Ecological interactions among species

With this unit, we're bridging the gap between population-level and community-level patterns and processes. The interactions we'll discuss here affect both population-level (distribution, abundance, dynamics) and community-level (species diversity, trophic structure, dynamics) phenomena.

I. Classifying interspecific interactions according to fitness consequences

II. Competition (Ch. 13)
  - A. general introduction
  - B. Studies of intraspecific competition provide evidence for resource limitation
  - C. The ecological niche reflects the environmental requirements of species and provides the conceptual foundation for understanding patterns of interspecific competition
  - D. Interspecific competition can have significant ecological and evolutionary influences on species and their niches
    1. Competitive exclusion occurs when the strength of interspecific competition is greater than the strength of intraspecific competition.
    2. Coexistence is possible if the strength of intraspecific competition is greater than the strength of interspecific competition.
  - E. Interspecific competition may help regulate population size
  - F. The effects and prevalence of interspecific competition have been controversial issues in ecology

III. Exploitation (Ch. 14)
  - A. Definitions and complexities
  - B. Exploitation is a strong selective force for both exploiter and exploited
  - C. Predation, parasitism, and pathogens can affect the distribution, abundance, and population structure of prey/hosts
    1. caddisfly larvae reduce population size in benthic stream algae, bacteria
    2. *Cactoblastis* affects both size and distribution of *Opuntia* populations in Australia
  - D. Exploitation leads to complex interactions among species within a community
    1. parasites can change host behavior
    2. predation can moderate the effects of interspecific competition
  - E. Interactions among exploiters and exploited populations are dynamic and complex
  - F. To persist in the face of exploitation, hosts/prey need refuges
    1. spatial
    2. numerical
    3. size

IV. Commensalism and mutualism (Ch. 15)
  - A. Commensalism is not well studied; four major categories are currently recognized
  - B. Mutualisms are +/+ interactions of great importance to the structure and diversity of the biosphere
    1. General overview
    2. Selected examples illustrate the complexity of mutualistic interactions

I. Classifying interspecific interactions according to fitness consequences

Ecologists have developed a lot of terms to describe specific kinds of interactions among individuals within and among species.

A. Grouping interactions according to common effects lets us study them in a more systematic fashion; improve understanding

B. Arguably most important effect = effects on fitness:

   1. effects on fitness = effects on birth, death
   2. therefore, effects on fitness translate into effects on population structure and dynamics

C. Although some disagreement among textbook authors, the essentials of the classification we'll use are pretty standard:

   1. -/- interactions have negative fitness consequences for all participants: **competition**
   2. +/- interactions have positive consequences for one, negative for the other: **exploitation** (includes **herbivory**, **parasitism**, **predation**, **pathogenesis**)
   3. +/0 interactions have positive consequences for one, no consequences for the other: **commensalism**
   4. +/+ interactions have positive consequences for both: **mutualism**

D. Note on terminology: **symbiosis** often used to refer to one or more of the above interactions

   1. term means, literally, “living together”; generally used to describe interactions involving intimate physical contact between individuals
   2. most often used to describe mutualistic interactions, but frequently used to describe others as well
   3. because of variability in use among ecologists, I don’t find term very useful; we won’t use it.

II. Competition

A. General introduction

1. Story: Threespot damselfish inhabit coral reefs of the north coast of Jamaica; each defends a territory of < 1m^2 containing shelter, food, and spawning grounds. Territories are patrolled regularly; fish attack any intruder. Not all individuals in the population have territories; some live on "margins" of territories. If a territory-holding fish dies (or is removed by an experimenter), other fish appear quickly to claim territory -- some threespot, some of other species. They fight for a few minutes until one "wins" –usually another threespot.
2. Story illustrates several important features of many (most?) **biological communities** (groups of individuals of different species inhabiting same area and interacting with each other):
   a. **resource limitation**:
      i. presence of non-territorial fish on margins plus quick "filling" of vacant territories indicates that territories are important resources, but not enough to go around.
      ii. At K, all populations face some kind of resource limitation -- food, space, etc. --and it's the limiting resources that set up the potential for competition.
      iii. note, though, that populations don't necessarily have to be at K to face resource limitation and competition
   b. **intraspecific competition**: territorial defense against conspecifics indicates that members of same species are in competition with one another for limiting resources
   c. **interspecific competition**: that individuals of other damselfish species also try to win vacant territories indicates that these species require the same limiting resource (space on reef) and compete for it
   d. **(a)symmetry of effects**:
      i. that threespots usually "win" indicates that they are "better" competitors than other species -- effects are "less -" for them than for individuals of other species
      ii. can get whole range of symmetries, from very symmetrical to very asymmetrical,

depending on species and resources involved

3. Other general points:
   a. by definition, competition (intra- or inter-specific) is a -/- interaction; fitness is harmed as a consequence of
      i. time, energy spent on competitive activities
      ii. loss of resources to competitors
   b. competition can take two general forms:
      i. **interference** = “direct” interactions among individuals (can involve actual fighting, ritualized displays, etc. -- not always tooth and fang!)
      ii. **exploitation** = more indirect; one individual exploits/monopolizes resource before another can get to it

B. Studies of **intraspecific competition** provide evidence for resource limitation: **note that competition generally inferred from obviously negative effects on fitness**

1. Grass *Sorghastrum nutans* competes for access to nitrogen
   a. as soil N increases, get increased shoot:root (grass grows taller, produces more above-ground biomass), indicating that N is a limiting resource
   b. experiment: plants grown at high and low densities across a range of N availability. Compared to low-density plants, high-density had (OH)
      i. higher root:shoot (allocating more energy to competition than above-ground growth)
      ii. lower biomass
      iii. lower growth rates
      iv. much lower response to increasing N
   c. conclusions:
      i. N is a limiting resource (because increasing N increases shoot:root)
      ii. competition for N increases with density (inferred from effects of crowding; lack of response to increased soil N)
      iii. in this case, fitness consequences fairly symmetrical among competitors
2. Many kinds of plants exhibit self-thinning (e.g., creosote from earlier)

a. density high as seedlings germinate, then declines over time (negative outcome = death!)
b. result of intraspecific competition for space (light), HOH, nutrients (in soil)
c. over time, density decreases as the biomass of survivors increases (OH)
d. note that, in this case, consequences asymmetrical -- some individuals “win” (survive, grow), others “lose” (die)
e. note also, though, that even “winners” presumably have lower fitness than they would have if they didn’t face competition

3. Planthoppers compete with each other for access to food
   a. *Prokelesisia marginata* feeds on sap of *Spartina* (marsh grass)
   b. experimenter enclosed Planthoppers at various densities comparable to those found in natural populations
   c. as density increased, saw (negative fitness consequences)
      i. decreased survivorship
      ii. decreased body size
      iii. slower development time
   d. at same time, sap from plants exposed to highest planthopper densities had
      i. less protein
      ii. less chlorophyll
      iii. less water
   e. conclusions similar to above:
      i. Planthoppers have limited food resources
      ii. competition for food increases with density
   f. note one important feature this study added (compared to others): study of plant sap <u>demonstrated decline in resource availability</u> with increase in density -- strengthens conclusion for resource limitation and competition
4. Conclusions from these kinds of studies (zillions done!)
   a. natural populations, at least at higher densities, face some form of resource limitation
   b. because individuals of the same species have the same resource requirements,

expect to see competition among individuals as density increases relative to the resource base

c. the outcome of competition is always negative for all competitors, but can vary from ~ symmetric (fitness losses ~ = among competitors) to highly asymmetric (big differences in fitness losses among competitors)

5. Now, extend these ideas to interactions among species:
   a. when species share similar resource requirements and resources limited, expect to see **interspecific competition**
   b. effects will be negative for individuals of both species
      i. because of negative effects on individuals, we expect to see effects manifested at the population level (i.e., effects on abundance, distribution, dynamics)
      ii. in fact, in many studies, population-level effects will be used to infer interspecific competition
   c. effects may range from ~ symmetric to highly asymmetric

C. The ecological niche reflects the environmental requirements of species and provides the conceptual foundation for understanding patterns of interspecific competition

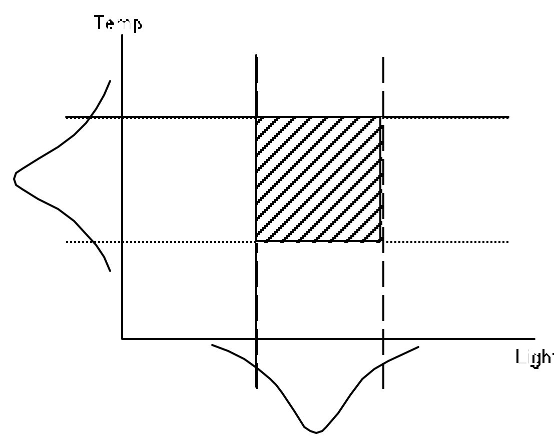
1. Concept of the niche was developed originally in early 1900's (1917, 1927)
   a. Joseph Grinnell -- CA ornithologist, first director of the Museum of Vertebrate Zoology at U.C. Berkeley: focused primarily on abiotic components of the niche (1917)
   b. Charles Elton -- early British animal community ecologist focused primarily on the biotic components (1927)
   c. combining concepts, niche = "role" played by an animal in its environment, including interactions with both abiotic and biotic components
2. The concept of the niche became more important with the work of Gause (population ecologist working in Russia) in early 1930's on population dynamics
   a. found that when 2 species of *Paramecium* using the same food were grown together, one died out and one maintained viable population
   b. concluded that populations of two species with the same requirements can't coexist in

nature -- the better competitor will eliminate the weaker competitor

c. his conclusion was reframed using the concept of the niche as a way to describe the requirements:
   i. two species with the same niche can't coexist in nature (or, two species can't occupy the same niche at the same time)
   ii. principle now called **principle of competitive exclusion**

d. with that formulation, the niche concept provided framework for trying to understand species interactions in natural communities

3. next advance came from G. Evelyn Hutchinson, British ecologist who spent much of professional career at Yale (and trained a generation of incredibly important and influential ecologists) in 1957:
   a. defined niche in quasi-mathematical terms as an **n-dimensional hypervolume**
      i. axes of volume = all the biotic and abiotic factors necessary for the species to maintain viable populations (e.g., water, food, temp, etc.)
      ii. "shape" determined by tolerance limits along each axis
      iii. e.g., using two dimensions to illustrate:
         a) axes = temp, light
         b) tolerance ranges from performance curves set "shape"
         c) niche = filled space



      iv. provided way to think about measuring niches vs. simply describing them
   b. distinguished between two "types" of niche:
      i. **fundamental niche** = sum of abiotic conditions under which species can establish, maintain viable populations (i.e., the sum of all abiotic conditions falling within the tolerance limits of the species)
      ii. **realized niche** = conditions under which species actually exists in nature

a) will usually be more restrictive than fundamental niche because of biotic interactions -- like competition -- among species sharing same fundamental niche

iii. ON YOUR OWN: How do Connell's barnacles (*Balanus* and *Chthalamus*) illustrate the difference between fundamental and realized niches?

4. practical considerations: how useful is the concept?
   a. in reality, impossible to fully characterize either fundamental or realized niche for most species (number of biotic and abiotic interactions huge, and many hard to measure)
   b. in practice, can often identify and measure a few key "niche dimensions" that play major role in species ecology -- e.g.
      i. beaks in Galápagos finches
      ii. tidal depth in barnacles
   c. even when can't pin down in detailed, quantitative way, useful concept for comparing features of communities whose species composition is different, but that we might expect to have some similarities (e.g., communities in same biome on different continents)

D. Interspecific competition can have significant ecological and evolutionary influences on species and their niches

1. **competitive exclusion** occurs when the strength of interspecific competition is greater than the strength of intraspecific competition:
   a. In this situation, selection will favor adaptations that make an individual better at competing against individuals of another species than at competing with individuals of its own species
   b. result will be a restriction in the realized niches of competing species such that species no longer occupy the same habitat – one excludes the other
   c. **competitive replacement** is a special case of competitive exclusion – and a major problem in conservation
      i. can happen when

a) exotics invade new habitats (especially problematic on islands); e.g.,
   i) European starlings outcompeting bluebirds and other cavity nesters
   ii) alewife and other introduced fish outcompeting native species for food
   iii) kudzu, multiflora rose, and exotic weedy plant species competing with natives for space, nutrients

b) habitat alteration changes the competitive relationships among species – e.g., *Phragmites*
   i) native marsh grass that thrives in distuburbed wetlands
   ii) when wetlands are disturbed, populations expand rapidly, outcompeting other plant species and the organisms that depend on them
   iii) result is ~ *Phragmites* monoculture, with much lower overall species diversity

d. Competitive exclusion is very difficult to demonstrate in the field (how do you test "why is this species absent"?) – but is often thought to be responsible for species replacement in space (similar species having adjoining, but non-overlapping, distributions)

2. Coexistence is possible when the strength of intraspecific competition is greater than the strength of interspecific competition, but resources must be shared somehow:

a. **niche partitioning** = species share the same geographic range, but have non-overlapping ecological ranges – two famous examples

i. Tansley (1917) studied competitive exclusion in bedstraw (*Galium saxatile* and *G. sylvestre)*

a) in nature, *G. saxatile* lives on acidic and *G. sylvestre* on basic soils

b) in lab, both germinate and grow on both soil types (but both do less well on acid soils) -- fundamental niches overlap

c) when grown in mixed plantings:
   i) in basic soils: *G. sylvestre* overgrows and eliminates *G. saxatile* within a year
   ii) in acidic soils, *G. saxatile* overgrows and eliminates *G. sylvestre*, but takes

6 years because both grow more slowly on acid soils

d) conclude: interspecific competition restricts realized niche of both species

ii. Joseph Connell's barnacles (from prev. discussion):

a) *Balanus* and *Chthalamus* both settle throughout middle intertidal, but only *Balanus* persists

b) grown alone, *Chthalamus* can survive well in middle intertidal (fundamental niches overlap)

c) Connell did removal experiments on several sites across intertidal

i) in upper intertidal, removal of *Balanus* had no effect on *Chthamalus* densities (B. densities too low to have any effect to begin with)

ii) in mid-intertidal, removal of B. greatly increased *Chthamalus* survivorship

d) other studies indicated that B's competitive advantage due to dense settlement and rapid growth -- it crowds out *Chthamalus*

b. **morphological character displacement** = evolutionary change in the morphology of species such that, where the two species co-occur, they occupy different fundamental niches

i. This idea was developed by Brown and Wilson (1956); formal definition = **the morphology of two species is more similar where they occur in allopatry than where they occur in sympatry**

ii. because morphology assumed to be correlated with niche, can restate in terms of niches: niches are more similar in allopatry than in sympatry

iii. reasoning:

a) as morphological (niche) similarity increases, so does competition

b) where species coexist, selection should favor those individuals in both populations that compete the least

c) those should be the individuals who are most different from each other (have the least niche overlap)

d) therefore, should get directional selection on populations of both species, increasing the differences

e) in allopatry, no competition –> no selection pressure to change

iv. best e.g.: Galápagos finches: OH

a) beak size in *Geospiza fortis* alone on Daphne Major overlaps that of *G. fuliginosa* on Los Hermanos

b) where both occur on Santa Cruz, no overlap

i) *G. fortis* much larger than on Daphne Major

ii) *G. fuliginosa* much smaller than on Los Hermanos

c) have lots of evidence from years of study by Peter and Rosemary Grant et al. that

i) beak size is strongly correlated with size of seeds eaten

ii) birds compete intra- and interspecifically for access to seeds

d) consequently, reasonable to conclude that differences in beak size are long-term, evolutionary result of interspecific competition on Los Hermanos

v. unfortunately, as nifty as the hypothesis is, it's actually very difficult to find good examples -- ones where we can demonstrate not only the morphological pattern itself, but the role of competition in producing it.

E. Interspecific competition may help regulate population size in coexisting competitors

1. As mentioned earlier, the negative fitness effects of competition on individual competitors should be reflected at the population level – specifically, should affect population size

a. remember that shared resource is in limited supply

b. if populations of two species are using the same limited resource, neither will be as large as if only one species were present

c. NOTE: this premise is the basis for using removal experiments to test interspecific competition – a very common approach!

2. test with removal experiments: excellent e.g. = work done by Jim Brown et al. on LTER at Portal, Arizona

a. Chihuahuan desert community; major food resource = seeds of annual plants

b. numerous studies have demonstrated that seeds are a limited resource that affect the abundance, distribution of populations of many species (mammals, birds, ants, lizards)
c. small mammal community includes variety of rats and mice
   i. some specialized granivores (k-rats, pocket mice, some deer mice)
   ii. two species of insectivores: grasshopper mice
d. based on information from other studies, hypothesized that granivorous rodents competed for seeds (but obviously not enough for complete competitive exclusion)
e. tested using removal experiments:
   i. fenced in 50x50m study plots: fences deep & high enough to prevent rodents from digging under/climbing over
   ii. in control plots, made openings big enough to allow all rodents free access
   iii. in experimental plots, made openings small enough to exclude large granivores (k-rats), but not small granivores (pocket mice) or insectivores (grasshopper mice) -- call system “semipermeable fences”!
   iv. removed k-rats from experimental plots
   v. predicted that, if granivores competed for seeds, removal of large granivores should result in
      a) increase in small granivore populations (**competitive release**)
      b) no change in insectivore populations
   vi. results confirm predictions, hypothesis
f. important caveat for removal experiments: because species within communities interact in complex ways, increase in population of one species following removal of another isn’t always a consequence of competitive release, so isn’t always evidence for competition
   i. simplistic hypothetical e.g.s:
      a) black-footed ferrets prey(ed) on prairie dogs; burrowing owls use prairie dog burrows for nesting
      b) remove ferrets, burrrowing owl population could increase – but not because they were competing with ferrets!

ii. phenomenon called **apparent competition** -- important to be sure (through natural history, appropriate experimental design, etc.) that's not what's going on

F. The effects and prevalence of interspecific competition have been controversial issues in ecology

1. After mathematical, laboratory models developed in early 1900's, lots of theoretical work (esp. Robert MacArthur et al.) into 40's, 50's, 60's; interspecific competition often assumed or inferred based on relatively little evidence
2. As investigators began testing theoretical models in the field, began to find patterns inconsistent with the theoretical models -- period of 1970's and '80's saw lots of controversy over assumptions of models, validity of conclusions of earlier studies, most appropriate methods for studying, etc.
3. Upshot was/is debate over relative importance of competition as ecological and evolutionary factor
4. Among other things, generally accepted now that competition has its greatest effects in favorable, stable habitats; it will be less important a process in disturbed, unpredictable, resource-limited environments

II. Exploitation:

A. Definitions and complexities:

1. By definition, exploitative interactions are those in which one species benefits at the expense of another (+/- fitness effects)
2. Lots of different terms describing different forms of exploitation:
   a. **herbivory**: animals eat plants, usually without killing
   b. **predation**: animals eat other animals; prey is killed
   c. **parasitism**: one organism derives ongoing nourishment from another at the other's expense; usually without killing host
   d. **parasitoid**: larvae of one species of insect feeds on and kills host insect
   e. **pathogen**: microorganism causing disease = fundamental alteration in the physiology of host

3. Note some complexities: these terms don't really express full diversity of interactions in nature
    a. distinctions among forms sometimes subtle: e.g., parasite vs. parasitoid; pathogen vs. parasite; herbivore vs. parasite
    b. some kinds of interactions don't fit neatly: e.g.
        i. granivores sometimes called seed predators
        ii. parasites sometimes kill hosts
        iii. detritivores don't kill anything, or even "harm" their prey
4. We'll generally lump all together under heading "exploitation"; examples will come mostly from predation, parasitism

B. Exploitation is a strong selective force for both exploiter and exploited
1. Think of any kind of organism -- among the most obvious adaptations will be those that allow it to feed (exploit) and avoid being eaten:
    a. E.g. plant defenses against herbivory: spines, chemicals, dropping infected leaves
    b. E.g. animal feeding adaptations: jaws/claws, traps, venoms/toxins
    c. E.g. animal defensive adaptations: crypsis, chemical defenses/warning colors, mimicry
    d. Less obvious (but pretty cool) are adaptations of, e.g.
        i. parasites, pathogens to infect hosts (more later)
        ii. host anatomical, immunological defenses against parasitism, disease

C. Predation, parasitism, and pathogens can affect the distribution, abundance, and population structure of prey/hosts
1. Should be self-evident that all three will have the effect of increasing death rates and decreasing birth rates (at least latter 2); consequently, can clearly affect r
2. E.g. of direct, dramatic effect of exploiter on prey populations: caddisfly larvae and benthic algae, bacteria (note sophistication of exp. design -- not always easy to do this with most predator/prey populations!)
    a. caddisfly larvae = benthic stream inverts; major inverts in NA streams
    b. *Helicopsyche borealis* larvae graze on algae, bacteria on exposed surfaces of

submerged stones etc.

c. investigators studied populations in Big Sulfur Creek, CA:
   i. over summer and fall, larvae attain densities of 4,000 individuals/m^2; comprise 25% of benthic animal biomass
   ii. did exclusion experiment to test the effects of larvae on food supply:
      a) control "plot" = unglazed ceramic tiles placed on streambed:
         i) available for colonization by algae, bacteria
         ii) accessible to larvae & other invertebrates
      b) experimental "plot" = same number, arrangement of tiles elevated above streambed on supports that prevent larvae from climbing up onto tiles (demonstrated this in preliminary exp.)
         i) available for colonization by algae, bacteria
         ii) inaccessible to larvae, but accessible to other inverts
      c) even though algae, bacteria on experimental "plot" available to other inverts as food, saw greatly increased density due to exclusion of larvae

3. E.g. of effect of exploiter on pop size and distribution: *Cactoblastis* and *Opuntia* in Australia : an example of biological control
   a. *Opuntia* introduced into Australia mid-1800's as ornamental and to establish cochineal (red dye produced by insects) trade; "escaped" from cultivation
   b. by 1930, covered over 24 million ha in stands of up to 12,000 ind/ha -- obvious problem!
   c. Aus. gov't hired biologists to come up with control agent; came up with moth *Cactoblastis cactorum*
      i. females deposit eggs on Opuntia pads
      ii. larvae hatch, burrow into pads, feed on pads (are they herbivores or parasites?)
      iii. burrowing of caterpillars also introduces variety of fungi, bacteria that also attack internal tissues
      iv. combined effects of caterpillars, microbes reduce internal tissues to mush; cactus

collapse and die

d. Two years after release of *Cactoblastis*, *Opuntia* population densities reduced from 12,000 ind/ha to 27/ha; area covered fell to a few thousand acres

e. other effect was on *distribution* of populations: remaining pop's highly dispersed; get dynamic interactions now

   i. individual pop's not as easily found by moths -- able to grow

   ii. eventually, moths find them, invade -->pop's decline

   iii. meanwhile, other pop's in other areas growing, etc.

f. Note about success of biological control

   i. one key to success of biological control is that "control agent" remain specific to its target – in many cases, that doesn't happen

   ii. in Australia, *Opuntia* is introduced and that's the only thing the moth larvae feed on – it works

   iii. in the Caribbean and in Florida, problem is arising:

      a) moth was imported to control *native* species that prevented conversion of land to agriculture and ranching

      b) has now migrated into south Florida, where it attacks native *Opuntia* there, including some very rare species

4. Of course, for many species, predation highly age-dependent, so has major affect on survivorship and age structure of populations as well

D. Exploitation leads to complex interactions among species within a community

1. parasites can change host behavior so as to increase transmission from host to host (cool!)

   a. note that many parasites require multiple hosts to complete their life cycles; traits that increases transmission from one host to the next will be selectively favored

   b. spiny-headed worms (Acanthacephalans) well known for this; e.g. = *Plagiorhyncus cylindraceus*, isopod (pill bug) *Armadillidium vulgare*, and European starling *Sturnus vulgaris* studied by Janice Moore:

i. Parasite life cycle =
    a) adults in birds lay eggs shed with feces
    b) amphipod (intermediate host) ingests eggs; parasite hatches; in 60-65 days larvae developed enough to infect vertebrate host
    c) bird eats amphipod, parasites complete life cycle (including reproduction) attached to host intestinal walls
ii. Moore demonstrated in lab experiments that
    a) compared with uninfected isopods, infected individuals
        i) spent more time on light vs. dark substrates
        ii) spent more time in low-humidity than high humidity sites
        iii) spent less time in sheltered than unsheltered sites
    b) these traits correspond to more open microenvironments in the field, where amphipods are presumably more susceptible to predation
    c) also demonstrated that
        i) in the lab, starlings eat more isopods from light-colored than from dark-colored substrates,
        ii) in the wild, starlings eat a higher proportion of infected isopods than predicted if they fed at random on available isopods
iii. conclusion = parasite alters isopod behavior in very specific way -- to increase transmission
iv. lots of other e.g. from this group of parasites

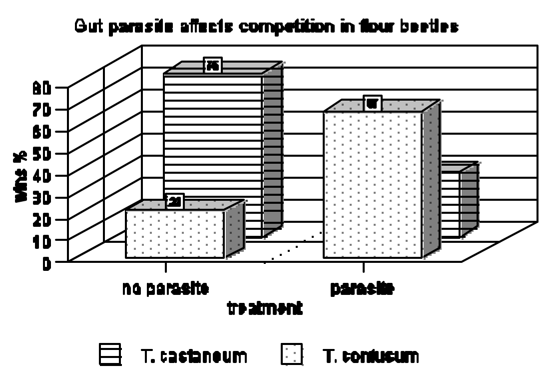
c. fungal plant parasite alters development and morphology (= "plant behavior") to increase own reproductive success:
    i. parasite = rust *Puccinia monoica*; host = mustard *Arabis* from Rocky Mountains
    ii. rust requires outcrossing for sexual reproduction
    iii. normal host life cycle =
        a) spend few months - several years as low-growing "rosette", storing energy underground
        b) when has enough energy, "bolts" (= rapid growth of stalk), flowers, sets seed.

iv. when rust infects:
   a) attacks rosette stage in late summer, invading meristem tissue in the following winter
   b) manipulates development such that rosettes produce elongated stalk with high density of bright yellow leaves
   c) at top of stalk, leaves form “pseudoflower” resembling buttercups
   d) tissues of pseudoflowers include fungal tissues, esp. reproductive cells and sexually receptive hyphae
   e) fungus also produces sweet, sticky fluid containing repro. cells

v. butterflies, bees, flies attracted to flowers, fluid; transfer repro cells from pseudoflower to pseudoflower (just as they would pollen!)

vi. changes to development generally truncate development of host, often killing it outright (so is it a parasite or predator?)

2. Exploitation can moderate/alter the effects of interspecific competition by altering the dynamics of competitor populations
   a. competitive interactions between species of flour beetles affected by gut parasite
      i. *Tribolium castaneum* and *T. confusum* = popular laboratory model species for studying effects of competition etc.
      ii. interspecific competition includes predation; mostly of *T. castaneum* on *T. confusum.* (so is it competition or exploitation?)
      iii. gut parasite *Adelina tribolii* transmitted when infected beetle eaten by another beetle (so which sp. should have higher infection rates?)
      iv. when parasite absent, *T. castaneum* usually outcompetes *T. confusum*
      v. when parasite present, reverse happens



   b. Predatory starfish reduces competition among tidepool invertebrates (very famous study by Paine)

i. Starfish *Pisaster ochraceus* feeds on variety of chitons, mussels, barnacles in intertidal zone

ii. experimental removal of *Pisaster* led to reduction of # of species from 15 ->2 after 5 years (competitive exclusion!):

a) lost barnacles, several algae, chitons, limpets, sponges & their nudibranch predators, etc.

b) only spp left after 5 years were one mussel, one barnacle

c) mussel, barnacle left outcompeted other spp. for space

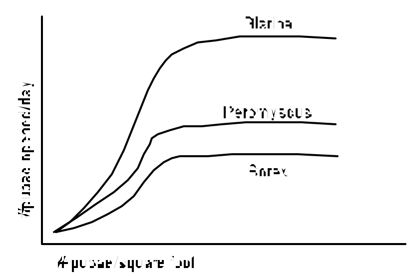
d) mussel = one of *Pisaster*'s preferred prey items in that system

iii. conclusion: presence of predator keeps populations of strong competitor low enough to prevent competitive exclusion of other spp.

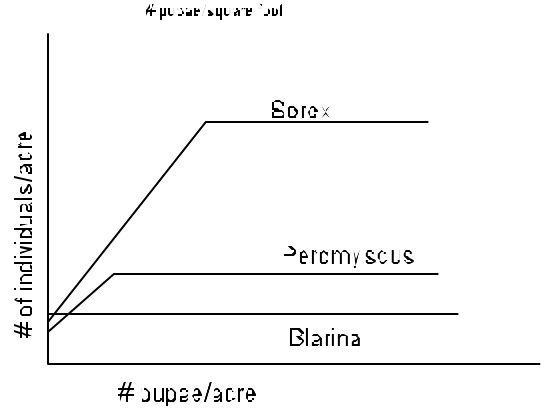
E. Interactions among exploiters and exploited populations are dynamic and complex

1. over relatively short time spans, predator density may or may not change with changes in prey density: as prey densities increase can get

   a. **functional response** = rate at which predators feed increases, then levels off (why?) – e.g., small mammals feeding on pine sawfly larvae



   b. **numerical response**: predators increase in number (increase r) e.g., from same system:



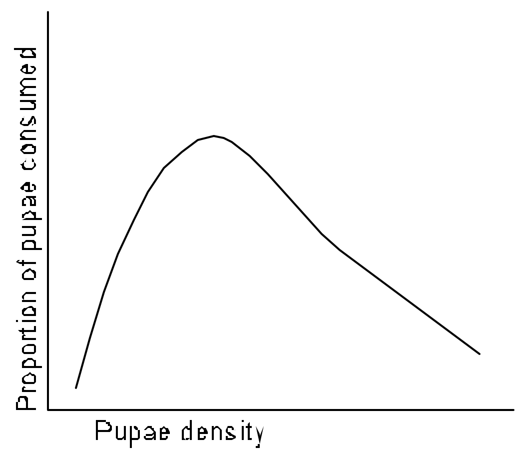
2. over long time periods, interactions among predators, prey, and prey's food species can produce complex population patterns -- famous e.g. = population cycles of Canadian lynx and snowshoe hare

   a. initial data from Hudson Bay Company trapping records; has been studied more recently as well

b. pattern = coordinated cycles over ~ 10-yr periods, with lynx populations lagging just behind hare populations
c. obvious explanation:
   i. as hare pop's increase, lynx pop's increase (with bit of lag) = numerical response
   ii. as lynx populations increase, have greater effect on hare pop's, causing hare pop's to decline
   iii. as hare pop's decline, lynx decline (with bit of lag)
   iv. decline in lynx pop's allows hare pops to go back up
d. now realize situation more complex than that: interaction includes hare's food supply as well:
   i. snowshoe hares have very high r: can double pop size in 1 generation
   ii. in winter, feed on the buds, small stems of shrubs
   iii. as hare populations increase, get
      a) numerical response in lynx population (with lag)
      b) increasing levels of herbivory (one population found to decrease biomass from 530 kg/ha in November to 160 kg/ha in March)
      c) high feeding rates induce plants to produce secondary chemicals (defensive compounds) making plants unpalatable – these can last up to 2 years
   iv. so, get increasing predation and declining food supply (direct due to feeding; indirect due to increased defensive chemical concentrations) -> hare populations decline rapidly
   v. as hare pop's decline, lynx decline and plants begin to recover
   vi. cycle starts again as predation pressure minimal and plants more palatable
e. note that lots of animal populations exhibit complex cycles; not all involve predation (causes not always understood, even now)

F. To persist in the face of exploitation, hosts/prey need refuges: = ways to "escape"or avoid predation. These can take several forms, e.g.
   1. spatial
      a. on a local scale, obvious spatial refuge = place to hide from predator

b. on a larger spatial scale, habitat patches can be refugia for whole populations
   i. e.g., *Cactoblastis* populations don't prey on *Opuntia* pop's at high elevation (too cold) or on poor soils (nutritional quality of tissues too poor)
   ii. immigration from "refugia" can maintain local populations in spite of predation pressure
   iii. conservation implications?
2. numerical: "safety in numbers" can happen for several reasons
   a. mutual protection
   b. large numbers of individuals can cause visual confusion in predators (e.g., schooling fish)
   c. **predator satiation**: as prey density increases to high level, proportion of individuals preyed upon decreases
      i. results from combined effects of functional and numerical responses
      ii. using previous example, response looks like:



         a) as prey density increases, individual predators eat more (functional response) & have more offspring (numerical response) –>proportion of prey consumed goes up
         b) past some threshold, individuals can't eat any more or reproduce any faster
         c) as prey densities increase past that point, "extra" individuals relatively safe; **proportion** consumed declines
      iii. in nature, many kinds of "prey" seem to use this strategy:
         a) **masting** in trees = widespread, synchronous seed and fruit production follows this pattern

b) periodic cicadas = insect example

3. size
   a. predation almost always size-selective (i.e., predators select limited sizes from among the range of sizes available in prey population)
   b. reason matter of cost/benefit:
      i. capturing, subduing, handling, consuming prey all takes energy (collectively = **handling cost**)
      ii. energy cost of handling often increases with prey size
      iii. at some point, energy benefit of large prey outweighed by extra energy cost of handling (some prey just too big to be profitable)
      iv. therefore, large size is a type of refuge from predation
         a) one reason for Type III survivorship curves
         b) can lead to anatomical and behavioral adaptations to give the appearance of large size
            i) frog puffs up body, stands up on legs
            ii) birds/mammals may “fluff up” feathers/fur
            iii) insects alter posture

IV. Commensalism and mutualism

A. Commensalism is not well studied; four major categories are currently recognized
1. By definition, commensalisms are +/0 interactions
   a. Compared to other kinds of interactions, these have received relatively little attention
   b. Four general types are recognized:
      i. **trophic**: one species receives a food benefit; considered fairly rare
      ii. **transport**: one species gets dispersal or other transport from the other (e.g., passive dispersal of plant seeds; flower mites on humming birds); fairly common
      iii. **structural/support**: one species gets space, position from another; very common in tropics (epiphytes) and in aquatic systems (e.g., barnacles on whales; algae on corals, etc.) – but note that we often assume no cost without carefully examining the

system

iv. **shelter**: probably among most common in both terrestrial (burrows) and aquatic (nooks and crannies in corals, sponges) systems – very important interaction! – e.g., aardvark burrows are used by at least 12 different vertebrate species (including whole families of warthogs and one species of bat)

c. To the extent that one member of interaction receives important benefit, commensal relationships are important consideration in conservation efforts (e.g., gopher tortoises, indigo snakes in longleaf pine)

B. Mutualisms are +/+ interactions of great importance to the structure and diversity of the biosphere

1. General overview
   a. As we'll see, mutualistic interactions are very common
   b. Coral reef and the majority of terrestrial plant communities depend on mutualisms -- those alone make mutualism critical to the structure and diversity of the biosphere!
   c. Mutualisms can be classified two ways:
      i. by "necessity" of mutualism to species involved:
         a) **facultative** provide benefits, but not necessary for individual survival
         b) **obligate** are required for individuals to survive
      ii. by kind of benefit received: usually, one member of the mutualistic pair receives energy and/or nutrients; the other can receive other benefits: OH
         a) **trophic**: species have complementary ways of acquiring nutrients - e.g.s of extremely important trophic mutualisms are
            i) plants and mycorrhizae
            ii) corals and zooxanthellae
         b) **defensive**: one species provides a protective function in return for energy/ nutrients; examples include
            i) "cleaner" fish remove parasites from other fish
            ii) ants and acacias (and other ant-plant associations): ants protect acacias

from herbivores and from competing plant species; trees provide shelter (thorns) and food (Beltian bodies + sugary exudates)

iii) root nodules on leguminous plants provide shelter (a type of defense) for nitrogen-fixing bacteria

c) **dispersive**: organisms receive energy in exchange for dispersing gametes, propagules; really important examples are from plants

i) pollination

ii) seed dispersal

2. Selected examples illustrate the complexity of mutualistic interactions

a. The “strength” of mycorrhizal mutualisms can vary with soil fertility (environmental condition)

i. general system:

a) mycorrhizae help plants acquire HOH, mineral nutrients (especially nitrogen, phosphorous) from soil

b) fungi feed off soluble carbohydrates (exudates) released by plant roots

c) in general, the amount of exudate decreases with soil fertility (as fertility increases, exudate decreases -- why?)

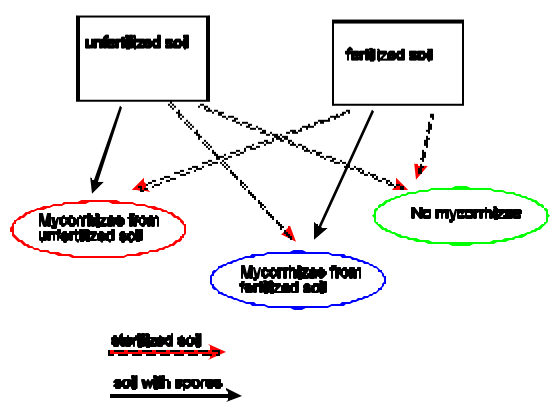
ii. Nancy Johnson predicted that increasing soil fertility would select for less mutualistic mycorrhizal species:

a) reasoning: as fertility increases, selection favors strains that can live with less exudate; these likely to be more aggressive in the acquisition of carbs, at the expense of the host plant

b) experimental test: compared soils from abandoned fields with and without a history of added fertilizers

i) different mycorrhizal species dominated each type of soil

ii) grew grass (big bluestem,



Andropogon) on both kinds of soils with and without mycorrhizae; with and without extra nutrients

c) results:

i) graph 1: grass w/mycorrhizae grew larger at all 4 nutrient levels (mycorrhizae benefit plants)

ii) graph 2: adding nutrients and mycorrhizae reduced root:shoot ratios; slight difference in +N+P treatment between mycorrhizae from fertilized vs. unfertilized soils

iii) graph 3: plants with mycorrhizae produce more flowers; plants with mycorrhizae from unfertilized soils produced most flowers

b. Corals, zooxanthellae, and crustaceans have 3-way mutualism:

i. Zooxanthellae (algae) live w/in coral tissues at densities ~ 1 million cells/cm^2 of coral surface (note -- not all coral species do this!)

ii. Zooxanthellae photosynthetic; provide coral with photosynthate

a) corals regulate excretion of photosynthate by producing molecules that increase permeability of zooxanthellae membranes

b) in presence of coral, zooxanthellae produces fixed carbon at higher rate than without; excretes 90-99% of fixed carbon for corals

c) by regulating fixed-carbon production and secretion, coral also regulates zooxanthellae pop growth

iii. Zooxanthellae receive nutrients from coral (by-products of coral's predation on zooplankton); especially nitrogen and phosphorous

iv. Corals from several genera have mutualistic relationship with several crustacean species:

a) crustaceans protect coral from predation by sea stars

b) one investigator (Glynn) also noted that protected corals have overall better tissue health/integrity (less invasion of dying tissues by tunicates, algae, sponges)

c) crustaceans get food and shelter (like ants!):

- i) corals have tight branching structure, providing protective shelter
- ii) corals provide lipid-rich mucous secretions for crustaceans
  - a) in some species, crabs stimulate mucus production by inserting legs into polyps
  - b) in others, lipid is concentrated into fat bodies -- produced at higher rate in presence of crabs than without crabs
- iii) release of lipids with mucus may constitute up to 40% of daily photosynthetic production of zooxanthellae (bringing system full-circle!)

c. Humans in Africa seem to have evolved a mutualism with honeyguides (birds)

- i. interaction is between traditional honey gatherers and the greater honeyguide (*Indicator indicator* - member of woodpecker family)
- ii. honey gathering at least 20,000 yrs old (rock art that old)
- iii. mutualism is facultative: honeyguide lives on beeswax and bees (all stages); can live independently of humans
- iv. will actively guide humans and ratels (honey badgers) to bees nests by flying close to a human and calling; it then flies off toward the nest, stopping to call periodically -- humans whistle, bang on wood, etc., to “keep the bird interested”
- v. both species benefit: humans find hives more easily; bird gets food more easily as humans raid hives
- vi. Isak (member of tribe of traditional honey gatherers) studied birds and humans to test three assertions of honey gatherers: that birds inform them of
  - a) <u>direction of nest</u>: by direction of flight
    - i) induced birds to guide to same nest from same starting point on 5 occasions
    - ii) induced birds to guide to same nest from different starting points
    - iii) results: birds consistently led toward nest (OH)
  - b) <u>distance to nest</u>: by decreasing three things as distance decreases:
    - i) time spent out of sight between first encounter and first stop
    - ii) distance between stops on way to nest
    - iii) height of perch on way to nest

iv) results: all three consistently decrease with distance to nest

c) when they arrive at the location of the nest: by changing vocalization and behavior -- Isak observed

i) when guiding, birds emit distinctive call and answer human calls by increasing frequency of guiding call

ii) when reaches nest, bird perches and gives special “indication” call repeated a few times; doesn’t “answer” human calls

iii) when reaches nest, if approached by human, flies in a circle around the location before perching again.

iv) these results (which are pretty cool in and of themselves!) prompted Robert May to wonder how much important ecological knowledge we’re losing as a result of loss of traditional cultures -- important to think about!

3. ON YOUR OWN:

a. read example of bullshorn acacia & ant mutualism; answer review question #5

b. read example of ant-sunflower mutualism, with special attention to the characteristics of this system that favor facultative, but not obligate, mutualism