Competition

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Introduction

- [http://nsm1.nsm.iup.edu/rgendron/seuss.shtml Nutches]

Inter-species interactions

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

()	helps	neutral	hurts
helps	mutualism	commensal	exploitation
neutral		neutral	???
hurts			competition

Competition

- Competition occurs when two species both depend on the same resource(s)

- Each species growth rate is reduced by the other's presence

- Species may be very similar, or very different

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

- *Model species*: ecology in the laboratory
- There is a series of experiments where researchers allow two species of flour beetles (*Tribolium*) to compete in different laboratory environments
- The larger species survives better in drier conditions, and the smaller species reproduces faster in moister conditions
- What are the possible outcomes of such an experiment?
- What if we "tune" the conditions to something in between (neither species always does better than the other)?

Figure 1: *Tribolium castaneum*

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

Population model with competition

Model

- 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?

Carrying capacity

- For this unit, we will mostly ignore Allee effects
- Therefore, we expect each species to have a *carrying capacity* K (or K_1 and K_2)

- If the species is alone, the carrying capacity is that species' stable equilibrium, defined by:
- $b(K) = d(K)$

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?

Logistic model

- 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

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.
- The total population is $\bar{N} = N_1 + N_2$.
- Our equations are now
- $\frac{dN_1}{dt} = (b_1(\bar{N}) - d_1(\bar{N}))N_1$
- $\frac{dN_2}{dt} = (b_2(\bar{N}) - d_2(\bar{N}))N_2$
- What happens in this case?

Competitive exclusion

- Why does one species always win in equal competition?
- Competition is mediated by only one quantity, $\bar{N}$.
- Whichever species can reproduce up to a higher value of $\bar{N}$ is going to win; there is no basis for a **tradeoff**
- Reminder:
- $\frac{dN_1}{dt} = (b_1(\bar{N}) - d_1(\bar{N}))N_1$
- $\frac{dN_2}{dt} = (b_2(\bar{N}) - d_2(\bar{N}))N_2$
- If $K_1 > K_2$, then species 1 can always increase when species 2 can; and sometimes when it can't

Dominance (dynamics vs. time)

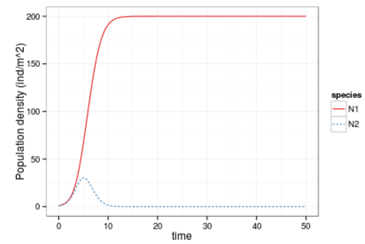

Figure 2: plot of chunk comp1

Dominance (phase plane)

Dominance (comparison)

Dominance (multiple starting points)

Dominance reversed

Units of α

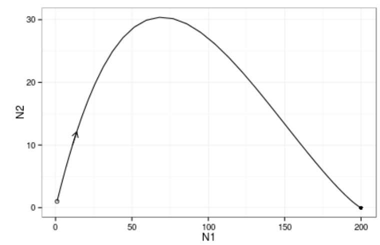

Figure 3: plot of chunk comp1__pp

- $\tilde{N}_1 = N_1 + \alpha_{21} N_2$;
- $\tilde{N}_2 = N_2 + \alpha_{12} N_1$
- 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}?
- Since α has units, we don't expect there to be anything special about $\alpha = 1$

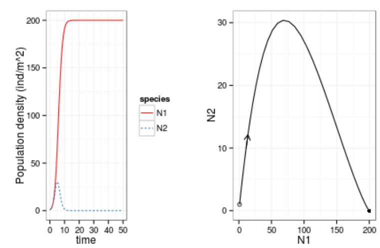

Figure 4: plot of chunk comp1B__pp

- **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

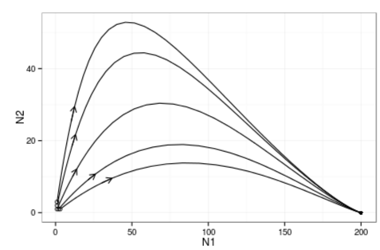

Figure 5: plot of chunk comp2

- Two plants compete with each other for water. α_{21} is 4individuals of sp 1/individuals of sp 2
- Which species is bigger?
- If they're only competing for water, what's the value of α_{12}?

Balanced competition

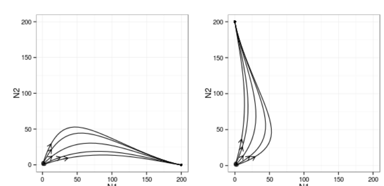
Figure 6: plot of chunk comp3

- What results do we expect from balanced competition?
- Balanced competition works just like equal competition
- 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?
- C measures the relative effect of between-species and within-species competition
- $C = 1$ means competition is balanced
- $C < 1$ means there is more **intraspecific** competition (within species: tendency for coexistence)
- $C > 1$ means there is more **interspecific** competition (between species: tendency for founder control)

Neutral competition

- Competition is balanced, and neither species dominates: **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"

Unbalanced competition

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 $C < 1$
- Why might individuals have relatively weaker competitive interactions with members of the other species?

Coexistence (1)

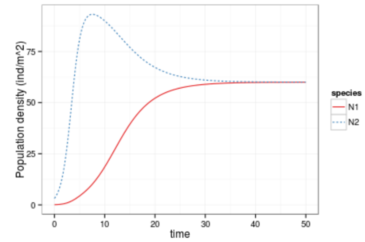

Figure 7: plot of chunk coex1

Coexistence (2)

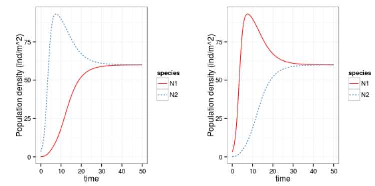

Figure 8: plot of chunk coex2

Coexistence (phase plot)

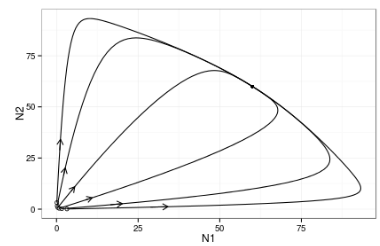

Figure 9: plot of chunk coex3

Founder control

- Founder control *may* occur when $C > 1$
- Why might individuals have relatively stronger competitive interactions with members of the other species?
- Somewhat related to Allee effects

Founder control (1)

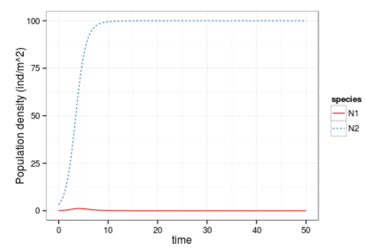

Figure 10: plot of chunk fc1

Founder control (2)

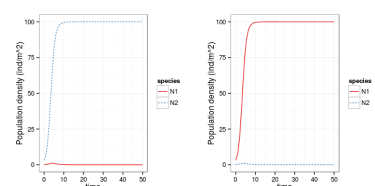

Figure 11: plot of chunk fc2

Founder control (phase plot)

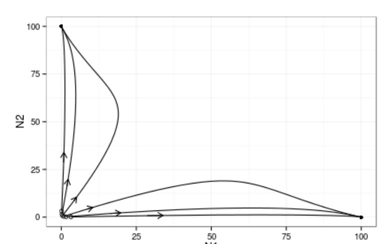

Figure 12: plot of chunk fc3

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
- C tells us what will happen *if* neither species is dominating

Population-level interactions

Invasion theory

Invasion theory

- The competitive relationship between two species can be investigated by studying *invasion*:
- What happens if one species is established, and the other one tries to invade (ie., some individuals are introduced)?

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

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:

- The amount of competition species 1 feels when trying to invade a population of species 2 is:

- 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

- If both Es are > 1, they both exclude each other

- If one E is > 1, the large-E species can exclude the other

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
- $C = \alpha_{21}\alpha_{12} = E_{21}E_{12}$
- Do we have a *tendency* for founder control or coexistence?
- To know results for specific parameters, we need to know the actual values of E.

Founder control

- Up until now, we've thought of founder control as a single outcome
- But to competing species, it's pretty important which one of them gets control
- What should determine that

Growth rate and founder control slides

- Slides here

Colonization and co-existence

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
- $r - K$ tradeoff
- r strategists do better in the short term; K strategists do better do better in the long term
- When can you survive by doing better in the short term?

Growth rates

- The maximum growth rate (for each species) is $r_0 = (b(0) - d(0))$:
- 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

r-K tradeoff

- slides here

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?
- Dr. Seuss

Fundamental niches

- **Fundamental niche**: the conditions under which an organism could make a living (in other words, survive with $R > 1$ *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

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?

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 1 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 hits zero and gets stuck there
- **Drift**: 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