Unit 4: Community Ecology

See topic and resource outline for readings, activities

I. Overview:
   A. Communities are groups of individuals of different species that live in the same place and interact with one another.
   B. We’ll focus on two basic aspects of community structure and function because they are the most important for understanding the potential consequences of human impacts on the environment and how we can best avoid or mitigate them:
      1. biodiversity within communities
      2. interactions among species within communities

II. Biodiversity: how much is there and why does it vary?
   A. The simplest way to conceive of biodiversity is to think of how many different species live in a community. But that's an oversimplification. To see why, consider the two “communities” below:
      1. Intuitively, we perceive Community A as being more diverse, even though it has the same number of species as Community B
      2. That's because Community B has 4 individuals of one species and only 1 individual each of 3 species; Community A has 2 of each.
   B. In formal terms, this example illustrates that biodiversity is a bit more complex than just the number of species:
      1. Biodiversity has two components that must be taken into account:
a. **species richness** = the number of species in a community

b. **species evenness** = the relative abundance of each species

2. This makes sense ecologically – a community that is dominated by one species will have fewer different kinds of ecological interactions than will a community that has a more equal abundance of each of its component species.

a. Note the important implication here – biodiversity can be reduced even if no species are actually lost from their community!

b. Ecologists use a variety of different ways to measure, calculate, and illustrate biodiversity – but all of them take these two components into account.

C. Biodiversity varies enormously among communities (think of tropical rainforest vs. arctic tundra).

1. Ecologists have been trying to determine why some communities are more diverse than others for a long time, but good general explanations are hard to find.

2. Two general patterns are common enough to mention (but note that they aren’t universal):

a. **Biodiversity is often higher in more structurally complex communities than in structurally simple communities.** Compare, e.g., a typical deciduous forest with a typical grassland:

   (1) The forest will often have at least four distinct layers of vegetation: low ground cover, shrubs, small trees, and tall trees; the grassland will have one or two (if there are a few shrubs or trees)

   (2) Because it has a more complex structure, the forest presumably has more ecological niches (roughly, ways organisms can “make a living” in the habitat) – and can therefore support a greater diversity of species than can the grassland.

   (3) This pattern becomes important when we try to restore
b. **Biodiversity is often higher in communities that experience periodic, mild disturbance than it is in communities that are either heavily disturbed or not disturbed at all.**

(1) E.g., the Great Plains – U.S. grasslands. Important disturbances there are fire and grazing.

(a) Grasslands that are overgrazed show a reduction in biodiversity as the species grazers like to eat are replaced by a few unpalatable species

(b) Grasslands where fire and grazers are both completely eliminated show a reduction in biodiversity as a few strong competitors replace other species.

(c) Grasslands with natural (intermediate) levels of fire and grazing show the greatest diversity.

(2) The explanation here has to do with competition and adaptation to abiotic conditions:

(a) When communities are heavily disturbed, there are often only a few species adapted to tolerate the conditions the disturbance creates.

(b) When communities are not disturbed at all, the best competitor often “takes over.”

(c) At intermediate levels of disturbance, many species can tolerate conditions and no one species can outcompete the rest.

(3) Understanding disturbance and its effects on communities is also very important in conservation – particularly when we’re trying to manage/restore communities.

D. Application: Restoring the Kissimmee River – combining principles of habitat complexity and moderate disturbance
1. Introduction to rivers and floodplains
   a. Rivers + floodplains are complex, dynamic landscapes whose elements include river, riparian forest, marsh, oxbow lakes, and wet meadow ecosystems
   b. Flooding is a critical process that “connects” river with floodplain and influences many important processes:
      (1) floods affect the complexity of landscape structure by
          (a) depositing silt on floodplains
          (b) isolating oxbow lakes
          (c) creating new river channels
      (2) Floods influence nutrient cycling and decomposition
      (3) many species of river fish use flooded floodplains as spawning and nursery grounds
      (4) many species of plants require flooding for germination and seedling establishment
      (5) rates, timing, and extent of these processes are a function of the rate, timing, and extent of the “flood pulse”
   c. Human management of riverine systems has focused primarily on flood control, which has had the overall effect of “disconnecting” rivers from floodplains and disrupting the processes above
   d. After decades of this type of management, we now recognize that flood management efforts result in loss of water quality and biodiversity.
   e. This has led to efforts to restore riverine systems
2. Natural history of the Kissimmee River:
   a. The Kissimmee River flows from headwaters in Lake Kissimmee (near Orlando) south into Lake Okeechobee (in the heart of the Everglades).
   b. The historical landscape included
      (1) highly braided, meandering channel ~ 103 miles long
(2) floodplain 1-2 miles wide & 56 miles long that included 35,000 acres of wetland
(3) a variety of ecosystems, including oxbow lakes and four types of marshes
c. Flooding generally inundated 94% of floodplain for ~ 6 months at a time – river flooded more of its floodplain for longer periods than any other river in NA
d. Because of extent and duration of inundation, river “acted” much like large tropical river – the tight linkage between river and floodplain was very important to organisms living there
e. Before its modification, this complex landscape supported
   (1) 48 species of fish
   (2) 16 species of wading birds
   (3) 22 species of ducks and other water birds
   (4) hundreds of species of aquatic invertebrates
3. Human population growth in early 1940’s plus extensive flooding in 1947-1948 prompted flood control efforts – they included
a. channelizing the river: river converted into system of
   (1) 5 reservoirs connected by
   (2) a straight canal 30 feet deep, 300 feet wide, 56 miles long
b. This eliminated 30,000 acres of floodplain wetlands within the landscape and filled in former river channels
c. This effort
   (1) Reduced the complexity of the landscape (made it structurally simpler) and
   (2) Reduced the level of disturbance by eliminating the natural flood pulse
d. The effects on the the river system included:
   (1) reduced winter waterbird populations by 92%
(2) large mouth bass populations replaced by non-game species that tolerate low oxygen concentrations
(3) populations of riverine inverts replaced by inverts typical of ponds and lakes
(4) reduction of exchange of nutrients, organic matter, and organisms between river and floodplain
(5) loss of spawning and foraging habitat for adult fish
(6) loss of “safe” habitats and nursery areas for larval/juvenile fish
(7) excessive agricultural runoff (pesticides, fertilizer) into Lake Okeechobee and the Everglades

4. By mid-1980s, people realized that effects of channelization were, on balance, negative; restoration was mandated and a test project began in 1984 – the project included
   a. building weirs to divert water from canal into remnant river channels
   b. fluctuating water levels within one of the reservoirs to restore flooding
   c. In other words, restoration included restoring structural complexity and moderate levels of disturbance.

5. The results were fairly quick and impressive: within just a few years,
   a. native vegetation returned; exotics declined
   b. flow through remnant channels cleared detritus and restored channels
   c. riverine inverts recolonized remnant channels
   d. fish moved into flooded areas
   e. fish requiring high dissolved oxygen returned
   f. wetlands attracted more waterfowl

6. Consequence is that a major restoration project was authorized by Congress in 1992; major features will include
   a. restoring historical landscape structure by restoring complex channel network and reestablishing floodplain marshes
   b. restoring flood pulses to “reconnect” river with floodplain
c. In total, “The project will restore over 40 square miles of river/floodplain ecosystem including 43 miles of meandering river channel and 27,000 acres of wetland.” (Kissimmee River Restoration Project website, http://www.sfwmd.gov/org/erd/krr/)

d. On your own, read about the completion of Phase I in 2004 – how did it go?

III. Interactions among species within communities

A. Introduction to interactions: interactions among species in communities become very complex very quickly! We’ll look at interactions based on how they affect the fitness of individuals or the status of populations that engage in them, with the goal of understanding how natural communities work and how invasive species can disrupt them. Note that I use slightly different terms than does the text:

1. **Competition** among species happens whenever two species require the same important resources; whether direct or indirect, it harms both parties.

2. **Exploitation** includes all the interactions in which one individual benefits from an interaction and another is harmed. The most important exploitative interactions in communities are
   a. predation/herbivory
   b. parasitism

3. **Commensalism** is a relationship in which one individual benefits and one is neither harmed nor benefited. Commensal relationships are often extremely important in maintaining biodiversity.

4. **Mutualism** is a relationship in which both parties benefit. Much of the diversity of life in both terrestrial and marine communities depends on mutualistic relationships.

B. **Competition** can happen within species and among different species. We’ll focus here on competition among species = interspecific competition.

1. The **ecological niche** reflects the environmental requirements of species
and provides the conceptual foundation for understanding patterns of interspecific competition
a. Concept of the niche was developed originally in early 1900’s;
b. combining concepts developed by several biologists working independently, ecological niche = “role” played by an animal in its environment, including interactions with both abiotic and biotic components
c. e.g., the ecological niche of white-footed mice includes:
   (1) eat acorns, gypsy moth pupae, berries, etc.
   (2) climbs trees
   (3) is active at night
   (4) breeds in the spring, but may breed throughout the year
   (5) rears young in protected nests
   (6) does not hibernate
   (7) requires relatively mild temperatures
   (8) can’t tolerate extremely dry environments

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
   (1) one species will inevitably have adaptations that make it better at acquiring resources than the other
   (2) this better competitor will eliminate the weaker competitor from the habitat
c. Later, his conclusion was reframed using the concept of the niche as a way to describe the shared requirements that lead to competition:
two species with the same niche can’t coexist in nature (or, two species can’t occupy the same niche at the same time)

(2) principle now called principle of competitive exclusion

3. In natural communities, the degree to which niches are similar can vary – so we can get different degrees of competition and a wide range of outcomes

a. Competition isn’t strong enough to eliminate either species, but

regulates population size of both. E.g. – effect of competition among seed-eating rodents in Chihuahuan desert = work done by Jim Brown et al. on LTER at Portal, Arizona

(1) Chihuahuan desert community; major food resource = seeds of annual plants

(2) Numerous studies have demonstrated that seeds are a limited resource that affect the abundance, distribution of populations of many species (mammals, birds, ants, lizards)

(3) Small mammal community includes variety of rats and mice

(a) some specialized granivores (“seed-eaters” such as kangaroo rats, pocket mice, some deer mice)

(b) two species of insectivores: grasshopper mice

(4) Based on information from other studies, hypothesized that granivorous rodents competed for seeds (but not enough for complete competitive exclusion)

(5) Tested using removal experiments:

(a) fenced in 50x50m study plots: fences deep & high enough to prevent rodents from digging under/climbing over

(b) in control plots, made openings big enough to allow all rodents free access

(c) 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”!

(d) removed k-rats from experimental plots

(6) 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

(7) results confirm predictions, hypothesis

b. Competition is too strong for complete coexistence, but not strong enough for complete exclusion. This results in **niche or resource partitioning** -- species still live in same habitat, but use different resources within the habitat. Concept was developed from a famous study by Robert MacArthur on warblers (small insectivorous birds) in New England

(1) 5 species with very similar niches lived in the same habitat and fed in the same trees:

(a) All five were about the same size, shape; all fed by picking insects off bark, needles of spruce trees

(2) Clearly, competitive exclusion wasn’t working the way Gause predicted. Based on preliminary observations (discovery science!), MacArthur predicted that species avoided competitive exclusion by feeding in different regions in the trees.

(3) Performed careful observational study quantifying how much time individuals of different species spent foraging in different parts of the trees – hypothesis was confirmed.

(4) Conclusion: Species could coexist in same habitat in spite of many similarities in niche because they divided up one very important resource. That made the niches different enough to permit
c. Competition is strong enough, and one species a good enough competitor, to eliminate another species from all or part of the habitat. This is true **competitive exclusion**. Classic e.g. = Joseph Connel’s studies of intertidal barnacles:

1. *Balanus* and *Chthamalus* are barnacles that settle as adults onto rocks in the intertidal zone of the North Atlantic.
2. Both settle throughout middle intertidal zone (the region between high and low tide), but only *Balanus* persists there; *Chthamalus* only persists in the upper intertidal (higher up on the rocks)
3. Grown alone, *Chthamalus* can survive well in middle intertidal – the niches of the two barnacles overlap.
4. Connell did removal experiments on several sites across intertidal
   a. in upper intertidal, removal of *Balanus* had no effect on *Chthamalus* densities (*Balanus* densities too low to have any effect to begin with)
   b. in mid-intertidal, removal of *Balanus* greatly increased *Chthamalus* survivorship
5. other studies indicated that *Balanus*’ competitive advantage due to dense settlement and rapid growth -- it crowds out *Chthamalus*

d. **Competitive replacement** is a special case of competitive exclusion – and a major problem in conservation. It results in one species completely replacing another across a wide geographic area. Competitive replacement is common when

1. exotics invade new habitats; e.g.,
   a. European starlings outcompeting bluebirds and other cavity nesters
   b. alewife and other introduced fish outcompeting native species for food
(c) kudzu, multiflora rose, and exotic weedy plant species competing with natives for space, nutrients

(2) habitat alteration (often caused by humans) changes the competitive relationships among species – e.g., *Phragmites*

(a) *Phragmites* is a native marsh grass normally co-occurs with other marsh plants; under natural conditions, it can’t outcompete the others.

(b) *Phragmites* thrives – and is a very strong competitor – in disturbed wetlands. So, when wetlands are disturbed, populations expand rapidly, outcompeting other plant species and the organisms that depend on them.

(c) result is ~ *Phragmites* monoculture (large expanses of wetlands dominated by this one species), with much lower overall species diversity.

(d) Many invasive plant species work this way – they thrive on human-disturbed areas like roadsides and invade other habitats from there – e.g., spotted knapweed invading millions of acres of western pastureland

4. **Summary of competition:**

a. Competition occurs when two species occupy the same niche (or parts of the same niche).

b. Competition among species can have several outcomes, each of which is important in helping determine the structure and diversity of ecological communities.

(1) Species may co-exist, but at lower population densities than either would achieve if it occupied the community by itself.

(2) Species may partition resources, which allows them to share the habitat.

(3) One species may exclude another from all or part of the habitat.
C. **Exploitation** shapes many of the adaptations of plants and animals and has important consequences for community structure and function.

1. Definitions and complexities: Again, my terms are a little different from the text. The problem here is that exploitative interactions (one species benefits at the expense of another) are complex!
   a. **Herbivory**: animals eat plants, usually without killing them
   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

2. Note some complexities: these terms don’t really express full diversity of interactions in nature.
   a. What should we call a granivore? It’s an animal eating a plant part (seed = embryo), but it’s obviously killing an individual plant. So granivores are sometimes called seed predators.
   b. If a parasite kills its host after some period of time, should we call it something else?

3. Exploitation is a strong selective force for both exploiter and exploited. **Parasites** have many adaptations to deal with their hosts – here we’ll look at two examples in which parasites change their hosts’ behavior to increase the likelihood of their own survival and reproduction.
   a. Many animal parasites require multiple hosts to complete their life cycles; traits that increases transmission from one host to the next will be selectively favored – e.g. from a group called spiny-headed worms. The parasite infects pill bugs at one stage and European starlings at a later stage. Janice Moore studied this system:
      (1) Parasite life cycle =
          (a) Adults in birds lay eggs shed with feces
(b) Pill bug (intermediate host) ingests eggs; parasite hatches; in 60-65 days larvae developed enough to infect vertebrate host

(c) Bird eats pill bug, parasites complete life cycle (including reproduction) attached to host intestinal walls

(2) Moore demonstrated in lab experiments that

(a) compared with uninfected pill bugs, 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 pill bugs are presumably more susceptible to predation

(3) She also demonstrated that

(a) in the lab, starlings eat more pill bugs from light-colored than from dark-colored substrates,

(b) in the wild, starlings eat a higher proportion of infected pill bugs than predicted if they fed at random on available pill bugs

(4) Conclusion = parasite alters pill bug behavior in very specific way - to increase its own transmission

(5) lots of other e.g. from this group of parasites

b. Fungal plant parasites can alter the development and morphology (= “plant behavior”) of their hosts to increase own reproductive success – e.g. from a parasitic rust that infects wild mustard plants in the Rocky Mountains.

(1) Rust requires outcrossing for sexual reproduction

(2) Normal wild mustard (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.

(3) When rust (fungal parasite) infects:
   (a) attacks rosette stage in late summer, invading actively growing 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 reproductive cells

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

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

4. Some important invasive species are parasites that are able to attack new hosts that aren’t adapted to defend against them. E.g.:
   a. Whirling disease is a disease in trout and other salmon relatives.
      (1) It’s caused by a parasitic microorganism that invades the developing tissue of the brain and spinal cord of juvenile fish.
      (2) It probably got to North America when we began importing brown trout from Europe as sport fish – these fish were deliberately introduced throughout the U.S.
      (3) It is currently a major problem in trout fisheries throughout the Western U.S.
   b. Avian malaria in Hawaii is a problem of two parasites, both introduced:
      (1) Culex mosquitoes were probably introduced by North American
sailors dumping water barrels into streams to clean/refill them. These mosquitoes are parasites on birds.

(2) When exotic birds were introduced to Hawaii, many carried *Plasmodium*, a parasitic microorganism that lives off host red blood cells and causes avian malaria.

(3) Double whammy: *Culex* transmits *Plasmodium* from infected to uninfected birds.

(4) Avian malaria is a leading cause of decline (possibly even extinction) of endemic Hawaiian forest birds.

5. Predators/herbivores and their prey also have a variety of adaptations to make them better predators/less susceptible prey. Here we'll look at just a few kinds of adaptations of predators/herbivores and their prey.

a. **Animal defenses against predators**:

   (1) **Camouflage**: background matching, outline disruption, etc.

   (2) **Mechanical defenses** – spines (large – like porcupines, or small – like the “hairs” on caterpillars), claws, jaws (think ant bites), stingers, etc.

   (3) **Chemical defenses** are very common – chemicals that either taste bad or are toxic are found in a wide variety of invertebrates and vertebrates, sometimes in conjunction with mechanical defenses –

      (a) e.g.’s include

         i) Dart poison frogs – all amphibians have poison glands, but not all make effective defenses

         ii) Many kinds of fish have toxins associated with spines – e.g. lionfish

         iii) Wasps and bees deliver toxin via stingers

         iv) Monarchs and other butterflies acquire poisons (cyanide, in their case) from the plants they eat and store them in
v) Nudibranchs (marine “slugs”) that eat tentacles of sea anemones, absorb the stinging cells into their own skin to use as defense.

(b) Note that chemical defenses will only work if they’re “advertised” to the predator – otherwise the predator won’t learn to avoid the prey. That’s why species with chemical defenses have **warning coloration** – usually very bright and high-contrast to stand out from the background.

(4) Chemical defenses and warning coloration sets the stage for another important defense. **Mimicry** involves one species “copying” the defensive adaptations of another species; it depends on the ability of predators to learn to avoid well-protected prey and can take two forms:

(a) **Batesian mimicry** is the best known: a harmless mimic looks like a harmful “model” species. E.g.’s include moth eyespots, flies that look like bees/wasps, moth larvae that look like snakes, etc.

(b) **Müllerian mimicry** is less familiar to non-biologists: two or more harmful species look like each other – each still benefits from predators learning to avoid the other. E.g.’s include wasps and bees (most are yellow/orange with black stripes); Monarch and Viceroy butterflies, etc.

b. **Plant defenses against animals:**

(1) **Mechanical defenses:** like animals, plants use spines and stinging “hairs”

(2) **Isolation:** Plants can’t “run away” from herbivores, but they can sometimes isolate them:

(a) some drop leaves that have been “infected” by small
herbivores
(b) some form galls = swellings of tissues that block the herbivore off away from the main part of the plant

(3) Chemical defenses are most plants’ main weapons – all produce a wide array of chemicals with a variety of effects on herbivores. Some that we’re more familiar with include:
(a) chemicals that affect our own physiology: examples include the poisons strychnine, cyanide, curare; the drugs morphine, nicotine, mescaline, caffeine, etc.
(b) chemicals that we use to flavor and/or preserve our foods: cloves, cinnamon, mint
(c) others like tannins, the various chemicals that give evergreens their smell, etc.

c. Animals preying on other animals need tools to capture and subdue their prey:
(1) appropriate sensory systems: e.g., bat sonar, snake infra-red heat detectors, fish motion detectors
(2) “jaws and claws”, plus speed, agility: e.g., jumping spiders, preying mantis, large mammalian predators
(3) venom to subdue prey: all spiders, all Cnidarians (jelly fish, sea anemones, coral polyps, etc. have venom delivered by stinging cells), some snakes, two mammals (short-tailed shrews, duck-billed platypus)
(4) traps: spider webs

d. Herbivores need adaptations to avoid plant defenses:
(1) against mechanical defenses, adaptations like tough mouths/tongues (giraffes, e.g.), biting or stripping off thorns
(2) physiological adaptations to plant chemical defenses include
(a) enzymes to break down plant chemicals
(b) symbiotic microorganisms (bacteria, ciliates especially) that can break down plant chemicals

6. Exploiters and the species they exploit are locked into an “evolutionary arms race” – selection favors better defenses against exploiters, which in turn selects for better adaptations to deal with prey defenses. This often leads to **co-evolution**: reciprocal adaptations in two or more species that occur because changes in one act as selective pressures on the other.

a. E.g., sonar-detecting moths
   
   (1) Many bat species prey on moths, using sonar to detect them in flight
   
   (2) One family of moths has members who have evolved specific adaptations against bat sonar: ears specifically “tuned” to the frequency of bat sonar
      
      (a) some simply detect the sonar and “drop” out of the air
      (b) others can emit sounds of their own that jam the bat’s sonar
   
   (3) Bat response – some species shift the frequency of the sonar out of range of moths’ hearing . . .

b. E.g., *Heliconius* and the passionflower vine:

   (1) Passionflower produces toxins to defend against *Heliconius* larvae.
   
   (2) Larvae have evolved enzymes that break down the toxins.
   
   (3) Passionflower has evolved a cool adaptation to help defend itself against the larvae – it produces sugar deposits that look like *Heliconius* eggs. This is adaptive for two reasons:
      
      (a) Mature female Heliconius butterflies avoid laying eggs on leaves where others have already laid eggs (why might that be?)
      
      (b) Sugar deposits attract ants and wasps that prey on the *Heliconius* larvae
7. Exploitation can affect the structure and biodiversity of a community.

Three good examples:

a. Famous study by Robert Paine in 1960’s led to the development of the concept of **keystone predators** = species that have a disproportionate affect on their communities because of what they eat. He found that predatory starfish reduces competition among tidepool invertebrates, ultimately increasing diversity in tidepools.

   (1) Starfish *Pisaster ochraceus* feeds on variety of chitons, mussels, barnacles in intertidal zone

   (2) experimental removal of *Pisaster* led to reduction of # of species from 15 ->8 with 2 species dominating after 5 years (competitive exclusion!):

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

      (b) dominant spp left after 5 years were one mussel (*Mytilus*), one barnacle

      (c) mussel, barnacle left outcompeted other species. for space

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

   (3) Conclusion: presence of predator keeps populations of strong competitor low enough to prevent competitive exclusion of other species.

b. Keystone species don’t have to be predators – they can also be herbivores. E.g., red crabs on Christmas Island

   (1) Red crabs are land crabs – they live in the forest interior of the island, returning to the ocean only to re-hydrate, mate, and disperse offspring.

   (2) Red crabs eat seeds, seedlings, and plant litter. By doing so, they

      (a) keep the forest floor open (few seedlings are present) with
little litter
(b) reduce the diversity of insects and other animals that might otherwise live in/on the forest litter
(c) keep weedy species out of the forest interior
(3) They are considered keystone species because they have such a strong effect on forest structure and diversity
(4) A current major problem on Christmas Island is the invasive crazy ant
(a) Crazy ants compete with land crabs for space in the forest; they also kill crabs, apparently by producing so much formic acid that the crabs die from it.
(b) Where ants are present, they can reach densities of more than 1000 per square meter of forest floor!
(c) By excluding the land crabs, they change the structure and biodiversity of the forest:
   i) double the amount of standing litter
   ii) seedling densities 30x higher
   iii) seedling species diversity 4x higher
   iv) increase number of weedy species able to invade the forest

c. Predation on keystone species can have a strong effect on their communities – the case of the declining sea otters:
   (1) Sea otters are keystone predators in near-shore communities in the Northern Pacific (from California north to Alaska):
      (a) sea otters’ primary prey is sea urchins
      (b) sea urchins feed on kelp – large algae that form “kelp forests” that support a huge diversity of marine organisms
      (c) when sea otters are abundant, sea urchin populations are kept in check and kelp forests thrive
(2) Sea otters were hunted nearly to extinction during the 1800’s, then recovered after they were protected by international treaties. But, ~ 20 years ago, numbers began to decline in large areas off the coast of Alaska.

(a) With loss of sea otters, sea urchin populations have increased and kelp forests are being destroyed (along with the diversity of species they support).

(b) Culprit appears to be killer whales, who are shifting prey from seals and sea lions (and possibly from great whales before that) – seal and sea lion populations declining due to pollution, disease, and overfishing of their prey

8. Even without an effect on keystone species, many of the world’s most important invasive species are predators/herbivores who eliminate prey species:
   a. Brown tree snakes
   b. Mongooses
   c. Black, Norway, and ship rats
   d. Feral dogs, cats
   e. Cattle, goats, sheep
   f. etc.

9. Exploitation and biological control – a very important practical issue! When exotic species invade a new habitat, they’re usually successful in large part because of a lack of exploiters (predators and parasites) to keep their populations in check. This gives them a strong competitive advantage and can lead to competitive replacement of native species. The obvious “defense” is to bring in a predator or parasite as a biological control agent.
   a. Example of successful control: Prickly pear cactus (*Opuntia*) in Australia.

   (1) *Opuntia* introduced into Australia mid-1800’s as ornamental and to
establish cochineal (red dye produced by insects) trade; “escaped” from cultivation

(2) by 1930, covered over 24 million ha in stands of up to 12,000 ind/ha -- obvious problem!

(3) Aus. gov’t hired biologists to come up with control agent; came up with moth *Cactoblastis cactorum*
   (a) females deposit eggs on Opuntia pads
   (b) larvae hatch, burrow into pads, feed on pads (are they herbivores or parasites?)
   (c) burrowing of caterpillars also introduces variety of fungi, bacteria that also attack internal tissues
   (d) combined effects of caterpillars, microbes reduce internal tissues to mush; cactus collapse and die

(4) 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

(5) Note that Opuntia wasn’t completely eliminated – isolated populations persist in a dynamic balance with the moths:
   (a) individual pop’s not as easily found by moths -- able to grow
   (b) eventually, moths find them, invade -->pop’s decline
   (c) meanwhile, other pop’s in other areas growing, etc.

b. Note about success of biological control – it doesn’t work successfully very often!

(1) one key to success of biological control is that “control agent” remain specific to its target – in many cases, that doesn’t happen
   (a) in Australia, *Opuntia* is introduced and that’s the only thing the moth larvae feed on – it works
   (b) in the Caribbean and in Florida, problem is arising:
      i) The same moth was imported to control *native* prickly
pear species that prevented conversion of land to agriculture and ranching

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

(2) In many cases, a biological control agent switches to a new target, often causing great harm to native communities – e.g.,

(a) mongooses in Hawaii and other islands:
   i) humans established sugar cane plantations, introducing rats and other pests that feed on the sugar cane
   ii) mongooses were imported to feed on the rats
   iii) mongooses are generalist feeders; they prey instead on birds, native lizards, etc. that lack anti-predator adaptations

(b) Rosy wolfsnails in Hawaii introduced to control African giant snails (introduced as garden ornamentals) – wolfsnails decimating native land snails instead

(c) Cane toads in Australia (we’ll see a film about those!)

10. **Summary of exploitation:**

   a. *Exploitation includes predation, herbivory, and parasitism; in this kind of interaction, one species benefits and one is harmed.*

   b. *Exploitation is a potent selective force on both “partners” and leads to numerous adaptations in both. Because of the reciprocal interactions between exploiters and exploited (predator and prey, e.g.), exploitation sometimes leads to co-evolution. In this process, adaptations in one species create selection pressure favoring new adaptations in the other.*

   c. *Exploitation can have a strong influence on community structure.*

   (1) Keystone predators maintain biodiversity through their feeding
interactions by changing the competitive interactions among species.

(2) Keystone herbivores and scavengers affect community structure.

(3) When keystone predators themselves become prey, their communities may lose diversity.

d. Many invasive species are devastating because they are very good exploiters.

e. Exploitation is at the heart of the problem of many invasive exotic species and biological control agents.

(1) Invasive parasites are often successful because their hosts lack adaptations against them.

(2) Invasive exotics are often successful because they lack exploiters in their new environments.

(3) Invasive species may have a disproportionate affect on communities by affecting keystone species.

(4) Biological control involves introducing a predator or parasite in hopes of controlling the exotic species.

(5) Biological control only works if the introduced control agent affects only its target species; this has rarely been the case thus far.

D. **Commensalism** refers to interactions in which one individual benefits and the other is neither benefitted nor harmed.

1. Compared to other kinds of interactions, these have received relatively little attention – probably because it’s difficult to imagine interactions in which one species is completely unaffected. But some commensalisms seem to be very important community interactions, so we’ll take a look at a few.

2. Commensalism is generally broken down into four categories, depending on the type of benefit the “benefitting” species gets:

   a. **Trophic**: one species receives a food benefit; these are considered
fairly rare, but examples might include

(1) Birds (e.g., cattle egrets) that feed on insects flushed out of the vegetation by grazing mammals

(2) Interaction between scale insects and sooty molds = fungal disease that attacks plants
   (a) Scale insects feed on plant sap, which contains sugars.
   (b) As they feed, they “leak” sap onto the surface of the plants.
   (c) The mold uses the sap as food – airborne spores land on sap and the fungus takes hold from there.
   (d) So the scale insects aren’t affected, but the fungus benefits

b. **Transport**: one species gets dispersal or other transport from the other (e.g., passive dispersal of plant seeds; flower mites on humming birds);
   (1) These are probably fairly common
   (2) To the extent that dispersal to new habitats is important for maintaining populations of a species, these can be important for maintaining biodiversity

c. **Structural/support**: one species gets space, position from another
   (1) We can easily identify potential candidates:
      (a) Many trees provide “growing platforms” for a wide variety of plants (oaks and “Spanish moss”, tropical trees and epiphytes).
         i) Some, like misteltoe, are parasitic
         ii) Some, like “strangler figs” in the tropics will kill the trees;
         iii) Many plants don’t seem to harm the trees that support them – however, the interactions between trees and the plants growing on them haven’t often been studied in detail.
      (b) In aquatic systems, examples would include barnacles on
whales; algae on corals, etc. Again, however, these haven't been studied, so we often just assume that there's no cost to the interaction.

d. **Shelter**: one species lives/hides in a burrow or other space provided by the other species.

   (1) This is probably the most common kind of commensalism in both terrestrial (burrows) and aquatic (nooks and crannies in corals, sponges) systems

   (2) It's a very important interaction because shelter creates critical habitat for many different species.

      (a) E.g., aardvark burrows in African savannahs are used by at least 12 different vertebrate species (including whole families of warthogs and one species of bat) – that doesn't count all the insects, fungi, etc.

      (b) Prairie dog burrows and surrounding areas provide critical habitat for hundreds of species – including some endangered species.

      (c) Animals that build structures (like packrat nests, termite mounds) may have similar effects

      (d) Many species of marine algae and invertebrates live in the nooks and crannies of sponges and corals

(3) Remember the *Culex* mosquitoes in Hawaii – they benefit from a type of shelter commensalism with another introduced species – pigs.

   (a) Pigs were likely brought to Hawaii by the original Polynesian colonists.

   (b) Pigs feed by rooting through the soil, leaving behind depressions in the ground.

   (c) When depressions fill with rain, they create great breeding
habitat for *Culex* mosquitoes – which makes the malaria situation even worse!

E. **Mutualism** is an interaction in which both partners benefit.

1. As we’ll see, these interactions are extremely important determinants of the structure and diversity of communities and ecosystems on a global scale (hint: multicellular life, coral reefs, virtually all plant communities, and all plant-eaters depend on mutualistic interactions with other species)

2. Mutualism can be classified by the kind of benefit each partner receives. One usually receives energy and/or nutrients, so we classify based on what the other partner receives

   a. **Trophic:** species have complementary ways of acquiring nutrients - so each benefits by gaining food/energy that it wouldn’t be able to get on its own. Four extremely important trophic mutualisms are

      (1) plants and mycorrhizal fungi (read opening essay, chapter 17):

         (a) Remember that the Fungi is the kingdom that includes yeasts, molds, mushrooms

         (b) The fungi we’re talking about are often the same ones that produce mushrooms. Most of the time, these fungi exist as underground masses of thread-like structures called hyphae.

         (c) The hyphae can grow around and even into plant roots, forming **mycorrhizae** (literally, “fungus roots”). The plants and fungi both benefit from this interaction:

         i) fungi receive food and energy from plant sap

         ii) in turn, the fungi help the plants acquire water and minerals (especially phosphorus) and protect plants against soil microbes that cause disease.

      (d) Fossil evidence shows that the oldest known land plants associated with mycorrhizal fungi; the interaction may have been necessary for plants to colonize land (remember that no
(e) Currently, virtually all plants form mycorrhizal associations, and these associations are extremely important for allowing plants to persist!

(2) Legumes & nitrogen-fixing bacteria

(a) Legumes = plants in the pea/bean family (including acacias, mimosas, vetches, alfalfa as well as peas/beans)

(b) Nitrogen-fixing bacteria establish swellings = nodes on legume roots

(c) Bacteria generate usable nitrogen, enriching soil fertility (for host plant and for other plants)

(d) Host plant provides food to bacteria

(e) This is why alfalfa, soybeans, peanuts used in crop rotation

(f) This type of mutualism can also help an exotic species become a troublesome invasive: e.g., Autumn olive is an invasive shrub whose nitrogen-fixing root nodules help it invade and thrive on poor soils.

(3) Corals and zooxanthellae:

(a) Coral reefs are the “rainforests of the ocean”; they support the most diverse aquatic ecosystems on earth.

(b) The hard structures we call corals are the “skeletons” of tiny animals called polyps – related to sea anemones.

(c) Many coral species have mutualistic relationship with zooxanthellae (algae – specifically diatoms) that live w/in coral tissues at densities ~ 1 million cells/cm² of coral surface (note -- not all coral species do this!)

(d) Zooxanthellae are photosynthetic; provide coral with energy-rich carbon compounds

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

(f) Importance of the interaction becomes clear when corals bleach – environmental disruption (excess heat, pollution) causes corals to expel algae – coral animals die, reefs are overrun with sponges, diversity decreases.

(4) Herbivores & gut symbionts

(a) Many bacteria, protists live in guts of plant-eating animals
(b) Receive food (& shelter) from hosts
(c) Provide food services, including
   i) detoxifying plant defensive chemicals
   ii) breaking down cellulose for its energy (most animals can’t do this on their own)
   iii) synthesizing vitamins and other compounds for hosts
(d) Examples:
   i) termites – critical decomposers/recyclers in many ecosystems
   ii) ruminant mammals: deer, antelope, cows, sheep, goats, giraffes – symbionts allow them to live on plants w/relatively poor nutritional quality
   iii) humans! – *E. coli* in guts help digest food, synthesize vitamins
(e) Plants as food sources wouldn’t be as possible without this mutualism

b. **Defensive**: one species provides a protective function in return for energy/ nutrients; examples include

(1) Eukaryotes & cell organelles (mitochondria, chloroplasts)
   (a) mitochondria, chloroplasts = ancient symbiotic bacteria
   (b) both provide chemical energy for cells in exchange for shelter
(c) mutualism at least 1.5 billion years old; set the stage for evolution of complex multicellular life!

(2) “Cleaner” fish and shrimp remove parasites from other fish

(3) Ants and acacias (and other ant-plant associations): ants protect acacias from herbivores and from competing plant species; trees provide shelter (thorns) and food

(4) Ants and “honeydew” producing insects

(a) Ants typically require both a good source of protein (usually from other insects, other small animals) and a good source of sugars.

(b) Many ant species get sugars from aphids and scale insects that feed on plant sap – these insects usually suck up more sap than they can absorb, and the excess is excreted as “honeydew”, which is rich in sugars.

(c) Ants will tend the honeydew producers, protect them from potential predators, and even move them around from plant to plant.

(d) Remember the crazy ants from Christmas Island – they are also scale-insect tenders. Where ant densities are high, the density of scale insects increases tremendously, causing:
   i) canopy dieback (the insects are so dense they actually kill trees) and
   ii) an increase in sooty mold

c. Dispersive: organisms receive energy in exchange for dispersing gametes, propagules; really important examples are from flowering plants – another example of mutualisms that have shaped our global environment:

(1) pollination

(2) seed dispersal
(3) Another double-whammy:
   (a) One of Hawaii’s worst plant invasives is strawberry guava, a vigorous shrub that grows in dense thickets that outcompete native plant species.
   (b) One of Hawaii’s worst mammal invasives is the dwarf mongoose, which eats native lizards and birds.
   (c) Dwarf mongooses also eat strawberry guava fruits, dispersing its seeds.
   (d) So here we have a mutualism between two invasive species!

3. A human example: people in Africa seem to have evolved a mutualism with honeyguides (birds)
   a. Interaction is between traditional honey gatherers and the greater honeyguide (*Indicator indicator* - member of woodpecker family)
   b. Honey gathering at least 20,000 yrs old (rock art that old)
   c. Mutualism is facultative: honeyguide lives on beeswax and bees (all stages); can live independently of humans
   d. 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”
   e. Both species benefit: humans find hives more easily; bird gets food more easily as humans raid hives
   f. Isak (member of tribe of traditional honey gatherers) studied birds and humans to test three assertions of honey gatherers: that birds inform them of
      (1) **direction of nest**: by direction of flight
          (a) induced birds to guide to same nest from same starting point on 5 occasions
          (b) induced birds to guide to same nest from different starting
points
(c) results: birds consistently led toward nest (OH)

(2) **distance to nest**: by decreasing three things as distance decreases:
(a) time spent out of sight between first encounter and first stop
(b) distance between stops on way to nest
(c) height of perch on way to nest
(d) results: all three consistently decrease with distance to nest

(3) **when they arrive at the location of the nest**: by changing vocalization and behavior -- Isak observed
(a) when guiding, birds emit distinctive call and answer human calls by increasing frequency of guiding call
(b) when reaches nest, bird perches and gives special “indication” call repeated a few times; doesn’t “answer” human calls
(c) when reaches nest, if approached by human, flies in a circle around the location before perching again.
(d) 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!

F. **Summary of interactions:****

1. **Interactions among species can be classified by whether or not “partners” in the interaction benefit or are harmed.**
   a. **Competition**: both partners are harmed
   b. **Exploitation**: one partner benefits at the expense of the other
   c. **Commensalism**: one partner benefits, the other is neither harmed nor helped
   d. **Mutualism**: both partners benefit
2. **Interactions among species are varied and complex; they have important consequences for the evolution of individual species and for the structure and biodiversity of ecological communities.**

3. **Invasive species can be devastating because of the many ways they can disrupt the normal interactions among community members.**