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Competition
11 Competition

• Competition for Resources
• General Features of Competition
• Competitive Exclusion
• Altering the Outcome of Competition
A. G. Tansley did one of the first experiments on competition in 1917.

He wanted to explain the distribution of two species of bedstraw: *Galium hercynicum*, which was restricted to acidic soils, and *G. pumilum*, restricted to calcareous soils.
Tansley found that if grown alone, each species could survive on both acidic and calcareous soils.

But when grown together, soil type determined which would survive.

Tansley inferred that competition restricted the two species to particular soil types in nature.
Interspecific competition is an interaction between two species in which each is harmed when they both use the same limiting resource.

Intraspecific competition can occur between individuals of a single species.
Competition occurs between species that share the use of a resource that limits the growth, survival, or reproduction of each species.

Organisms compete for resources—features of the environment that are required for growth, survival, or reproduction, and which can be consumed to the point of depletion.
Examples of resources that can be consumed to depletion:

- Food.
- Water in terrestrial habitats.
- Light for plants.
- Space, especially for sessile organisms.
- For mobile animals, space for refuge, nesting, etc.
Figure 11.3  Space Can Be a Limiting Resource
Species are also influenced by factors that are not consumed, such as temperature, pH, salinity.

These factors are not considered to be resources.

**Physical factors** affect population growth rates but are not consumed or depleted.
Experiments using two species of diatoms (single-celled algae that make cell walls of silica, $\text{SiO}_2$) were done by Tilman et al. (1981).
Figure 11.4 Competing Organisms Can Deplete Resources (Part 1)

(A) Asterionella alone

(B) Synedra alone

ECOLOGY, Figure 11.4 (Part 1)
Figure 11.4 Competing Organisms Can Deplete Resources (Part 2)

(C) Interspecific competition

- **Silica concentration**
- **Asterionella**
- **Synedra**

![Graph showing population density and silica concentration over time for Asterionella and Synedra](image)
Competition should increase in intensity when resources are scarce.

Competition in plants might be expected to increase in importance when they are growing in nutrient-poor soils.

Using a perennial grass species, Wilson and Tilman (1993) were able to demonstrate this.
The grass species was transplanted into plots with and without nitrogen fertilizer added.

Each plot type had 3 treatments:

1. Neighbors left intact.
2. Neighbor roots left intact but neighbor shoots tied back.
3. Neighbor roots and shoots both removed.
Figure 11.5 A Resource Availability Affects the Intensity of Competition

(A)

Index of competition intensity

- Low nitrogen
- High nitrogen

Belowground competition
Aboveground competition
Total (Belowground and aboveground competition)
Figure 11.5 B Resource Availability Affects the Intensity of Competition
How important and widespread is competition in ecological communities?

Results from many studies have been compiled and analyzed to answer this question.

Schoener (1983) found that of 390 species studied, 76% showed effects of competition under some conditions; 57% showed effects under all conditions tested.
Connell (1983) found that competition was important for 50% of 215 species in 72 studies.

Gurevitch et al. (1992) analyzed the magnitude of competitive effects found for 93 species in 46 studies. They showed that competition had significant effects on a wide range of organisms.
Potential biases in these analyses include failure of researchers to publish studies that show no significant effects, and a tendency for investigators to study species they suspect will show competition.

Still, they document that competition is common, though not ubiquitous.
Competition, whether direct or indirect, can limit the distributions and abundances of competing species.

Competition is often classified into two general types:
**Exploitation competition:** Species compete indirectly through their mutual effects on the availability of a shared resource.

Competition occurs simply because individuals reduce the availability of a resource as they use it.

Examples: Trees competing for access to light; diatoms for nutrients
**Interference competition:** Species compete directly for access to a resource.

Individuals may perform antagonistic actions (e.g., when two predators fight over a prey item, or voles aggressively exclude other voles from preferred habitat).
General Features of Competition

Interference competition can also occur in sessile species.

Example: The acorn barnacle often crushes or smothers nearby individuals of another barnacle species as it grows. As a result, it directly prevents the other species from living in most portions of a rocky intertidal zone.
Allelopathy: A form of interference competition in which individuals of one species release toxins that harm other species.
It also releases a toxin called catechin into surrounding soils, which has been shown to reduce germination and growth of native grasses.

Cattle do not eat spotted knapweed, giving it an edge over native plants that cattle do eat.
Figure 11.6  Chemical Warfare in Plants (Part 2)

**B**

![Graph showing seed germination for Festuca and Koeleria with and without catechin treatment.](image)

**C**

![Graph showing biomass for Festuca and Koeleria with and without catechin treatment.](image)

- **Seed germination (%)**
  - **Festuca**: Catechin treated (0), Without catechin (60)
  - **Koeleria**: Catechin treated (40), Without catechin (20)

- **Biomass (g)**
  - **Festuca**: Catechin treated (0), Without catechin (1.5)
  - **Koeleria**: Catechin treated (0), Without catechin (2.0)

**ECOLOGY, Figure 11.6 (Part 2)**
General Features of Competition

For a resource in short supply, competition will reduce the amount available to each species.

In many cases the effects of competition are unequal, or asymmetrical, and one species is harmed more than the other.

Example: When one species drives another to extinction.
Competition can also occur between distantly related species.

In experiments with rodents and ants that eat the same seeds, Brown and Davidson (1977) set up plots with four treatments:
1. Wire mesh fence excluded seed-eating rodents.

2. Seed-eating ants were excluded by applying insecticides.

3. Both rodents and ants were excluded.

4. Undisturbed control plots.
Where rodents were excluded, ant colonies increased by 71%.

Where ants were excluded, rodents increased in both number and biomass.

Where both were excluded, the number of seeds increased by 450%.
Figure 11.7 Ants and Rodents Compete for Seeds

- **Rodents**
- **Ants**

The graph shows the percentage of seeds consumed by ants and rodents across different seed size categories (mm):<br>
- <0.64<br>- 0.64–0.69<br>- 0.70–0.82<br>- 0.83–0.98<br>- 0.99–1.16<br>- 1.17–1.39<br>- 1.40–1.63<br>- 1.64–1.97<br>- 1.98–2.35<br>- 2.36–2.78<br>- 2.79–3.32<br>- 3.33–3.95<br>- 3.96–4.69
When either rodents or ants were removed, the group that remained ate roughly as many seeds as rodents and ants combined ate in the control plots.

In natural conditions, each group would be expected to eat fewer seeds in the presence of the other group than it could eat when alone.
Competition can also limit distribution and abundance of species.

Connell (1961) examined factors that influenced the distribution, survival, and reproduction of two barnacle species, *Chthamalus stellatus* and *Semibalanus balanoides*, on the coast of Scotland.
Distribution of larvae of the two species overlapped throughout the upper and middle intertidal zones.

Adult distributions did not overlap: *Chthamalus* were found only near the top of the intertidal zone; adult *Semibalanus* were found throughout the rest of the intertidal zone.
Figure 11.8  Squeezed Out by Competition

Semibalanus

Chthamalus

High tide

Chthamalus adult distribution

Semibalanus adult distribution

Low tide

ECOLOGY, Figure 11.8
Using removal experiments, Connell found that competition with *Semibalanus* excluded *Chthamalus* from all but the top of the intertidal zone.

*Semibalanus* smothered, removed, or crushed the other species.

However, *Semibalanus* dried out and survived poorly at the top of the intertidal zone.
Competition can also affect geographic distribution.
Chipmunk species in the southwestern U.S. live in mountain forests.

Patterson (1980, 1981) found that when a chipmunk species lived alone on a mountain range, it occupied a broader range of habitats and elevations than when it lived with a competitor species.
Figure 11.9 A “Natural Experiment” on Competition between Chipmunks

Nevada

Ruby Mountains

Snake Range

Pilot Peak

New Mexico

Organ Mountains

Mt. Taylor

Magdalena Mountains

Neotamais umbrinus

Neotamais dorsalis

Neotamais quadrivittatus
If the overall ecological requirements of a species—its *ecological niche*—are very similar to those of a superior competitor, that competitor may drive it to extinction.

**Concept 11.3:** Competing species are more likely to coexist when they use resources in different ways.
In the 1930s, G. F. Gause performed laboratory experiments on competition using three species of *Paramecium*. Populations of all three *Paramecium* species reached a stable carrying capacity when grown alone. When paired, some species drove others to extinction.
Figure 11.10 Competition in *Paramecium* (Part 1)

(A) Population density (measured by volume) of *P. aurelia* over days.

(B) Population density (measured by volume) of *P. caudatum* over days.

(C) Population density (measured by volume) of *P. bursaria* over days.
Figure 11.10  Competition in *Paramecium* (Part 2)

(D)

![Graph showing population density of P. aurelia and P. caudatum](image)

(E)

![Graph showing population density of P. caudatum and P. bursaria](image)
**Competitive Exclusion**

*P. aurelia* drove *P. caudatum* to extinction. They may have been unable to coexist because both fed on bacteria floating in the medium.

*P. caudatum* and *P. bursaria* were able to coexist, although they were clearly in competition—the carrying capacity of both species was lowered.
P. caudatum usually ate bacteria floating in the medium, while P. bursaria usually fed on yeast cells that settled to the bottom.

Unless two species use available resources in different ways, one can go extinct.
The **competitive exclusion principle**: Two species that use a limiting resource in the same way can not coexist.

Field observations are consistent with this explanation of why competitive exclusion occurs in some cases, but not others.
Resource partitioning: Species use a limited resource in different ways.

Example: Four species of *Anolis* lizards on Jamaica live together in trees and shrubs and eat similar food.

Schoener (1974) found that the lizards used the space in different ways, resulting in a reduction in competition.
Figure 11.11 Resource Partitioning in Lizards

(A) Large Small

- Anolis opalinus
- Anolis grahami
- Anolis lineatopus
- Anolis valencienni

(B) Thick branches Thin branches
The competitive exclusion principle: Two species that use a limiting resource in the same way cannot coexist.
Derivation: Competition model
Competitive Exclusion

Competition was first modeled by A. J. Lotka (1932) and Vito Volterra (1926).

Their equation is now known as the Lotka–Volterra competition model.

\[
\frac{dN_1}{dt} = r_1 N_1 \left( \frac{K_1 - N_1 - \alpha N_2}{K_1} \right)
\]

\[
\frac{dN_2}{dt} = r_2 N_2 \left( \frac{K_2 - N_2 - \beta N_1}{K_2} \right)
\]
Competitive Exclusion

\[ N_1 = \text{population density of species 1} \]
\[ r_1 = \text{intrinsic rate of increase of species 1} \]
\[ K_1 = \text{carrying capacity of species 1} \]
\[ \alpha \text{ and } \beta = \text{competition coefficients—constants that describe effect of one species on the other.} \]
α is the effect of species 2 on species 1; 
β is the effect of species 1 on species 2.

α measures the extent to which the use of resources by an individual of species 2 decreases the per capita growth rate of species 1.

When α = 1, individuals of the two species are identical in their effects.
Box 11.1  What Do the Competition Coefficients $\alpha$ and $\beta$ Represent?

When $\alpha < 1$, an individual of species 2 decreases growth of species 1 by a \textit{smaller} amount than does an individual of species 1.

When $\alpha > 1$, an individual of species 2 decreases growth of species 1 by a \textit{larger} amount than does an individual of species 1.
Figure 11.12 Graphical Analyses of Competition

(A) \( \frac{K_1}{\alpha} \) vs. \( N_2 \)

- \( N_1^* \)
- \( N_1^A \)

- \( A \)

- Arrows indicating movement

(B) \( K_2 \) vs. \( N_2 \)

- \( N_1 \)
- \( \frac{K_2}{\beta} \)

- Arrows indicating movement
The straight lines are **zero population growth isoclines**: The population does not increase or decrease in size for any combination of $N_1$ and $N_2$ that lies on these lines.

Zero growth isoclines can determine the conditions under which each species will increase or decrease.
Figure 11.13 A, B  Outcome of Competition in the Lotka–Volterra Competition Model

(A)  
- $K_1/\alpha$  
- $N_2$  
- $K_2$  
- $K_2/\beta$  
- $N_1$  
- $K_1$

(B)  
- $K_2$  
- $N_2$  
- $K_1/\alpha$  
- $K_1$  
- $K_2/\beta$  
- $N_1$
When the isoclines do not cross, competitive exclusion results.

Depending on which isocline is above the other, either species 1 or species 2 always drives the other to extinction.
Figure 11.13 C, D  Outcome of Competition in the Lotka–Volterra Competition Model

ECOLOGY, Figure 11.13 (Part 2)
The Lotka–Volterra model supports the idea that competitive exclusion is likely when competing species require very similar resources.
Coexistence occurs when the values of $\alpha$, $\beta$, $K_1$, and $K_2$ are such that the following inequality holds:

$$\alpha < \frac{K_1}{K_2} < \frac{1}{\beta}$$

If $\alpha$ and $\beta$ are equal, and close to 1, the species are equally strong competitors, and have similar effects on each other.
Competitive Exclusion

Example: If $\alpha = \beta = 0.95$

$$0.95 < \frac{K_1}{K_2} < 1.053$$

Coexistence is predicted only within a narrow range of values for the carrying capacities, $K_1$ and $K_2$. 
Example: If $\alpha = \beta = 0.1$

$$0.1 < \frac{K_1}{K_2} < 10$$

Coexistence is predicted within a much broader range of carrying capacities.
Model assumptions

• Competition coefficients and carrying capacities are constant
• Linear density dependence
• Resources are in limited supply
• No genetic structure
• No age or size structure
• No time lag
• No I or E
Altering the Outcome of Competition

The outcome of competition can be altered by environmental conditions, species interactions, disturbance, and evolution.

Environmental conditions or species interactions (e.g., predation) can result in a competitive reversal—the species that was the inferior competitor in one habitat becomes the superior competitor in another.
Figure 11.14  Herbivores Can Alter the Outcome of Competition
Disturbances such as fires or storms can kill or damage individuals, while creating opportunities for others.

Example: Some forest plant species require abundant sunlight and are found only where disturbance has opened the tree canopy.

As trees recolonize and create shade, these plants can not persist in the patch.
Such species are called **fugitive species** because they must disperse from one place to another as conditions change.

The brown alga called sea palm coexists with mussels, a competitively dominant species, in the rocky intertidal zone because large waves sometimes remove the mussels, creating temporary openings.
On shorelines with low disturbance rates, competition runs its course, and mussels drive sea palms to extinction.
Figure 11.15 Population Decline in an Inferior Competitor

The diagram shows a graph with two lines and several data points. The x-axis represents Density (N/m²) in year x, ranging from 0 to 200. The y-axis represents Density (N/m²) in year (x+1), ranging from 0 to 80. The graph includes a red line and a blue line, with data points indicated by black circles. The title of the graph is "ECOLOGY, Figure 11.15."
Competition has the potential to cause evolutionary change, and evolution has the potential to alter the outcome of competition.

This interplay has been observed in many studies.
In spite of competition, natural communities contain many species sharing scarce resources.

Resource partitioning is one explanation for this.

Other mechanisms include environmental variation and disturbance. Species may coexist if different species are superior competitors under different environmental conditions.
Lecture end