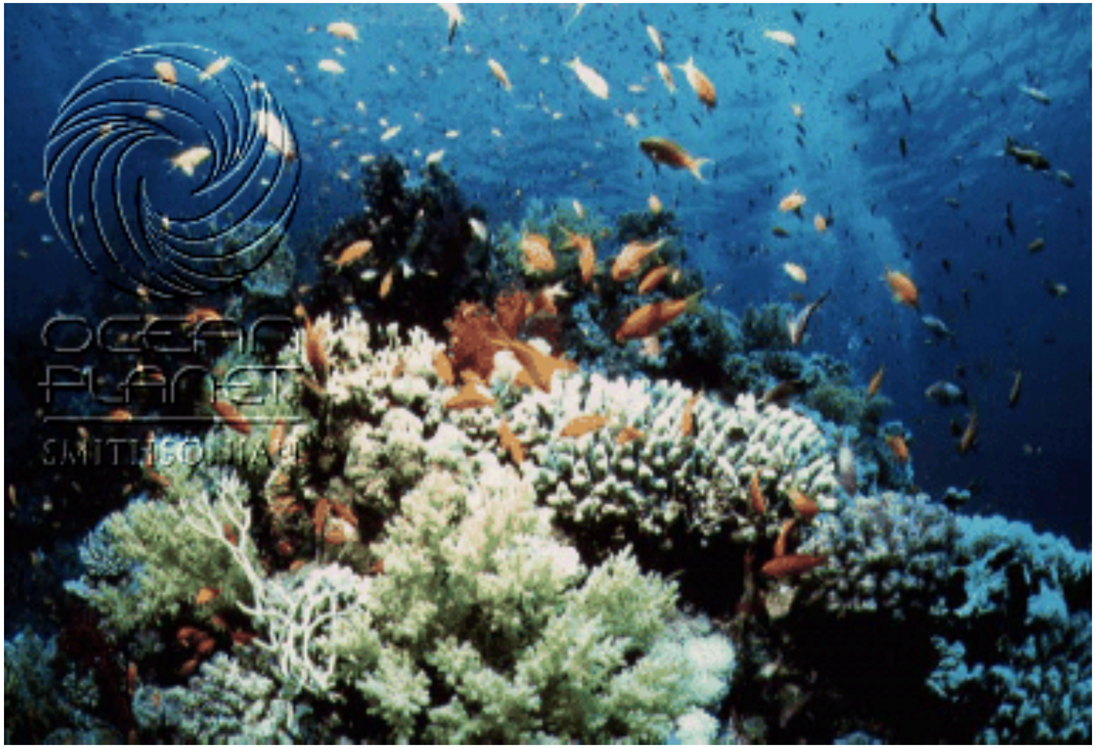
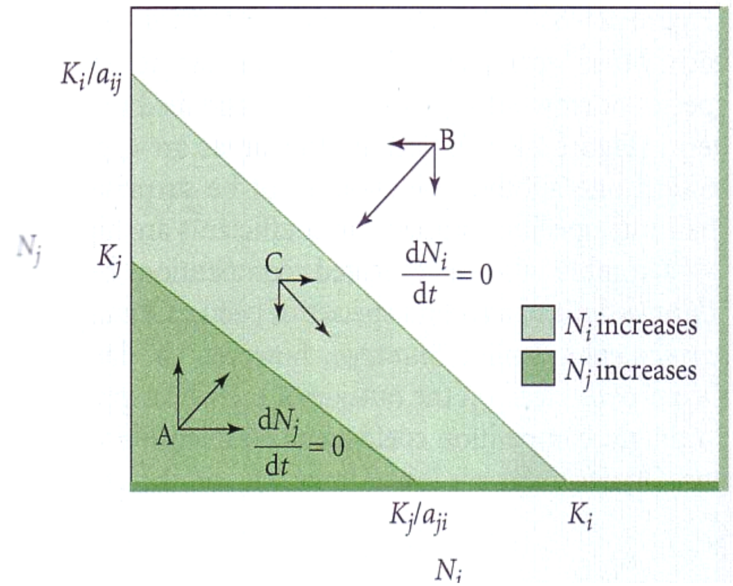




Ecology – Competition

Competitive Relationships in Natural Communities

How did we define *Symbiosis*?

- Symbiosis can be defined as the interaction or relationship between two species (or among several)
- This definition includes ***all*** types of biotic relationships that organisms may encounter in their community
- These relationships can be very subtle (as is true for many competitive interactions – our subject matter today)

Our possibilities again

Species 1 Species 2	+	0	-
+	Mutualism	Commensalism	Predator/Prey or Parasite/ Host
0	Commensalism	No Effect?	Amensalism
-	Predator/Prey or Parasite/ Host	Amensalism	Competition

Interspecific relationships

- In many ways, our consideration of the influence of one species on another is a matter of "degree"
- The more imposing or severe the impact, and the more it is an issue of life and death and therefore the greater the selective pressure – how do we measure this?
- First, let us look at resources

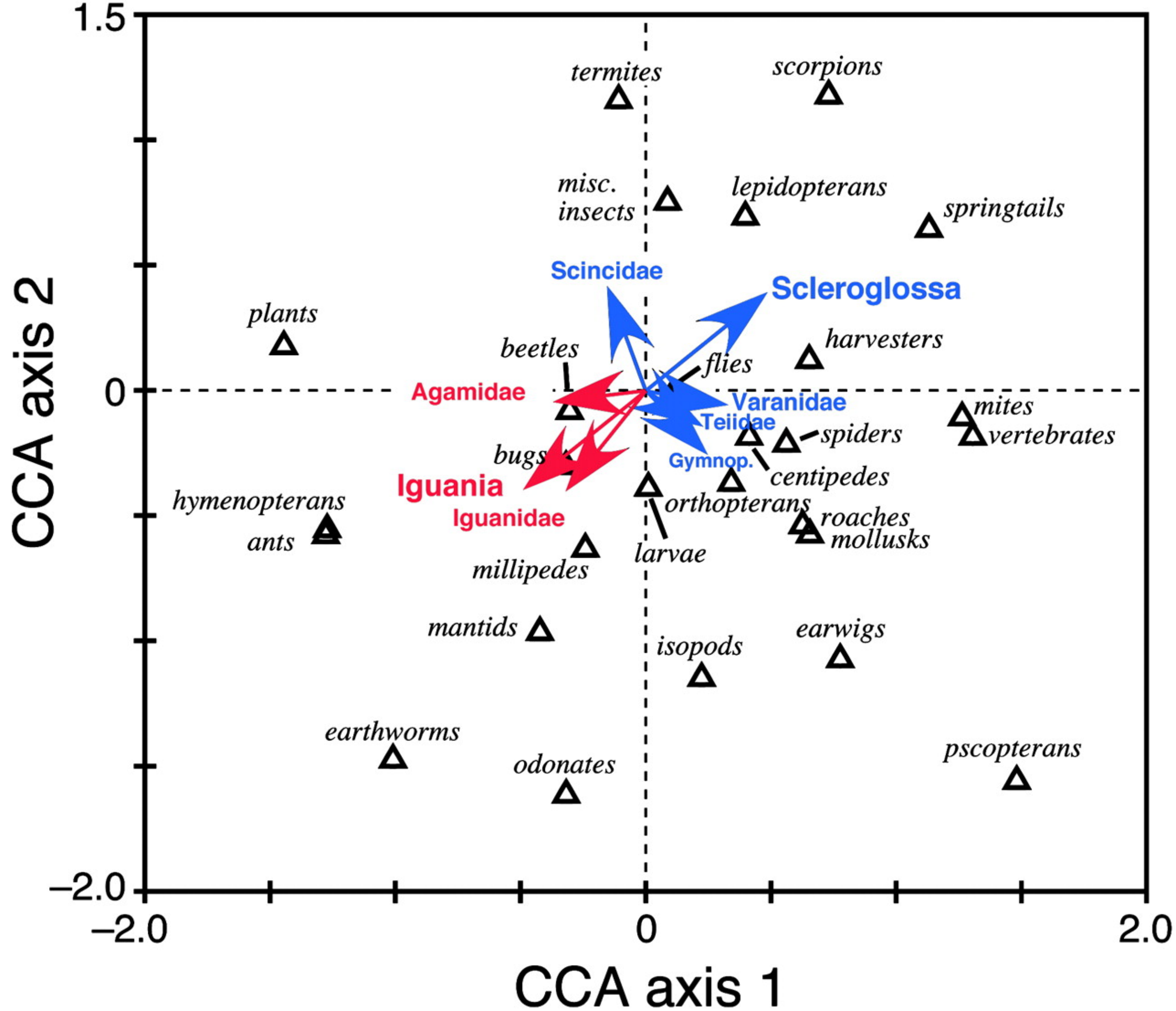
Resources

- What is meant by the term ***resource?***
- A resource is something that is required by the organism for survival and reproduction
- These can be renewable, or nonrenewable depending upon if these are constantly regenerated
- Example of a nonrenewable resource?

Limiting Resources

- We have not really faced the issue of an organism’s **niche** to this point
- How might we define the term niche?
- By the book – “the organism’s role in the community, which includes its required resources and conditions in which an organism lives” (this includes its role as prey or host too!)
- This is usually visualized as some *n*-dimensional space with regard to resources

We could also represent this with multivariate statistical tools



Historical treatment of resources

- One of the early considerations was in regard to the nature of limitations to population size in nature (intraspecific competition and logistic growth)
- When we are modeling such a system, it is often difficult to deal with multiple resources as limiting factors
- ***And***, not all limiting factors are resources – think back to our physiological ecology!

Consumers and Resources

- Consumers of resources come in a variety of forms – predators, parasitoids, parasites, herbivores and detritivores
- But at the basis of most symbiotic relationships, we have resources as the common denominator (and very often this is based on food)
- Competition is based on limited resource availability driving that interaction

What happens with two species experiencing limited resources?

- That is, what happens when two consumers are feeding on a single resource
- Well, ultimately, this use **reduces the level** of that resource in the environment
- From what we know already, what do we expect to happen to the populations of the competing species?

Evaluation of Competitive Relationships

- When we look at the competitive interactions between species, we can identify two broad categories of competition –
  - 1) Exploitive Competition
  - 2) Interference Competition
- What does each imply?
- Are there more detailed ways of looking at competitive interactions?

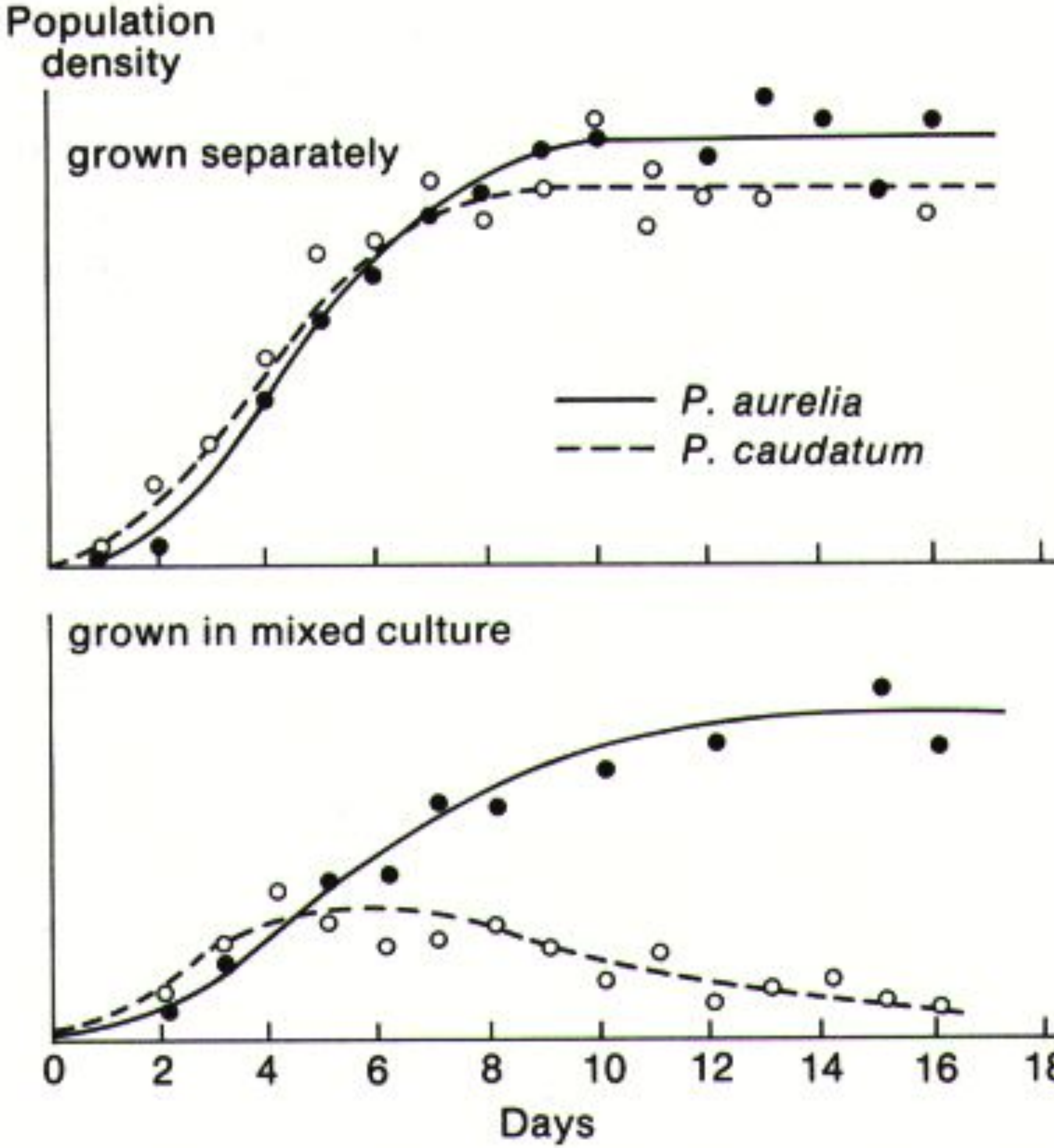
Foundations for Competition

- We can identify several different ways in which competition might occur
  - **Consumptive competition** – nutrient utilization
  - **Preemptive competition** – occupation of an open space
  - **Crowding competition** – limits a species by either crowding or covering another
  - **Chemical competition** – effect of toxin on neighbors (allelopathy)
  - **Territorial competition** – defense of a space
  - **Encounter competition** – chance or temporary events

Competition as a real phenomenon

- Early treatments of symbiosis and the relationships among organisms did not consider competition as an important factor
- Experimental work by Tansley and Gause provided evidence to the contrary, identifying competition as one of the primary factors that is either **shaping or "has shaped"** the structure of the community


μm


Population density
grown separately
P. aurelia
P. caudatum
grown in mixed culture
0
2
4
6
8
10
12
14
16
18
Days

When we consider competition -

- We are looking at a relationship *limiting* the species involved in this interaction – by definition
- The question becomes, how good are the respective species at their jobs? That is, in evaluation of their competitive abilities, is one a better competitor than the other?
- Now, what are we getting at with this question?

We want to predict the ***outcome***

- In a general sense, there are two alternatives; either one is a better competitor than the other and the inferior competitor is driven to extinction, or the two competitors find a way to coexist
- The former situation is the competitive exclusion principle, a.k.a. Gause's Principle – ***two species with similar ecologies cannot live together in the same place at the same time*** (i.e. they cannot occupy the same ecological niche)

This sounds great, right?

- However, we often see very similar species coexisting in nature. So what about the competitive exclusion principle?
- Two species with the ***identical ecological niches*** cannot coexist
- Realistically, two species that use the same resource will differ in other respects – but, are they different enough?

Let us look at the modeling of this

- From our earlier work on population growth, we know the predicted rate of population growth based upon the logistic model
- Here, we are considering *intraspecific* competition for species *i*

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i \left(1 - \frac{N_i}{K_i}\right),$$

But in the general sense…

- We are generally concerned with the effect of one species on another, that is *interspecific* competition
- Just as with intraspecific interactions, we are looking at limitations in the resource base, whatever form that might take

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i N_i \left(1 - \frac{N_i}{K_i} - \left[\begin{array}{c}\text{competitive effect}\\ \text{of } j \text{ on } i\end{array}\right]\right). \tag{21-2}$$

Now, look specifically

- The rate of population growth for species ***i*** is given by:

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i} - \frac{a_{ij} N_j}{K_i}\right),$$

- The rate of growth for species ***j***:

$$\frac{dN_j}{dt} = r_j N_j \left(1 - \frac{N_j}{K_j} - \frac{a_{ji} N_i}{K_j}\right).$$

What does the relative magnitude of the competition coefficient suggest about the impacts on the respective species?

Now, what are the possibilities?

- Well, we already know the possible outcomes; species ***i*** outcompetes species ***j*** and ***j*** goes extinct, species ***j*** outcompetes species ***i*** and ***i*** goes extinct, or they coexist
- We can look at this graphically and look at the conditions in which these possibilities might occur

Soooo, what is the bottom line?

- What are the conditions for a ***stable*** system of coexistence?
- And, qualitatively, what does that suggest about the level of inter- vs. intraspecific competition?
- This is really powerful stuff! We can predict population growth rates of multiple species based upon the influences of species on one another

But not always…

- We cannot always make predictions about outcomes, even with the best modeling
- We can look at situations and recognize that sometimes the starting conditions will dictate the results of competition
- Sometimes physical conditions will define the winners and losers
- And sometimes, there are ***outside*** forces at work in the community – any thoughts?

First, let us consider a predator

- That is, the effect of a predator on the growth of a given species or species pair in a symbiotic relationship
- Now, we are considering more of the actual influencing factors in a given environment
- And as you would expect, this is another *restricting* force with regard to growth

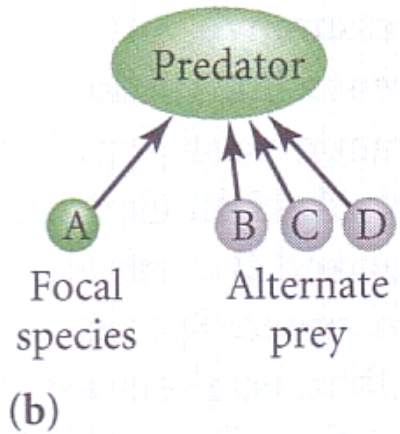
The whole point to this argument

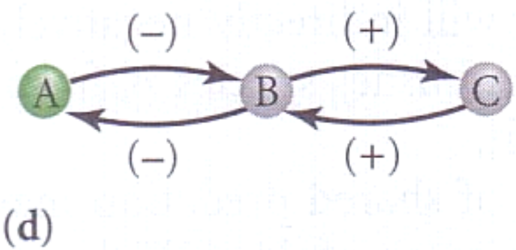
- “Simple” competition could result in the competitive exclusion of one species
- However, the prey species will be limited (or may be limited) by the influences of the predator
- This ultimately reduces the potential for exclusion of the inferior competitor(s). So, what does that mean to the superior competitor?

Let us return to our subject and consider *Apparent* Competition

- These are situations where interactions exist between species that are in fact negative in nature, but not competition for resources
- These relationships may result from interactions with a common predator or with another potential competitor
- And, these relationships can be direct or indirect

The influences of predation





Break Time

Now, what about the environment?

- Back to our model – the logistic growth predictions inherently include some level of stability
- But, what would environmental unpredictability add to our considerations?
- Look at this on a different level – what about anthropogenic disturbances to habitats?

Environmental Variability

- The variability associated with some environments leads to a situation of density-independent population limitations
- That is, the random fluctuations in unpredictable environments may result in the chance elimination of a population of individuals – and this could be the superior competitors
- The inferior competitors may be spared the influence due to competition

Habitat Disturbance

- Anthropogenic activities may have profound effects on the habitats of species in nature, depending upon the particular habitat under consideration
- Aside from the direct introduction of exotics or extinctions of forms, the changes of the physical environment (habitat destruction) often yield conditions very different from the norm

Evidence for Competition

- There are several issues that are persistent critiques of competition theory
  - First the complicating factors associated with interactions (e.g. predation) may not be competition at all, but *apparent competition*
  - Second, evaluation of the levels of competition in an interspecific and intraspecific sense is quite difficult
  - Third, the nature of the limiting resource or resources is difficult to identify
  - Finally, we observe, typically, the **results** of these interactions, not the interactions *per se*

Review of the modes of competition

- We can identify several different ways in which competition might occur (please note many of these can be exploitive ***or*** interference)
  - Consumptive competition – nutrient utilization
  - Preemptive competition – occupation of an open space
  - Crowding competition – limits a species by either crowding or covering another
  - Chemical competition – effect of toxin on neighbors (allelopathy)
  - Territorial competition – defense of a space
  - Encounter competition – chance or temporary events

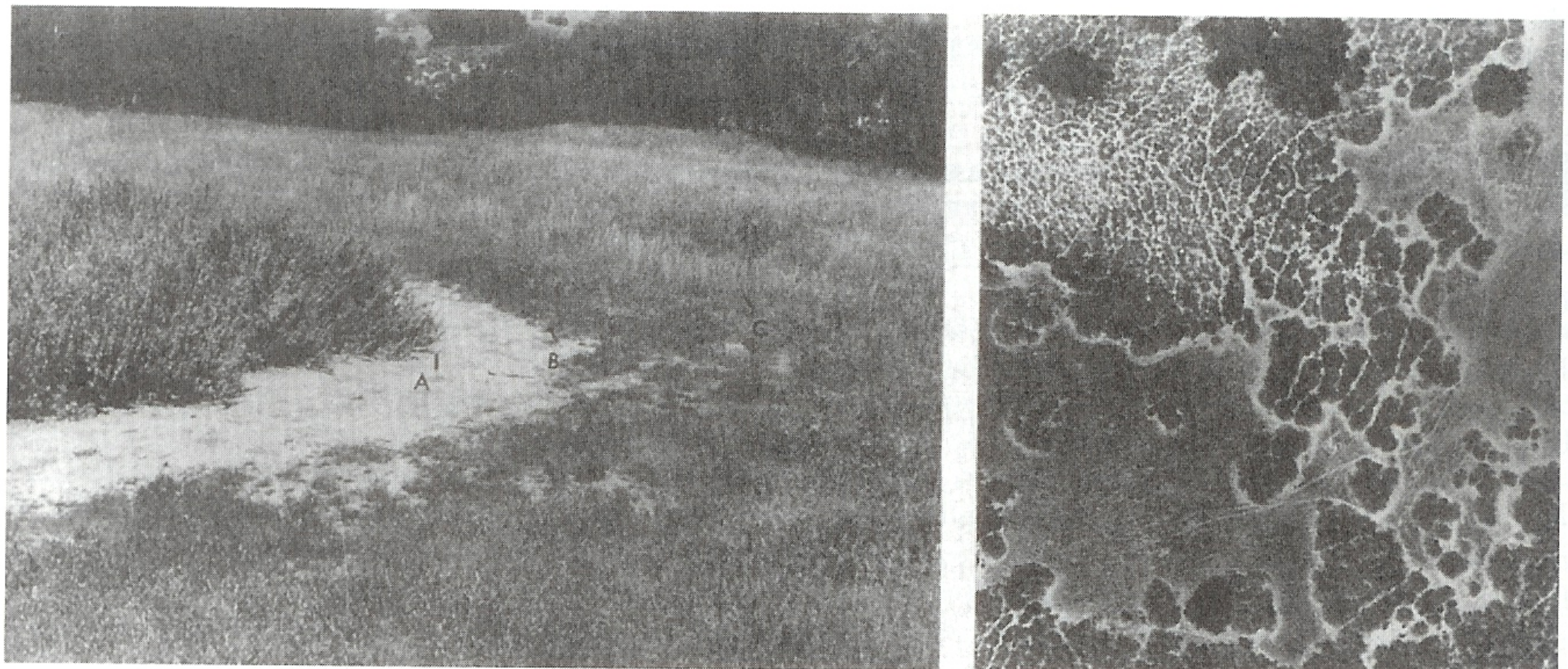
So, what do field studies suggest?

TABLE 22-1 A survey of proposed mechanisms of interspecific competition in experimental field studies

	Mechanism						
Group	Consumptive	Preemptive	Overgrowth	Chemical	Territorial	Encounter	Unknown
Freshwater							
Plants	0	0	1	1	0	0	0
Animals	13	1	0	1	1	5	2
Marine							
Plants	0	6	4	1	0	0	0
Animals	9	10	6	0	7	6	0
Terrestrial							
Plants	28	3	11	7	0	1	9
Animals	21	1	0	1	11	15	6
Total	71	21	22	11	19	27	17

(Data from Schoener 1983.)

Evidence for allelopathy?



(a) (b)

FIGURE 22-1 (a) Bare patch at edge of a clump of sage includes a 2-meter-wide strip with no plants (A-B) and a wider area of inhibited grassland (B-C) lacking wild oat and bromegrass, which are found with other species to the right of (C) in unaffected grassland. (b) Aerial view shows sage and California sagebrush invading annual grassland in the Santa Inez Valley of California. (*Courtesy of C. H. Muller; from Muller 1966.*)

Best evidence for competition?

- Unfortunately, some of the best evidence for competition is due to the introduction of exotic species
- Sometimes this is intentional, e.g. for the control of pest species
- And sometimes this is by accident as in the introduction of many “hitch-hiker” species

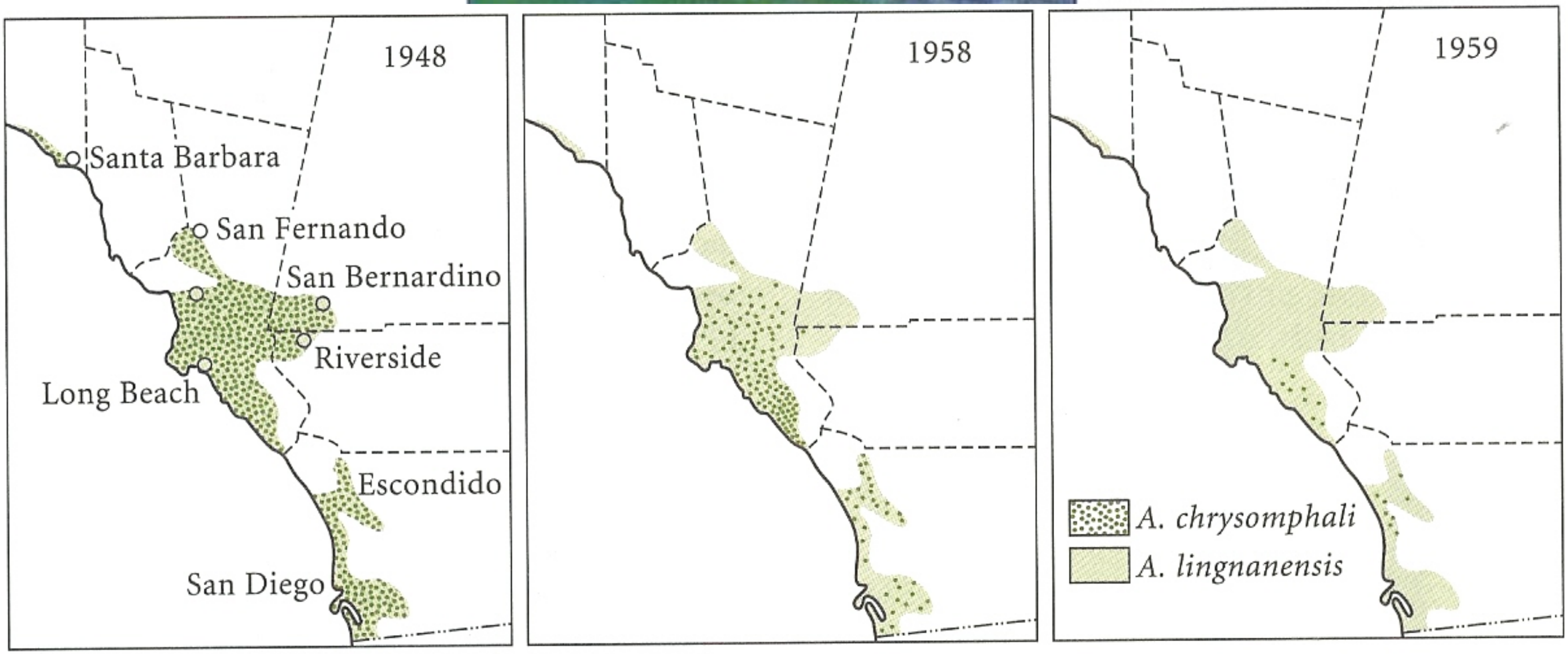


FIGURE 22-4 Successive changes in the distribution of *Aphytis chrysomphali* and *A. lingnanensis*, wasp parasites of citrus scale, in southern California. *A. lingnanensis* was first released in 1948 and rapidly replaced *A. chrysomphali* throughout the region. (*After DeBach and Sundby 1963.*)

Experimental manipulations

- Experiments have also provided valuable evidence regarding competition
- The organisms used in these studies include both plant and animal species in control and manipulation studies
- Of interest are the various levels at which competition can occur and sometimes these are very subtle effects

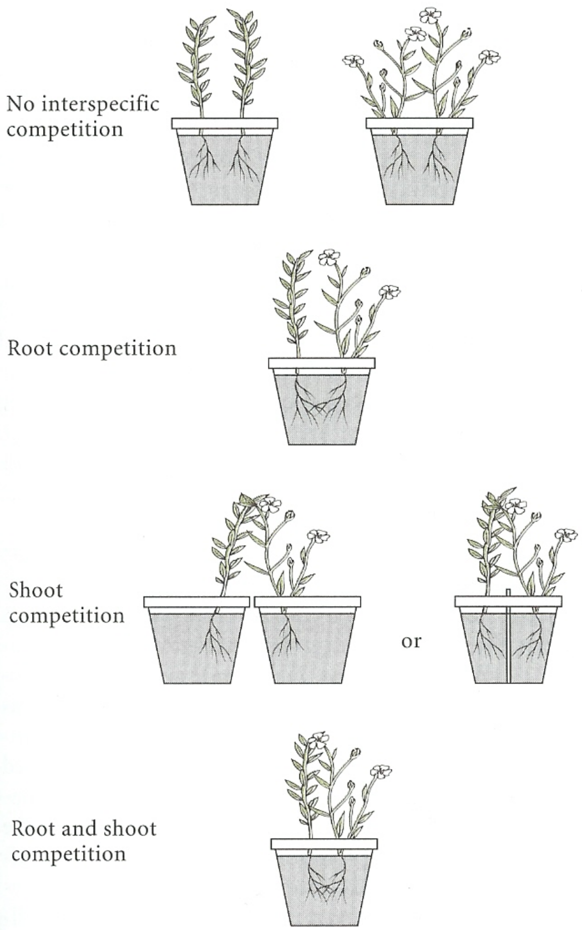


FIGURE 22-8 Experimental method for examining the relative strengths of root and shoot competition between two species of plants. Interspecific competition may be eliminated by placing plants of each species in separate pots. (Intraspecific competition is controlled by using the same density in each plot; see Figure 22-13.) Root competition in the absence of shoot competition is arranged by placing competing plants in pots in such a way that the leaves of the plants are not in close proximity to each other. Shoot competition in the absence of root competition is created by placing two pots close together or by partitioning the soil of a single pot so that the roots do not compete. Root and shoot competition together occur when the plants are placed close to one another in a single pot. (*After Silvertown and Doust 1993.*)

Look at the potential effects between species on two levels, shoot competition and root competition. Both can be very important contributors to the outcome of an interaction

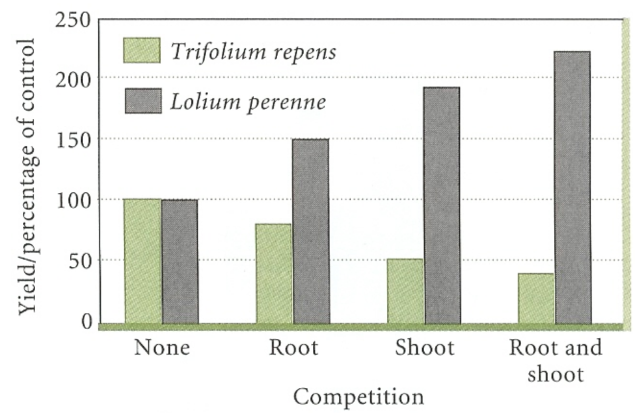


FIGURE 22-9 Results of an experiment to determine the relative effects of root and shoot competition between white clover (*Trifolium repens*) and a perennial ryegrass (*Lolium perenne*). The measure of interest is the yield as a percentage of the yield of control plants (no root or shoot competition), which is shown in the graph as 100%. The results indicate that the ryegrass wins in both root and shoot competition. (*From Martin and Field 1984.*)

It is not just growth!

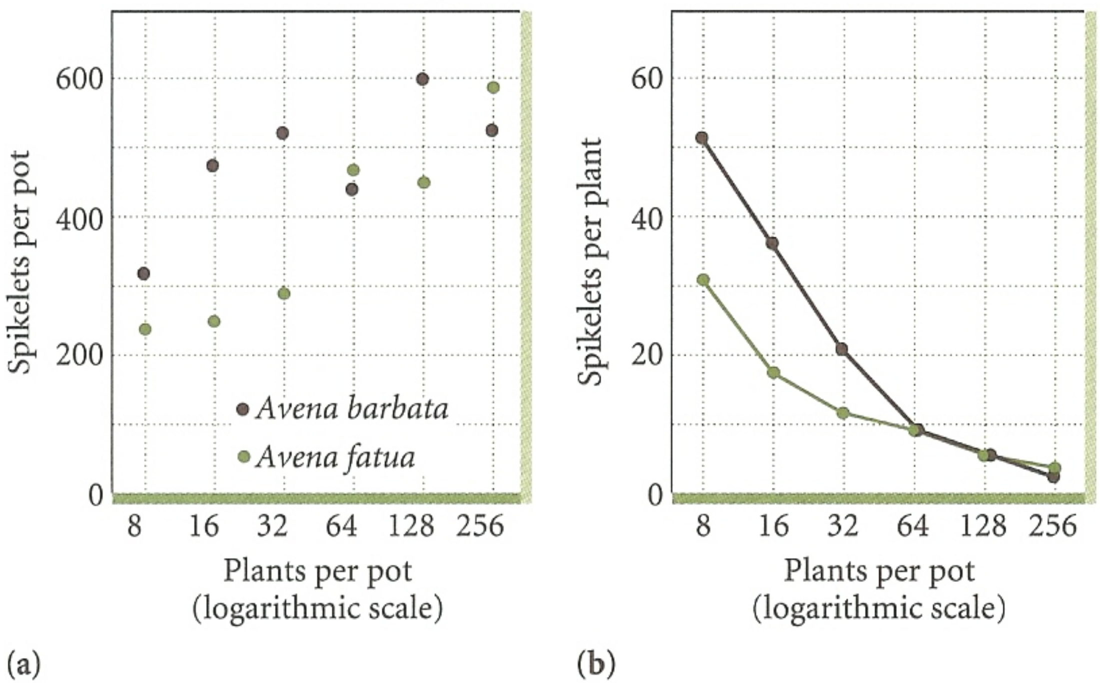


FIGURE 22-13 When pure cultures of two species of oats (*Avena*) were planted at different densities, the total number of spikelets per pot (a measure of reproductive output) increased with density (a), but the number of spikelets per plant decreased (b). (*After Marshall and Jain 1969.*)

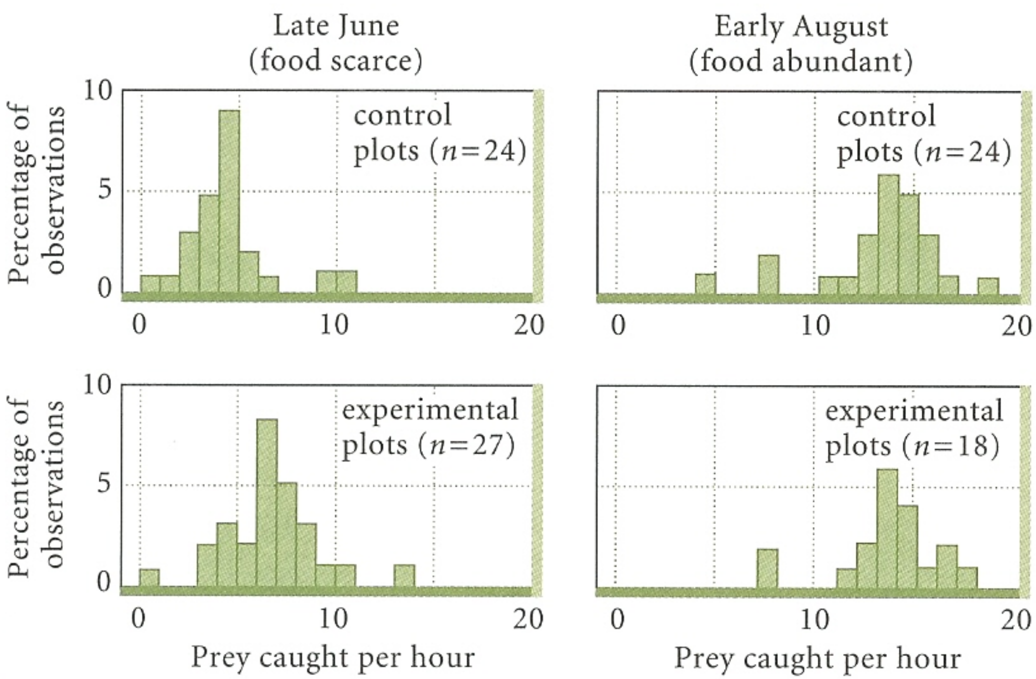


FIGURE 22-19 Feeding rates of adult male *Urosaurus ornatus* on experimental plots from which *Sceloporus merriami* were removed and on unmanipulated control plots. These results suggest that the intensity of the competition between these species is greater when food is limited. (*From Dunham 1980.*)

We must also consider coexistence

- A sometimes false assumption of our models is that there is extinction of one of the taxa involved in the relationship, but as we know from observations, that is not necessarily true
- One situation is where the competing species have a lesser effect on one another than they do on themselves
- But even if the nature of the relationship would suggest the extinction of one of the species, that is not always the case

Distribution of Barnacles

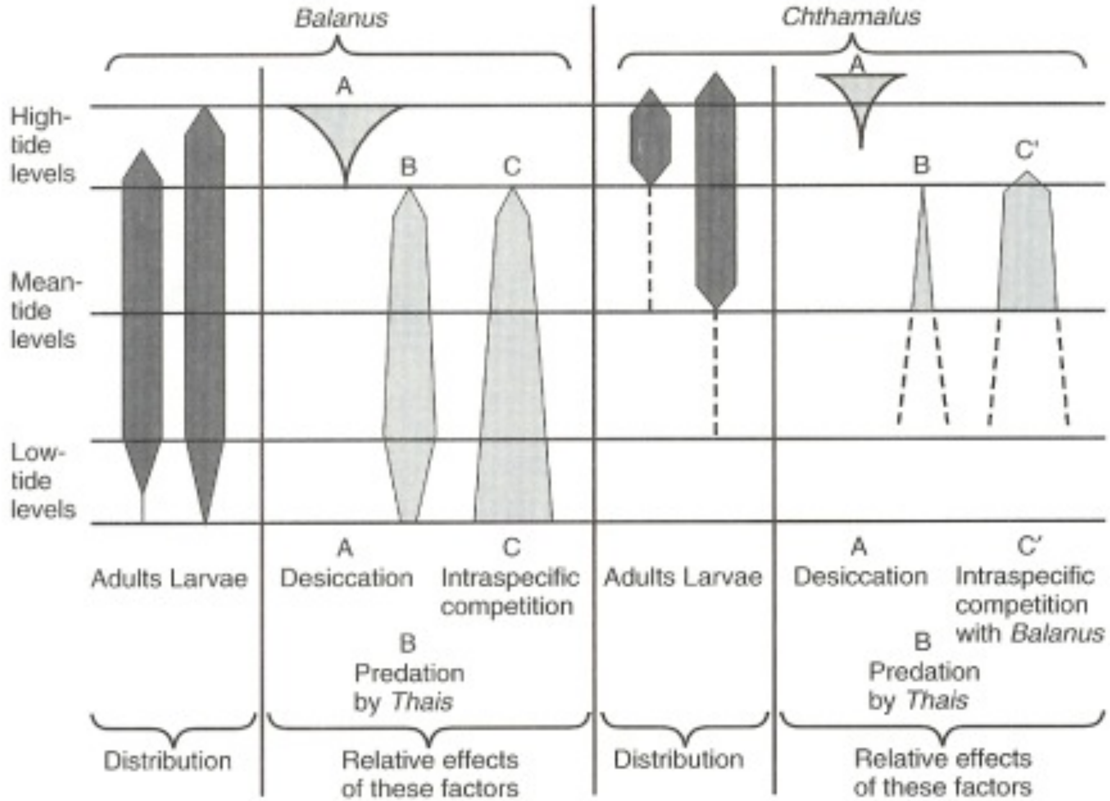


FIGURE 14.5 The distribution of adult and newly settled larvae of two species of barnacles. The upper limit to the distribution is set by desiccation, while the lower limit is set by a combination of competition for space and predation by a species of snail.

Source: Redrawn from Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–23.

This is Resource Partitioning

- Here we need to talk about niches again and the recognition that the niche we generally consider is based upon observational information regarding that organism
- It is important here to distinguish the differences between the ***potential*** niche and the ***realized*** niche. What do these mean?

A related concept is…

- **Character displacement** is the observation that characteristics are more divergent in sympatric populations of two species than in allopatric populations of the same two species
- These changes are coevolution in action, where the species involved in a competitive relationship (either one or both) change in response to resource limitations in the environment

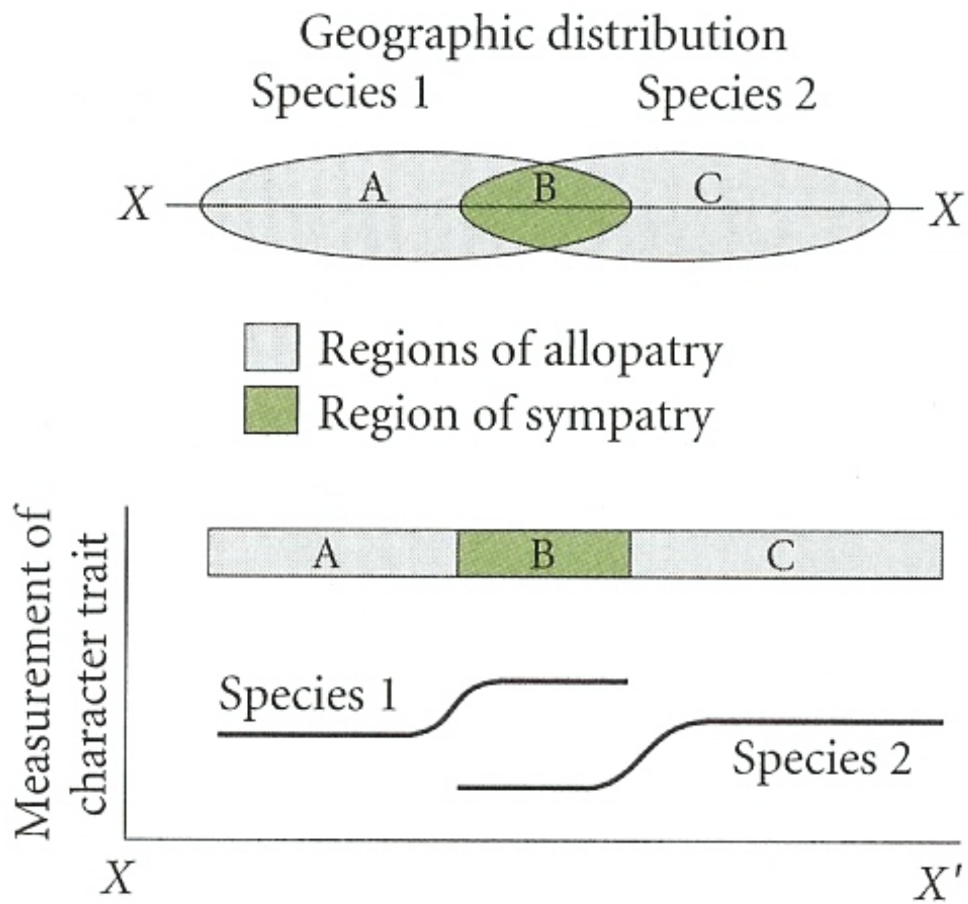


FIGURE 22-25 The phenomenon of character displacement, in which character traits of two closely related species differ more where they occur in sympatry than in allopatric portions of their geographic ranges.

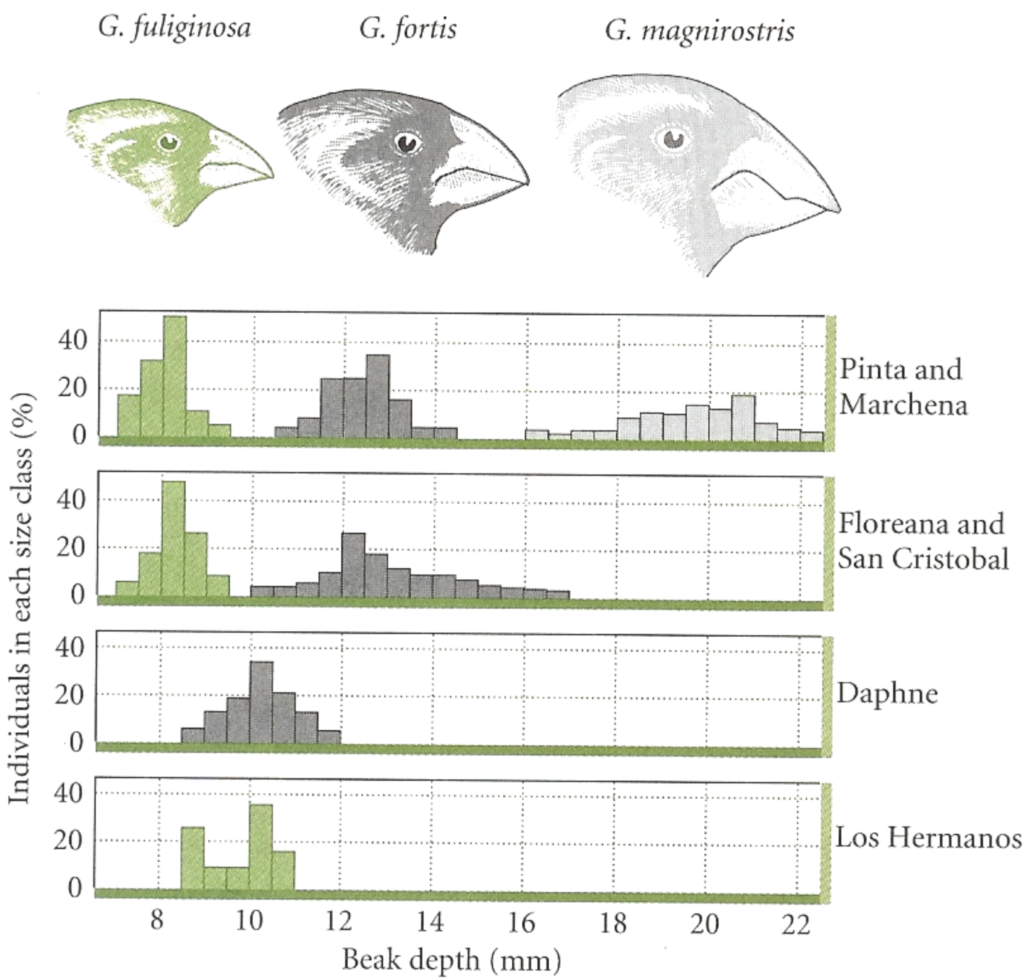


FIGURE 22-26 Proportions of individuals with beaks of different sizes in populations of ground finches (*Geospiza*) on several of the Galápagos Islands. This pattern is a possible example of character displacement. (*After Lack 1947.*)