BIOL 3340 Ecology Study Guide for Exam 2: Lecture 10: Competition and Facilitation

Source: the lecture slides (text, figures and slide notes). No textbook.
Each heading is one Study Lab objective. [L13 s08] = Lecture 13, slide 8.
(teal italics) = plain meaning of the word before it. ⚠ **Do not mix up = a look-alike pair to keep apart.** **Amber dotted words** = names printed on the figure beside them.

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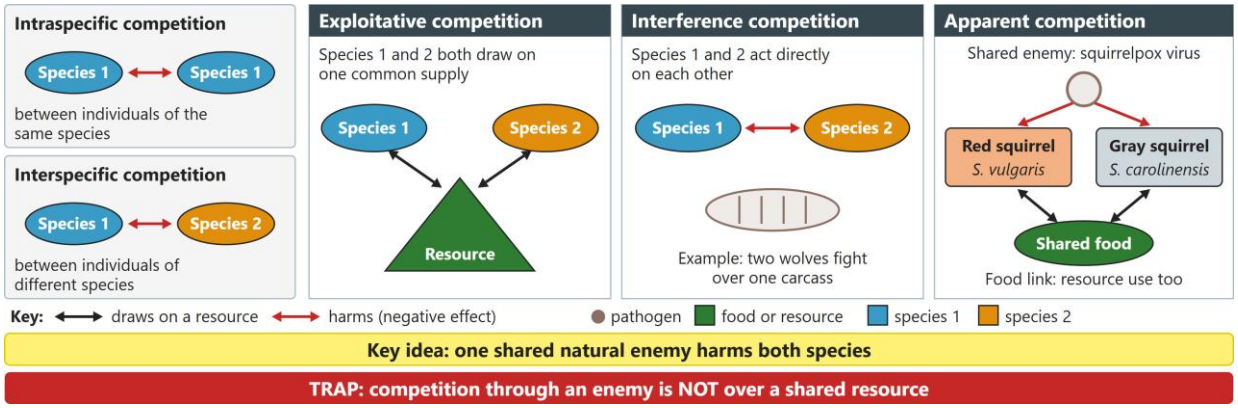
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L10.1 Species interactions and types of competition

⚠ **Do not mix up: Apparent competition is NOT a shared resource: it is a shared natural enemy.** [L10 s10]

Species interactions *(how species affect each other)*: interactions among populations, usually of different species, in the same area. [L10 s05]



Intraspecific, interspecific, exploitative, interference and apparent competition side by side [L10 s09]

On the figure: Intraspecific competition · Interspecific competition · Exploitative competition · Interference competition · Apparent competition · squirrelpox virus

Intraspecific competition *(within one species)*: between individuals of the same species. [L10 s07]
Interspecific competition *(between species)*: between individuals of different species. [L10 s07]
Interspecific competition is the main focus, but individuals within a species compete strongly. [L10 s07]
Types of competition: interference, exploitation, apparent; also amensalism *(one species harmed, other unaffected)* and allelopathy. [L10 s60, L10 s06]
Exploitative competition: species **1** and species **2** both draw on the same shared resource. [L10 s08, L10 s09]
Interference competition: species **1** and species **2** act directly on each other. [L10 s08, L10 s09]
Apparent competition: involves a shared natural enemy. [L10 s10]
It is different from exploitative and interference competition. [L10 s10]
Squirrels: red squirrel (S. vulgaris) and gray squirrel (S. carolinensis) share the **squirrelpox virus**. [L10 s10]
The two squirrels also share a food resource, which is exploitative competition. [L10 s10]

Review question: why is apparent competition different than competition? [L10 s11]

Answer: apparent competition runs through a shared natural enemy, not shared resources or direct contact. [L10 s10, L10 s11]

Species interactions and their signs

Interaction	Species A	Species B
Competition	-	-
Amensalism	-	**0**
Predation, herbivory, parasitism	+	-
Mutualism	+	+
Commensalism	+	**0**
Neutralism	**0**	**0**

Table source: [L10 s06]

Three types of competition

Type	Diagram	Example
Exploitative	Two arrows from the species to one shared resource	Overlapping root systems
Interference	One arrow directly between species **1** and species **2**	Two wolves snarling over a carcass
Apparent	Both species linked to a shared natural enemy	Red and gray squirrels, squirrelpox virus

Table source: [L10 s08, L10 s09, L10 s10]

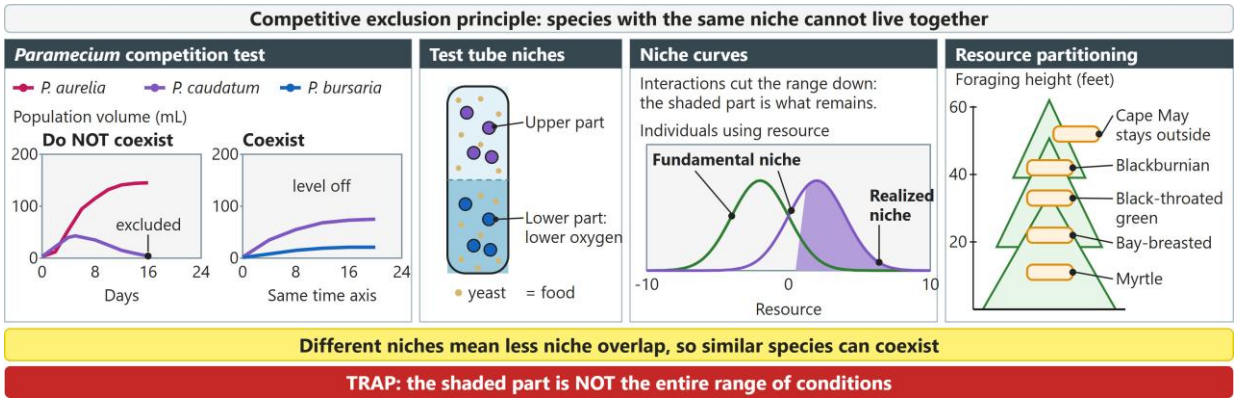
L10.2 Competitive exclusion, niches and resource partitioning

⚠ **Do not mix up: Realized niche is NOT the full possible range: that is the fundamental niche.** [L10 s17, L10 s18]

Competitive exclusion principle: species with exactly the same requirements cannot live together. [L10 s13]

Cannot live together means cannot use the same resources in the same place (the same niche). [L10 s13]

This is thought to be true of any species forced to compete: microbes, mammals, plants. [L10 s13]



Paramecium results, test tube niches, niche curves and warbler heights in one view [L10 s18]

On the figure: Paramecium · P. bursaria · P. caudatum · Fundamental niche · Realized niche · Resource partitioning · Blackburnian

Paramecium test: species grown alone, then in pairs; population volume (mL) tracked over days. [L10 s14]

Why the difference? Different resource use can prevent competitive exclusion. [L10 s14, L10 s15]

P. bursaria uses yeast in the lower part of the test tubes, where oxygen is lower. [L10 s15]

P. caudatum uses yeast in the upper part of the test tubes. [L10 s15]

These different niches are proposed to keep P. caudatum from excluding P. bursaria. [L10 s15]

Eltonian niche: the role of an organism in an ecosystem. [L10 s16]

Niche: the range of conditions within the environment where an organism can exist. [L10 s16]

The course primarily uses this second definition of niche. [L10 s16]

Fundamental niche *(every condition where it could live)*: the entire range of conditions a species could exist in. [L10 s17]

Most species do not exist across that entire range. [L10 s17]

Realized niche *(the part it actually uses)*: **only** part of that range. [L10 s18]

Competition, predation, parasitism or some other interaction cuts the range down. [L10 s18]

Resource partitioning *(splitting resources)*: differentiation of niches in space and time that lets similar species coexist. [L10 s19]

Warblers in spruce trees: five warbler species in New England. [L10 s19, L10 s20]

Four of the species used different heights and portions of the tree. [L10 s19]

Each probably fed on a different range of insects. [L10 s19]

The Cape May warbler attacked flying insects more than the **Blackburnian** did. [L10 s19]

The Cape May warbler also tended to remain on the outside of the trees. [L10 s19, L10 s20]

Result: reduced niche overlap, which promotes coexistence. [L10 s19, L10 s20]

Each warbler prefers a different height and portion of the tree, which reduces competition. [L10 s20]

Allopatric *(living apart)*: each finch alone, fuliginosa on **Los Hermanos**, fortis on **Daphne Major**. [L10 s21]

Sympatric *(living together)*: both finch species on the same islands, San Cristobal and **Santa Maria**. [L10 s21]

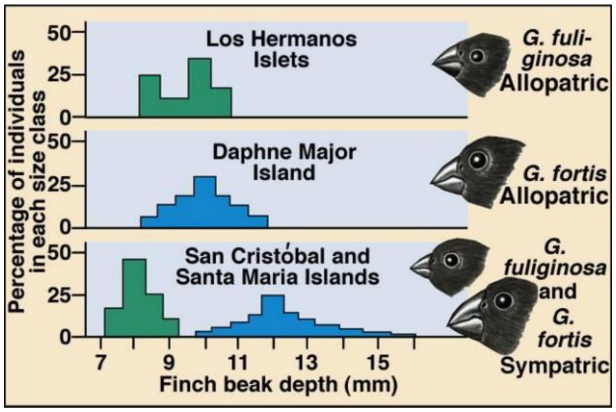
Galapagos finches: the Small Ground-Finch (Geospiza fuliginosa) and Medium Ground-Finch (Geospiza fortis). [L10 s22]

Character displacement *(traits shift apart)*: the trait measured is **beak depth**. [L10 s21]

Allopatric: the two beak depth ranges overlap. [L10 s21]

Sympatric: the two beak depth ranges shift apart, so beaks differ more. [L10 s21]

Niche: the resources a species uses and its interactions with other species define it. [L10 s23]



Beak depth of two finches alone and together: sympatric beaks shift apart [L10 s21]

On the figure: Allopatric · Sympatric · beak depth · Los Hermanos · Daphne Major · Santa Maria

Species a, b and c show large overlaps on the first niche dimension. [L10 s23]

Overlaps are smaller on the second niche dimension. [L10 s23]

With two dimensions together, the actual overlap (hatched area) is small. [L10 s23]

Paramecium competition results

Grown	Result
Each alone	All three level off
P. bursaria with P. caudatum	Coexist: both level off
P. aurelia with P. caudatum	Do **NOT** coexist: P. caudatum dies out

Table source: [L10 s14]

L10.3 Testing for competition: barnacles and caddisflies

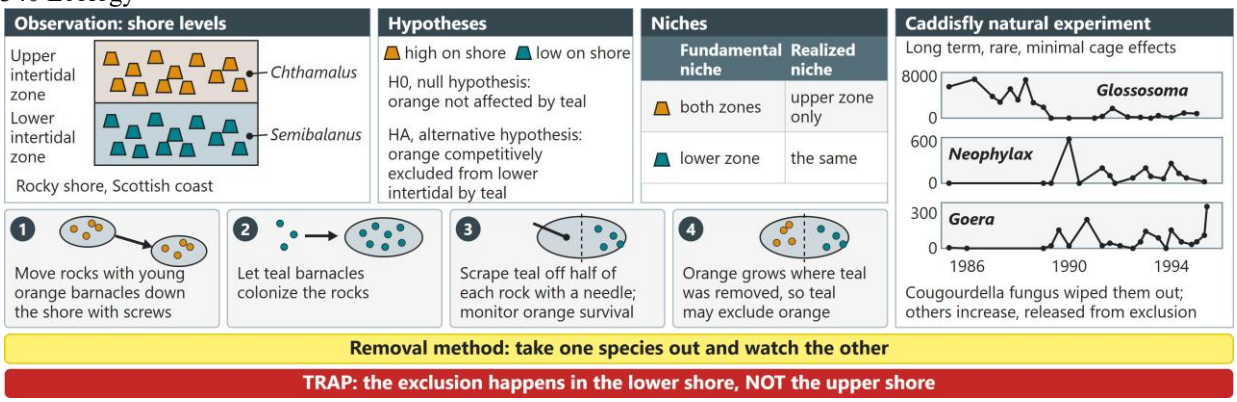
⚠ **Do not mix up: Semibalanus excludes Chthamalus from the LOWER zone, not the upper zone.** [L10 s27, L10 s28, L10 s29]

Competition can be an evolutionary force, strong enough to cause non-overlapping distributions between species. [L10 s24]

How can we test for competition and competitive exclusion experimentally? [L10 s25]

Removal method: temporarily remove one species and examine the effect on the other. [L10 s26]

This is one of the best tools for studying competition between two species. [L10 s26]



Barnacle removal steps, niches of the two barnacles, and the caddisfly long term record [L10 s29]

On the figure: Chthamalus · Semibalanus · Glossosoma · Removal method · Fundamental niche · Realized niche · H0

Barnacle experiment: a classic removal study of competition between two barnacle species. [L10 s26]

Observation: the two barnacle species occur at different levels of the rocky intertidal zone. [L10 s27]

Chthamalus stellatus *(upper shore barnacle)* occurs in the upper areas of the zone. [L10 s27]

Semibalanus balanoides *(lower shore barnacle)* is more abundant in the lower zone. [L10 s27]

Question: does competition restrict the ranges of these two barnacle species? [L10 s27, L10 s28]

H0 *(null hypothesis)*: Chthamalus are not affected by the presence of Semibalanus. [L10 s28]

HA *(alternative hypothesis)*: Chthamalus are competitively excluded from lower intertidal by Semibalanus. [L10 s28]

Setting: rocky shores of the Scottish coast, where the two species do not coexist. [L10 s29]

Result: Semibalanus may exclude Chthamalus from certain habitats. [L10 s29]

Chthamalus: **fundamental niche** covers both zones, **realized niche** **only** the upper zone. [L10 s29]

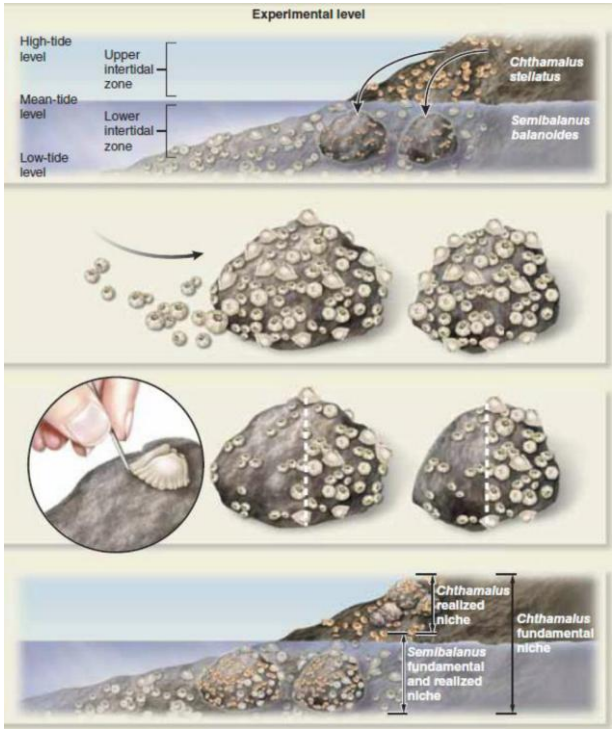
Semibalanus: fundamental and realized niche are the same, the lower zone. [L10 s29]

Glossosoma caddisflies: fungal pathogens (Cougourdella sp.) wiped them out in Michigan streams. [L10 s30]

This is a long-term natural experiment, a rare example with minimal cage effects. [L10 s30]

After Glossosoma was eliminated, other herbivorous insect species **increased** in density. [L10 s30]

They were released from exclusion via competition. [L10 s30]



Barnacle zones on the shore with realized and fundamental niche ranges [L10 s29]

On the figure: Chthamalus stellatus · Semibalanus balanoides · realized niche · fundamental niche

Barnacle removal experiment

Step	What was done
1	Remove rocks with young Chthamalus from upper zone, screw them down in lower zone
2	Allow Semibalanus to colonize the rocks
3	Remove Semibalanus from half of each rock with a needle, return rocks to lower zone, monitor Chthamalus survival on both sides
4	Chthamalus grows on the side where Semibalanus was removed

Table source: [L10 s29]

L10.4 Lotka-Volterra and R* models

⚠ **Do not mix up: Alpha is the effect of species 2 on species 1, NOT species 1 on species 2.** [L10 s34]

Lotka-Volterra competition model: based on the logistic equation of population growth. [L10 s31]

r1 is the per capita growth rate of species **1**; r2 is that of species **2.** [L10 s32]

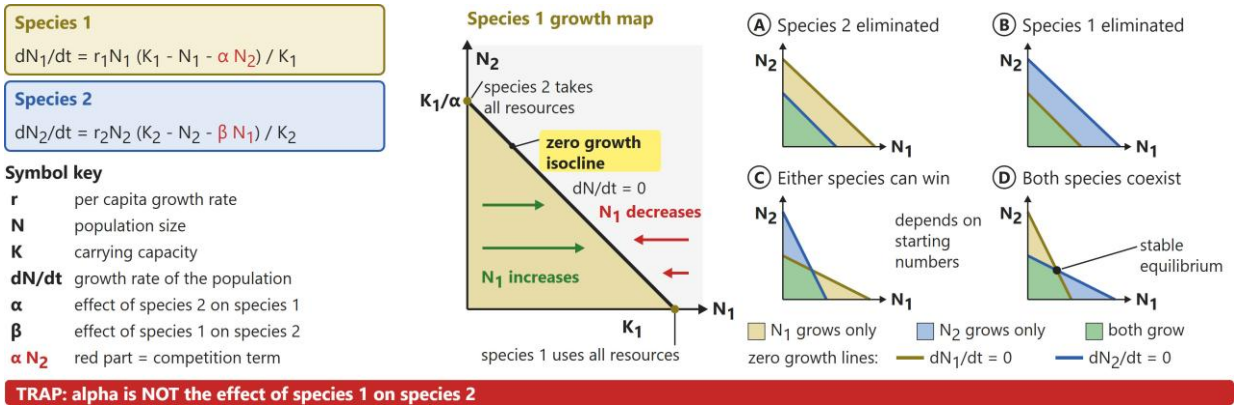
Start with the logistic equation for each species: dN1/dt = r1N1 (K1 - N1) / K1. [L10 s33]

Then add a competition term for each species effect on the other. [L10 s33]

Species **1**: dN1/dt = r1N1 (K1 - N1 - α N2) / K1. [L10 s34]

Species **2**: dN2/dt = r2N2 (K2 - N2 - β N1) / K2. [L10 s34]

These equations describe how the abundance of both species changes together. [L10 s34]



Competition equations, zero growth isocline with arrows, and the four outcomes [L10 s37]

On the figure: Zero growth isocline · Species 1 · Species 2 · K1/α · alpha

Zero growth isocline *(line where growth stops)*: the diagonal line where dN/dt = **0.** [L10 s35]

Axes: **species 1** size (x), **species 2** size (y); line runs **K1/α** to K1. [L10 s35]

Shaded area: species **1 increases** (arrows point right) and settles on the diagonal. [L10 s35]

Unshaded area: species **1 decreases** (arrows point left) until it reaches the diagonal. [L10 s35]

At K1 on the x axis, species **1** uses all resources and no N2 is present. [L10 s35]

At K1/α on the y axis, species **2** takes all resources; none remain for species **1.** [L10 s35]

Each species competes more strongly against its own species at high density. [L10 s36, L10 s37]

So each species limits itself more than it limits the other species. [L10 s36, L10 s37]

Colors: tan = N1 **increases only**, blue = N2 **increases only**, green = both **increase**. [L10 s36, L10 s37]

Dotted lines show vector addition *(adding the two solid arrows)* of the two solid line vectors. [L10 s37]

Tilman R star model *(resource level model)*: Tilman criticized the Lotka-Volterra model. [L10 s38]

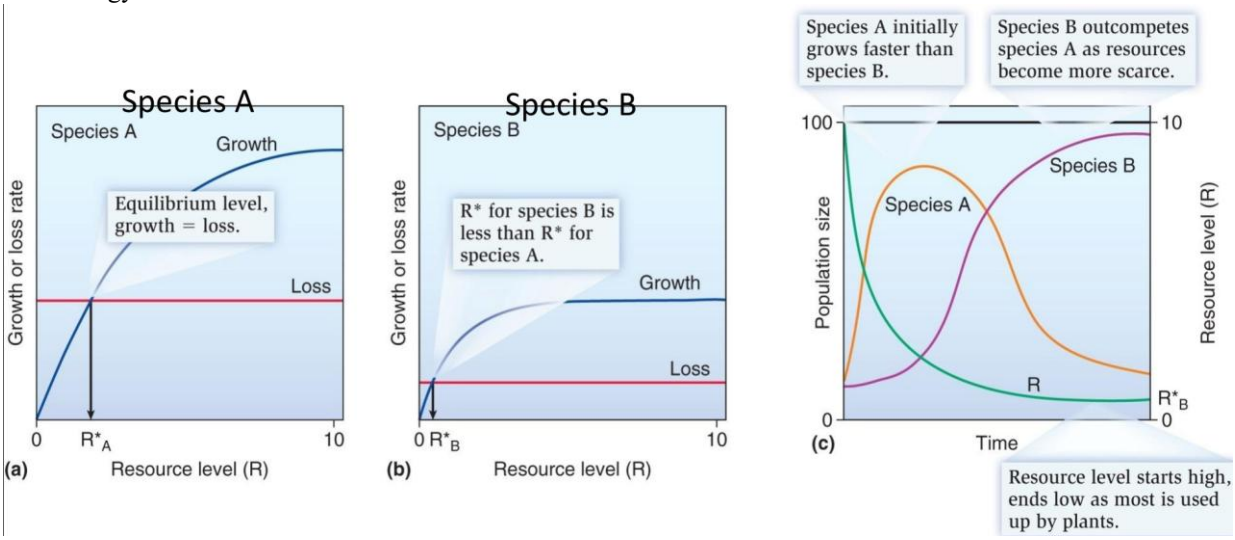
We need to know the mechanism by which competition occurs. [L10 s38]

Knowing the mechanism enables better predictions of the outcome. [L10 s38]

R star: the resource level where gains by growth equal losses to predators or disease. [L10 s38]

At R*, population size neither **increases** nor **decreases**. [L10 s38]

R* predicts the outcome of competition from resource use. [L10 s38]



Growth against loss for species A and B, and population and resource over time [L10 s39]

On the figure: Species A · Species B · resource level · Time

Species A: R* is where its rising growth curve meets the flat loss line. [L10 s39]

Species B: growth is slower than A, and R* for B is below R* for A. [L10 s39]

Over **time** species A first grows faster, peaks, then declines. [L10 s39]

Species B outcompetes species A as resources become scarce. [L10 s39]

Lower R star wins: species B has the lower R*, so it displaces species A. [L10 s39]

Species B drives the **resource level** down to R* of B. [L10 s39]

Resource level starts high and ends low, as most is used up by plants. [L10 s39]

Two resources: imagine a second resource where R* is lower for species A than B. [L10 s39]

They coexist if some habitat has more of resource **1** and some more of resource **2.** [L10 s39]

What the model teaches: competition is predicted to lead to local extinction of one species. [L10 s40]

Local extinction fails to occur if intraspecific competition is greater than interspecific competition. [L10 s40]

That means each species limits its own growth rate more than it limits the other species. [L10 s40]

Studies of R* show coexistence can occur when species require differing levels of the same resource. [L10 s40]

Summary: Lotka-Volterra models and the R* concept help explain species coexistence. [L10 s60]

Symbols in the model

Symbol	Meaning
r	per-capita rate of population growth
N	population size
K	carrying capacity
Subscripts 1, 2	refer to species **1** or species **2**
α (alpha)	per capita competitive effect of species **2** on species **1**
β (beta)	per capita competitive effect of species **1** on species **2**

Table source: [L10 s31, L10 s32, L10 s34]

Parts of the logistic equation

Part	Meaning
N1	population size
r1	per capita growth rate
dN1/dt	growth rate of the population

Table source: [L10 s33]

Four consequences of the model

Outcome	Result
A	Species **2** is eliminated
B	Species **1** is eliminated
C	Either species can win; it depends on the starting numbers
D	Both species coexist at a stable equilibrium

Table source: [L10 s37]

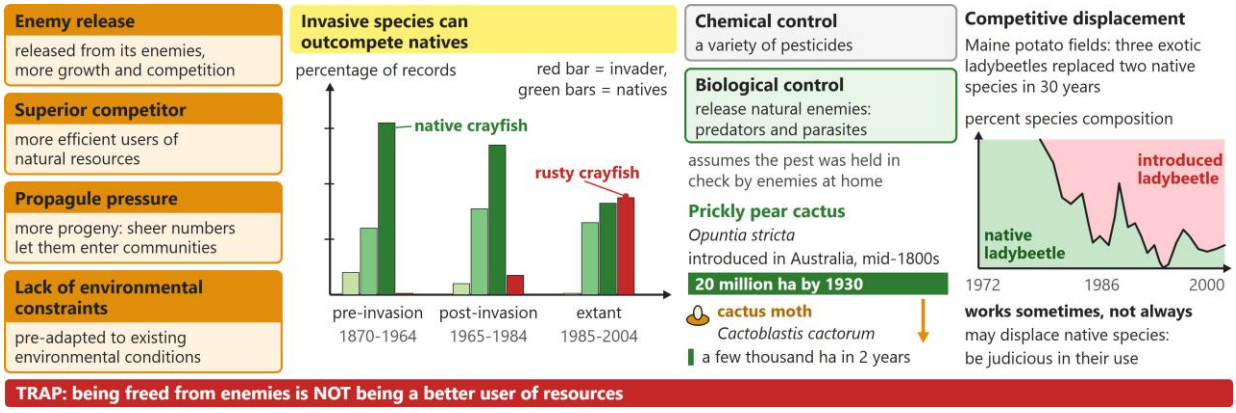
Two competition models

Model	Key idea	Prediction
Lotka-Volterra	Competition terms α and β added to logistic growth	Four outcomes, including coexistence
R* (Tilman)	Mechanism of competition, based on resource use	Species with the lower R* wins

Table source: [L10 s31, L10 s34, L10 s37, L10 s38, L10 s39]

L10.5 Invasive species and biological control

⚠ **Do not mix up: Enemy release is NOT efficient resource use: that is the superior competitor hypothesis.** [L10 s42]



Invasiveness hypotheses, crayfish records, biological control and ladybeetle displacement [L10 s41]

On the figure: Enemy release · Superior competitor · rusty crayfish · native crayfish · Biological control · Prickly pear cactus · Cactus moth · Competitive displacement

Invasive species can outcompete natives: an example is the **rusty crayfish** in Wisconsin. [L10 s41]
Competition from the rusty crayfish (red bar) reduced **native crayfish** abundance. [L10 s41]
Rusty crayfish records rose across three time periods while native O. virilis records fell. [L10 s41]
Four hypotheses are currently being tested to account for invasiveness. [L10 s42]
Enemy release also leads to evolution of **increased** competitive ability. [L10 s42]
These four hypotheses have rarely been tested concurrently. [L10 s42]
Summary: lack of natural enemies lets introduced species outcompete natives. [L10 s60]
Pest control is of paramount importance to agriculture, with two main methods. [L10 s43]
The enemies released are often those believed to control the pest in its native country. [L10 s43]
Biological control assumes the enemy release hypothesis is correct. [L10 s43]
Otherwise there is no reason to bring an enemy from the native country. [L10 s43]
Prickly pear cactus (Opuntia stricta) was introduced in Australia in the mid-**1800**s. [L10 s44]
Populations eventually established in the wild. [L10 s44]
It covered **20** million ha by **1930.** [L10 s44]
Cactus moth (Cactoblastis cactorum) was introduced; spread was hypothesized to come from lack of natural enemies. [L10 s45]
Opuntia cover dropped to **only** a few thousand ha in **only 2 years**. [L10 s45]
Competitive displacement: in Maine potato fields, three exotic ladybeetles replaced two native species in **30 years**. [L10 s46]
Biological control species sometimes (but not always) control the pest species. [L10 s46]

Introduced control agents may outcompete natives, so we must be judicious in their use. [L10 s46]

Four invasiveness hypotheses

Hypothesis	What it suggests
Enemy release	Invasives are released from natural enemies and devote more resources to growth and competition
Superior competitor	Invasives are more efficient users of natural resources than natives or non-invasives
Propagule pressure	Invasives produce more progeny than some natives, and sheer numbers let them enter communities
Lack of environmental constraints	Some invaders are pre-adapted to existing environmental conditions

Table source: [L10 s42]

Two methods of pest control

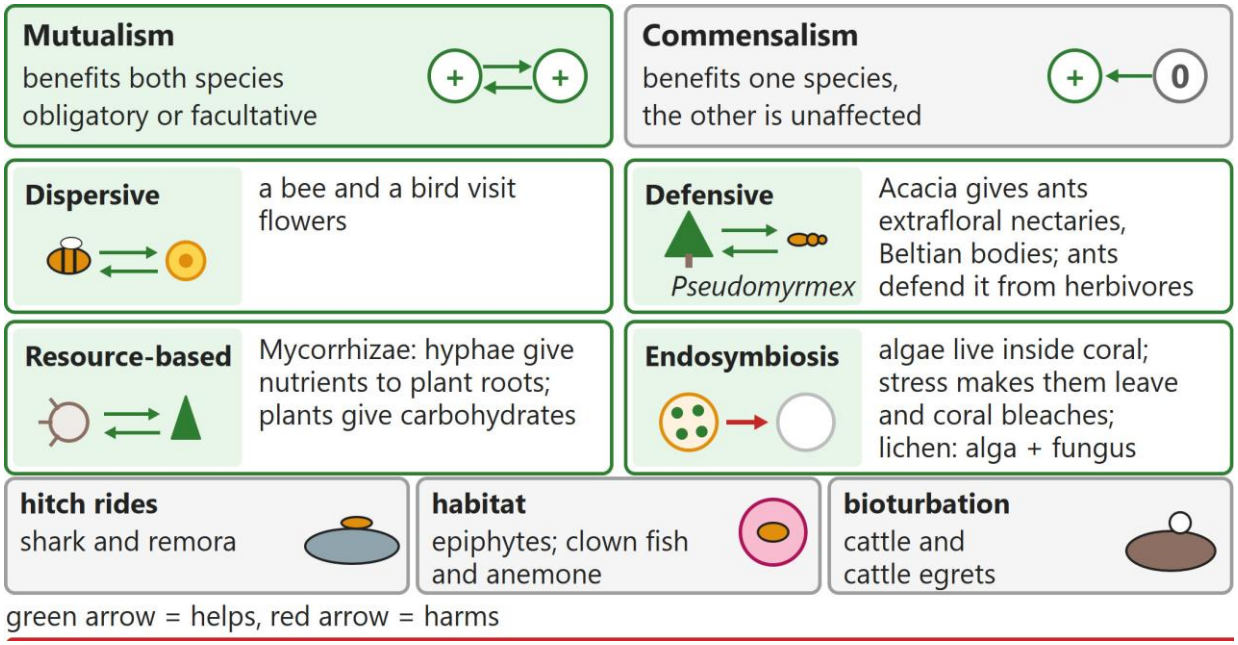
Method	How it works
Chemical control	A variety of pesticides is used
Biological control	Natural enemies such as predators and parasites are released against pests

Table source: [L10 s43]

L10.6 Facilitation: mutualism and commensalism

⚠ **Do not mix up: Commensalism is NOT mutualism: in commensalism one species benefits and the other is unaffected.** [L10 s48]

Facilitation *(one species helping another)*: the heading that covers mutualism and commensalism. [L10 s48, L10 s49]



Mutualism and commensalism signs with the kinds of mutualism and commensalism [L10 s06]

On the figure: Mutualism · Commensalism · dispersive · defensive · resource-based · endosymbiosis · remora · bioturbation

Mutualism: association between two species that benefits both species. [L10 s48]

Mutualism can be **obligatory** *(required)* or **facultative** *(optional)*. [L10 s48]

Commensalism: association between two species that benefits one species, while the other is unaffected. [L10 s48]

Signs: mutualism is + and +, commensalism is + and **0.** [L10 s06, L10 s48]

Mutualism may be **dispersive**, **defensive**, **resource-based**, or **endosymbiosis** *(partner living inside the other)*. [L10 s49]

Acacia and ants: acacia trees provide extrafloral nectaries *(nectar glands outside the flower)* to Pseudomyrmex ants. [L10 s50]

Acacia also provides protein-rich food nodules called **Beltian bodies.** [L10 s50]

In exchange, the ants defend the acacia tree from herbivores. [L10 s50]

Mycorrhizae *(root fungi)* form critical mutualisms with plants. [L10 s51]

Mycorrhizae are more efficient at obtaining nutrients. [L10 s51]

Hyphae *(fungal threads)* invade plant roots and receive carbohydrates from the plants. [L10 s51]

In exchange, the hyphae give nutrients to the plants. [L10 s51]

Coral bleaching: coral and **algae** depend on each other to survive. [L10 s52]

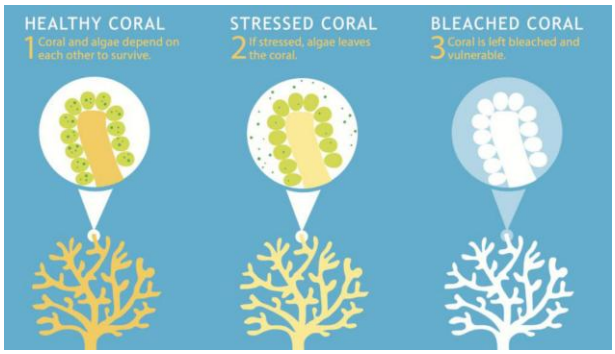
The algae are zooxanthellae *(tiny algae in coral tissue)*, the coral's primary food source, and give it color. [L10 s52]

Stress from **increased** ocean temperature or pollution makes the algae leave the coral tissue. [L10 s52]

Without algae the coral loses its main food, turns white, and is more prone to disease. [L10 s52]

Lichens: a mutualism between a photosynthetic organism and fungi. [L10 s53]

Commensalism examples include organisms that hitch rides, such as sharks and **remora** *(fish that ride on sharks)*. [L10 s54]



Healthy, stressed and bleached coral: algae leave and the coral turns white [L10 s52]

On the figure: coral · algae

Some use other organisms for habitat without damaging them: **epiphytes** *(plants growing on other plants)*, clown fish and anemone. [L10 s54]

Bioturbation *(organisms stirring soil or sediment)*: cattle and cattle egrets. [L10 s54]

Types of mutualism

Mutualism type	Example
Dispersive	A bee on a flower and a bird on a flower head
Defensive	Acacia trees and Pseudomyrmex ants
Resource-based	Mycorrhizae and plants
Endosymbiosis	Coral and algae; lichens

Table source: [L10 s49, L10 s50, L10 s51, L10 s52, L10 s53]

Coral bleaching steps

Step	Coral state	What happens
1	Healthy coral	Coral and algae depend on each other to survive
2	Stressed coral	If stressed, the algae leave the coral
3	Bleached coral	Coral is left bleached and vulnerable

Table source: [L10 s52]

Commensalism examples

Commensalism kind	Example
Hitch rides	Sharks and remora
Habitat use without damage	Epiphytes; clown fish and anemone
Bioturbation	Cattle and cattle egrets

Table source: [L10 s54]

L10.7 Facilitation in stressful environments

⚠ **Do not mix up: Neighbors do NOT mainly hurt high elevation plants: removing them lowered flowers and survival.** [L10 s57, L10 s58, L10 s59]

Plant mutualisms are more common in stressful environmental conditions, according to the evidence. [L10 s55]

Hypothesis: plants at higher elevations benefit more from neighboring plants. [L10 s55]

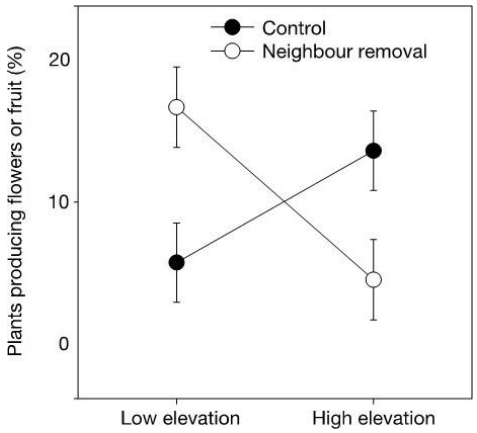
The reason is **facilitation** *(neighbors helping each other)*. [L10 s55]

Neighbors help by providing shade, protection from disturbance like wind, and herbivore protection. [L10 s55]

Global experiment: neighboring plants were removed at high and low elevation plots. [L10 s56]

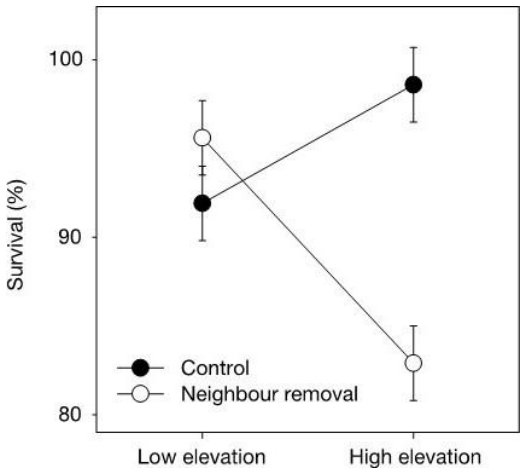
The experiment used **11** different locations. [L10 s56]

Plants at high elevation (more stressful) produced fewer flowers when neighbors were removed. [L10 s57, L10 s58]



Flowers or fruit at low and high elevation with and without neighbors [L10 s58]

On the figure: high elevation · low elevation · flowers



Survival at low and high elevation: removing neighbors cuts survival high up [L10 s59]

On the figure: survival · high elevation · low elevation

Plants at high elevation also had reduced survival when neighbors were removed. [L10 s59]

At low elevation, removing neighbors raised flowers, not lowered them. [L10 s58]

Take-home: facilitation in stressful environments might matter more than in ideal conditions. [L10 s60]