INTRASPECIFIC competition – the main mechanism for density-dependent population regulation – can to reduced population growth by affecting birth or death rates when some resource becomes limiting. **INTER**SPECIFIC competition may do more than simply slow a populations growth.

Experiments by Gause with *Paramecium* species in lab culture in early 20th century: with constant environment and food supply, each species, grown alone, shows something like logistic growth to carrying capacity. When they are grown together in mixed culture, *P. aurelia* always drives *P. caudatum* to extinction. (NOTE, however, that the effects of competition on population growth are seen ONLY when populations are large enough that resources become limiting). From these studies, Gause formulated what has come to be known as the 'Principle of Competitive Exclusion'. If two species are too similar they're unlikely to coexist because one will prove the superior competitor. More rigorously*: Two populations can't coexist if actively limited by the same resource*. Whichever is the most efficient user of that resource will out-compete the other. Note that this allows coexistence if populations are regulated by something other than resource competition EVEN IF they're very similar.

Competition between two species of flour beetles of the genus *Tribolium* at different temperatures and relative humidities
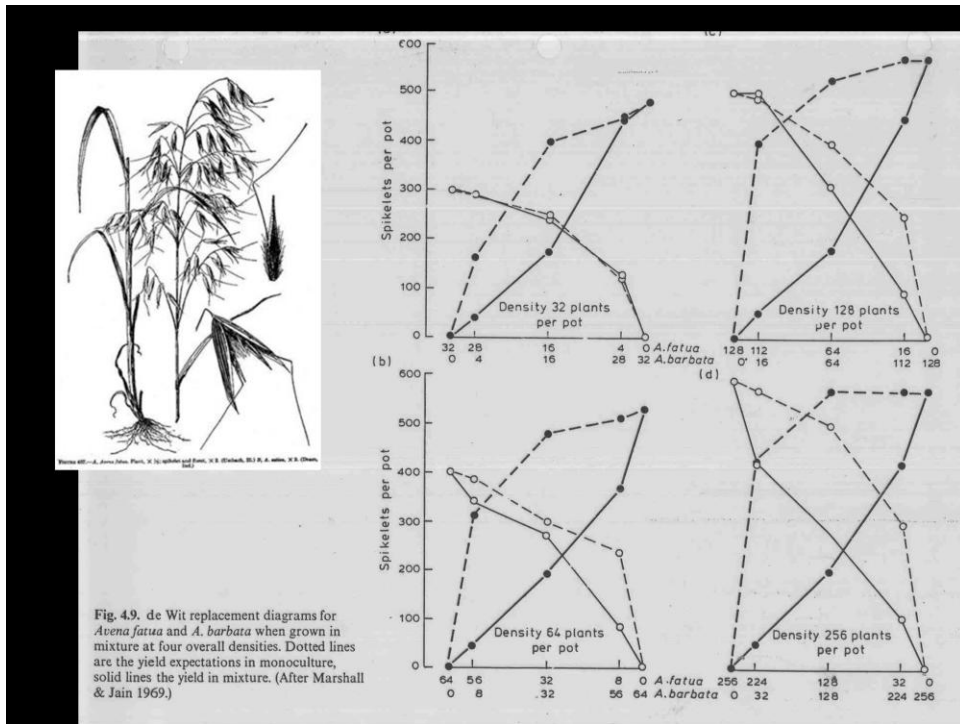
Temperature	Humidity	EQUILIBRIUM POPULATION SIZE*		PERCENTAGE OF CONTESTS WON BY†	
		T. confusum	*T. castaneum*	*T. confusum*	*T. castaneum*
Cool	Dry	26.0	2.6	100	0
	Moist	28.2	45.2	71	29
Moderate	Dry	29.7	18.8	87	13
	Moist	32.9	50.1	14	86
Warm	Dry	23.7	9.6	90	10
	Moist	41.2	38.3	0	100

*Number of adults, larvae, and pupae per gram of flour.
†Based on 20–30 contests in each combination of temperature and humidity.
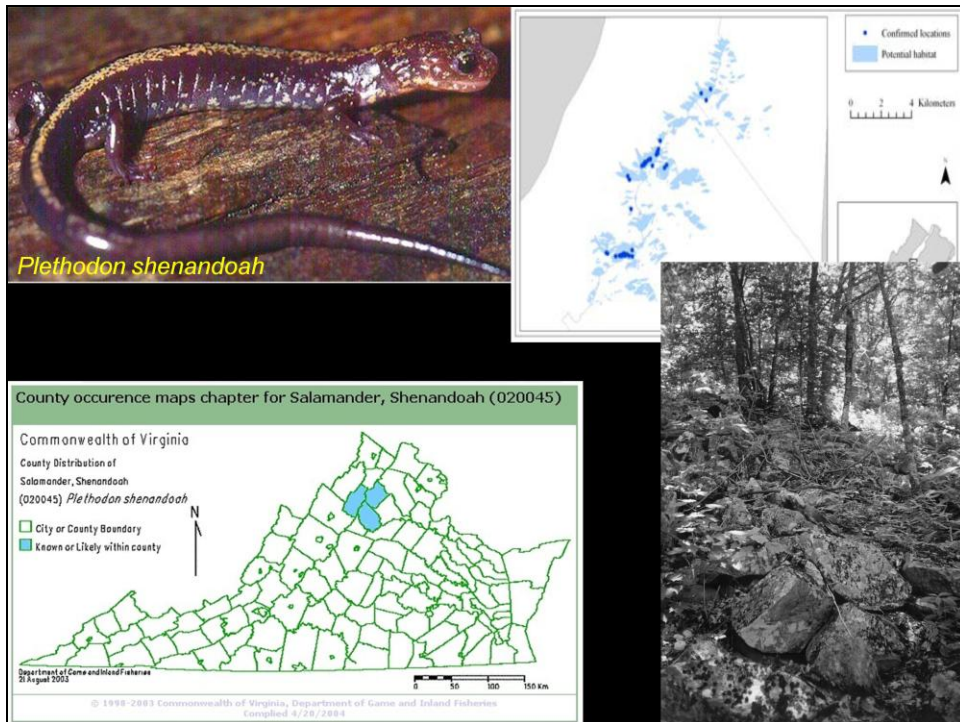(Data from Park 1954, 1962.)

The potential for competitive exclusion was further explored in the lab by Park in the 1950s. He used two species of 'stored grain products beetles' (genus *Tribolium*) to explore the possibility of coexistence, but found that, in uniform habitats (flour barrels at any particular temperature and humidity), one or the other species would ultimately 'win' and the other would be eliminated. Competitive exclusion again. What was more interesting was that *which* species won was not the same in all conditions, but was to some extent *predictable*. In cool, dry conditions, *Tribolium confusum* always won; in warm, moist cconditions, *T. castaneum* always won. In intermediate conditions there could be some uncertainty as to which would win, but one or the other species always did eventually displace the other. These results suggest that competitive ability can be influenced by environmental circumstances, and that there may be **trade-offs**; species that are particularly strong competitors in some circumstances may, as a consequence be *less effective* competitors elsewhere; each species *specializes* in doing one sort of things. This kind of thinking will come up again in the context of *life-history theory.*

Fig. 4.9. de Wit replacement diagrams for *Avena fatua* and *A. barbata* when grown in mixture at four overall densities. Dotted lines are the yield expectations in monoculture, solid lines the yield in mixture. (After Marshall & Jain 1969.)

A classic, elegant experiment that offers yet deeper insight into the effects of *interspecific competition*. The study uses two closely related (and therefore presumed to be ecologically rather similar) annual grasses. What might you expect concerning effects on one another of *similar* species (as compared to very different species)? The experimental design controls for overall density of individual plants in terms of effect on plant growth; this allows researchers to tease apart the effects of *intraspecific* and *interspecific* competition. Here, the measure of population growth or vigor is the number of spikelets (seed-bearing structures) per pot – a measure of reproductive output. Each graph shows results of experiments using constant *total* plant density (different density in each graph), but comprised of different proportions of the two species. The solid lines show spikelet production in these mixed plantings. The dashed lines show what each species would do if the same number of plants were planted WITHOUT the other species (e.g., instead of 112 of *A. fatua* and 16 of *A. barbata* – upper right – just 16 of *A. barbata* for the second filled circle on dashed line.). This type of experiment also shows a strong 'winner' or dominance by one species (probably would result in full competitive displacement over a few growing seasons at higher densities)

But testing for competition and potential competitive exclusion *in nature* is difficult because it is extremely difficult to control for other factors than competition that might limit occurrence of species. You must establish that presumed competitors would have higher r (lower death rate or higher birth rate) if competition were removed *and nothing else altered*. Here (on a mountain range in Nevada), a working hypothesis is that bristlecone pine is a superior competitor on the light-colored limestone in the center of the picture (where mineral nutrients are likely limiting, but water can be accessed in deep cracks in the rock), sagebrush on sandstone (where water may be limiting; there is no deep reservoir, and the dark stone gets hotter so that water evaporates quickly). Consider experiments that would allow you to test that hypothesis against the alternative (null) hypothesis that one or both species simply can't tolerate the other environment, and wouldn't grow there even without competition (think about transplants, removals, supplementation of resources, proper controls…).

County occurence maps chapter for Salamander, Shenandoah (020045)

Commonwealth of Virginia

County Distribution of
Salamander, Shenandoah
(020045) *Plethodon shenandoah*

☐ City or County Boundary
☐ Known or Likely within county

Confirmed locations
Potential habitat

Plethodon shenandoah

Another classic scenario and study closer to home: *Plethodon shenandoah* is a narrowly endemic lungless salamander, living on bouldery (talus) slopes in three counties in the Blue Ridge Mountains of Virginia. It's range is very restricted. Map at upper right 'zooms in' and shows that it is found only in a very small part of that three-county area; dark blue areas are where it is known to occur; pale blue areas are talus habitats that seem appropriate for the species.

5

Redback Salamander
Plethodon cinereus

Jundt
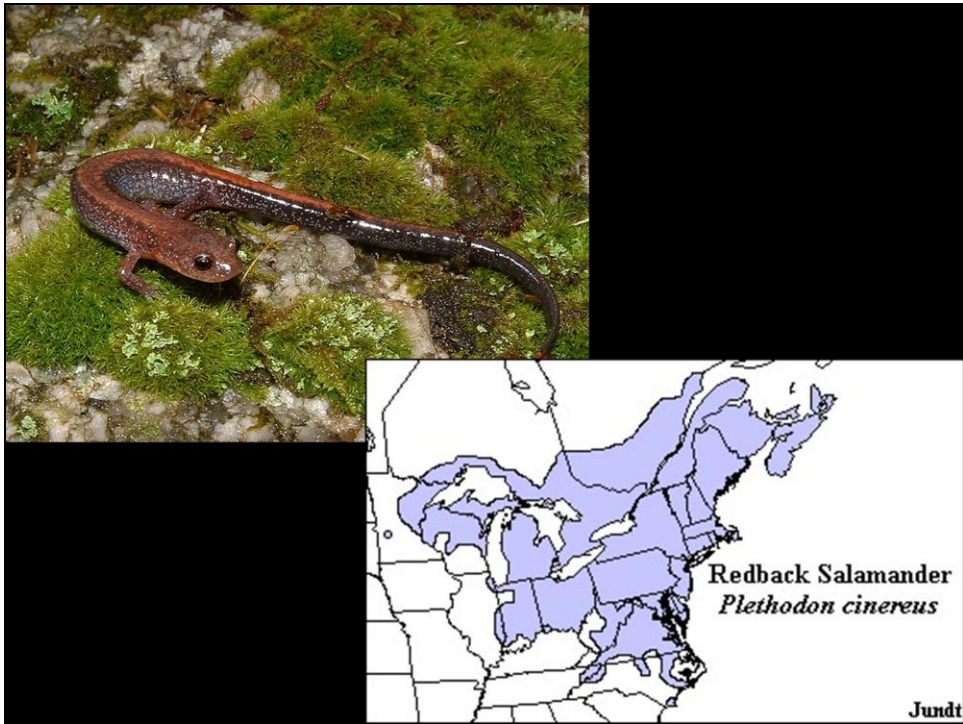
The closely related and very similar *P. cinereus* (red-backed salamander) is abundant and wide-spread in forest habitats (in fact, it's been claimed that it is the most abundant native terrestrial vertebrate in eastern North America), and its range completely encompasses that of *P. shenandoah*

Late Spring 1972   FOOD AS A LIMIT
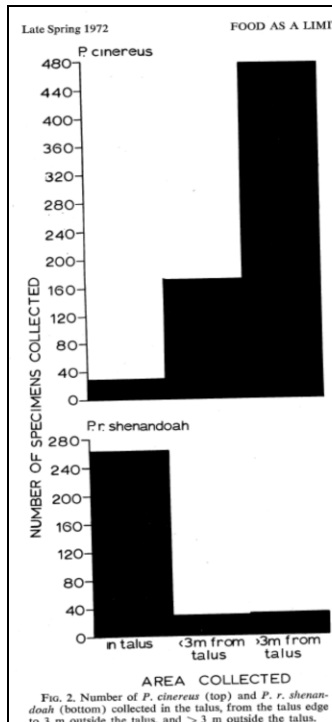
Food as a Limited Resource in Competition between Two Species of Terrestrial Salamanders
Robert G. Jaeger
Ecology, Vol. 53, No. 3 (May, 1972), pp. 535-546

FIG. 2. Number of *P. cinereus* (top) and *P. r. shenandoah* (bottom) collected in the talus, from the talus edge to 3 m outside the talus, and > 3 m outside the talus.

Robert Jaeger suggested that *shenandoah* is competitively excluded from the 'better' (moister, less stressful, more productive) habitat of forests surrounding the talus slopes by competition with *cinereus,* but it is able to persist on the talus slopes because it can *tolerate* the more severe conditions there (specifically, they're drier), while *cinereus* can't. This is a common scenario/hypothesis; one species is a better competitor, but less tolerant of environmental extremes. Again, note the idea of *trade-offs* in adaptations. Think about it from a selective/evolutionary perspective. Data here show pronounced 'turnover' of the two spp at the talus margin. HOWEVER, to show that this hypothesis is correct, it is necessary to demonstrate that a) *cinereus* is unable to survive on the talus when *shenandoah* is absent, and b) *shenandoah* CAN survive in the moister forests off the talus if *cinereus* is absent. How could you test the hypothesis?
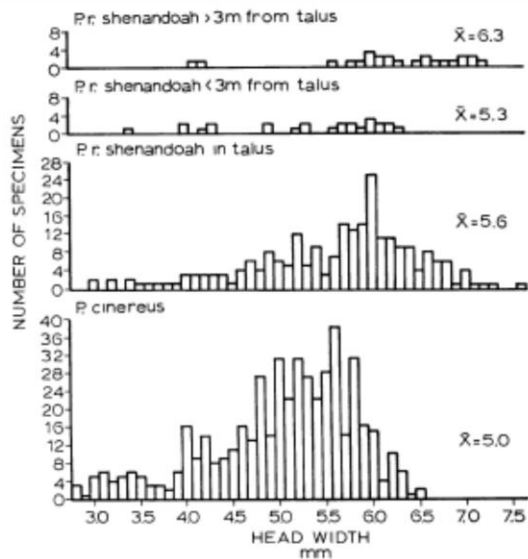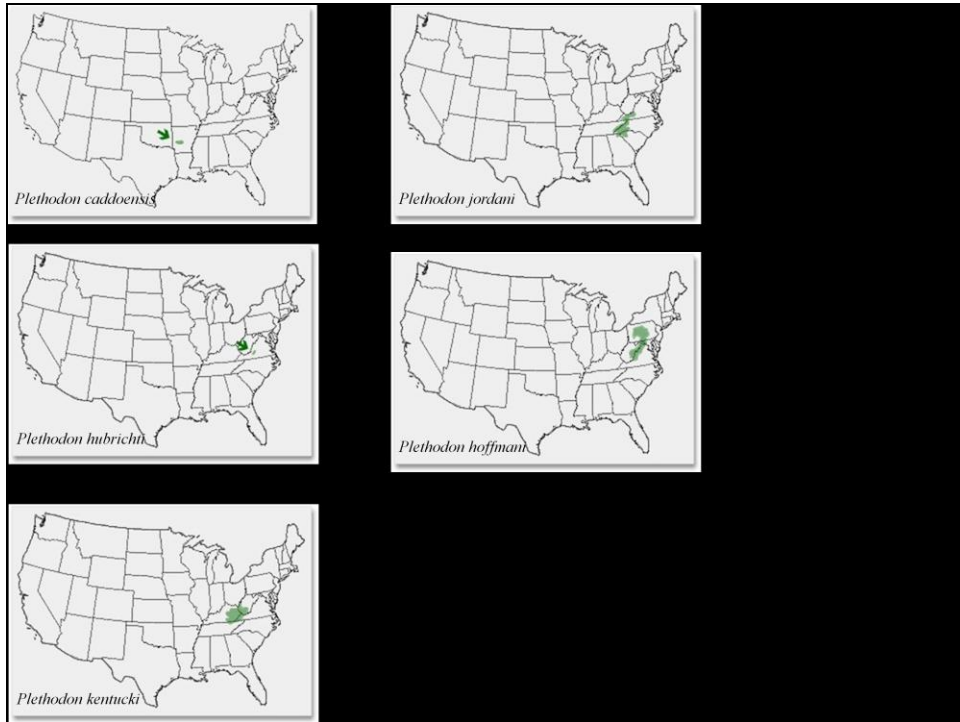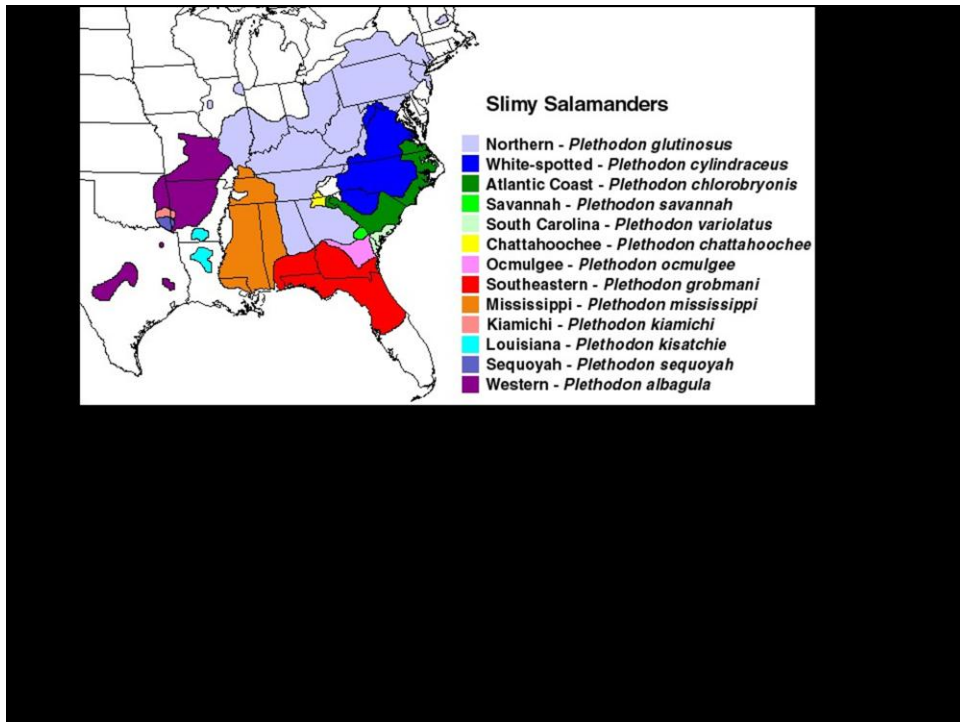
FIG. 4. The number of *P. r. shenandoah* of given head widths found (1) > 3 m outside the talus, (2) < 3 m from the talus, (3) in the talus, and (4) the total number of *P. cinereus* of given head widths collected. Mean head width for each group is given.

Examine SIZE distributions from different habitats: For *P. shenandoah* found >3 m away from talus (top), near, but not in the talus (2nd from top), and in the talus (3rd from top), and for *P. cinereus* (bottom). (This graph shows head width; similar patterns are seen for length). Salamanders are aggressively territorial and fight by biting and locking jaws, so head size matters. Only big *shenandoah* ever occur off talus; small ones restricted to talus. But *shenandoah* gets a little bigger (would this have anything to do with tolerating drought on talus?). Think about what these patterns suggest… Transplants of salamanders in and out of talus strongly support the competitive exclusion and environmental tolerance hypotheses proposed by Jaeger.

Plethodon caddoensis

Plethodon jordani

Plethodon hubrichti

Plethodon hoffmani
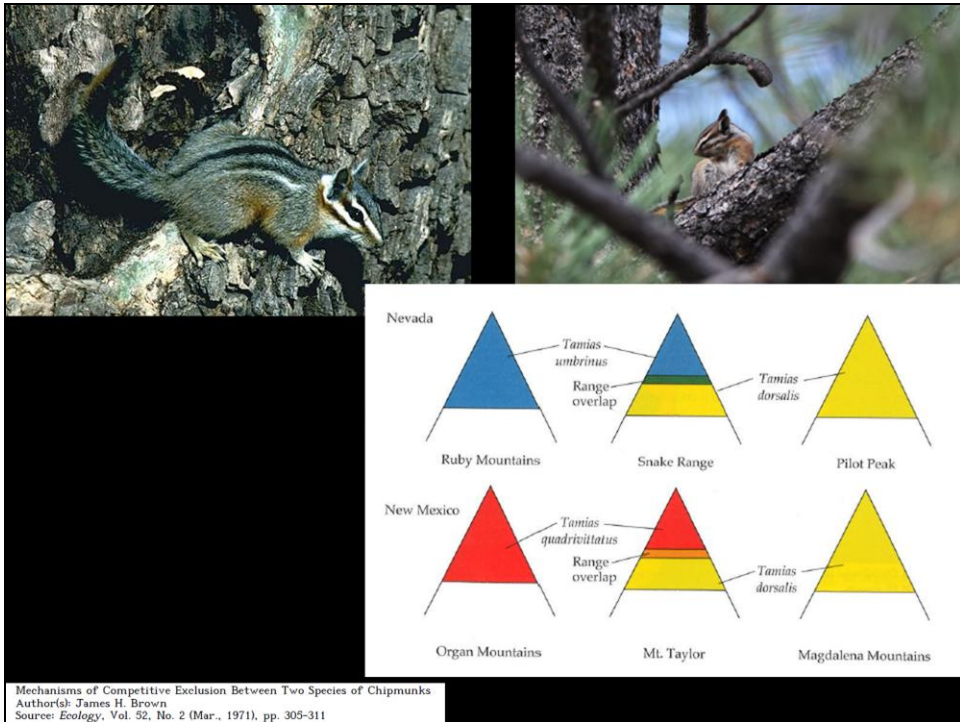
Plethodon kentucki

And this is probably a common phenomenon: there are several other narrowly distributed endemic members of the genus *Plethodon*; perhaps these are all 'specialized' species living in their locally distinctive habitat, surrounded by 'generalist' species like *P. cinereus* dominating the broader landscape. Again, this suggests *adaptive trade-offs* where one set of traits that 'solves' the problem of living in a special habitat may have the consequence of making an organism less competitive in another habitat. (This also offers a useful scenario for thinking about evolution by natural selection; we'll come back to that…)

Slimy Salamanders

Northern - *Plethodon glutinosus*
White-spotted - *Plethodon cylindraceus*
Atlantic Coast - *Plethodon chlorobryonis*
Savannah - *Plethodon savannah*
South Carolina - *Plethodon variolatus*
Chattahoochee - *Plethodon chattahoochee*
Ocmulgee - *Plethodon ocmulgee*
Southeastern - *Plethodon grobmani*
Mississippi - *Plethodon mississippi*
Kiamichi - *Plethodon kiamichi*
Louisiana - *Plethodon kisatchie*
Sequoyah - *Plethodon sequoyah*
Western - *Plethodon albagula*

A similar pattern of widely distributed common species and a few narrowly distributed ones in another group of *Plethodon* salamanders – but *none of these ranges overlap much!* Is this because competitive exclusion by each species of its 'neighbors'?

Mechanisms of Competitive Exclusion Between Two Species of Chipmunks
Author(s): James H. Brown
Source: *Ecology*, Vol. 52, No. 2 (Mar., 1971), pp. 305-311

Can competitive exclusion be more confidently demonstrated in nature? Here's a 'natural experiment' with chipmunks on mountain ranges in western U.S. (this research is by James Brown – the same guy who did the kangaroo rats and ants work a few slides back). Chipmunks live only in the forested upper elevations of these ranges (lower elevations are sagebrush or desert scrub), where they eat, mostly, conifer seeds. Some ranges have just one species, some have two. Where only one of some pairs is present, it occupies full range of forests, but where both are present, each is limited to only part of the elevational range of forests. High elevation forests are closed spruce-fir forests; lower forests are more open-canopy ponderosa pine. In the upper series of ranges (there are more examples than those shown), *T. umbrinus* is an arboreal species that harvests pine cones while they're still on the trees. *T. dorsalis* is terrestrial; it generally waits for the cones to fall. *T. dorsalis* is a very aggressive and territorial species; *umbrinus* always loses in confrontations with *dorsalis*. Think about the mechanisms that might be at work if this is, indeed, an example of competitive exclusion. This example also illustrates the notion of the *ecological niche*. The niche concept is built around interspecific resource competition and is one of the most important organizing concepts in ecology.

Fig. 1. Sizes of native seeds harvested by coexisting ants and rodents near Portal, Arizona. A total of 11,518 seeds were collected from the cheek pouches of 134 rodents representing five species, and 1052 seeds were collected singly from ants representing seven species. These were sized by passing them through a graded series of sieves (Tyler). Although ants take some seeds smaller than those utilized by rodents, there is extensive overlap (5).
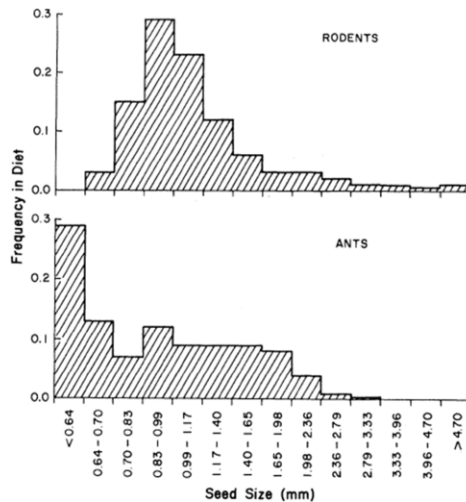
Competition Between Seed-Eating Rodents and Ants in Desert Ecosystems

James H. Brown; Diane W. Davidson

Science, New Series, Vol. 196, No. 4292. (May 20, 1977), pp. 880-882.

But competitors are not necessarily closely related, similar organisms. Some species of rodents and ants are both seed-eaters in the desert (so are birds). In this respect, they constitute and ecological *guild* – a set of species that are, in some manner, ecologically similar – doing the same 'job'. A famous study by James Brown and his students, at the University of New Mexico, looked at interactions between two groups of seed-eaters in the Chihuahuan Desert – ants and rodents. First, they establish that resource-use (in terms of sizes of seeds consumed) overlaps – there is the *potential* for competition.

Table 1. Summary of the results of experiments in which ants or rodents were eliminated from plots and the unmanipulated taxon was repeatedly censused. Values in first three columns are totals of all censuses. Ants were censused five times, and there were two replicates of each treatment for a total of ten comparisons. There were 25 comparisons of rodent censuses: 13 censuses of the first replicated set of plots (established in August 1973) and 12 censuses of the second set (established in December 1973). The last column gives the fraction of the comparisons in which the experimental census exceeded the control census.

Taxon	Total			Increase relative to control (%)	Experimental > control
	Rodents removed	Ants removed	Control		
Ant colonies	543	—	318	70.8	9/10
Rodents					
Number	—	144	122	18.0	15/25*
Biomass (kg)	—	5.12	4.13	24.0	16/25†

*In five comparisons, the experimental equalled the control census. †In three comparisons, the experimental equalled the control census.

They did mutual "exclusion" experiments, with controls. Results strongly support notion that the two groups compete – although they do coexist, suggesting that they may not be 'total' competitors (refer back to seed-size distributions used by each to speculate as to how they manage to coexist). In results not shown here, they also showed that the number of seeds left unconsumed was about the same when ants were removed and when rodents were removed. However, when *both* ants and rodents were removed, the number of seeds left unconsumed increased by over five-fold. (image lower right shows rodent exclosure fences from the air)
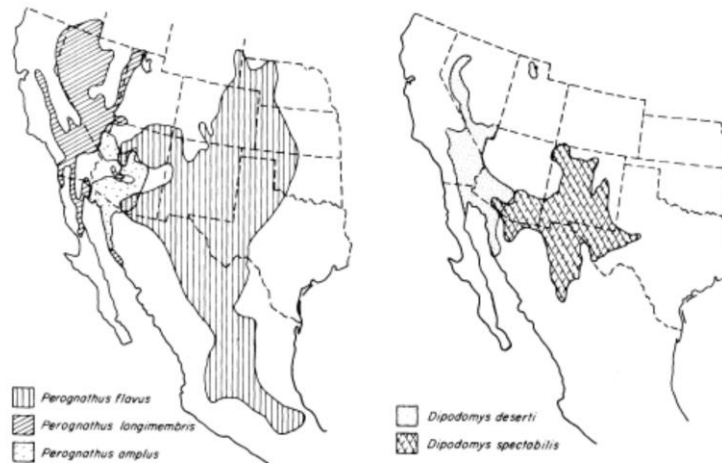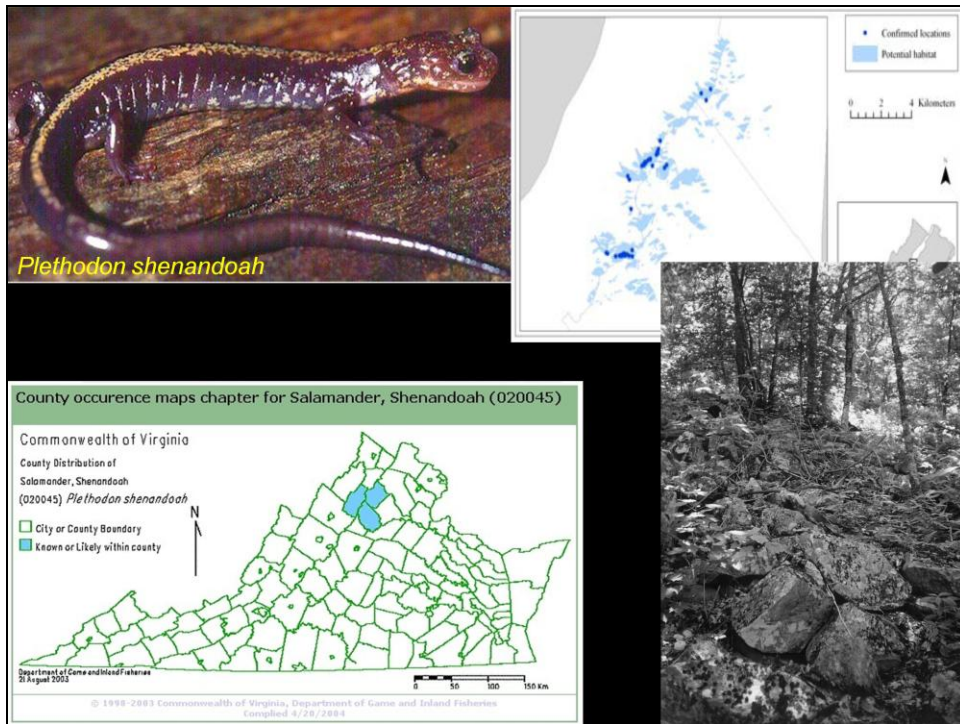
FIG. 2. Geographic ranges of small pocket mice (*Perognathus* spp., body mass <11 g) and of large kangaroo rats (*Dipodomys* spp., body mass >100 g). Redrawn from Hall and Kelson (1959). Note the extremely small overlap in geographic ranges of the species of similar size.

NON-overlapping distributions of generally similar organisms is sometimes taken as evidence for competitive exclusion – here, several species of pocket mice (*Perognathus*) and two species of kangaroo rats (*Dipodomys*). It's important to remember that this is evidence that has to be assessed carefully; there are other reasons for such distributions that might not involve competition as the primary driver (think about it – maybe you could generate a couple of alternative hypotheses). Remember the salamander studies and the sagebrush-bristlecone pine scenarios; the important thing is to think about how hypotheses suggested by such patterns can be tested…

Plethodon shenandoah

County occurence maps chapter for Salamander, Shenandoah (020045)

Commonwealth of Virginia

County Distribution of
Salamander, Shenandoah
(020045) *Plethodon shenandoah*
□ City or County Boundary
■ Known or Likely within county

Department of Game and Inland Fisheries
21 August 2003
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Compiled 4/28/2004

TRANSLATE ALL OF THIS INTO **NICHE THEORY** – one of the most useful general concepts in ecology… Think of an organism's 'niche' as the range of resources and conditions in which it *can* survive and succeed. In the case of the *Plethodon* salamanders, the common *P. cinereus* can't survive/tolerate the drier, harsher talus habitat; it's niche is limited to moister conditions. The endemic *P. shenandoah* can tolerate these conditions as well as the broader forest conditions; it has a broader niche. BUT, *shenandoah* fails in competition with *cinereus* and is excluded from part of it's potential niche when *cinereus* is present; there appears to be an adaptive *trade-off* between tolerance of severe conditions and general competitive ability... Thus, we speak of *fundamental* or potential niche (conditions suitable for the organism when it does not face competitioni), and the *realized* niche (conditions where it lives when competitors are present). The fundamental niche may be thought of as a biological property of the organism; the realized niche is clearly variable and conditioned by what potential competitors are present.

Competition between two species of flour beetles of the genus *Tribolium* at different temperatures and relative humidities

Temperature	Humidity	EQUILIBRIUM POPULATION SIZE*		PERCENTAGE OF CONTESTS WON BY†	
		T. confusum	T. castaneum	T. confusum	T. castaneum
Cool	Dry	26.0	2.6	100	0
	Moist	28.2	45.2	71	29
Moderate	Dry	29.7	18.8	87	13
	Moist	32.9	50.1	14	86
Warm	Dry	23.7	9.6	90	10
	Moist	41.2	38.3	0	100

*Number of adults, larvae, and pupae per gram of flour.
†Based on 20–30 contests in each combination of temperature and humidity.
(Data from Park 1954, 1962.)

Tribolium confusum

In the case of the classic experiment with *Tribolium,* these two species of flour beetles exhibit overlapping *fundamental* niche; the realized niche of each is reduced if the other is present die to differences in their relative tolerance of temperature and humidity conditiions; you can think of the relevant *resource space* (in the Hutchinsonian sense) being defined in just two dimensions (one for temperature, one for moisture). Most 'real-world' niche structures might require more dimensions for a full representation of important variables.

Figure 1 Effects of single-species and mixed infections on the intraintestinal distribution of the tapeworm *Hymenolepis diminuta* and the acanthocephalan *Moniliformis dubius*. Tapeworms are represented by solid dots and lines, and acanthocephalans by open dots and broken lines. The data points are from Holmes (84). The curves were drawn by eye.
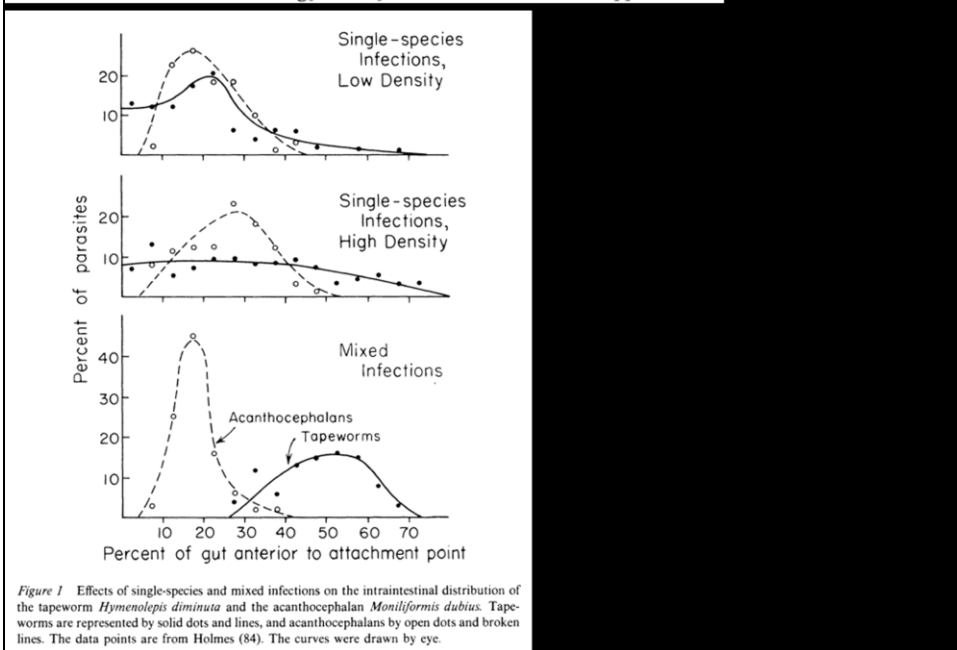
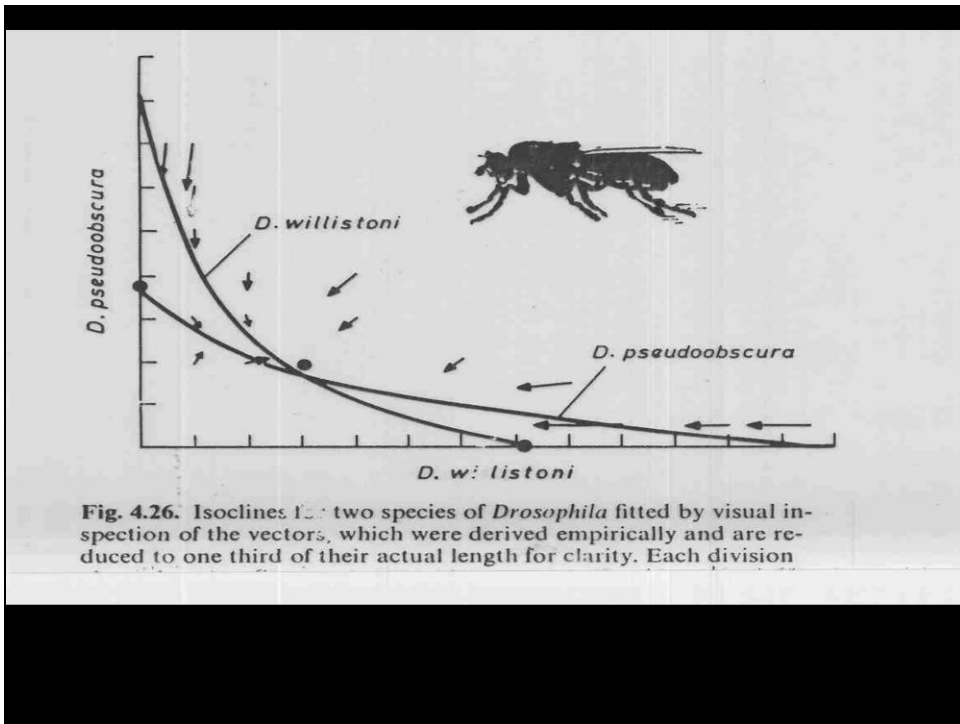Another example of a natural experiment suggesting niche-space partitioning by competitors – here, two types of gut-parasite worms. 'single-species' infections suggest that, in general, tapeworms are generalists relative to acanthocephalans – they can exploit a wider range of gut habitat ('% of gut anterior to attachment' is a measure of how far down the gut they reside; 'anterior' means 'head-ward'). In competition, the more specialized acanthocephalans seem to exclude tapeworms from the top of the gut. Consider which part of the gut axis represents the 'best' habitat. Is it likely/predictable that arrangement shows some trade-off between specialization/competitiveness for a 'good resource' vs. tolerance of a wide range of condition? Is this something that might be generalized?

Fig. 4.24. The outcomes of competition generated by the Lotka-Volterra competition equations for the four possible arrangements of the N_1 and N_2 isoclines. Vectors, generally, refer to joint populations and are de... as indicated in (a). For further discussion, see text.

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha_{12} N_2)}{K_1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \alpha_{21} N_1)}{K_2}$$
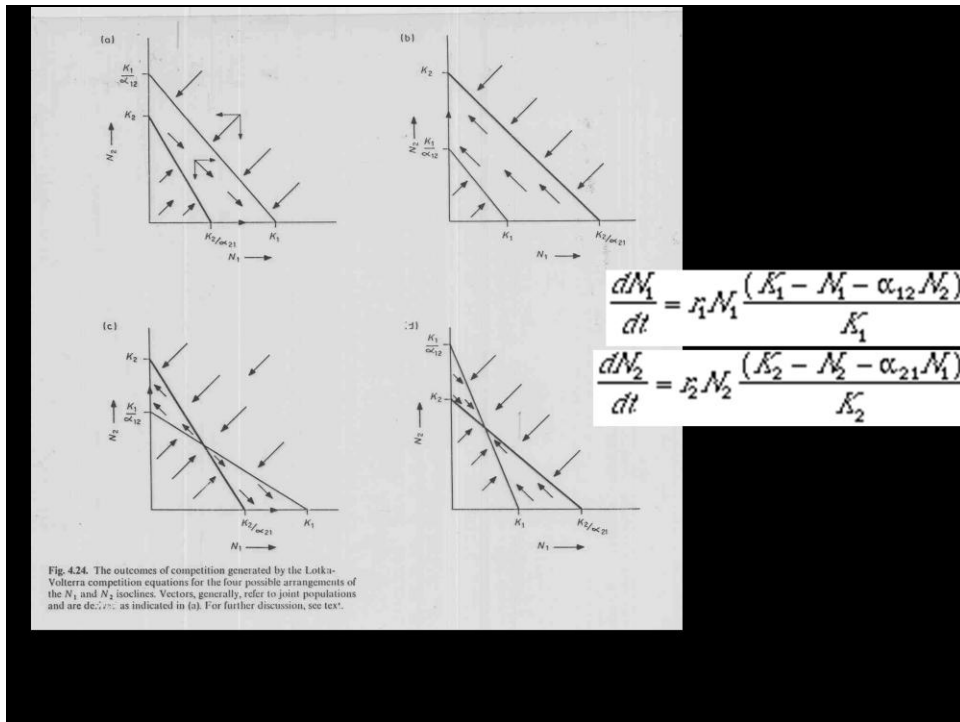
The Lotka-Volterra equations: View these as another idealized formalization of competitive interactions in a two-species system. They're based on the same kind of logic as the logistic growth mode. The formulae are derived from the logistic population growth model by adding competition terms (competition coefficient times population size of the 'other' species) that account for the competitive effects on each species' population of the number of individuals of the other competing species. Presence of individuals of one species consume resources required by the other in some amount proportional to the numbers of that species, effectively reducing carrying capacity for the second. The equations can be explored graphically on a plane is defined by the numbers of the two competing species (N1 and N2). The lines are Zero Growth Isoclines; any possible combined population sizes can be shown as a point; if it's above/'outside' a species' ZGI that species will experience negative population growth; if it's below/within, that species' population will grow. The arrows on the graph show how the 'system' (combined populations) will move in any area of the graph. Results change depending on how the competititon coefficients. A simple statement of the results; if each species has more competitive impact on its *own population than on the other*, there can be a *stable equilibrium where both populations coexist* (lower right). In upper graphs, one or the other species is simply universally the better competitor. In lower left situation, there's an equilibrium point, but it's *unstable*; most situations move towards one or the other species winning/displacing the other – but which one wins depends on where you start (relative abundances initially). Try placing a point on one of the graphs and working out its trajectory. *Note that the graphs and the equations are equivalent* here; it's often possible to use equations or graphs interchangeably. Here's a website that lays the equations out AND offers a little applet to show poulation dynamics:
http://fisher.forestry.uga.edu/popdyn/LotkaVolterraCompetition.html Here's another:
http://www.tiem.utk.edu/~gross/bioed/bealsmodules/competition.html. These equations involve most of the same assumptions as the logistic model and so are too simplistic to precisely describe most real-world situations -

Fig. 4.26. Isoclines for two species of *Drosophila* fitted by visual inspection of the vectors, which were derived empirically and are reduced to one third of their actual length for clarity. Each division

But they can come close! Here are empirically derived ZGIs for two species of fruit flies; they differ from those generated by Lotka-Volterra equations only in being some what concave upwards.
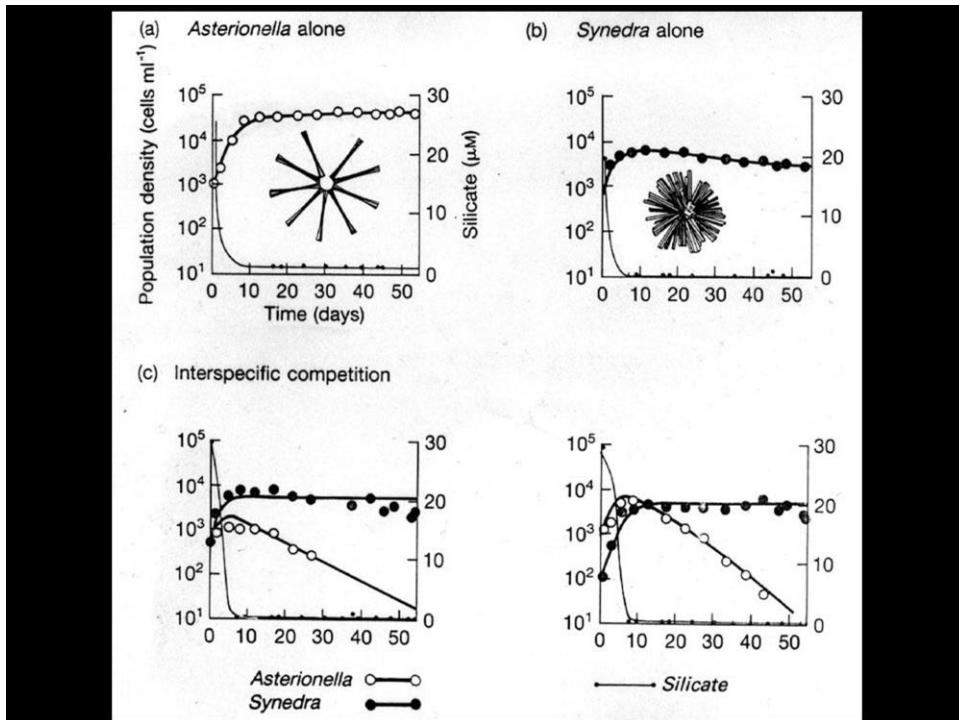
Some theory: David Tilman (U. Minnesota) did experiments with diatoms, structured similarly to Gause's work with *Paramecium*. However, he also monitored the depression of resource concentration as populations grew (note the 'silicate' curves; axis on right). He predicted, from top two experiments (with each species alone), that *Synedra* would win in competition BECAUSE it depressed silicate levels further than *Asterionella* – that is, it was able to keep increasing in density at the silicate level where *Asterionella* population stopped growing. Experiments with species in same cultures showed this to be the case. (AGAIN, nutrients are continuously suppied at a constant rate.) If silicate is limiting, *Asterionella* ALWAYS wins, competitively displaces *Synedra,* even if the experiment starts with much higher abundance of *Synedra*.
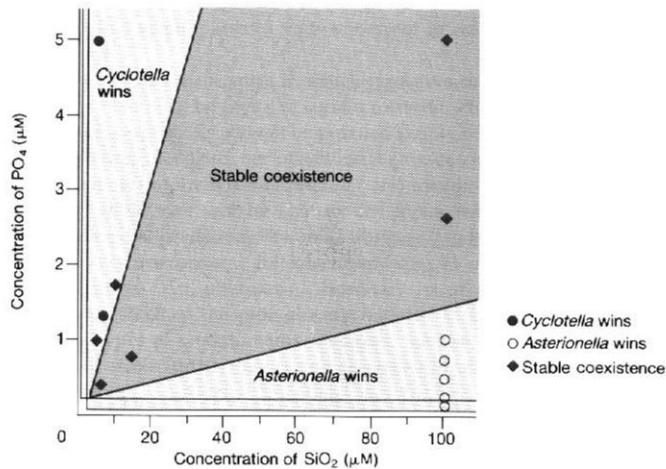
Figure 7.25. The observed ZNGIs and consumption vectors of two diatom species, *Asterionella formosa* and *Cyclotella meneghiniana*, were used to predict the outcome of competition between them for silicate and phosphate. The predictions were then tested in a series of experiments, the outcomes of which are depicted by the symbols explained in the key. Most experiments confirmed the predictions, with the exception of two lying close to the regional boundary. (After Tilman, 1977, 1982.)
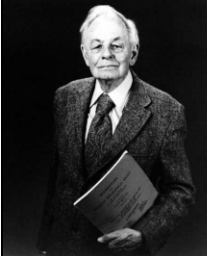
BUT, Tilman reasoned, different species might be superior competitors when limiting resource changes. Here, *Cyclotella* replaces *Synedra*, but the concept is the same. The thin solid lines are 'zero growth isoclines'; above or to right of its ZGI, a species can maintain positive population growth; below or to left, it declines. Think about each axis separately, then the 2-D space. Recognize that, if you begin (start the 'system') in conditions where both populations grow, they will deplete availability of resources and the position of the 'system' here will move down or to left depending on who's growing and how fast. Once the position hits a ZGI, the affected species stops growing… Play with it!
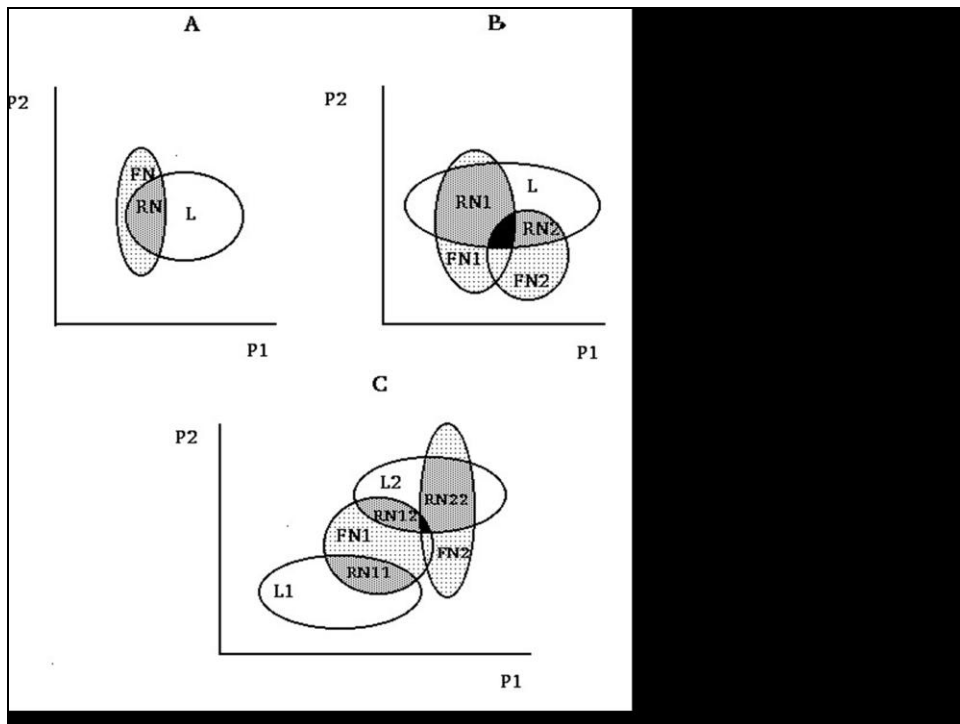
NICHE CONCEPTS
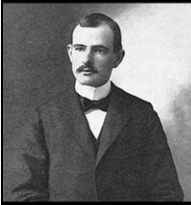
Joseph Grinnell (1917): the range of values of environmental factors that are necessary and sufficient to allow a species to carry out its life history

Charles Elton (1927): the 'role' a species plays in community (""[W]hen an ecologist says 'there goes a badger,' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, 'there goes the vicar.'")
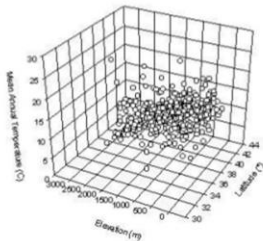
G. Evelyn Hutchinson (1957): The n-dimensional hypervolume defined by range of all environmental and resource conditions where a species' fitness is > 0.

The notion of the ECOLOGICAL NICHE has evolved over the last hundred years through successively more rigorous formulations, successively incorporating ideas of competitive exclusion and adaptive 'trade-offs' among coexisting species. It has become one of the most important and powerful concepts in ecology – 'powerful' because it can be usefully structure a wide range of hypotheses and tests of hypotheses, and because it seems to generalize to a very wide range of situations -- but also one that is often mis-used or confused. In fact, various definitions of the ecological niche have not been entirely consistent with one another. NOTE that early notions of the niche were qualitative and descriptive; e.g., a 'species role in a community', while later ones were progressively more rigorous and quantitative.

A conceptual illustration of the Hutchinsonian concept of niche. Axes define availability of two different resources – OR range of values for some environmental 'condition', like temperature – so the area of the graph can be thought of as the 'space' of possible habitat conditions (habitat space or resource space). If each ellipse is some species' fundamental niche, then competition can occur in conditions where ellipses overlap (CAN occur, but WILL occur if and only if resources are limiting). Who 'wins' – is the better competitor -- in those overlap areas will determine *realized niche*; one species may claim all of the habitats described by the overlap area, or it might be partitioned in some manner – no easy way of predicting this. BUT OFTEN (think back to the salamanders) a species with a large *fundamental niche* (in other words, a generalist) may not be a good competitor with a species that is specialized (specifically adapted) for a narrow range of conditions (and so has a narrower fundamental niche). This would constitute an *adaptive trade-off*; in this case one of the basic trade-offs; you can be capable of dealing with a wide range of conditions, or really good at dealing with a narrow, specific set of conditions – but you probably can't be both at the same time! Think about how this would play out in 'niche space'.

Modern ecologists largely adopt G. Evelyn Hutchinson' formal definition of the niche. A species niche is the 'region in an N-dimensional hypervolume (you can call this "NICHE SPACE" – an abstract space where all combinations of environmental conditions can be mapped…) where its fitness is > 0' – it's the range of resource availability and conditions, taking all such dimensions into account, where populations can persist. Note that this concept includes 'conditions' like temperature as well as consumable resource availability; see niche axes at top. Thus, even more than with Elton, a species' niche is a fundamental property of the species' adaptations. BUT, now there's a problem; competition from other species might prevent a particular species from 'occupying' all of the parts 'niche space' where it's capable of living without competition (another way of putting 'competitive exclusion'). So Hutchinson recognized that we have to think of two types of niches. The *fundamental niche* is a property of the organism – essentially genetic; it's observed niche in the absence of competition. BUT with competitors presence, we might not observe the organism using parts of this 'niche space' because it's competitively limited to a subset of the full fundamental niche: the observed niche in the presence of competiton is the *realized niche*. The realized niche *can change depending on the combination of competitors present. Tribolium* species can each live in all parts of the humidity-temperature spectrum without competition – but they partition it when both are present (Note that 'temperature' is an example of a 'condition' dimension, as contrasted with a 'resource' dimension…)

NICHE CONCEPTS

Joseph Grinnell (1917): the range of values of environmental factors that are necessary and sufficient to allow a species to carry out its life history

Charles Elton (1927): the 'role' a species plays in community (""[W]hen an ecologist says 'there goes a badger,' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said, 'there goes the vicar.'")

G. Evelyn Hutchinson (1957): The n-dimensional hypervolume defined by range of all environmental and resource conditions where a species' fitness is > 0.

T. S. Geisel:

A fourth thinker has contributed further insights to modern thinking about the niche

And NUH is the letter I use to spell Nutches
Who live in small caves, known as Nitches, for hutches,
These Nutches have troubles, the biggest of which is
the fact there are many more Nutches than Nitches.
Each Nutch in a Nitch knows that some other Nutch
Would like to move into his Nitch very much.
So each Nutch in a Nitch has to watch that small Nitch
Or Nutches who haven't got Nitches will snitch.

Here is the initial formulation of the 'Geiselian' niche, due to Theodore S. Geisel.

Also know as Dr. Seuss.

So what does it take for species to coexist? EITHER

Subdivide habitats spatially at fine scale (so they coexist at coarse
Scale but not at finer scale – like the salamanders

OR subdivide resources by taking different 'strategies' (like warblers,
Different plants in same area) so *not limited by same resource.*

=> *"Life-history strategies"*

https://www.youtube.com/watch?v=Atg-5Nqszxw

Magnolia Warbler Male · Magnolia Warbler Female · Cape May Warbler Male · Black-throated Blue Warbler Male · Black-throated Blue Warbler Female · Cerulean Warbler Male · Cape May Warbler Female · Yellow-rumped Warbler Male · Yellow-rumped Warbler Female · Cerulean Warbler Female · Chestnut-sided Warbler Male · Chestnut-sided Warbler Female · Black-throated Green Warbler Male · Black-throated Green Warbler Female · Yellow-throated Warbler Male · Bay-breasted Warbler Male · Bay-breasted Warbler Female

But it's almost never just two species competing. Here is a 'guild' of insectivorous birds – warblers --native to northeastern forests; as many as six or seven may nest in the same stands, suggesting complex competitive relationships.
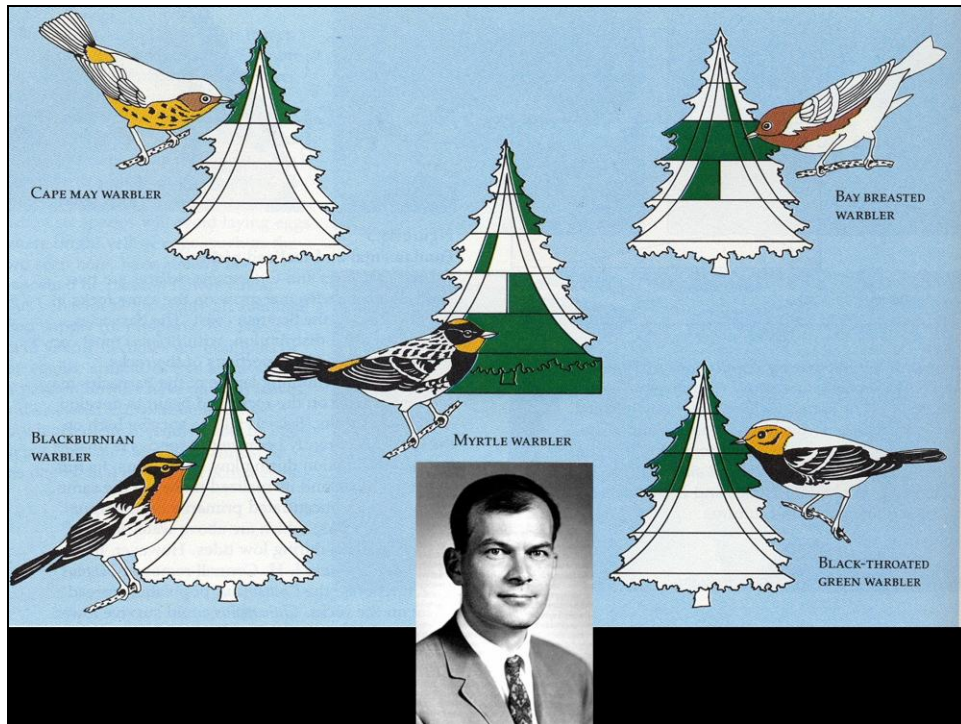
Robert MacArthur (of Island Biogeography fame) did graduate research on several warblers coexisting in mountain forests of New Hampshire. He established that they 'partitioned' resources – in this case with respect to how they foraged ('hawking' for flying insects, gleaning from leaves or twigs, prying under bark, rummaging on the ground, etc.) and what part of the canopy they used. (Note that this does not tell us whether each could use the resources the others use if the others weren't there – it does not establish that they're actively competing.   H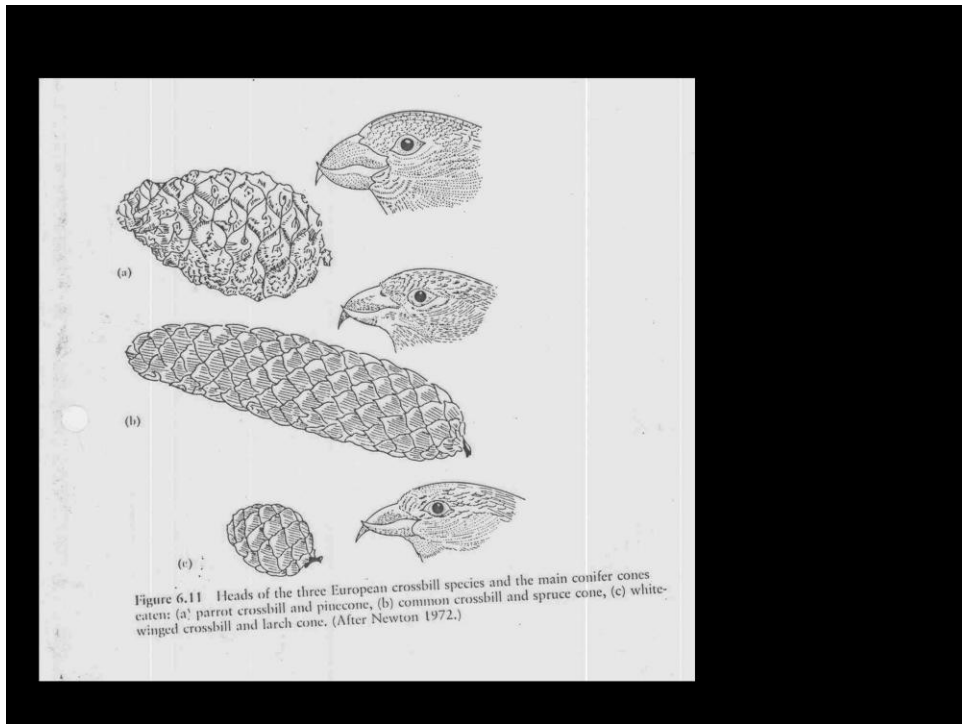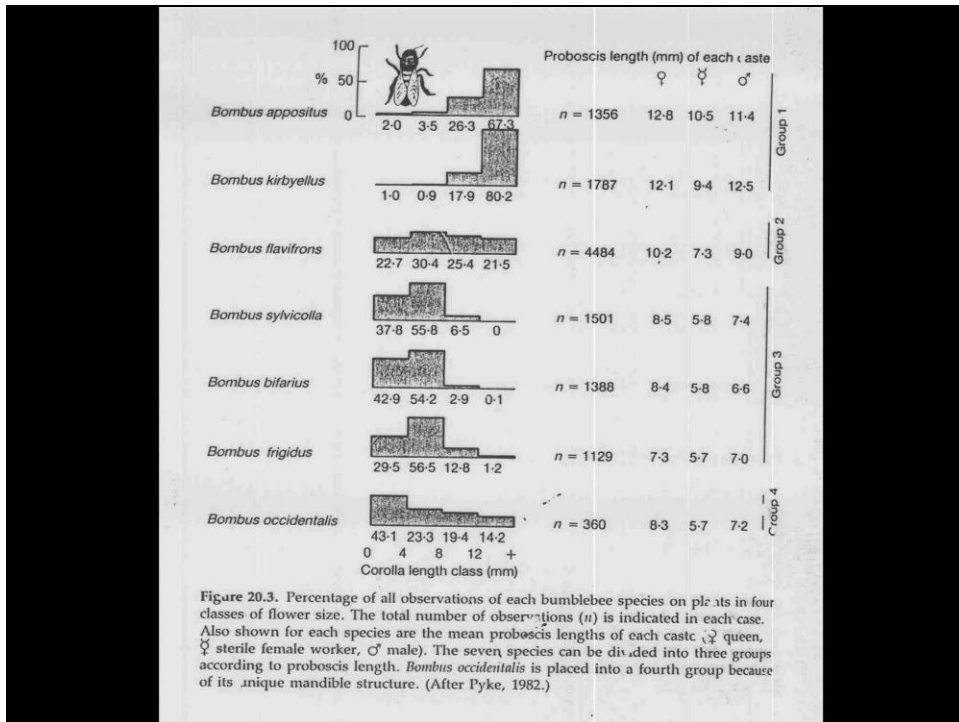ow would you do that?). This was a classic illustration of NICHE STRUCTURE – how different species partition the resource/environment world they live in. This is the rather informal sense of the ecological niche as defined by Elton, who coined the term in this context. He simply thought of the niche as a species 'place' in the natural economy of an ecosystem. NOTE that the niche is *a property of the organism*; you can't talk about it in the absence of the organism! He suggested that if species' niches were too similar, they'd be unable to coexist if numbers were allowed to increase – another way of putting the competitive exclusion principle. Coexisting species should demonstrate 'niche separation'.

Figure 6.11 Heads of the three European crossbill species and the main conifer cones eaten: (a) parrot crossbill and pinecone, (b) common crossbill and spruce cone, (c) white-winged crossbill and larch cone. (After Newton 1972.)

There are many situations that look very much like guilds of organisms partitioning resource space according to different adaptation – or, equivalently, inhabiting different but adjacent parts of niche space. Here, cross-bills, which specialize on prying seeds from conifer cones – but different species (with different beak sizes) use different types of cones. – BUT REMEMBER that it's tricky to tell whether competition is actually occurring in the wild…

	Proboscis length (mm) of each caste		
	♀	☿	♂
Bombus appositus — 2·0 3·5 26·3 67·3	n = 1356	12·8	10·5	11·4	Group 1
Bombus kirbyellus — 1·0 0·9 17·9 80·2	n = 1787	12·1	9·4	12·5	
Bombus flavifrons — 22·7 30·4 25·4 21·5	n = 4484	10·2	7·3	9·0	Group 2
Bombus sylvicolla — 37·8 55·8 6·5 0	n = 1501	8·5	5·8	7·4	
Bombus bifarius — 42·9 54·2 2·9 0·1	n = 1388	8·4	5·8	6·6	Group 3
Bombus frigidus — 29·5 56·5 12·8 1·2	n = 1129	7·3	5·7	7·0	
Bombus occidentalis — 43·1 23·3 19·4 14·2	n = 360	8·3	5·7	7·2	Group 4

Corolla length class (mm): 0   4   8   12   +

Figure 20.3. Percentage of all observations of each bumblebee species on plants in four classes of flower size. The total number of observations (*n*) is indicated in each case. Also shown for each species are the mean proboscis lengths of each caste (♀ queen, ☿ sterile female worker, ♂ male). The seven species can be divided into three groups according to proboscis length. *Bombus occidentalis* is placed into a fourth group because of its unique mandible structure. (After Pyke, 1982.)

Here several coexisting species of bumblebee generally have different proboscis lengths, and partition the nectar resource on the basis of flower structure (sometimes males and females of the same species seem to similarly partition – show niche displacement!). The last species on the list is a 'nectar thief', accessing nectar by cutting through the base of the flower (it does no pollinate in the process – it's a parasite on the flower…).
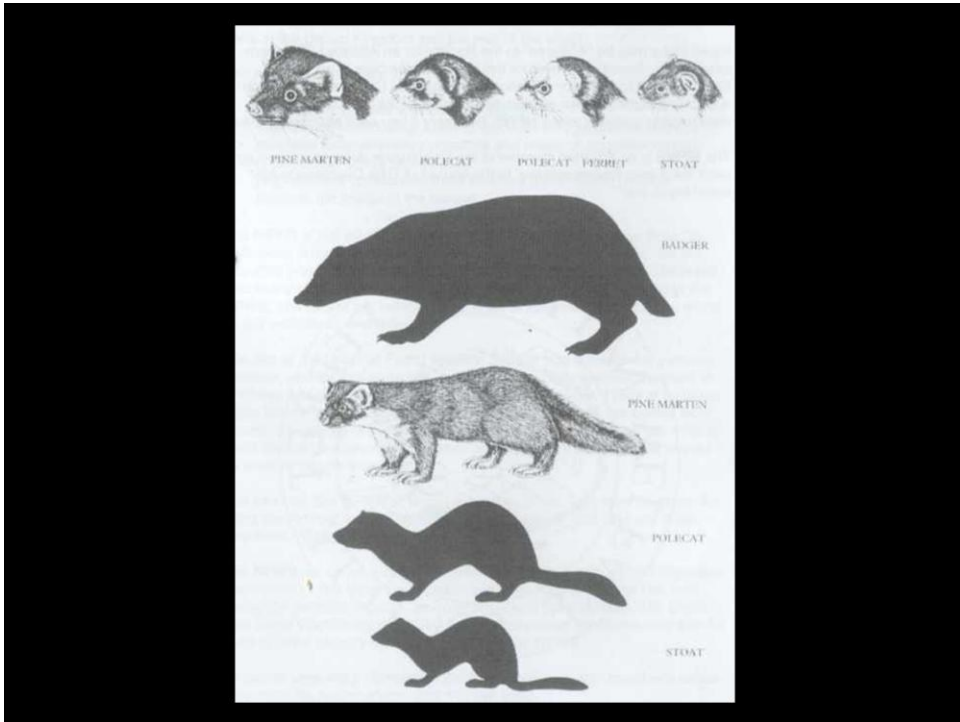
Nonetheless, competition seems to be pretty important and general in structuring things. For example, guilds of coexisting organisms (here, members of the weasel family – Mustelidae – in Europe), in fact, often are very evenly spaced along a size axis – looks like a sort of niche separation… Is it real?
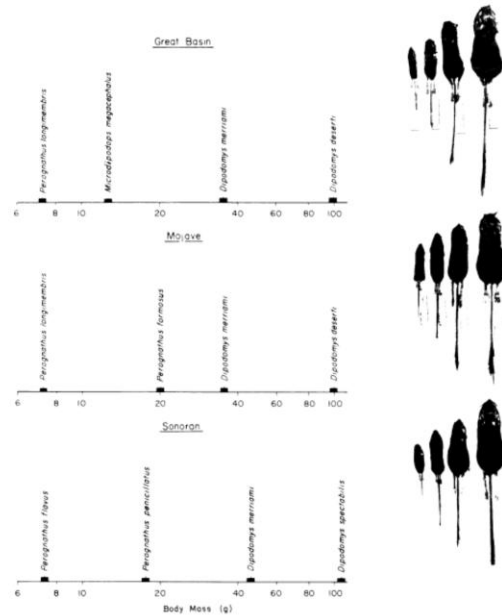
FIG. 1.   Distribution of body sizes (plotted on a logarithmic scale so that equal spacing indicates equal ratios) in arbitrarily chosen, diverse communities in three deserts (see text). Note that the size distributions of species are very similar even though the identity of species often differs between deserts.

In desert southwest, several species of seed-eating rodents coexist in different areas; here sympatric assemblages of ground-foraging species are shown for three regions. In each case there are four species -- and the 'spacing' along a body-mass axis is much more even than a random selection of species would produce. This kind of pattern might be produced by competition 'sorting' the species available – BUT there's also a suggestion that species might be 'shaped' evolutionarily to reduce similarity (or 'fundamental niche' overlap!). There is some theory to suggest that the *ratio of body mass* between 'adjacent' species in such size-ordered guilds should be about constant. That would produce even spacing on a logarithmic scale as is used here.

Figure 20.10. The conventional musical ensemble of recorders, which appears to conform to Hutchinson's size-ratio rule. (After Horn & May, 1977.) (Instruments kindly lent by Russel Acott, Oxford. photograph courtesy of B. Roberts.)
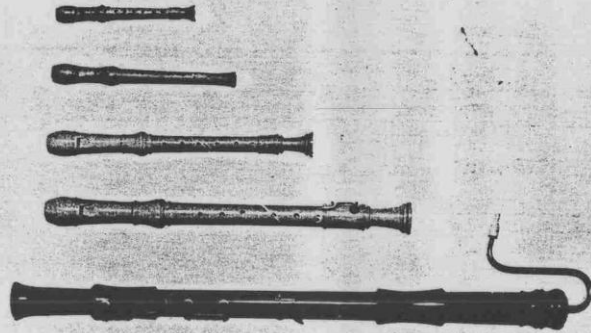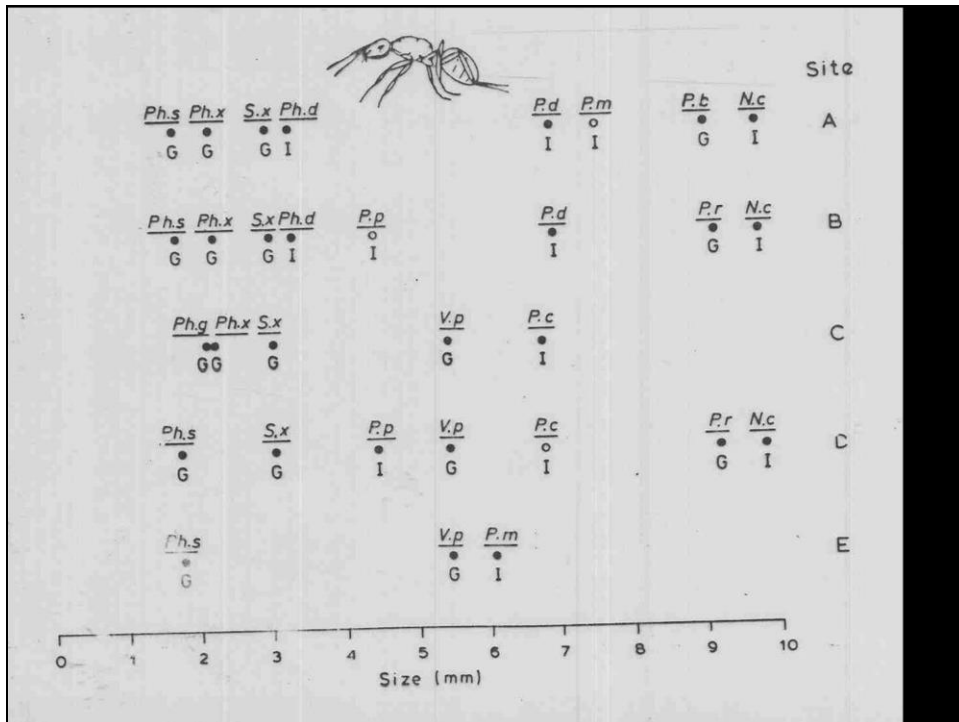
And coexisting ant species tend to be of different sizes (and body size is correlated with mandible size, which is correlated with size of seeds eaten). Here, each row is a single study-site. "G" and "I" represent different foraging strategies (on ground, in shrubs…). MOSTLY, species of very similar size coexist at same site only if they're different in foraging strategy. This is all consistent with competitive structuring of coexistence and the notion of competitive exclusion coming into play if species are TOO similar in how they make their livings (niche structure). *HOWEVER,* there are some exceptions to this rule, especially among smaller species; *either* some populations here are not limited by competition but by something else, *or* they're differentiated in some other niche dimension than seed size. It's tempting to think that it's all about competition – but sometimes there are patterns of coexistence that are hard to explain by thinking only in terms of niche differentiation.

For example, these two species of long spring forest wildflowers ('Dutchman's breeches', *Dicentra cuccularia*, top, and 'squirrel corn', *Dicentra canadensis,* below) are closely related and very similar in growth form and habitat requirements – seemingly likely competitors – yet they often occur in closely intermingled populations. Are populations not limited by competition? Or is there some axis of niche differentiation that we do not understand? What permits their coexistence?
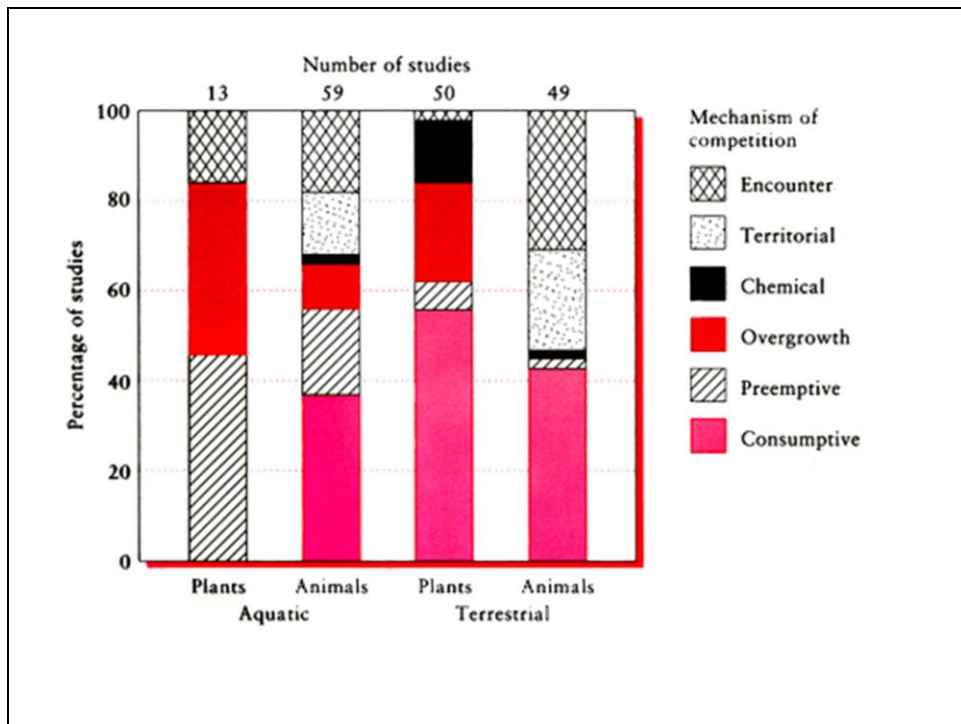
In this context, worth reminding ourselves that populations can be limited by things other than competitive dynamics. We've talked about shade-tolerance differences among local forest trees. Very tolerant species like hemlock tend to outcompete other species when light is limiting (left). Why aren't our forests (at least old-growth stands like these) all hemlock and/or beech (or whatever the most shade-tolerant species is locally)? What if *sometimes* other factors than light are what matter – like ability to withstand or regnerate in response to a big disturbance like high wind? Can you think of this in the same terms as in other cases – a trade-off between 'specialists' who are going to win in competition (assuming the specialize in capturing the resource that's most limiting) and generalists who may never persist long in face of competition, BUT can get around and make use of a wide range of resources as long as they're not being subject to severe competition…
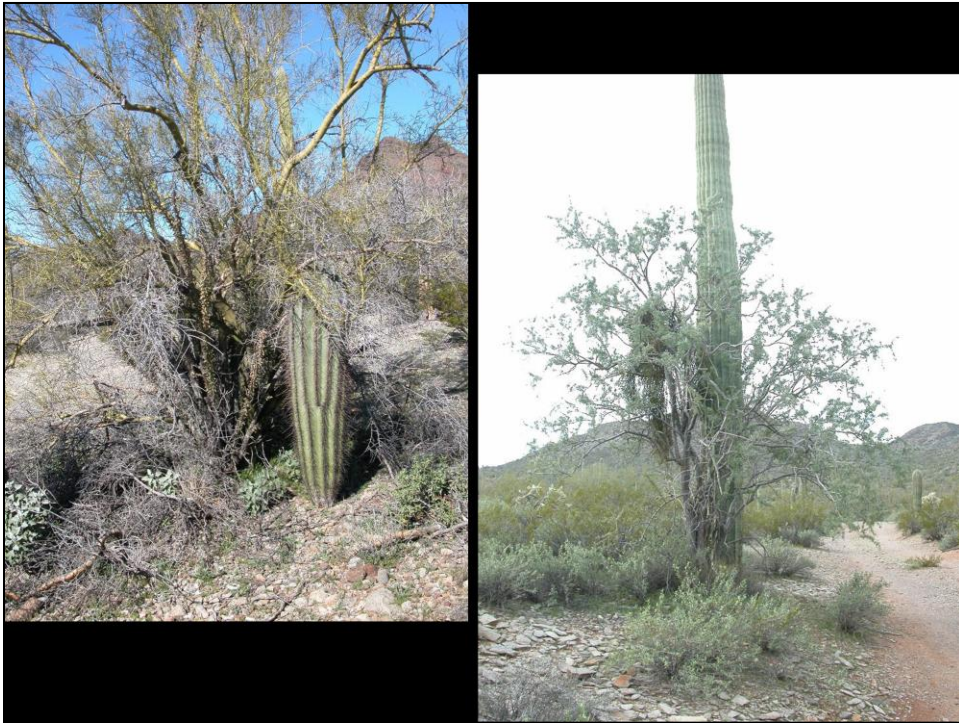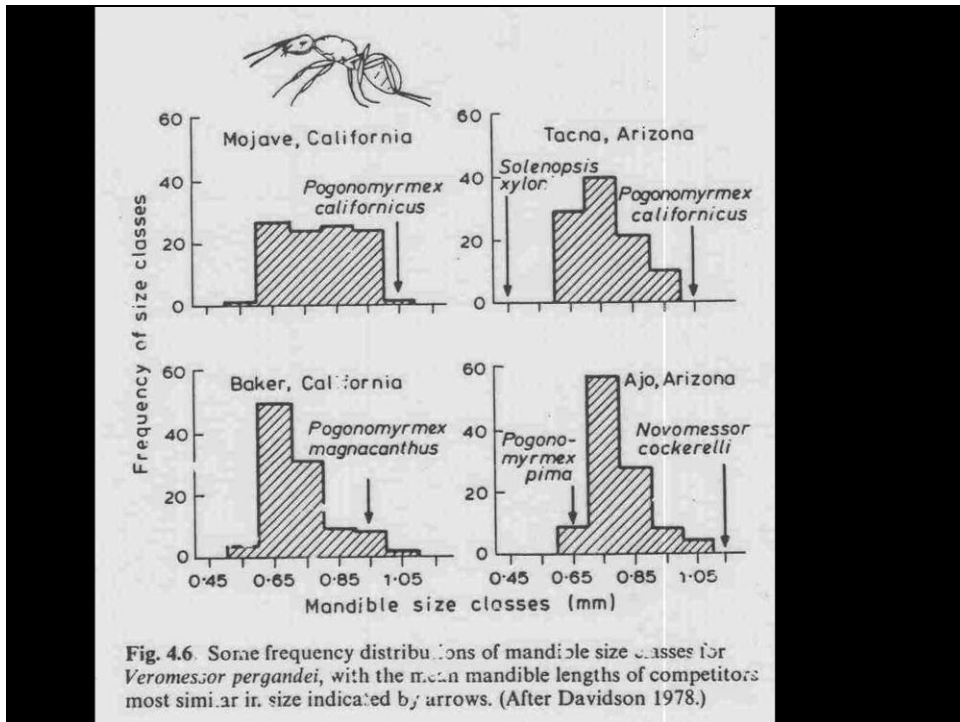
And, of course, in the real world, interactions among species don't always fall into our neat categories of competition, predation, mutualism without confusion. Young saguaro cactus in the Sonoran deserts of the southwest require some protection from night-time cooling to survive; young cacti are often restricted to the cover of 'nurse shrubs' (on left, a palo verde tree). This is an example of a sort of a one-sided mutualism (sometimes called 'comensalism'). As the cactus grows larger, it becomes massive enough that it can hold enough heat through the cold nights to avoid having it's growing tip frozen and so can survive without the 'nurse'. But saguaro specialize in capturing rainfall efficiently with an extensive network of shallow roots (they store that water for dry periods, and so can continue growing into drought periods); the nurse trees depend on collecting water stored in deeper soils. But the large cactus can stop most of the rainfall reaching the deeper soils and so can competitively deprive the nurse shrub/tree of water, ultimately even killing it (right; the nurse tree here is a desert ironwood). Mutualism becomes competition. In pollination interactions, mutualism often tips into parasitism and vice versa…

Fig. 4.6. Some frequency distributions of mandible size classes for *Veromessor pergandei*, with the mean mandible lengths of competitors most similar in size indicated by arrows. (After Davidson 1978.)
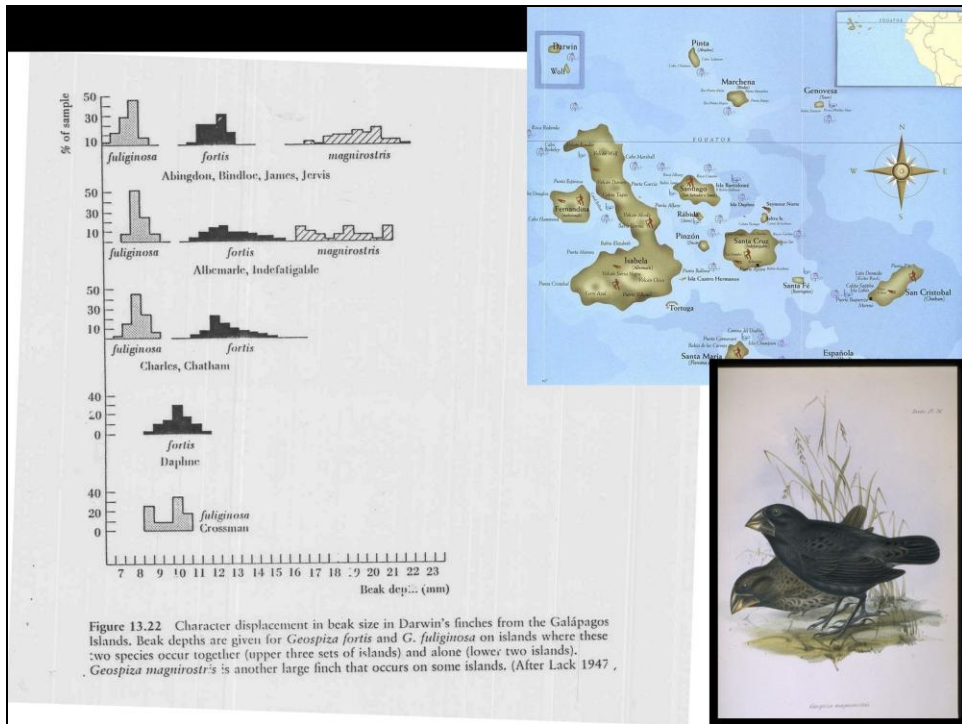
Finally, even fundamental niche dimensions can vary within a species. Here are distributions of mandible sizes for a single species of desert seed-eating ant for four different areas/populations. Mandible size is pretty much genetically determined and determines what seed sizes an ant *can* eat – i.e., mandible size would seem to be an indicator of *fundamental* niche. So fundamental niche seems to vary among these populations. The arrows show the *average* mandible sizes for species of coexisting (sympatric) seed-eating ants…

Think about it.

Figure 13.22 Character displacement in beak size in Darwin's finches from the Galápagos Islands. Beak depths are given for *Geospiza fortis* and *G. fuliginosa* on islands where these two species occur together (upper three sets of islands) and alone (lower two islands). *Geospiza magnirostris* is another large finch that occurs on some islands. (After Lack 1947)
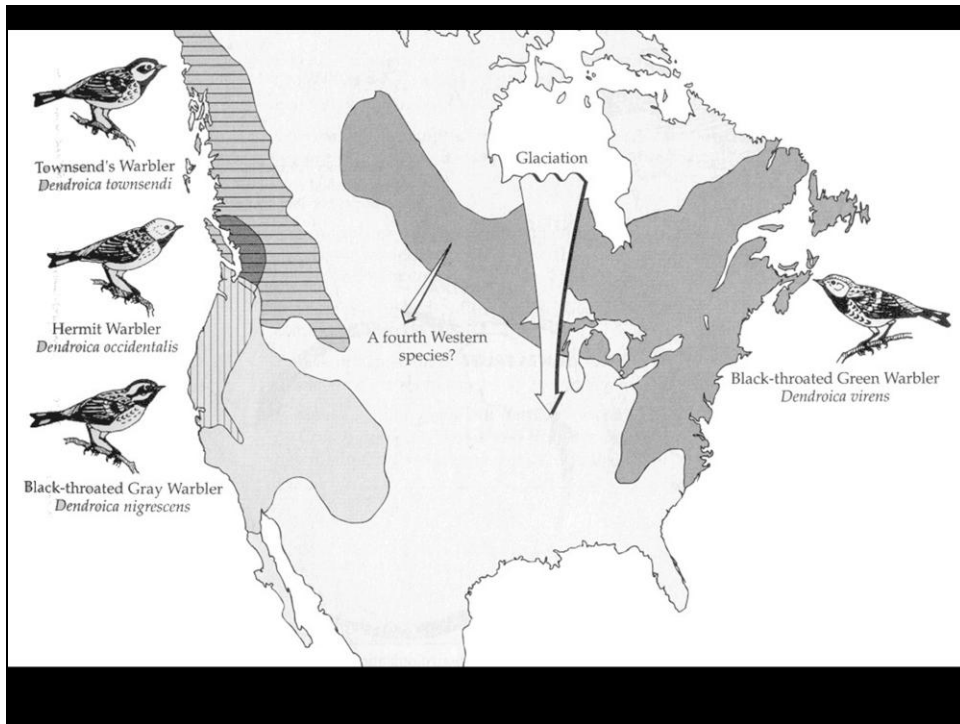
Ant think about it some more. Look at beak depth distributions for *Geospiza fortis* (one of Darwin's finches) on different islands where it co-occurs with 0, 1, or 2 other species of finches. We'll talk more about this.

ulvae (open circles) and *H. ventrosa* (filled circles) at a variety of sites t which they coexist or live alone. (b) Distributions of food p ... .ze of the same species at typical sites at which they coexist or ...ve alone. (After Fenchel 1975.)
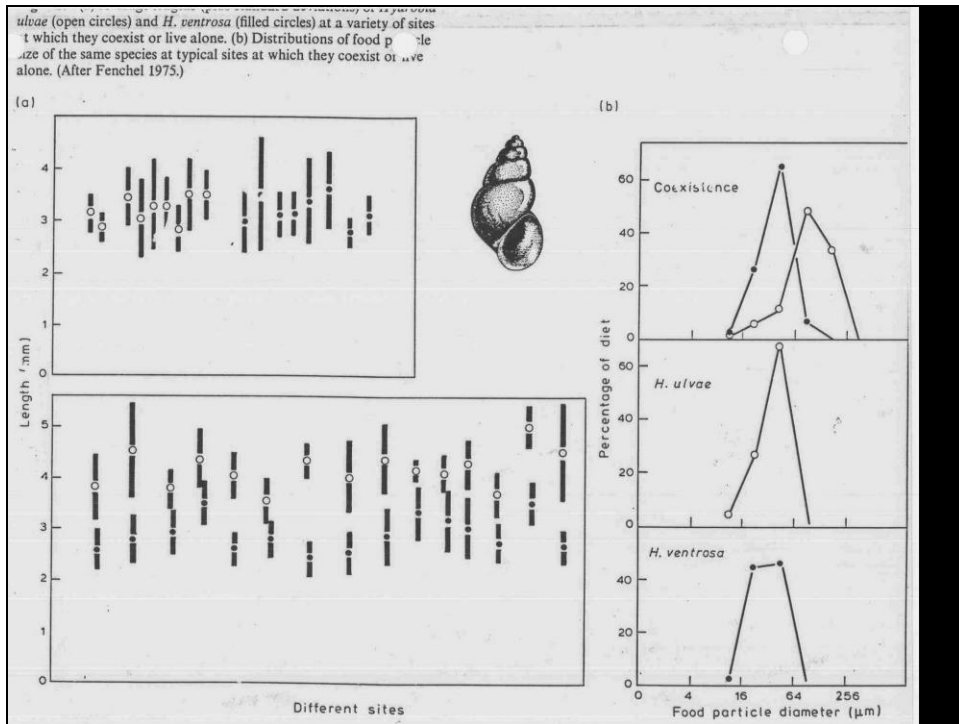
A similar scenario with snails on lots of different islands. Graphs to left show average (and range of) shell sizes for populations of two snail species. The upper graph shows populations on islands where only one or the other species (solid or open dots) exists without the other (technical term: they are *allopatric* – not overlapping in distribution). The lower graph shows shell sizes for islands where the same two species coexist (technical term: here, the two species are *sympatric* – overlapping in distribution).

This pattern, along with the Galapagos finches on previous slide, is taken to suggest that there've been *changes in shell size* over time – shift in *fundamental niche* (see right-hand graph; shell size is indicative of food particle size), or the fundamental properties of the organism. *If these differences are related to genetic differences, this represents evolutionary change…*

Townsend's Warbler
Dendroica townsendi

Hermit Warbler
Dendroica occidentalis

Black-throated Gray Warbler
Dendroica nigrescens

Glaciation

A fourth Western species?

Black-throated Green Warbler
Dendroica virens

And add deep history: Glaciers have displaced species ranges multiple times over the last 2 million years. Combining competitive dynamics with this history and with natural selection offers a window into the deeper 'problem of diversity'. It's not just 'how do diverse species coexist'; it has to be extended to, "HOW DO YOU GET SO MANY SPECIES IN THE FIRST PLACE?"