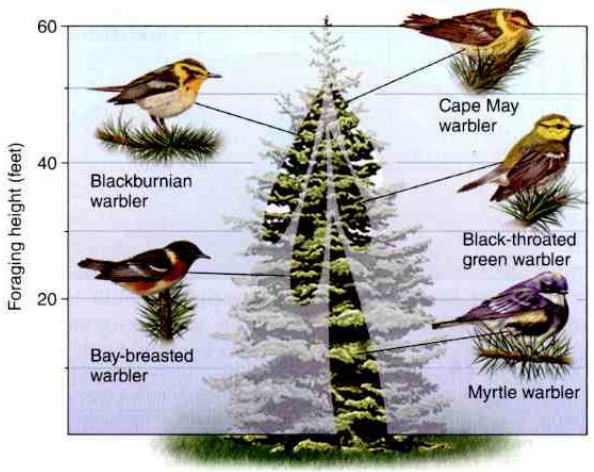
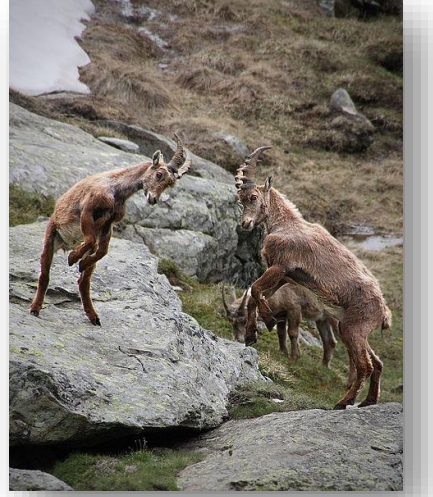
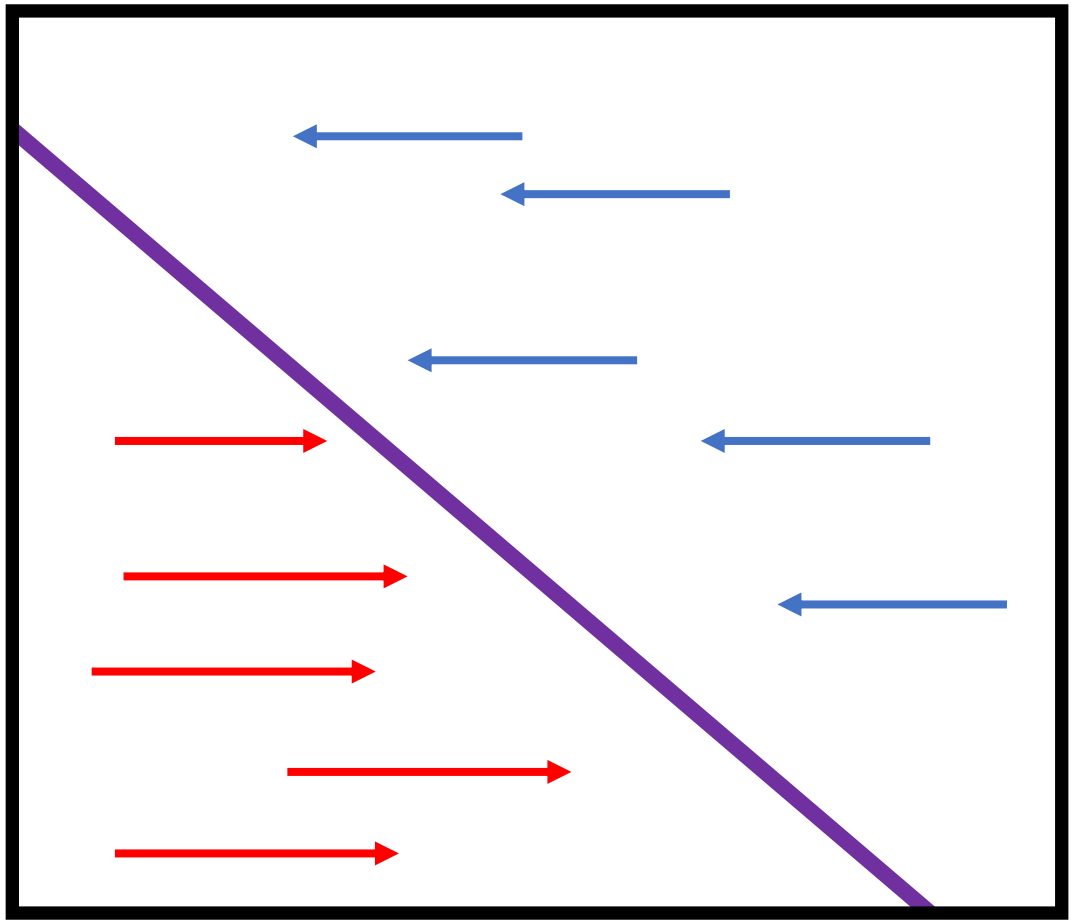








Competition and Facilitation



The ten principles of ecology

1. Evolution organizes ecological systems into hierarchies.
2. The sun is the ultimate source of energy for most ecosystems.
3. Organisms are chemical machines that run on energy.
4. Chemical nutrients cycle repeatedly while energy flows through an ecosystem.
5. dN/dt = B-X+I
6. dS/dt = D-X+I
7. Organisms interact – do things to each other - in ways that influence their abundance.
8. Ecosystems are organized into webs of interactions.
9. Human populations have an outsized role in competing with, preying upon, and helping other organisms.
10. Ecosystems provide essential services to human populations.

Topics for today

- Species interactions:
  - Competition, amensalism, predation, herbivory, parasitism, mutualism, commensalism, neutralism
- Competition
  - Intra- vs. interspecific
  - Types: interference, exploitation, apparent (also, ammensalism, allelopathy)
  - Invasive species, *Chthalamus/Semibalanus,* and *Glossosoma* examples
  - Lotka-Volterra models,
- Species coexistence (niche theory, resource partitioning)
- Facilitation
  - Mutualisms, commensalisms
  - Facilitation in stressful environmental conditions

Species interactions

- Interactions among populations (usually of different species) living in the same area

Species interactions

- Interactions among populations (usually of different species) living in the same area

Interaction	Species A	Species B
Competition	-	-
Amensalism	-	0
Predation, Herbivory, Parasitism	+	-
Mutualism	+	+
Commensalism	+	0
Neutralism	0	0

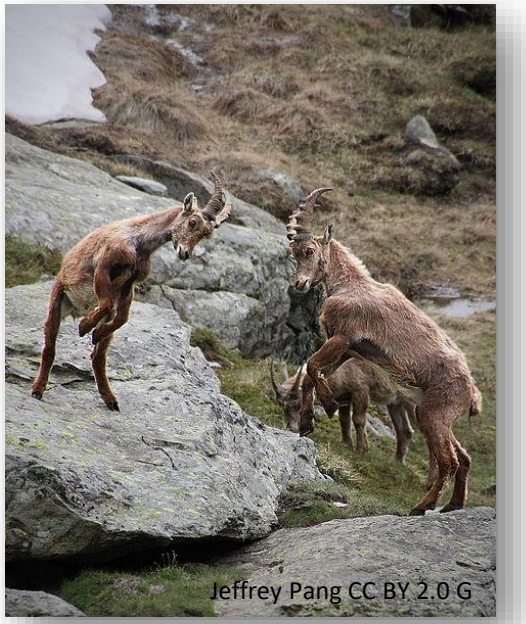
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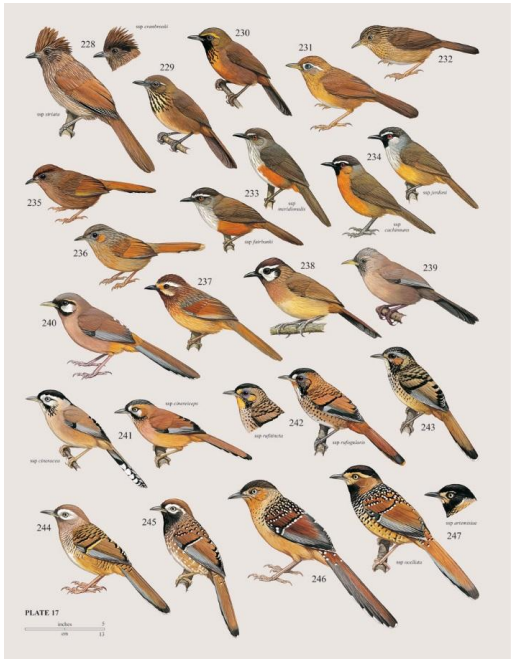
Types of competition

Competition may be **intraspecific**, between individuals of the same species or **interspecific**, between individuals of different species.

- We will focus on interspecific competition, but remember that individuals within a species compete strongly.

Intraspecific

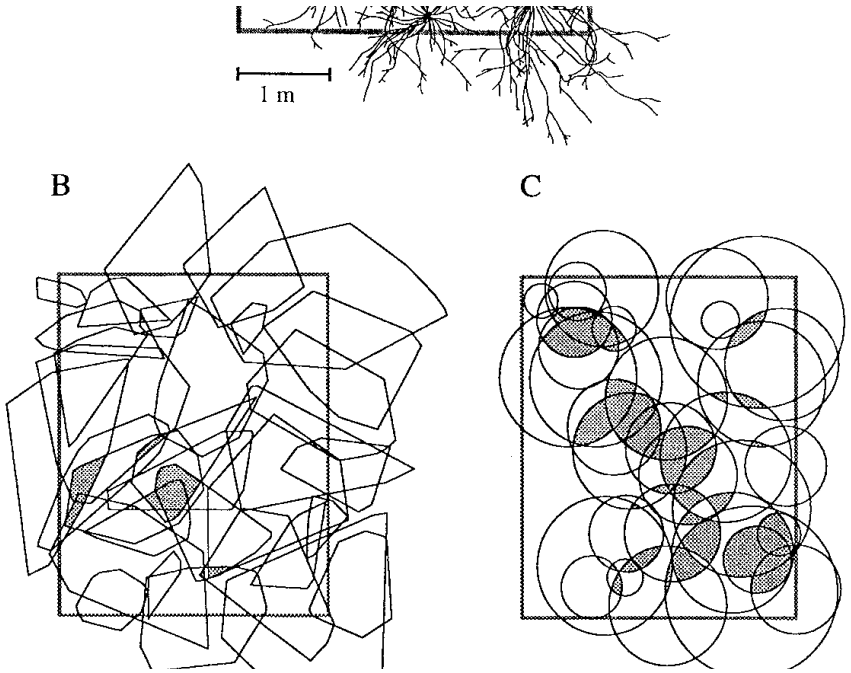




Interspecific

Types of competition

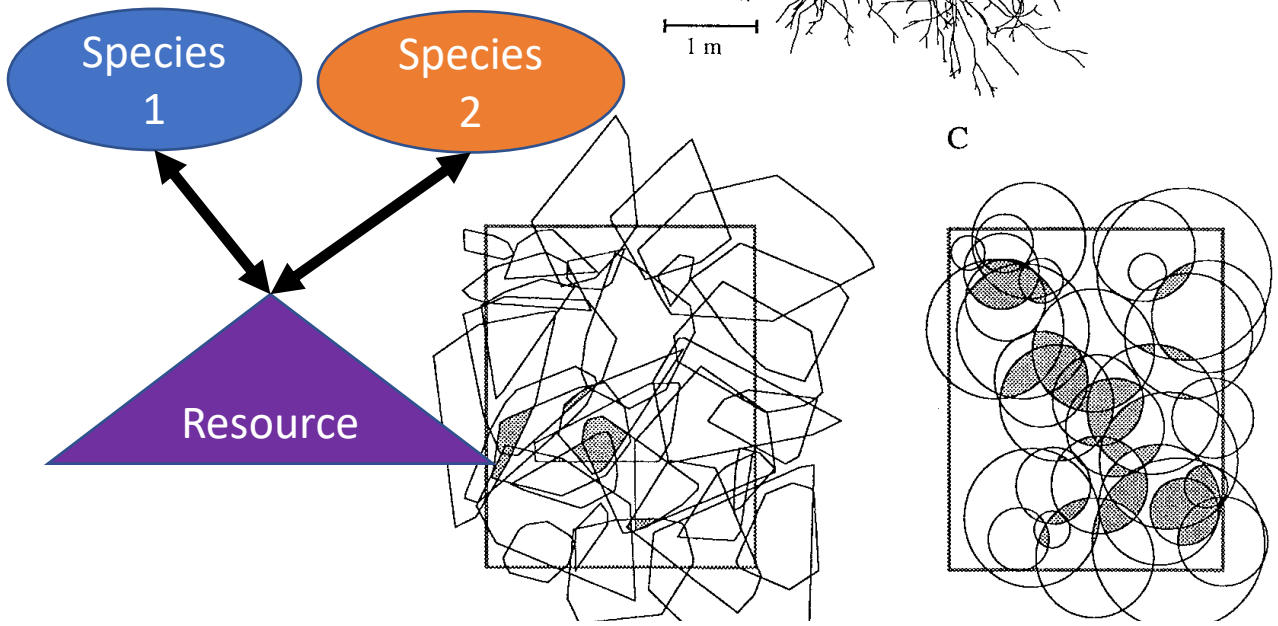
- Competition may also be ***exploitative*** or via ***interference***



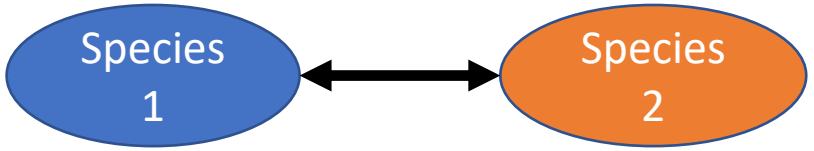


Types of competition

- Competition may also be ***exploitative*** or via ***interference***

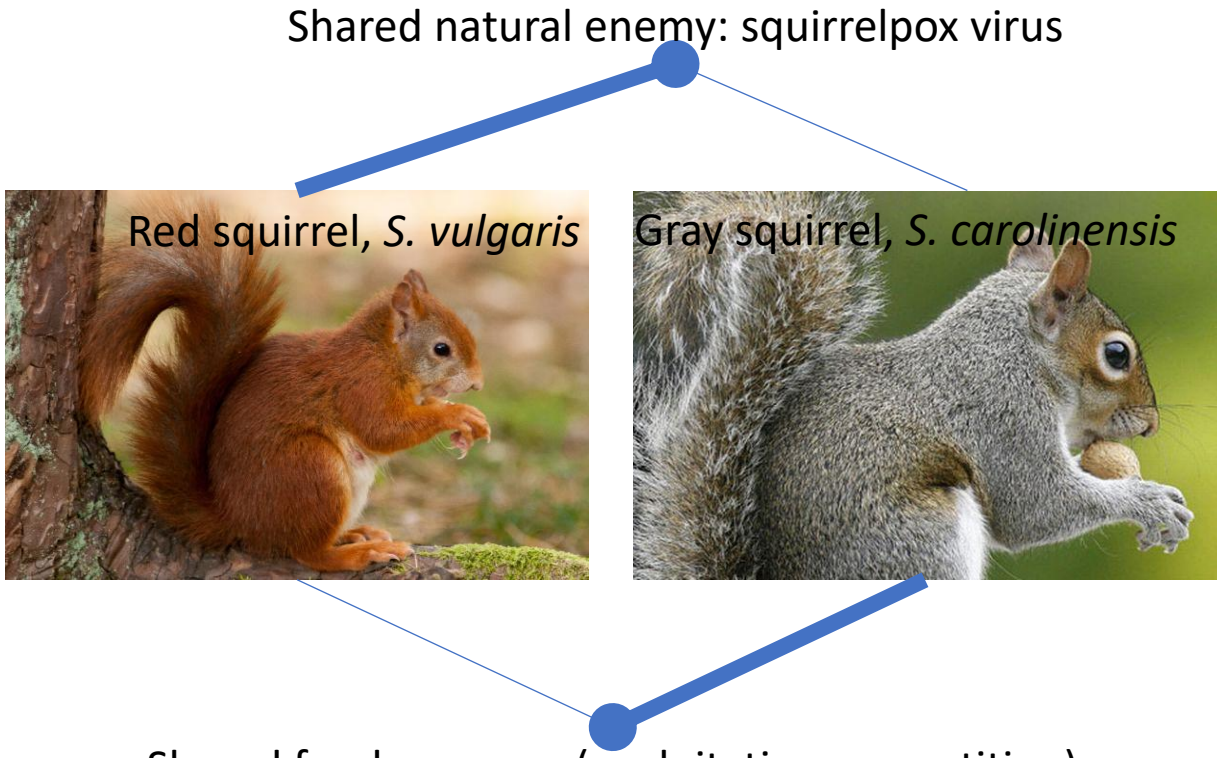






Types of competition

- **Apparent competition** involves a shared natural enemy, and is different than exploitative/interference competition.



Why is *apparent* competition different than competition?

Topics for today

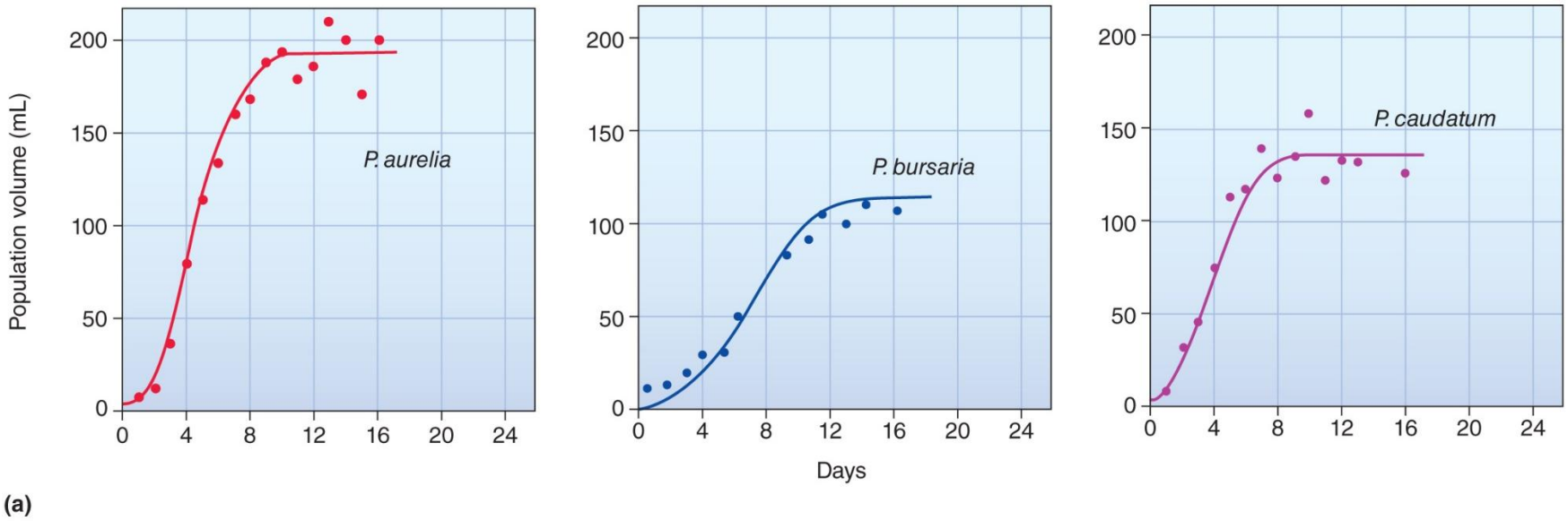
- Species interactions:
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  - Types: interference, exploitation, apparent (also, ammensalism, allelopathy)
  - ***Chthalamus/Semibalanus,* and *Glossosoma* examples**
  - **Lotka-Volterra models, R***
  - **Invasive species, biological control**
- Facilitation
  - Mutualisms, commensalisms
  - Facilitation in stressful environmental conditions

Competition can cause competitive exclusion

The **competitive exclusion principle** states that species with exactly the same requirements cannot live together in the same place and use the same resources (i.e. occupy the same *niche*).

This is thought to be true of any group of species that are forced to compete (microbes, mammals, plants, etc.)

Paramecium bursaria and *Paramecium caudatum* coexist



P. aurelia and *P. caudatum* do NOT coexist. Why the difference?

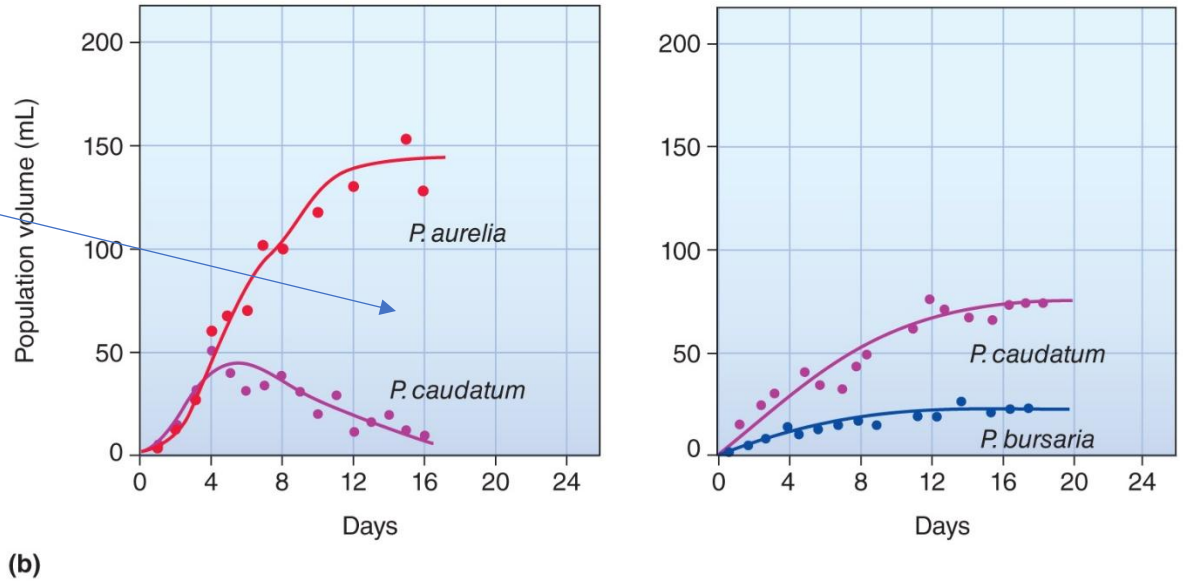


Fig. 11.21

Use of different resources can prevent competitive exclusion

- *P. bursaria* uses yeast in the lower part of test tubes where oxygen levels are lower
- *P. caudatum* utilizes yeast in the upper part of the test tubes
- These different **niches** are proposed to allow coexistence by preventing *P. caudatum* from excluding *P. bursaria*

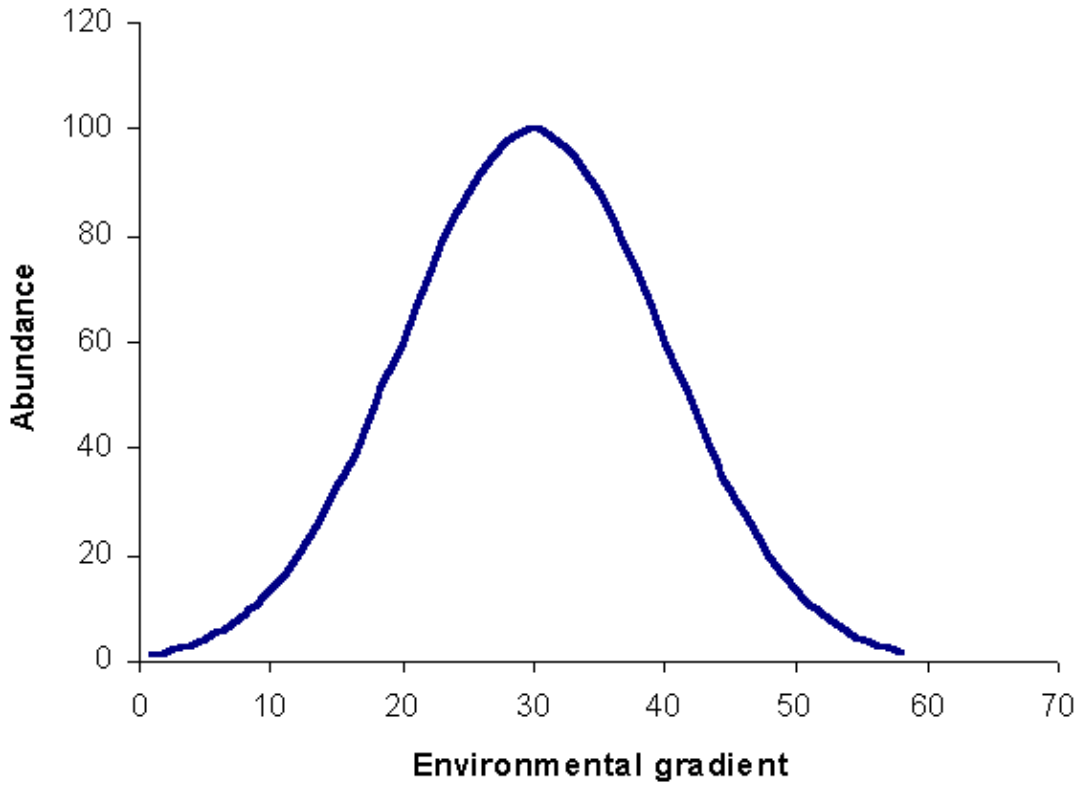
Use of different resources can prevent competitive exclusion

- (Eltonian) Niche - The role of an organism in an ecosystem

- Niche - The range of conditions within the environment within which an organism can exist
  - We will primarily use this definition

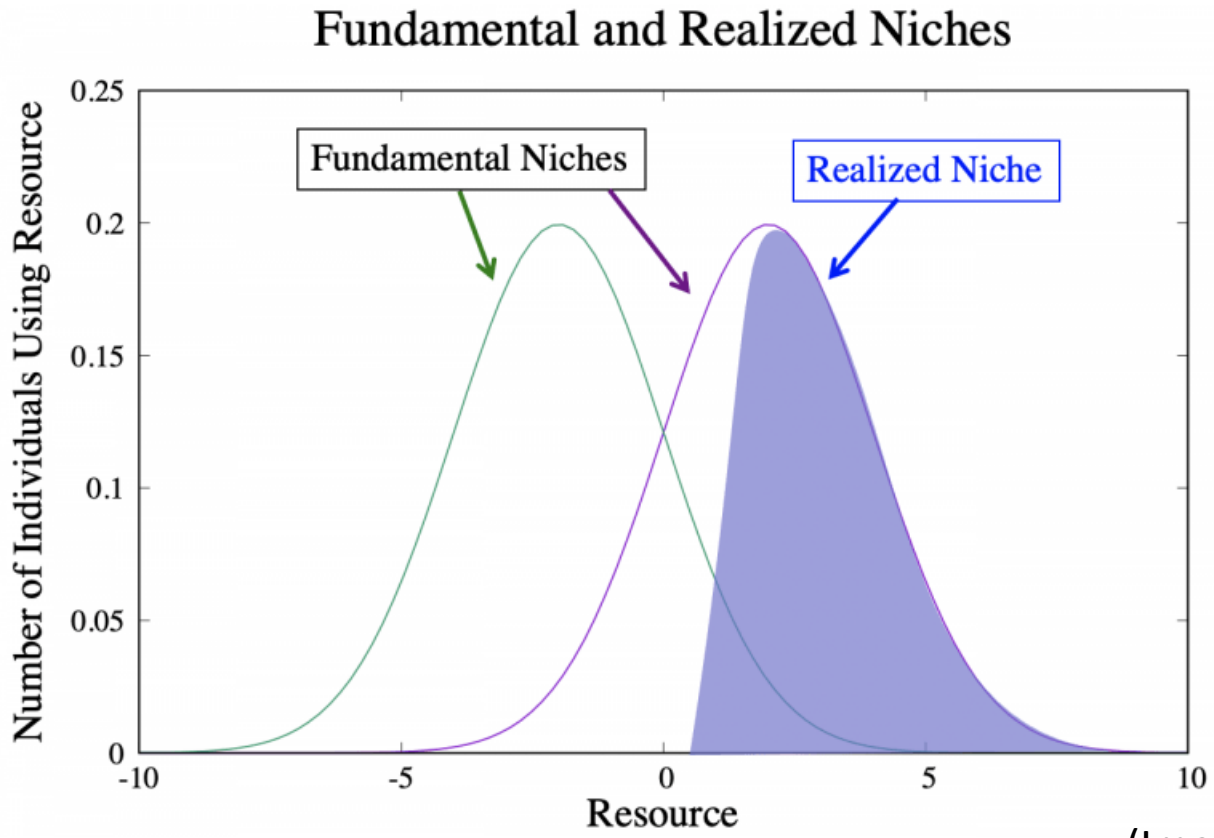
Definition of a niche

In reality, most species do not exist across the entire range of conditions under which they could exist (**fundamental niche**)



Definition of a niche

Instead, They only exist under part of that range (**realized niche**) due to competition, predation, parasitism or some other interaction



(Image Credit: Joe Montoya CC-BY-NC-SA)

Reductions in niche overlap

Species May Partition Resources

Promoting coexistence.

The term **resource partitioning** describes the differentiation of niches, both in space and time, that enables similar species to coexist in a community.

- Robert MacArthur examined coexistence between five species of warblers feeding within spruce trees in New England.
- MacArthur found that four of the species occupied different heights and portions in the tree and each probably fed on a different range of insects.
- Foraging habits also differed. The Cape May warbler attacked flying insects more than the Blackburian and tended to remain on the outside of the trees.

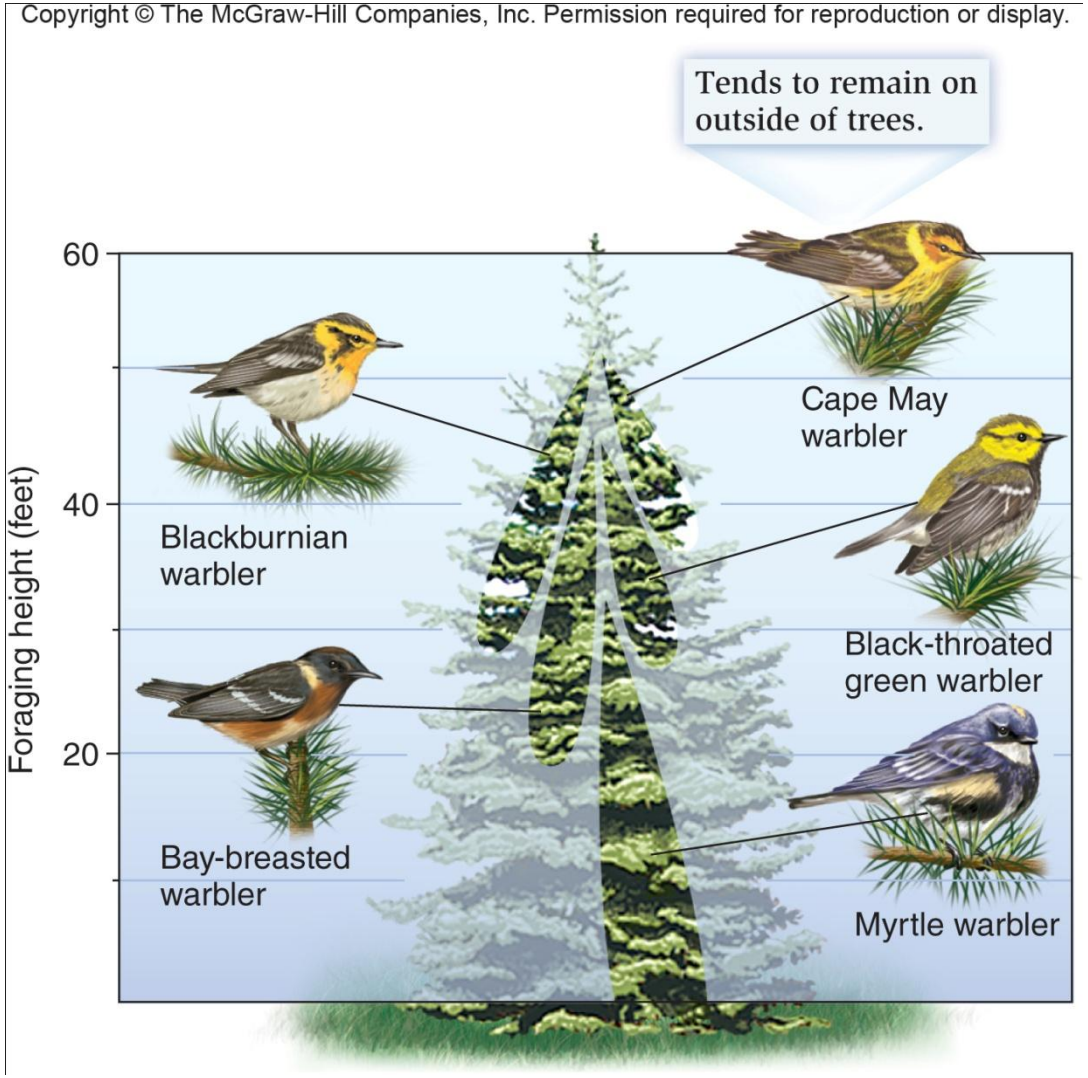
Reductions in niche overlap

Resource Partitioning

Figure 11.22 Resource partitioning.

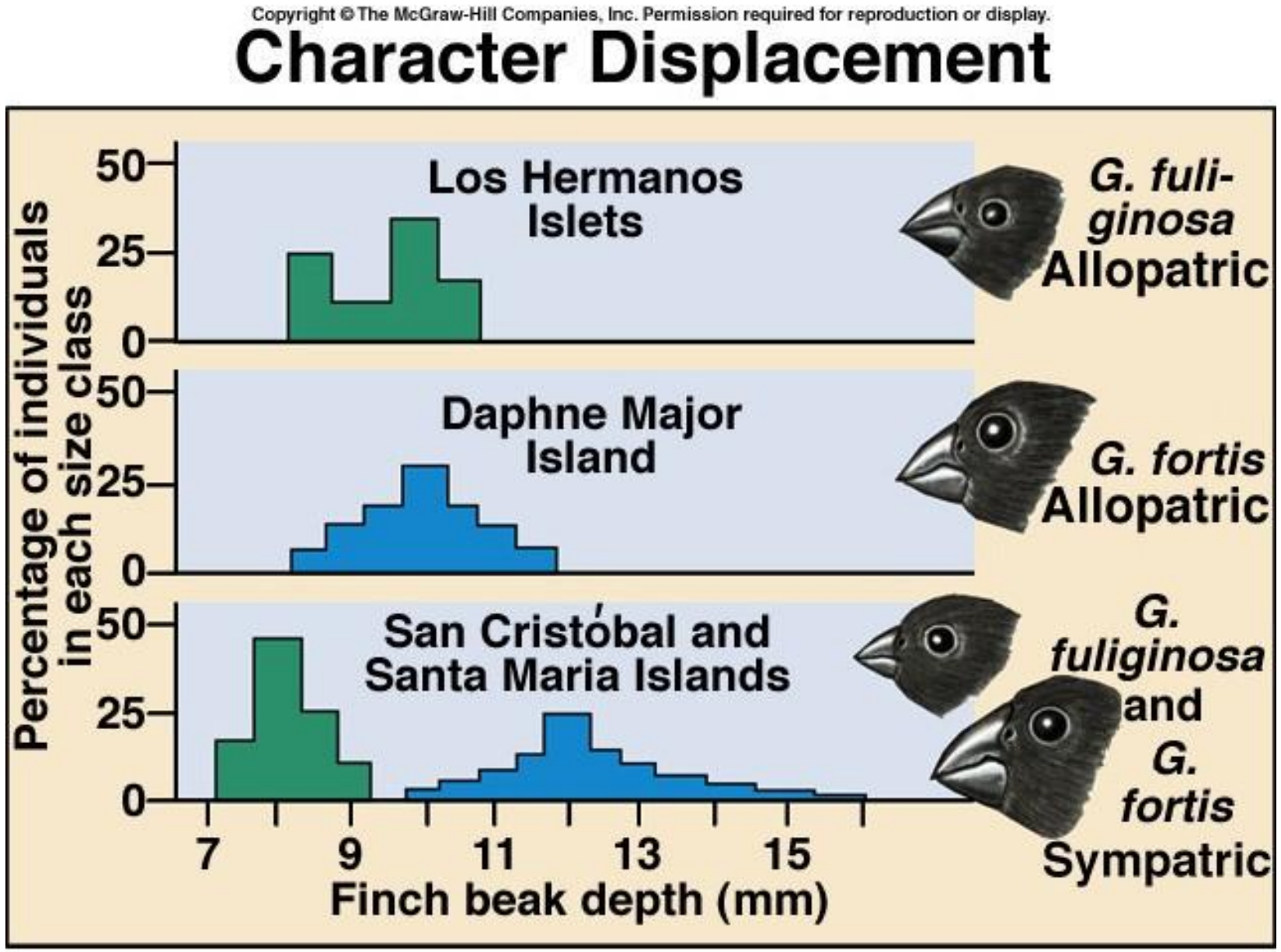
Among five species of warblers feeding in North American spruce trees, each warbler species prefers to feed at a different height and portion of the tree, thus reducing competition.
(Redrawn from McArthur 1958)

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Competition and niches

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Allopatric

Sympatric

Competition and niches



Small Ground-Finch (*Geospiza fuliginosa*)

The
Galapagos Finches

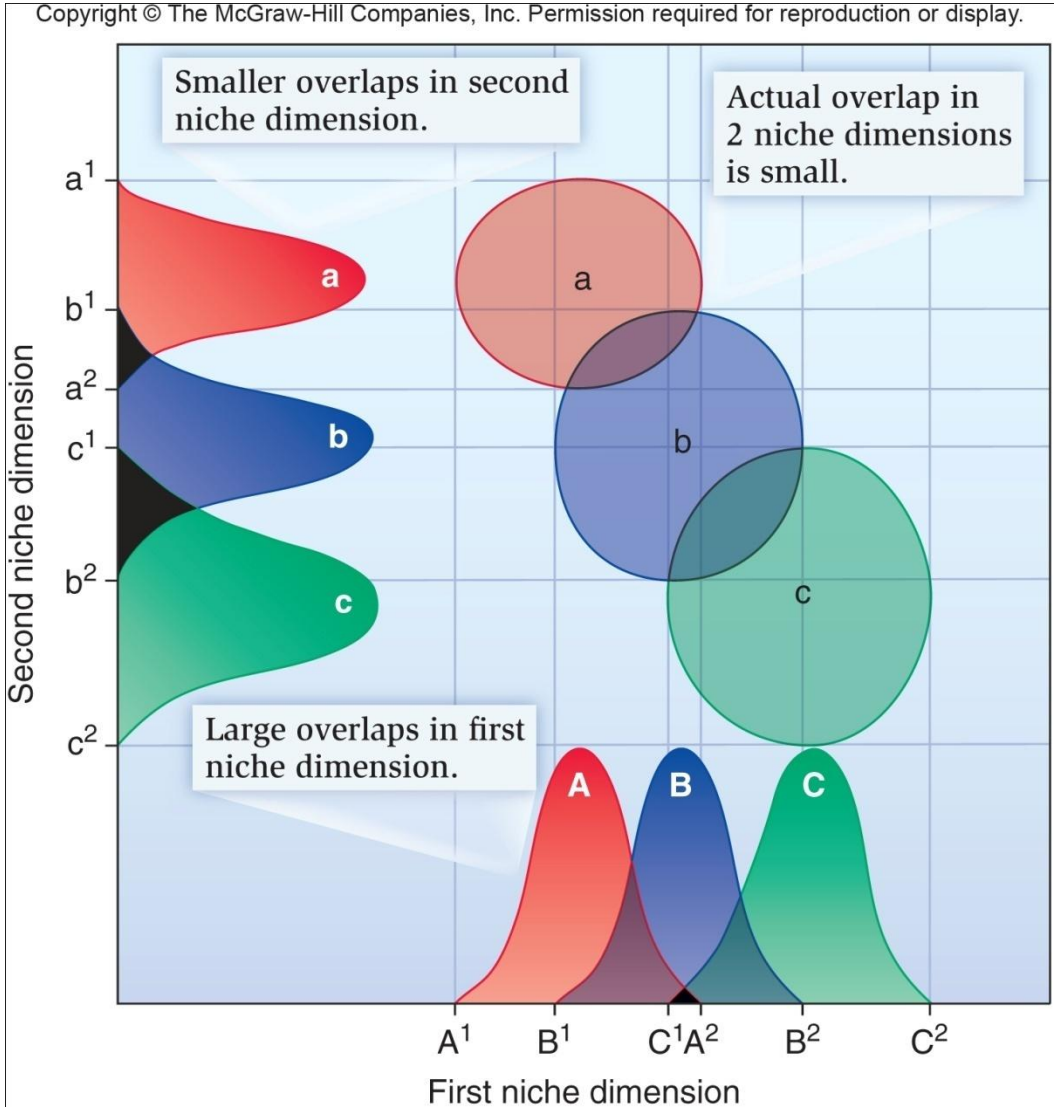


Medium Ground-Finch *Geospiza fortis*

The resources a species uses and interactions with other species defines its niche

Figure 11.25 Division of resources along two niche dimensions

Although overlaps are broad along the first niche dimension, overlap is minimized when two niche dimensions are considered (hatched area).



Use of different resources can prevent competitive exclusion

Competition can be an evolutionary force in nature, strong enough to cause non-overlapping distributions between species.

Use of different resources can prevent competitive exclusion

- How can we experimentally test for competition and competitive exclusion?

Use of different resources can prevent competitive exclusion

- One of the best tools we have to study competition between two species is to temporarily remove one of them and examine the effect on the other.

- The following is a classic example of this method involving a study of competition between two species of barnacles.

Chthamalus stellatus and *Semibalanus belanoides*

- Observation: two barnacle species tend to occur at different levels of the rocky intertidal zone
  - *Chthamalus* occurs in upper areas of the zone
  - *Semibalanus* more abundant in the lower zone
- Question: does competition restrict the ranges of these two barnacle species?

- H_0:
- H_A:





Chthamalus stellatus and *Semibalanus belanoides*

- Observation: two barnacle species tend to occur at different levels of the rocky intertidal zone
  - *Chthamalus* occurs in upper areas of the zone
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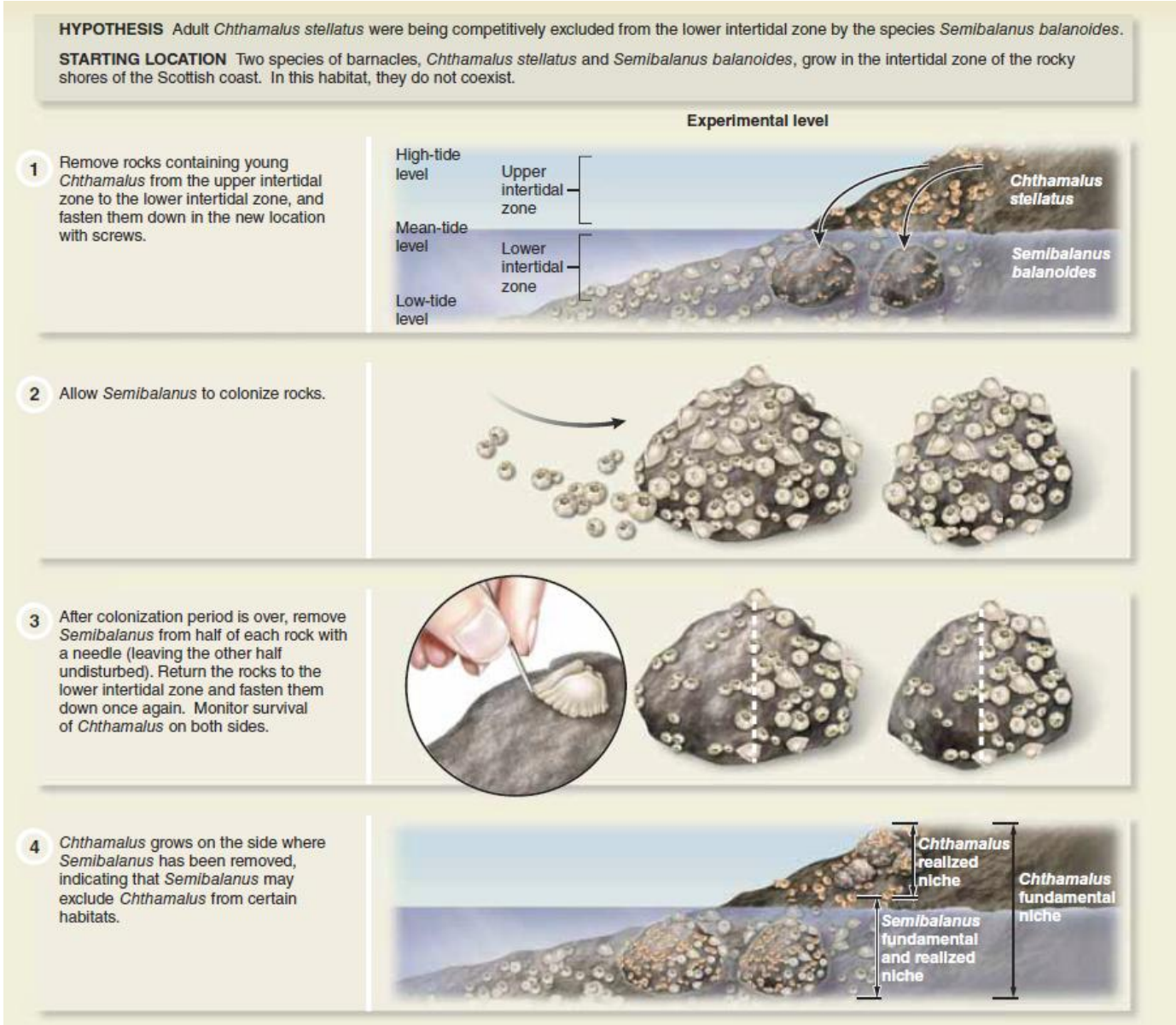
- H_0: *Chthamalus* are not affected by presence of *Semibalanus*
- H_A: *Chthamalus* are competitively excluded from lower intertidal by *Semibalanus*





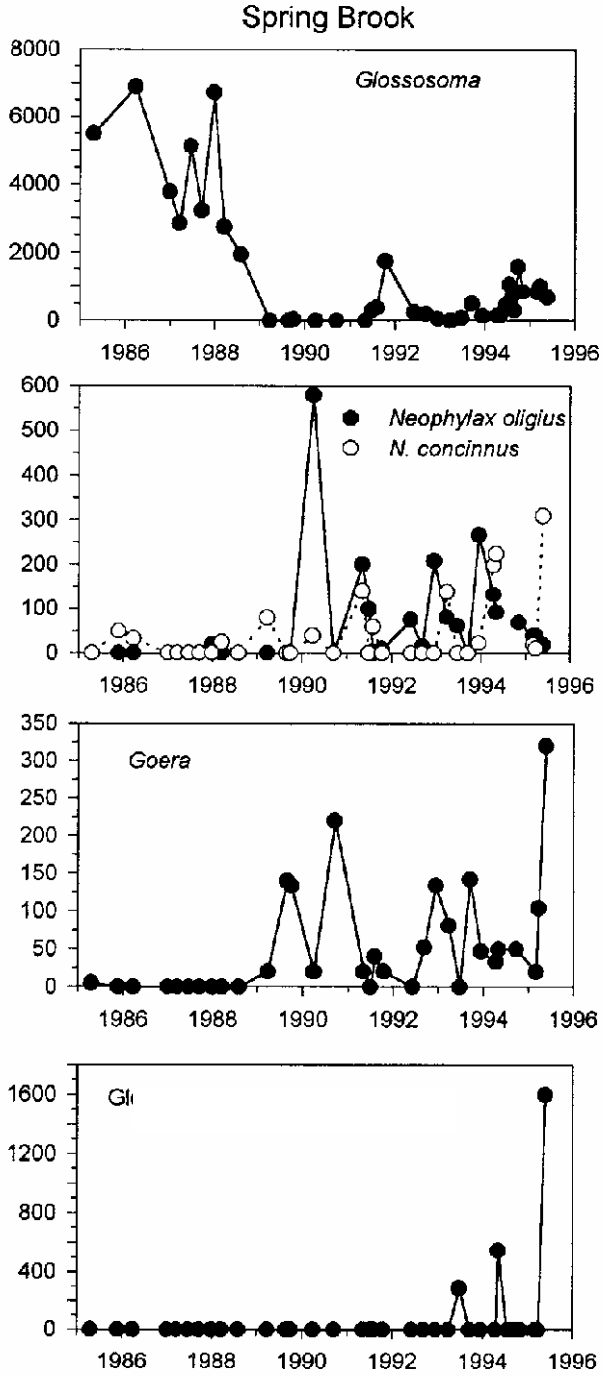
Use of different resources can prevent competitive exclusion

Figure 11.4 Connell's experimental manipulation of species indicated the presence of competition.



Evidence of competition in nature: *Glossosoma* caddisflies





- Fungal pathogens (*Cougourdella* sp.) wiped out *Glossosoma* caddisflies in Michigan streams
- Long-term, natural experiment – rare example with minimal cage effects
- With elimination of *Glossosoma,* other herbivorous insect species increased in density – released from exclusion via competition

Kohler and Wiley, 1997 *Ecology*

Lotka-Volterra competition model

Based on the logistic equation of population growth.

- r is the *per-capita* rate of population growth
- N is the population size
- K is the carrying capacity

Lotka-Volterra competition model

Subscripts are used to refer to particular species.

- r_1 is the per capita population growth rate of species 1.
- r_2 is the per capital population growth rate of species 2.

Lotka-Volterra competition model

Species 1

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1)}{K_1}$$

Growth rate of population → $\frac{dN_1}{dt}$

r_1: *Per capita growth rate*

N_1: *Population size*

$\frac{(K_1 - N_1)}{K_1}$: *(carrying capacity – population size) / carrying capacity*

Species 2

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2)}{K_2}$$

Start with the logistic growth equation for each species.

Then, we need to add a competition term that quantified the effects of species 1 on species 2, and vice-versa.

Lotka-Volterra competition model

α is the per capita competitive effect of species 2 on species 1, and

β is the per capita competitive effect of species 1 on species 2.

Species 1

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha N_2)}{K_1}$$

Species 2

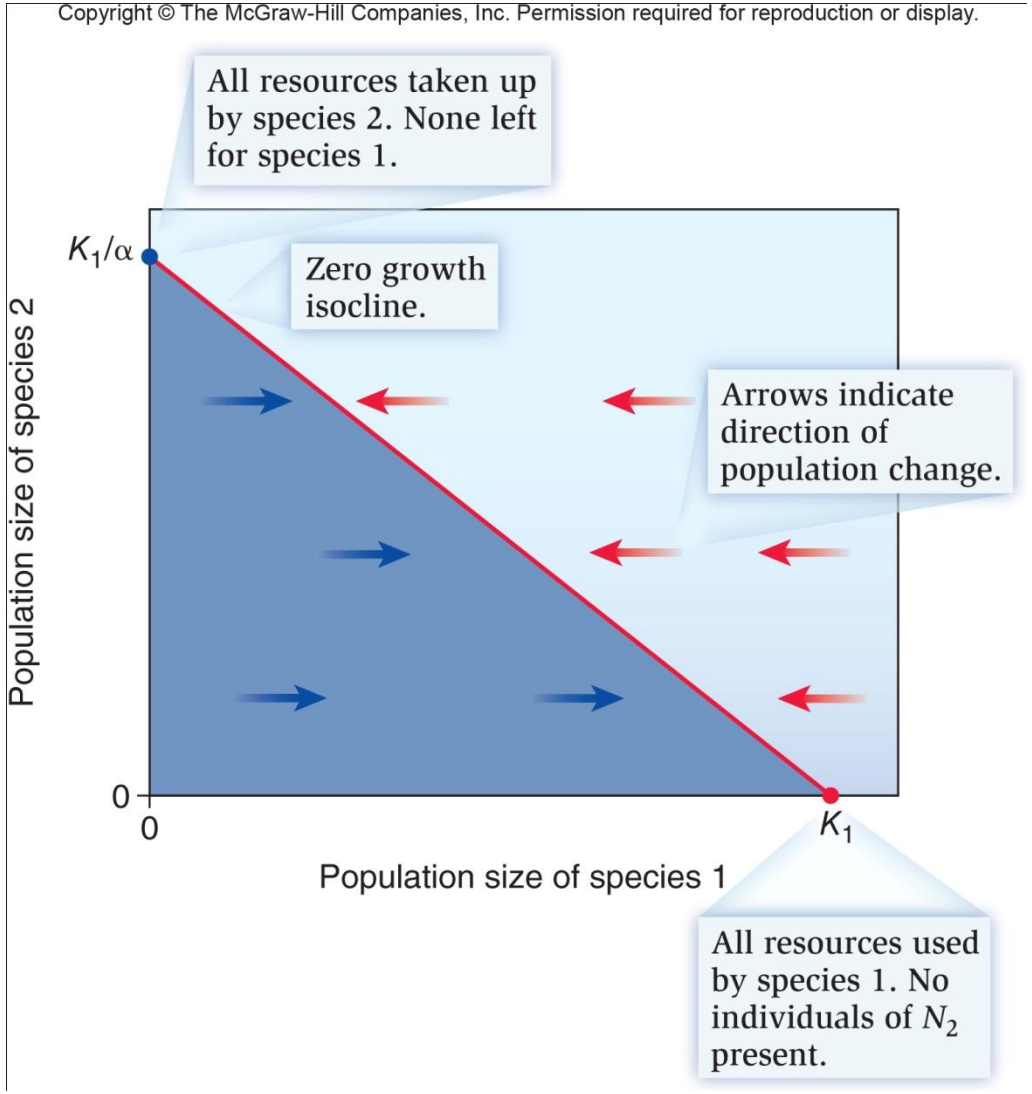
$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \beta N_1)}{K_2}$$

These equations can be used to describe how the abundance of both species changes *together*.

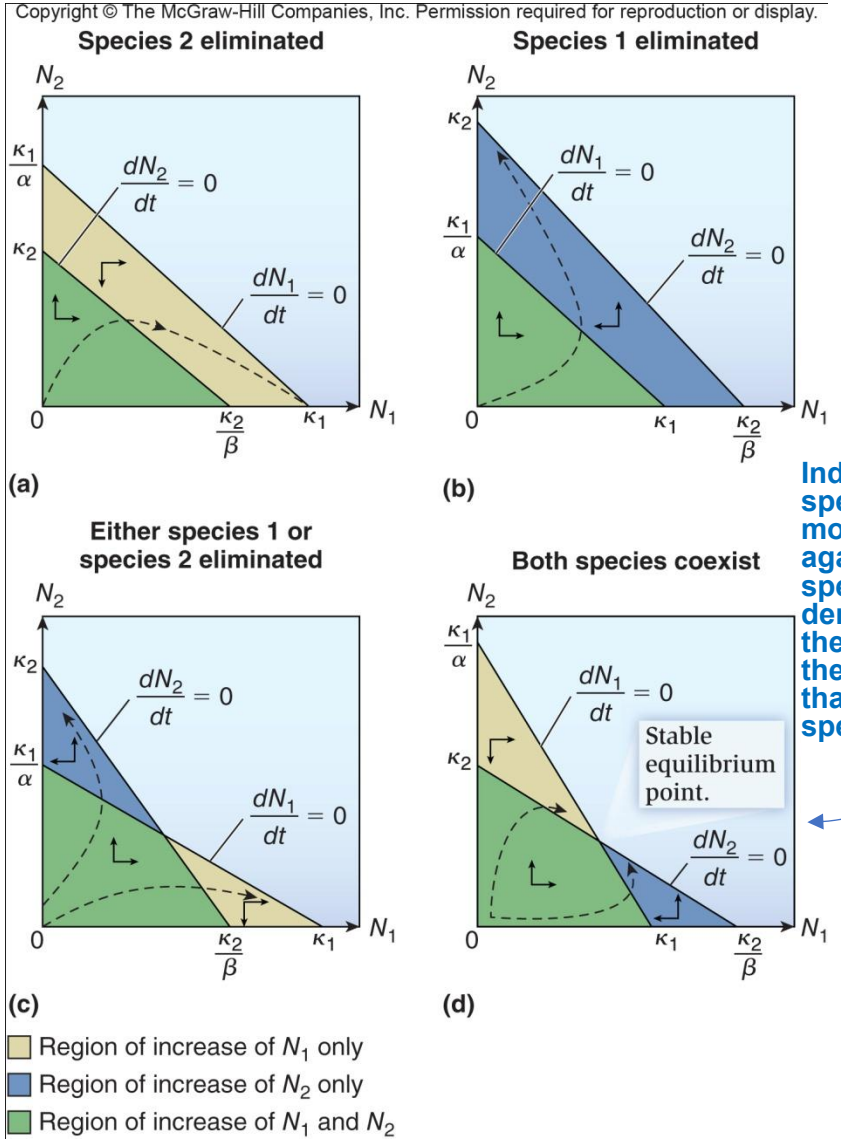
Lotka-Volterra competition model

Figure 11.16 Changes in the population size of species 1 when competing with species 2.

Populations in the shaded area will increase in size and will come to equilibrium at some point on the diagonal line. At any point on the diagonal there is no further population growth, i.e., dN/dt=0. Populations in the unshaded area will decrease in size until they reach the diagonal line.



Lotka-Volterra competition model

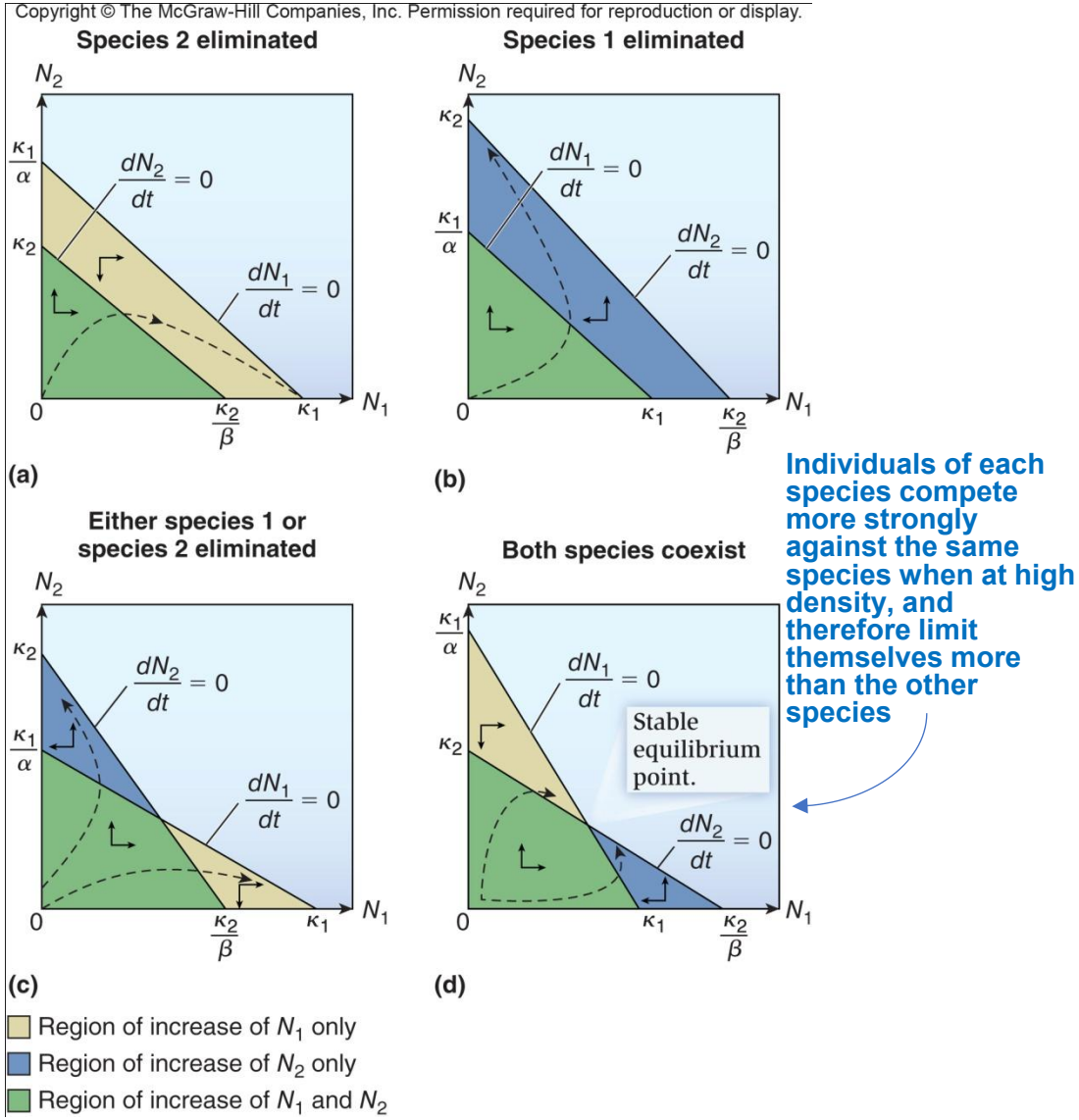


Individuals of each species compete more strongly against the same species when at high density, and therefore limit themselves more than the other species

Lotka-Volterra competition model

Figure 11.17 The four consequences of the Lotka-Volterra competition equations.

Axes are population size of species 1 and species 2. Dotted lines represent the results of vector addition of the two vectors shown by the solid lines. There are four possible outcomes: A. species 2 is eliminated, B. species 1 is eliminated, C. either species 1 or species 2 is eliminated, depending on who has fewer individuals when the competition begins, or D. both species coexist at a stable equilibrium.



Individuals of each species compete more strongly against the same species when at high density, and therefore limit themselves more than the other species

Re-thinking Lotka-Volterra competition model

Tilman's R* Models

Predict the outcome of competition based on resource use.

David Tilman criticized the Lotka-Volterra model of competition and emphasized that we need to know the mechanism by which competition occurs. *Knowing the mechanism will enable better predictions of the outcome.*

- Tilman's alternative was the **R* (R star)** concept.
- R* is the resource level at which organismal gains by growth equal losses to predators or disease (population size neither increases nor decreases).

R* model

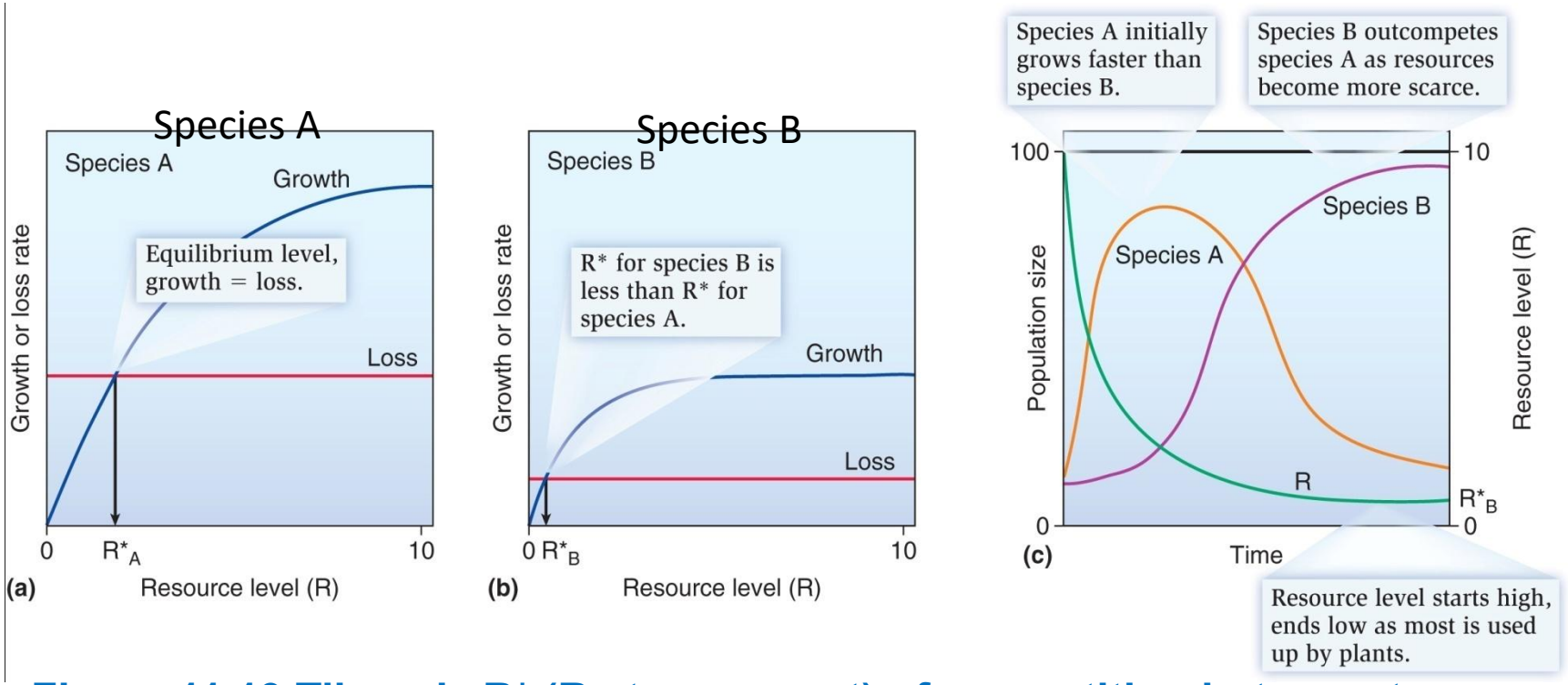


Figure 11.19 Tilman's R* (R star concept) of competition between two species, A and B, based on their resource utilization curves.

(a) Resource-dependent growth and loss for species A. The resource concentration at which growth equals loss is R_A*. **(b)** Resource-dependent growth and loss for species B and its R_B*. Growth is slower than for species A, **(c)** Dynamics of resource competition between species A and B. Note that species B, which has the lower R*, displaces species A and drives the resource concentration down to R_B*. (Reproduced from Tilman 1997)

Now imagine there is a second resource and R* for this resource is lower for species A than B. These two species can coexist if some habitat contains more of resource 1 and some habitat contains more of resource 2.

What have we learned from the Lotka-Volterra competition model?

- Competition predicted to lead to the local extinction of one of the species

- Local extinction fails to occur if ***intraspecific*** competition is greater than ***interspecific*** competition
  - (each species limits its own population growth rate more than the population growth rate of the other species)

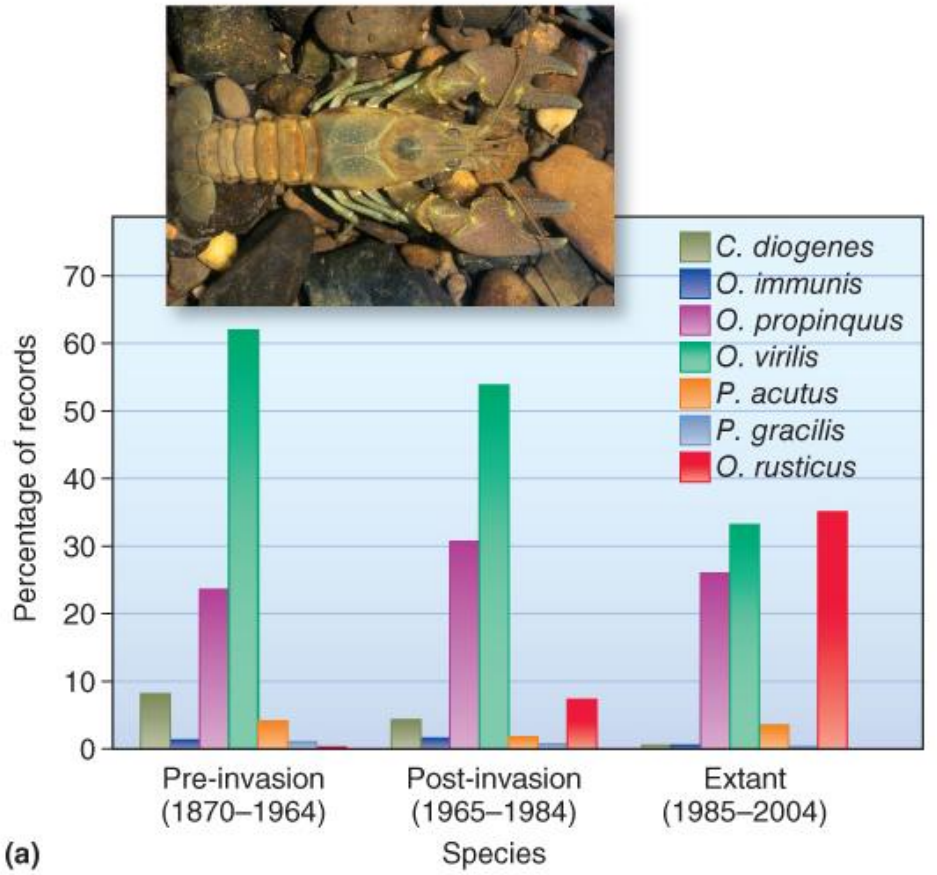
- Studies of R* have shown that coexistence can occur when species require differing levels of the same resource.

Invasive species can outcompete natives

Figure 11.11 Competition from the rusty crayfish (red bar) has reduced native crayfish species abundance (other colored bars) in Wisconsin.

(a) Comparison of pre-invasion data (1870-1964) with post invasion data (1985-2004). (From Olden et al. 2006)

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Invasive species

There are four hypotheses currently being tested to account for invasiveness.

Enemy Release Hypothesis	Superior Competitor Hypothesis	Propagule Pressure Hypothesis	Lack of Environmental Constraints Hypothesis
• Suggests invasives are released from their natural enemies and can devote more resources to growth, and thus competition. • This leads to the evolution of increased competitive ability.	• Suggests invasives are more efficient users of natural resources than natives or non-invasives.	• Suggests invasives produce more progeny than some native species, and by sheer weight of numbers this permits them entry into natural communities.	• Suggests pre-adaptation of some invaders to existing environmental conditions.

These hypotheses have rarely been tested concurrently.

Invasive species control

The control of pests is of paramount importance to agriculture. Two main methods of control exist:

Chemical control	Biological control
A variety of pesticides is used.	Natural enemies such as predators and parasites are released against pests. Often these natural enemies are the ones that are believed to control the pest in its native country.

Biological control assumes the enemy release hypothesis is correct…there's no reason to introduce an enemy from the native country into a new country unless you think the pest species was being controlled by the enemy in its native country.

Invasive species control

- Prickly pear cactus (*Opuntia stricta*) introduced in Australia in mid-1800s
- Eventually populations established in the wild
- Covered 20 million ha by 1930



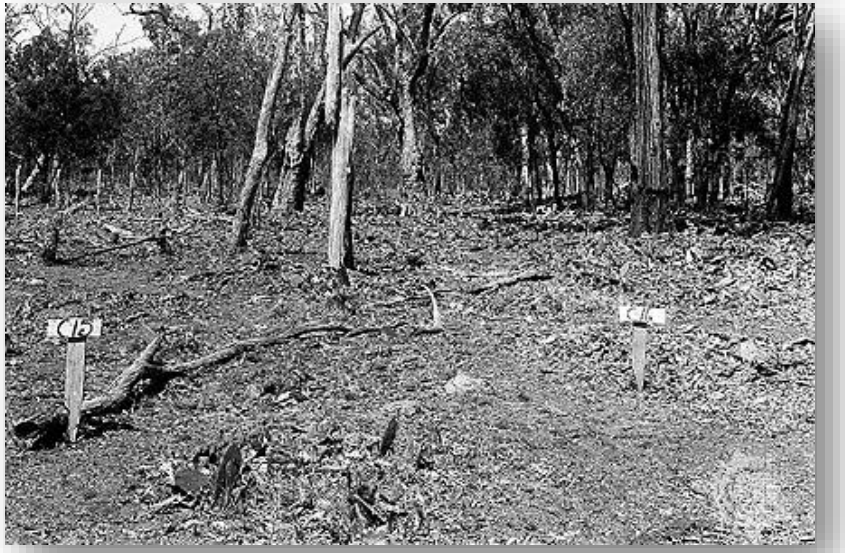
Invasive species control

- Hypothesized spread was due to lack of natural enemies
- Introduced cactus moth *Cactoblastis cactorum*
- *Opuntia* populations decreased to cover only a few thousand ha in only 2 yr

Cactus moth, *Cactoblastis cactorum*







Invasive species control

Biological control species sometimes (but not always) control the pest species.

However, introduced biological control agents may outcompete native species so we must be judicious in their use.

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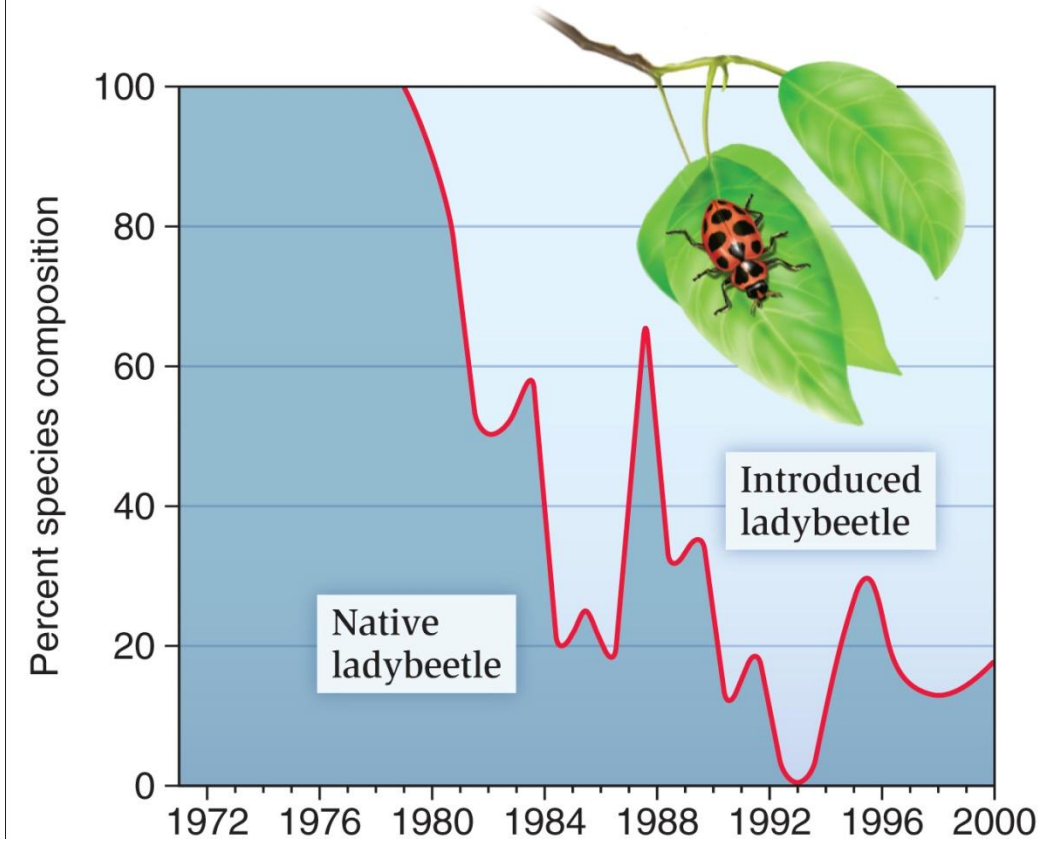


Figure 11.14 Competitive displacement.

In the potato fields of Maine, three exotic species of ladybeetles replaced two native species over a 30-year period. (After data in Alyokhin and Sewell 2004)

Topics for today

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  - Intra- vs. interspecific
  - Types: interference, exploitation, apparent (also, ammensalism, allelopathy)
  - Invasive species, *Chthalamus/Semibalanus,* and *Glossosoma* examples
  - Lotka-Volterra models
- Species coexistence (niche theory, resource partitioning)
- **Facilitation**
  - Mutualisms, commensalisms
  - Facilitation in stressful environmental conditions

Facilitation

- Mutualism
  - Association between two species that benefits both species
  - Can be obligatory, or facultative
- Commensalism
  - Associations between two species that benefits one species, and the other species is unaffected

Facilitation

- Mutualism
  - May be **dispersive**, defensive, resource-based, endosymbiosis





Facilitation

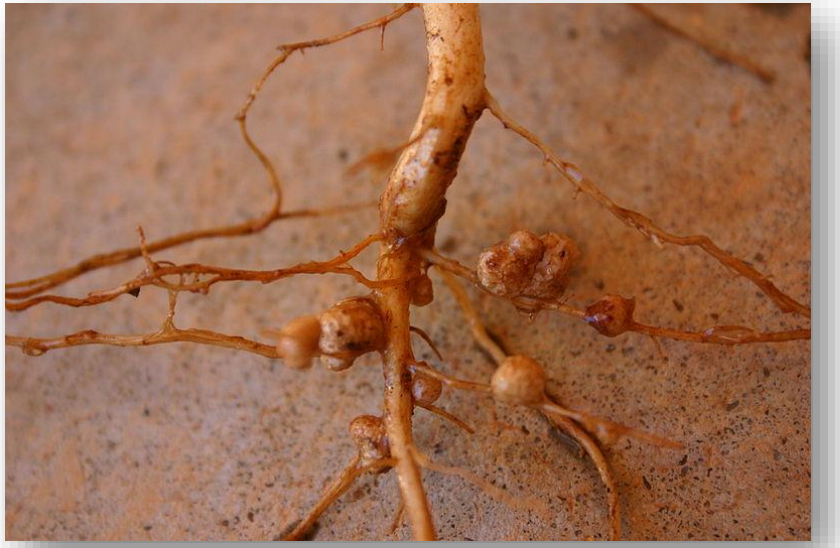
- Mutualism
  - May be dispersive, **defensive**, resource-based, endosymbiosis



- *Acacia* trees provide extrafloral nectaries and protein rich food nodules called Beltian bodies to *Pseudomyrmex* ants
- In exchange, the ants defend the acacia tree from herbivores

Facilitation

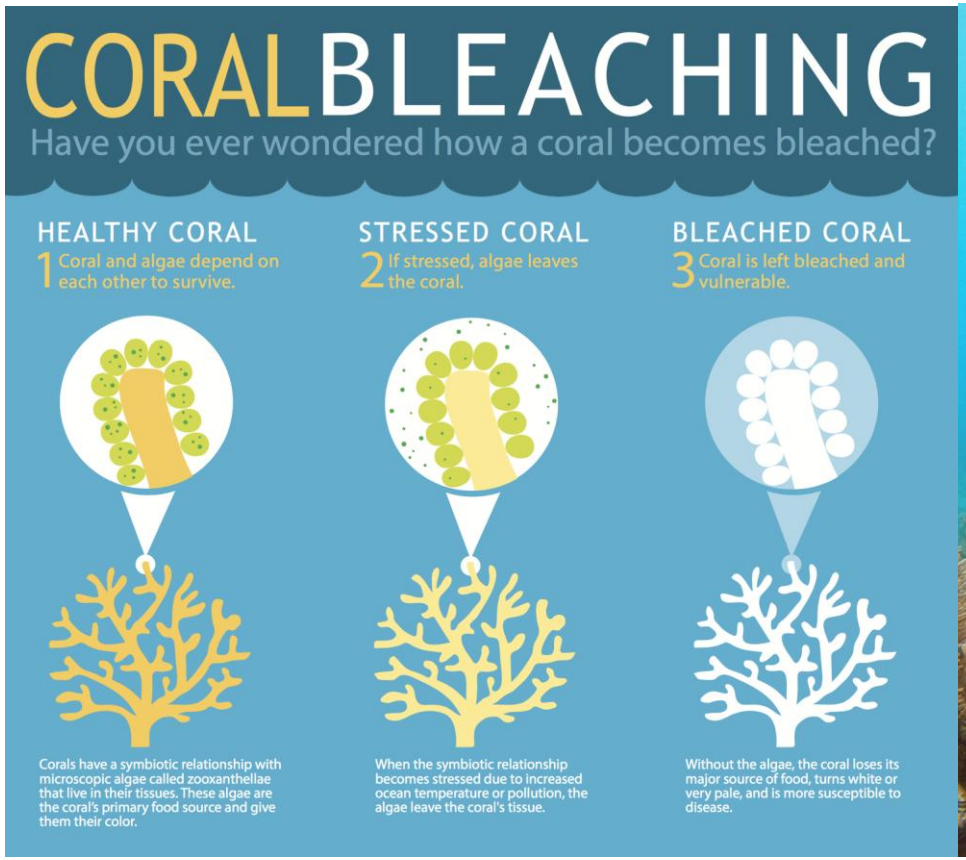
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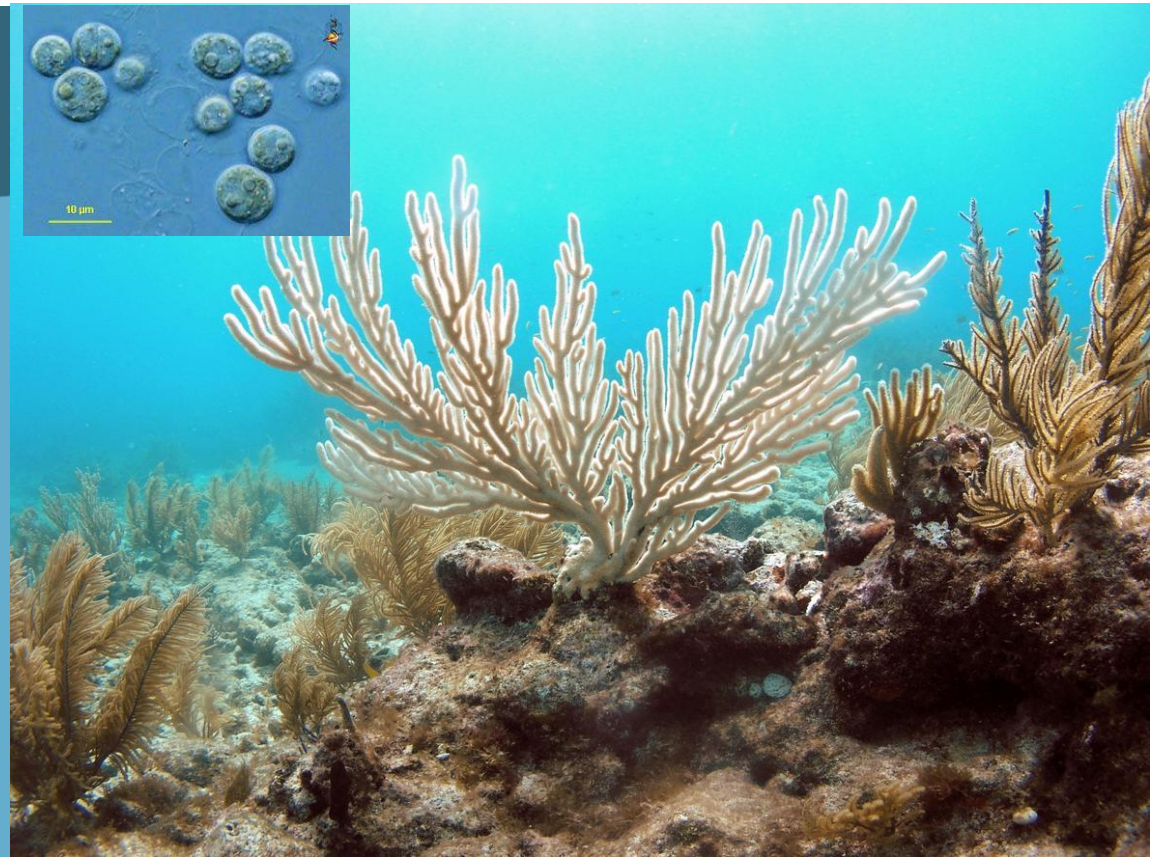


- Mycrorrhizae form critical mutualisms with plants
- Mycorrhizae are more efficient at obtaining nutrients
- Hyphae invade plant roots, receive carbohydrates from the plants in exchange for nutrients

Facilitation

- Mutualism
  - May be dispersive, defensive, resource-based, **endosymbiosis**





Facilitation

- Mutualism
  - May be dispersive, defensive, resource-based, **endosymbiosis**

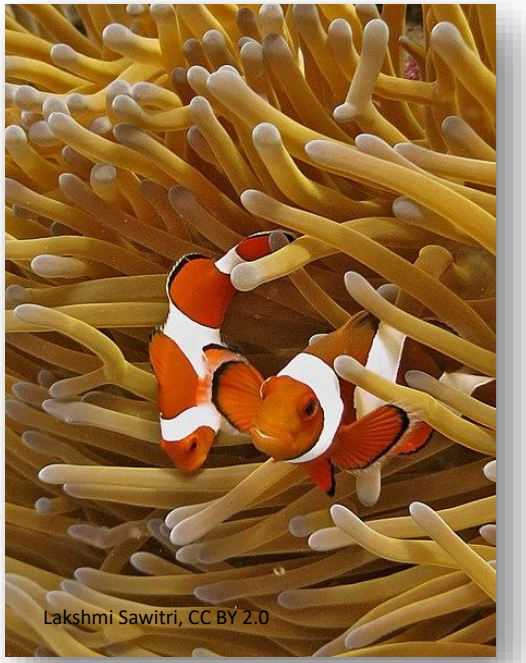


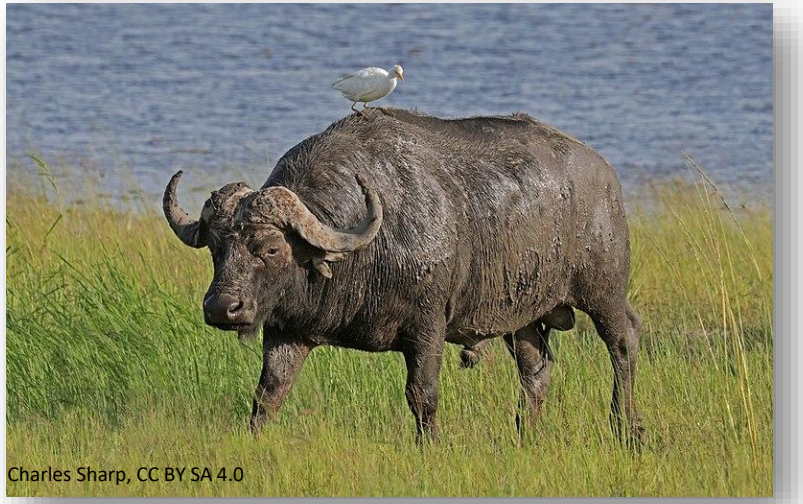
Lichens are a mutualism between a photosynthetic organism and fungi

Facilitation

- Commensalism
  - Common examples include organisms that hitch rides (sharks/remora), use other organisms for habitat without damaging them (e.g., epiphytes, clown fish/anemone), and bioturbation (cattle/cattle egrets)







Facilitation

- Evidence that plant mutualisms are more common in stressful environmental conditions

Positive interactions among alpine plants increase with stress

Ragan M. Callaway*, R. W. Brooker†, Philippe Choler‡, Zaal Kikvidze§, Christopher J. Lortie‖, Richard Michalet¶, Leonardo Paolini#, Francisco I. Pugnaire☆, Beth Newingham*, Erik T. Aschehoug*,, Cristina Armas☆, David Kikodze§ & Bradley J. Cook***

Hypothesized that plants at higher elevations would benefit more from neighboring plants, because of **facilitation**
(via provision of shade, protection from disturbance like wind, and herbivore protection, etc.)

Facilitation

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Tested their hypothesis with global experiment – removed neighboring plants at high and low elevation plots in 11 different locations

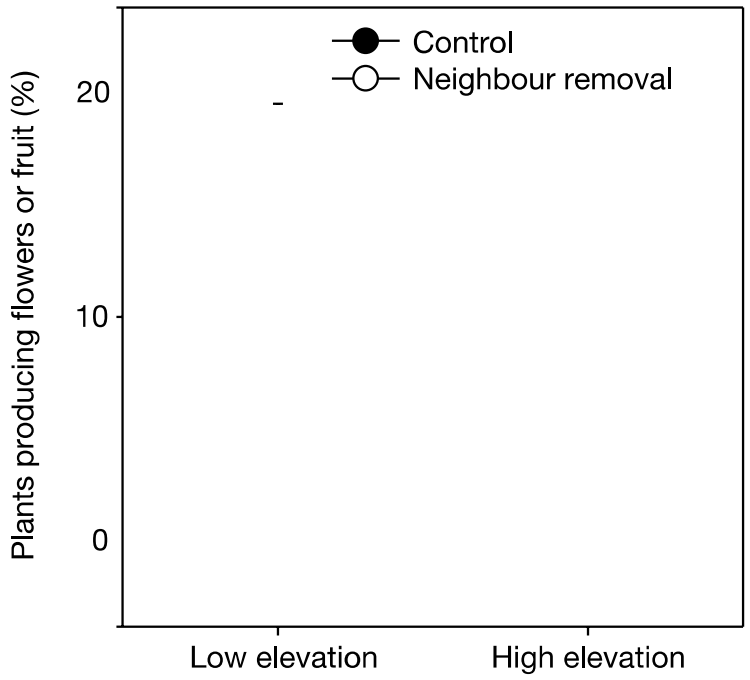
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Plants at high elevation (more stressful environment) produced *fewer flowers* when neighboring plants were removed



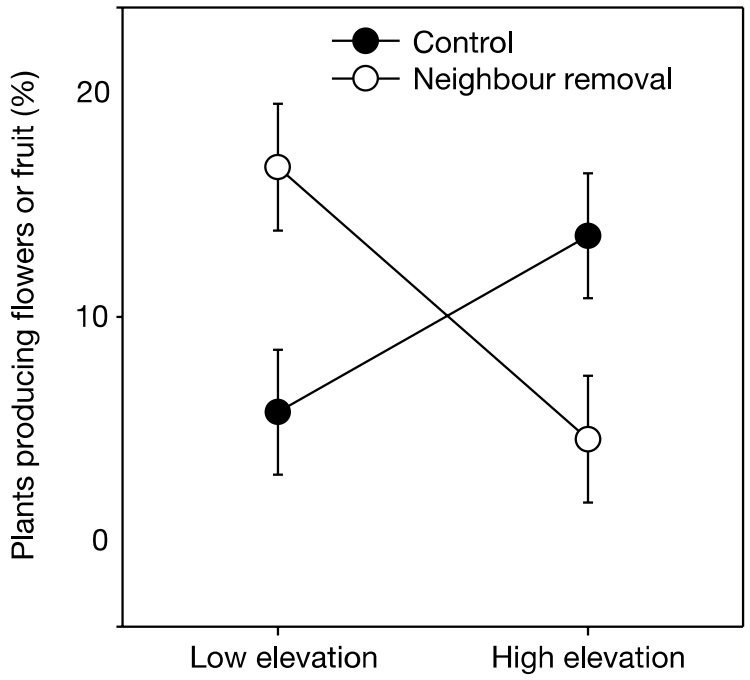
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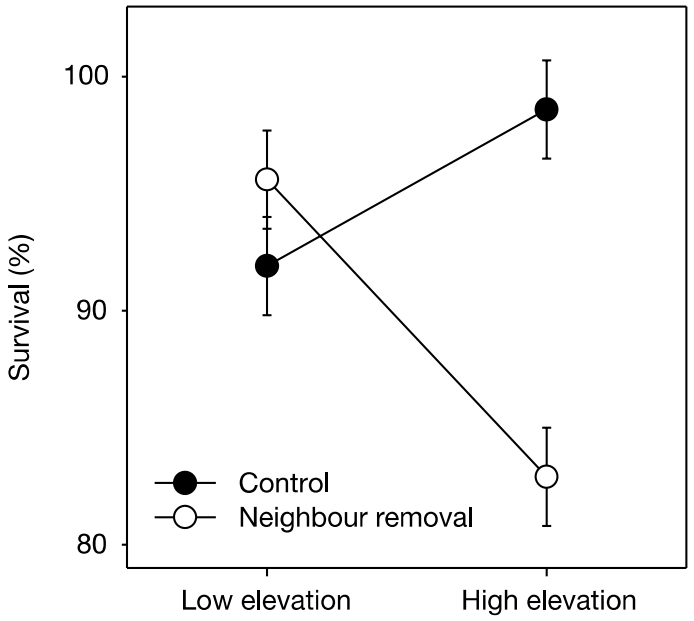
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Plants at high elevation (more stressful environment) had *reduced survival* when neighbors were removed



Topics for today

- Competition
  - Can be within the same species, or between different species
  - Types: interference, exploitation, apparent (also, amensalism, allelopathy)
  - One potential mechanism for species invasion is lack of natural enemies, allowing introduced species to outcompete natives
  - Lotka-Volterra models and R* concept help explain species coexistence
- Species coexistence (niche theory, resource partitioning)
- Facilitation
  - Mutualisms, commensalisms - several interesting examples
  - Facilitation in stressful environmental conditions might be more important than in ideal conditions.