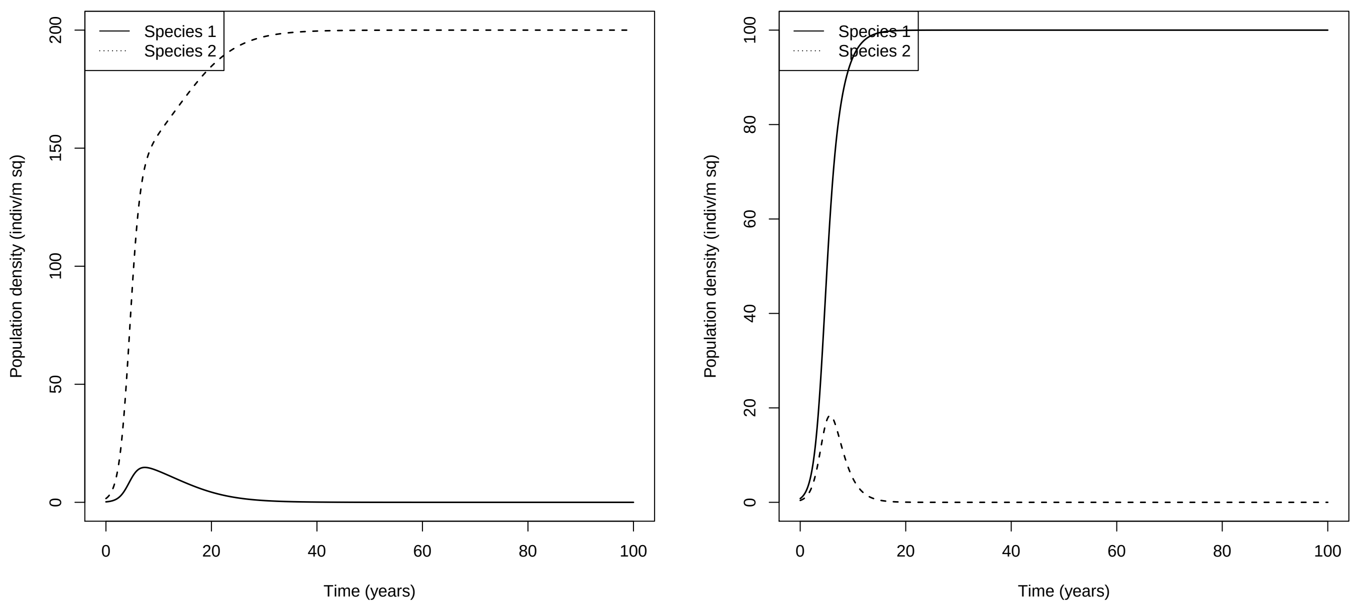
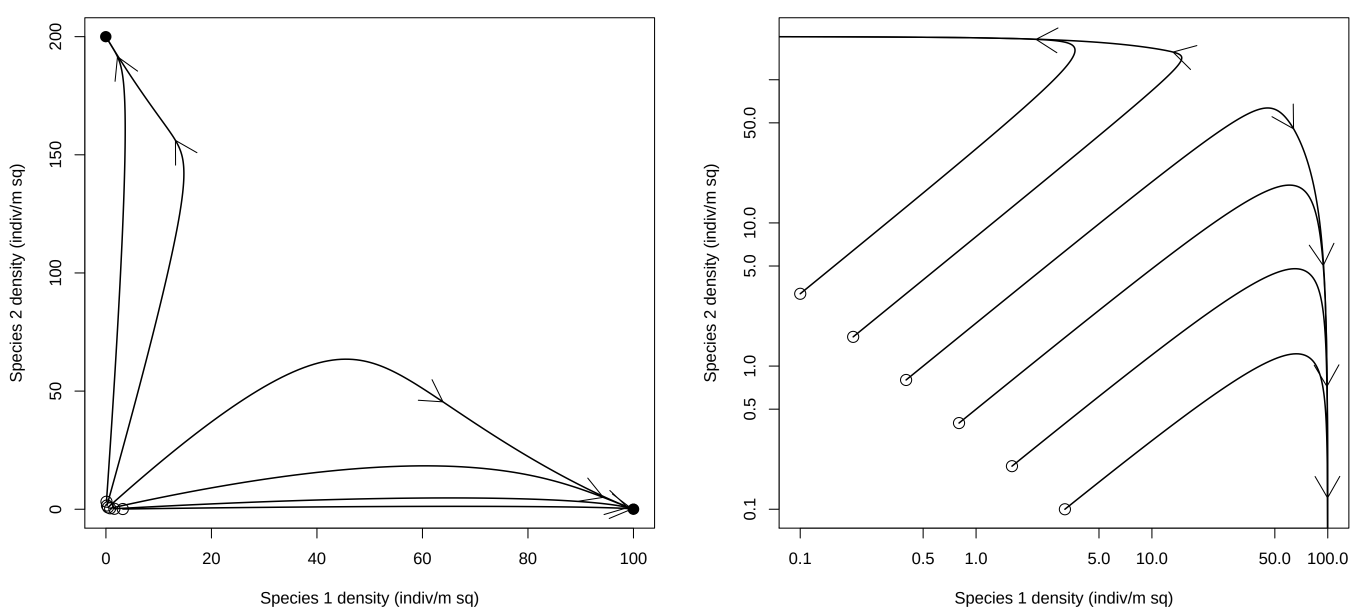
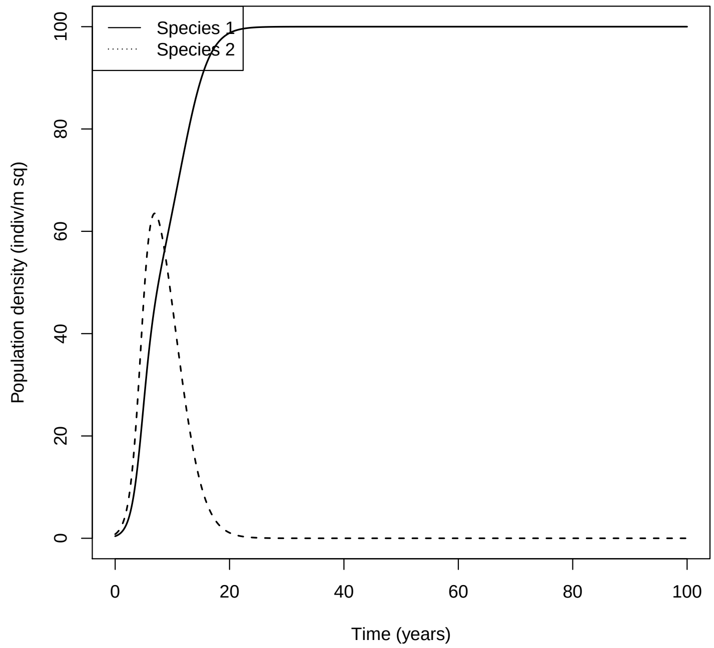
Founder control



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.
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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)?
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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?
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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:
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- The amount of competition species 1 feels when trying to invade a population of species 2 is:
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- 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
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- If both Es are > 1, they both exclude each other
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- If one E is > 1, the large-E species can exclude the other
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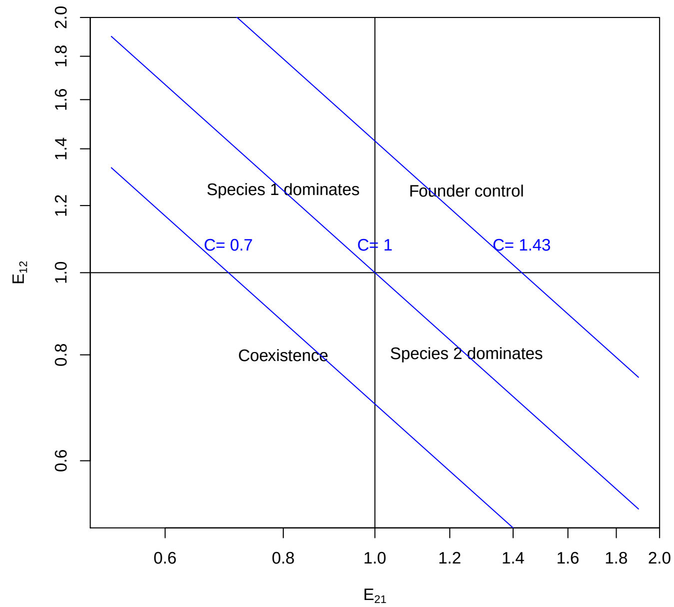
Results of competition



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?
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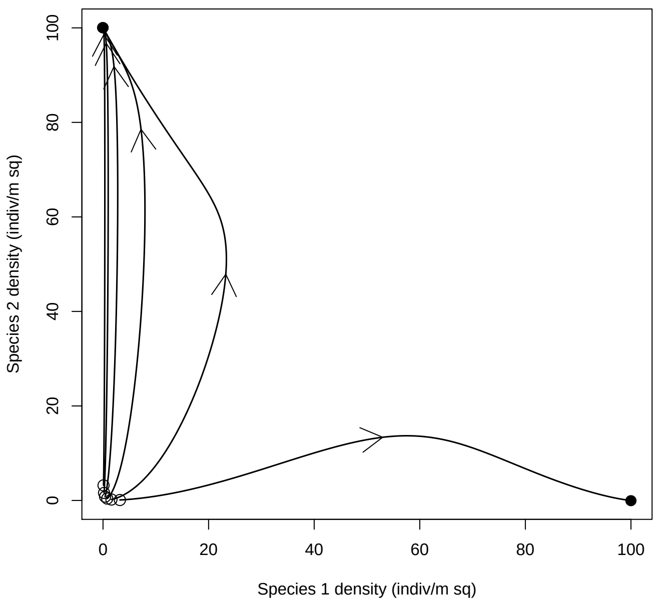
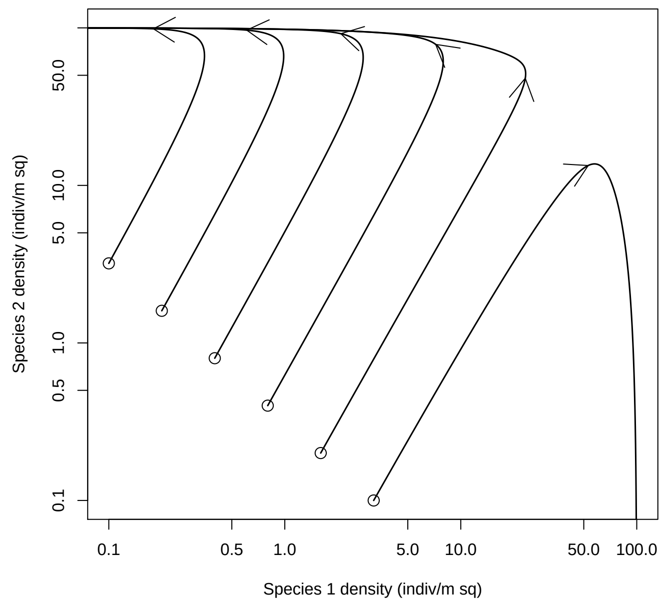
Growth rate and founder control





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?
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Growth rates

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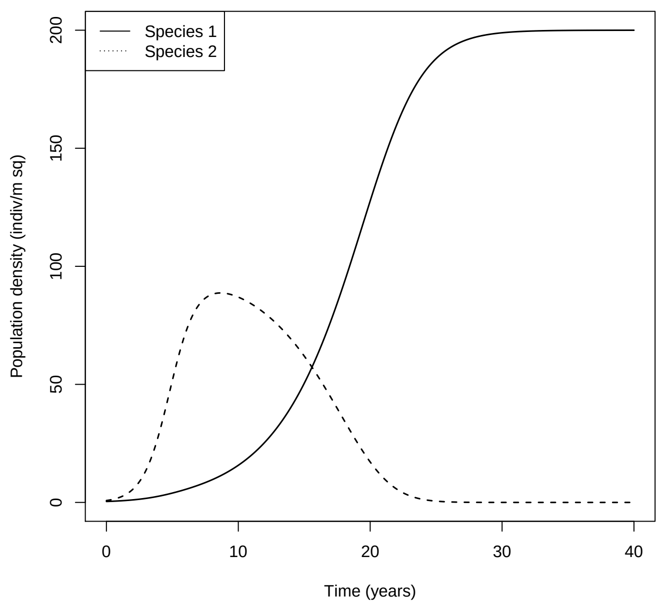
- The species with the better r_0 should do better in the short run
  - Faster exponential growth
- If patches are very stable, then K species wins
- If they are very unstable, then r species wins
- In between, we get coexistence at the level of multiple populations
  - i.e., at the landscape level species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

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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 outcompetes 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?

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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)

Exclusion and drift

- Even if the two species were *exactly* equal in efficiency, we expect one species to go extinct at random
- Due to the randomness of births and deaths, we expect the proportions to fluctuate at random until one proportion reaches 0 and gets stuck there
    - We call this process "drift", and it is strongly analogous to genetic drift

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?
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